
Chapter II

Regional variations in cell structure of the cerebral cortex.

1. The general rules of variability.

Developmental studies have shown that the primitive lamination of the cerebral cortex undergoes far-reaching local modifications during ontogeny, by means of which completely new patterns emerge that do not reveal their common origin from a basic six-layered type without detailed examination. They are the source of the numerous and diverse local specialisations that characterise the mature cortex of the adult. The architectonic rearrangements involve either the number and particular structure of individual layers, or the density and size of cellular elements through the whole cortex and within given layers, or the total thickness of the cortex and the relative thickness of the different layers. They sometimes result in sharp linear borders, as shown in Figures 10 to 12, 15, 20 to 22 and 24 to 26, sometimes in subtle transitions (Figures 17, 23 and 28 to 32).

The rules for local variations in cytoarchitecture depend on the above criteria. They will now be discussed in detail and, as far as feasible, explained by illustrations. There are microphotographic records of many of them in my earlier works on histological localisation; especially in my third and seventh communications on the cortical structure of monkeys and prosimians. Firstly, one should distinguish two major categories of architectonic transformation of

the primitive cortex that occur throughout the whole mammalian class.

1. Architectonic variations in established six-layered cortex. We call all examples of this type "*homotypical formations*" for they maintain the same basic pattern throughout life.

2. Extreme variants with altered numbers of layers or "*heterotypical formations*", that no longer have the six layers in the mature brain because of the secondary transformations described above.

I. In homotypical formations, where **the number of layers remains the same**, the cellular structure of a cortical section can be modified in the following ways.

a) Through changes of cell packing density or, in other words, cell number per unit volume. It is not rare for the whole depth of the cortex in one part of the hemisphere to become more or less cellular, or the process may be restricted to a single layer. Figures 20, 21 and 22 are typical examples of the former case with a sharply delimited zone of increased cell density appearing over the whole depth. Figure 23 provides an example of the second case; in an area of otherwise rather even cell density the inner granular layer (IV) of the prepirietal area (between $\downarrow 1$ and $\downarrow 2$) suddenly becomes much more densely cellular. The degree that local differences in cell density can attain can be judged from a comparison of later higher-power micrographs of human, monkey and kinkajou cortex, especially Figures 50 to 52.

b) Through changes of cell size or specific cell type in one or more layers. Two categories of such modifications can be distinguished: either the cells at a particular place take on new forms more or less abruptly, for example their average size decreasing so that granule-like elements predominate, or an entirely new cell type appears in a single layer. Calcarine cortex (Figure 12) is the chief example of the first case, giant pyramidal cortex (Figure 7) and prepirietal cortex (Figures 16 and 23) of the second, these last types presenting cells of unusual volume in their ganglion cell layer (V). The surprising differences in cell size in various parts of the cortex are also clearly visible in the high power micrographs of Figures 43 to 57, in which sections from the large-celled giant pyramidal and small-celled calcarine cortex are compared.

c) Through changes in the relative thickness of individual layers. A layer can thicken considerably at the expense of neighbouring layers and vice versa; one sees such an isolated thickening especially frequently in the pyramidal (III) and ganglion cell (V) layers. But the spindle cell layer (VI) also frequently undergoes considerable variations in thickness that are often sudden in onset. A typical example of this is the transition from the occipital type of cortex to the calcarine, as Figures 21 and 22 show clearly. Also the transition from archipallium to neopallium, that is from homogenetic to heterogenetic cortex (*63), illustrates the same process. Three identical transition zones in monkeys and prosimians can be compared in Figures 24 to 26.

d) Through increase or decrease of the whole cortical thickness. The cortex can become thinner or thicker overall while the relative thicknesses of individual layers do not change.

II. Extreme variations in cortical architecture accompanied by an **altered number of layers**, or *heterotypical formations*, may result from an increase or decrease of the basic or primitive layers.

1. An increase in the layers arises:

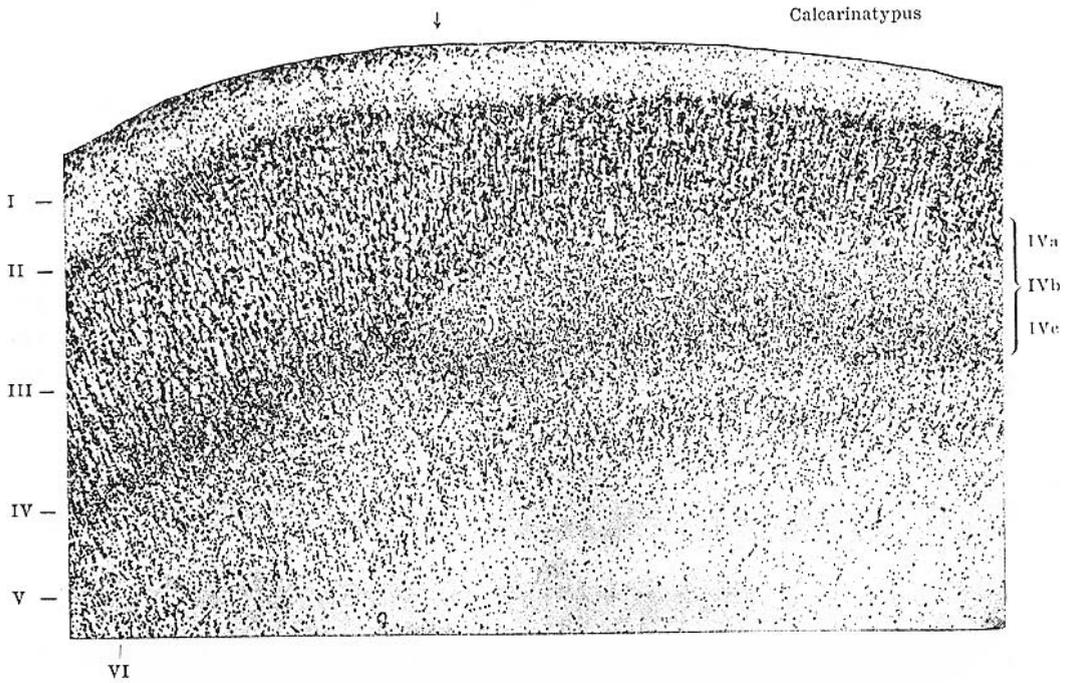


Fig. 20. Human foetus aged 8 months. 46:1, 10 μ m. Site of transition to calcarine cortex (↓) with sudden increase in cell density and laminar rearrangement. Cell density even changes in layer I at ↓ (See page 46.)

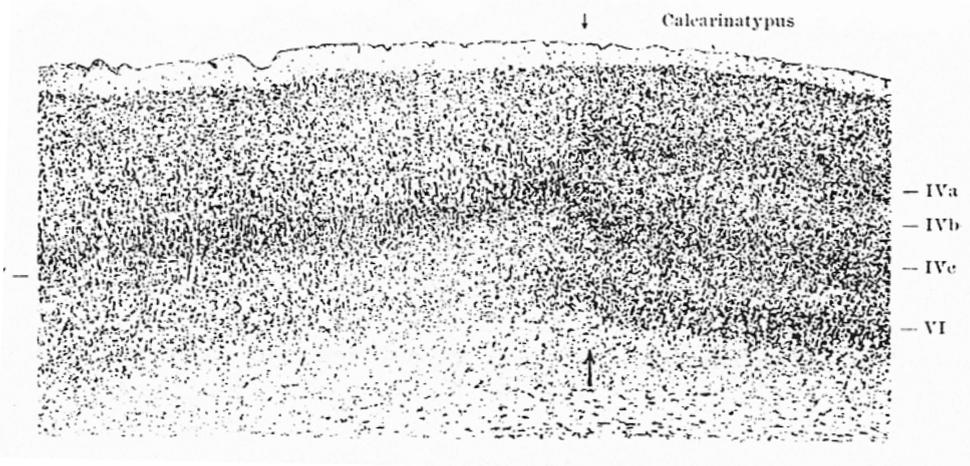


Fig. 21. Black-eared marmoset (*Hapale pennicillata*) (*62). 25:1, 10 μ m. Sharp transition from calcarine cortex (area 17) to occipital cortex (area 18 of the brain map) as in Fig. 20. There is increased cellularity in all layers throughout the whole cortical depth.

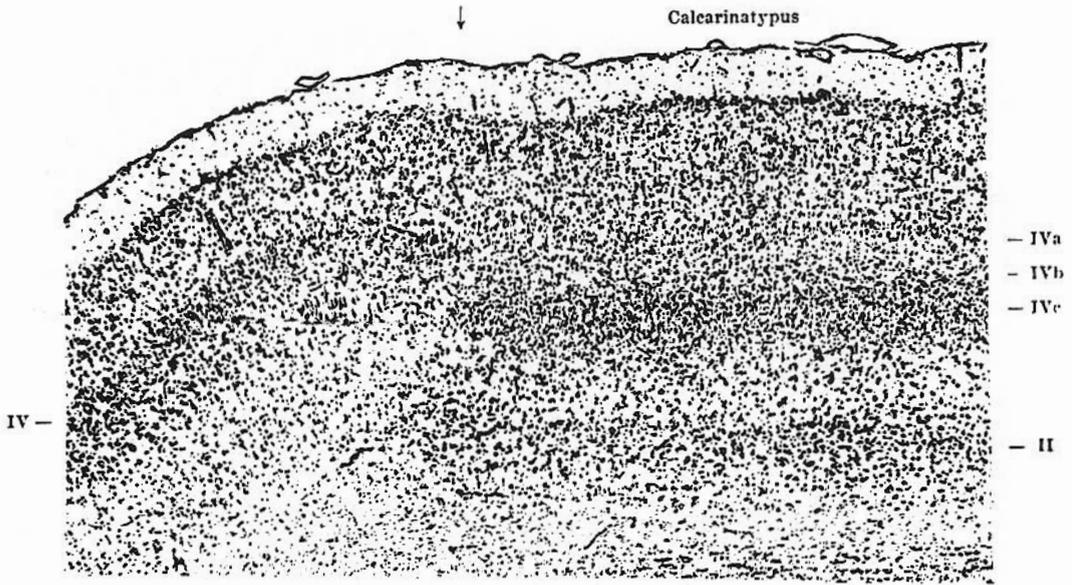


Fig. 22. Adult wallaby (*Macropus dorsalis*). 25:1, 10 μ m. The same as in the previous figure. Increase in cell density over the whole cortical depth, especially in layers IV and VI. Deepening of the whole cortex. Alteration of thickness of layers.

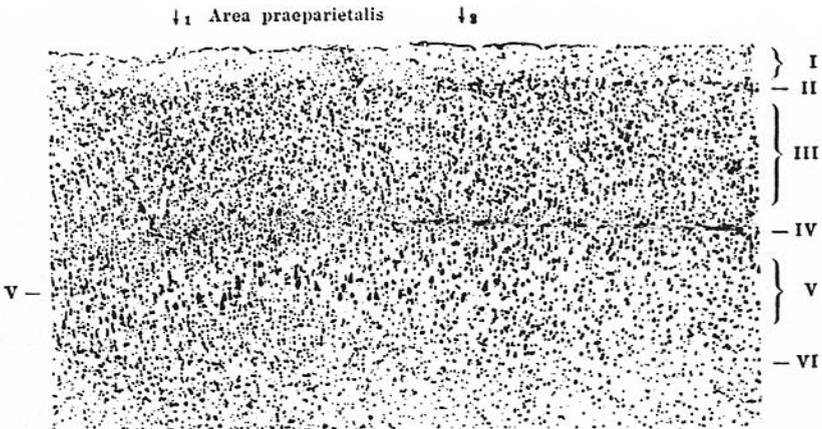


Fig. 23. Prosimian (*Lemur macaco*). 25:1, 10 μ m. Transition from preparietal cortex to the parietal area on the one hand (\downarrow 2) and to the postcentral area on the other hand (\downarrow 1). The preparietal cortex is characterised by very large ganglion cells in layer V and an increase in granule cells in layer IV, while the cell density remains the same in the rest of the cortical thickness.

