The Isocortex of Man

By PERCIVAL BAILEY and GERHARDT VON BONIN

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Volumes I, II, and III of this series were issued under the title Illinois Medical and Dental Monographs.

THE ISOCORTEX OF MAN

Supratemporal plane

Parietal operculum

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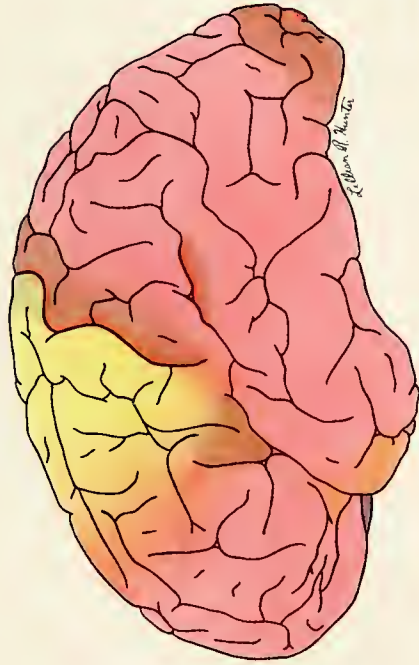
Island
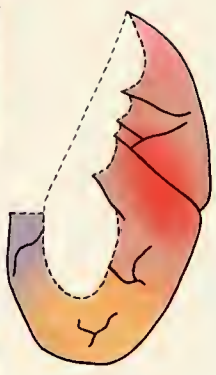
KEY TO FRONTISPIECE (*see Chapter VI*)

Red: granules
Yellow: no granules
Blue: allocortex
Gray: large pyramids in *iiic*

THEREFORE:

Red: koniocortex
Yellow: agranular cortex
Blue: allocortex
Pink: eulaminate cortex

Purple = pink + blue: juxtallocortex
Orange = yellow + pink: dysgranular cortex
Brown = pink + gray: parakoniocortex
Green = blue + yellow: mesocortex

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REMOTE STORAGE

To the memory of

PAUL FLECHSIG

Therefore the surgeon in seeking a thoroughly reliable knowledge must duly prepare a dead body....It should be the body of someone who had neither been excessively old, nor one who died of poison, nor of a protracted disease.

SUŚRUTA (III, 5)

PREFACE

It is safe to say that interest in cortical architecture has not been widespread since the appearance of Brodmann's *Vergleichende Lokalisationslehre der Grosshirnrinde* in 1909. Brodmann's contention (p. 305), frequently reiterated by the Vogts, that each cortical area is an organ in itself, tied up cortical architectonics with a theory of cortical function that threatened, under the influence of holistic views in psychology and biology, to become more and more outmoded. The minute parcellation of the cortex by the Vogt school, moreover, made this theory less and less tenable.

The subject became not only difficult and abstruse, but doubts about the reliability of cytoarchitectonics grew until, "Unless the criteria are clearly stated and objectively verifiable . . . architectonic charts of the cortex represent little more than the whim of the individual student," could be written, amidst widespread applause, by Lashley and Clark (1946).

In 1927, G. Elliot Smith, who twenty years previously had published a brain map of his own, in reviewing the work of Economo and Koskinas, wrote: "It can be confidently said that such a survey will not have to be done again, and that this work will become a standard treatise of reference on the topography of the human cerebral cortex. No doubt in the future much detailed work will be done upon particular regions, perhaps introducing small points of modification, but the work as a whole is bound to stand as a permanent achievement."

The work is a standard reference and a permanent achievement, yet there seem good reasons why the human cerebral cortex should be investigated once more, why it would be worth a considerable outlay of time and money to go over a ground that seemingly has been worked over so carefully. The number of brains that have actually been examined is not very large, nor was the state of their preservation always as good as one might have wished. Campbell (1905), by his own account, examined three hemispheres completely for nerve cells and nerve fibers, and two others incompletely. Brodmann never gives precise information about his material. The Brain Institute under Vogt's direction possessed, when Brockhaus (1940) published his paper, at least seven hemispheres. We find, in the last two volumes (49, 50) of the *J. f. Psychol. u. Neurol.* mention of eleven normal human brains serially sectioned for anatomical study. These brains were removed about ten hours postmortem (C. & O. Vogt, 1942) and put into a 10 per cent neutral formalin solution. When it is realized that one brain was not fixed until twenty-four hours after death, and when one of Vogt's pupils (Strasburger, 1937) mentions that the staining occasionally had to be corrected by means of a camel's-hair brush, one's desire for corroboration grows. Economo and Koskinas evidently had three brains, but took "most" of their photographs from one and the same hemisphere. Their material was fixed by immersion into formalin at some unstated time after death. Only for the occipital lobe (Economo, 1930a) the supratemporal plane (Economo and Horn, 1930; Kakeshita, 1925) and a few other areas do we have more plentiful information except for that which is contained in the studies of the Brain Institute of Moscow (only the first four volumes of which were available to us), difficult to

obtain and in Russian. According to Blinkow and Poliakov (1938) the Moscow Institute possessed at that time "over 30 series of complete microscopic sections through the entire brain hemispheres of an adult." Whatever might be the meaning of this ambiguous statement, the study of yet another brain, properly fixed and stained, seemed desirable in any event.

The importance of proper material for anatomical study was known already to the ancient Hindus. Through the kindness of Colonel J. E. Ash, then Director of the Armed Forces Institute of Pathology, we came into possession of a particularly perfect brain removed from a young healthy adult male, who died of an accident without injury to the head. The brain was removed within one hour of death after perfusion through the arteries with a 4 per cent aqueous solution of formaldehyde; it weighed, after fixation, 1,347 gm.; and will be referred to henceforth by the symbol *H*. Subsequent study proved the brain to be uniformly fixed throughout.

The unsuitability of the brains removed many hours after death, and fixed in the usual way by immersion in formalin, should be evident to anyone, and the histological preparations made from them show clear evidences of pathological alteration. We might cite, as an example, the drawing of the cortex given by Ramón y Cajal (1911, tome II, Fig. 334, p. 522). It could serve well, without alteration, in a textbook of neuropathology to illustrate severe acute degenerative changes of the ganglion cells. The superiority of brains immediately injected through the arterial system over those removed after the body has been kept in refrigeration for twenty-four hours, or even those removed immediately and immersed in the fixing fluid, has been recognized by M. Rose (1929), Bartelmez and Hoerr (1933), Barnard (1940), and many others.

The immediate reason why we decided to embark on this renewed investigation of the human cerebral cortex is found in our previous work on macaque and chimpanzee. That work was undertaken to lend precision to the results of physiological neuronography performed on these primates and to be applied, so it was hoped, to man. But, in the process of our studies, it became clear that the precise homology of which we had dreamed could be achieved only when maps of all three primates— man, chimpanzee, and macaque—had been drawn up by the same observers.

As our work on cytoarchitectonics progressed, it became increasingly apparent to us that more than local patchings were required, as Lashley and Clark have also found. What was needed was to state as objectively as possible those architectural types that can be clearly distinguished, but to refrain from giving quite secondary, obviously unimportant, details the same critical value. Anybody can see, to give an example, the difference between Brodmann's areas *17* and *18*. But the differences between his *18* and *19* are quite tenuous and very difficult to recognize. To draw a map on which these three areas are given three different markings—such as dots, cross-hatchings, and broken lines—is to create an entirely misleading impression. Useful as such maps are for the description of corticocortical connections, they do not translate accurately cytoarchitectonic data. The frontispiece of this monograph is drawn on a different principle (see opposite title page) from those used for the macaque (Bonin and Bailey, 1947) and chimpanzee (Bailey, Bonin, and McCulloch, 1950). In those maps colors were used mainly to facilitate the portrayal of regions of transitional structure and many areas were distinguished largely for the purpose

of describing the findings of the method of physiological neuronography without much regard for degree of differentiation.

This is not to deny that such subtle and minute distinctions can be made; it is, however, to deny that, at least at present, they serve any useful purpose. Coming from subhuman primates we are more impressed, as will appear in the course of this monograph, by the astounding homogeneity of the human cortex than by its divisibility into a host of elemental organs as Brodmann would have it. To present a new analysis of the adult human cerebral cortex to modern neurologists, who do not rush at once to questions of functional localization, seemed amply justified.

Most students of cytoarchitecture have been "arrested in the Nissl stage" as Rioch (1948) put it to one of us. But how can we progress beyond it? That myelo-architectural studies are less reliable than cytoarchitectural ones was noted by Vogt (1906a) and confirmed by Brodmann (1909), although some of their pupils seem to have forgotten it. Myelin preparations show only a fraction of the axonal plexus, but no dendrites. The way in which the axons break up into telodendria, the unmyelinated collaterals, as well as the type of the synapses can be seen only in Golgi preparations. Lorente de Nó's (1949) description of the cerebral cortex is based on Golgi preparations of the mouse. His account may be valid for man, but we have only fragmentary data with which to check it, mostly old observations of Ramón y Cajal (1911). Other silver preparations are utterly unsuited for archi-tectural studies, as Cajal noted long ago. They show so many bewildering details that one cannot see the wood for the trees. In the case of Golgi preparations, so few cells are impregnated that again the architecture of a given area cannot be made out. Unfortunately, the full details of the axons and their collaterals in the adult brain cannot be demonstrated by any method. The Golgi method will im-pregnate them only in newborn material where they are most probably not yet fully developed; Ramón y Cajal (1911, vol. 2, p. 536) remarked that collaterals are not demonstrated by the Golgi method until 1–1.5 months after birth. It is well to keep these limitations in mind. The microphotographs of Flexner and his co-workers (see Peters and Flexner, 1950) suggest the phaseshift microscope as a promising tool. We became aware of it only after our brain had been sectioned and stained.

Racial differences in the sulcal pattern have frequently been discussed, and their existence is indeed implicitly assumed, or at least suspected, in many of the titles which the studies of the sulcal pattern bear. Weinberg (1905), Landau (1911, 1914), Shellshear (1926, 1937), van Bork-Felkamp (1930), Connolly (1950) could be cited. It is true, of course, that thoughtful anatomists such as Tiedemann (1836), Stieda (1908), or Kohlbrugge (1908) were skeptical about racial differences and loath to interpret individual differences in the sulcal pattern as signs of mental inferiority or superiority. "My intention was to shake the belief in the importance of gross exami-nation of the brain and to undermine the opinion that individual differences of gyri and sulci are of importance for mental functions" was Stieda's concluding sentence.

It is, however, the architecture of the cerebral cortex which is the main topic of this study. The incredibly complicated spatial pattern in which the neurones are arranged within the cerebral cortex still defies a thorough understanding, as the following pages should make clear. But this lack of understanding is precisely the

reason why repeated discussions are necessary, or at least felt to be so, by those who disagree with what has been said before.

Although convinced that structure determines function, we do not believe that one can discourse about function by taking one's eyes off the microscope and leaning comfortably back in one's chair. That needs further work, of a different kind, outside the scope of this study. What we propose to do here is to analyze the architecture of the cortex. The reader has been told how best to preserve a brain for such studies. From now on, we are afraid, the cortex will be dead; to bring it back to life we must leave to others.

