CONNECTIONS OF THE CEREBRAL CORTEX

I. THE ALBINO RAT. A. TOPOGRAPHY OF THE CORTICAL AREAS

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FIVE TEXT FIGURES AND EIGHT PLATES (EIGHT FIGURES)

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INTRODUCTION

Of all of the main divisions of neurological study the connections of the cerebral cortex are perhaps least advanced at this time. The spinal cord and the brain stem are relatively well understood; being smaller in size they are more easily sectioned; and having marked local variations in structure, points may be more easily identified. Until recently the thalamus and hypothalamus were neglected, probably because of their larger size and lack of striking local variation in structure. It is now known that most of the thalamic nuclei receive specific afferents and project to specific regions of the cerebral cortex and that there are few interthalamic or other connections. This has unexpectedly simplified the problem of diencephalic functions but it has shifted it to the cerebral cortex.

The study of the cerebral cortex is hampered by an intensification of the difficulties which have made the thalamic study more recondite than brain stem or spinal cord investigations. The cerebrum is much more massive than the diencephalon, discouragingly void of easily perceived variations in structure, either of the cortex or of the medullary centers and in many animals is thrown into a welter of irregular convolutions which make it impossible to obtain comparable sections in any one conventional plane. Local divisions are, however, discernible, but the study of them has constituted a specialty in itself. Unfortunately for the progress of our knowledge of the connections it is necessary first to be able to identify the cortical areas with which we are working. Moreover, in the case of any of the commonly used experimental animals it is necessary to work this out de novo. Only then can one make a proper experimental study of cortical connections in anatomical material. Connections determined and any conclusions based on them must be referred to the cortical areas, which constitute functional units, as has been so abundantly shown, particularly in the case of the larger brains. Even at this point the major difficulties are not ended, for the problem remains of recording, visualizing and localizing the findings
in any one example in terms of the general brain; and a pictorial representation of these findings in such a way as to be comprehensible demands special planning.

With practical difficulties in mind, and desiring to know more of the connections and mechanisms of the cerebral cortex, this investigator has decided to begin the study of this problem with a small and presumably simplified brain, that of the albino rat. Numerous minute lesions have been made in all parts of the cortex. These have been traced by means of reconstructions to portray the resulting degenerations from these lesions. However, before such findings can be understood it is necessary to have an accurate plan of the topographical distribution of the cortical areas and a clear picture of the normal structure of each. This has been the object of the study here reported. The observation and synthesis of the connections revealed by the experimental work will be the subject of a later paper.

It seems peculiar that the architecture and topography of the cortical areas of the albino rat have never been investigated. The rabbit and the mouse and Mus decumanus have been studied, but irrespective of whatever appraisal may be made of the accuracy of the findings these results cannot be directly applied to the detailed study of the albino rat. Particularly is this true when one is making lesions of a millimeter diameter accurately placed with a stereotaxic machine. The design of such a machine and the localization of the various parts of the brain in terms of specific coordinates are described in another place. The object of this paper is merely to determine the identity and local habitation of the cortical area units, to establish their normal structure, and to make it possible to do investigation on cortical mechanisms and connections with the security of an accurate knowledge of the position and identity of the units of which it is composed.

The material used in this study consists of the brains of normal albino rats, sectioned in celloidin at 40 μ, in various planes, conventional and unconventional, and stained by thionin and the Weil myelin stain. The main evidence on which
this paper is based consists of a critical series of cross sections of an adult albino rat brain, with alternate sections stained for cells and fibers. An atlas showing the extent of each cortical area visible on every fourth section was prepared and this was used as a basis for building a wax plate reconstruction. This reconstruction shows the external form of the cortex of the right cerebral hemisphere with the topography of the cortical areas marked on it.

In studying a series of cross sections of the cerebrum, even in the case of small lissencephalic animals, only a part of the cortex is cut in radial section. This is immaterial in a mere partitioning of the cortex into areas. Sections oblique to the radial plane cannot be used when characterizing or analyzing cortical areas. For this reason a number of brains have been oriented in such a manner that every part of the cortex is sectioned in a truly radial direction in one or other example.

The report of this investigation will be divided into two parts, which form separate papers. The part A, forming the present paper, is concerned with the identity, topography and relations of the several areas. Part B deals with the pattern, lamination and distinguishing features of each of the areas and correlates the appearances of cell- and fiber-stained sections. These two aspects should be considered together, as they are interdependent.

FRONTAL REGION

The frontal region of the rat is, of course, small when compared with higher mammals, nevertheless it includes six areas. It forms a rostral cap to the cerebral hemisphere but does not have an equal extent on all aspects. Dorsomedially it extends half way back. Much of this projection is formed by area 4. Passing laterally it rapidly shortens, until at the lateral edge it only extends about one quarter of the way caudally. Basally, it is limited by the rhinal fissure and medially it is non-existent, as the cortex here is included with the cingular region. It comprises areas 10, 6, 4, 8, 8a and 11.
CORTICAL AREAS OF ALBINO RAT

Area 10: area frontopolaris (FD) \(^2\) (fig. 2, 3, 6, 11). This constitutes the frontal polar area or region and cannot be further homologized with Brodmann's designations since, as has been shown by others, he has inaccurately subdivided the frontal area. It perhaps corresponds to the areas included in FD and FE of von Economo. This region occupies the entire dorsal aspect of the frontal pole from the tip to about one quarter of the way back.

Area 6: area precentralis (agranularis) (FB) (fig. 2, 7, 11). This area, corresponding perhaps to the premotor area, is in general quite similar in structure to area 10. It occupies a narrow strip lateral and caudal to area 10 but does not participate in the formation of the frontal pole at all, beginning about one-quarter back and running a little further caudally than area 10, becoming shifted medially to occupy for a short distance the dorsomedial angle left vacant by the disappearance of area 10.

Area 4: area gigantopyramidalis (FA) (fig. 2, 7). This area is a thin but distinct strip beginning rostrally between area 6 and the parietal cortex but placed more caudally in a series of transverse sections. When area 6 disappears caudally, area 4 is shifted medially to the dorsomedial angle and broadens. Its caudal end is half way through a series of transverse sections of the cerebrum.

Those investigators who have identified functional cortical areas exclusively on the basis of cell studies might have made their analogies better if they had given more attention to connections. The extent of the area from which distinct somatic movements can be elicited in the rat does not coincide with area 4, according to Lashley ('21), but includes the regions occupied by 10, 8, 6 and 4, the regions of the body being distributed in rostro-caudal order within the entire frontal lobe. Unpublished Marchi studies have shown that all of the frontal areas send numerous fibers into the pyramids.

\(^2\)Letters in parenthesis refer to von Economo's designations of comparable human areas.
Perhaps the shift to area 4 is a later specialization, and the extensive origin of the pyramidal tracts is consonant with the motor activities of the premotor areas observed in higher mammals after destruction of area 4.

*Area 8: area frontalis intermedia (FC) (fig. 3, 6).* Included in the frontal region must be the area designated by both Brodmann and Rose as area 8. Possibly it conforms better to the human area 47. It extends to the frontal pole and along the entire frontal region forms the ventrolateral quadrant. Above, it is adjacent to 10. Below and medially are areas 11 and 51b. As it extends caudally, however, it becomes reduced from above by the forward end of area 2 of the parietal region. It disappears at a level nearly one-third through a transverse series of sections. Basally this region forms the dorsal lip of the rhinal sulcus, but in the middle of its extent the structure of this lip is markedly altered. To this modified region the designation 8a is here given.

