THE DUAL STRUCTURE OF THE NEOPALLIUM: ITS HISTORY AND SIGNIFICANCE

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INTRODUCTION

Even at the primitive stage of cerebral evolution represented by the reptilian fore-brain, considerable structural diversity of cortical pattern is already apparent. Despite the neurological investigations carried out during the present century, we are still far from understanding how that pattern arose and, until we have unravelled the reptilian pattern, the mammalian cortex will remain correspondingly obscure.

Over a decade ago I was approaching this problem by a morphological study of the striate body (Dart, 1920). By force of circumstances these studies were interrupted until the present year, when, with Dr J. Gillman's assistance, I was enabled to occupy several workers in my laboratory with the material for a more exhaustive analysis of the cortical areas in various South African Reptiles such as *Agama*, *Zonurus*, *Gecko*, *Testudo*, *Chameleon*, etc., by means of accurate maps.

Extending the precedents of Campbell, Brodmann and others with Mammals we have been accumulating records of the fore-brain pattern in these Reptiles, after treating them according to the methods of Nissl and Cajal. The results of these investigations will appear in due course; but one particular outcome of the work is so novel in character and of such morphological importance that it justifies the present preliminary communication.

A neopallial primordium has been recognised in the reptilian fore-brain by all recent workers, and has been identified as that part of the brain which lies between the hippocampal and pyriform formations, and to which a special group of fibres (the forerunner of the internal capsule) penetrates from the thalamus by way of the corpus striatum.

In order to understand the limits of the cortical areas in general and of this neopallial primordium in particular we plotted on graph paper projected views of the fore-brain from its several aspects. The figures used as illustrations here are copies of such projected views (see figs. 1, 2, 3 and 4).

In general explanation of the figures it should be pointed out that there is considerable overlapping of adjacent cortical fields in Reptiles. Where such overlap occurs the borders of these areas are shown in interrupted lines, and the convention of lines or dots, used to represent the area, is thinned or decreased in size in the portion overlapped. Various names and homologies have been suggested for the individual cortices represented in these diagrams; but I will not discuss them here because Mr Segal, one of the workers referred to, will give them special consideration in his memoir on the cortices of *Agama nigricollis*. He presents there the evidence for interpreting the areas according to the nomenclature adopted.

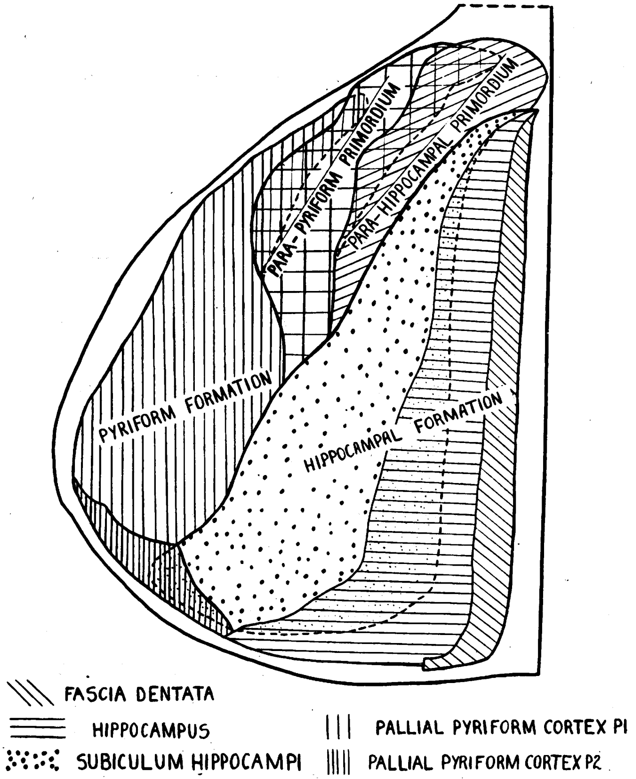

Fig. 1. Dorsal projection of fore-brain areas in *Agama nigricollis*. × 29.

THE DUAL STRUCTURE OF NEOPALLIAL PRIMORDIA

In the district interpolated between the hippocampal and pyriform formations we discovered to our surprise not one homogeneous cyto-architectonic field but two primordial neopallial areas (para-pyriform and para-hippocampal respectively, of almost equivalent area), distinct from one another and from the other areas in cell structure and fibre connections (*vide* fig. 1). In fig. 1 the lateral or *para-pyriform neopallial primordium* is seen overlapping the pyriform cortex, and is in turn overlapped by the medial or *para-hippocampal neopallial primordium*.

To find two neopallial rudiments, where we had anticipated only one, was so unexpected that I hesitated to draw any far-reaching inferences from the conspicuous arrangements in *Agama*; until the regular presence of a similar duplication of neopallial primordia had been confirmed independently by Dr A. Galloway in *Zonurus*; by Dr J. Gillman in the gecko, *Platydactylus bibroni*; by Dr Gillman and Mr Segal in *Mubuia striata*, and *Eremias lugubris*; by Mr W. Girdwood in *Chameleon vulgaris*, and by Mr G. W. H. Schepers in *Testudo geometrica*. Subsequently an analysis of the literature showed that previous authors have unwittingly recognised corresponding areas in their descriptions of the reptilian fore-brain.

