THE THALAMUS OF ELEPHANTULUS

by

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Part 1 - Text.

THE THALAMUS OF ELEPHANTULUS.

INTRODUCTION.

The thalamus in space.

The thalamus is a large area of mixed grey and white matter, interposed between the telencephalon on the one hand and the brain-stem on the other. The thalamus has thus a key position in the brain and the great majority of connections between the telencephalon and bulbo-spinal regions pass through it.

Those connections passing upwards to the telencephalon tend to lie above the descending fibre systems, and the dorsal thalamus is intimately related to the ascending lemniscal or sensory systems. Very nearly all somatic sensory fibres are relayed in the dorsal thalamus before they reach the telencephalon, mostly the cerebral cortex. These final relays or thalamic projections lie in the thalamic radiations and internal capsule. It follows from this intimate relationship between the dorsal thalamus and telencephalon that progressive enlargement and elaboration of the telencephalon in evolution is accompanied by a corresponding increase in size and structural complexity of the dorsal thalamus.

The *ventral thalamus* or *subthalamus*, on the other hand, is connected with the ventral or descending fibre system. It lies centrally in the diencephalon, between dorsal thalamus and hypothalamus, and is intimately related to the descending lenticular connections of the lateral forebrain bundle, i.e. to the motor and motor-co-ordinating systems of the brain. Increase in the size and importance of the subthalamus in evolution is consonant with increase in telencephalic control of movement, found particularly in mammals, and most of all in Primates.

The thalamus in time.

One of the characteristics of the progressive evolution in vertebrates is enlargement and increase in complexity of the forebrain, culminating in the elaboration of the cerebral cortex and related structures in man. The salient features of development in the telencephalon of different groups of animals have been studied in detail. As a result of this intensive study, and because the different elementary areas in this part of the brain are reasonably distinct, we have a great deal of accurate knowledge of telencephalic structure in all vertebrates. We know, for example, that a hippocampus of simple type is found in Amphibians, and that a primordium of the true cerebral cortex or neopallium is present in reptiles (see the excellent reviews of ELLIOT SMITH (1910) and JOHNSTON (1923)). Extending these original studies, WRIGHT (1947) has provided satisfactory objective criteria for distinguishing the basal telencephalic areas in the brain of any vertebrate.

While telencephalic development is thus on the whole well understood, very few students of the forebrain have concerned themselves with the thalamus, and our knowledge of comparative thalamic morphology is limited and unsatisfactory. This is the more surprising since the thalamus occupies a very significant position in the brain: it lies between the brain-stem and spinal cord on the one hand and the telencephalon on the other; it has strong reciprocal connections with the telencephalon, and upon thalamically relayed impulses the sensory cortex is entirely dependent; it undergoes a progressive differentiation not less spectacular than that in the cerebral cortex. As ELLIOT SMITH (1910) pointed out, the key to the interpretation of the structure of its rich cortical component of the cerebral hemispheres which is found in mammals - the neopallium - lies in an intensive study of the thalamus.

Quite recently, the importance of the thalamus has been realized by workers on the mammalian brain. Our knowledge of forebrain morphology has been considerably advanced during the past two decades by numerous detailed studies of the thalamus and of the relationship of the thalamus to the telencephalon. In spite of the difficulties involved, a more or less consistent nomenclature of the various cell-masses and fibre-tracts has been developed, and applied to such widely separated groups as primates (see WALKER, 1938), rodents (GURDJIAN, 1925 and 1927), ungulates (SOLNITZKY 1938), insectivores (LE GROS CLARK, 1929 and 1929a) edentates (PAPEZ, 1932) and masupials (BODIAN, 1939, 1940 and 1942, and GOLDBY, 1941).

Unfortunately, no attempt has been made to apply the fruits of these recent researches generally to other groups of vertebrates. Quite different terms are employed in analysing and describing the thalami of the several classes. In fishes and amphibians subdivision of the thalamus is based upon the position of sulci or depressions in the ventricular wall. The difficult problem of comparison of the thalamus of reptiles with that of amphibians on the one hand and mammals on the other has been avoided completely; a method of subdivision of the thalamus and nuclear terminology applying only to reptilian brains has been developed, having very little resemblance to terms used either in amphibian or in mammalian studies. This reptilian terminology is applied with a few embellishments to avian brains. The unsatisfactory and indiscriminately used criteria make homology impossible.

Thus, while the telencephalon, hindbrain and all other regions of the central nervous system - with the possible exception of the midbrain - of craniotes are on the whole adequately compared, so that we know at least the major structural modifications in each, our knowledge of the comparative structure of the thalamus is quite inadequate. It follows from the different and incompatible procedures of analysis and description used in the several groups of animals that it is impossible to assess even the outlines of development in this important area of the brain. The original researches may be regarded merely as provisional attempts at analysis of the thalami of different animals in the absence of more complete data embracing a wide series of species.

At present an extensive reanalysis of the structural pattern in the thalamus of different animals - from fishes to primates - is being conducted, using the accepted neurological techniques of study. Evidence has already accummulated to show that in the thalamus, just as in the telencephalon and hindbrain, the various subdivisions found in the different classes of animals can be identified and compared, and the emergence and differentiation of new areas traced throughout the vertebrate phylum. In the thalamus the problem of comparison is perhaps more difficult than in other parts of the brain, by reason of the relatively diffuse and complex arrangement of the cell-bodies and systems of fibres; but the problem is none the less capable of more satisfactory solution.

Why Elephantulus ?

The brain of Elephantulus was chosen as material for the preliminary stages of this study, because some rather simply organized placental mammalian brain type had to be used as a basis for comparison, and fresh brains of Elephantulus were available. The previous studies of LE GROS CLARK (1928) and WRIGHT (1945) on the structure of the forebrain of Elephantulus had shown an inordinate development of the subsplenial hippocampus, relatively large basal telencephalic areas and pyriform cortex, and a relatively small and undifferentiated neopallium. Originally, this study of the thalamic morphology of Elephantulus was undertaken for two reasons: first, to see what sort of a thalamus an animal with this unusual arrangement of telencephalic areas might have, i.e. what structural modifications are found in a brain with so high a degree of visceralization; secondly, to add to the general body of information being collected in our University about this interesting little mammal. The opportunity was taken at the same time of reviewing the terminology used and of introducing some small, but none the less long overdue, changes.

For these reasons alone detailed study of the thalamus of the elephant shrew seemed justified. As the investigation proceeded it soon became clear, however, that the study had considerably more to offer. In the first place, because of the large size and relatively clear differentiation of the basal telencephalic areas and hippocampal formations in Elephantulus, it has been possible to analyse the connections between these areas and the diencephalon with a degree of accuracy hitherto unparalleled. The results of this analysis may be profitably applied to the study of other brains, and throw additional light upon the academic theory of forebrain structure, allowing a new and more satisfactory interpretation of certain forebrain commissures.

Moreover, Elephantulus occupies a unique position in mammalian classification, a position that is not yet finally settled. Older systematists grouped the family Macroscelididae, to which Elephantulus belongs, with the family Tupaiidae to form the sub-order Menotyphla, as distinct from the Lipotyphla, which included the rest of the Insectivora. LE GROS CLARK (1934) demonstrated the many points of similarity between the Tupaiidae and the smaller Primates: however, he denied a similar position to the Macroscelididae since he regarded their hippocampal development as evidence of marked specialization. More recently EVANS (1942) has reasserted the close relationship between the Macroscelididae and Tupaiidae, and has shown that the former have almost all of the lemuroid features found in Tupaia. Studies on the morphology and embryology of Elephantulus carried out in this University have emphasised the close relationship between Elephantulus and Primates: VAN DER HORST and GILLMAN (1941), for instance, have described the elaborate menstruation in the elephant shrew. As HUXLEY (1941) has pointed out, in the early stages of evolution of different groups, considerable variability of form is to be expected, and it is likely that Elephantulus occupies a position closer to the Primate stem of evolution than is generally admitted. In any event, comparison of structural features between Elephantulus and Primates is justified.

On the other hand, Elephantulus exhibits many markedly primitive features. In a detailed study of the cell-masses of the telencephalon, WRIGHT (1945) showed clearly the similarity between Elephantulus and other primitive metatherian and eutherian forms. This affinity was found as well by GILBERT (1944) in her study of the embryology of the venous system of the elephant shrew, and has been lent further support by the chromosomal studies of BRENNER (1946).

In this study, the close relationship between Elephantulus and other primitive mammalian forms has been readily confirmed. The brain of Elephantulus is, on the whole, very similar in structure to brains of not only primitive placental mammals, e.g. the Edentate Tatusia, but also of the marsupials Didelphys and Trichosur~~ie~~us. Many features of thalamic morphology in Elephantulus are undoubtedly primitive: the relatively small size of the dorsal lateral geniculate and ventral nuclei, the large area of midline nuclei, and the lack of emphasis upon cerebral projection in particular. These considerations make Elephantulus specially valuable in comparative studies as a link between ~~S~~submammalian and mammalian forms. Armed with detailed knowledge of thalamic structure in Elephantulus one can turn to the thalamus of Reptiles with new insight.

General nuclear configuration and relations in the mammalian thalamus.

The mammalian thalamus conforms to a pattern of structure as reflected in the disposition of the nuclear masses and related systems of fibres. The various nuclei have constant general relations, although they vary considerably in details of size and structure from one species to another. Two main groups of nuclei may be recognised, namely, the principal nuclei and intralaminar nuclei.

The principal nuclei are usually well-defined, having a more or less uniform structure, and delimited by the surrounding fibre condensations or medullary laminae. Of the principal nuclei, ventral, lateral, anterior and medial dorsal complexes are recognised, according to their position in the thalamus. The relations of the principle nuclei to the systems of fibres in the thalamus is on the whole well-known from experimental investigations. These experiments, carried out on primates, carnivores, rodents and even marsupials, have established a similar arrangement, so it is reasonable to assume that a single pattern of organization is present through the class of mammals.

The second group, the intralaminar nuclei is represented by cells of various types, often closely packed, small and fusiform, within the medullary laminae.

In some cases the cells of the intraliminar nuclei comprise the peripheral zones of the adjacent principal nuclei, their appearance being modified by the fibres which are interwoven in their substance. The precise relation of the intralaminar nuclei to the systems of fibres in which they are embedded is obscure.