The identification of area 8 seems to have been confused by Rose in the mouse. In his figure 5, he has marked the area here designated as 8 by 13–16. It is uncertain whether or not he means our area 8a to correspond to 51b; it would seem not in his figures 7 and 8. In plates 1 and 2 he makes no distinction between 8 and 8a. Area 8 is directly rostral to 13 and 16 in Rose, but when 8a is traced backward in this series it seems to have the same structure through the entire region designated. The insular region 13 to 16 comes in dorsally at the more caudal part of 8 and its structure contrasts sharply with that of 8. 8a, however, loses its identity some distance before 8 disappears.

There are two areas on the basal surface of the frontal lobe (fig. 3) in contact with the olfactory bulb. Thus they fill in the sector between areas 8 and 25. The rostral one seems to be an unspecialized type of frontal cortex and is here designated...
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Figure 1
as area 11. The other has the uniform granular appearance of cingular cortex. It will be called area 25a. The identity of these areas can be recognized properly only in sagittal section; the grain is so oblique here that in transverse sections parts of two areas occupy the same swath. This area was missed by Rose.

**Parietal Region**

The parietal region in the rat is well defined and quite uniform. It occupies approximately the regions covered by the parietal bones, i.e., the dorsolateral middle third of the cerebral cortex. It is bordered anteromedially by the frontal region, posteriorly by the occipital, and ventrally by the insula in front and temporal region behind. Six parietal areas may be recognized in the rat (3, 1, 2, 7, 39, 40). The differences between them are not striking but are definite. All of the parietal areas have structural similarities so it is easy to decide whether a given area belongs to this region.

*Area 2: area postcentralis caudalis (PC)* (fig. 2, 3, 4, 7, 8) dominates the parietal cortex and may be taken as the prototype of the parietal pattern. Rostrally it occupies the lateral wall of the cerebrum and extends well forward towards the frontal pole, abutting directly on areas 10 and 8. It occupies a wide sector of the cortex and extends back a great distance but is gradually reduced ventrally by area 40. It is quite uniform in structure in spite of its large size, although less so than area 17. Local modifications exist but it has been impossible to reduce them to any system, except for the ventral half of the middle third of its extent, recognized as area 2a. Whether it constitutes a separate area will not be known until the results of specific lesions are analyzed.

*Area 3: area postcentralis oralis (PA).* The specialization of parietal cortex which is immediately adjacent to the motor-area is designated here as area 3, appropriately, it seems (fig. 2, 11). It forms a squarish region of middle size in the middle of the dorsal surface. Laterally and caudally it is bounded by parietal cortex (2, 7).
Area 1: area postcentralis intermedia (PB, PD) forms a short, narrow strip between 3 and 2 (fig. 2, 8). This is the smallest of the parietal areas and resembles the structure of the adjacent cortex except for concentration of cells in layers iv and vi, where they are noticeably sparser. Thus, except
for the pyramidal cells in \( v \) the whole cortex here has a uniform appearance. This decrease in cell concentration is a reciprocal of the increase in myelinated fibers visible in Weil preparations. It would hardly merit separation as a separate area on the basis of structure alone, but it corresponds so well to von Economo's area PB, which equals Brodmann's 1, that it may be shown to have some significance. Thus, the sequence 3-1-2 characteristic of man can be upheld in the rat, since the areas 3, 1 and 2 represent perhaps the principal projection area of the somesthetic thalamus in man. The sector of the brain designated here as 3-1-2 in the rat has a similar relation to the thalamus. Rose designates as area 7 much of the caudal part of area 2 as here given. The topology of the projection from the thalamus will test this.

*Area 7: area parietalis superior (PE)* (fig. 2, 4). Caudal to the 3-1-2 complex is another area of parietal type. On the basis of its relations it is regarded as area 7. It is sandwiched between the dorsomedial part of the primary parietal cortex and the occipital region, and these are the relations of 7 in higher forms.

*Area 40: area supramarginalis (PF)* (fig. 2, 3, 4, 8) is a triangular area, placed below the caudal part of 2, above the insular cortex and in front of the auditory cortex. As the second portion of this paper will show, this cortex is of parietal type, but generalized. A parietal area placed here would be best designated as the germ of area 40. In higher forms the auditory cortex (41) lies inferior to 40, rather than behind, as it does in the rat, but this shift is due to the development of the temporal lobe which causes a forward shift of the areas on the caudolateral part of the cerebral hemisphere.

*Area 39: area angularis (PG)* (fig. 2, 3, 4, 9). The remaining area of the parietal region is more caudally placed than the other components. It fills the triangular chink between the more rostral part of the parietal region, the auditory receptive cortex (41) and the area occipitalis (18). In the cell maps of higher forms the only area which meets these conditions is 39. As will be shown in the second section of
Fig. 3 Rostro-ventro-lateral view of right cerebral cortex with areas differentiated.
this paper, this area here meets the conditions required as being associative between the main sensory areas adjacent to it, so may fairly be regarded as forming the germ of the large parietal association area and the designation area angularis (39) is given it.

TEMPORAL REGION

The temporal region comprises two areas, the large auditory receptor area 41 and an intermediate area between this and the so-called insular area, which is here designated area 20, though it perhaps represents the germ of the temporal areas 20, 21, 22 and possibly more. The temporal areas have a late development phylogenetically and it is not surprising that they are in such a rudimentary state in the rodent.

*Area 41*: *area auditoria* (TD) (*fig. 2, 4, 9, 10) occupies a round area at the greatest lateral prominence of the cerebrum in the caudal third of a transverse series of sections. It was not recognized in the rodent, either by Brodmann or by Rose. They regard as temporal cortex the entire lateral prominence of the cerebrum between the insula and perirhinal areas below and the somesthetic and striate areas above, dividing it into 4 oblique bands which they designate as 36, 20, 21 and 22 from below upwards, making no allowance for auditory receptive cortex. The area here designated as 41 is known to be auditory receptive cortex, since degeneration was found to conform to this cytoarchitectural area after a specific lesion of the auditory radiation as it left the medial geniculate body. The cortex containing degenerated fibers was shown to conform neatly to the areas which so clearly represent the unit in both cell and fiber preparations. We believe this sort of evidence takes priority over any amount of purely cytologic study, particularly when, as we have already seen, histologic criteria cannot be projected indiscriminately down the scale of mammals.

*Area 20*: *area temporalis*. In contrast to the great development of the auditory area the remainder of the temporal lobe is very poorly developed. It includes the narrow strip between
the auditory area proper and the cortex immediately adjacent to the rhinal fissure here designated area 20, area temporalis, and also the triangular area immediately caudal to area 41, here designated area 36. It is difficult to understand how Brodmann and Rose could have relegated such large areas to 20, 21 and 22 when it is well known that the temporal lobe is the latest of all to develop and no area had been assigned as auditory receptive cortex.

*Area 36: area ectorhinalis (TF).* Immediately caudal to the auditory cortex is an undifferentiated cortical region which is here designated area 36, area ectorhinalis (TF) (fig. 4). It is fairly large and fills in the triangular space between the occipital and perirhinal regions as they approach each other.