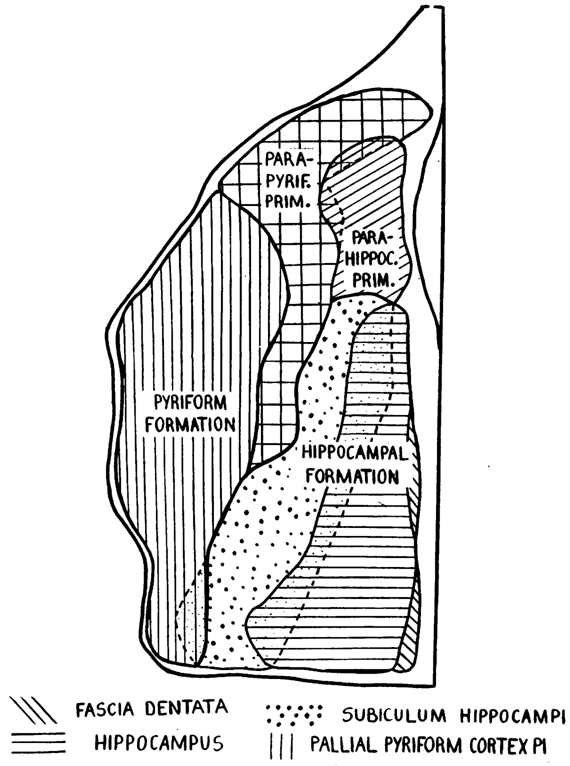

Fig. 2. Dorsal projection of fore-brain areas in *Chameleon vulgaris*. × 29.

Cartographic studies of this sort display a rather amazing variety in the disposition of the component fore-brain cortices in Reptiles. In the terrestrial *Agama* there is a general all-round development of the hippocampal and pyriform cortices and also of the neopallial primordia. Thus the fore-brain (fig. 1) assumes an elongated form in which each of the cortices shares. In the arboreal *Chameleon*, on the other hand, the hippocampal formation is restricted to the posterior two-thirds of the dorso-medial region (see fig. 2). The pyriform formation is tolerably expanded laterally; but the neopallial primordia are relatively very large. The elongated para-pyriform primordium completely excludes the pyriform lobe from the dorsum in the anterior third and intrudes even on the medial margin of the brain. The para-hippocampal primordium meantime widens and extends downwards along the septal wall in front of the hippocampal formation.

In the particular gecko depicted in fig. 3 a reversal of the chameleon arrangement is seen. In the antero-posteriorly and medio-laterally compressed and almost globular fore-brain of these innocuous, terrestrial and nocturnal lizards, the hippocampal formation is relatively gigantic and its lateral third (or subiculum) is almost entirely covered by the more medial portions (i.e. hippocampus and fascia dentata) of the formation. The pyriform formation is of moderate extent, but the huge fascia dentata—which forms the whole anterior pole of the fore-brain—has carried, as it were, the medial or para-hippocampal neopallial rudiment around with it to the lateral aspect of the brain; so that it comes to lie, paradoxically enough, lateral to the lateral or para-pyriform primordium. It was only by the anchorage of the para-pyriform primordium between the pyriform and hippocampal cortices posteriorly, and the similar attachment of the para-hippocampal primordium to the hippocampal structures anteriorly—as well as by the study of the fibre tracts—that Dr Gillman and I were able, after a couple of months' mapping and study, to solve the riddle of the complex superimpositions this brain presents. In

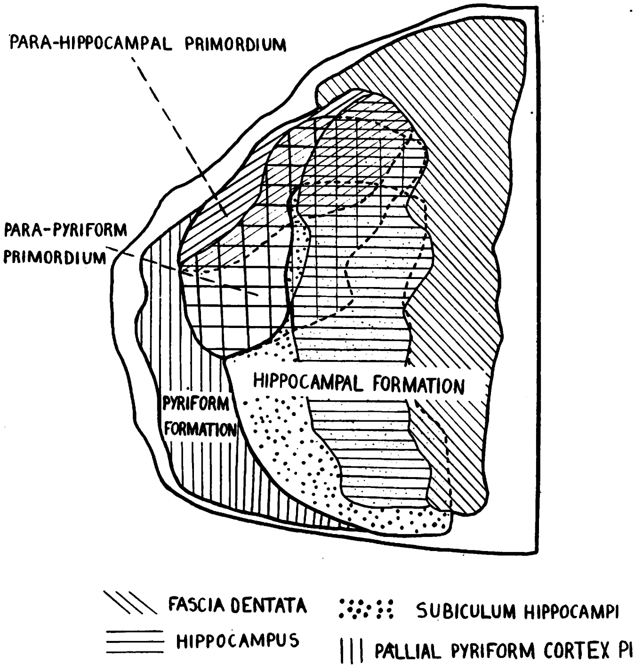

Fig. 3. Dorsal projection of fore-brain areas in *Platydactylus bibroni*. ×29.

certain parts two, and even three, cortical regions are overlapped by the middle (or hippocampus) component of the hippocampal formation, when viewed in projection from the dorsal aspect.