Broadly speaking, four categories of nuclear organization may be distinguished in the thalamus. Nuclei in the first series receive connections from and send axons to other parts of the diencephalon, midbrain or the basal areas of the telencephalon, but have no cerebral projections. The midline nuclei are included in this complex, since they are most intimately related to the hypothalamus through the periventricular system. The habenular nuclei may be included, since they receive fibres from the stria medullar~~u~~is and send axons, by way of the habenulo-peduncular tract, to the tegmentum. The pretectal and ventr~~al~~o- lateral geniculate nuclei are included too, although they receive special sensory fibres direct from the optic tract; because their relays pass to the tectum and tegmentum, not to the cerebral cortex.

The second series is represented by the anterior nuclear group, which receives afferent connections from the hypothalamus and basal areas of the telencephalon and projects fibres to the retrosplenial and cingular areas of cerebral cortex. In primates this projection arises predomi antly from the anteroventral nucleus which is, consequently, very much longer than the anterodorsal and anteromedial nuclei.

The third series of nuclei receives the main sensory tracts and sends relay fibres direct to the cerebral cortex. This series comprises three main sets of nuclei: the ventral nuclear complex, concerned mainly with somatic sensation, the dorsal lateral geniculate nucleus, concerned entirely with vision, and the medial geniculate nucleus, concerned with audition. The ventral nucleus is the relay-centre for all somatosensory fibres in the lemnisci and for fibres passing from the cerebellum through the brachium conjunctivum. As the importance of cerebral projection of these impulses increases as one ascends the scale of mammals towards the higher primates and man, so the ventral nucleus becomes relatively larger and more differentiated. In the primates - and to a lesser extent in other species orders - several divisions of the ventral nucleus may be recognised: the most important of these are the ventral posterior nucleus which receives somatosensory fibres and projects them to the sensory cortex of the postcentral gyrus, and the ventral lateral nucleus, which receives the cerebellar fibres and sends projections to the precentral motor cortex.

The dorsal lateral geniculate body receives terminal fibres of the optic tract and projects through the optic radiations to the striate area of cerebral cortex. Where cerebral projection of visual impulses is important, as in primates, the ventral lateral geniculate nucleus is small, while the dorsal nucleus is greatly developed and has its cells disposed in concentric laminae. The medial geniculate nucleus receives auditory fibres through the brachium of the superior colliculus and the lateral lemniscus, and relays them on through the auditory radiations to the temporal cortex.

The fourth series of nuclei receives impulses from the main sensory stations just described and projects to the cerebral association areas: these, are the lateral, lateral posterior or pulvin~~o~~ar, and medial dorsal nuclei. Axons of the lateral complex terminate in the parietal association cortex. The medial dorsal nucleus has a double projection: the medial part of the nucleus relays fibres to the visceral areas of the frontal cortex; the rest of the nucleus to the frontal association areas. In primates, and most of all in man, where the association areas are much expanded, there is a corresponding enlargement of the lateral nuclear complex and principal part of the medial dorsal nucleus.

These main categories of nuclei have been distinguished in all mammals, placental and non-placental, so far subjected to detailed analysis. They may be combined in various ways: in primitive mammals like the marsupial Didelphys, the insectivore Erinaceus, and the edentate Tatusia, the fourth series is hardly represented at all while the third series is only moderately developed; in primates the fourth and third series are enormously enlarged, and so on. Thus, in analysing any mammalian thalamus, it is necessary first of all to recognise the several nuclei as they are disposed in the particular species under consideration, and then to assess the degree of development of the various nuclear groups. This is done for Elephantulus in the following pages.

MATERIAL AND METHODS.

On the interpretation of neurological material, with special reference to the thalamus.

All nervous activity may ultimately be reduced to a least common denominator, the nerve impulse, which varies in itself and which is woven into a complex and intricate pattern in the central nervous system. In this pattern of activity, differences in arrangement or organization of impulses produce widely different results. Thus, in the nervous system one must study not only the general principles according to which cells are arranged and interconnected - common to muscles, glands and so on as well - but also the patterns of organization of neurons.

Nervous activity depends upon, first, a certain degree of independence and preservation of structural and functional individuality of nerve cells; second, upon variance in the types and reactivities in different cells; and third, upon variance in modes of reciprocal relationships of nerve cells. Of these three prerequisites, the latter two are amenable to direct anatomical study: we can pick upon variances in cells, even though our crude techniques may not reveal anything like the delicate variations in reactivity which must be present in the living, active, nervous tissue; and we can determine, at least to an extent, the reciprocal relationships existing between different areas of cells in the central nervous system.

Because of their structural peculiarity in having greatly elongated processes, neurons in widely separated areas in the central nervous system can be related to one another. Thus, study of nervous activity resolves itself into a study of tracts and their origins from, and endings in, groups of cell-bodies. This is in some cases relatively easy; areas of the brain having segmental connections, i.e. in the spinal cord, medulla and parts of the midbrain, are on the whole clearly demarcated and consist of neurons of fairly characteristic type. Thus, it is easy enough to distinguish a dorsal from an intermediolateral or ventral horn of the spinal cord, or a sensory from motor trigeminal nucleus. This is in keeping with the physiological finding of somatotopic localization in the segmental centres.

In the forebrain the situation is far more complex. Together with increased functional differentiation of these suprasegmental parts of the brain in evolution has gone the development of a very elaborate organization of neurons.

There is no somatotopic localization. Often the neurons are more or less diffusely arranged. It is the difficult task of the anatomist to get some idea of the structural relationships in these areas: to sort out the neurons and group cell-bodies together where they have common features into small divisions or cell-masses; and then to determine the connections of such masses with other areas of the brain through their projections in various fibre-tract

In the telencephalon this grouping of cell bodies is usually obvious: thus cells of a certain type may clearly constitute a single large area of hippocampus, or a layer of cerebral cortex or olfactory bulb. But in the thalamus this problem is most acute. The observer is faced with a very large area of cell-bodies and fibres, showing only rarely characteristic structural features which at once differentiate them from their surroundings. Under these conditions the observer must make full use of every possible criterion of separation of cells. Differences in size, shape and intensity of staining of neurons are sought first. Quite as important as these are differences in myeloarchitecture: differences in arrangement and intensity of staining of fibres in different areas. In material prepared by a standard myelin technique some of the cell-masses which were only poorly differentiable when cell-bodies were studied alone are clearly outlined, either because of the rich plexus of medullated fibres in them, or because they remain unstained and skirted by fibres. All these criteria must be used in combination and rigorously applied, as they have been in this dissertation.

When it is possible to employ it, the experimental method is an invaluable supplement to anatomical investigation on normal material. In the thalamus, retrograde degeneration in thalamic nuclei following upon localized experimental lesions in the cerebral cortex has recently served to refine considerably the results of previous investigations. What is more, this experimental work has shown the justification of minute areal subdivision of the thalamus into a large number of cell-masses: each of these cell-masses or nuclei has a characteristic projection to a brain area that in its turn, can be defined on objective anatomical and physiological criteria. Thus the medial dorsal nucleus projects to area 8 of the frontal cortex, and the medial geniculate nucleus to the auditory cortex. Indeed, different parts of one nucleus project to different regions: the ventral posterior nucleus projects to the sensory cortex of the postcentral area, the ventral lateral nucleus to the motor cortex of the precentral area. Unfortunately, no experimental work on Elephantulus has been possible, but this study has been conducted at least armed with the results of previous experimental investigations.

When grouping fibre projections together, considerable difficulties are encountered. Sometimes, as in the fornix and optic tract, compact bundles of fibres occur, to which the term "tract" is readily applied. But such cases are exceptional - in the forebrain: more usually series of diffuse connections are found. It has been customary to subdivide connections in as detailed a manner as possible into a legion of small tracts. Often the wood cannot be seen for the trees: because of the detailed accounts the general features of structure and relations are missed. It seems most satisfactory, in order to analyse and describe such connections, to consider them as systems of fibres, each system forming a whole, related in a particular way to other systems and having components from a number of different sources. Thus, the stria medullaris and medial forebrain bundle systems overlap in their origins from the basal areas of the telencephalon, though their later courses are distinct. There is at present no anatomical or physiological justification for further splitting of the several systems.

Material and Methods used in this study:

For the purposes of gross dissection and examination under a binocular microscope formalin fixed brains of Elephantulus myurus jamesoni were available.

For the microscopical study, seven sets of serial sections were used. They were prepared in the department from fresh brains as follows:

3 formalin-fixed, paraffin-embedded brains were sectioned in three planes at 20 μ and stained with cresyl violet to display the cell masses;

2 formalin-fixed, paraffin-embedded brains were sectioned transversely and horizontally at 20 μ, and stained with Weils' technique for myelinated fibres;

and 2 brains were impregnated with silver by the modified method of Rasmussen described by Wright (1945), embedded in paraffin, and cut transversely and horizontally at 20 μ.

These series of sections were the best of much Elephantulus material available in the department and showed well the conformation of the cell masses and fibres.

In these sections the thalamic nuclei were for the most part reasonably well-defined. In doubtful cases, reference to fibre connections often helped to delineate more precisely the boundaries of individual cell masses.

The material was unfavourable for detailed cytological study, but differences in cell size, shape and intensity of staining were manifest and were used as criteria for separating the various masses. It was found most difficult to determine with any precision the origin and termination of any but the most well-defined fibre systems, and the conclusions reached are only tentatively offered for consideration in the absence of experimental confirmation.

In the drawings, outlines of the sections were prepared with the aid of a Seltz projection apparatus and the structural detail filled in from sections under the microscope. An attempt was made to preserve in the illustrations some of the cytoarchitectural and myeloarchitectural features of the sections, but the representations are necessarily somewhat diagrammatic. Drawings of the fibre tracts were made from projected outlines, with details filled in from sections prepared by the Weil and silver pyridine techniques.

Complete sets of drawings of transverse sections of cell masses and fibre tracts appear in the plates, together with a series of drawings of horizontal sections showing cell masses.

In the description which follows, the relations of the cell masses and fibre systems will be given only in outline since much of the detail of these relationships will be illustrated by the several figures.

GROSS MORPHOLOGY OF THE DIENCEPHALON.

The general anatomical relationships of the base of the diencephalon are shown in plate 1, fig.2. Rostrally the diencephalon joins the preoptic region (M.PR.R.) and its large lateral condensation, the olfactory (T.OLF.). The prominent optic tracts (TR.OP) enclose the tuber cinereum (T.CIN) as they diverge at a wide angle behind the chiasma (O.CH) and pass dorsolaterally between the amygdala (AMYG.) and diencephalon. The mammillary bodies (MAM.B.) appear as slight bilateral elevations on the brain base; they are replaced caudally by the tegmentum of the mid-brain.