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**Fig. 4** Dorso-lateral-caudal view of right cerebral cortex with areas differentiated.
toward the occipital pole. It is best seen in horizontal sections, since it faces obliquely caudally. It should be grouped with the temporal areas, but whether it corresponds more closely to 36 or 37 is a question. From its position as here delimited homologization with 37 should be more appropriate. Brodmann and Rose have recognized a 36 and not a 37 in the rodent, but their 36 forms a long strip just above 35 and not a broad area.

**OCCIPITAL REGION**

The occipital region consists of the visual receptive center, 17, and its satellite areas 18, 18a and 36. The rhinal area climbs up on the caudal aspect of the occipital lobe, but, strictly speaking, does not belong to this section of the brain. This region has considerable uniformity of structure and has certain characteristics of its own. It is always highly granulous and there is little differentiation of the various layers. Large pyramidal cells are found in only one location. There are relatively few myelinated fibers in this cortex. It is bordered caudally and medially by the retrohippocampal lobe, ventrally by the temporal lobe and frontally by the parietal lobe.

**Area 17: area striata (OC)** (fig. 2, 4, 9, 10) is a large pyriform field forming a large part of the posterior third of the dorsal aspect of the hemisphere. It has a uniform structure and a sharp border separating it from area 18. In spite of the fact that it does not have the highly stratified development found in the striate area of the higher mammals its extent can always be determined.

Area 17 is bordered medially by a special type of cortex termed **area 18, area occipitalis (medialis)** (fig. 2, 8–10) (OB), since it conforms to the position of the area of similar designation given by Brodmann and by Rose. Its rostral and caudal extremities correspond well with those of area 17. It has the form of a longitudinal strip, and lies near the median plane, but separated from the medial surface by 29c, except that it
forms the caudo-medial angle of the cerebrum. It is longitudinally coextensive with 29c as well as 17.

On its lateral and caudal aspects area 17 is bounded by a more generalized type of occipital cortex which has an essential uniformity of structure. Now, Brodmann and Rose carried the temporal areas up to the visual receptive area in

Fig. 5 Ventro-caudo-medial view of right cerebral cortex with areas differentiated.
rodents, though in all higher forms Brodmann recognized at least one occipital zone (18) lateral to area 17, and generally another (19). In rodents they found area 18 only medially. In an attempt to effect a compromise between Brodmann's designations of this region we here refer to it as 18a, area occipitalis (lateralis) (fig. 2, 4, 9, 10), but it must be understood that structurally it has no relation to the strip medial to area 17, here designated as 18.

INSULAR REGION AND RHINAL SULCUS

It is difficult to say just how far the insula should extend in a rostral and caudal direction, and it is somewhat questionable to what extent the region ordinarily assigned to the insula in rodent brains really corresponds with the insula of the brain of higher forms. Regarding the insula as coextensive with the cortex which overlies the claustrum, though a convenient criterion, is a specious one. The only definite sulcus on the rat brain is the rhinal sulcus, which runs the entire length of the brain and lies rather uniformly at its ventrolateral quadrant, though it turns dorsally at the occipital region to end at the occipital pole. Broadly speaking, the area insularis ventralis, area 13 (fig. 2, 3, 7, 10), may be taken as occupying the middle two quarters of the region of the rhinal fissure, yet the cortex bordering the rhinal fissure at all points has a certain amount of uniformity in its character and has modifications which take place abruptly at this fissure and are possibly the cause of it.

Area 14: area insularis dorsalis (IA) (fig. 2, 3, 7, 8) forms a long strip below parietal region 40 and above the portion of the insula invaded by the rhinal fissure (13). This area appears between parietal area 2 and frontal area 8 rostrally, and at the beginning of the temporal region caudally.

CINGULAR REGION

The cingular region is the dorsal subdivision of the limbic lobe of the brain. In spite of an extreme diversity of structure, this limbic region is recognized as a loosely organized
unit because of the combination of olfactory and hippocampal connections with connections to the somatic cortex. The ventral subdivision receives the primary olfactory tract, but the cingular area receives very few direct olfactory connections, though it has strong, well marked associations with the hippocampal gyrus, which is not necessarily entirely olfactory. The cortex of the cingulum is basically of the six-layered type, though it may be considerably modified, that is, it is allocortex. That of the ventral portion of the limbic lobe is for the most part isocortex, so on structural grounds the primary division mentioned is a reasonable one.

Area 24: area cingularis anterior ventralis (LA) (fig. 5, 6, 7) occupies most of the medial aspect of the frontal pole rostral to the genu of the callosum and extends over the top of the callosum directly in contact with it for a short distance.

Area 32: area cingularis anterior dorsalis (area praelimbica of Rose) (fig. 5, 6) is a subdivision of the cortex of the cingular type. It lies ventral to 24 immediately in front of the callosal genu and blends with that area. Just below 32 and immediately above the pyriform cortex is the tiny area 25, area subgenualis (FM) (fig. 5, 6). It extends forward, somewhat transformed, as a tenuous strip along the ventromedial shoulder of the frontal pole.

On the basal aspect of the frontal lobe, just above the line of junction with the olfactory bulb is a small area for which provision must be made. It is not visible in the reconstruction but may be visualized as caudal to 11, medial to 8, lateral to 25 and joining abruptly with 51a in the rostral extreme of the rhinal sulcus. Its structure shows a marked resemblance to the undifferentiated cingular cortex of areas 32 and 25, so it is here termed 25a. Rose seems to confuse it with 51a.

Area 23: area cingularis posterior ventralis (LC2) is a small region lying on the corpus callosum directly behind area 24 (fig. 5).

Areas 29b and 29c area retrosplenialis granularis b and c (LE) (fig. 5, 8, 9, 10) always easily identified and easily distinguished from one another, occupy the caudal half of the
supracallosal region and extend beyond the splenium as far as the occipital surface. Area 29c lies immediately dorsal to 29b, occupying the dorsomedial shoulder of the cerebral hemisphere all the way back to where the occipital cortex begins to diverge from the median plane.

It is interesting to note that each cingular area exactly corresponds to an adjacent area of more definitely somatic cortex. Thus 24 is contiguous to 10 and 6, 23 next to 4, and 29 related to 18.

PYRIFORM REGION

The ventral part of the limbic lobe occupies the olfactory bulb and the entire ventral aspect of the cerebral hemisphere with the exception of a part occupied by the amygdaloid nucleus and extends dorsally along the posteroinferior aspect of the occipital lobe. In general it includes the area between the rhinal sulcus and the di-telencephalic boundary. Most of this constitutes the pyriform cortex and is lumped into area 51, area pyriformis, although 51 can be subdivided into some 5 quite distinct areas.

Taking now the various divisions of 51 in order, we will begin with 51a (fig. 3, 5-9). This cortex forms the principal substance of the stalk of the olfactory bulb. It is present on the entire circumference of the olfactory bulb so that at the base of the bulb it forms a ring but farther distally forms a C whose limbs nearly meet, the open part of the C being filled by the olfactory bulb formation, 51g. When the bulb joins the cerebral hemisphere proper 51a is continued on the ventral aspect. This area continues over more than two-thirds of the length of the brain, always keeping an extreme ventral position. It is unique among the cortical areas in being covered by a large myelinated tract rather than merely a fibrous lamina as the cingular areas are. This is the olfactory tract. Caudally, it expands somewhat and thins, but rostrally the tract is large and oval, indenting the cortex.