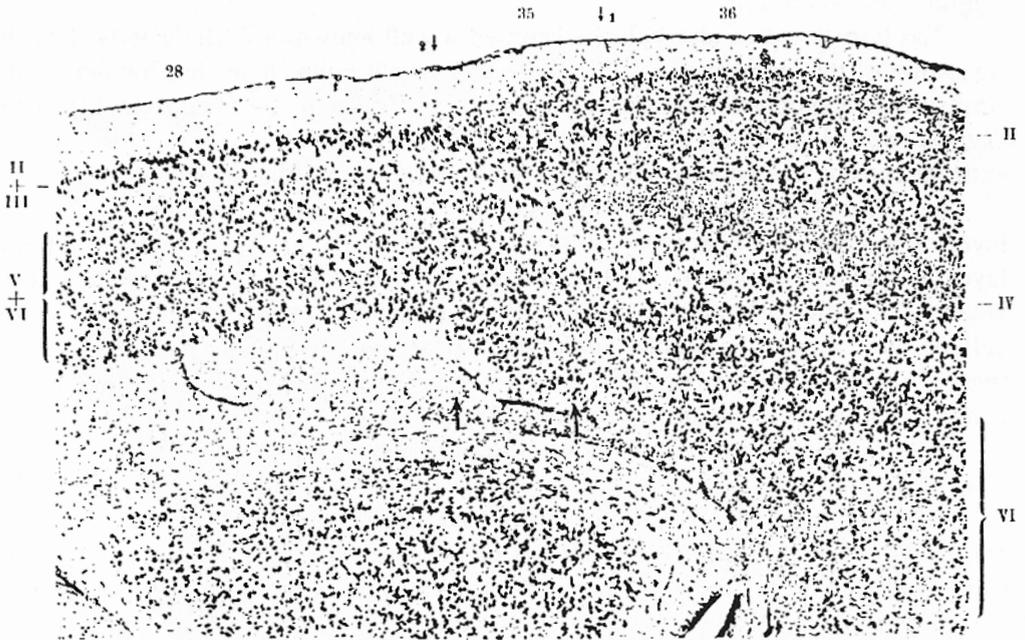


Fig. 24. Marmoset (*Hapale jacchus*). 25:1, 10 μ m. Transition of the homogenetic cortex of the neopallium (right) to the heterogenetic cortex of the archipallium (left): narrowing of the total cortical depth, widening of layers I and VI with sharp narrowing of layers II and III and loss of layer IV (\downarrow 1). Between \downarrow 1 and \downarrow 2 is the *perirhinal cortex* (area 35 of the brain map), to its right the *ectorhinal cortex* (area 36) and to the left the *entorhinal cortex* (area 28). cf. Part II.

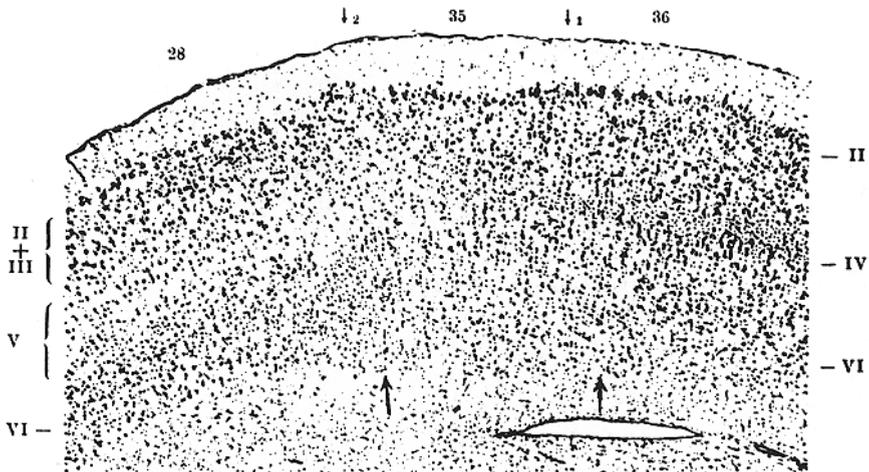


Fig. 25. Prosimian (*Lemur macaco*). 25:1, 10 μ m. The same as in Fig. 24. The cortical thickness does not change at the site of transition, only layers V and VI widen at the expense of layers II and III. Layer IV stops quite sharply at \downarrow 1. Layer I becomes narrower rather than wider.

a) Through splitting of a basic layer into two or more sublayers. A typical example of this pattern is the calcarine cortex, where the original single inner granular layer (IV) divides into three sublayers, a superficial, an intermediate and a deep (Figures 20, 21 and 22).

The insular cortex also belongs here; as is well known, it is characterised by the formation of the claustrum as a deep cell-rich structure which, as developmental and comparative anatomy demonstrate conclusively, is formed by the breaking off from the deepest cortical layer (VI) of a cellular strip close to the white matter that traverses the extreme capsule and becomes more and more independent (Figures 36 to 37) (*64).

b) Through differentiation and parcellation of new cell types within a principle layer of the basic cortical type. In this way a sublayer separates within the original layer. A typical example is the human occipital cortex (Figure 27) in which there develops a particularly clear division of the pyramidal layer (III) into an outer small-celled layer (*parvopyramidal sublamina*, IIIa) and an inner large-celled layer (*magnopyramidal sublamina*, IIIb). Similar processes are numerous, for instance in the ganglion cell layer (compare, for example, Figures 16, 17 and 23).

2. A reduction in the number of layers can also occur through a double mechanism.

a) One of the original layers of the basic architectonic pattern may disappear completely more or less abruptly. We can observe this process in various parts of the frontal cortex, part of the insula and in the anterior part of the cingulate gyrus, where the prominent inner granular layer (IV) of foetal life later disappears completely, by its granular elements regressing or becoming dispersed within adjacent layers, so that it can no longer be considered to exist. There is also a reduction in the number of layers at the transition from neopallium to archipallium where the inner granular layer suddenly ceases, as shown in Figures 24 to 26.

An especially characteristic and physiologically important example of the sudden interruption of a basic cortical layer, that is to say a reduction in layers, is provided by the transition from the giant pyramidal cortex (area 4) to the postcentral cortex (areas 1 to 3). The same essential architectonic transition can be traced through the whole mammalian class as will be explained elsewhere. In all animals the inner granular layer (IV) stops quite abruptly in this region to be substituted by the appearance of Betz giant cells in the underlying ganglion cell layer (V). In Figures 28 to 31 this transition is illustrated for four different animals.

b) Several layers that were originally separate in the basic pattern may fuse together and form a single layer in the mature brain. This is encountered especially in certain areas of the retrolimbic region that I described in detail for lemurs in my seventh communication. However, the most striking illustration of this category of laminar reorganisation comes from the fact that Meynert's outer granular layer (II), that is clearly expressed as a separate cell layer throughout the immature brain and shown in Figures 1 to 3 and 5 to 11, frequently regresses so much in the adult that it can hardly be distinguished from the underlying pyramidal layer (III), if at all (Figures 12, 13, and 16 to 18). As I have argued repeatedly, this situation is precisely the reason why most authors have not recognised an outer granular layer and have arrived at an erroneous

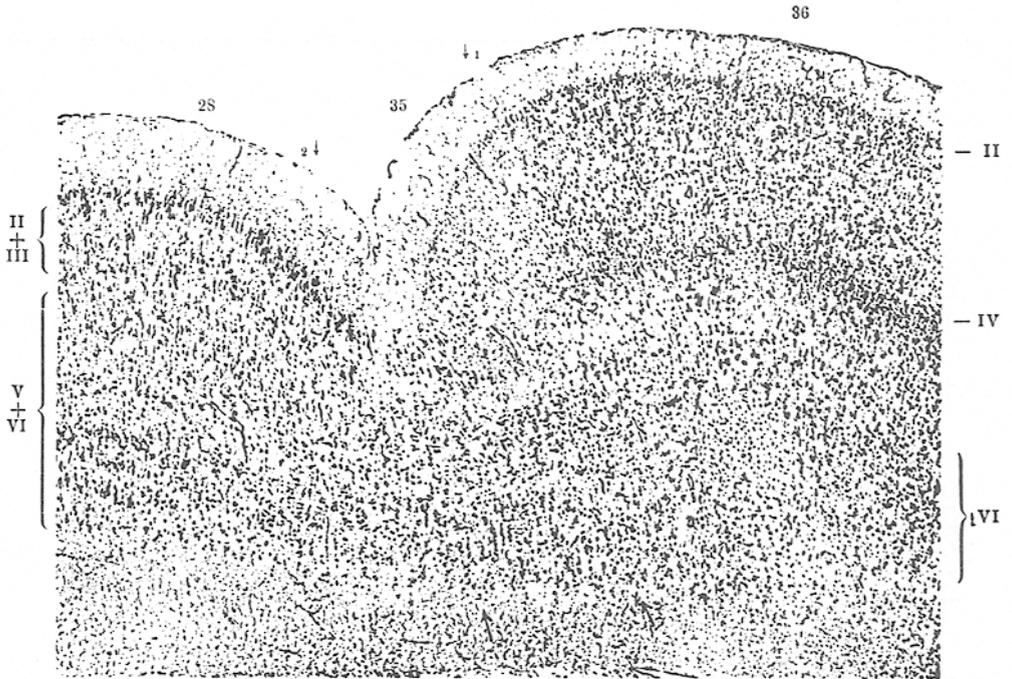


Fig. 26. The same architectonic transition as in Figs. 24 and 25 in the rhesus monkey (*Macacus rhesus*). 25:1, 10 μ m. The transition site in the archipallium is marked by a sulcus, the posterior rhinal sulcus. The labels are the same as in Figs. 24-26.

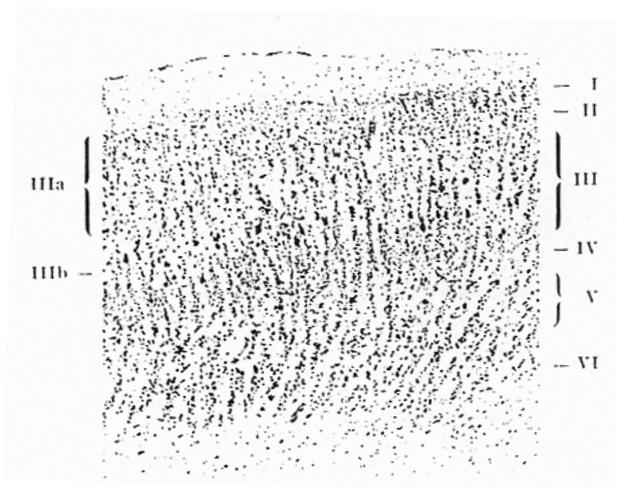


Fig. 27. Human occipital cortex. 25:1, 10 μ m. Division of the pyramidal layer (III) into two sublayers: the parvopyramidal IIIa and the magnopyramidal IIIb. (see also Fig. 42).