The optic tracts course dorsally round the lateral aspect of the diencephalon, passing a small but distinct elevation, the medial geniculate body (M.GEN., fig. 3), and so fan out thereafter over the posterior aspect of the large lateral geniculate body (L.GEN.). Some fibres pass under the prominent anterior colliculus (A.COL.). The posterior colliculus (P.COL.) is very much smaller than the anterior colliculus.

Rostral to the pineal body (PIN.) on the dorsal side of the diencephalon the distinct striae medullares (STR.MED.) converge on the habenula (HAB.); they separate medial elevations on the dorsal surface of the thalamus, sometimes termed the anterior tubercles but not comparable to these bodies in primates, from less prominent lateral elevations.

The lateral forebrain bundle (l.CAPS) appears as a large group of fibres between striatum and diencephalon. Over the dorsal surface of the lateral forebrain bundle passes the stria terminalis (STR. TERM), dipping down to the amygdala caudally and reaching the preoptic region rostrally. The stria terminalis marks the lateral limit of the dorsal thalamus.

Further back the mid-brain overlies the caudoventral extremity of the diencephalon. The dorsal thalamus reaches relatively further forward in Elephantulus than in other mammals on account of the large size of the pretectal nucleus and tectum: the lateral geniculate nuclei, consequently, appear in the same plane of transverse section as the optic chiasma.

In plate 1. fig. 1, a drawing of a sagittal section through the brain in the median plane, the large size of the massa intermedia (M.INT.) is indicated. It divides the third ventricle (V111) into dorsal and ventral parts behind the foramen of Monro (FOR.MON.) The ventral division of the ventricle has well-defined preoptic (PR.R.) and hypophysial (HYP.R.) recesses. The pineal recess of the dorsal division of the ventricle is also large.

MICROSCOPICAL STRUCTURE OF THE THALAMUS.

The thalamus of Elephantulus has typical mammalian structural relations. It occupies the entire dorsal area of the diencephalon, lying between the telencephalon on the one hand and the brain-stem on the other.

The thalamus has the following detailed relations. It is continuous rostroventrally and rostrolaterally with the preoptic region of the basal telencephalon. The ventral neighbour of the thalamus along the greater part of its extent is the hypothalamus. Dorsally, the thalamus forms part of the free surface of the brain. Laterally, the thalamus lies medial to the basal ganglia and internal capsule at its rostral extremity, while further back it is bounded by the optic tract. Caudally the thalamus is continuous with the tectum, and caudoventrally with the tegmentum, of the mid-brain. Medially the thalami of the two sides are fused together for the greater part of their extent, forming a large massa intermedia.

Over the dorsal surface of the thalamus lies a thin fibre layer, the stratum zonale. A fine sheath of fibres, the internal medullary lamina, runs ventromedially from this stratum and divides the thalamus into separate parts or groups of cell masses. Some of the cell masses lie within the medullary lamina and are, consequently, designated "intralaminar." The external medullary lamina is a sheet of white matter near the lateral surface of the thalamus paralleling the internal capsule and continuous ventromedially with the ventral medullary lamina. The latter separates the dorsal thalamus from the subjacent subthalamus.

It is usual in descriptions to distinguish a series of nuclear groups, each of which has a characteristic position in the dorsal thalamus. The *habenular group* lies dorsomedially in the diencephalon, the *anterior group* in the rostral part of the thalamus, the *midline group* in the massa intermedia, the *medial group* within the limits of the internal medullary lamina, the *ventral and lateral group* between the internal and external medullary laminae, and the geniculate and pretectal nuclei form a *posterior group* lying outside the external medullary lamina in the lateral and caudal areas of the thalamus. These groups are used in this dissertation chiefly to facilitate description; they are not intended to indicate necessary structural or functional affinities between the several nuclei in each group.

Cell Masses of the dorsal thalamus. → Cap

Pineal Body.

The pineal body (PIN, figs. 13 and 14, 23, 33 and 34) lies in a plane slightly caudal to the habenular nuclei, above the habenular and posterior commissures. It appears in sections as a rounded, compact mass of intensely staining cells.

Isolated bundles of fibres from the habenular and posterior commissures enter the pineal body: some, after a short aberrant course in the pineal tissue rejoin the main bodies of commissural fibres; others appear to divide and end in small loops and bulbs among the pineal cells.

Habenular group.

Classically, the habenular nuclei are grouped together with the pineal body to form a distinct subdivision of the diencephalon, the epithalamus. This subdivision seems unsatisfactory since it fails to recognise the close relationship that undoubtedly exists between the habenular and other thalamic nuclei and since it includes in the same complex structures so morphologically and physiologically different as the habenula and pineal body. In this dissertation the term "epithalamus" is abandoned and the habenular nuclei are treated as a separate dorsal thalamic nuclear group, lying in the most dorsal and medial region of the diencephalon.

Medial habenular nucleus, (N.HAB.M., figs. 5-11 and 22): This nucleus is a prominent mass of small, deeply basophilic cells situated immediately under the ependyma of the third ventricle. The nucleus is related, in particular, medially to the paraventricular nuclei, laterally to the paratae~~m~~nial nucleus, and, further caudally, to the scattered cells above the medial dorsal nucleus; ventrolaterally it joins the more widely spaced cells of the lateral habenular nucleus.

The medial habenular nucleus is intimately related along the whole of its length to the stria medullaris, from which it receives fibres. The nucleus appears to contribute elements to the habenular commissure which is situated immediately above its caudal extremity.

Lateral habenular nucleus, (N.HAB.L., figs. 7-11 and 22): This nucleus, because of the scattered arrangement of its medium sized cells, is less conspicuous than its medial companion. The lateral habenular nucleus is heterogeneous and divisible into a series of smaller groups of cells, each with a characteristic small or large cell type, as

MARBURG (1944) has found in the corresponding nucleus in human material.

On its dorsal side the lateral habenular nucleus is related to the stria medullaris, ventrally to the medial dorsal nucleus,and laterally to the lateral central nucleus.

Both habenular nuclei appear to receive fibres from the stria medullaris and to contribute elements to the habenular commissure. Many finely myelinated fibres leave the substance of the nuclei and converge to become the habenulo-peduncular tract. Of the fine, diffuse connections between the habenula and related cell masses, those with the medial dorsal nucleus, tectum and posterior paraventricular nucleus are the best defined.

Anterior Nuclear Group.

The anterior nuclear group in Elephantulus is large and occupies the greater part of the rostral pole of the dorsal thalamus. It comprises the three elements recognised by most authors - anterodorsal, anteroventral and anteromedial nuclei. The relative size and relations of the three nuclei differ appreciably from those observed in most mammals, resembling most nearly the situation described by LE GROS CLARK (1929a) in Macroscelides.

Anterodorsal nucleus (N.A.D., figs 4-9, 18-20): This nucleus shows relatively most development of the anterior nuclei. It occupies a considerable area and is characterised by the large size, angular shape and deep staining of its neurons.

It appears in transverse sections at the level of the caudal extremity of the anterior commissure; as these sections are followed caudally, the nucleus rapidly assumes a rounded and then an oval shape, reaching to the dorsal surface of the diencephalon adjacent to the stria medullaris. Ventrolaterally the nucleus is bounded by the fornix. Furthe caudally, triangular areas free of cells lie on the medial sides of the bilateral anterodorsal nuclei and, about the level of the optic chiasma, a thick, well-defined, medullated bundle of fibres crosses the midline between the nuclei, forming an extensive *interanterodorsal commissure*, (CO.I.A.D., fig. 28).

The small mass of spindle-shaped cells horizontally disposed in the region of this decussation has been termed the *interanterodorsal nucleus*, (N.I.A.D., fig.7):

it appears to be a differentiation of midline elements produced by the commissural fibres below the rhomboid nucleus.

Further caudally, the anterodorsal nucleus does not reach the dorsal surface of the thalamus, and at this level a triangular condensation of relatively small cells lies on the dorsolateral extremity of the nucleus. As transverse sections are followed in a caudal direction, the anterodorsal nucleus becomes wedge-shaped and diminishes in size until, at the level of the caudal limit of the optic chiasma, the nucleus is represented by only a few large cells scattered about the mammillo-thalamic tract.

The anterodorsal nucleus at about the level of the interanterodorsal commissure is pierced by numerous bundles of fibres from the mammillo-thalamic, lateral preoptico-habenular and lateral cortico-habenular tracts; many of these fibres join the thick network of finely medullated fibres present throughout the anterodorsal nucleus. Other bundles from the lateral cortico-habenular tract pass through the nucleus to join the stria medullaris which lies superjacent to it. There are strong indications that at least some of the fibres from these several tracts end in the anterodorsal nucleus itself; some cross in the interanterodorsal commissure. It is likely, too, that fibres from the anterodorsal nucleus are contributed to the stria medullaris.

Anteromedial nucleus (N.A.M., figs. 4-8, 16 and 17): At its rostral extremity, the anteromedial nucleus appears in transverse sections as a prominent, triangular mass of large, deeply-stained cells lying beside the dorsal tip of the preoptic recess of the third ventricle, above the fornix and anterior commissure. More caudally, the nucleus extends in a lateral direction as far as does the anterodorsal nucleus.

At this level, and further caudally, there is in the anteromedial nucleus a well defined mass of smaller cells dorsal and medial to the large cells already described. This mass of small cells fuses with its fellow of the opposite side, forming a robust interanteromedial nucleus (N.I.A.M., fig.6) in the midline below the interanterodorsal commissure. The cells of the interanteromedial nucleus are for the most part small and similar to those of the adjacent midline nuclei. Consequently, clear separation of the individual cell masses is not possible in this region.

Further caudally, a triangular mass of large cells is detached from the main body of the anteromedial nucleus; as transverse sections are followed in a caudal direction this triangular mass sinks ventrally and eventually joins the large cells of the paraventricular hypothalamic nucleus. By means of this cellular link, the paraventricular nucleus is continuous with the anteromedial nucleus, and this is, in turn, continuous with the anterodorsal nucleus.

The main body of the anteromedial nucleus continues caudally as far as the posterior extremity of the optic chiasma.