No useful purpose can be served by describing in more detail the variations and modifications, which occur in the cortical districts in general and the neopallial rudiments in particular, of various lizards; nor will I attempt to describe their histological structure. My single intention has been to demonstrate briefly that the two neopallial primordia described are constant structures and occupy definite areas in the reptilian fore-brain. But it will be profitable to discuss their usual topography, and to demonstrate that they both satisfy all the known criteria of neopallial architecture.

For descriptive purposes it is simpler to consider the more generalised type, e.g. *Agama*. There the more lateral of the two primordia customarily occupies the position antero-medial to the pyriform formation and overlying the antero-lateral (neostriatal) portion of the striate body, a position which has been regarded hitherto as diagnostic of a primordium neopallii. I have termed it, from its topography, the *para-pyriform primordium of the neopallium*. Histologically, too, this para-pyriform primordium merges so gradually into the pyriform cortex postero-laterally, that it presents the appearance of having arisen from the antero-medial extremity of the pyriform cortex. It usually extends farther posteriorly than its companion primordium; and thus, its backward prolongation is the only cortex intervening between the pyriform and hippocampal formations in that region. The para-pyriform primordium is the destination of those thalamic fibres which, coming from the lateral fore-brain bundle, perforate the neostriatum (or hypopallium of Elliot Smith) and enter the primordium on its deep or striatal aspect, in the fashion recognised and described for the neopallium by De Lange, Crosby, Elliot Smith, Kappers and others. There is therefore no need to add to the proofs submitted by these observers of its neopallial nature.

The more medial area, however, has not hitherto been recognised as being a distinct cortical element nor as being neopallial. It is not related to the neostriatal portion of the corpus striatum, nor is it connected by fibres with that portion of the striate body. Although it is a distinct cortical area, it seemed then, at first, illogical and a denial of well-established criteria to regard it as a neopallial rudiment. But actually it satisfies all the tests of neopallial architecture for it is a strip of cortex lying between the hippocampal and pyriform formations; stimulation of the region evokes muscular responses; and it receives a thalamic radiation which passes forwards not through the neostriatum on the lateral side but, strangely enough, through the *palaeostriatum* on the medial side of the fore-brain. I have therefore termed it the *para-hippocampal primordium of the neopallium*. Because of the significance attaching to the recognition of this new element in the reptilian cortex we will consider in detail how the criteria apply to the region in question, so that we may the better understand why it has been called neopallial.

In the first place it lies between the hippocampal and pyriform formations; its position is such that its medial border skirts the lateral and anterior margins of the three constituent parts (subiculum, hippocampus and fascia dentata) of the hippocampal formation; but the anterior portion of the area is so expanded, that it intrudes on to the medial aspect of the hemisphere in front of the hippocampal formation medially and into the base of the olfactory peduncle dorsally. The histological structure of the cortex traced backwards, merges almost imperceptibly into that of the area designated as subiculum (the *general cortex* of Johnston, Crosby and others). The cortex presents thereby the appearance of having arisen from the antero-lateral portion (or subiculum) of the hippocampal formation. The para-hippocampal primordium usually extends well in front of the para-pyriform primordium and completely separates it from the anterior extremity of the hippocampal formation and the septal region. Topographically therefore the cortical element must be regarded as neopallial and para-hippocampal.

In the second place the cortical stimulation experiments, carried out by Bagley and Richter (1924) and by Bagley and Langworthy (1926) upon the crocodile, show that the para-hippocampal primordium functions in a neopallial manner. These authors discovered that coordinated movements of the body, limbs and tail were elicited by simulating the whole of the region corresponding with that comprehended in the para-pyriform and para-hippocampal primordia here described. In their attempt to correlate their experiments with Johnston and Crosby's identification of the primordium they were disappointed to find that the excitable area did not coincide absolutely with any one definite cyto-architectonic field described by these authors; and were surprised that the area "extended from the mesial over the dorsal surface to the dorso-lateral border tapering almost to a point at its outer extremity."

It is clear from our maps that the experimenters were stimulating not one homogeneous, but two heterogeneous cyto-architectonic fields of which the para-hippocampal is the one which extends so far medially. It is the duplex nature of the neopallial primordium too which must be responsible for the two differing responses encountered on stimulating the medial and lateral parts. Stimulation of the mesodorsal part caused combined head and tail movements of a lashing character, while the outer portion of the area favoured movements of the legs as in walking. These differing responses will be referred to again at a later stage. In the second reported group of experiments it was rightly recognised that the excitable area included the anterior part of what Crosby calls the "general cortex," i.e. the subiculum, and "extends mesially into the hippocampus." The correspondence of the medial part of the excitable field with the *para-hippocampal primordium* described here is therefore absolute.