It is impossible to present a subject such as cortical architecture in an inductive manner as it can be—and generally is—approached in the experimental sciences. For a classification into types, be it of species or genera or be it of cortical areas, is still arrived at by intuition rather than by objectively stated rules. Our study proceeds, therefore, in the same way as those of our predecessors. The architectural types are described first, although the method of induction would demand them to be put last. We shall then tax the reader's patience by taking him through the whole cortex block by block. The next chapter will discuss the brain map which appears to us the logical outcome. It differs from those given previously, hence it is necessary to take issue with those authors from whose opinions we differ. We hope to justify our beliefs without unduly sharp criticisms. The chapters that follow, on cortico-cortical and afferent and efferent connections, tend to round out our picture of the isocortex of man, of which the last chapter will give an impressionistic sketch.

CONTENTS

Chapter I: Historical Introduction

It must, however, be owned, that all that both Ancients and Moderns have told us about the Brain is so uncertain, that the Books which contain the Anatomy of this Organ may be said to be chiefly a Collection of Doubts, Disputes and Controversies; but still a great advantage may be made of their Labour, and even of their Mistakes.

<div align="right">

Nicolaus Stenonius (1665)

</div>

A white line in the cortex near the calcarine fissure had been noted independently by Gennari in 1782 (see Fulton, 1937) and Vicq d'Azyr (1786). It was known to Blumenbach (cited after Soemmerring, *loc. cit.*, p. 70) and Soemmerring (1788). But this line of Gennari (or of Vicq d'Azyr, as it later became known) remained for long an isolated, purely anecdotal fact. This is hardly surprising, for at that time the cerebral cortex was held to be quite unimportant functionally, consisting probably of minute glands. Nerve fibers almost exclusively held the attention of anatomists who looked upon the white matter, the centrum ovale of Vieussens, or upon the ventricles where the fibers were thought to end, as the seat of the mind. Baillarger (1840) was the first to investigate seriously the structure of the cerebral cortex. He demonstrated the intimate connection between the white matter and the gray matter of the cortex and thus ushered in our modern conceptions of cortical function. Meynert (1867–68) first attempted to relate regional structural differences in the cerebral cortex to its function. He avowedly set out to prove or refute certain theories about the brain. To quote him verbatim: "The main function of the central organ is to transmit the fact of existence to an ego gradually shaping itself in the stream of the brain. . . . If we look upon the cortex as an organ functioning as a whole then all that can be said is that it subserves the processes of the mind. . . . To think further about the cortex is impossible and unnecessary . . . but our hope to understand eventually the function of the hemispheres is raised again by the opposite assumption which leads us straight to an organology of the cortical surface. . . . Between these two theoretical possibilities the facts have to decide." Meynert gives then a detailed account of the structure of the cerebral cortex in general, of what is now known as the visual area in particular where he describes the solitary cells which still bear his name, and devotes a large space to an analysis of the hippocampal formation, the olfactory lobe, and the septum pellucidum. He ends by distinguishing between cortex with gray surface and cortex with white surface. The former is subdivided once more into 5-layered and 8-layered cortex; the latter is subdivided into the three types just mentioned.

To speak in modern terms, Meynert thus divided allocortex from isocortex, and analyzed within the isocortex in detail the peculiar structure of the striate area. His formulation of the problem and his term "organology of the cortex" are perhaps of equal historical importance.[1]

[1]"Späte Fischer werfen dann die Netze,
　　Späte Taucher in den Tiefen späh'n
　　Und es segnet uns'res Erbes Schätze
　　Ein Geschlecht, für das wir untergeh'n."
to quote Meynert once more.

Soon afterward the motor area was discovered by Betz (1874). In the precentral region of man, of the chimpanzee and other primates, and of the dog, he described the giant pyramidal cells which still bear his name. Comparing his findings with the results of electrical stimulations, he deduced the motor function of the cortical center which he had discovered. In 1881 Betz published, in both French and German, a brief account of his cytoarchitectonic studies. These accounts are evidently translations from a Russian original. Each text contains obvious errors, usually readily corrected by comparison with the other, but some points remain obscure. Nevertheless, the account seems to us of sufficient importance that we have prepared an English version, as accurate as has seemed to us possible without having the original Russian text at our disposal. Unfortunately, the atlas promised in the last paragraph was never published (Benedikt, 1906).

By means of the present communication, I shall try to give the anatomical proof of the existence of specific regions in the human cortical substance, which are distinguished from one another as much by the form as by the disposition of their integral parts.

These regions of the cortical substance are found at the surface of the human brain in definite and constant situations. The variations in their structure may serve as criteria for their different physiological functions.

The general type of the structure of the human cerebral cortex is the following: the cortical substance consists of five different layers which, from without inward, are superimposed on one another in the following manner:

The first layer consists of a thick network called *neuroglia* in which are strewn, here and there, small granular bodies.

The second layer contains, besides the *neuroglia* (which, moreover, all the layers contain) pyramidal cells not too large which, not very near each other, have their apices directed toward the first layer, the base toward the bottom.

The third layer is composed of the same pyramidal cells, only two or three times larger, but in compensation less numerous and further apart from one another.

The fourth layer, called the granular layer, consists of small, round or elliptical cells.

The fifth layer finally consists of specific fusiform cells.

This structure of five layers may be considered as the general type of the cortical substance. Up to the present time, one has observed only a few particularities relative to the structure of the cortical substance, and for only a few parts.

Thus, Meynert has demonstrated that the third layer (pyramidal layer) is lacking in the cortical substance around the calcarine fissure, but that instead one encounters there two granular layers separated one from the other by layers of nerve fibers. In these layers of fibers are found, solitary or in pairs widely separated, pyramidal cells of considerable size. Besides that, it is mentioned that the cortical substance of the hippocampus contains principally elements of the third layer and that the claustrum is composed of elements of the fifth layer. Finally, according to my investigations, the cortical substance of the anterior central convolution and of the lobulus paracentralis contains gigantic nerve cells situated by groups in the form of nests.

That is all which, up to the present time, one knew on the subject of the peculiarities of certain regions of the cerebral cortex. By the study of 5,000 preparations examined by me during recent years, and coming from the right and left hemispheres of the same individuals (male brains, female, of all ages, even of an embryo of seven months, of newborn and infants of six weeks), I have obtained the following results:

Almost every part of the cortical substance of man, even the most insignificant, be it in the form of a lobule or a characteristic convolution, be it in the form of a part of a convolution, is distinguished by a specific structure.

This last consists of quantitative variations (different thicknesses) of each of the five elementary layers of the cortical substance which, sometimes larger, sometimes smaller, occasionally separated by elements not corresponding to the general type, present sometimes

new forms of cells or cells grouped differently or finally are distinguished by the total lack of certain layers. It is especially the disposition of the third layer which varies. One finds it more or less large, more or less dense, in its proper place or replacing the second layer; sometimes it is found above the fifth layer.

These principal characters of the peculiarities of the structure of the cortical substance of man are repeated precisely in the same regions on the surface of the most different brains.

It happens that the type corresponding to certain convolutions occupies, on one brain or on one hemisphere, a larger extent; in this case one finds in the corresponding region of the cortical substance a greater or lesser number of convolutions or lobules. Certain parts of the cerebral cortex are distinguished by the most remarkable constancy of the limits of their characteristic structure which, in the most different brains, never exceeds a certain region.

As specially characteristic are distinguished the structure of the following regions of the cortical substance:

> Of the anterior central convolution;
> Of the arciform convolution (gyrus cinguli);
> Of the hippocampus;
> Of the third frontal convolution;
> Of the lobulus paracentralis;
> Of the gyrus lingualis;
> Of the lobulus extremus; and
> Of the ventral extremity of the polus temporalis.

The anterior central convolution, from the superior limit of the inferior third toward the vertex, shows the following peculiarities: in the first place one encounters, above the fifth layer, large cells, solitary or in pairs, very far apart from one another. Higher up, these cells are grouped by threes or fours, in the form of nests, and less distant. Still higher up, these groups are composed of a larger number of cells; they contain at least four, sometimes five, and even as many as seven. At the same time these cells pass, from their first place above the fifth layer, to the third, where they are disposed in the form of a continuous line; moreover, one finds them isolated in the second and fourth layers, or even in the fifth. Toward the lobulus paracentralis, this layer breaks up again into nests and, in the lobulus paracentralis itself, the cells are distributed in layers one above another or in nests differently grouped. The nearer one approaches this lobulus the larger these cells become until, in the lobulus itself, they have the appearance of true giant cells.

They are found only in the anterior central convolution, but never [sic] extending to the posterior central convolution.

They reach the deepest parts of the central fissure, and it is only in brains of older subjects that they are situated in the very depths of the fissure and are found isolated on the base of the posterior central convolution.

Before advanced age, sometimes already in the adult, one encounters these cells in the superior part of the posterior central convolution, there where it passes into the lobulus paracentralis.

The arciform convolution [gyrus cinguli], at its origin above the anterior part of the lamina terminalis, is composed only of two layers: of the superior layer and of the fifth; the pyramids of the second layer are scarcely encountered and those which are found there are very small.

In this region, the particularity which characterizes the fifth layer consists in the disposition of those cells which, instead of being distributed as everywhere else along the base of the convolution, are situated vertically to its section, as are the cells of the third layer of the other convolutions.

These fusiform cells of the gyrus cinguli are much larger than those of the fifth layer (two, or even three times as large).

Near the knee of the corpus callosum these cells are found, one might say, pushed toward the bottom by the second layer, here very thick. In the middle of this convolution, there appears again the granular layer, as well as the pyramidal cells of the third layer, but these last are much smaller than in the other convolutions.

There where the gray layer touches the transverse fibers of the corpus callosum, above this

latter, appear three new layers, beginning at the posterior half of the gyrus cinguli. One of these layers, the inferior layer, consists of longitudinal fibers, which form an arc above the superior part of the corpus callosum. The second, the gray layer, is composed of small pyramidal cells or of fusiform cells of considerable dimensions. As these layers approach the posterior extremity of the gyrus cinguli, they gain in dimension, occupying nevertheless only the inferior border and the internal inferior face of this convolution.

There where the gyrus cinguli passes over into the hippocampal gyrus the layer of large cells enlarges suddenly and forms the internal layer of cells of the hippocampal convolution (already known). The new granular layer becomes the known granular layer of the hippocampal convolution, and the white layer of longitudinal fibers of the gyrus cinguli spreads along the surface of the hippocampus and, enlarging always, forms its granular white substance (substantia reticularis alba); then it transforms itself into the very substance of the hippocampus where, as the imperfect white wall, it has been described by Meynert under the name of granular sheet (Kernblatt), a denomination moreover which is not justified.

In this way, what the authors call *taenia tecta et fasciola cinerea* are the integral parts of the hippocampus developed independently on its posterior half and sometimes even more anteriorly. As a peculiarity of the extremity of the hippocampal convolution and of the entire extremity of the polus temporalis, one must remark that one there encounters the pyramidal cells of the third layer again immediately under the first layer. It is here that they are disposed quite singularly in the form of great round groups separated from each other by considerable intervals; the pyramidal cells of these very groups lie in the most different directions; their distribution resembles a ball of yarn. It is for this reason that I call them cortical balls (*glomerula corticalia*).

On the third frontal convolution one discerns three segments which may be distinguished by their cortical substance. The posterior segment reaches from the extremity of the anterior central convolution to the ascending branch of the fissure of Sylvius; the middle segment, from the latter place to the beginning of the orbital part of the third frontal convolution; the third segment finally (inferior segment) extends from the extremity of this convolution to the polus insulae. The first segment shows sometimes, in its third layer, pyramidal cells larger than those of the other convolutions of the frontal lobe. Here and there, especially in the brains of aged subjects, are found giant cells of lesser caliber which, sometimes, extend to the inferior extremity of the anterior central convolution. In some brains they occupy a considerable part of that extremity; this is something I have never encountered in the brains of subjects still young.