The lateral side of the nucleus is pierced by bundles of fibres of the lateral cortico-habenular tract and the superior thalamic radiations, and small fasciculi of fibres converge at the ventrolateral extremity of the nucleus to form the circumscribed mammillo-thalamic tract. The anteromedial nucleus is relatively free of myelinated fibres. It receives fi~~v~~bre contributions from the anterior periventricular system, including a distinct fascicle from the paraventricular nucleus of the hypothalamus. The anteromedial nucleus receives some fibres of the thalamic radiations, and fibres from the preoptic region as far laterally as the pyriform cortex. Many fibres of the mammillo-thalamic tract appear to terminate in the nucleus.

Anteroventral nucleus (N.A.V., figs. 5 and 6, 15): This is the smallest of the anterior nuclei. It appears in transverse sections as a rounded mass of multipolar cells of medium size, lying in the angle between anterodorsal and anteromedial nuclei. Further caudally the anteroventral nucleus assumes a more triangular shape, and the medial angle fuses with the midline elements in this region. The anteroventral nucleus becomes rapidly smaller as transverse sections are traced in a posterior direction; the nucleus is replaced caudally by the intramedullary nuclei which form its ventrolateral boundary and which separate it from the reticular nucleus.

The only well-defined connections of the small anteroventral nucleus are with the telencephalon through the thalamic radiations.

Midline Nuclear Group.

In Elephantulus there is a considerable area of fusion in the midline of the thalami of the two sides.

In the large massa intermedia so formed lies a series of unpaired cell masses, which together form the midline nuclear group. These cell masses have small neurons of periventricular type and are in all probability functionally allied to the periventricular system. In addition, they serve to relate the bilateral thalami by means of commissural connections.

Anterior paraventricular nucleus (N.PAV.A., figs. 4-5, 16-21): This condensation of midline elements lies below the third ventricle in the rostral diencephalon, separated from the adjacent medial group of nuclei by the periventricular system of fibres. It is related in turn to the medial division of the parataenial nucleus and to the medial dorsal nucleus. Ventrally it is continuous with the rhomboid nucleus and caudally, at the level of the habenula, with the posterior paraventricular nucleus.

The fine fibre connections of the anterior paraventricular nucleus appear to be for the most part with the anterior periventricular system.

Posterior paraventricular nucleus (N.PAV.P., figs. 6-12, 22): This nucleus replaces the anterior paraventricular nucleus caudally and is iteself replaced at the level of the posterior commissure by the central grey surrounding the cerebral aqueduct. The nucleus forms a lamina of small cells below the ventricle, closely associated with the periventricular system. The most important lateral relations of the nucleus are the posterior extremities of the medial habenular and medial dorsal nuclei and, more caudally, the pretectal nucleus.

The only well-defined connections of the posterior paraventricular nucleus are with the posterior periventricular system: many of these fibres pass down into the midbrain as the dorsal longitudinal bundle.

Rhomboid nucleus (N.RH., figs. 5-9, 19 and 20): This nucleus is a condensation of midline cells ventral to the anterior paraventricular nucleus and dorsal to the interanteromedial and central nuclei. It lies between the medial dorsal nuclei on either side, and at its level of greatest development has in transverse sections the appearance of a diamond, with lateral extensions in the angles between the bilateral medial dorsal and anterodorsal nuclei. Above and behind the interanterodorsal commissure, the rhomboid nucleus is more triangular in shape, with its apex limited dorsally by the intermediodorsal nucleus and its broad base joining the central nucleus. The rhomboid nucleus is replaced by the central nucleus caudally.

The only clear connections of the rhomboid nucleus are commissural.

Central medial nucleus (N.CENT.M.,figs.9-11, 16-20): This nucleus is a conspicuous mass of cells, lying in the midline from the caudal extremity of the interanteromedial nucleus to the level of the habenular commissure. The central medial nucleus fuses laterally with the paracentral nucleus. Dorsally it is related in turn to the interanteromedial nucleus, the rhomboid nucleus and the medial dorsal nuclei; ventrally it is separated by periventricular fibres from the nucleus submedius.

The only reasonably distinct connections of the central medial nucleus are with the hypothalamus by way of the periventricular system.

Nucleus reuniens(N.REU., figs.8-11, 16 and 17): The nucleus reuniens is distinguished by the loose arrangement of its cells from the central medial nucleus which lies superjacent to it. Rostrally, the nucleus reuniens lies between the anterior poles of the ventral nuclei; caudally it fuses with the interventral nucleus.

The nucleus reuniens appears to receive fine fibres from the hypothalamus, and is associated with some small bundles of the inferior thalamic radiations.

Medial Nuclear Group.

The nuclei of the medial group lie within the region of the internal medullary lamina or between the internal medullary lamina and the midline group, with which they are for the most part closely related. The medial group comprises the parataenial, medial dorsal, submedius, paracentral, central lateral, parafascicular, subparafascicular and medial ventral nuclei, and the centrum medianum.

Parataenial nucleus (N.PAT., figs. 4 and 5, 20 and 21): This is a column of mixed small and medium-sized cells in the rostral thalamus, immediately ventromedial to the stria medullaris. Its caudal extremity joins the lateral habenular nucleus and extends over the dorsolateral side of the medial dorsal nucleus. The nucleus is clearly divisible into a lateral more scattered part with relatively large cells and a medial compact part which is closely related to the anterior paraventricular nucleus. The band of cells crossing the midline in this region is distinguished by some authors as the interparataenial. nucleus. (N.I. PAT., fig.5).

The parataenial nucleus receives fine fibres from the midline and has very fine connections with the medial dorsal nucleus.

Medial dorsal nucleus (N.M.D., figs 6-11, 20 and 21): This nucleus is a cigar-shaped mass of cells of medium size replacing the parataenial nucleus caudally. It is very intimately related to the anterior paraventricular nucleus, and at one level a mass of medial dorsal cells extends across the midline: this corresponds to the intermediodorsal nucleus (N.I.M.D., figs. 8 and 21) of other authors.

The medial dorsal nucleus is related in turn on its ventrolateral side to the anterodorsal, paracentral and lateral central nuclei. The nucleus extends from the rostral third of the diencephalon to the level of the posterior commissure, where it is replaced by the parafascicular nucleus.

The medial dorsal nucleus of Elephantulus appears to correspond to the medial part of the corresponding nucleus recognised in Primates by WALKER (1940) and others. In the medial dorsal nucleus of Elephantulus there are to be found, however, the three subdivisions described in other mammals, a principal part, a dorsolateral part and a ventral part. The principal part is composed of cells of medium size in a thick matrix of fibres; the dorsolateral part has small cells in relation to the parataenial and habenular nuclei, and the ventral division large cells in relation to the anterior, paracentral and parafasicular nuclei.

The only well-defined connections of the medial dorsal nucleus are with the superior thalamic radiations. Fine fibres relate the nucleus to the adjacent thalamic cell masses.

Nucleus submedius (N.SUBM., figs. 10 and 11, 18.): This nucleus is ovoid in transverse section and lies below the paracentral nucleus and internal medullary lamina and lateral to the central medial nucleus. Ventrolaterally it is bounded by the medial ventral and ventral nuclei. The submedius nucleus has mostly small scattered cells with little chromidial substance and small nuclei.

The only well-defined connections of the submedius nucleus appear to be with the adjacent midline and intralaminar systems.

Paracentral nucleus (N.PAC., figs. 9-11, 18 and 19): This nucleus is a lateral extension of the central medial nucleus, from which it is not clearly distinguishable. It is a group of small, deeply staining, spindle-shaped cells arranged with their long axes horizontally in the internal medullary lamina. The paracentral nucleus at its level of greatest development is triangular in cross section, with its base connected with the central medial nucleus and its apex continuous with the lateral central nucleus. Dorsally the paracentral nucleus is related to the large cells of the medial dorsal nucleus, ventrally to the nucleus submedius. Caudally the paracentral nucleus is replaced by the lighter stained cells of the centrum medianum. Connections from widely separated thalamic nuclei pass in the internal medullary lamina through the paracentral nucleus, but most of these appear to be fibres of passage. From the paracentral nucleus a ring of fine fibres passes round the inner and ventral surface of the medial-dorsal nucleus; other fibres pass to the lateral and ventral nuclei.

At least some of the axons in the paracentral nucleus are commissural.

Lateral central nucleus (N.CENT.L., figs. 7-10, 20 and 21):

This intralaminar nucleus is crescentic in section and closely applied to the ventrolateral and lateral border of the medial dorsal nucleus, which it separates from the lateral and ventral nuclear masses. Rostrally and dorsally the lateral central nucleus adjoins the anterior nuclei; ventromedially it is continuous with the paracentral nucleus. The cells of the lateral central nucleus are for the most part small, fairly deeply stained, and fusiform or polygonal in shape.

The chief connections of the lateral central nucleus are in the internal medullary lamina, and their origin and termination is indeterminate.

Parafascicular nucleus (N.PAF., figs. 12 and 13, 19-21): This is the most caudal of the medial nuclei. It is continuous at its rostral extremity with the similar but more widely spaced cells of the medial dorsal nucleus. Medially, the bilateral parafascicular nuclei fuse to form what might be described as an interparafascicular nucleus (N.I.PAF., figs. 12 and 21.) In cross section, the parafascicular nucleus has typically a triangular shape and is pierced by the habenulo-peduncular tract. Laterally, the parafascicular nucleus is continuous with the centrum medianum.

Besides more diffuse connections with the neighbouring cell masses, the parafascicular nucleus receives fibres from the thalamic radiations and from the tectum.

Subparafascicular nucleus (N.S.PAF., figs. 14 and 18): This small nucleus lies caudal and ventral to the parafascicular nucleus. Medially, it is related to the periventricular gray and the habenulo-peduncular tract; laterally it is adjacent to the ventral and interventral nuclei. It consists of small fusiform or angular cells with little chromidial substance.

The subparafascicular nucleus appears to have short connections with the adjacent thalamic and tectal cell masses.

Centrum medianum (N.C.M., figs. 13 and 20): The centrum medianum is relatively small in Elephantulus. It replaces the lateral central nucleus caudally, and forms a thin lamina lateral to the parafascicular nucleus and between the ventral and pretectal nuclei. The centrum medianum extends laterally towards the lateral posterior nucleus and is distinguished from the related cell masses by the relatively small size and pale staining of its neurons.

The connections of the centrum were not determinate in the normal material examined.