The experimenters went further; they found that, when the flap of excitable cortex was elevated and reflected, so that it was attached to underlying structures only on its medial (or para-hippocampal) side, stimulation of this medially attached flap gave the same reactions as those recorded in the normal brain. When the flap was attached only on its lateral (or para-pyriform) side, electrical stimulation gave no motor reaction at all. Moreover, while stimulation of the underlying corpus striatum (neostriatum) in both cases gave negative results, "stimulation of the medial wall gave results similar to those recorded after cortical stimulation, but usually with less current in accordance with the fact that the fibres from the convexity run down the mesial wall, fornix fashion." These experiments corroborate the appearances presented in our Cajal serial sections, that both the para-pyriform and para-hippocampal primordia discharge their impulses medially through the most anterior portion of the "fornix" fibre system in Reptiles. The experiments, as a whole, prove that both the lateral and the medial (and more particularly the medial or para-hippocampal) primordia are neopallial in their functional response to stimuli.

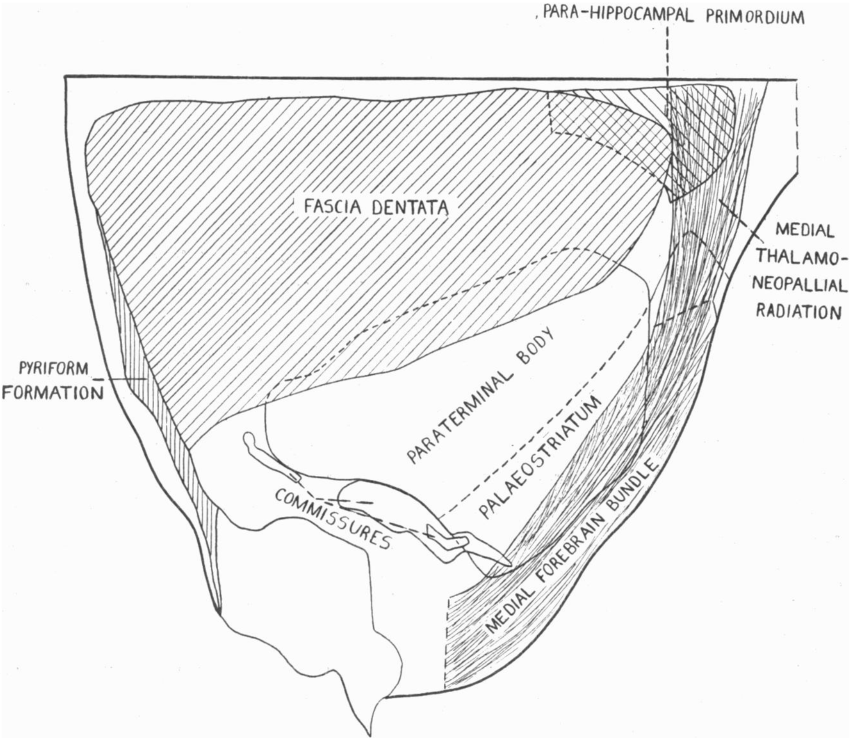

Fig. 4. Medial projection of fore-brain areas in *Agama nigricollis*. ×29.

In the third place the *para-hippocampal primordium*, while not receiving fibres radiated through the corpus striatum by way of the lateral fore-brain bundle, *does* receive thalamic fibres and by this criterion also is to be regarded as neopallial. These fibres have been mapped in our series; they pass up by way of the medial fore-brain bundle (*vide* fig. 4); escape from the medial (or palaeo-striatal) portion of the striate body at its antero-medial extremity; penetrate partially through, but chiefly anterior to the paraterminal body or septum; skirt up the medial wall of the hemisphere as a compact band anterior to the hippocampal formation; and enter the para-hippocampal primordium principally at its medial margin and on its anterior and superficial aspects. Their direction of approach is responsible neurobiotactically for "pulling" the para-hippocampal primordium forwards and downwards toward the septum in front of the fascia dentata.

This fibre tract corresponds in part with the "septo-mesencephalic tract" of Edinger and Wallenberg, and in part with the "olfactory bundle" of Zuckerkandl, or "septo-cortical fibre system" of various authors. The latter system is supposed by most comparative neurologists to link the septum with the hippocampal formation; but the main, if not the only, destination of its fibres is *not* the hippocampal formation but the more anteriorly-lying para-hippocampal primordium.

It is natural that, having overlooked the separate existence and nature of the cortical area which we have termed the para-hippocampal primordium, observers should have imagined the fibre tracts in this vicinity to have been destined for the hippocampal formation. Despite the presence of a hippocampus in anosmatic Mammals, these seemingly direct connections between lower olfactory centres and the hippocampal formation have been used to support the idea that the hippocampal formation is olfactory and receives afferent olfactory fibres on its medial aspect. I do not deny the existence of such septal olfacto-hippocampal connections in Reptiles and in Mammals but we have found little positive evidence of their presence in *Agama*. On the other hand, we found convincing proof that there is this *ascending palaeo-striato-neopallial* fibre tract lying anterior to the hippocampal formation (*vide* fig. 4). In explanation of the curious outline presented by the medial aspect of the brain in fig. 4, it must be stated that, in mapping, the dorsal border of the brain was regarded as a straight line.