The second segment of the third frontal convolution contains, in the second and third layers, little oblong pyramidal cells with very long apical processes. These cells are crowded close to one another. They have, as have their processes, an oblique position, so that they are, one may say, interlaced with one another. The third segment of the frontal convolution, finally, contains for the most part cells of the type of those of the fifth layer, approaching in dimension the cells of the claustrum; they are disposed mostly perpendicularly to the transverse section of the cortex; sometimes one encounters cells of the third layer, but they are always very small.

One can make the same assertion concerning the insula, where one encounters also groups of small pyramidal cells with oblong processes, as well as cells of the fifth layer, analogous in dimensions to the cells of the beginning of the gyrus cinguli. At the very root of the operculum Blumenbachii on the convolution of the insula of the adult, one encounters often, in the third layer, large pyramidal cells, sometimes solitary, sometimes in groups, resembling giant cells of medium caliber.

The gyrus lingualis is distinguished among all the others by its structure. One may distinguish in it eight layers, although the cortical gray substance of this convolution is thinner than that of all the others. From without inward, these layers are as follows: (1) layer o neuroglia, (2) layer of very small pyramidal cells, (3) granular layer, (4) layer of longitudinal fibers—the fibers lie horizontal to the base of the cortical gray substance—(5) second granular layer, (6) second layer of longitudinal fibers, (7) layer of triangular pyramidal cells very far from one another, (8) layer of fusiform cells, corresponding to the type of the cells

of the fifth layer in the general type. In some parts of this convolution, especially in the middle, are encountered, in the fifth and sixth layers, sometimes even still higher, large pyramidal cells analogous to the cells of the third layer of the general type.

The limits of the fusiform lobe, at the internal face of the cuneus and at the entire extremity of the polus occipitalis, present the same structure.

The nearer one approaches the lobulus extremus, the more one sees the seventh layer disappear and, arrived at the extremity of the gyrus descendens, all the layers fuse, one may say, with one another and form a compact substance of granular cells and a little line of fusiform cells.

The external face of the occipital lobe offers already the second and the third layer of pyramidal cells of the general type, and sometimes one encounters these cells of a considerable dimension; one finds them large especially at the convexity of the convolution. The same structure of the cerebral cortex is remarked in the three occipital convolutions of the gyrus angularis, which often is transformed into a lobulus, even a lobe, and in the transitional superior gyrus (*pli de passage*) of Gratiolet. In this last, the solitary cells of the third layer are much larger than the cells of this same layer in the lobus occipitalis and, by their appearance, this convolution is clearly distinguished from the extremity of the superior temporal convolution. In ripe age, and sometimes even at a young age, one sees, in certain parts of the gyrus angularis and at the extremity of the anterior limit of the occipital convolutions, that the third layer is separated into two belts superimposed and separated by a layer of small pyramidal cells. This same structure extends just to the temporal convolution, where it stops abruptly.

The posterior central convolution and the superior and inferior parietal lobules offer a structure of general type.

Sometimes, in aged brains, the third layer of the posterior central convolution penetrates into the second layer and almost always one encounters, at the superior extremity of this convolution, giant cells. I have already mentioned this fact.

Often one finds in the third layer of this convolution, in its superior part, pyramidal cells of considerable dimensions.

The three temporal convolutions are distinguished by the great dimensions of their fifth layer and by the little cells of their third except, nevertheless, the polus temporalis which was mentioned above.

The two hidden temporal convolutions (gyri parietotemporales et gyri temporales transversi) recall, by their structure, the posterior central convolution. There one encounters also, here and there, sometimes solitary, sometimes grouped, cells which by their dimensions resemble small giant cells. The structure of the lobulus quadratus (praecuneus internus) is the same as that of the superior parietal lobe but, on the highest part of its border, one encounters, in the third layer and above the fifth layer, two lines of pyramidal cells. The frontal convolutions, with the exception of the inferior, are distinguished by the following peculiarities: The superior frontal convolution and its internal face contain, in the third layer, rather large pyramidal cells. This layer is thick and extends to the fifth, from which it results that the granular layer (fourth layer) is very small and enlarges only over the anterior third of this convolution. As the granular layer augments, the third layer diminishes toward the extremity of this convolution, just as its elements which become smaller and rarer.

One can make the same affirmation concerning the second frontal convolution, although on this last the granular layer, from its beginning, is more distinct.

In older brains, one encounters sometimes giant cells of lesser dimensions, but they are only found at the beginning of the frontal convolutions.

The gyrus rectus resembles greatly the anterior part of the gyrus cinguli. The other orbital convolutions are not to be distinguished essentially from the extremity of the frontal convolutions. Nevertheless, the granular layer predominates there. Only as one advances toward the point of this triangular lobe, one sees the pyramidal cells diminish in size and number. At the posterior and internal extremity of these convolutions one sees the fifth layer gain in dimensions; it becomes especially of a considerable size.

My atlas of the surface of the human brain will treat in more detail of what I have just said, as well as of the structure of the convolutions.

The locations of the areas which Betz described are fairly clear except for the lobulus extremus. We have been unable to find any such term in the older descriptions of the gyri of the human brain. His account of its structure seems to fit best the retrosplenial region.

From Benedikt (1906), who knew Betz personally, we learn that he gave up his position in the University of Kiev to become physician to the Southern Russian Railroad and that his atlas was never published. He was a perfectionist, never satisfied with his work, as Benedikt adds. Betz saw very clearly the import of his work on our conception of the cortex. "It follows from what has been said that the present conception of the topography of the surface of the human brain, based as it is sometimes on the most detailed investigation of the sulci, sometimes on comparative anatomy and, finally, sometimes on ontogeny, is inapplicable to the adult brain. The brain and its convolutions can be subdivided only on the basis of differences in the anatomical structure."

A remarkably detailed subdivision of the cortex was achieved by Flechsig (1898) by the myelogenetic method, i.e., by studying the spatio-temporal distribution of myelination of the fibers in the white substance immediately subjacent to the cortex. In 1898 Flechsig described forty cortical fields. Numbers 1–8 were primordial areas; numbers 9–32 intermediate ones; and numbers 33–40 terminal ones. Flechsig considered the first eight as sensory areas, the others as association areas. The terminal areas were those which distinguished the human brain most clearly from those of the anthropoids [the third frontal convolution nowhere belongs to them]. Throughout, Flechsig alludes frequently to local differences in cortical architecture, even in the brain of the hamster, without, however, ever giving details. Flechsig's papers and books contain a wealth of information and ideas; they deserve much closer study than is now generally devoted to them. In spite of Vogt's adverse criticism (1906a) it may be doubted whether cyto- and myeloarchitecture would ever have led to such detailed maps without Flechsig's example. Later Flechsig made alterations in his map and increased the number of areas. Although he protested (1901) when Hitzig drew a map without his authorization, we have taken the liberty of drawing one from his data given in 1920 (Fig. 1). In this map the cross-hatched zone is myelinated at birth; the zone of parallel lines is myelinated between birth and one month after birth; the clear zones are myelinated later.

Analysis of the cerebral cortex received another impetus from Hammarberg (1895). This young Swedish worker, whom a fatal appendicitis removed far too soon from a promising career, was primarily concerned with the brains of idiots. To do a thorough job, however, he had to describe and measure normal brains and, in the course of that work, he demonstrated the cytoarchitecture of some areas, giving the only numerical data available before Economo and Koskinas (1925).

Cytoarchitecture in the modern sense of the word got under way shortly after the turn of the century, with Campbell (1905) and Brodmann (1907). "Localization" appears in the title of both their studies, since they both took function localization for granted. That this conception had its root in the phrenology of Franz Josef Gall is too well known to need retelling. Its early history, particularly as it relates to the study of aphasia, has been given by Head (1926). In the latter part of the nineteenth century, the facts about the sensory and the motor function
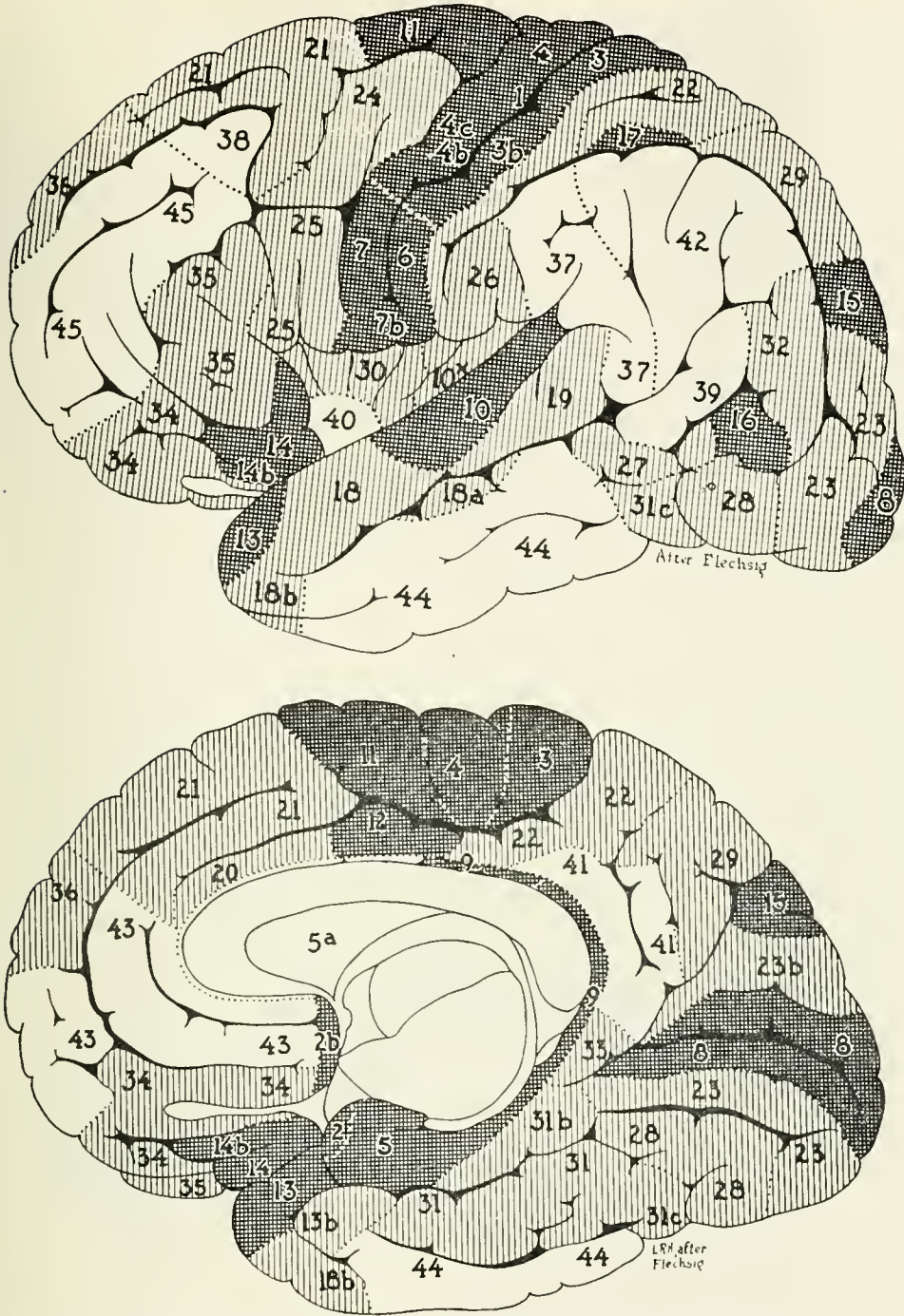
FIG. 1. Myelogenetic map of the cerebral cortex. Redrawn and altered slightly from Flechsig. Cross-hatched—primordial areas; lined—intermediate areas; plain—terminal areas.

of the cortex added, or so it seemed, new proofs to the theory of localization of function. That these functions were based more on extrinsic connections of these areas with other parts of the nervous system than on their intrinsic structure was, if not overlooked, then at least not investigated systematically.