Medial ventral nucleus (N.M.V., figs. 9-12, 17 and 18):

This nucleus replaces the interanteromedial nucleus caudally. The medial ventral nucleus lies below the submedius nucleus and internal medullary lamina, lateral to the central medial nucleus. Ventrolaterally it is bounded by the mammillo-thalamic tract and laterally by the ventral nucleus. It is composed for the most part of small and medium-sized, moderately well-stained cells.

The main connections of the medial ventral nucleus appear to be with the midline and intralaminar elements. Some fibres of the inferior thalamic radiations are distributed to the medial ventral nucleus.

Lateral and ventral nuclei.

These nuclei lie in the lateral and ventral areas of the dorsal thalamus, where they are intimately related. The lateral nuclear group comprises the lateral nucleus proper, the lateral posterior nucleus and the reticular nucleus.

Lateral nucleus (N.L., figs. 5-11, 20-22): This nucleus appears in transverse sections about the same level as the habenular nuclei as a rounded mass of medium-sized cells arranged regularly in a fibre-free matrix lying lateral to the lateral central nucleus. The lateral nucleus is related ventrolaterally to the bed nucleus of the stria terminalis and ventromedially to the anterior nuclei; more caudally, the nuclei of the lateral geniculate body and the reticular nucleus are consistent lateral relations of the lateral nucleus.

The ventral area of the lateral nucleus, pierced by fibre bundles of the thalamic radiations, is distinguishable from the rest of the nucleus by reason of its larger, somewhat more angular, cells. This area appears to correspond to the nucleus lateralis A of LE GROS CLARK (1929), and is continuous with the ventral nucleus. The rest of the nucleus (nucleus lateralis B) has more numerous and smaller cells.

Caudolaterally, the lateral nucleus is continuous with the lateral posterior nucleus; caudomedially it is replaced by the pretectal nucleus. The lateral nucleus receives fibres from the superior thalamic radiations, and has fibre interchanges with the ventral nucleus, the pretectal nucleus and the intralaminar nuclei.

Lateral posterior nucleus (N.L.P., figs. 12-15, 20-22): This nucleus replaces the lateral nucleus caudal to the habenular commissure. It forms a broad band of angular, moderately deeply-stained cells from this region to the medial geniculate nucleus. Medially, the lateral posterior nucleus is related to the pretectal nucleus; laterally it is related to the dorsal nucleus of the lateral geniculate body. Ventrally it is related to the posterolateral part of the ventral nucleus.

The lateral posterior nucleus has fibre connections with the thalamic radiations, ventral nucleus and apparently with the tectum. It is traversed by bundles of optic tract fibres on their way to the pretectal nucleus.

Reticular nucleus (N.RET., figs. 6-11, 16-18): This nucleus is a prominent mass of deeply basophilic, fusiform or subangular cells of medium size, crescentic in transverse section, situated among the fibre bundles of the thalamic radiations. The reticular nucleus extends from a position below the bed nucleus of the stria terminalis in the rostral thalamus to the level of the habenular commissure. The reticular nucleus is related to the striatum and internal capsule laterally and the lateral and ventral nuclei medially. Dorsolaterally the reticular nucleus joins the ventral nucleus of the lateral geniculate body, ventromedially the subthalamus.

Since the reticular nucleus is interposed in the fibres of the thalamic radiations its own connections are difficult to determine. It is probable that the reticular nucleus acts as a true bed nucleus (i.e. a mass in which fibres relay) of the lateral forebrain bundle.

Ventral nucleus (N.V., figs 8-14, 16-19): This nucleus is characterised by the division of its elements into groups or columns by the passage through it of fibre bundles of the thalamic radiations. The ventral nucleus is limited dorsomedially by the paracentral nucleus in the internal medullary lamina, and ventrolaterally by the external medullary lamina and reticular nucleus. Dorsolaterally, the ventral nucleus joins the lateral nucleus ; other lateral relations are nuclei of the lateral geniculate body and, more caudally, the medial geniculate nucleus. Medially, the ventral nucleus joins the medial ventral and submedius nuclei. At one level, a strong band of cells connects the bilateral ventral nuclei across the midline, thus forming an interventral nucleus (N.I.V., figs. 13 and 18). Caudal to this level, the ventral nucleus appears as a triangular cell mass of gradually diminishing size; it ends above the most anterodorsal extremity of the red nucleus, medial to the medial geniculate body.

The ventral nucleus can be divided, as in other mammalian species, into three divisions, anterior, intermediate and medial. The anterior division has relatively small cells, scattered in the fibres of the thalamic radiations behind the anterior nuclei. The intermediate division of the ventral nucleus lies below the lateral nucleus and has larger cells, while the medial division, adjacent to the medial ventral nucleus, has somewhat smaller neurons.

The ventral nucleus has important connections with the medial lemniscus and thalamic radiations, and other less-defined fibre interrelations with the lateral, medial ventral, medial dorsal and lateral habenular nuclei.

Posterior Group.

The posterior group comprises a series of nuclei situated in the caudal areas of the thalamus, in the junctional region between diencephalon and midbrain and in relation to the terminal fibres of the optic tract. The nuclei of the lateral geniculate body are included for convenience in the posterior group, even though in

Elephantulus they lie dorsolaterally rather than caudally in the thalamus.

Dorsal nucleus of the lateral geniculate body (N.GEN.L.D., figs. 6-13, 20-22): This nucleus lies dorsolateral to the lateral nucleus and, more caudally, lateral to the lateral posterior nucleus. It is situated above the ventral nucleus of the lateral geniculate body, from which it is separated by a narrow zone free of cells. Ventromedially at one level the nucleus joins the main body of the ventral nucleus.

The nucleus consists of medium-sized cells stained with moderate intensity. There is no distinct lamination of the cells in the nucleus, as has been reported in Primates (WALKER, 1938), the Insectivore No!! Tupaia (LE GROS CLARK, 1929), and the Marsupial Trichosurus (GOLDBY, 1941).

Ventral nucleus of the lateral geniculate body (N.GEN.L.V., figs. 7-14, 19-22): This is an oval mass of small cells lying in the lateral diencephalic wall from the level of the optic chiasma to the level of the posterior commissure. The nucleus is related dorsally to the dorsal nucleus of the lateral geniculate body, medially to the lateral and ventral nuclei and ventrally to the reticular nucleus.

The whole rounded outer surface of the nucleus is related to the optic tract, from which it receives many fibres. Other axons of cells in the nucleus are contributed to the optic tract as the latter passes on towards the tectum as the brachium of the superior colliculus.

Nucleus of the optic tract (N.TR.OP., figs. 13 and 23): This is a narrow, irregular cellular lamina above the pretectal nucleus, intercalated in the course of the brachium of the superior colliculus. In transverse sections about the level of the posterior commissure the nucleus has a more or less triangular shape and contains, in addition to larger, more basophilic, cells, smaller cells embedded in a thick matrix of fibres medial to the lateral posterior nucleus. More caudally, the nucleus of the optic tract disappears below the lateral margin of the anterior colliculus.

The nucleus appears to be primarily a bed nucleus of the brachium of the superior colliculus. It has also short connections with the pretectal nucleus.

Medial geniculate nucleus (N.GEN. M., figs. 15, 19-21): This is a rounded mass of moderately basophilic cells at the extreme caudolateral extremity of the thalamus, where it forms a distinct tubercle on the surface of the brain (fig.3). The medial geniculate nucleus is related particularly to the optic tract anterolaterally, the suprageniculate nucleus dorsomedially and the brachium conjunctivum ventromedially.

The medial geniculate nucleus receives distinct lemmiscal contributions and some optic tract fibres. Probably the latter fibres are not retinal in their origin but are elements of GUDDEN'S commissure. Other connections exist between the medial geniculate nucleus on the one hand and the suprageniculate nucleus and adjacent cell masses on the other. The brachium of the inferior colliculus is well developed. Anteromedially, cells of the medial geniculate nucleus are scattered among the more caudal bundles of the thalamic radiations as far forward as the ventral nucleus.

Pretectal nucleus (N.PRET., figs 12-15, 19-22): The pretectal nucleus is a well-defined mass of cells of small and medium size, situated caudomedial to the lateral nucleus and ventral to the anterior colliculus. The pretectal nucleus in Elephantulus is relatively very large and its size accounts for the prominence of the anterior colliculus which lies like a cap over the nucleus. The pretectal nucleus is related laterally to the lateral posterior nucleus and dorsolaterally to the nucleus of the optic tract.

The pretectal nucleus lies ventromedial to the optic tract, from which it receives many fibres. It lies for the most part among tectothalamic fasciculi and is tra~~ns~~versed by a considerable number of elements of the medial lemniscus. Many axons in the pretectal nucleus appear to be fibres of passage, but some, at least, appear to end in the nucleus itself. The better-defined short connections of the pretectal nucleus are with the lateral geniculate nuclei, nucleus of the optic tract, and the adjacent tectal grey masses. The pretectal nucleus receives contributions from the posterior periventricular system, and many fibres from the pretectal nucleus cross in the posterior commissure.

SUBTHALAMIC CELL MASSES.

The subthalamus is that region of the brain ventral to the dorsal thalamus and dorsolateral to the hypothalamus, closely associated with the descending extrapyramidal connections of the lateral forebrain bundle. In Elephantulus the cell masses of the subthalamus are very similar to those described in the rat by GURDJIAN (1927) and in the opossum by BODIAN (1940). They comprise the more circumscribed subthalamic nucleus and the more diffuse entopeduncular nucleus, zona incerta and field of Forel.

Subthalamic nucleus (N.SUB., figs. 13 and 14, 16 and 17): This is a prominent mass of cells of medium size, oval in section and closely applied to the dorsomedial aspect of the cerebral peduncle. The nucleus is related to the zona incerta medially, anterodorsally it is continuous with the reticular nucleus, and caudally it is rather poorly demarcated from the substantia nigra.

The subthalamic nucleus receives cortical fibres through the internal capsule, and is connected with the striatum by the ansa lenticularis. It is connected with the contralateral subthalamic nucleus by fibres in the supramammillary decussation, and fibres of the supraoptic decussations reach its rostroventral border.

Entopeduncular nucleus (N.ENTOP., fig.10): This is a rather diffuse mass of cells in the rostrolateral subthalamus. It is represented by large, moderately deeply staining, triangular or fusiform cells scattered among the fibres of the ventral peduncle of the lateral forebrain bundle. Laterally the entopeduncular nucleus reached the striatum; medially it joins the zona incerta. The entopeduncular nucleus is closely associated with the descending lenticular systems, for which it forms a true bed nucleus.