Cajal (1900–6) opposed the view that the hippocampal formation received afferent tracts from the medial side in Mammals; according to him they came in from the lateral side, from the posterior part of the pyriform lobe. He also definitely denied that Zuckerkandl's bundle came from the olfactory cortex, and regarded the analogous, if not homologous, septal (or precommissural) fibre systems in Mammals as being two: "one descending and centrifugal from the gyrus fornicatus and forming the *fornix longus* of Forel and the other ascending and centripetal coming from the pedunculus cerebri and ending in the septum." The tract running through the palaeostriatum to the para-hippocampal primordium in *Agama* is apparently the reptilian homologue of Cajal's tract. Le Gros Clark (1932–3) has shown experimentally that in Mammals, e.g. rats (Rodentia) and cats (Carnivora), the fibres proceeding forward from the anterior thalamic nuclei pass through the striatal formation under the caudate nucleus and at the level of the septal region turn abruptly medially and run along the dorsal surface of the corpus callosum to reach the whole length of the cingular gyrus (fornicatus).

Thus Cajal's idea, that the ascending portion of the septal system terminated in and never transgressed beyond the septum, has been proved erroneous. His "descending" tract contains both descending and ascending fibres. It proceeds beyond the septum to a para-hippocampal pallium (i.e. the gyrus fornicatus) in Mammalia and to the corresponding (and apparently homologous) primordium we have called para-hippocampal in Sauropsida. There is no experimental proof as yet of the thalamic origin of this "septal" system in Reptiles, but the strictly homologous "septal" system in Birds, like that of Mammals, is known experimentally to be connected with the thalamus and with more posteriorly situated portions of the avian brain. Even in Fishes the corresponding, but not so highly evolved, septal region is also known to be directly linked with the thalamus and hypothalamus. Unless something fantastic has taken place in the reptilian brain the appearances in Cajal sections are reliable and the para-hippocampal cortex in Reptiles receives a thalamic radiation and, by this criterion also, justifies its title to be regarded as a neopallial primordium.

THE DUAL STRUCTURE OF THE NEOPALLIUM

Having recognised the dual nature of the primordium neopallii in Reptiles, it is important to examine from that standpoint the arrangement of the mammalian cerebral cortex. The existence of a double neopallial primordium in Reptiles emphasises a most important aspect of the aforementioned experimental investigations by Le Gros Clark and Boggon (1933) on the thalamus. They have proved in fact that the mammalian cortex is also dual in structure and function; although they seem to have overlooked the phylogenetic import of the discovery.

They have shown that the cingular and prefrontal cortices of the mammalian brain belong to a separate thalamo-cortical projection zone (from the anterior and dorso-medial thalamic nuclei) which we may call *medial*; whereas the remainder of the neopallium belongs to the thalamo-cortical projection zone of the ventral thalamic nucleus and the geniculate bodies, which may be called *lateral*. I designate the two zones in this fashion because the neopallial tracts projected from the *lateral* zone of the thalamus reach the cortex by passing through the lateral portion of the internal capsule, i.e. through its neostriatal or *lateral fore-brain bundle* portion. The neopallial tracts projected from the *medial* zone of the thalamus form "the most medial fibres of the internal capsule" and are in close topographical relation to the septal region near the medial surface of the hemisphere. They therefore utilise the more ancient *pallidal* or palaeostriatal pathway of the *medial fore-brain bundle* portion (*vide* Dart, 1925).

In the mammalian brain the thalamo-cortical and cortico-thalamic systems of both zones have increased to such an extent, as almost to obliterate any appearance of division between these ancestrally distinct, lateral and medial fore-brain bundle systems. Their divergent destinations in the thalamus, however, exhibit the *duality of the mammalian neopallium,* and throw into relief the reality of the distinctions which, I am of the opinion, should be drawn between the para-hippocampal (or cingular and prefrontal cortices) moiety of the neopallium, on the one hand, and the para-pyriform (or the remainder of the neopallium) moiety on the other.

It may seem bold to extend the terms para-hippocampal and para-pyriform in this fashion to embrace such heterogeneous cortical formations in Mammals; and to hypothesise, as I am doing, that the respective primordia, so named in Reptiles, are ancestrally related to these two major subdivisions of the mammalian neopallium. No greater leap of the imagination, however, is demanded by this conception, than by the original suggestion that a homologue of the whole mammalian neopallium is present in the reptilian primordium. Indeed, this conception confirms, while it expands that earlier, valid and generally accepted hypothesis.

Significant, as illustrating the value of this hypothesis of a dual mammalian neopallium, are the studies of Shellshear (1929) on the mammalian cerebral blood supply. Because the greater part of the neopallium in the monotreme *Echidna aculeata* (i.e. the spiny ant-eater) is supplied by branches from the posterior cerebral artery (or "hippocampal" artery of Reptiles), Shellshear suggested that this neopallium differs from the neopallium of other Mammals "in being to a great extent *para-hippocampal* in origin." He similarly regards the cortex usually supplied by the middle cerebral artery (or "pyriform" artery of Reptiles) in Mammals as developing "in response to a differentiation of the general pallium on the pyriform side" and in short as *para-pyriform.* His terminology is extremely happy and I am glad to have been able to extend it in the manner previously indicated. Whether it will be possible finally to utilise blood-vascular supply to determine the limits of para-hippocampal and para-pyriform cortices in other Mammals in this fashion still remains to be demonstrated; but Shellshear's idea was well conceived and receives abundant corroboration in the discoveries of the double primordium in Reptiles and the double neopallial projection system from the thalamus in Mammals.