Brodmann and Campbell followed Flechsig's example in publishing cortical maps (Figs. 2 and 93, see p. 190), and soon one textbook after another copied at least one of them. Brodmann never gave a detailed description of the areas indicated on his map of the human brain. He had done that only for the cercopithecus (1905); external circumstances and his untimely death prevented him from publishing a similarly thorough analysis of the human brain. It is strange that for many years the scientific world has accepted statements, and built upon them, for which no direct proof had ever been given.

The forty odd years which have elapsed since the classical period of cytoarchitecture have seen attempts in two directions. There was clearly a job for the comparative anatomist. Brodmann and Campbell had made forays into that field, but there was obviously work for several generations. Mott, Woollard, and LeGros Clark in England, the Vogts and their associates in Germany contributed to our knowledge, which was reviewed, as far as it was germane to anthropogenesis, by LeGros Clark (1934). Brodmann's original conception of an increasing differentiation during evolution seemed amply confirmed. It is well to remember that, for Brodmann, differentiation meant higher perfection. It seemed to him logical, therefore, to expect and to search for ever more detailed subdivisions of the human cerebral cortex. Indeed, the Vogts and their coworkers described more than a hundred different areas in the human brain on the basis of myeloarchitectural studies. This was imposing, but also quite bewildering. For not everyone saw the subtle distinctions which the Vogts described and, while politely admired, the teachings of the Vogts had little influence (except for Foerster) on general neurological thought. Even the grandiose attempt of Economo who, with Koskinas (1925), published a voluminous atlas and gave a detailed description of each area, did not mend matters a great deal. By and large, Economo (1927) kept close to Brodmann's areas. Lorente de Nó (1949) once called it an "unsystematic elaboration" of Brodmann. M. Rose's (1935) account of the isocortex is little more than an abstract of Economo and Koskinas.

Since Brodmann's classification was based on ontogenesis, there was need for more detailed knowledge of cortical development. M. Rose (1926) has published an elaborate classification of the cerebral cortex based on its histogenesis as follows:

I. Cortex semiparietinus sive striatalis [semicortex (Regio praepyriformis, Tuberculum olfactorium, Regio periamygdalaris, Regio diagonalis, Septum pellucidum)].
II. Cortex totoparietinus sive pallialis (Totocortex).
    a) schizoprotoptychos (Schizocortex).
        α) parvumstratificatus (Regio praesubicularis, Area perirhinalis).
        β) multistratificatus (Regio entorhinalis).
    b) Holoprotoptychos (Holocortex).
        α) bistratificatus (Cornu Ammonis, Subiculum, Taenia tecta, Fascia dentata, Regio retrobulbaris).
        β) quinquestratificatus (Regio infraradiata, Regio subgenualis, Regio retrosplenialis granularis, Regio retrosplenialis agranularis).
        γ) septemstratificatus (Regio frontalis, Regio parietalis, Regio temporalis, Regio occipitalis).
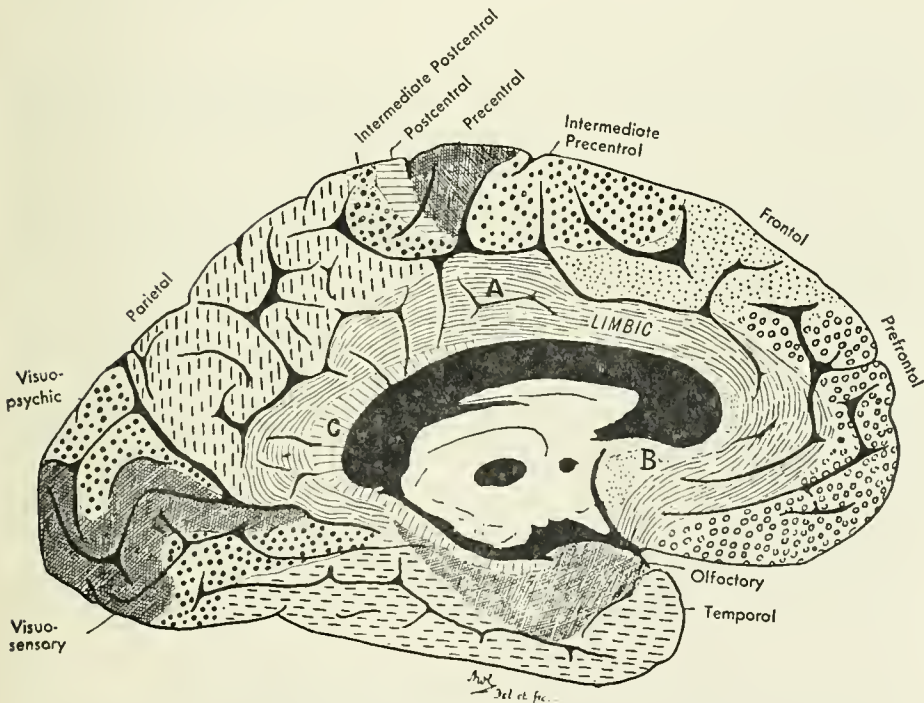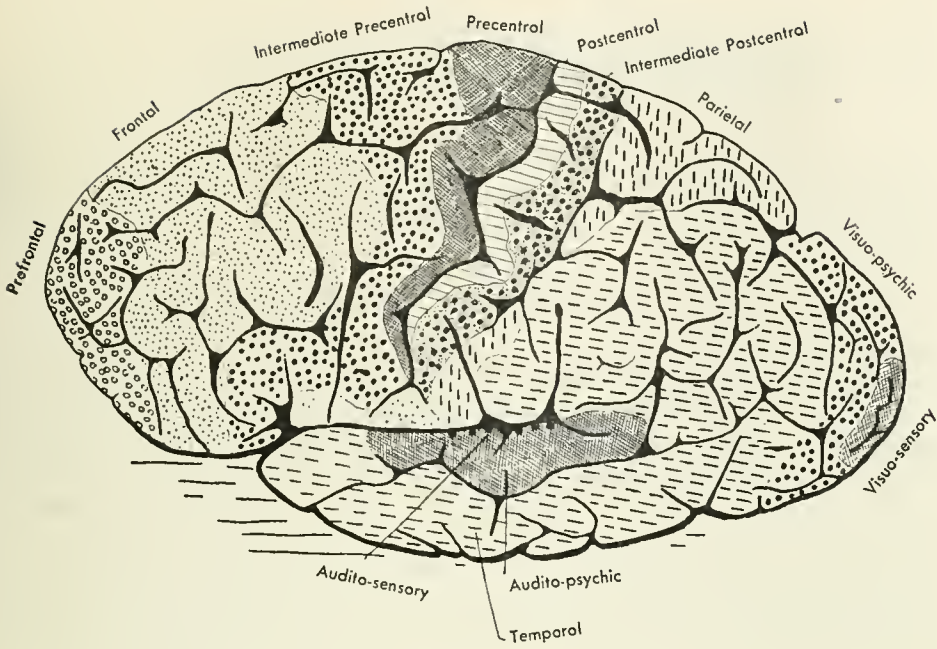
FIG. 2. Campbell's map of the cerebral cortex.

III. Cortex pallio-striatalis sive bigenitus (Bicortex).
        α) quatuorstratificatus (Area praepyriformis I).
        β) septem- (octo) stratificatus (Regio insularis agranularis).
        γ) novemstratificatus (Regio insularis granularis et propeagranularis).

After a long, detailed study of the morphogenesis of the cerebral cortex, Ed. Beck (1940) concluded that "Rose's teaching concerning the histogenesis of the cortex is incorrect in all of its statements and, therefore, has shown itself to be erroneous."

Filimonoff (1947) has also criticized the system of Rose. He states:

Our classification is based on quite another concept than that of Rose which, in our opinion, is particularly erroneous with respect to his "schizocortex." Rose considers this portion of the cortex in contrast to his "holocortex," presented in his scheme as a unit and including such actually heterogeneous structures as the isocortex and Ammon's cortex. Our investigations would show that the relations are just the reverse: The schizocortex ("periarchicortex" in our terminology) occupies a place intermediate between Ammon's cortex (archicortex) and the isocortex, since Ammon's plate can by no means be considered as a homologue of the isocortical plate. Our understanding of the semicortex (cortex semiseparatus, not cortex semiparietinus in the sense of Rose) is also entirely different. The cortex bigenitus occupies an intermediate place between the isocortex and the allocortex both in our classification (perisemicortical zone) and in the Rose system (between the cortex totoparietinus and the cortex semiparietinus). However, we understand this intermediate position in a quite different sense, since our concept of the genetic character of the claustrum is quite a different one.

Filimonoff summarizes his system as follows:

The main territories of the cerebral cortex are designated in our scheme as cortex completus or isocortex (after O. Vogt); cortex incompletus, or allocortex (after O. Vogt), but with considerable limitations (allocortex *sensu strictiori*), and cortex intermedius, or periallocortex.

The cortex completus, or isocortex, includes the whole territory within which the end brain wall is characterized, even in relatively early stages of development (27 mm. stage in our material), by the presence of all the fundamental layers of His, including the clearly differentiated cortical plate.

The cortex incompletus, or allocortex *sensu strictiori*, includes, first, the semicortex, or semicortical zone, to which belong the tuberculum olfactorium, the diagonal zone, the septum pellucidum, the periamygdalar region, and the prepiriform region, but the latter only partly, since, as a matter of fact, it presents a transition from the semicortex *sensu proprio* to a cortex of higher type, namely, the cortex intermedius (perisemicortex). The second main territory of the allocortex is represented by the archicortex, or the archicortical, or Ammon's zone, which includes the subiculum, the cornu ammonis, the fascia dentata, and the tenia tecta (indusium corporis callosi).

The cortex intermedius, separating . . . the semicortical and archicortical zones (forming together the cortex incompletus) from the cortex completus, is divided, like the cortex incompletus, into two zones—the perisemicortical and the periarchicortical zone.

The perisemicortical zone includes the intermediate insular formations and partly also the prepiriform region, which can thus be referred to the semicortex in a rather conventional sense.

The periarchicortical zone includes the presubicular and the entorhinal region.

The presubicular region is situated in the immediate neighborhood of the archicortical zone and surrounds it almost completely. It is, accordingly, represented not only by the temporal but also by the retrosplenial, supracallosal and subgenual parts.

Most of this controversy is irrelevant to our study, since we deal with the iso-cortex, but it should be remarked that we propose to include under this term most of the insular cortex and the anterior limbic cortex which Rose did not include in his holocortex septemstratificatus.

Recently Eduard Beck (1950) has begun to publish again and Elisabeth Beck (1949), in England, has made a study of the orbital frontal cortex which differs little from the analysis of Economo. The attempts of Mettler (1949) to reconcile Brodmann and Economo might also be mentioned. These latter studies have been provoked by the extirpations of neurosurgeons in their attempts to found a psycho-surgery.