Zona incerta (Z. INC., figs. 13-19): This area of scattered medium-sized cells occupies the dorsal part of the subthalamus, immediately ventral to the ventral medullary lamina. The zona incerta lies rostrally above the lateral forebrain bundle and subthalamic nucleus, and more caudally above the red nucleus; ventrally and medially it merges with the field of Forel.

The zona incerta is closely related to the lateral forebrain bundle throughout its length, and receives from it a considerable number of fasciculi. Other fibre bundles pass from the zona incerta dorsally to reach the dorsal thalamus, particularly the submedius nucleus. Fibres from the Zona incerta are contributed to the ventral part of the dorsal supraoptic decussation, to the subthalamic decussation, to the hypothalamus and, caudally, to the pretectal nucleus, tectum and tegmentum.

Field of Forel (FF in figs 14 and 15): This area of small and medium-sized cells is ill-defined and is recognised only by its position in association with the radiations of Forel. It is continuous laterally with the Zona incerta and dorsally with the ventral medullary lamina. Medially it adjoins the hypothalamus. Caudally the field is replaced by the tegmentum.

The cells of the field are connected with the basal ganglia and dorsal thalamus by the fasciculus lenticularis and ansa lenticularis, and has diffuse connections with the Zona incerta, posterior hypothalamic area and tegmentum.

MAIN THALAMIC FIBRE SYSTEMS.

As each cell mass was described in the preceding paragraphs, the more important of its connections were described briefly. The following is a short account of the arrangement of the more important tracts in the thalamus of Elephantulus. It is given in a general way, since it was not possible in normal material to determine the origin, course and termination of stained connections with any precision.

Most of the fibre systems, particularly the internal capsule and thalamic radiations, are very similar to those described in the detailed published accounts of GURDJIAN (1927) and BODIAN (1940). Others, like the stria medullaris, have a characteristic arrangement in Elephantulus: these are, consequently, considered in more detail.

Study of the tracts was carried out on sections prepared by both the WEIL and SILVER pyridine techniques, and, since rigid distinction between medullated and unmedullated material seems unnecessary, both types of connections are described together.

CONNECTIONS BETWEEN DIENCEPHALON AND TELENCEPHALON.

All connections between diencephalon and telencephalon may be considered as belonging to four systems, the lateral and medial forebrain bundles, fornix and the stria medullaris. These systems all pass through the preoptic region, which forms, thus, a fibrous and cellular link between the two subdivisions of the forebrain, telencephalon rostrally and laterally and diencephalon caudally and medially.

The fornix and medial forebrain bundle, passing from the hippocampus and basal forebrain areas to the hypothalamus and brain stem, will not be given any consideration in this account of the thalamus proper.

Stria medullaris system.

The stria medullaris is prominent and well-developed in Elephantulus. In it are readily distinguished the following components:

medial cortico-habenular tract, septo-habenular tract, amygdalo-habenular tract, lateral cortico-habenular tract, lateral preoptico-habenular tract and medial preoptico-habenular tract. The preoptico-habenular tracts pass from the preoptic region to the thalamus, and correspond to the olfacto-habenular tracts of other authors.

These individual tracts overlap to some extent in their origin and distribution, and it seems better to consider them as parts of a single stria medullaris system than as distinct entities. The fibres from basal forebrain areas are very intimately associated with components of the medial forebrain bundle in the earlier part of their course; those from the hippocampus are similarly related to the fornix, those from the amygdala to the stria terminalis, and those from the basal ganglia and neopallium to the thalamic radiations. Moreover, it seems certain that many stria medullaris fibres are distributed to thalamic areas other than the habenula. Becuase of these considerations, complete separation of stria medullaris elements from other tracts is difficult and artificial.

Medial cortico-habenular tract (TR.C.HAB.M., fig. 24): This appears as a prominent bundle of fibres passing from the dorsolateral side of the fornix in the rostral diencephalon and collecting below the ventricle to form the main body of the stria medullaris (STR.MED., fig. 25). The medial cortico-habenular tract is related particularly to the bed nucleus of the stria terminalis ventrolaterally and to the parataenial nucleus dorsomedially. Its more caudal fibres are in very intimate contact with the cells of the anterodorsal nucleus, in which nucleus many fibres appear to terminate. The tract provides thus a pathway between the hippocampus on the one hand and the anterior nuclei and habenular complex of the dorsal thalamus on the other.

Septo-habenular tract (TR.S.HAB., fig. 24): The contributions from the septum, particularly the bed nucleus of the anterior commissure, to the stria medullaris are fine and scant, and are scarcely distinguishable from other elements of the stria.

Amygdalo-habenular tract (TR.AM.HAB., fig.25): This is the name given to fibre interconnections occurring between the stria terminalis and stria medullaris where the two systems are closely related spatially. There seems to be no doubt that in available preparations fibres from the stria medullaris (i.e. from the hippocampus chiefly) join the stria terminalis for distribution as well as the reverse. The name amygdalo-habenular tract is to be preferred to the ambiguous term "strio-habenular tract", used by some authors.

Lateral cortico-habenular tract, (TR.C.HAB.L., fig.26): This tract arises from the medial aspect of the internal capsule at a level just rostral to the interanterodorsal commissure. Many distinct fibre bundles curve medially and dorsally, where they are associated with preoptico-habenular fibres. Many elements are contributed to the rich network of fibres in the anterodorsal nucleus, and others pass dorsally to the stria medullaris.

Lateral preoptico-habenular tract, (TR.PR.HAB.L., fig.26): This is a robust bundle of fibres passing dorsomedially from the olfactory tubercle and lateral preoptic region. In its course it passes lateral to the fornix columns and through the anterodorsal nucleus, to which cell mass many fibres are contributed; other fibres pass to the stria medullaris above.

Medial preoptico-habenular tract, (TR.PR.HAB.M.fig.27): This tract, in contrast to its lateral companion, contains relatively few fibres passing rostrodorsally from the medial preoptic region and anterior hypothalamic area to the region of the anterior nuclei. Some fibres are lost in the anterior nuclei and others join the stria medullaris near the habenula.

Stria medullaris proper, (STR.MED., figs 26-29): The main body of the stria medullaris, formed by the junction of the tracts described above, passes back along the dorsolateral surface of the thalamus. In its course it passes the parataenial nucleus, lateral nucleus and anterodorsal nucleus. Many fibre components of the stria pass through the anterodorsal nucleus, and the nucleus itself appears to contribute elements to the main body of the stria which lies above it. The terminal bundles of the stria are expended in the habenular nuclei themselves and in the rich plexus of fibres associated with the lateral habenular nucleus. At least some stria fibres cross in the habenular commissure. There is no evidence whatever to indicate the direction in which fibres of the stria medullaris conduct impulses.

Lateral forebrain bundle.

Lateral to the rostral extremity of the diencephalon, bundles of the internal capsule pass through the basal ganglia and between basal ganglia and thalamus (l.CAPS., figs 24-30). They travel ventrally, caudally and medially, and become separated into dorsal and ventral peduncles. The dorsal peduncle of the lateral forebrain bundle divides into the lateral cortico-habenular tract and the thalamic radiations; the ventral mass continues as the far smaller and more circumscribed cerebral peduncle (PED.CER., figs 31-34). The cerebral peduncle passes above the optic tract and curves ventrally and medially towards the medial forebrain bundle, giving off fibres to the Zona incerta and subthalamic nucleus. It emerges on the base of the mid-brain and passes on down the brain-stem in a superficial position. Besides fibres of passage, the lateral forebrain bundle carries fibres between the thalamus on the one hand and the basal ganglia and cerebral cortex on the other.

Thalamic radiations, (TH.RAD., figs 28-30): These are several series of fibres arising from the medial and dorsal aspects of the internal capsule as it passes from the region of the basal ganglia through the lateral diencephalic wall. These fibres enter the lateral side of the dorsal thalamus, in the nuclei of which they are ditributed. They are divided more or less arbitarily into three groups, the superior, inferior and intermediate thalamic radiations, as described by GURDJIAN (1927) in the rat.

The superior thalamic radiations are bundles of fibres arising from the internal capsule all along the lateral aspect of the diencephalon. They pass through the most dorsolateral part of the reticular nucleus, and, as they are distributed, their fibres are not clearly separable rostrally from those of the lateral cortico-habenular tract. Fibres from both enter the anterior nuclei. Other fibres of the superior radiations, together with those of the intermediate radiations, supply the dorsolateral aspect of the ventral nucleus and the medial dorsal nucleus. Bundles of the superior radiations enter the lateral nucleus, and caudally these form a thick mass of fibres, triangular in cross section, lying between the lateral forebrain bundle and external medullary lamina. Many of these fibres pass back to the pretectal nucleus and tectum.

The inferior thalamic radiations are other bundles passing from the ventromedial surface of the internal capsule through the ventral part of the reticular nucleus. They course through the thalamus medial to the mammillo-thalamic tract and are distributed more ventrally and medially than the fibres of the superior and intermediate radiations. The more rostral fibres of the inferior radiations, together with others of the intermediate radiations, are contributed to the maze of fibres in the anterodorsal nucleus, where they are quite closely related to the original fibres of the mammillo-thalamic tract. Other elements of the inferior radiations reach the ventral and medial aspects of the medial and midline nuclei in this region.

The intermediate thalamic radiations are groups of fibres, described together, which pass from the internal capsule to the dorsal thalamus in between the bundles of the superior and inferior radiations. For the most part they merge for distribution dorsally and ventrally with the adjacent parts of the superior and inferior radiations. Rostral to the mammillo-thalamic tract the fibres of the radiations are distributed together to the lateral aspect of the anterior nuclei. More caudally, the great majority of intermediate radiation fibres enter the ventral nucleus; some continue medially to the region of the medial and midline nuclei, particularly the medial dorsal nucleus. Caudally, many radiation fibres reach the medial geniculate nucleus, suprageniculate nucleus, pretectal nucleus and dorsal nucleus of the lateral geniculate body.