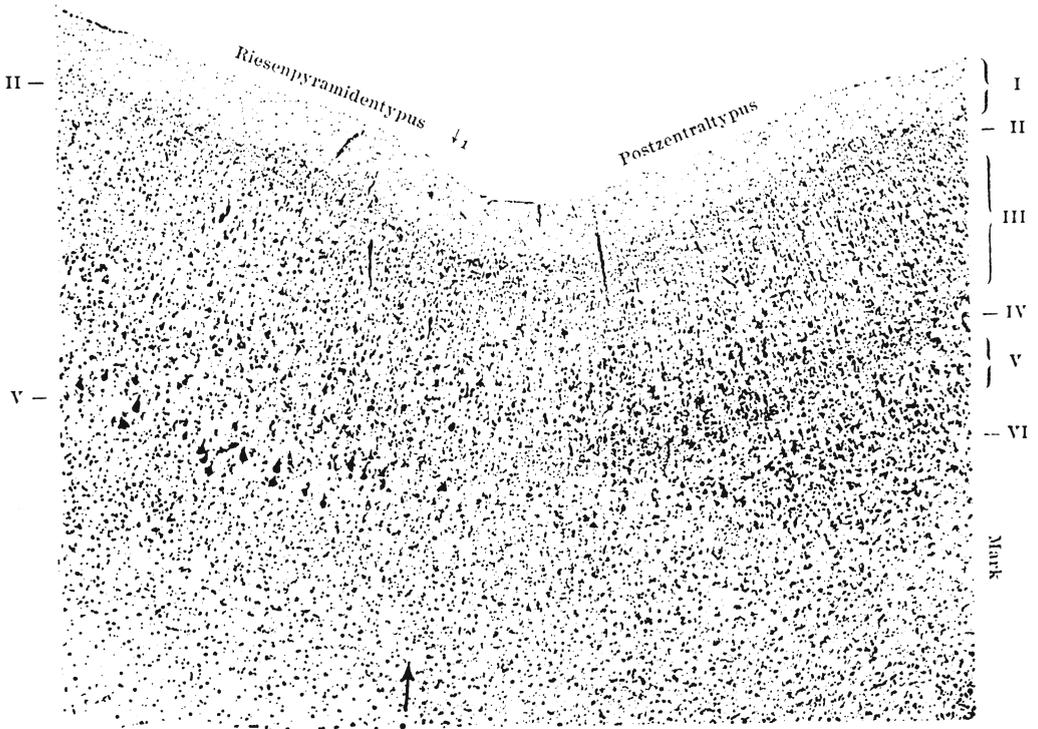


Fig. 28. Adult human. 20:1, 20 μ m. (For explanation, see Fig. 31).

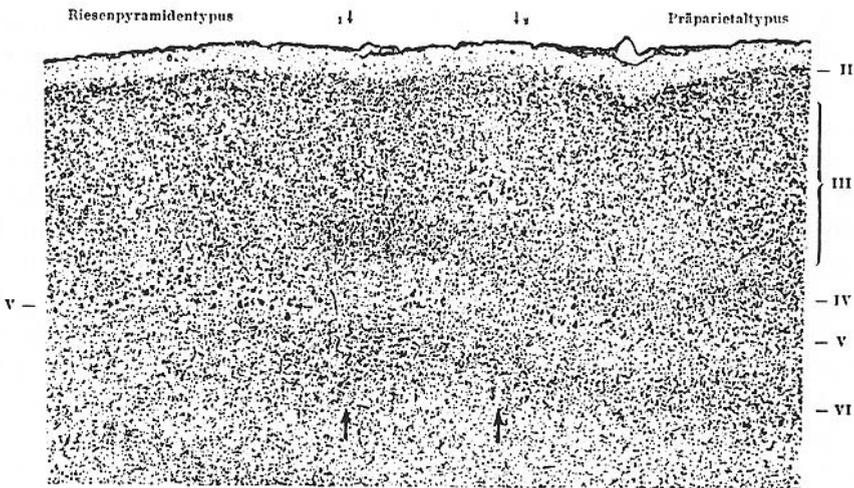


Fig. 29. Marmoset (*Hapale penicilata*). 25:1, 10 μ m. Transition from the giant pyramidal cortex to the postcentral cortex (\downarrow 1) and then to the preparietal cortex (\downarrow 2). The borders are very sharp. In the preparietal cortex large ganglion cells appear in the ganglion cell layer (V), similar to the actual giant pyramids.

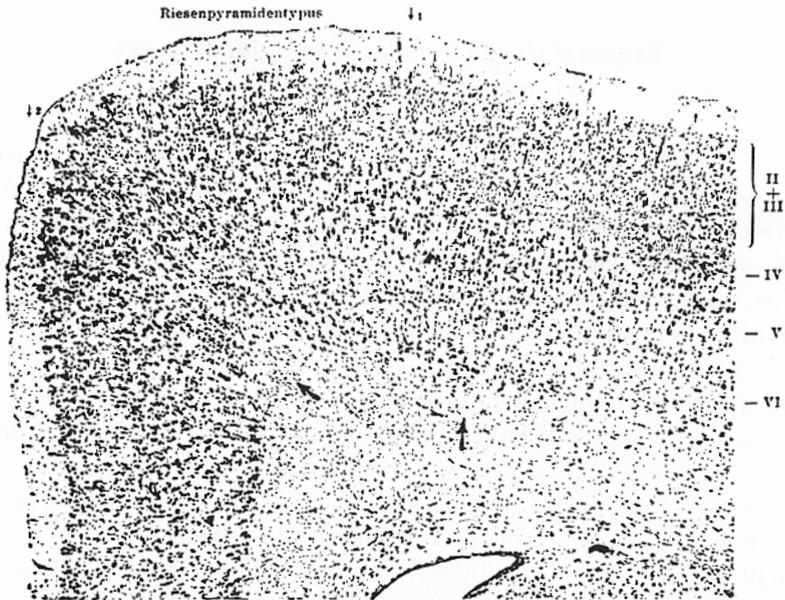


Fig. 30. Rabbit (*Lepus cuniculus*). 25:1, 10 μ m. Transition from the giant pyramidal cortex to the postcentral cortex (\downarrow 1) on one side, and the prelimbic cortex on the other (\downarrow 2).

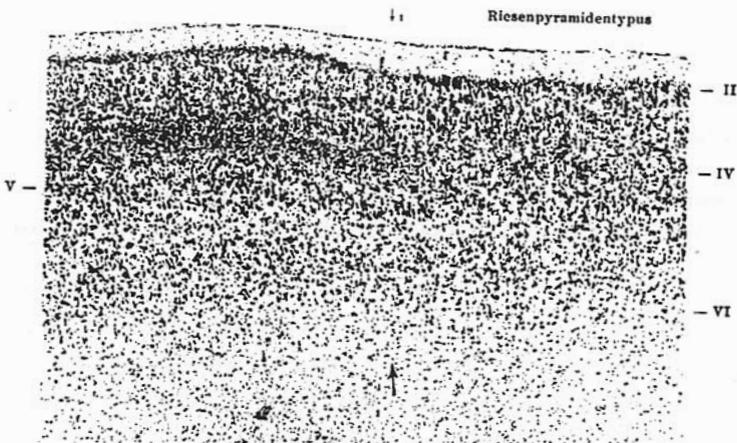


Fig. 31. Foetal wallaby (*Onychogale frenata*). 25:1, 10 μ m. The same as in the previous figure. There is a sharp end to the inner granular layer (IV) at \downarrow 1.

Figs. 28-31. Transition from the giant pyramidal cortex to the postcentral cortex in man, marmoset, rabbit and wallaby (*65). In the giant pyramidal cortex the inner granular layer (IV) is absent, instead of which the giant pyramids appear in layer V; in the postcentral cortex, on the other hand, a distinct layer IV is formed, whereas the giant pyramids are absent. One can compare the differences in cortical thickness, cell density and the laminar pattern in the different animals.

interpretation of the layers. In marsupials layer II remains clearly separate from the pyramidal layer (III) throughout life in many areas (Figures 15, 19 and 22).

Another form of fusion of two layers is found in those not uncommon cases where the cellular elements of the ganglion cell layer (V) and the fusiform layer (VI) mix in such a way that they appear to form a single layer. Examples in man include the rostral portion of the cingulate gyrus (areas 24, 25 and 33), certain frontal areas (6 and 8), and areas 30 and 35 of my brain map. Illustrations in support of this are not provided here, but can be found in my third and seventh communications.

c) Complete overlap and fusion of all cortical layers can be observed in several regions of the frontal lobe in man and other animals which were clearly laminated and possessed an inner granular layer during foetal development (Figures 32 and 33).

2. Regional characteristics of individual layers. (Constancy and variability.)

We have based our arguments so far on the primitive six-layered pattern as a whole and examined the general principles by which differentiation and reorganisation can take place. It emerges that modifications of cellular lamination respect the same rules in all mammals. There is either regression, for example fusion of individual primitive layers, or duplication and differentiation of sublayers from an elementary layer or, thirdly, there can be less radical changes in the thickness of layers, cellular density and size, and specific cell shape.

For the following comparative anatomical studies it will be helpful to examine each individual layer of the basic cortical pattern separately once again in terms of their regional variations.

This is necessary first of all because the changes in the cortical layers we have discussed are frequently not manifested suddenly and abruptly in a single region, but arise gradually over a broad area. In such cases only the comparison of widely separated regions permits the untrained eye to detect differences in a layer. Thus if one wishes to obtain an accurate picture of the degree of modification of a layer, one must treat each layer as an entity to be examined throughout its whole extent over the cortical surface. From the foregoing arguments the important fact emerges that, in general, certain of the basic layers can be assumed to be very constant and unchangeable and the others highly inconstant and variable. It can further be taken as established that those layers that undergo only slight regional modifications in man, on the whole also change little in other mammals, while on the contrary those layers that undergo marked local changes in man usually show an equally great variability throughout the whole mammalian class.

a) (*66) One can regard layers I and VI - the molecular and spindle cell layers - of the basic pattern as the most constant in this sense. They are not absent in any species or in any cortical area, and also appear in certain abortively developed zones of the cingulate gyrus and hippocampus. Their cellular structure varies within much narrower limits than that of all other basic layers.

The *molecular layer*, the extreme outer cortical layer (I), essentially only

Chapter IV.

Description of individual brain maps.

Unlike the preceding descriptions of details of individual cortical fields according to lobes or gyri, the next section will deal with the division of the surface of the hemispheres of different animals into major, structurally homogeneous zones that only partially coincide with the morphological formations of earlier nomenclatures, such as lobes, lobules and gyri, each of which may encompass several architectonic areas. The basis for this is essentially comparative anatomy and depends on the following considerations. One can indeed roughly subdivide the hemispheres of man and related gyrencephalic animals into morphologically homologous lobes. Nevertheless what corresponds in lower orders, such as small rodents and insectivores, to the frontal or temporal lobes is unfortunately impossible to determine by external inspection. However, it is quite possible to identify histological structures, and a number of such structural areas can be demonstrated in all mammals.

We therefore group together large zones of similar composition as individual structural entities, the so-called "regions" as opposed to the individual fields or "areas". So from now on we shall no longer merely differentiate the fields of the frontal, temporal, occipital lobes etc. but shall take regions as our point of departure, within which the individual areas are delimited according to their histological homogeneity.

A considerable number of such homologous regions can be distinguished in man and the other mammals (*99). They are the:

1. postcentral region
2. precentral region
3. frontal region
4. insular region
5. parietal region
6. temporal region
7. occipital region
8. cingulate region
9. retrosplenial region
10. hippocampal region
11. olfactory region

Many of these regions are massively developed in the higher orders and have a rich variety of individual areas, while demonstrating a simple organisation in lower orders. Other regions show an opposite trend, with more differentiation in lower, more primitive species than in more highly organised animals. Certain zones, like the olfactory region, are extremely reduced in certain animal groups and only developed in a rudimentary way so that they cannot be represented on the brain map, while in other orders, like the macromammals, they occupy a considerable portion of the cortical surface.