Morphologically, however, one of the chief advantages of recognising the structural duality of the reptilian neopallial primordium and the mammalian neopallium is that it enables us for the first time to understand the cortical arrangements in the avian fore-brain. The gap existing in our knowledge hitherto has rendered it confessedly impossible for investigators (e.g. Huber and Crosby, 1929) to homologise the cortical arrangements in Birds with those of Reptiles and of Mammals. The filling of that gap demonstrates that Craigie's (1930) "neo-cortex" in the Kiwi is a genuine neopallial structure and corresponds with the para-hippocampal primordium in Reptiles. It corroborates Kappers' (1921) idea that Edinger's *cortex medio-dorsalis* in birds is "a sort of neopallium" and shows that his criteria, namely that this "neopallium" was non-olfactory, and the source of a cortico-fugal fibre-system, were justifiable. The neopallial cortical apparatus of Birds, especially its para-hippocampal component, is more extensive, more highly laminated and more patently connected through the "septum" with the mid-brain than appears anywhere amongst Reptiles.

I will not analyse the anatomy of the avian neopallial primordia at this juncture. They will be more advantageously discussed when the cartographic records of their distribution, which we are in the process of preparing, are concluded. Neopallial primordia are present in Birds and can now be homologised with those of Reptiles and Mammals. That the primordia play a significant rôle in avian life cannot be doubted, when we know (*vide* Huber and Crosby) that the cortico-septo-mesencephalic tract is one of the most striking features of the avian brain and places this cortical region (particularly its "para-entorhinal" or para-hippocampal portion) in direct communication with the mid-brain and even more posteriorly placed centres of the brain.

THE HISTORY OF THE DUAL NEOPALLIUM

As I have already indicated, the double structure of the mammalian neopallium is inextricably linked with the two parts (palaeostriatum and neostriatum) of the corpus striatum. The double neopallium owes its existence to the two major phylogenetic phases in the forebrain's striatal history; and as I am about to suggest that the divergent functions of the two parts of the mammalian neopallium are dependent upon the striatal history, I will discuss briefly the nature of the palaeostriatum and neostriatum.

Since Hunt (1917) first demonstrated how the clinical phenomena following pallidal (or palaeostriatal) lesions differed from those following striatal (or neostriatal) lesions, we have come to understand more clearly that the palaeostriatum and neostriatum still perform in Mammals (including Man) the same type of functions they were first evolved to execute in Fishes and Reptiles respectively (*vide* Tilney and Riley, 1933). The palaeostriatum was elaborated to correlate and control the body- and corresponding fin-movements of fishes (which are characterised by their constancy, rhythmicity, intersegmental association and automatic nature) in such a way as to produce directive body movement in the water. The assumption of terrestrial life necessitated a marked change. The constant unremitting, undulant movement of the whole, relatively rigid, body, indispensable for maintaining bodily orientation in the fluid water medium, becomes distinctly disadvantageous on land.

Here inconstant undulatory movements, subject to protracted intervals of complete inhibition, are manifest. During walking or running, the further necessity arises for maintaining the general musculature of the body, which supports its mobile and articulated vertebral column, in a state of tonicity; while the controlled extensor and flexor movements of particulate, jointed portions of the body, i.e. the limbs, are synchronised in such a fashion as to produce progression of the equilibrated body while elevated from the ground.

The neostriatum emerges simultaneously with this reptilian need for holding in check the constant, rhythmical and automatic body-wide movement of the palaeostriatally-equipped fish and so producing orderly movement on land.

The transference from sea to land entailed many other neurological changes. In an earlier paper (Dart, 1925) I took advantage of the revolution it caused in the whole structure of the mouth and nose apparatus to demonstrate how that revolution was accompanied by, and permanently recorded in, the pattern of the mammalian fore-brain in general and the corpus striatum in particular. But the transference revolutionised not only the olfactory apparatus and the mechanics of bodily progression and its neural control, but also the entire structure of the branchial region. It transformed the rigid neck, with its rhythmically-opening gills and upper digestive tract, into a mobile head and neck containing a naso-pharynx equipped with a swallowing apparatus, a mouth furnished with a movable projectile tongue, and a larynx controlling the ingress and egress of the air column. The novelties of body movement were accompanied by fundamental alterations in head, neck, jaw and throat movements associated with the new feeding, drinking, respiratory and vocal habits of land life.

Thus it comes about in Man that *palaeostriatal* lesions, which lay bare the activities of the piscine palaeostriatum, are characterised by the rhythmical tremor of paralysis agitans, which occurs even when the body is at rest and is increased by movement and by emotional excitement; by gradually increasing general muscular rigidity throughout the entire body, which causes inertia in initiating movements and inability to restrain them once they have been initiated; and finally by the suppression of normal automatic associated movements. In *neostriatal* lesions, on the other hand, which reveal the functions of the reptilian neostriatum, tremors are reduced or absent and muscular tone is reduced rather than increased; the outstanding features of the affection are the mobile and variable muscular spasms, which produce athetoid and choreiform movements of localised body parts, especially of the limbs, jaws and neck, and the exaggeration of normal automatic associated movements. Thus movements carried out voluntarily or mimetically in such patients bear the character of clambering or climbing movements, while dysarthria and dysphagia are commonly associated with the disease. It is well known (*vide* Cunningham's *Anatomy*) that, in Man, the *ansa lenticularis* comes from the lentiform nucleus (neostriatum) and proceeds to the thalamus. Elliot Smith states that "this system of fibres is very old, being the most primitive efferent tract from the cerebral hemisphere" and that its connections with the thalamus, red nucleus and substantia nigra "afford some explanation of the difficulties of articulation and swallowing after damage to the striate body."