Area 51b (fig. 2, 3, 7-10) lies immediately lateral to that part of 51a caudal to the olfactory bulb but it extends some-
what further caudally, lying lateral to the cortical amygdaloid nucleus and thus nearly to the occipital pole. It is replaced occipitally by area 28. Rostrally it forms the ventral lip of the rhinal sulcus, but becomes increasingly narrower until finally it is only a few cells wide, nevertheless it still shows its characteristic pattern. This is one of the most eloquent arguments for specificity of structure of cortical areas.

51e (fig. 5) forms a small area in the transitional region between the anterior junction of the cingulate and ventral olfactory areas. It lies between areas 25 above and 51f and the olfactory tubercle below. Area 51f is another very small one forming the ventromedial quadrant of the caudal part of the olfactory bulb where it is joining the cerebrum. Area 51g forms the anterior part of the olfactory bulb on all aspects and continues backwards medially farther than on any other aspect.

The olfactory tubercle is not usually considered a part of the cortex proper. Nevertheless, it has a heavy outer cellular lamina continuous with that of 51a. The olfactory tubercle begins at the same level as the genu of the corpus callosum and continues caudal for several mm, always forming a ventromedial extreme of the C-shaped section of the cortex as far as it extends.

The designation 51h, nucleus of lateral olfactory tract, may be applied to the minute ovoid compact group of dark cells at the caudal end of the olfactory tubercle. Though minute, it is striking in appearance, even in fiber preparations, as it sends an intensely black, compact funiculus dorsally as component 1 of the stria terminalis. It was described and illustrated by Loo in the opossum ('31).

RETROHIPPOCAMPAL REGION

The pyriform areas 51a–h occupy almost the entire basal aspect of the cerebral hemisphere below the rhinal sulcus, except along the medial edge where non-cortical structures exist (olfactory tubercle, amygdala). They are succeeded caudally by another group of areas (35, 28) which in the rat
are placed for the most part on the caudal aspect of the hemisphere, of which they occupy the greatest part. They are in turn succeeded by the presubicular areas 49 and 27 and finally by the subiculum, fascia dentata and hippocampus proper. They may be together regarded as the retro-hippocampal region. Their inclusion as a unit is only a convenience in low mammals, but in higher forms and in man all these areas are distorted into long, narrow strips concentric with the hippocampus and are always considered together. In describing these areas we will begin laterally and continue medially, i.e., toward the hippocampus.

The first of these is area 35, *area perirhinalis* (*HB, TH*) (*fig. 4, 12*), which occupies the continuation of the rhinal fissure on the occipital surface of the cerebrum. It forms a narrow strip whose surface is slightly depressed, extending halfway up the caudal aspect of the hemisphere. Lateral to it is the undifferentiated occipital cortex, 36, and medial to it is 28b, immediately to be considered.

28b, *area entorhinalis b* (*HA*) (*fig. 4, 5, 12*) lies immediately medial to the rhinal fissure, in other words it adjoins area 35 and forms a strip lying in an oblique but almost frontal plane. Its position is best visualized in horizontal sections where it may be seen to occupy most of the caudal aspect of the hemisphere.

*Area 28a, area entorhinalis a* (*HB*) really differs considerably from 28b in appearance and in cell type, but the apparent triple layered arrangement can be followed clearly from 28b. This cortex lies medial to 28b; hence in most of its extent exactly at the caudal sharp edge of the cerebrum. Thus, it could be missed in transverse sections.

The caudal pyriform areas are succeeded medially by a group which may be regarded as transitional to the hippocampal formation. Following Lorente de Nó's terminology they constitute the presubiculum and prosubiculum (area 28 forming the parasubiculum). Much detailed analysis has been made of the subicular and hippocampal regions by Cajal and
by Lorente de Nó, not because this region is any more complicated than other cortical regions, but rather because it is relatively simpler and allows or offers some hope of interpretation in Golgi and other preparations. We will continue to proceed from laterally to medially in the morphological sense.

The outermost of these band-like areas concentric with the hippocampus is area 49, area parasubicularis (HC) (fig. 5). It is the most elusive of all the cortical areas in transverse series, as it is a narrow strip whose long axis is vertical and thus it occupies only a few sections; moreover, it is placed just at the sharpest part of the occipital tuck, where all areas are difficult to trace. In horizontal sections it is very distinctive, though small (fig. 12). It is wedge-shaped in cross section, so that its base is very narrow.

The next medial component of the group is area 27, area presubicularis (HD), which is distinctly divided into parts a and b (fig. 5, 10-12). It is succeeded medially by the subiculum itself. 27b is the dorsal of the two. In transverse sections it lies on the medial wall of the cerebral hemisphere below 29b. It corresponds rather precisely to the concave ventromedial end of the posterior forceps. It lies in front of 49, from which it is distinguished with difficulty in cell preparations. 27a forms the ventral half of this arc or strip of cortex. Being narrow, it is seen in only a few of a series of transverse sections; but in horizontal sections it may be identified easily as the last cortical zone which has more than one cell layer.

The subiculum (HE) (fig. 5, 10-12) is the cortical area transitional to the hippocampus proper. It is directly continuous with the full extent of the front or medial edge of 27. Thus, it extends from the splenium of the callosum ventrally, medial to the posterior forceps, onto the basal surface of the brain. In this region, though 27 is replaced by the amygdaloid formation, and though the subiculum is quite narrow, and has a greatly reduced structure, it can always be recognized.

The frontal or medial edge of the subiculum is succeeded by the striking appearance of the hippocampus, which in turn is
replaced by the fascia dentata. These formations of Ammon’s horn are familiar to all, and have not been reconstructed.

Between the caudal part of the pyriform region and the hippocampal formation is a considerable area which differs in structure from all other regions. This is the exposed part of the amygdala, constituting the cortical and medial amygdaloid nuclei (Johnston, ’23).

The medial amygdaloid nucleus (Am. m.) (fig. 5, 9) (Loo, ’31) is the more rostral and medial of the two. Rostrally it forms the medial edge of the cerebral hemisphere and is in contact with the nucleus of the lateral olfactory tract while laterally it borders on 51a. However, it is bounded in its caudal part, medially by fascia dentata and subiculum, and laterally by the cortical amygdaloid nucleus in addition to 51a. This is the region termed amygdala by Brodmann and Rose in the mouse.

The cortical amygdaloid nucleus (Am. c.) (fig. 5, 10) (Loo, ’31) is placed caudal and lateral to the former. Medially it is continuous with area 49 in its caudal part, while laterally it is bounded by 51b and 28a, from before backwards.

DISCUSSION

A. Comparison with previous studies

The areal plan of the rat has been studied adequately only by Fortuyn (’14). Brodmann divided the cortex of the rabbit and the spermophile into cortical areas in 1909. Rose has published lengthy papers on the cortex of the mouse (’30) and the rabbit (’31). Zunino (’09) studied the fiber structure of the cortical areas in the rabbit. Lashley (’41) examined the work of Rose and made an attempt to project it to the cortex of the rat but apparently did not make detailed observations. These papers are not widely discrepant, but differing terminologies are used. If one’s object were only to reconcile and systematize the nomenclature in an animal as important as the rat one would make a useful study. Here, however, the intention is to furnish an exact basis for the
tracing of the various connections by means of experimental studies, the determination of the functions of the areas, the analysis of their structure and neuron connections and their comparison with the connections of the areas of other forms, including man. Experimental cortical lesions must be localized in terms of cortical areas involved and this requires a rather precise delimitation if the stereotaxic machine is used for the lesions. The construction of a stereotaxic machine for the rat, and an atlas of coordinates for the cortical areas is the subject of a separate communication (46).