In Figures 83 and 84 the regions of the human cerebral cortex (except the insular region that is shown in Figure 89) (*100) are represented schematically from the medial and lateral aspects of the hemispheres. As can be seen, they only partially coincide with the subdivisions habitually used so far; it should be especially noted that the morphologically homogeneous "Rolandic region" is structurally divided into two separate regions, precentral and postcentral, each of which in turn contains several areas. Also, to avoid erroneous interpretations it should again be stated that not all these regions are demarcated from each other by sharp borders but may undergo gradual transitions as, for example, in the temporal and parietal regions.

I. The human brain map (Figures 85 and 86).

I first gave a brief description of the human cortical pattern in 1907 and at the same time drew up the accompanying surface map of the subdivision of the whole cortex into areas. In general I have nothing to remove from it, nor anything essential to add. I could thus content myself with a reference to that description. Nevertheless, in view of later comparative studies I shall give a detailed description here of the whole extent of the cortex and a precise delineation of the more physiologically or clinically important fields in relation to their position and their topographic relations to sulci and gyri. There will also be a general discussion of the sulci.

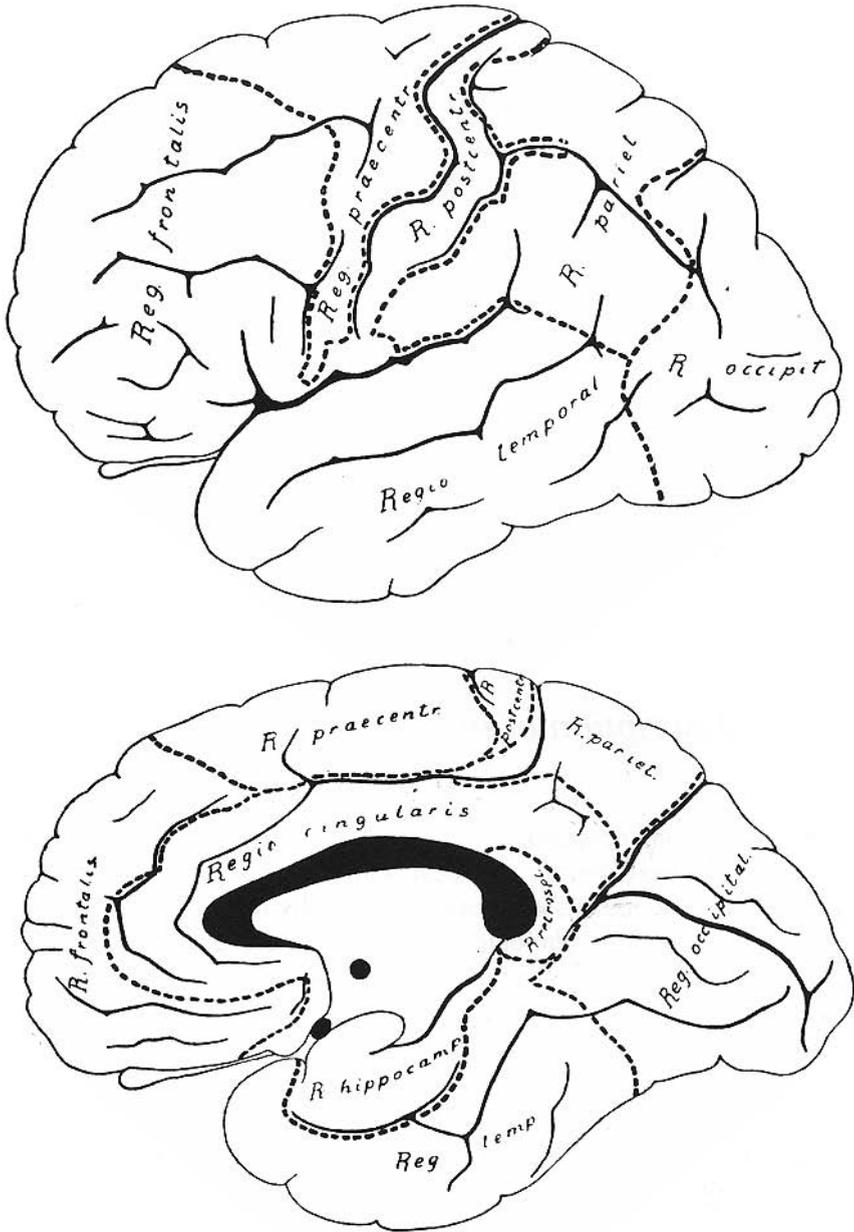


Fig. 83 and 84. The cytoarchitectonic regions of man. The olfactory region is not indicated.

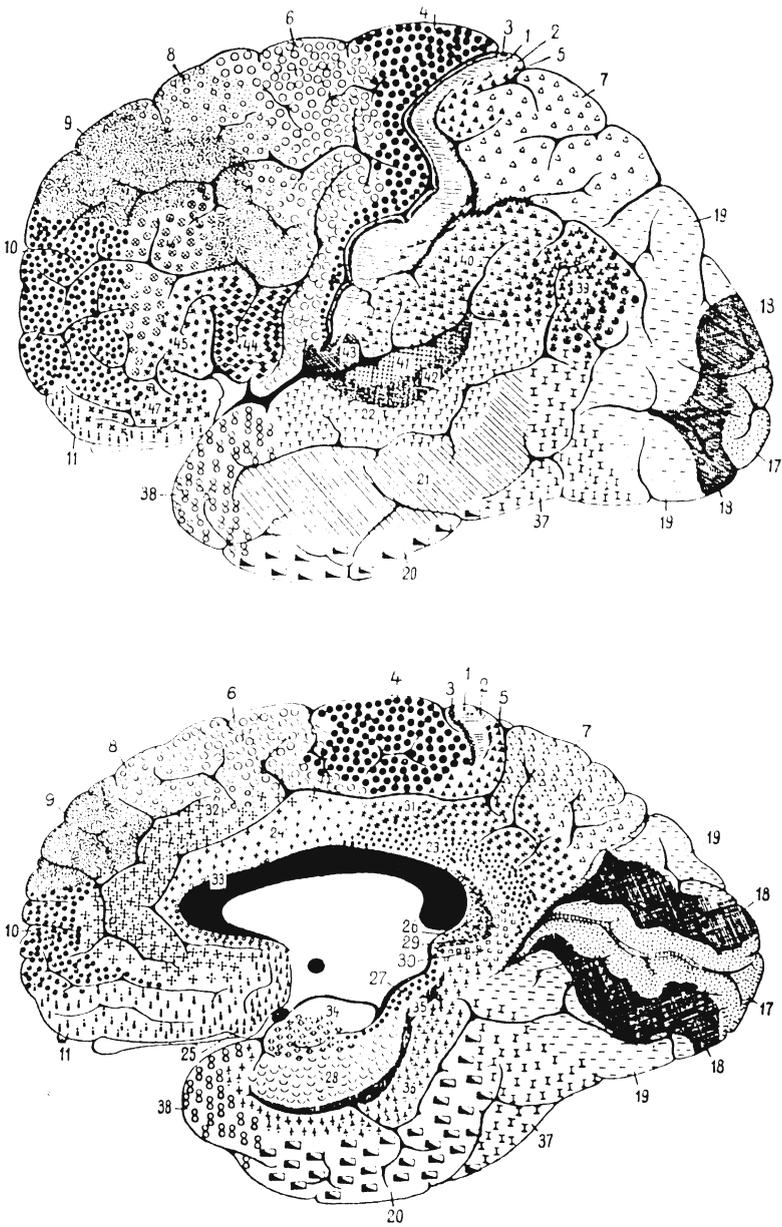


Fig. 85 and 86. The cortical areas of the lateral and medial surfaces of the human cerebral hemispheres. (Sixth communication, 1907.)

Postcentral region.

Concerning the cortical areas of the pericentral gyri, I wrote in 1902/03: "The Rolandic region of man is split by the central sulcus through its whole dorsoventral extent into two anatomical zones that are totally different in their cytoarchitectonic structure; the anterior zone is characterised by the appearance of giant pyramids and the lack of an inner granular layer, the posterior one by the presence of a distinct granular layer and a lack of giant pyramids. The border between the two zones is largely formed by the bottom of the sulcus apart from a short transition zone possessing a mixture of both structural types. At the dorsomedial end of the central sulcus this border continues on the paracentral lobule such that it forms a linear prolongation of the central sulcus as far as the junction with the callosomarginal sulcus, thus separating the paracentral lobule into two histologically different fields, an anterior one of which the structure corresponds in all respects to that of the giant pyramidal cortex, and a posterior one that represents the prolongation of the postcentral gyrus and has the same cytoarchitecture" (my first communication, *Journal f. Psychol. und Neurol.* Vol. 2, p.93/94).

This already contains the description of the splitting of the Rolandic region into two histological zones, that I now distinguish as the postcentral and precentral regions.

The postcentral region lies directly behind the central sulcus and comprises essentially the postcentral gyrus as well as its medial prolongation on the caudal third of the paracentral lobule (except the most posterior part of this gyrus that is occupied by area 5) and the greater part of the Rolandic operculum. Topographically it is further subdivided into four architectonically related, but substantially different, structural types: areas 1, 2, 3 and 43.

Area 1 - *intermediate postcentral area*. - This area lies in the middle of the granular postcentral region, that is between areas 2 and 3, separated from them by a quite distinct, but certainly not absolutely sharp, border and occupies a narrow band approximately along the whole length of the apex of the postcentral gyrus. At the upper margin of the hemisphere it follows the curve of the postcentral gyrus onto the medial surface as a quite narrow strip on the caudal (retrocentral) part of the paracentral lobule. Its main expanse on the lateral convexity varies in width, being extremely narrow and constricted at the upper margin of the hemisphere and extending more widely in the middle of the gyrus. In places the area also encroaches somewhat on the cortex of the depths of the central sulcus and the postcentral sulcus, compressing the adjacent areas 2 and 3 into the fundus of these sulci. At the lower end of the postcentral gyrus it narrows markedly, its structure changes somewhat and its borders with areas 2 and 3 become less distinct so that a sort of mixed cortical type appears. This transitional form is demarcated quite sharply from the subcentral cortex (area 43) on the Rolandic operculum.

Area 2 - *the caudal postcentral area* - forms, like area 1, a narrow stripe-like zone, that includes chiefly the posterior aspect of the postcentral gyrus

and, therefore, the anterior bank of the postcentral sulcus. Its borders are not everywhere sharp and constant; sometimes it does not extend forwards entirely to the apex (*101) of the gyrus, while more often it crosses the fundus of the postcentral sulcus posteriorly and encroaches on the superior parietal lobule (*102). In the course of the intraparietal sulcus (*103), where it is continued as the postcentral sulcus, a narrow strip extends fairly far caudally. Elliot Smith equally described this stripe-like zone and tends to regard it as a special field, the “*sensory band β* ” (*104) although he has to concede that it is not possible to separate it from the caudal postcentral area or from the inferior parietal area. There are undoubtedly considerable individual differences concerning this, as there are in the sulcal pattern, that require further special study. Cytoarchitectonically speaking, it is not very feasible in my opinion to separate this strip round the intraparietal sulcus from area 2 without arbitrariness.