Various pupils of the Vogts have been elaborating on the old Vogt scheme, using cell- as well as myelin-preparations. Gerhardt (1940) has analyzed in detail the parietal lobe, Ngowyang (1934b) and Strasburger (1937) the frontal lobe, M. Rose (1927) the limbic lobe, Brockhaus (1940) the island, Kreht (1936) and Knauer (1909) the inferior frontal gyrus, and Lungwitz (1937), M. Vogt (1929) and Ngowyang (1934a) the occipital region.

The Russian school at the Brain Institute in Moscow has followed traditional lines, using the terminology of Brodmann. We possess now four elaborately illus-trated volumes of their studies. Their chief characteristics are the insistence on limitrophic regions and on variations from brain to brain (O. Vogt, 1929; Blinkow & Poliakov, 1938).

The efforts of all these authors were meticulous to the point of hair-splitting, yet they suffered, so it would seem, from a basic weakness in our understanding of the functional importance of architectural differences and merely served to make our knowledge of the cortex anatomically top-heavy. Indeed, until the advent of Berger's encephalography and the oscilloscope, introduced to neurophysiology by Gasser and Erlanger, no method to assess architectonic differences from a functional point of view was available. What the differences in the Nissl picture or in the dis-tribution of myelinated fibers meant for the intrinsic function of the cortex was hardly ever asked; as early as 1899, Hans Berger, then an assistant in Binswanger's clinic, noted the inadequacy of the available methods of study for the functional analysis of the cerebral cortex and embarked on the search which finally led him to the development of electroencephalography. It enabled, for the first time, an attempt to justify the areal subdivisions by appeal to other than anatomical methods. Kornmüller (1937) made the first systematic investigation on the rabbit. His statement that each "area" has its characteristic pattern of electrical activity has, however, not been generally accepted. Garvin and Amador (1949) found in the macaque significant differences from the general type in the pre- and postcentral regions, and in the occipital region, but were otherwise unable to correlate the type of spontaneous activity (under Dial or local anesthesia, recorded with ink-writers) with the cytoarchitecture.

The electroencephalographic record is difficult to interpret in any case since the exact way in which it arises is not yet understood. Rosenblueth and Cannon (1942) showed that the electrical response of different parts of the cortex to an artificial stimulus varies and, therefore, the intrinsic structure of the cortex influences the pattern of response. This still leaves the recognition of the responsible histological

differences an unsolved problem. One might expect help from theoretical work. Experimental information about the properties of single nerve cells has been provided by Lorente de Nó (1947) and the neuronal processes underlying the electrical activity of the brain have been studied and analyzed by Bremer (1949), O'Leary (1949), Walter (1950), and many others, yet the theoretical work has not been carried far beyond the stage of simple random nets (see Ward, 1950). In short, we are still severely hampered in any effort to evaluate the areal differences as to their functional significance and any subdivision of the cortex can, therefore, be only tentative.

Chapter II: Growth and Weight of the Brain

Since the babe is born with a forebrain almost entirely devoid of myelin, hence chemically very different from that of the adult, man begins his pilgrimage on this earth without cerebral hemispheres.

P. FLECHSIG (1896)

In the young embryo, the cranial end of the neural tube is beyond that of the notochord. It is known from numerous experiments that the notochordal tissue acts as an organizer during the next stages of the development of the neural tube. Obviously, the prechordal part of the neural tube will undergo a different development than that of the epichordal part. To distinguish between an acrencephalon and chordencephalon (Dalcq, 1946) appears, therefore, of greater significance than the traditional distinction of three and, later, five vesicles. The acrencephalon is identical with the primitive prosencephalon, the chordencephalon comprises the mesencephalic and the rhombencephalic vesicles. Kingsbury (1922) held many years ago that the acrencephalon never possesses a true floor plate and basal plate but consisted exclusively of alar plate and roof plate. Even now, when it is recognized that the differentiation into these components is brought about by the notochord, Kingsbury's ideas still serve to demonstrate the futility of applying the concepts of segmental anatomy to the forebrain.

That the differentiation of the prosencephalon into telencephalon and diencephalon follows the development of optic vesicle and olfactory placode was shown experimentally in amphibia. But one has only to glance at Hochstetter's (1919, 1929) or Retzius' (1896) figures to convince oneself that the telencephalon shows, in man, a vigorous growth from the very beginning, much too vigorous to be explained by the influence of an olfactory placode alone. "The development of the nervous system is the result of many factors. Among these factors some . . . are inherent in certain regions of the embryonal nervous system, and are evidently inherited. . . . " (May, 1945).

The differentiation of the telencephalon into pallium, basal ganglia, and rhinencephalon is too well known to be retold here once more in detail. The formation of the cortex within the pallium was studied by Vignal (1888), His (1904), and Ziehen (1906). Vignal (1888) recognized the gradual change in the character of the cells constituting the cortex. He saw the first appearance of the molecular layer at the end of the first month and the differentiation of the white matter between the second and third months. His (1904) appears to have been the first to put forward the conception that the cells forming the cerebral cortex migrate from the ependyma to their definitive position, a conception that was to be elaborated by M. Rose (1926) and made the basis for a complicated system of cortical types (see p. 8). This migration begins at about eight weeks of embryonal life; it continues— with gradually diminishing density, one should expect—all through fetal life and even a short time after birth (Mellus, 1912). But the prenatal growth of the cortex is not an approximately linear function of time. In the pig's fetus Flexner, Flexner,

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and Strauss (1941), who give excellent photomicrographs, observed from 55 to 61 days a rapid growth of the cortex. The cells increase in size, change from a round to an oblong shape, and show an increase in Nissl substance. Then things appear to settle down for a while, to be followed by another spurt between 90 and 108 days, when the cells begin to assume the shape of adult neurons and when, a few days later, fissuration of the cortex begins. In the fetal guinea pig Peters and Flexner (1950) observed "a series of sharply defined morphologic and biochemical changes" at a gestation period of 41 days. In man, Scammon and Hesdorffer (1935a) found a "very rapid increase" of the cerebral surface in the fourth lunar month and "a very vigorous increase" in the seventh and eighth lunar months. One is tempted to generalize to all mammals. Koch's (1913) observations show, however, that the time scale may vary widely from species to species. The newborn rat's cortex is, as far as its chemical composition is concerned, as immature as that of a 100 mm. pig embryo. Areal differences of the human cortex can be distinguished in the seventh month (Lorente de Nó, 1934; Wen, 1933) and are well pronounced at birth. But the cortex of the newborn (Conel, 1939) is still immature. Its cell density is higher than it is later. The fibers of the white matter subjacent to the cortex as well as those within the cortex are in many areas (see p. 7) still without stainable myelin sheaths. Moreover, the areal differentiation has not yet attained its full measure.

The increasing importance of cytochemical and similar studies makes it desirable to review briefly some chemical investigations on the fetal cerebral cortex before considering the growth after birth.

Hydén (1947) has recently pointed out that the outgrowth of axons during maturation demands a tremendous increase of substance, e.g. an axon of an anterior horn cell contains about one thousand times more volume than the perikaryon from which it stems. This order of magnitude may also be correct for the cortical cells which give origin to the pyramidal tracts. From the very beginning, the cytoplasm of nerve cells and their nucleoli are rich in polynucleotides. That the increase in proteins as well as in lipids progresses unevenly has been known for a long time and has recently been reviewed by Needham (1931) and May (1945). As Koch and Koch (1913) pointed out, proteins and some phosphatids are the main constituents of the brain during the early stages of development. After birth, when medullation begins [Koch and Koch worked on the rat], phosphatid formation flares up. During a concluding period of growth, the increase in all substances, excepting cerebrosides, slows down. These latter "come into view [in the rat!] between the 20th and 40th day after birth. . . . They contribute a large share towards medullation."

An increase in cerebrosides after birth was found in man by Schuwirth (1940) who investigated the lipids of the growing human brain with modern methods.

Klüver (1944 a and b) showed that the white matter of the cerebral hemisphere contains a coproporphyrin. Investigating growing rats he found that it appears first in the spinal cord, and later at successively higher levels. The postnatal development of the nervous system is characterized by an "ascending porphyrinization."

Some enzyme systems have recently attracted attention. Flexner and Flexner (1946) investigated the fetal pig. At the first spurt of growth the content of succinic

dehydrogenase increases and continues to do so until birth when it reaches the adult level. At the same time, i.e., about the sixtieth day of gestation, the cytochrome content, very low previously, begins to rise, to reach a little less than 50 per cent of the "mature" level at birth (Flexner, Flexner, and Strauss, 1941). In the rat's brain Potter, Schneider, and Liebl (1945) found a sharp increase of succinic dehydrogenase after birth, together with a similar, although not quite so sharp, increase of adenosinetriphosphatase.

The human cerebral cortex is, as everyone knows, by no means "mature" at birth. Conel (1939, 1941, 1947) has traced its histological differentiation up to the third month after birth and Aldama (1930) investigated the brains of children of one and of five years respectively. But we know, ever since Flechsig published his myelogenetic studies (for a review see Flechsig, 1920), that the cortex is not fully provided with myelinated fibers until long after birth. The third frontal convolution, i.e., Broca's area, appears to have been the favorite object. Its myelogenesis was studied by Aranovich (1939), the cytoarchitectural changes were investigated by de Leonardis (1948), who found an increase in cell size paralleled by a decrease in cell density, up to three years of age.

Since the brain increases in mass, although less than many other organs, up to about twenty-five years, when the basilar suture of the skull finally is obliterated, there must be some slight further development of the cortex, although of a less spectacular and profound character than during the prenatal period and early childhood. Aldama (1930) found indeed that the cortex of the five-year-old still showed a greater cell density than that of the adult and Kaes (1907) reported an increase in myelinated fibers up to about the fortieth year of life (see Economo and Koskinas, 1925, p. 22).

The increase of the brain in mass was analyzed on the basis of several series of previous observations by Dunn (1921), Scammon and Dunn (1922), Pearson (1925), Scammon and Hesdorffer (1935 a and b, and 1936) and Grenell and Scammon (1943), who list most of the older literature. All authors studied the growth of the brain as a function of time. This promises indeed to throw more light on the basic processes of growth than "allometric" formulae (also given by Dunn) representing growth as a function of body weight, which itself depends upon those processes within the different organs one sets out to elucidate. For prenatal growth, Dunn (1921, Fig. 34) demonstrated for the brain as a whole as well as for its major parts what has become known since as the "neural" type of growth (Scammon, 1930). The curve rises very gently up to the third month. Between the third and seventh month, increase becomes more and more rapid, to continue at an even pace for the rest of the intra-uterine development. The brain appears serenely to go its way, undisturbed by the disproportionate development of the liver, by the stormy events in the kidney or by the hesitating progress of the intestinal tract.

A similar behavior was found for the postnatal development of the brain by Scammon and Dunn (1922) on the basis of 2,951 observations recorded in the literature but not cited explicitly in their short communication. They felt justified in pooling males and females, and arrived at a smooth curve rising very steeply during the first year or so, and then gradually flattening out. After five years of age, the increase amounts to about 15 per cent.

Pearson (1925) analyzed the German data of Wendt, Marchand, and Bischoff as well as the English data of Boyd and found—evidently by inspection; details are not stated—a growth curve which shows a "pubescent dip" which, to quote him verbatim, "is not a mere point of contraflexure but an actual depression." While Pearson does not take issue with Scammon and Dunn, his conclusions are obviously in sharp contrast to the concept of neural growth.