The work of Fortuyn is a comparison of the plan of cortical areas in a number of rodents, one of which is a rat, Mus decumanus. Fortuyn's investigations are based entirely on sections of two specimens fixed "within 24 hours after death." They were sectioned at 10μ in paraffin and stained by the old Nissl soap-methylene blue recine. Practically no illustrations of the cross sections or of sample strips are published and these are diagrammatic. However, he gives projections of the cortical hemisphere in three views with the cortical areas outlined which are adequate in making comparisons. He gives a table of histological characteristics but the "inflated cells" which he so frequently refers to are not found in material critically fixed, so it makes some comparisons difficult. His delimitations of areas seem in general to have been carefully done and agree in general with the results of the present study. He uses lower case letters for designation and these have no relation to any other published cortical plans. An attempt has been made in this work to conform as far as possible to Brodmann's designations, not because they are better than Fortuyn's or others' but because for experimental and for clinical work they have by usage become standard. In his discussion section Fortuyn attempts to equate his literal designations with the numerical designations of Brodmann. If one makes a comparison between the regions included in Fortuyn's areas and those identified in this study, it will be seen at a glance that in some cases Fortuyn's areas include several of the areas recognized here.
This is especially true for k, o and p. On the other hand, in the retrosplenial region he carries the subject even further and the designations are not easily to be equated with the ones given here. The separation of \( f' \) from \( f \) causes him to miss areas 4 and 6, and the parietal region might have been further subdivided with significance. It is in area p that the widest discrepancy occurs and includes considerably more than the auditory cortex. It would be difficult to use Fortuyn’s paper as a guide for identification of areas on a series of sections in any casual study. Once the areas have been laboriously identified, outlined in an atlas and made into a reconstruction it is quite feasible to make a comparison, but if one is going to do work which depends on exact identification of cortical areas it is indispensable to have clear illustrations of spaced sections with the sectors identified. This is particularly important if cortical structures are analyzed in detail. It is important to have myelin stained sections, preferably alternating with the thionin stained sections, as the fiber picture is usually as characteristic as the cell picture.

In his classic book, Brodmann (’09) illustrates the plan of cortical subdivision in the rabbit and in the spermophile by means of two diagrammatic drawings of a cerebral hemisphere of each of these forms. His total textual material on the rodent occupies but four pages, consequently one is thrown on an identification based on somewhat crudely made diagrams. Nevertheless, they prove tremendously useful for anyone studying the rat. Fortunately, however, M. Rose, his student, published a paper in 1912 giving in great detail the histologic localization in the cerebrum of a number of lower mammals using the mouse as the type form. The plan he settled on (his figure 31) is quite similar to that of Brodmann and the work was presumably executed under Brodmann’s supervision. Thus the detailed comparison of Rose’s findings, or of those in the present work, with Brodmann’s is unnecessary.

Turning then to Rose’s earlier account, it may be said in general that a fairly close agreement with that presented here
can be made. There are some substantial differences in the subdivision of the neocortex which do not depend on a difference in structure in the two species but on a different interpretation. The plans of subdivision of the limbic areas agree quite well, however, and Rose’s work here was a great help in the present study.

Turning to the neocortex, the subdivision into areas has been made more precise in some cases and probably conforms closer to the cortical areas distinguished in higher forms, thus somesthetic, visual, and auditory areas have been localized and the somesthetic has been subdivided into distinct regions which are believed to correspond to those seen in higher animals. Thus, in place of a mixed area 1, 2, 3 and 5 distinguished by Rose there are distinct areas 3, 1, 2, 2a, 7, 39, and 40, while the separation off of areas 3 and 1 from the main somesthetic cortex (3–1–2) must be regarded as conjectural at the present time. By comparing these areas with those observed in the human cortex and illustrated by von Economo, the identification suggested here may have some factual basis. Rose’s area 7 probably includes the areas here identified as 7 and 39 but there are two distinct structures in this region. Even in a cortex as low as the rat’s one can expect that there would be a germ of the extensive areas of 39 and 40 in the human brain. This region should be in the triangular zone between the three main sensory areas. It is now generally recognized that Brodmann and Rose were quite mistaken in their identification of 20, 21 and 22 in the temporal area of all of the lower forms on which they worked. They made no provision for the auditory cortex and included too large an area for the temporal associative areas. Area 41 fills most of this area and, as was stated previously, is the verified auditory receptive area. Any temporal associative area in the rat must be extremely reduced and should lie ventral to the auditory area but dorsal to the rhinal fissure. This leaves only the region here identified as 20 which may be taken to represent in undeveloped form that portion of the cortex included in higher forms and man as 20, 21, 22, 37 and 38. This agrees in spirit
with what is known of the evolution of the cerebral cortex. The area striata (17) can be easily identified and the author is in close agreement here with Rose and with Brodmann. The remainder of the occipital area, however, is not so entirely clear. In most higher mammals area 17 is nearly or quite completely surrounded by 18 and there seems to be no good reason why this should not be true in the rat also. Rose has placed area 18 as only medial to 17 where it is easily recognized on account of certain structural peculiarities. There is, however, a specialized zone of cortex continuing laterally of 17 and capping it caudally but not rostrally. In fiber preparations this cortical area can be seen to be closely associated with area 17 and hence belongs to the visual system of the occipital lobe. It does not, however, correspond in structure to the medial area already identified as 18. It is here termed area 18a in an attempt to be as conservative as possible with new designations. It would not seem right to equate it with area 19 since 19 always is peripheral to 18 in the higher forms and perhaps represents a later stage of development. Areas 18 and 18a form a distinct and complete ring entirely surrounding 17 except possibly at the occipital pole where the structure of the occipital region seems to undergo a gradual modification.

In the frontal region certain changes have been made toward a greater specificity of areation. Rose groups areas 4 and 6 together and has 8 extending quite to the frontal pole. Thus, he distinguishes no truly frontal regions. There are, however, distinct differences in this region which would seem to make it possible to separate a motor, a premotor and a frontal polar area. The designation of the polar area as 10 in the present work is meant to include the undifferentiated anlage of the dorsal human frontal areas and possibly others, but there is no further differentiation in the rat. The ventrolateral part of the frontal pole is distinct and was identified by Rose and Brodmann as area 8; but from position and what is now known of its connections (to be described in a later paper) it is more likely that this area corresponds better to area 47.
The region of and immediately dorsal to the rhinal sulcus is identified by Rose and Brodmann as the insula and the area was not further subdivided, being lumped together as areas 13 and 16. It is quite feasible, however, to separate the cortex of the rhinal sulcus from that lying more dorsally on the basis of structure, yielding areas 13 and 14 of the present account.

The cingular region conforms to the plan of Rose and Brodmann except that 29a is not distinguished. The caudal part of the limbic lobe corresponds well to the earlier papers but area 48 could not be separated from 27b and is left out of the present account. Thus, 27b is placed in contact with 29b. The areas in this region require close study and vivid visualization as they curve rapidly out of any plane of section.