Area 3 - *rostral postcentral area* (*105). - This area covers the anterior extent of the postcentral gyrus, thus forming the posterior bank of the central sulcus along its whole length. Its borders are sharper than those of area 2; it is especially sharply demarcated from the agranular area 4 (giant pyramidal area) anteriorly. The transition to the giant pyramidal area is not always precisely in the deepest part (fundus) of the central sulcus, but is sometimes markedly anterior to it and in other places posterior. Thus the area has a variable width at different locations along the central sulcus, a feature that is also determined by the varying depth of the sulcus. At the upper (medial) and lower (lateral) ends, area 3 encroaches on the precentral gyrus around the central sulcus thus, as it were, pushing area 4 anteriorly. At these places, as well as in the retrocentral part of the paracentral lobule and in the posterior section of the Rolandic operculum, there is a noticeable obscuring of the borders such that the adjacent fields seem partially fused, forming composite areas and making parcellation very difficult in some brains.

Instead of my areas 1 to 3, Campbell differentiates only two fields on the postcentral gyrus, a “*postcentral area*” and an “*intermediate postcentral area*”, while Elliot Smith leaves the question open as to whether two or three different areas should be recognised.

Area 43 - *the subcentral area* - is formed by the union of the pre- and postcentral gyri at the inferior end of the central sulcus and thus lies on the Rolandic operculum. From its architecture, this area belongs to the postcentral cortex. Its anterior border is quite sharp and coincides approximately with the anterior subcentral sulcus; posteriorly it disappears gradually around the posterior subcentral sulcus in the retrocentral transition zone and in the anterior portion of the supramarginal area (40). It extends widely over the inner surface of the operculum, that is to say in the depths of the Sylvian fissure; in this region it has a distinct boundary with the insular cortex.

In his Plate 1 (*106) Campbell also pointed out a small region on the Rolandic operculum but did not describe it as a special area but rather as a mixed zone. Elliot Smith equally delimits a narrow strip (z) (*107) at the same place but he takes it to be a continuation of his “*area postcentralis A*” (my rostral

postcentral area) that he extends round the inferior end of the central sulcus as far as the vertical ramus of the Sylvian fissure anteriorly, in spite of a change in structure, and erroneously in my opinion.

Precentral region.

This consists of the territory lying directly anterior to the central sulcus and is chiefly characterised by the lack of an inner granular layer. It extends rostrally beyond the Rolandic region as it is usually understood, in that the dorsal half of its anterior border crosses the precentral gyrus and encroaches significantly on the superior and middle frontal gyri. Its anterior borders are rather clear but vary between individuals, while the posterior boundary is everywhere sharply demarcated from the postcentral region (*108), and particularly from area 3, by the depths of the central sulcus, although, as mentioned above, the border does not always correspond to the deepest part of this sulcus.

Within the precentral region two distinctly different fields - areas 4 and 6 - can be identified, both characterised cytoarchitectonically by the lack of an inner granular layer, and area 4 further distinguished by the presence of Betz giant cells that do not appear in area 6. (See Figures 94 and 95, page 130)

Area 4 - *the giant pyramidal area* - is one of the most strikingly differentiated and cytoarchitectonically delimitable structural regions of the whole human cerebral cortex.

It consists of a wedge-shaped cortical segment along the course of the central sulcus, narrowing from superior to inferior and enclosed entirely within the precentral gyrus and the adjacent part of about the middle third of the paracentral lobule. On the medial aspect of the hemisphere it covers approximately the middle third of the paracentral lobule. Laterally it only includes the whole width of the precentral gyrus near the superior edge of the cortex - often encroaching somewhat on the base of the superior frontal gyrus - and then, more ventrally, becomes restricted to the posterior half of this gyrus, narrowing progressively (with individual variation) and withdrawing to the buried cortex of the posterior bank of the precentral gyrus, where its sharp border ceases quite a distance above the lower end of the central sulcus as it fuses with area 6.

I have already described its borders elsewhere, in complete agreement with Campbell. They are very variable, especially in the paracentral lobule; it is not uncommon for area 4 not to extend as far medially as the callosomarginal sulcus, but to only include the dorsal half of the paracentral lobule, sometimes precisely to the level of an unimportant secondary sulcus that has been appropriately named the medial subcentral sulcus ¹⁾. Rostrally the borders give way gradually to area 6, caudally they lie in the central sulcus, sometimes somewhat anterior or posterior to its deepest point. Ventrolaterally area 4 does not quite

¹⁾ Contrary to the usual nomenclature, Elliot Smith calls this sulcus the sulcus paracentralis.

reach the lower end of the central sulcus; in many cases it stops 2 to 3cm higher in the depths of the sulcus.

I must definitely classify as erroneous the idea, proposed by Elliot Smith, that the anterior subcentral sulcus is "a limiting furrow" for area 4, especially as Elliot Smith himself admits that the precentral fields vary considerably in their boundaries and that macroscopic analysis in unstained preparations is often unsatisfactory ²).

Campbell's suggestion that the myeloarchitectonic border of area 4 (his *precentral or motor area*) extends 1 to 2mm further anteriorly than the "cell area" takes on a special importance ³).

The rostral border of the giant pyramidal area on the convexity of the gyrus is rather unclear and variable, for areas 4 and 6 undergo a gradual transition and because isolated Betz giant cells occur in "solitary" fashion more or less extensively rostrally, such that the identification of the line of transition is purely subjective and can only be determined from numerous individual brains. On the upper edge of the cortex the border usually lies just ahead of the superior part of the precentral sulcus but then soon runs backwards and downwards on the superior frontal gyrus to continue approximately down the crest of this gyrus. At the superior frontal sulcus the field bulges out, widening anteriorly once again, after which it becomes pushed towards the posterior edge of the gyrus, and in the lower half of the gyrus, or even somewhat higher, retreats onto its posterior bank so that from here down the the field is restricted to the cortex deep in the central sulcus, only being visible as a narrow strip.

Within this circumscribed zone, as has been known since the work of Lewis and Clarke, there emerge considerable local differences in the number, size and distribution of the giant pyramids, in addition to individual variations. Lewis and Clarke claimed to observe column-like accumulations of these cells corresponding to the physiological centres for the legs, the trunk, the arm and the face, but later their views did not enjoy universal confirmation and also require verification by physiological experiments. It is however clear that the size and number of the Betz giant cells decrease on average from superior to inferior, that is from the paracentral lobule laterally, and also that the dense cell clusters gradually disappear toward the ventral end of the central sulcus, making way for a more scattered arrangement of these cells. It can further be noted that the distribution of the giant pyramids in the upper third of the field and at the summit of the gyrus is essentially "cumulative", while it becomes almost entirely solitary or laminar more ventrally. Equally, the total cortical thickness decreases ventrally. However, the cytoarchitecture is not sufficiently

²) "The naked-eye appearances of the praecentral areas is subject to a wide range of variation" (Elliot Smith, 1907, p.246).

³) "A discrepancy which must be mentioned, however, is that the fibre area is one or two millimetres more extensive than the cell area; to understand this difference we have only to take note of the size and extensive ramifications of the enormous dendrons possessed by these cells, as well as the numerous collaterals given off by their axis cylinder processes, and also remember that the existence of cells of great size has a marked influence on the fibre wealth of the part and apparently makes its presence felt at a considerable distance" (Campbell, 1905, p.35).

characteristic to enable a subdivision of the giant pyramidal area into spatially circumscribed subfields, in spite of the above-mentioned regional differences.

Area 6 - the *agranular frontal area* - could be considered part of area 4 on account of its lack of a granular structure, and for convenience is included with the latter in a major regional division, separate from other frontal types that possess an inner granular layer. It is very similar to area 4 in shape and extent. Area 6 consists of an upper very broad zone, becoming increasingly narrow inferiorly and laterally, and covering the whole vertical extent of the frontal lobe from the callosomarginal sulcus to the upper bank of the Sylvian fissure. The following gyri contribute to it: medially, the anterior part of the paracentral lobule with the neighbouring parts of the superior frontal gyrus, and in many cases also almost the whole dorsal bank of the callosomarginal sulcus except its posterior third; laterally, the bases of the superior and middle frontal gyri, and further inferiorly the whole precentral gyrus except where it is occupied by area 4.

Campbell also includes in this area (his intermediate precentral area) the whole inferior frontal gyrus, but according to my studies this is undoubtedly to be separated as a special region, the opercular, triangular and orbital areas (44, 45 and 47), as it possesses a distinct inner granular layer, a feature that Campbell overlooked.

Elliot Smith divides my area 6 into a dorsal *area frontalis superior* and an *area frontalis intermedia*. I admit that area 6 gradually changes its structure in a dorsoventral direction (this also applies to the myeloarchitecture). However, the cell structure gives no conclusive indication for a division into two specific fields, and even Elliot Smith concedes that the difference is not always clearly manifested ("This contrast has not been sufficiently clearly" - p.249) (*109).

Frontal region.

The frontal region is by far the most extensive region of the human cerebral cortex in terms of area; it includes the whole of the frontal lobe anterior to the central sulcus, with the exception of the precentral region, and the precingulate region on the medial surface. This constitutes, as a surface estimate, around 20% of the total cortical area of a hemisphere. It should be treated as a single frontal structural region because, in contrast to the agranular precentral region, all its subdivisions again contain a compact inner granular layer. We shall study the major importance of this architectonic feature in more detail below when we make comparisons with other brain maps. Its limits are easy to enumerate: caudally it gives way to the agranular frontal area at well-marked boundaries, rostrally it extends round the frontal pole, and on the medial surface to near the callosomarginal or superior rostral sulci. However, as can be seen from the map, the borders do not correspond exactly to these sulci.

I distinguish eight individual fields in the frontal region of man, namely areas 8, 9, 10, 11, 44, 45, 46 and 47. Of these, areas 44, 45 and 47 on the

inferior frontal gyrus form a particularly homogeneous subgroup on the grounds of major cytoarchitectonic similarities, that can be termed the *subfrontal region*. The exact parcellation of these areas (with the exception of the subfrontal zones) is often fraught with great difficulties, for the architectonic differences in cell preparations are sometimes not at all striking. Elliot Smith also draws attention to this with the words: "The accurate mapping out of this area (frontal) presents great difficulties, because the contrasts between adjoining areas are often exceedingly slight and at times quite impossible to detect." (*110) Elliot Smith divides the frontal lobe into eight fields, similar to my divisions, even though in many respects differences exist in relation to individual areas.

Campbell only differentiates two subfields within the whole region, a "frontal area" and a "prefrontal area". He includes the inferior frontal gyrus in his "intermediate precentral area", and thus, mistakenly, in an agranular structure.

Area 8 - the *intermediate frontal area* - consists of a strip-like zone, wide superiorly and narrowing laterally which, like the agranular frontal area (6), crosses from the callosomarginal sulcus on the medial surface over the upper edge of the hemisphere onto the lateral surface; but there it only reaches to about the middle frontal gyrus before gradually vanishing without distinct borders. Especially on the lateral convexity of the hemisphere it is much less extensive than area 6.

Area 9 - the *granular frontal area* - is a field of similar shape and position to the preceding area, but much more extensive. On the medial surface its only approximate morphological boundary is provided by the callosomarginal sulcus, and on the lateral surface it stops ventrally in the region of the inferior frontal sulcus.

Area 10 - the *frontopolar area* - covers the frontal pole, that is approximately the anterior quarter of the superior and middle frontal gyri on the convexity of the hemisphere, but does not extend medially quite as far as the callosomarginal gyrus. Inferomedially it is fairly precisely demarcated by the superior rostral sulcus. It corresponds approximately to the frontal area of Elliot Smith.

Area 11 - the *prefrontal area* (*111) - forms the rostroventral part of the frontal lobe on its orbital and medial surfaces, thus including most of the straight gyrus (*112), the rostral gyrus and the extreme anterior end of the superior frontal gyrus. The borders are: medially the superior rostral sulcus, laterally approximately the frontomarginal sulcus of Wernicke, and on the orbital surface the medial orbital sulcus.