The thalamic radiations constitute a series of connections between the dorsal thalamic nuclei on the one hand and the cortex and basal ganglia on the other. Probably most of the fibres have their cells of origin in the thalamic nuclei and are, thus, thalamofugal. Their precise origin and termination, and the nature of thalamic projection in Elephantulus, must remain for experimental investigation to discover. It seems likely that many fibres are thalamo-striatal. Whether there are fibres conducting impulses from telencephalon to diencephalon in the radiations is still a moot point.

No definite inferior thalamic peduncle, such as has been described in other mammals, was identified, and this tract seems to be part of what is included here in the more general term inferior thalamic radiations.

Ansa lenticularis, (ANSA.L., fig. 29): The fibres of the ansa lenticularis pass medially from the basal ganglia below the internal capsule, and turn caudalward between the cerebral peduncle and medial forebrain bundle. They are distributed to the entopeduncular nucleus, subthalamic nucleus, Forel's field, hypothalamus, and to the tegmentum caudally.

Fasciculus lenticularis, (FASC.LENT., fig. 31): This is a diffuse mass of fibres passing medially to the zona incerta dorsal to the cerebral peduncle . Its fibres originate in the basal ganglia and are distributed to the subthalamic nucleus, zona incerta and field of Forel.

INTRADIENCEPHALIC CONNECTIONS.

Although accurate knowledge of the intradiencephalic connections in any mammal is a pressing need, it is impossible to sort these connections out of the maze of fibres seen running all ways, in and out of the medullary laminae, in sections prepared from brains of normal animals. Such fibres include short and long axons and axons of passage to and from areas other than the diencephalon. From normal material, however carefully prepared and examined, it is thus possible to make but few, guarded generalisations; the niceties of local diencephalic connections and their relation to more distant projections remain obscure.

Mammillo-thalamic tract, (TR.M.TH, figs. 29-32): This is the only circumscribed tract connecting different diencephalic centres. It is a well-defined bundle of fibres passing between the mammillary region of the hypothalamus and the anterior nuclei of the dorsal thalamus. The tract arises chiefly from the medial mammillary nucleus, though some fibres enter it from the lateral mammillary nucleus and supramammillary area, and travels rostrodorsally. It has a characteristic position at first above the fornix, lateral to the tuber nuclei of the hypothalamus, and then ventrolateral to the medial ventral nucleus of the dorsal thalamus. More rostrally the tract divides into fascicles as it enters the anteromedial nucleus. Fibres are contributed to the anteromedial and anteroventral nuclei, but the great majority end in the anterodorsal nucleus. Some cross the midline in the interanterodorsal commissure, and some appear even to reach the stria medullaris above.

Most, if not all, of the fibres in the tract are mammillo-thalamic; whether there are or are not as a general rule any thalamo-mammillary fibres must remain undecided.

Habenular commissure, (CO.HAB., figs. 30-32): The habenular commissure is a band of fibres crossing the midline above the caudal end of the habenular complex. It receives fasciculi in particular from the stria medullaris and habenular nuclei, and contributes elements to the habenulo-peduncular tract. Some bundles enter the pineal body, but these may be only fibres of passage which later rejoin the main mass of commissural axons.

Posterior commissure, (P.CO., figs. 32-34): Though most of its fibres are not diencephalic, this commissure is considered here for convenience. It is relatively well-developed, and can be divided, as in reptiles, into two parts. A dorsal division connects chiefly the tecta and superior colliculi of either side; a ventral division has fibres bringing in particular the pretectal nucleus, posterior praventricular nucleus and the nucleus of the medial longitudinal bundle into relation with the contralateral cell masses.

Optic nerves and tracts: The course of optic fibres in Elephantulus is essentially the same as that described repeatedly in other species and reviewed by LE GROS CLARK (1942).

The majority of fibres in the optic nerves, (N.OP., figs 24 and 25), cross in the optic chiasma, (O.CH., figs. 26-28), and continue their course as the optic tracts (TR.OP., fig. 22 et seq.). The tracts pass back dorsolaterally, round the diencephalon, to reach the geniculates and tectum. Each tract passes over the cerebral peduncle and fans out over the lateral geniculate body and pretectal nucleus (Fig.3).

Some fibres, forming the anterior accessory optic tract described by some authors, pass from the optic tract to the subthalamic nucleus, but it is doubtful if these fibres are of retinal origin. A small posterior accessory optic tract, (TR.OP.ACC.P., fig. 31), crosses the cerebral peduncle obliquely and terminates in the nucleus opticus tegmenti of the midbrain.

Myelin-stained sections show conspicuous connections of the optic tracts with the dorsal nucleus of the lateral geniculate body, the large-celled nucleus of the optic tract, the pretectal nucleus and pretectal nucleus. Other fibres enter the ventral nucleus of the lateral geniculate body. It is not possible to decide in normal material which of these fibres are of retinal origin, as the work of BODIAN (1937) has shown.

Periventricular system and dorsal longitudinal bundle. It has been convenient, following the suggestion of BODIAN (1940), to divide the periventricular system, (PEV.S., figs. 27-31), into two groups of connections.

The anterior periventricular system consists of a series of short fibres which pass vertically along the walls of the third ventricle, connecting the medial and midline cell groups of the dorsal thalamus with the more central nuclei of the hypothalamus. These fibres are most numerous in the tuber region.

The posterior periventricular system is a group of very finely myelinated and unmyelinated fibres arising from the more caudal and dorsal centres of the hypothalamus and passing upwards and backwards to the region of the posterior paraventricular nucleus. From the caudal thalamic nuclei the fibres are relayed as the dorsal longitudinal bundle, (DLB., fig. 24), around the cerebral aqueduct, to the midbrain. It is probable that most of the fibres in the dorsal longitudinal bundle are descending to as yet undetermined mesencephalic and bulbar centres.

CONNECTIONS OF DIENCEPHALON AND MID-BRAIN.

Afferents to the thalamus include the rather diffuse lemniscal system and brachium conjunctivum, the brachium of the inferior colliculus, and ill-defined connections from the tectum and tegmentum to the dorsal thalamus and subthalamus. Efferents include, in addition to the well-defined habenulo-peduncular tract, several series of short relay fibres from the pretectal and adjacent thalamic nuclei to the tectum and tegmentum.

Habenulo-peduncular tract, (TR.H.P., figs. 32-34): This is a prominent, circumscribed bundle of fibres passing from the caudal end of the habenula to the tegmentum of the mid-brain. It receives fibres from the neuropil of the lateral habenular nucleus, from the habenular commissure and from the medial habenular nucleus. As it passes, caudoventrally, the tract pierces the parafascicular nucleus and passes the subparafascicular nucleus. The tract terminates in the interpeduncular nucleus of the tegmentum.

Lemniscal system (LEMN. M., figs. 33 and 34): The fibres of the lemniscal system pass up from the midbrain dorsomedial to the cerebral peduncle. Many fibres terminate in the mid-brain, and, as the system passes the pretectal nucleus, many bundles pass dorsorostrally through the substance of the nucleus. Other lemniscal fibres are contributed to the medial geniculate body.

The main body of the medial lemniscus flattens out in the ventral medullary lamina under the ventral nucleus. Many lemniscal fibres pass upwards round the ventral nucleus, which receives lemniscal contributions from above, below, and behind.

Brachium conjunctivum, (BR. CONJ., fig. 34): The brachium conjunctivum passes up from the region of the red nucleus as a diffuse mass of medullated fibres medial to the medial geniculate nucleus. In the maze of fibres in the region, it is not possible to separate out the terminations of the lemniscal system and brachium conjunctivum in the ventral thalamic nucleus.

DISCUSSION.

1. The structural peculiarities of the thalamus of Elephantulus.

In the foregoing pages a general account of the nuclear configuration of the mammalian thalamus was given, and this was followed by a detailed description of the thalamus of Elephantulus. It is possible now briefly to review the structural peculiarities found in Elephantulus and to assess their significance in relation to the rest of the brain.

In the midline complex: The massa intermedia is well-developed and the midline nuclei within it occupy a large area. This appears to be more than a merely relative large size resulting from lack of emphasis of the other groups of nuclei. Probably the development of the midline nuclei may be correlated with the concurrent development of the hypothalamus and basal telencephalic olfactory and visceral areas with which the midline mass is known to have close connection.

In the habenula: The habenular nuclei of Elephantulus are prominent and extend over a larger area than they occupy in most mammals. Again, this appears to be more than a mere relative size increase: active enlargement in the habenular nuclei is related to the high degree of development of the stria medullaris and its components.

In the anterior complex: The anteromedial and, particularly the anterodorsal nuclei are large in Elephantulus, while the anteroventral nucleus forms only a very small, circumscribed mass. The magnitude of the anterodorsal and anteromedial nuclei is in all probability related to the unusual expansion of the hippocampus and basal telencephalic areas. There is strong evidence in favour of connections between the hypothalamus, hippocampus and basal telencephalic areas on the one hand and the anteromedial and anterodorsal nuclei on the other. In this way these two anterior nuclei are in contact with widely separated visceral areas in the brain, and most probably they project visceral impulses through the thalamic radiations to the retrosplenial and cingular areas of cerebral cortex, as in other species. It is noteworthy that these are the only cerebral areas in Elephantulus that are greatly differentiated.

In the special sensory systems: The eyes and optic nerves of Elephantulus are large, and the optic tracts terminate for the most part in the pretectal nucleus and anterior colliculus. These structures, and the ventral nucleus of the lateral geniculate body which sends fibres to them, are relatively well-developed. The striate area of cerebral cortex is not clearly differentiated, and cerebral projection of visual impulses seems comparatively unimportant. Accordingly, the dorsal nucleus of the lateral geniculate body, from which the cerebral projection fibres arise, is small and its cells show no distinct lamination. This is very different from the arrangement in the insectivore Tupaia (LE GROS CLARK, 1929) and in primates (WALKER, 1938), in which the mechanism of vision is predominantly cerebral, the striate area is elaborately differentiated, and the dorsal lateral geniculate nucleus is correspondinglylarge, with cells disposed in concentric laminae.

Similarly, auditory connections in the midbrain are well-developed and complex. Most lateral fillet fibres end in the posterior colliculus. The medial geniculate nucleus, and its projection area of cerebral hemisphere, the auditory cortex, are much less developed than in other mammals.

<u>In the general sensory system</u>: The usual terminal centre for the somatosensory or fillet systems, the ventral nucleus, is in Elephantulus relatively small and its constituent divisions are not very clearly distinguishable. Many somatosensory fibres appear to terminate in the midbrain. Certainly, fewer fillet fibres reach the thalamus than is found in most mammals. Nor is the sensorimotor area of cerebral hemisphere to which the

ventral nucleus projects elaborately differentiated. Cerebral projection of somatosensory impulses, as of visual and auditory impulses, is but little emphasised.