In other words, the palaeostriatum is a mechanism whereby the natural tone of the body musculature is inhibited, steadied and adjusted; so that *movements of the whole body* in response to cerebral activities can be executed with rapidity, smoothness and ease, after the fashion exhibited by the perfection of body movement in Fishes. The neostriatum, on the other hand, is a mechanism whereby, in Sauropsida, there can be superimposed upon, or isolated within, these smooth whole-body movements the relatively disjunctive and spasmodic *movements of individual parts* (e.g. the limbs, head, neck, jaws and throat) of the body, whose synchronisation and coordination is essential to orderly progression and vital existence on land.

Because the fore-brain has passed through these two striatal phases in its evolution, two paths are now available for the passage of thalamic radiations to the cortex. They may enter by way of either the medial or the lateral fore-brain bundle (*vide* Dart, 1925) and so theoretically two types of neopallium may arise—and this, in point of fact, happened.

THE SIGNIFICANCE OF THE DUAL NEOPALLIUM

The distinctive attribute of the neopallium in Mammals is regarded as the further progressive isolation, control and coordination of muscular movements in order to bring about the bodily, and more particularly the appendicular, mobility, dexterity and skill characteristic of the class. This isolating and coordinating function is, however, more manifestly exercised in Mammals by what we have termed the *para-pyriform moiety of the neopallium*, in which are coordinated proprioceptive and exteroceptive information relayed to the cortex from the organs of muscle and joint sense, touch, hearing, equilibration and vision. This information reaches the para-pyriform neopallium by way of tracts passing through the *neostriatum*; that part of the neopallium having been developed, as it were, to receive the surplus of the thalamo-neostriatal radiation. It is natural therefore that this neopallium should exhibit in a still more exaggerated way, than does the neostriatum, the capacity to control and coordinate "isolated movements." The para-pyriform neopallium controls *the muscular display of skill.*

The para-hippocampal moiety of the neopallium, by contrast, is not concerned with "isolated movements" but governs widespread muscular and sympathetic reactions associated with the expression of the emotions. It has developed, as it were, to receive the surplus of the thalamo-palaeostriatal radiation. By incising the prechiasmatic region of the fore-brain 3–4 mm. in front of the chiasma and from the mid-line to the olfactory radiation to a depth of only 2–3 mm. on both sides of the brain, Fulton and Ingraham (1929) changed three cats (2 castrated males and 1 female), which previously were characterised by their friendly and playful behaviour, into chronically angry beasts provoked upon the slightest stimulation into violent bodily manifestations of ungovernable rage.

As Le Gros Clark (1932) pointed out, this lesion probably involved the course of the fibres, which run from the frontal pole back to the dorso-medial nucleus of the thalamus and in the reverse direction, and which provide in this way a means for harnessing the thalamic emotional responses. He showed that the medial thalamic nucleus is linked up with the whole peri-ventricular system and, as has been recognised for a long time, motor activities at the thalamic level are characterised by their exaggerated emotional or affective tone. But Le Gros Clark showed the cingular cortex to be reciprocally linked by fibres to the anterior thalamic nucleus (and as we know, through that nucleus with the bundle of Vicq d'Azyr and the mammillary bodies), so that probably it, as well as the frontal cortex, is concerned with this thalamic emotional control. At any rate there is no evidence at present available for separating the cingular cortex functionally from the prefrontal cortex; and we have seen that they are rationally grouped together as para-hippocampal neopallium on the basis of their position and thalamic connections.

Those pre-chiasmatic lesions, then, severed the medially-situated fibres which link the para-hippocampal neopallium with the thalamus. The emotional mass-reactions of the body musculature and the sympathetic system, elicited by the lesions, conspicuously differ from the localised spastic paralytic reactions, which follow in the train of comparable lesions in the lateral part of the internal capsule. The para-hippocampal neopallium controls the *muscular display of emotion.*

Skill or emotion in the final resort are both displayed chiefly in terms of muscular activity and accompanying sympathetic phenomena. They do not differ in the mechanisms called into action; they have this further feature in common, that the play and variety of emotional activity depends directly upon, and varies directly according to, the degree of bodily skill which the animal group, genus or species possesses. But whereas skill, on the one hand, depends on the capacity to isolate the activities of individual muscle groups, and the accompanying sympathetic phenomena are finely adjusted to the needs of the delicately-poised muscular activity; emotional responses, on the other hand (such as those of fear, rage and mating), especially in lower animals, tend to involve the entire body musculature and are associated with gross vaso-motor and other exhibitions of sympathetic nervous system activity, of an explosive and immoderate character. It is in keeping with this explosive, widespread and immoderate character of the responses, that the palaeo-striatum serves as the channel of passage for emotion-controlling impulses from the para-hippocampal cortex. The palaeo-striatum first emerged for whole-body response and the higher cortico-thalamic tracts, that emerge for still further direction of these massive muscular responses, are laid down within this pre-existing scaffolding.