The rostral part of the pyriform area forming the base of the brain corresponds rather closely to the findings of Rose. The several parts of 51 are identified except that it is difficult to see on what basis he distinguishes 51d.

Rose gives detailed descriptions of the structure of each of the cortical areas, both as regards the cytoarchitectonics and myeloarchitectonics and describes the location of each area on the cortical surface. In spite of the excellence of the heliogravures forming the atlas appended to his work one is sometimes left in doubt as to the identification of certain of the areas. His map of the surface extent and arrangement of the areas leaves much to be desired. The paper as a whole is, however, a useful guide for one studying the cortex of a related form.

In 1930 Rose wrote a long paper on the cortical areas of the mouse and in 1931 published a similar one on the rabbit. Both of these articles have a detailed description of each cross section illustrated followed by a summary of the characteristics of the various cortical types. The numerous plates are large folding heliogravures of selected cross sections, supplemented by many higher power fields. His study seems to be based entirely on cross sectional series of thionin stained sections. In the rabbit 72 cortical types are recognized. Rose has here abandoned the numerical designations of Brodmann
used in his earlier study ('12) and has substituted a complicated array of names and abbreviations. The novelty of nomenclature and the very detailed descriptions conspire to make these papers difficult of comprehension, while the total lack of any regard for function, connections, or significance add a feeling of remoteness to the whole undertaking. In some regions Rose, in this and his later work, has carried his

### TABLE 1

*Comparison of areas recognized in this study with areas distinguished by Rose in the mouse ('30).*

<table>
<thead>
<tr>
<th>THIS STUDY</th>
<th>ROSE</th>
<th>THIS STUDY</th>
<th>ROSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>with T1</td>
<td>25a</td>
<td>Irba</td>
</tr>
<tr>
<td>2</td>
<td>Pc, T1 (caudally)</td>
<td>27a</td>
<td>Prsub2</td>
</tr>
<tr>
<td>2a</td>
<td>T2</td>
<td>27b</td>
<td>Prsub1</td>
</tr>
<tr>
<td>3</td>
<td>Par</td>
<td>28</td>
<td>e1–e4</td>
</tr>
<tr>
<td>4</td>
<td>Praeagr</td>
<td>29b</td>
<td>Rsag, Rsagβ</td>
</tr>
<tr>
<td>6</td>
<td>Praecag</td>
<td>29c</td>
<td>Rsag</td>
</tr>
<tr>
<td>7</td>
<td>Par</td>
<td>32</td>
<td>Irba</td>
</tr>
<tr>
<td>8</td>
<td>A1</td>
<td>35</td>
<td>Prh</td>
</tr>
<tr>
<td>8a</td>
<td>A1</td>
<td>36</td>
<td>Ecrh</td>
</tr>
<tr>
<td>10</td>
<td>Praeagr</td>
<td>40</td>
<td>Oc (in part)</td>
</tr>
<tr>
<td>11</td>
<td>Praecag</td>
<td>41</td>
<td>Ecrh, Oc (ventral part)</td>
</tr>
<tr>
<td>13</td>
<td>A2</td>
<td>49</td>
<td>e5 ?</td>
</tr>
<tr>
<td>14</td>
<td>Il, I2, Ecrh</td>
<td>51a</td>
<td>Prpy2, Prpy3, Pam1</td>
</tr>
<tr>
<td>17</td>
<td>Str</td>
<td>51b</td>
<td>Prpy1, Prpy3</td>
</tr>
<tr>
<td>18</td>
<td>Rsag, Pstr</td>
<td>51d</td>
<td>Rb</td>
</tr>
<tr>
<td>18a</td>
<td>Oc, Ecrh</td>
<td>51e</td>
<td>?</td>
</tr>
<tr>
<td>20</td>
<td>Ecrh (rostral end)</td>
<td>51f</td>
<td>t.t. (in part)</td>
</tr>
<tr>
<td>23</td>
<td>Irrβ, Irbβ, Irceβ</td>
<td>51g</td>
<td>B, ol.</td>
</tr>
<tr>
<td>24</td>
<td>Irrα, Irrβ, Irec</td>
<td>Am.m.</td>
<td>Pdm2, Pam3</td>
</tr>
<tr>
<td>25</td>
<td>Irba</td>
<td>Am.e.</td>
<td>Not separated</td>
</tr>
</tbody>
</table>
seems nearer the facts. The subdivision of the cingular and pyriform areas can be regarded as a matter of opinion, but his handling of the somatic cortex does not fit the facts of thalamic projection. Because Rose did not recognize the auditory cortex he confused the areas on the entire dorsolateral cortex, where the most important areas are located. This oversight stems from Brodmann, but it might have been corrected in the many years that Rose was preoccupied with cytoarchitectonics. As a result the occipital area is thrown far forward. Having to account for a fancied temporal lobe he lopped off the entire lateral part of the somesthetic area, which dominates the sensory cortex and arbitrarily designated it temporal (mouse: T1, T2). A casual observation of Weigert or of the proper Marchi sections would have corrected this. The differences between his account of the frontal areas and the present one are not so emphatic, as here the feasibility of separating a premotor from a motor area will not be settled until experimental material at hand is properly synthesized.

The study of the rabbit and the later study of the mouse agree well enough with one another. The partitioning in the rabbit is carried somewhat further, however. The mouse seems to resemble the albino rat more closely.

Zunino ('09) made a study of the myeloarchitectonics of the various cortical areas as distinguished by Brodmann. He does not propose any variation in Brodmann’s plan. His Kultschizky stains are superior to the Weil stained sections used in the present study and he publishes some beautifully detailed drawings of strips through each of the areas. He does not attempt any sort of analysis of mechanisms or functional interpretations.

Considering the work of previous writers on the rodent, it is evident that there is little disagreement or discrepancy between the various works, once the results have been translated into a common language. Certain differences in viewpoint are responsible for most of the differences in results. Fortuyn did not study minute differences in the somatic cortex though he subdivided the subicular region very minutely.
Rose, in his later work, particularly as evidenced by his work on man, seems to be bent on producing the highest possible number of fields that the human faculties can discriminate in thionin sections and gets further from correlations with fiber patterns or what little is known of fiber connections or functional significance. While under Brodman’s influence he was more conservative, Brodman seems the most level-headed of all and certainly had a wide experience with sections of the cerebral cortex. It has been possible to subdivide some of his areas somewhat but this is usually the case when epigoni restudy a master work. In spite of the time that has elapsed since Brodman’s study and the improvement of anatomical and functional knowledge it has not been seriously undermined. Brodman never published section illustrations for most of the areas in most of the forms that he studied, but his maps filled with symbols, crude as they are, seem to be pretty accurate. Much of the efforts of later workers would have been unnecessary if this genius’ life had not been cut short. The simplicity, universality, and early appearance of his scheme of numbering the cortical areas with Arabic numerals has made an appeal to all but the most specialized and it is now usual for clinicians and physiologists to designate cortical areas by the numbers which Brodman gave them. It is fortunate that there is now such uniformity among neurologists. However, if competing schemes are proposed such as those of Fortuyn, of Rose, or of von Economo only confusion will result in any but the minds of some half dozen specialists and there is no knowing where this subdivision will end. While it has sometimes been possible to subdivide the areas given by Brodman, there have been very few examples of discovery of new main types. Consequently, it seems feasible for originators to accept the Brodman numerical designations as far as possible and modify these as necessary by appended letters, or if the concepts or limits of an area are somewhat different from Brodman, to affix the initials of the originator in parenthesis after the numerical designation. Thus, the subdivision could be carried far enough to satisfy
any specialist and the experimenter or clinician would have a clearer idea of what was intended. These areas have a usefulness beyond that of designating anatomical entities as they are also the most practical way of designating the regions of the cerebral cortex, particularly in the case of smooth brains or when one has connections or function in mind. Thus, it is here urgently proposed that the designations of Brodmann be made a standard as far as this is possible.