From the data of Wendt (1909), Marchand (1902), and Bischoff (1880), which Pearson used, the means and standard errors given in Table 1 have been computed. The graph of Figure 3 shows these results once more and shows also, as could be proven arithmetically, that they are compatible with Scammon's conception of neural growth. Pearson's "pubescent dip" appears to be merely a vagary of random sampling.

Brain weight slowly decreases after the prime (twenty to twenty-five years) with advancing age, as Pearl (1905) showed with all statistical refinement. His results, so he stated, were "strong presumptive evidence of the essential correctness of the conclusion reached." This regression of brain weight with age has been confirmed by Appel and Appel (1942) (See our Fig. 4).

TABLE 1

Brain Weights of Males (Pooled German Data).

Age (years)	Means (grams)
7–8	1320 ± 25.0
9–10	1393 ± 45.0
11–12	1375 ± 37.2
13–14	1377 ± 25.3
15–16	1382 ± 23.2
17–18	1393 ± 20.0

To weigh the human brain is not as easy as it sounds. The definition of "brain" as everything cranial to the decussation of the pyramids might be considered as agreed upon. But the decussation is not a point and different observers, with different skills and perhaps different material, may sever brain from cord systematically at a higher or lower level. When the probable error of a mean, based on a large series, will be no more than a few grams, these differences in technique may become serious. How to treat the meninges and how to drain the cerebrospinal fluid are points that might be considered settled; they are, in any event, under the control of the observer and, therefore, can be standardized. What cannot be standardized, however, is the time elapsed between death and removal of the brain, or the temperature at which the cadavers are kept during that period. Chemical changes (in the widest sense of the word) affecting the brain weight go on after death, tending as Appel and Appel's (1942) curve (see Fig. 5) suggests, toward an equilibrium reached after several days, that differs appreciably from the original weight.

The sampling process, too, is by no means above reproach. Almost all series are based on the populations of large hospitals, and these are not true random samples of the population at large, but only of the lower social strata. How economic conditions can lead to changes in the dissecting room population—a much more highly selected group, it is true—and can lead to considerable changes in estimates of brain weight was dramatically told in a speech by the late T. Wingate Todd (1927).
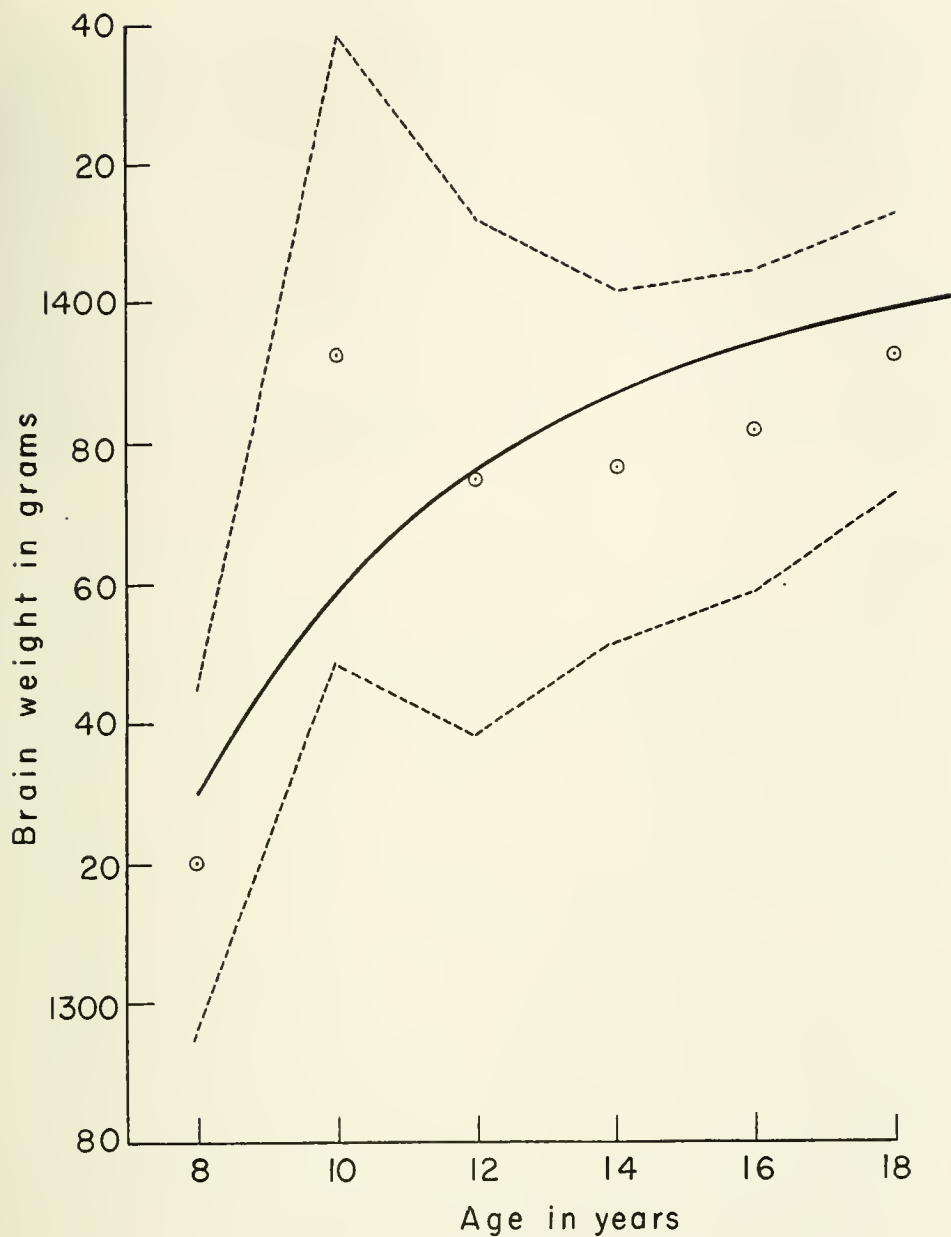
Fig. 3. Growth curve of brain between eight and eighteen years. Males of Wendt, Marchand, and Bischoff. ⊙ indicates means; – – – – indicates standard errors; ——— indicates drawn by inspection.

It is difficult, sometimes even impossible, to correct for all the factors just enumerated, and we generally have to accept the data as they are given. The older literature has been discussed and worked through by Pearl (1905); another American

series was worked up by Appel and Appel (1942) who enjoyed Pearl's advice until his death. Of late, interest in brain weight appears to have been lively in Italy and in Japan, but very few contributions from other countries are available. The male means and their standard errors, which could be computed, are given in Table 2. Males only have been given because they are for most series more numerous than females. We have, furthermore, only given series based on more than fifty specimens.
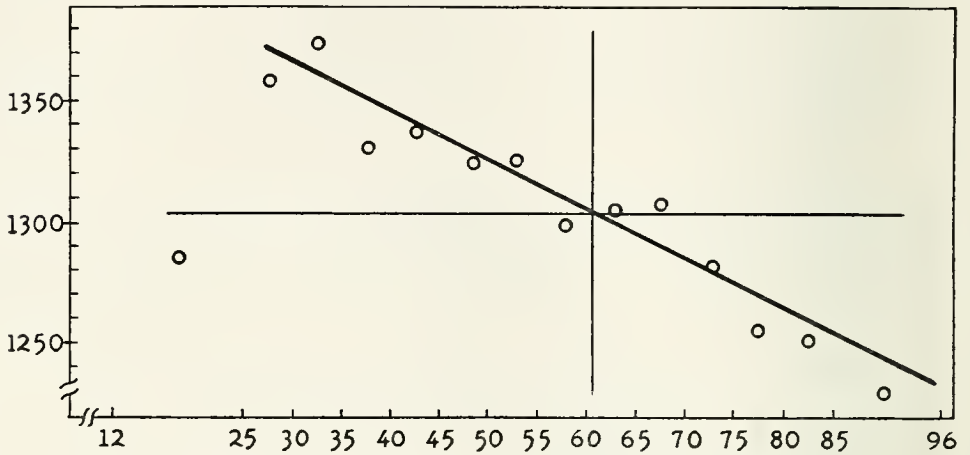
FIG. 4. Regression of brain weight with age at death (from Appel and Appel).
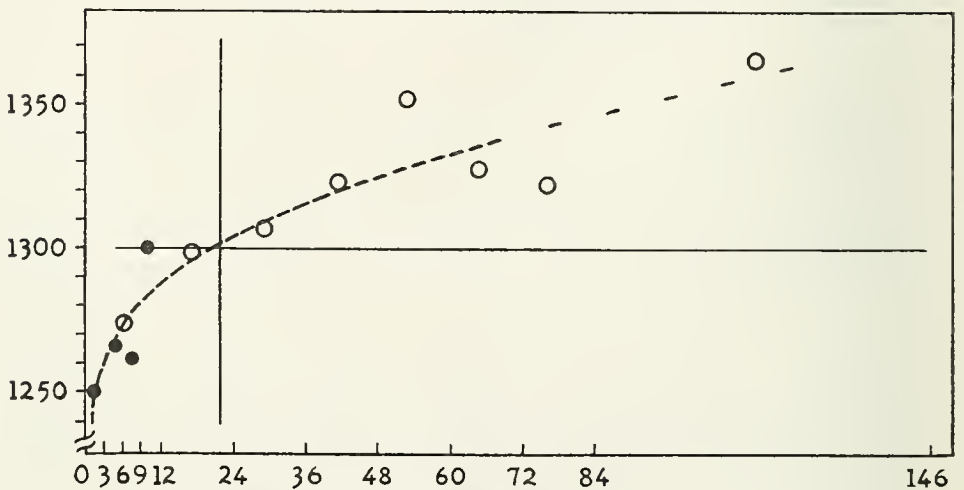
FIG. 5. Curve of brain weight after death (from Appel and Appel).

There is no significant difference between Bavarian, full-blooded Negroes, Florentines, Sardinians, Koreans, and Japanese. Higher than these are Hessians and Swedes who do not differ significantly from each other. The grouping is queer and reflects, one fears, differences in technique of measuring as much as differences due to "race." To accept, for the species *Homo sapiens* at large, a male weight of 1,345 gm. appears justified. (The weighted mean of all series is 1,343.6 gm.)

The surface of the cortex has been measured repeatedly and by several methods. Wagner (1864) covered the surface (of brains which had been fixed in alcohol) with gold leaf. He reports on the brain of the mathematician Gauss, the clinician Fuchs and of a workman and a woman. His figures in cm.² were 2,196, 2,260, 1,877, and 2,041, respectively. Henneberg (1910) used tissue paper instead of gold leaf and found an average of 2,226 cm.² for four brains. Calori (1870) was concerned with the difference between brachycephalics and dolichocephalics. From nineteen males of the former and sixteen males of the latter he obtained 2,438 ± 45 and 2,302 ± 40 cm.² (the difference, 136 ± 60 cm.², is barely, i.e., only on the 5 per cent level, significant). Aresu (1914), who gives a detailed account, added four males, with an average of 2,317 cm.², as well as four females with an average of 2,065 cm.² Leboucq (1929) covered the brain with a sugar solution of known concentration, determined quantitatively the amount of sugar used, and from these data the surface covered. Once the constants are known, the method is rapid. Thus

TABLE 2
Brain Weights of Males.