Having recognised the probable physiological significance underlying the duality of the neopallium in Mammals, and having appreciated that the anatomical architecture and the physiological functions of the constituent neopallial moieties are extensions of neostriatal and palaeostriatal functions, it is fitting to add a few final remarks concerning Sauropsida in general and Aves in particular, in order to show the applicability of our reasoning, and the possibility of utilising them for increasing our knowledge concerning the dually-functioning cortex.

In the cold-blooded fish and Amphibia with their primitive cortex a differentiation of bodily responses, as between skill and emotion, can scarcely be said to exist. With the life on land came courtship, cohabitation, hatching or parturition, and the nursing of young. Thus emotional response and bodily skill came to assume significance as two divergent aspects of animal behaviour; and the mechanisms established became available for their individualisation, control and orderly display. Hence it was in Sauropsida that Darwin found more liberal material for demonstrating the part that sexual selection played in evolution. The emotional reactions attendant upon the mating and fighting habits of Birds are well known, but the numerous and varied examples of comparable emotional display in Reptiles are sometimes overlooked. Such are the noisy combats of turtles and the splashing and roaring struggles of alligators for their mates, the defensive erection of frills, spines, pouches or other structures in lizards. Darwin concludes in explanation of their coloration and variegated appendages that "Sexual selection seems to have played almost as important a part with Reptiles as with Birds."

The cerebral structures in Sauropsida, which are responsible for these novel activities, are the neostriatum and the cortex; and we do not yet know to what extent they individually control these behaviour reactions. The experiments of Rogers (1922) seem to show that the cycles of avian behaviour in feeding, drinking, mating, nesting, incubation and rearing the young depend largely upon the integrity of the expanded neostriatum. He found so little disturbance in these cyclical functions when almost the whole avian cortex was removed, that he was inclined to regard the cortex as relatively insignificant, compared with the striate body, in controlling the rhythms of avian life. It may be that in this highly specialised group the neostriatum has taken over some of the functions that belong more properly to the para-hippocampal neopallium. But we need further critical experiments and more detailed behaviour studies before we shall be able to understand precisely what influence the avian cortex has on their skill and their emotions respectively. In Reptiles, on the other hand, from Bagley and Langworthy's experiments, head-deflection and tail-lashing movements are caused by stimulating the para-hippocampal cortex, and these cortically-controlled movements simulate the violent activities of these beasts under the powerful stimuli of rage or mating, and differ entirely from the tail-wagging movements resulting from stimulating the mid-brain. Stimulation of the para-pyriform field, on the other hand, causes movements of the limbs such as occur in walking.

Rogers (1922) did find that direct stimulation of the antero-medial portion of the cortical dorsum in Birds evoked depression of the feathers of the forehead and throat and various other sympathetic system phenomena which are associated with their emotional reactions. These suggestive experiments and Darwin's observations indicate a fruitful field of experimental research concerning the emergence of functional duality in the sauropsid cortex.

SUMMARY

The neopallial primordium in Reptiles is divisible topographically into para-hippocampal and para-pyriform moieties. The para-hippocampal primordium is now recognised for the first time as being neopallial. Stimulation of these neopallial primordia results in body movements of divergent character in Reptiles. Both primordia receive afferent fibre systems from the thalamus, the para-pyriform primordium receiving its tract by way of the lateral (neostriatal), the para-hippocampal by way of the medial (palaeostriatal) fore-brain bundle.

The neopallium of Mammals is also double and its duplicity corresponds with a duplicity of the thalamus and the thalamic projection zones. These two projection zones of the mammalian thalamus are the neostriatal and palaeo-striatal zones respectively and they correspond with the two projection zones of the reptilian primordia. The reptilian primordia are therefore the forerunners of the para-hippocampal and para-pyriform divisions of the mammalian neopallium, a division already suggested by Shellshear in consequence of his studies in reptilian and mammalian neopallial blood-vascular supply, and implicit in the thalamic studies of Le Gros Clark.

The double structure of the mammalian neopallium follows in the train of the two ancestral phases, water and land, palaeostriatal and neostriatal, of striatal history; and the exploitation, as I suggested in "The law of infiltration in fore-brain evolution," of both the palaeostriatal and the neostriatal pathways in vertebrate fore-brain evolution.

The striatal history affords a clue to the divergent activities of the two divisions of the mammalian neopallium, the parapyriform cortex controlling bodily skill, the para-hippocampal cortex controlling bodily emotion. The beginnings of that differentiation are traceable in Sauropsida and promise a valuable field of enquiry concerning the double functions of the cortex. The cortical arrangements in Reptiles, Birds and Mammals are now capable of being homologised with one another anatomically, and a structural basis is thereby provided for understanding any physiological correlations which may be discovered between them in the future.

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