It is possible to detect fine architectonic differences within this area and with some arbitrariness it can be subdivided. Thus one could separate the zone between the superior rostral sulcus and the inferior rostral sulcus from area 11 as a specific rostral area; equally the straight gyrus and the medial orbital gyrus that lies medial (*113) to it demonstrate certain structural differences, which in principle permit a division (into an *area recta* and a *medial orbital area*).

For reasons of clarity and because this whole area forms a histologically circumscribed zone, I have tentatively only included one area in the brain map, coinciding fairly precisely with the prefrontal area of Elliot Smith. (According to O. Vogt this region can be subdivided into a much larger number of individual areas myeloarchitectonically).

Area 44 - the *opercular area* - is a well-differentiated and sharply circumscribed structural region that on the whole corresponds quite well to the opercular part of the inferior frontal gyrus - Broca's area. Its boundaries are, posteriorly, approximately the inferior precentral sulcus, superiorly the inferior frontal sulcus and anteriorly the ascending ramus of the Sylvian fissure. Inferiorly or medially it encroaches on the frontal operculum and borders on the insular cortex. The area then stretches around the diagonal sulcus, and there are again minor structural differences between the cortex in front of and behind this sulcus to justify the separation of an *anterior opercular area* from a *posterior opercular area* by the diagonal sulcus. As there is much variability and inconstancy of these sulci one will find rather mixed topographical relationships of these structural areas in individual cases.

Area 45 - the *triangular area* - is cytoarchitectonically closely related to the previous area that corresponds approximately to the triangular part of the inferior frontal gyrus. Consequently its caudal border lies in the ascending ramus of the Sylvian fissure, its dorsal border in the inferior frontal sulcus and its rostral border near the radiate sulcus of Eberstaller, although it may extend in places beyond this last sulcus as far forward as the frontomarginal sulcus of Wernicke, and this area may also encroach partially on the orbital part; on the inferior surface of the inferior frontal gyrus it borders the insular cortex.

Concerning the exact morphological borders of the last two areas, that are so extremely important on account of their relationship to the motor speech area, I should like once again to expressly point out the great individual variations of the sulci in this region. As emerges from Retzius' great monograph "Das Menschenhirn" (*114), the diagonal sulcus is not infrequently fused with the inferior precentral sulcus or communicates with the ascending ramus, is often very strongly developed, but sometimes is entirely absent. The radiate sulcus and the ascending ramus vary widely in shape and structure so that naturally the relations of areas 44 and 45 to these sulci must be subject to major individual variations. Elliot Smith also recognised this with the words: "it must be admitted that its relations to these morphological boundaries is rarely, if ever, preserved with mathematical exactness" (Elliot Smith, 1907, p.249).

Area 47 - the *orbital area* - shares certain architectonic affinities with areas 44 and 45 such that it can be combined with them to form a *subfrontal subregion*. It lies essentially around the posterior branches of the orbital sulcus, generally well differentiated from area 11, but without constant morphological borders. Laterally it crosses the orbital part of the inferior frontal gyrus.

Area 46 - the *middle frontal area* - is not clearly distinguishable from neighbouring areas by its cell structure and can thus only be delimited with uncertainty. It includes about the middle third of the middle and the most

anterior part of the inferior frontal gyri at the transition to the orbital surface. There are no constant topographic relations to particular sulci.

Parietal region.

The parietal region coincides essentially with the parietal lobe, but the most posterior segment of the paracentral lobule with the ascending branch of the callosomarginal sulcus also belongs to it. In the inferior part of the parietal lobe it is especially difficult to differentiate it histologically and morphologically with certainty from temporal and even from occipital cortex; it is better distinguishable from the postcentral region for which the postcentral sulcus forms the approximate boundary. On the medial surface the subparietal sulcus and the parieto-occipital sulcus form approximate, but not precise, borders. Within its boundaries four or five individual areas can be distinguished.

Area 5 - the *preparietal area* - is a cytoarchitectonically well characterised area, clearly delimited from neighbouring areas, for which the major distinguishing feature is the presence in layer V of extraordinarily large pyramidal cells that sometimes attain the size of Betz giant cells, and in addition a thick inner granular layer (Figure 16). The cortical thickness noticeably exceeds that of the postcentral cortex. Although the architectonics of this area, especially the size of the pyramidal cells, varies considerably in individual cases, its position is essentially rather constant. The area begins in the most caudal portion of the paracentral lobule, and narrows markedly in the depths of the terminal branch of the callosomarginal sulcus on its rostral bank, extending over the edge of the hemisphere to the lateral surface; it forms a rather wider zone posterior to the superior postcentral sulcus that spreads out between the fork-like diverging terminal branches of the superior postcentral sulcus in the cases that I have examined. Thus overall area 5 has a sack-like shape. The characteristic lateral part of the cortex included in this area appears to be very constant and, from its histological structure, to be of great importance, corresponding in the literature to the anterior portion of the anterior arcuate parietal gyrus (Retzius). In spite of its conspicuous structure, the preparietal cortex has been neglected by all authors. Judging from comparative studies, it has a great biological importance as it can be traced down through much of the mammalian class.

Area 7 - the *superior parietal area* - corresponds essentially to the superior parietal lobule laterally, where this is not occupied by the preparietal area, and medially with the precuneus. The approximate boundaries are, medially the subparietal sulcus, laterally the intraparietal sulcus, posteriorly the parieto-occipital sulcus, and anteriorly the superior postcentral sulcus, with the limitations mentioned earlier. Its structure changes gradually from anterior to posterior so that one can distinguish a division at the superior parietal sulcus into an anterior and a posterior half, or an anterior and posterior superior parietal area (in Figures 84 and 85 this is shown by different densities of the symbols) (*115). This difference also struck Elliot Smith, although he did

not find it clearly expressed in all brains ⁴).

Area 40 - the *supramarginal area* - lies ventral to the intraparietal sulcus around the terminal branch of the posterior ramus of the Sylvian fissure, thus corresponding to the supramarginal gyrus. Anteriorly the supramarginal area abuts against the postcentral regions, notably areas 2 and 43, separated from it by the inferior postcentral sulcus and the posterior subcentral sulcus. Caudally it gradually gives way to the angular area with the sulcus of Jensen forming the approximate border. It has no sharp boundary with the temporal region (area 22).

Area 39 - the *angular area* - corresponds broadly to the angular gyrus, widening around the posterior end of the superior temporal sulcus, especially caudal to it. Its boundaries with the occipital and temporal regions (areas 19 and 37) are ill-defined; the border with the parietal area is formed approximately by the intraparietal sulcus.

Occipital region.

The occipital region includes the whole occipital lobe, that is laterally the superior, middle and inferior occipital gyri, medially the whole cuneus and the posterior portions of the lingual and fusiform gyri. Its borders are morphologically poorly defined on all sides and also architectonically indistinct. It is divided into three structurally very markedly different areas, the striate area, the occipital area and the preoccipital area.

Area 17 - the *striate area* - as we have seen above, is characterised by the most strikingly differentiated of all homogenetic cortical types, the so-called calcarine type (Figures 12 and 53). As a result of its remarkable structure this area is so easily recognisable, even with the naked eye, either in stained sections or in fresh specimens, that the precise delimitation of its extent can usually be determined macroscopically. This makes it all the more extraordinary that the topical localisation of this area was only established a few years ago and that even today many erroneous interpretations are still disseminated. I have described its situation and exact boundaries in detail in various places (my second, fifth and sixth communications); we shall come back to this below in the comparative discussion and the consideration of individual and species variations. In general the striate area corresponds to the cortex of the calcarine sulcus and closely neighbouring zones. At the posterior end of the calcarine sulcus it extends round the occipital pole onto the lateral surface of the hemisphere, but only very little in Europeans, at most no more than about 1cm; the bulk of the area lies on the medial side and includes a wider cortical field than would appear from the surface of the hemisphere, for the calcarine sulcus is very deep and often forms a true "calcarine fossa". The real extent of its deep spread can be judged from coronal sections of the region (Figures 87 and 88).

⁴ "In most specimens I have found it quite impossible to distinguish the cortex of the area in front of these furrows from that placed behind them" (Elliot Smith, 1907, p.245).

The borders of this area, especially laterally, are extraordinarily variable, which is particularly important for pathology. But even medially there are no regular and constant relationships to any "limiting sulci", and in particular the cuneate and lingual sulci cannot be taken as true upper and lower boundaries of the striate area (the *sulcus limitans superior* and *inferior* according to Elliot Smith), for it often extends beyond these sulci in places and in others does not reach them. Thus the cuneus and the lingual gyrus participate in the striate area to variable extents, depending on the degree of infolding of the calcarine sulcus, that is to say on its depth; usually the latter is more involved, that is the striate area extends further ventrally from the calcarine sulcus than dorsally. Above the union of the parieto-occipital and calcarine sulci, and not infrequently even before, the dorsal striate area retreats entirely from the surface and disappears in the depths of the sulcus, while ventrally this usually happens further anteriorly. The anterior end of the area always lies in the depths of the calcarine sulcus and always in its ventral bank, but only exceptionally in such a way that the sulcus forms the rostral boundary (the *sulcus limitans anterior areae striatae* of Elliot Smith); the area scarcely reaches it until right at the most anterior end of the sulcus.

Elliot Smith has described in detail the individual variations of the striate area and the organisation of its sulci, while Bolton, in 1900, studied the characteristics of the area, his *visuo-sensory area*, in blind and anophthalmic patients. (I have dealt with the characteristics of this area in certain foreign races of man elsewhere; see my fifth communication for the Javanese brain).

Area 18 - the *occipital area* - is represented as a crown-shaped field, as in simians and prosimians, that surrounds the striate area laterally and medially as a sometimes wide, sometimes narrow ring-like formation. On the lateral surface it extends quite far anteriorly along the lateral (superior) occipital sulcus and covers a wide zone, while on the medial surface, especially in the most anterior parts of the calcarine sulcus, its area is drastically reduced and it forms a narrow fringe only detectable by examining serial sections.

Area 19 - the *preoccipital area* - surrounds the occipital area (18) like a ring, as the latter surrounds area 17; it is also much reduced in size on its medial aspect. It is quite difficult to demonstrate, especially in the depths of the calcarine sulcus, so that it often seems doubtful whether that part of the area lying dorsal to the sulcus really unites spatially with the ventral part. In contrast, on the lateral surface it covers a wide zone and extends anteriorly over the interoccipital and parieto-occipital sulci. Its exact boundaries are just as little related to sulci as those of area 18.

In the course of the intraparietal sulcus a narrow band of similar structure to area 19 extends forwards sagittally. Elliot Smith puts this band in direct contact with the postcentral area and calls this whole strip running along the intraparietal sulcus the "visuo-sensory band". Further, Elliot Smith differentiates, in addition to the striate area, an area parastriata and an area peristriata, which correspond approximately to my areas 18 and 19; lateral to the latter he separates two small poorly differentiated zones, an *area temporo-*

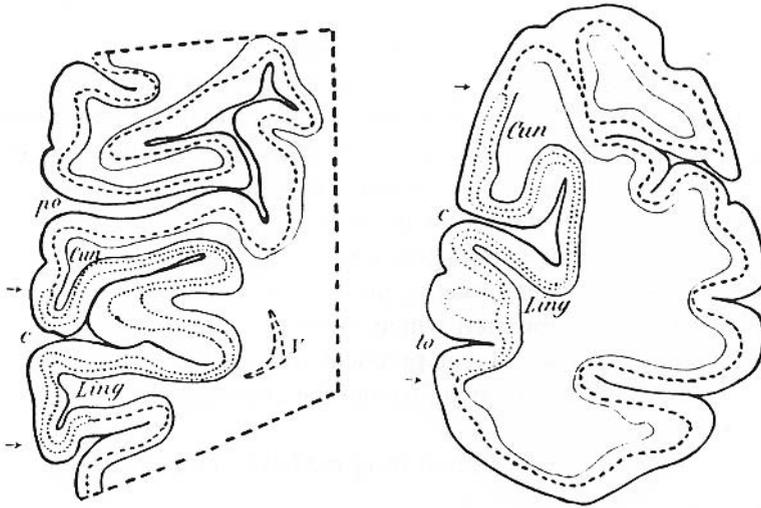


Fig. 87 and 88. Diagrams of coronal sections through the region of the calcarine sulcus. The double dotted line indicates the striate cortex; its extent is much wider within the sulcus than on the free surface.