In determining the identity of the cortical areas attempt was made to proceed entirely on the basis of the evidence presented by the sections and the details of the work of others on related forms purposely not studied out until a plan had been made. The boundaries in each section were decided on their own evidence and the series matched only after partitions had been set in all sections. Projection outlines were made, generally of every fourth section, and the observations were based on a close combination of cell-stained and fiber-stained sections. The background developed by existing publications was, of course, used as a basis for designation of areas and in several cases, notably areas 49 and 27, sections were restudied after the literature had been scanned. It is not suggested that any identification of or plan of division into areas should be regarded as definitive when based entirely on observations of thionin and Weil-stained sections. The distinguishing features observable are merely a visible expression of greater differences in intrinsic structure, patterns and connections. It is quite conceivable that two very different mechanisms might present the same picture when only one aspect of the complex is studied. Conversely, it is possible that cortical areas which may seem to differ considerably on the basis of the arrangement of the cells or fibers may actually present similar intrinsic connections. Thus, any "cytoarchitectonic" or "myeloarchitectonic" studies must be regarded as geography only, as a provisional division into areas which have natural boundaries that can be mutually agreed upon.

It is the belief of this writer that purely cytoarchitectural studies, valuable as they may have been in the early decades
of the century are incomplete expressions and, moreover, specious, since they are not based on the total available evidence. Broadly speaking, there seems to be a tendency on the part of "cytoarchitects" to narrow their range of observations as they extend their subdivisions. It is for these reasons that this work is put forward, not as a complete or final expression, but as a preliminary survey to a more extensive and critical study of what is behind the picture that is seen in cell stained and myelin stained sections. The experimental part of this work has already been performed. Over 100 minute lesions have been placed in various parts of the cortex and thalamus of the albino rat by a stereotaxic machine. These lesions have been localized and the complete picture of resulting fiber tract degeneration has been worked out in detail and illustrated by means of slice reconstructions. This will form another part of this series of publications. These observations are in turn to be referred to cortical areas and the results synthesized and expressed in terms of the functional division to which they may be classified. These results will form still another unit of the series. The writer hopes also to be able to make a contribution to the intrinsic structure and the connections of the various cortical areas. Such a study will deal with the significance of the patterns here observed. When and if the circuits may be tested electrically the cycle can then be regarded as completed.

**B. Development of plan of cortical areas**

This study and the results of previous workers have shown the cerebral cortex of the rat to be highly differentiated into numerous distinct areas. Whether or not the areas differentiated deserve the designations given them is of course a debatable question. In the case of many of them, the known connections and the obvious similarities of structure make close homologies feasible. The connections of the secondary areas are not as well known and their structure indicates that they are not as highly differentiated as in higher forms. Yet their existence in the proper relations to known areas is per-
haps adequate justification for drawing at least provisional homologies. This, however, is of secondary importance. The point is that the differentiation is present and visible and it remains to be accounted for. To attempt to fit them into the picture of brains in which the functions of the areas are better known rather than making a special classification is the more conservative approach and under the circumstances the justifiable one. Assuming then, for the present, that the areas have been correctly identified, certain conclusions and generalities are possible. Here is an animal comparatively low in the mammalian scale which has nearly all the cortical areas present in man. The increased size of the human brain and the greatly increased complexity of the intellectual life of man have not produced an overwhelming multiplication of distinguishable areas, as might be expected when viewed in one light. In general, areas have been laid down at an early stage of mammalian phylogeny and they only expand in the higher stages. Further differentiation is a subdivision coupled with an expansion of areas small in the lower form.

The early differentiation of the cortical areas would at first sight be a temptation toward a preformationist viewpoint. In submammalian forms there is practically no cortex, while in the lowly mammal a large number of cortical areas are distinguishable. These have a certain fundamental relation to one another which is altered only by known or knowable influences in the course of subsequent development. This relation must be fundamental. Thus, it remains to account for the relation of the elements in this complex mosaic dome of the cerebral hemisphere. There is no point in an extended study at which the careful person may feel himself justified in making philosophical generalities, yet there must be reflection, the summing up of significant results, if one is to escape being merely a geographer of the cortex.

Making use of the findings of others, particularly of Brodmann, one finds one's self coming to a naturalistic interpretation of the topography and differentiation of the cortical areas. The cerebral hemisphere of the most primitive mammal may
be thought of as divided into three sectors (fig. 13, A). Dorsally, where the hemisphere is attached to the thalamus, is the archipallium or hippocampus. Ventrally, is the paleopallium or pyriform region. These two areas join and so form the thick rim, or rather the main body, of the cup. The third portion is the neopallium or somatic cortex. It occupies the position of base of the cup or top of the dome. The hippocampus differentiates very little, its two areas of hippocampus proper and dentate gyrus being formed at the earliest known mammalian stage. The pyriform cortex develops a number of distinct areas at an early stage. Both of these areas are associated with the connections of the olfactory system—the pyriform area quite intimately since the lateral olfactory tract runs its length, the hippocampus less obviously so. Indeed, it is perhaps more constructive to question from the start any intimate relation of the hippocampus with the olfactory system. In the primitive brain the neocortex is small and undifferentiated, occupying perhaps a thin quadrant of the cross section of the cerebrum but it is in this area that the enormous differentiation and development are to take place.

What distinguishes the cortex of the mammal from that of any other class is the strong projection from the thalamus of the visual, somesthetic and auditory systems. This is well developed even in Ornithorhynchus (Hines, '29). So far as can be judged from any recent forms, these systems project simultaneously. The auditory sense is relatively less well developed in the lowest mammals. This is, of course, accompanied by an extensive development of the geniculate and ventrolateral nuclei of the thalamus.

The projection is a direct one. The location on the hemisphere of these three primary projections is predicated by the position in the thalamus that these nuclei happen to have. The geniculate nuclei, as representing special senses are further lateral than the more generalized somesthetic sense. Thus, we see extrapolated on to the cortex more by accident than principle, a manifestation of the primitive plan of
arrangement of elements in the neural tube. This will be more apparent when the motor division is considered. These three senses, then, project on to the neocortex in a triangular pattern shown in figure 13, b. This relation perseverates throughout the Mammalia, and is the fundamental predicator of later areal differentiations.