	N	Brain Weight (grams)	Reference
Negroes (Kenya)	324	1276 ± 7.1	Vint, 1934
Americans (white)	2080	1305.3 ± 1.9	Appel and Appel, 1942
French	292	1325 ± 7.1	Blakeman, 1905
English II	117	1328 ± 9.6	Blakeman, 1905
English I	340	1335 ± 6.7	Blakeman, 1905
Negroes (American)	139	1354.8 ± 10.2	Pearl, 1934
Japanese	342	1359.5 ± 4.0	Kusumoto, 1934
Bavarians	559	1363.2 ± 3.3	Pearl, 1905
Koreans	136	1369.5 ± 5.9	Shibata, 1936
Florentines	100	1373.2 ± 6.5	Castaldi and Bray, 1934
Russians (Irkutsk)	74	1383 ± 14.3	Chodos, 1929
Hessians	475	1391.7 ± 3.5	Pearl, 1905
Swedes	416	1400.5 ± 3.5	Pearl, 1905
Bohemians	372	1454.8 ± 4.0	Pearl, 1905

N = Number of individual observations.

for fourteen male brains, he obtained an average of 1,982 ± 26 cm.², a value that is significantly lower than that of Calori. Kraus, Davison, and Weil (1928) determined the cortical surface by measuring with a perimeter. Corrected for shrinkage they gave 2,895.4 cm.² for the entire surface of both hemispheres, and 639.18 cm.² for the visible surface (excluding the walls of the median longitudinal fissure).

The ratio of free to buried surface was given as 1:1.8–1:2.7 by Henneberg (1910), as 1:1.97–1:2.21 by Jensen (1875), but works out as 1:4.53 from the data of Kraus et al. if the surface in the walls of the median longitudinal fissure is ignored or 1:2.83 if it is included.

The volume of the cortex was directly determined by Jaeger (1914) [cited by M. Rose, 1936] using a planimeter on serial sections. He obtained 540–580 cm.³ for the cortex, and 400–490 cm.³ for the white matter of both hemispheres.

The total number of cells in the cerebral cortex was estimated by Economo and Koskinas (1925) as of the order of 10^{10}. Agduhr (1941) has given a critical review

of their procedure and pointed out that the Viennese authors had not taken into
account the varying size of the nerve cells. To quote Agduhr: "The number of
cells with a mean transverse diameter of 1 mm. (at a magnification of 100×) is
to be multiplied with 0.8, those ... with a diameter of 5 mm. by 0.333, etc."
Economo and Koskinas' estimate is, therefore, too high by a factor of 2 or 3.
Agduhr's concluding remarks, "These ... figures are impaired by such methodolog-
ical deficiencies that they cannot be accepted even as approximately accurate,"
are perhaps exaggerated. Nevertheless, the cell/gray coefficient, devised by
Economo (1929b) as a measure for the degree of organization of the cortex, and
given by him for the human brain, may be quite erroneous. We have not yet
determined it satisfactorily from brain *Hl*.

Chapter III: Fissures of the Brain

A science which hesitates to forget its own history is lost.

A. N. WHITEHEAD (1929)

With a few exceptions, the fathers of anatomy paid little attention to the cerebral cortex and it has rightly been remarked that their drawings of the cerebral hemisphere "resembled more a plate of macaroni than the organ of the human mind." Interest in the cerebral cortex began with Franz Josef Gall, of phrenological fame. After the Napoleonic Wars the sulci and gyri of the cortex excited the intense interest of many of the best minds among morphologists and neurologists. Leuret and his pupil Gratiolet (1839–52), who made the first grand attempt at a comparative anatomy of the cerebral cortex, set out to find a common type of fissures in all mammals. The premise that all mammals exhibited in their cerebral fissures only variations of a common theme, as it were, was tacitly accepted for a long time and is perhaps still held by some workers. For it is only gradually and quite recently realized that most classes of mammals, and among them certainly the primates, evolved from ancestors which were quite small and had lissencephalic brains. That these early ancestors were small can generally be directly demonstrated by their fossil skeletons or teeth, that they had lissencephalic brains can be inferred from the so-called law of Baillarger (1845) and Dareste (1852), pronounced first at about the time when Leuret and Gratiolet published their monumental work. A direct demonstration has only quite recently come forth in the case of the horse (T. Edinger, 1948).

"The comprehensive conception of the problem which Leuret had was abandoned by most subsequent workers," complained Meynert in 1877. More by instinct perhaps than by clear reasoning, of the sort just indicated, most authors who tried to elucidate the fissural pattern of the human brain by the comparative method restricted their studies to primates.

The list of authors who studied large numbers of human brains is imposing, and the job of describing the cerebral sulci appears to have been done with exhaustive thoroughness.

Many of these authors searched for racial differences in the sulcal pattern. Our knowledge of the racial anatomy of the human brain is still fragmentary, but enough is known, as we hope to show, to make it abundantly clear that a description of a few specimens is quite useless, that only longer series and the statistics deduced from them can form the basis for a physical anthropology of the brain.

Many of the series we have been able to gather from the literature come from Europe: Swedes (Retzius, 1896), Irish (Cunningham, 1892), Dutch (van Bork-Feltkamp, 1930), Germans (Connolly, 1950), Poles (Weinberg, 1905), Esthonians (Landau, 1910, 1911, 1914), Russians (Zernov, 1877). We are quite well informed about the Chinese (van Bork-Feltkamp, 1930; Chi and Chang, 1941; Shellshear, 1926) [Kurz's (1924) biased report on only seven brains has not been used]. We have some knowledge of the Negro's brain (Vint, 1934; Slome, 1932; Connolly,

21

1950) as well as of that of the Australian (Shellshear, 1937). To these we can add the Malay (Kohlbrugge, 1906). Some other accounts dealing with special features will be mentioned as occasion arises.

Most of these descriptions give no more than frequencies of fissural types and it is often doubtful, as will be seen, whether the interpretations of all authors were the same. Encephalometry, as laid down by Ariëns Kappers (1926) or by Economo (1929c), has only recently been employed. To a man, the older authors did not analyze their percentages statistically. With the information they had, they could not. But it is not difficult, and long overdue, to add the sampling errors to their data and thus to decide whether racial differences of fissural types exist or, when several series of presumably the same racial stock are available, whether various authors interpreted their material in a comparable manner.

The mathematical facts needed for such comparisons can be stated in a few words. The standard error e of a percentage p, based on a sample of N individual observations is

$$e = \sqrt{\frac{p(100 - p)}{N}}$$

and the standard error e_Δ of a difference Δ between two samples having standard errors e_1 and e_2 respectively is

$$e_\Delta = \sqrt{e_1{}^2 + e_2{}^2}.$$

The significance of a difference is judged by the quotient Δ/e_Δ. For samples in which $N > 30$ a value of 2 may be considered suggestive, of 3 or more, significant. For smaller samples, Student's t-test provides a more refined criterion (see R. A. Fisher, 1936).

The older anatomists followed Broca in distinguishing fissures from sulci. The former, so it was stated, were folds of the whole pallium, having therefore a counterpart in a ventricular eminence; the latter were merely indentations of the cortex. But this distinction appears to be of no morphological or functional importance and, moreover, breaks down completely in comparative anatomy. We shall therefore not be consistent. To redefine fissures as those furrows which are found in all gyrencephalic primates, and which we called primary fissures (Bonin and Bailey, 1947), and sulci as those furrows which we called secondary, might suggest itself but engenders confusion.

Even a superficial acquaintance with human cerebral fissures makes it clear that many of them are quite variable, that the first problem must therefore be to enumerate those fissures which are constantly present and of fairly regular shape. These fissures may be called the primary fissures.

To know the laws which govern the formation of cerebral sulci, or to know at least which features of cerebral fissuration are determined genetically, should help materially in directing our efforts. But the process of fissuration during ontogenesis has only rarely been studied. Until the fifth month of fetal life there are no sulci on the lateral surface of the human brain (Ecker, 1868). Previously described furrows have been proven postmortem or fixation artifacts. On the medial surface, however, a shallow groove appears in the third month which extends from the

region of the olfactory bulb to the tip of the temporal pole (Hines, 1922). This, Hochstetter (1924) says, is the sulcus parolfactorius posterior. Elliot Smith (1931, p. 269) agrees that there is no fissura hippocampi.

At the end of the fourth month, or the beginning of the fifth, there is an elongation of the occipital region of the cerebral vesicle. There are no sulci on the lateral surface of the cerebral vesicle at this age but the Sylvian depression is very evident, outlining the island. On the medial surface appears first the calcarine fissure and a couple of weeks later the parieto-occipital (Connolly, 1950).

At the beginning of the sixth month appears the central sulcus and, during the sixth month, also indications of the precentral and postcentral sulci. On the medial surface the sulcus cinguli appears.

At the beginning of the seventh month the intraparietal and parallel sulci develop. By the end of the seventh month most of the principal sulci are evident. The insula is beginning to be covered in its posterior portion. The anterior horizontal branch of the lateral fissure is formed. The olfactory sulcus is well developed. The fissuration of the brain of a human embryo thirty weeks old, from our collection, is shown in figures 6 and 7.

Until about the middle of the eighth month the course of development is fairly consistent. After that stage sulci appear rapidly in great confusion and inconstancy. To take an example, three frontal sulci, as classically described, may appear on one hemisphere, whereas the opposite hemisphere of the same brain may have an entirely irregular pattern. The same irregularity is to be observed in the parietal, temporal, occipital, and orbital regions and results in the obscuration of all but the primary sulci which were laid down before the end of the seventh month. During the eighth month the island is covered and the brain assumes its adult appearance.

The latest contribution by O. A. Turner (1948, 1950) summarizes the work begun by the late T. Wingate Todd and Y. T. Loo. Todd's death and Loo's return to his native China delayed the completion of this study. Turner had one fetal brain, twenty-two from birth to two years of age ("early postuterine") and twelve of individuals older than two years, i.e., of the "late postuterine" stage. We shall frequently have to cite his findings.

Interest in the genetics of cerebral fissures is quite recent. Karplus (1905, 1921), Sano (1916), Rössle (1937), Geyer (1939), and Higeta (1940) have reported on the cerebral fissures in identical twins. They noted such features as the behavior of precentral and of frontal sulci or the deep or superficial position of annectent gyri. No efforts at encephalometry were made. Rössle who reported on twenty-seven pairs of twins—whether identical or not was generally determined by examination of the twins, not of the fetal membranes or placenta—found that there was no complete concordance between the brains of uniovular twins. "The important dissimilarities can only be understood if we assume that the brain has a particularly high degree of 'developmental freedom.'. . . The brain is the most individualistic of all organs."

Higeta (1940), after examining ten identical and six other pairs of twin fetuses, came to much the same conclusion; his paper is the only one which gives concordances in tabular form. They are, for the characters tested, peculiarly low.