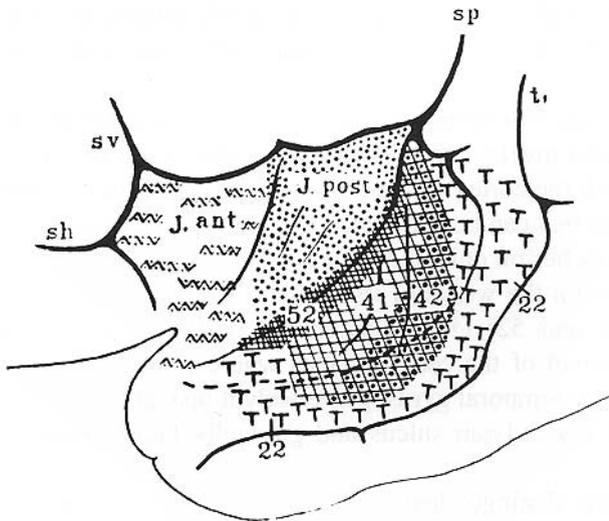


Fig. 89. Insular region and superior aspect of the superior temporal gyrus exposed. J. ant. = agranular anterior insular zone, J. post. = granular posterior insular zone, sp = posterior ramus of the Sylvian fissure, sv = vertical ramus of the Sylvian fissure, sh = horizontal ramus of the Sylvian fissure, t1 = superior temporal sulcus. On the superior aspect of the superior temporal gyrus are three areas: 52 = parainsular (*116) area, 41 = anterior or medial transverse temporal area, 42 = posterior or lateral transverse temporal area.

occipitalis and an *area parieto-occipitalis* (“often quite indistinguishable”).

Campbell only distinguishes next to the striate area a large occipital structural zone that he calls the “visuo-psychic area” in contrast to his visuo-sensory area (this author’s striate area).

Temporal region.

It also represents a morphologically well delimited and homogeneous region that, apart from its posterior border, is quite clearly circumscribed. It stretches from the posterior margin of the insula over the whole vertical extent of the temporal lobe to the rhinal sulcus or the temporal incisura (Retzius) and is thus the most voluminous region of the human brain after the frontal region. It is divisible into a large number of clearly different cytoarchitectonic areas of which certain, such as the transverse gyri and their surroundings, are extraordinarily characteristically structured and form a sort of subregion which, owing to their relationship to functional physiological centres, possess great practical importance. Those portions that directly abut the rhinencephalon (area 36) and the cortex of the temporal pole have a particularly variable structure.

We will undertake the description from medial to lateral on the brain map. (For area 35, see the Hippocampal region).

Area 36 - the *ectorhinal area* - lies, as its name implies, directly lateral to the rhinal sulcus and represents the first area of the neopallium adjacent to the archipallium, to which area 35 belongs. It possesses a markedly heterotypical architecture characterised by a distinct paucity of cells (and fibres) and also a massive development of the cells of layers V and VI, and forms a narrow band-like zone parallel to the outer edge of the rhinencephalon. Morphologically it represents the rostral extension of the lingual gyrus. I leave provisionally in abeyance whether the posterior portion of the zone delimited on our brain map as area 36 would be better differentiated as a “retrosubicular area”, as in many animals.

Area 37 - *occipitotemporal area*. - Such is the concept of a rather wide, but poorly circumscribed transition zone between the adjacent occipital and temporal cortices, which lies on the most posterior part of the temporal lobe, partly laterally and partly mediobasally. It is sufficiently distinct from the preoccipital area 19 as well as from the temporal area 20 that it is justifiable to differentiate it as an entity. Elliot Smith also proposed a specific structure denominated “area paratemporalis” in a corresponding situation.

Area 38 - the *temporopolar area* - corresponds in its position, as its name suggests, grossly to the tip of the temporal lobe, without any clear external delimitation; the field fuses laterally with the adjacent caudally situated areas 20, 21 and 22, and medially with area 36, and is characterised by its great cross-sectional depth.

Area 20 - the *inferior temporal area* - corresponds essentially to the inferior temporal gyrus and blends rostrally and caudally with the neighbouring areas 37 and 38 without sharp borders.

Area 21 - the *middle temporal area* - is situated approximately in the middle temporal gyrus, although its borders do not precisely follow the sulci that demarcate the gyrus; it also blends gradually, especially anteriorly and posteriorly, with the neighbouring areas.

Area 22 - the *superior temporal area* - is differentiated from the aforementioned areas in its cyto- (and myelo-) architecture more than these two areas between themselves. Together with the cortex of the transverse gyri of Heschl it forms a homogeneous structural region that can be contrasted with the other temporal areas. The superior temporal area encroaches on only about the posterior two-thirds of the superior temporal gyrus, and not even the whole of its free surface that is partially occupied by the deep areas (41, 42 and 52) (*117), as shown in Figure 89. Anteriorly it reaches approximately the level of the central sulcus where it climbs partly onto the medial surface of the superior temporal gyrus; posteriorly it just attains the level of the vertical terminal branch of the Sylvian sulcus and gradually blends with the supramarginal area.

Elliot Smith has distinguished localised areas that correspond precisely to my areas 20, 21, 22, 37 and 38; Campbell on the other hand includes the whole temporal lobe (except T1) with the inferior parietal area as a single field, his "Temporal area".

It has long been known that the transverse temporal gyri (Heschl) possess a structure that is different from the rest of the temporal lobe. More exactly, Campbell (1905) first differentiated a special field approximately within the confines of this gyral formation, the "audito-sensory area", contrasting it with the other temporal gyri, or "audito-psychic area". Elliot Smith, in agreement with this, writes (1907): "The two transverse gyri of Heschl represent a sharply-defined anatomical area of this cortex" (*118), but gives no precise topographical description of the region. Rosenberg describes a specific structure in the anterior transverse gyrus and without hesitation considers it possible to regard it as corresponding to "auditory cortex", in agreement with Flechsig.

In my sixth communication (1907) I myself differentiated two specific cortical types in the region of the gyri of Heschl, one anteromedially and the other posterolaterally. Recently I was able to divide off another band-like zone, medial to the medial area just before the beginning of the insula itself and parallel to its posterior margin, that I had earlier simply accepted as a mixed or transitional region. However, I was able to convince myself that it is distinguishable as a homogeneous area, well characterised from both the insular and the remaining temporal cortex by its specific structure.

The superior surface of the superior temporal gyrus thus includes, apart from area 22, the following three separate areas one after the other from medial to lateral: 1. the parainsular area, 2. the medial (anterior) transverse temporal area, 3. the lateral (posterior) transverse temporal area. After comes 4. the superior temporal area. Their mutual relations and their approximate extent are visible in Figure 89.

Area 52 - the *parainsular area* - forms a narrow band-like zone on the

superior bank of the superior temporal gyrus along the posterior margin of the insula and thus represents the transitional area between the temporal cortex and the actual insula. Anteriorly it extends almost to the limen of the insula, posteriorly it disappears gradually beneath its posterior margin near its posterior end.

Area 41 - the *medial (anterior) transverse temporal area* - corresponds approximately, but not precisely, to the anterior transverse gyrus and extends obliquely from anterolateral to posteromedial, descending gradually into the depths of the sulcus. It is bordered medially by the parainsular area from which it is sharply demarcated, while laterally area 42 forms an arc in contact with it. The transition to this last area is sometimes quite sharp, and in no way corresponds to the transverse sulcus, but lies in part in the middle of the apex of the anterior transverse gyrus. Both rostrally and laterally the area reaches beyond the anterior transverse gyrus.

Area 42 - the *lateral (posterior) transverse temporal area* - also extends obliquely from anterolateral to posteromedial over the superior bank of the superior temporal gyrus, but also lies on the free surface of the gyrus for a not inconsiderable distance. It forms a crescent along the lateral edge of area 41; caudally it extends deeply towards the posterior edge of the insula.

Insular region.

The insular cortex represents a well delimited, homogeneous region that is clearly differentiated from the surrounding regions thanks to an obviously recognisable specific laminar pattern (the claustrum). The region coincides approximately with the Sylvian fossa, but often extends over the margins of the circular sulcus of the insula and in particular may encroach partially on the under surface of the frontal and temporal opercula. The base of the insula also extends considerably beyond its anterior limiting sulcus, or at least the claustrum may be followed inwards as far as the orbital surface. One must therefore postulate a wider extent for the insula if one wishes to recognise the claustrum as an absolute criterion for identifying the insular cortex.

There are great difficulties in dividing it into individual fields, of which I described four in 1904. The most important aspect of differentiation within the insular cortex is to note that the insula divides basically into two separate halves along a line that is a prolongation of the central sulcus, one posterior and granular, the other anterior and agranular (Figures 36 and 37). Thus, like the central region, the insula is divisible according to the presence or absence of an inner granular layer into two totally different structural zones, the border of which lies in the prolongation of the central sulcus of Rolando but does not correspond exactly to the central sulcus of the insula. Figure 89 illustrates this relationship schematically. No other individual areas are illustrated. It should however be noted that on the edge of the anterior agranular half of the insula a cortical type of quite rudimentary structure can be distinguished, that I earlier called the olfactory portion of the insula. Also, the transitional zones

surface lying above the entire posterior half of the corpus callosum and whose homologue in primates, as we have seen, forms merely an extremely rudimentary zone next to the splenium. It is composed of the three characteristically organised and unequivocally identifiable areas 26, 29 and 30. The kinkajou occupies an intermediate position between the lemurs on the one hand and the rodents on the other in terms of size and histological differentiation of these areas. On the whole this region closely resembles that of the flying fox, except that in the latter the agranular retrosplenial area (area 30) is smaller and yet divisible into several subareas.

The **hippocampal region** also reveals a high degree of histotopical development that is manifested on the one hand by a marked expansion in area and on the other by a rich architectonic differentiation. It involves the absolutely largest surface area of all the brains studied so far and forms the major part of the very large *piriform lobe* that is clearly demarcated by the posterior rhinal sulcus. One can without difficulty distinguish the *presubicular area* (27), the *retrosubicular area* (48), the *parasubicular area* (49), the *perirhinal area* (35) and the *entorhinal area* (28). As in the rabbit and the flying fox, the last of these can be separated into two clearly different subareas, the medial and lateral entorhinal areas, as is also indicated on the map. Area 49 inserts itself between areas 27 and 28 to form a narrow dividing zone; in my material it has only also been demonstrable in the flying fox, the rabbit and the hedgehog, but in these remains inferior in size to that of the kinkajou.

The **olfactory region** forms approximately the anterior third of the piriform lobe and the largest part of the anterior olfactory lobe; it thus occupies a very large surface area, as in the flying fox, the rabbit and the ground squirrel, and is only exceeded in size by that of the hedgehog. Dorsally its border coincides with the rhinal sulcus, caudally it fuses gradually with area 28, and it reaches as far rostrally as the olfactory bulb. Within the olfactory region the specific rudimentary cortical formations of the *prepiriform area* (51), the *amygdaloid nucleus* (A) and the *olfactory tubercle* (Tol) can be distinguished.