In the lateral complex and medial dorsal nucleus: There is in Elephantulus no great development of the lateral and lateral posterior nuclei, nor clear separation of these nuclei from one another or from the adjacent ventral nucleus: in accordance with this, it is found that the parietal association areas of cerebral cortex, to which these thalamic nuclei project, is but poorly differentiated. In the case of the medial dorsal nucleus, a double projection is to be recognised: the medial part of the nucleus projects to the visceral areas of frontal cortex (the orbital surface in primates); this part includes most of the medial dorsal nucleus in Elephantulus; the rest of the nucleus, projecting to the frontal association area, is represented in Elephantulus only by a small area of scattered cells.

Thus the association areas characteristic of primates and, in particular, man, are rudimentary in Elephantulus.

In general: Much of the emphasis which in most mammals falls upon the cerebral cortex falls in Elephantulus upon other forebrain and midbrain areas. This is seen particularly in the visual system, but applies as well to the auditory and somatosensory systems. There is intimate connection between the thalamus on the one hand and the olfactory and visceral areas in the hippocampus and basal telencephalon on the other. A great deal of co-ordination carried out in other mammals by thalamic projection and cerebral association appears, in Elephantulus, to be carried out by connections within the diencephalon and midbrain, as in submammalian forms. Accordingly, cell-masses in the junctional region between forebrain and midbrain, in particular the pretectal nucleus, are developed to an unusual extent.

In the subthalamus: The subthalamus of Elephantulus has a pattern of organization very similar to that found in other mammalian species. The descending lenticular systems are rather smaller than the corresponding systems in primates, and the subthalamus less differentiated into component cell-masses. On the whole, however, the subthalamus remains relatively uniform in configuration while the dorsal thalamus and other regions of the brain undergo striking evolutionary changes.

Conclusions: Previous studies have indicated a close relationship between Elephantulus and other primitive mammalian forms. This has been readily confirmed: the thalamus of Elephantulus shows on the whole a simple, generalized mammalian pattern, in which all the characteristi component parts may be distinguished, but few are developed to any marked degree. There is close resemblance between the thalamus of Elephantulus and that of other primitive metatherian and eutherian forms, particularly the marsupials Didelphys (BODIAN, 1939 and 1940) and Trichosurus (GOLDBY 1941) and the edentate Tatusia (PAPEZ, 1932).

The thalamus of Elephantulus has, however, some specific features that are worthy of note. Foremost among these is the unusual development of the anterodorsal and anteromedial nuclei. The massa intermedia, and midline nuclei within it, are relatively very large. In general, cerebral projection of both general and special sensory impulses does not take place to the same degree as is usually found in mammals: thus cell-masses concerned with this cerebral projection - the ventral, dorsal lateral geniculate and medial geniculate nuclei - are not greatly developed. The frontal and parietal association areas, and the thalamic nuclei projecting to them - the lateral, lateral posterior and medial part of the medial dorsal nuclei - are little more than rudimentary.

2. The evolutionary development and structure of the thalamus.

The brain of Elephantulus, with its emphasis on midbrain association, is particularly suitable for comparison with submammalian forms. In the reptilian thalamus a configuration something like that in Elephantulus, but much less clearly differentiated, is found. In amphibians and primitive fishes there is hardly any separation of the thalamic tissue into different masses at all. Thalamic differentiation invariably parallels telencephalic differentiation precisely. It is thus possible to put forward an hypothesis of forebrain development different from that usually conceived:-

The diencephalon must originally have been a primordial mass very closely related to the adjacent preoptic region of the telencephalon. In no surviving vertebrate is this primitive condition found, for in fishes there is already a degree of specialization. The first dissociation of function came between a predominantly visceral area, the hypothalamus, and the predominantly somatic area, the thalamus. There soon followed separation of the dorsal thalamus, which is concerned with ascending fibres passing from brain-stem to the telencephalon, from the subthalamus, which is concerned with fibres passing from the telencephalon to the bulbo-spinal motor centres.

The dorsal thalamus retains throughout the vertebrate phylum intimate connections with the telencephalon. It is not surprising to find, then, that as the telencephalic masses differentiate structurally and functionally, there is corresponding differentiation in the thalamus. In the telencephalon this differentiation results in the formation first of all of the four primary regions - preoptic region, septum, striatum and pallium - and then in the subdivision of these regions. Thus arose, for instance, the amygdaloid mass, pyriform cortex, hippocampus and neopallium, and, within the neopallium itself, the various areas which are cytoarchitectonically distinguishable. In the thalamus this differentiation results in heterogeneity of cells, so that, in place of one homogeneous mass, a number of nuclei may be recognised. This differentiation is a fundamental feature of forebrain development: it is a single process applied to both parts of the forebrain, telencephalon and diencephalon, so that each nucleus so formed preserves a constant relationship to its corresponding telencephalic area. That each nucleus projects to one area is well-known experimentally: it is found in all mammals so far investigated, from marsupials to primates. The other finding of the experimental workers, that adjacent thalamic nuclei project to adjacent telencephalic areas lends further support to this hypothesis of forebrain development.

In this way there arose a number of complexes in the forebrain of mammals. As examples may be cited the somatosensory complex (ventral posterior nucleus - postcentral area), the visual complex (dorsal lateral geniculate nucleus - striate area), the visceral projection complex (anterior nuclei - retrosplenial and cingular areas) and the associated complex (lateral and lateral posterior nuclei-parietal association area). These complexes are to a certain extent independent, although they are naturally closely related, and each is developed to a particular degree, depending upon the general features of brain organization, in different species. Thus, in Elephantulus, only part of the anterior nuclear - cingular and retrosplenial complex is greatly developed: because of the emphasis which is given to midbrain association, as in submammalian forms, somatosensory, visual and auditory fibres are not projected to the cerebral cortex to the great extent found in other mammals. Thus, too, we find primates have the dorsal lateral geniculate - striate complex, the ventral posterior - postcentral complex and, in particular, the lateral and lateral posterior-parietal complex, all greatly developed. Modifications of the same fundamental plan of organization are found in all forebrains: description of the details in different species in beyond the scope of this discussion

The mammalian thalamus may be pictured, in the most general way, as a large part of the brain having a number of subdivisions which fall into four main groups. The first group, comprising the midline nuclei, is intimately related to the hypothalamus and has no cerebral connections. We know very little of the function of this group except that it is implicated in the most fundamental activity of the central nervous system, consciousness. The second group, comprising the anterior nuclei, has close connections with the visceral and olfactory regions of the brain, and relays to the retrosplenial and cingular areas. There is strong presumptive evidence that these connections are the pathway of emotional representation in the consciousness. The third group receives the tertiary sensory fibres and relays them direct to the sensory areas of the cerebral cortex. The ventral posterior nucleus is concerned with somatic sensation, the dorsal lateral geniculate nucleus with vision, and the medial geniculate nucleus with audition. Each of these nuclei plays an important part in the registration of sensation, so that, in higher mammals at any rate, a lesion in any one nucleus results in serious disturbance of the corresponding sensation. The fourth group, comprising the lateral and lateral posterior nuclei and the medial part of the medial dorsal nucleus, projects to the parietal and frontal association areas of the brain. Very little is known of the functions of this complex, which is so extraordinarily developed in man: further knowledge awaits better understanding of the association areas themselves. The four main groups, and the nuclei within each group, may be combined in diverse ways to give a thalamic configuration characteristic of each species of mammal and reflecting in an accurate way its entire central nervous organization.

SUMMARY.

The nuclear configuration and fibre systems of the thalamus of Elephantulus are described in detail as a basis for later comparison with submammalian brain types. In this study every possible criterion of nuclear differentiation was used, and rigidly applied in each case. In Elephantulus all the elements found in other mammals are present, but in rather unusual relation. The ventral nuclear group is, by comparison with other mammals, very small and only slightly differentiated into component parts. This is in keeping with the complexity of the tectum in Elephantulus and relative unimportance of cerebral projection of somatosensory impulses. Cortical projection of auditory and visual impulses, too, appears to be much less pronounced in Elephantulus than in other mammals: there is but poor differentiation of auditory and visual cortices, and the ventral lateral geniculate nucleus - which relays impulses to the tectum - is developed at the expense of the corresponding dorsal nucleus, from which cerebral visual fibres arise, and the medial geniculate nucleus. The lateral and lateral posterior nuclei in Elephantulus are readily recognised, but not greatly developed. This corresponds with the poor differentiation of the parietal association area of cerebral cortex, to which these nuclei project. The

greater part of the medial dorsal nucleus in Elephantulus probably represents the medial division of the corresponding nucleus in primates, which sends impulses to the visceral areas of the frontal cortex. The rest of the medial dorsal nucleus, which projects to the frontal association areas, is in Elephantulus scarcely distinguishable. It follows from the slight degree of development of other nuclei - chiefly the ventral, lateral and medial dorsal, that the habenular and midline elements are conspicuous in Elephantulus and occupy a relatively large area. The most significant development in the thalamus occurs in the anterodorsal and anteromedial nuclei. These cell-masses are intimately related to the hippocampal regions of the telencephalon which have undergone inordinate development in Elephantulus. The anteroventral nucleus, which in primates and other higher mammals is greatly enlarged, is in Elephantulus very small.

The mammalian thalamus may thus be visualized as a loose organization of different groups of cells. Each of these groups has a certain amount of distinctness and may alone undergo developmental modification. Thus, in primates, ventral, lateral, lateral posterior, medial dorsal and anteroventral nuclei are all emphasised: in Elephantulus development is practically confined to the anteromedial and anterodorsal nuclei.

It is possible, thus, to arrive at a picture of thalamic differentiation in the course of evolution. At first there is found a simple thalamic and related simple cerebral mass. Consonant with increasing differentiation of the cerebral primordium goes corresponding differentation in the thalamus. In the cerebral cortex this differentiation is represented by the formation of cytoarchitectonically and myeloarchitectonically distinct areas; in the thalamus by the formation of cytoarchitectonically and myeloarchitectonically distinct nuclei. Thus each thalamic nucleus projects to its corresponding cerebral area, and adjacent thalamic nuclei project to adjacent cerebral areas, as is found experimentally.

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