Along the periphery of each of these areas, both where they contact each other and where they touch the hippocampus and pyriform areas, is undifferentiated cortical tissue. One of the fundamental principles of cortical architecture is the tendency of one area to associate with another, to some extent directly, but more through mutual connection with a common pool. This tendency is expressed in the formation of secondary, limbic, or "psychic" areas. So, oversimplifying somewhat, we may think of each of these primary sensory areas as surrounded by a secondary area to which it in turn projects. Now we may get down to names and numbers. The somesthetic area is 3–1–2. The visual is 17 and the auditory is 41. The secondary areas of the somatic region perhaps constitute 7 and 40; that of the optic area 18, that of the auditory perhaps area 20. It is to be noted that where these three zones meet a triangular chink is left, potentially forming the basis for association between all three of the senses. This is area 39. Possibly, though not at all certainly, area 7 represents the common meeting ground for somesthetic and visual sensations. Area 18a as indicated in the present study would be a meeting place for visual and auditory stimuli, while possibly area 40 is the somesthetic-auditory connection. Area 39 and perhaps the germ of area 40 of the higher animals represents the great parietal associational area which is destined to receive so complex a development that it can function as a controlling cortex for at least a simplified life even in the complete absence of the premotor frontal cortex. Further concentric zones of differentiation of sensory psychic areas are of course possible but do not seem to have been carried far by the organism. The best example of these is 19 for the visual system. For the somesthetic system the differentiation
may lie in a distinction between 7a and 7b (or PEm and PEp in von Economo’s terminology). The limbic zones associated with audition develop and differentiate to the extent of the formation of the temporal lobe. This is so far out of proportion to the formation of tertiary association regions for the other senses that it is better to assume that the temporal lobe has special but at present unknown functions to perform, not directly associated with any one of the senses. The minute area 20 of the rat develops into areas 20, 21, 22, 37, and 38 in man, all of which are large. So much for the interrelations of the sensory areas.

An elaborate sensory registration zone or exchange would be unthinkable without the possibility of an effector mechanism and indeed, motor representation is very early laid down in the cerebral hemisphere. The difficulty of getting overt and discrete motor responses to electrical stimulation of the cortex must not be allowed to confuse the thinking here. Tonic influences on extrapyramidal mechanisms are about all that can be expected in a lowly brain, again reflecting the arrangement of nerve components in motor areas developed in the anterior part of the neocortex. This is partly due to the fact that this space was not preempted by the sensory radiation of the thalamus and also by the more direct connection possible with the motor elements which lie ventral in the brain stem and with the pallidus by direct descending connections. This area is at first diffuse and undifferentiated though not small. For brevity we may now speak of a frontal, parietal, occipital and temporal region or sphere of influence. The sensory systems at an early stage must send associative fibers to the frontal cortex. But as the differentiation of secondary and associative areas becomes more pronounced, some sorting out of the impulses is requisite and hierarchies must be made, until finally the primary motor area (4) becomes merely an effector mechanism or keyboard. As successive stages in the control of area 4 we may find an area 6, as let us say, a sorting mechanism, and an area 10 which is
a selector mechanism. Thus, we have an effector, a sorter and a selector for the motor system, which are in turn connected with the raw or integrated products of the sensorium.

Here then is a compact, self-contained and naturalistically developed mechanism. However, it does not include all of the elements of the cerebral cortex by far. Returning now to the original plan (fig. 13), the sensory areas are surrounded by undifferentiated cortex which is bounded peripherally by some part or other of the outer ring of hippocampal and pyriform cortex. The connection with the latter may be regarded as a correlating ground for the somesthetic, visual, and auditory senses on the one hand and olfactory on the other, while the cortical area adjacent to the hippocampus may likewise be considered as common ground for the neocortical activity and whatever the hippocampus does. In this way areas 13 and 14 are matured.

Between the neocortex and the hippocampus, however, there is an interesting development. There is some connection with the hippocampus as fiber preparations show, but how extensive or important this is is not clear. This is the area which developed into the cingulate region which shows a different pattern of differentiation from the other areas, and yet the plan of the various parts of the cingulum have a great deal in common. It is highly significant, perhaps, that in their early differentiation the areas which develop from the cingulum parallel in position the areas which they lie opposite. Thus, area 24 corresponds to areas 10 and 6, 23 is next to 4 (though the true relation may be with 3–1–2) and 29 connects with 17 and 18. It has recently been shown that there are close connections anatomically and functionally between the cingular cortex and the more dorsally or laterally lying cortical areas. Areas 31 and 32, the suppressor areas of the cingulum, are not developed in the rat but may be regarded as the tertiary stage of development, in an intermediate or undifferentiated position. In fact it may be that the suppressor areas as shown by McCulloch are all of tertiary origin and certainly what is known of their function would indicate
this. So whatever the hippocampus contributes meets the more differentiated sensori-motor system in the cingular region.

This accounts for the principal groups of cortical areas except the retrohippocampal. They are small elements and decrease relatively in size as the brain evolves, are distinct and have very definite connections. They have some special function to perform which is more significant in the lower mammal, is somehow connected with olfaction and apparently requires correlation with a wide extent of the cortex and connection with the anterior nucleus of the thalamus, as is evidenced by the extensive origin of the cingulum and the fiber layer which forms a lateral extension of it in the rat.

We have thus seen that the cortical areas, numerous as they are even in a low form, can be accounted for at least theoretically, but with considerable observational basis, on an entirely naturalistic plan. The unknown factors or the influences which must be calculated are relatively few. A great extension of the temporal region, the true rôle of the cingular region and the significance of the retrohippocampal areas are, of course, not understood. However, by a consideration of the primordial relations of these to one another we may speculate with greater probability of correctness than if we consider the mosaic of areas as created by some fiat.

LITERATURE CITED


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EXPLANATION OF PLATES

Figs. 6–12  Selected pairs of adjacent sections of cerebral cortex stained alternately for cells and myelin sheaths. The extents of the cortical areas which make up each section are designated.

PLATE 1

EXPLANATION OF FIGURE

6  Transverse sections 118 and 119, 18 ×
PLATE 2

EXPLANATION OF FIGURE

7 Transverse sections 175 and 176. 18 ×
CORTICAL AREAS OF ALBINO RAT

Figure 7

PLATE 2
PLATE 3
EXPLANATION OF FIGURE
8 Transverse sections 238 and 239, 18 X
PLATE 4

EXPLANATION OF FIGURE

9 Transverse sections 292 and 293. 18 X
PLATE 6

EXPLANATION OF FIGURE

11 Sagittal sections 156 and 157. 11 X
PLATE 7

EXPLANATION OF FIGURE

12  Horizontal sections 190 and 191. 24.5 X
CORTICAL AREAS OF ALBINO RAT
WENDELL J. S. KRIEG

PLATE 7
13 Diagrams to illustrate text on evolution of cortical areas.

a. Showing how the hippocampus (hip.) and fascia dentata (F.D.) on the one hand and the pyriform region (consisting of area 51 and the olfactory tubercle (T. ol.) on the other hand form the major part of the rim of the cerebral hemisphere. They are, however, kept from contact by the septum (Sep.) rostrally and the cortical parts of the amygdala (Amyg.) caudally.

b. Showing how relations of the primary sensory cortical areas are predicated by the positions of the thalamic nuclei from which they arise. A.R., auditory radiation; L.G., lateral geniculate; M.G., medial geniculate; S.R., somesthetic radiation; V., Ventral nucleus; V.R., Visual radiation.

c. Lateral view of cortex showing supposed formation of specific association areas by irradiation and combination.

d. Medial view of cortex showing (1) theory of formation of specific cingular areas through influence of neighboring somatic areas; (2) the related development of the hippocampal-retrohippocampal system, and (3) the independence of the olfactory system.