VI. Rodents (rabbit and ground squirrel). (Figures 106-109). (*98)

I have completed the study of the cerebral cortical field organisation of two rodents, the rabbit and the ground squirrel and summarised the results in maps. Isolated blocks from other families have also been examined. The description of localisation will be restricted to the rabbit brain, and only essential new findings will be considered. Any differences in the ground squirrel will be mentioned.

Little more need be said about the majority of the regions beyond what has already been discussed in relation to the flying fox. The main difference in surface topography in both rabbit and ground squirrel compared with higher mammals resides in the extraordinary expansion of the surface area and the rich differentiation of the retrosplenial region, the hippocampal region and the olfactory region that exceed even those of the flying fox. The retrosplenial

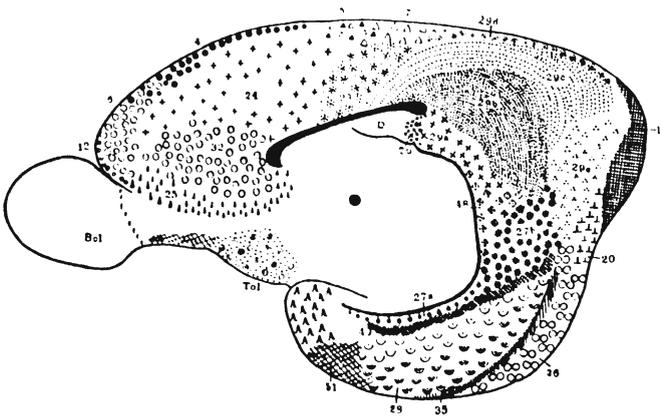
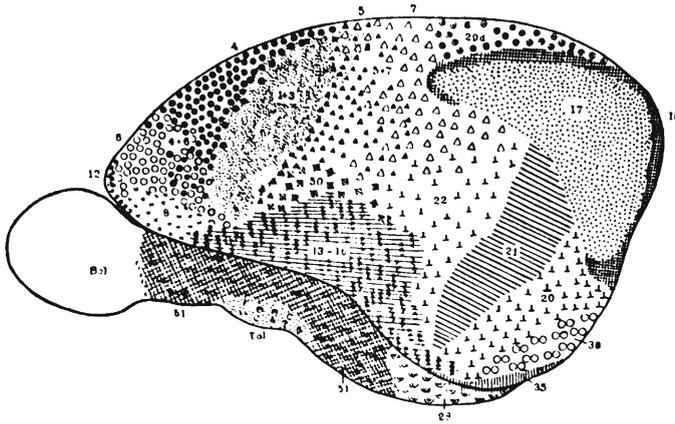


Fig. 106 and 107. The cortical areas of the rabbit (*Lepus cuniculus*). 2:1.

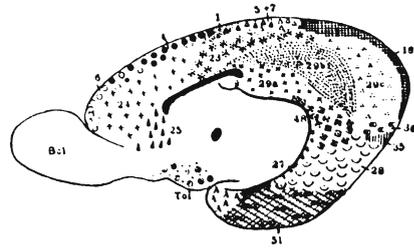
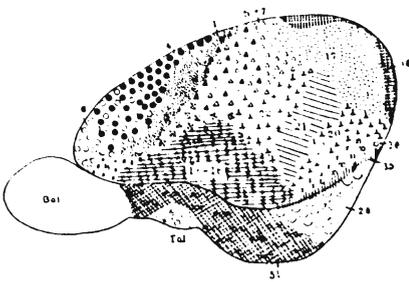


Fig. 108 and 109. The cortical areas of the ground squirrel (*Spermophilus citillus*). 2:1.

region alone in the rabbit ¹²⁾ can be divided into six different areas.

The **precentral region** lies very close to the frontal pole and stretches mainly horizontally along the superior margin of the hemisphere. It scarcely encroaches on the medial side as the cingulate region occupies most of the space above the corpus callosum. The laminar pattern of both areas 4 and 6 that characterises the region in primates is also suggested here, but actual separation of the areas can only be accomplished with difficulty. Therefore these areas are drawn as broadly superimposed in the maps, especially in the ground squirrel (Figures 108 and 109). At the frontal pole, yet another small field with a specific structure and shaped like an end-cap, area 12, but I cannot detect it in the ground squirrel. Whether this is the homologue of area 12 in the marmoset and the kinkajou I dare not decide in spite of its similar position.

Without doubt the whole agranular frontal cortex of both rodents (except perhaps area 12) belongs to the precentral region. There is no granular frontal region.

Concerning the **postcentral region** and the **parietal region** reference can be made to the description of the flying fox. They represent a large combined zone that is somewhat different in structure in its posterior portion from its anterior and, although certain features of the clearly separate individual areas of higher animals are revealed, they do not justify a precise spatial segregation into areas. In the brain maps the equivalents of areas 1, 5 and 7 are drawn with considerable overlap. (For areas 1 and 4 see Figure 63.)

The **occipital region** lies almost entirely on the lateral surface; it has obviously been forced from the medial side over the occipital margin of the hemisphere onto the lateral side by the overwhelming development of the retrosplenial region.

Once again the striate area (17) is the major field, as we saw in Part I, although in a considerably modified and simplified form (Figure 76). Caudally a crescent-shaped field borders area 17, that we have indicated as area 18, without wishing to insist upon its homology with the occipital area of higher mammals. (For area 17 see Figure 76.)

The **insular region** has undergone an even greater expansion than in the flying fox and the kinkajou. Due to the absence of any sulci it is entirely on the free surface which allows an easy estimation of its total area. It occupies at least a third of the vertical height of the hemisphere and its rostrocaudal length amounts to more than half that of the hemisphere. Ventrally it is sharply separated from the olfactory lobe by the rhinal sulcus; its other borders are indistinct, for its main architectonic feature, the claustrum, gradually merges with neighbouring zones. Even here a caudal granular and a rostral agranular subregion can be distinguished, each with two individual areas. Whether area 50, lying at the upper border of area 13, should also be counted in the

¹²⁾ Zunino has been able to demonstrate a myeloarchitectonic zone corresponding to each of the cytoarchitectonic areas that I have distinguished. - Journal f. Psychol. u. Neurol., XIV, 1909. (*141)

insular region I cannot decide for the present; I am equally doubtful about the allocation of area 8, that also demonstrates a quite specific and individual cellular structure, to any of the regions under consideration.

The **temporal region** is composed of four individual areas (20, 21, 22 and 36) and is characterised, as in the flying fox, by quite indistinct boundaries with the parietal and occipital regions. Areas 20, 21 and 22 are not very specifically differentiated and there are gradual transitions between them, but on the contrary the ventral areas 35 and 36, that lie across the rhinal sulcus, are differentiated very characteristically and it can be accepted with certainty that area 35 corresponds to the perirhinal area of man and area 36 to the ectorhinal area. Area 35, lying partially lateral to the rhinal sulcus and therefore in the temporal lobe, is better considered with the hippocampal region judging from its structure.

In the **cingulate region** of the rabbit, areas 23, 24, 25 and 32 of the flying fox are again found, but in the ground squirrel only 23, 24 and 25 are sure. As to the small stripe-like zones that surround the splenial sulcus in the flying fox (areas 30a, 30b, 31a and 31b of Figure 103), demonstrable homologues are absent in both the rabbit and the ground squirrel. There is little of significance to say about the position of the individual areas, except that area 25 extends very far rostrally, as far as the level of the frontal pole, unlike the situation in the previously mentioned animals.

The **retrosplenial region** is very differently constructed in the two closely related animals, the ground squirrel and the rabbit. Whereas in the former only four areas (26, 29a, 29b and 30) are distinguishable with certainty, one can clearly demarcate six structurally different areas (26 and 29a-e) in the equivalent region of the rabbit. Of these, area 26 corresponds to the ectosplenial area, while areas 29a-e must be considered as produced by further differentiation of the granular retrosplenial area of other species on account of their related structure. Thus area 29 has here differentiated into five subareas with specific structural features, although all (except area 29e) show marked evidence of being interrelated (Figures 65 and 66). Consequently the extent of this combined zone is unusually great. The retrosplenial region of the rabbit includes the whole medial surface of the occipital lobe, that is to say those extensive zones that in higher mammals belong to quite different cortical formations, notably the occipital region with the striate area, and which, looked at purely externally, are represented in man by the cuneus, the lingual gyrus and, partially, the precuneus. Its area in the rabbit represents at least about a tenth of the total cortical surface, whereas the homologous region in man cannot amount to any more than one three-hundredth of the surface. A cortical type corresponding to the agranular retrosplenial area (area 30) is absent in rodents. Area 29c takes on a peculiar aspect, especially due to its marked poverty in fibres (Zunino). Whether it corresponds to area 30 of prosimians is very questionable, but in any case it contrasts sharply from it cytologically (*142).

The **hippocampal region** also reveals an extraordinarily rich differentia-

tion. In the ground squirrel its predominant feature is its relative size, corresponding to the marked development of the piriform lobe; on the other hand the number of areas is greater in the rabbit. We distinguish in the latter one more area than in the flying fox, in that another special cortical type of related and yet quite specific structure is recognisable at the caudal end of the presubicular area (27), for which we propose the name *ectosubicular area* (27b). This area encroaches further along the hippocampal sulcus between areas 27 and 48, thus forming a sort of transition zone between them.

The other areas, 27, 28, 35, 48 and 49, are arranged in similar fashion to those of the flying fox and nothing essentially new can be said about them, except that it is worthy of note that area 28 demonstrates two clear architectonic variations so that it is justifiable to distinguish a *lateral entorhinal area* (28a) and a *medial entorhinal area* (28b) that are spatially sharply separated. In the ground squirrel no sure homology can be established for either area 49 or 27b, and even a similar division of area 28 cannot be accomplished easily.

The **olfactory region** of the rabbit, and even more so of the ground squirrel, is relatively more extensive than in the flying fox, but is likewise composed of three individual fields: 51, the amygdaloid nucleus (AA) and the olfactory tubercle (Tol). Area 51, or the *prepiriform area*, is of unusually large size, especially in the ground squirrel. The amygdaloid nucleus and the olfactory tubercle emerge very characteristically as circumscribed cortical fields in the rabbit and ground squirrel thanks to their atypical (heterogenetic), rudimentary cellular structure.

VII. The hedgehog (*Erinaceus europaeus*). (Figures 110 and 111).

The brain of the hedgehog occupies a special place in my research material in terms of its cortical architectonics as well as in the organisation of the cortical surface. The arrangement of the cellular laminae and the field distribution are so completely altered that great difficulties are encountered in trying to relate them to those of higher species. Only the study of intermediate situations and comparison with numerous other groups clarifies the organisational plan. This is an example of the importance and superiority of comparative anatomical methods. Anyone wishing to investigate the brain of the hedgehog or other insectivores in isolation without knowledge of the cortical structure of other orders, and understand their localisational organisation, would fail at the task. The only way to recognise the general principles of mammalian cortical structure is by means of ample comparative anatomical material comprehending the whole class. Therefore I consider the histological cortical parcellation of the insectivores proposed by Watson as generally erroneous, in spite of many correct isolated findings.

A characteristic of the hedgehog brain is the unusually large archipallium. The piriform lobe and the anterior olfactory lobe together account for between half and two-thirds of the total cortical surface. Corresponding to the massive expansion of this part of the brain one also finds very extensive heterogenetic