In a short communication—hardly more than a note—Geyer (1939) states that

Inferomedial-left
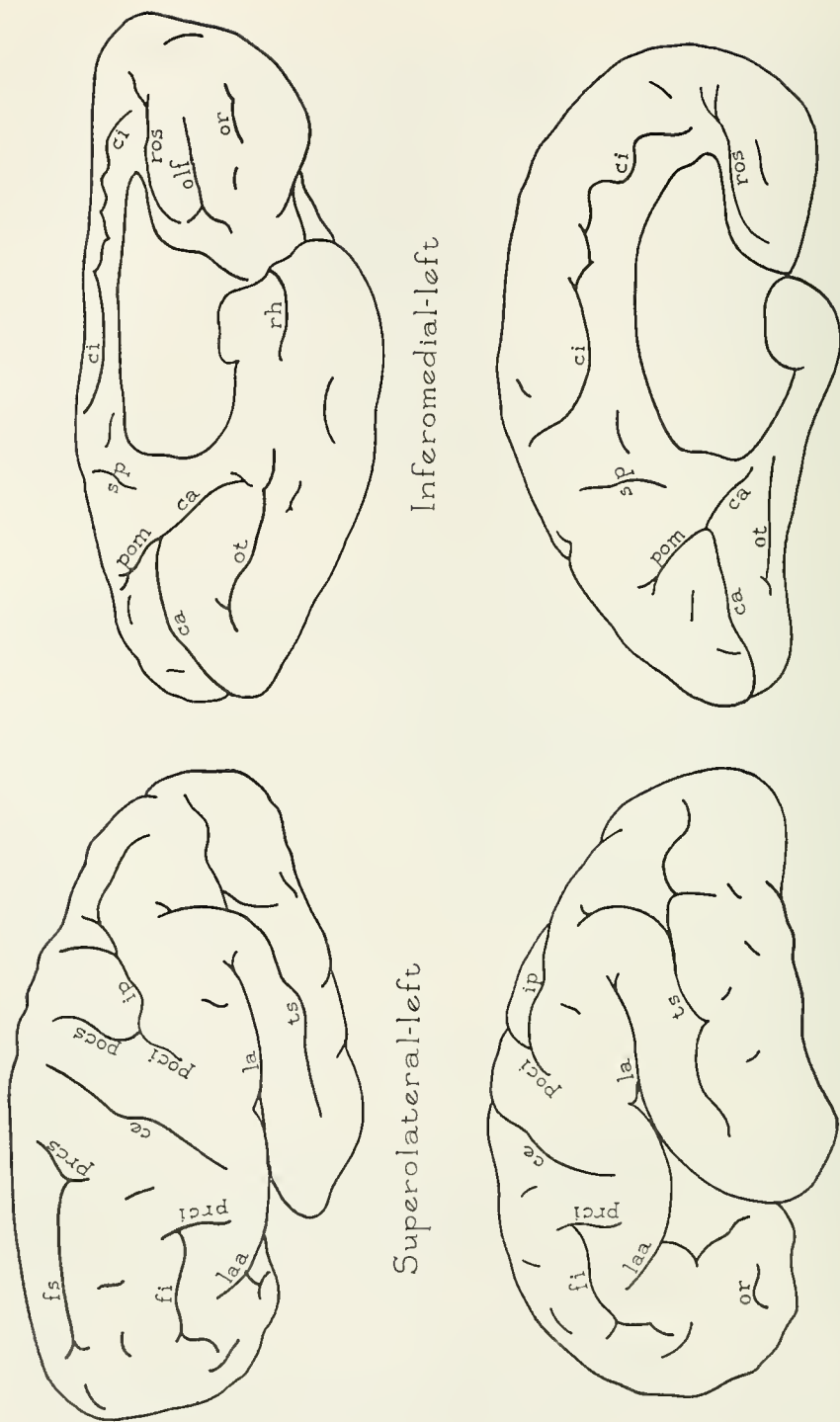
Medial-left

Superolateral-left

Lateral-left

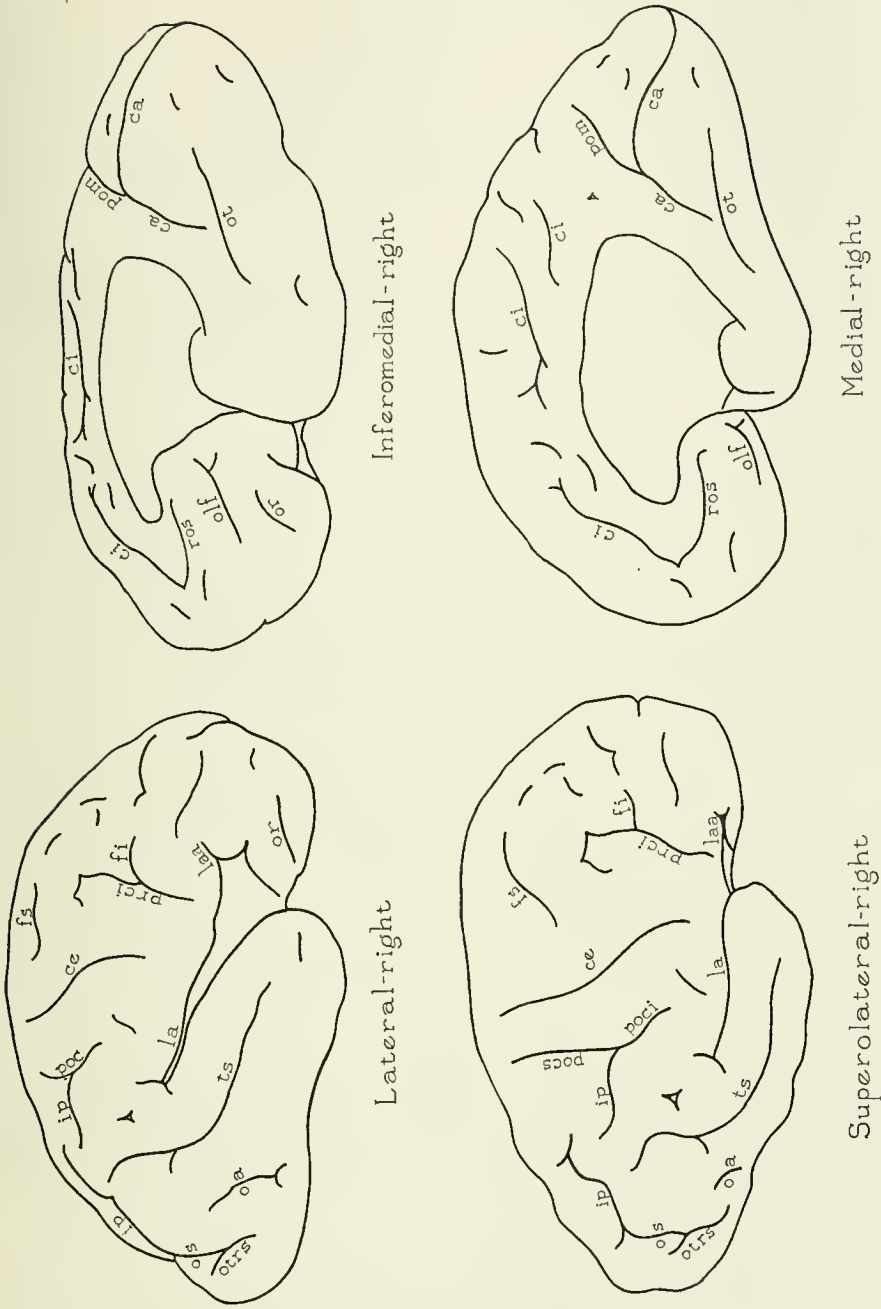FIG. 6. Sulcal pattern of left cerebral hemisphere of thirty-week embryo. For legends see page 28.

Fig. 7. Sulcal pattern of right cerebral hemisphere of thirty-week embryo. For legends see page 28.

the brains of identical twins differ no more than the right and left hemispheres of the same individual. He evidently disregarded, or was ignorant of, the asymmetries which exist between the two hemispheres.

The older anatomists attempted to define the primary fissures by other methods. Wernicke's (1876) was the comparative approach, and later workers such as Broca (1878), Kükenthal and Ziehen (1895), W. Turner (1891), and many others chose the same method. The ontogenetic approach was taken by His (1904), Cunningham (1892), and Retzius (1896). As an exponent of the purely descriptive method Zernov (1877) should be named, although his work, published in Russian, has not received the ample attention it deserves.

In most cases these different methods confirm each other. We adhere as previously (Bonin and Bailey, 1947; Bailey, Bonin, and McCulloch, 1950) to the comparative method. Our interpretations will become clear from what follows, in the study of which constant reference should be made to figures 8, 9, 10, 11, and 12.

I. THE PRIMARY SULCI

The primary sulci will be discussed in alphabetical order. Throughout, we shall have frequent occasion to refer to Dejerine's (1895–1901) classical description.

ca, the *calcarine fissure*. The fissure runs from a point just below and a little behind the splenium of the corpus callosum to the occipital pole where it generally ends in a bifurcation. Its course is at first obliquely dorso-occipital to bend more or less sharply ventro-occipital in its posterior third. At about its midpoint it fuses superficially with the medial parieto-occipital fissure (*pom*, see p. 38).

At its origin the calcarine fissure is separated from the hippocampal fissure by a narrow, sometimes submerged gyrus, the isthmus antecalcarinus of Dejerine (1895), the *pli temporo-limbique* of Broca (1878).

Near the fusion with the parieto-occipital fissure there is another submerged *pli de passage*. This *pli*, as Filimonoff (1932) explained, brings it about that the parieto-occipital and calcarine fissures unite in the depth at a point (φ'' of Filimonoff) appreciably anterior to that (φ') at which they appear to fuse on the free surface. In Filimonoff's eight brains (thirteen hemispheres) the average distance between these two points was 1 cm.

Cunningham (1892) considered it of "deep morphological significance" to distinguish between an anterior and posterior calcarine fissure, divided by the point of fusion with the parieto-occipital fissure. For the two parts arise from different primordia, that of the retrocalcarine appearing later, and only the anterior calcarine fissure has its counterpart in the calcar avis on the wall of the posterior horn. Elliot Smith (1904 a and b) strongly supported Cunningham's conception after a detailed study of the distribution of the striate area. He pointed out that the retrocalcarine (as he called Cunningham's posterior calcarine) was an axial sulcus of the striate area, while the anterior calcarine was a superior limiting sulcus to that area (see also p. 227).

There are generally two submerged gyri within the retrocalcarine sulcus, namely the anterior and posterior cuneolingual fold (Dejerine's π cla and π clp). The posterior one, just behind the fusion of the parieto-occipital and calcarine fissures, is more apt to become superficial than the anterior one. There appear to be no

appreciable differences between right and left or between males and females. Retzius gives 15 ± 3.6 per cent, Cunningham 15.7 ± 3.2 per cent for a superficial posterior cuneolingual fold. The anterior was superficial in only 3 ± 1.7 per cent in Retzius' one hundred hemispheres. Cunningham does not supply numerical data. Van Bork-Feltkamp (1930) gives data for the occurrence of these *plis de passage* but adds that they "were rarely on the surface." Zernov (1877) saw an interrupted calcarine fissure (it is not clear whether the anterior or posterior fold was involved) only once. From Shellshear's (1937) figures it would appear that a posterior *pli de passage* is common among Australians. Inspection of his figures leads to a frequency of 34 ± 8 per cent, not quite significantly higher than that of other races yet certainly suggestive.

The shape of the bend or hook of the retrocalcarine sulcus varies evidently considerably, but no correlation with cranial (i.e., cerebral) index or anything else has been definitely established. Van Bork-Feltkamp (1930) stated that a hook was more frequent in Chinese than in Dutch brains. Huard and Nguyen (1938) report a hook in 32 ± 5.2 per cent among Tonkinese. In Chinese brains Wen (1933) observed a pronounced hook in 44 ± 6.9 per cent on the left, and 13 ± 4.6 per cent on the right hemisphere. This would indicate a significant asymmetry.

The calcarine fissure ends almost always (Zuckerkandl, 1906, gives 96 per cent) in a bifurcation close to the occipital pole. In almost one-half of known cases (46 per cent in Zuckerkandl's European, 51 ± 5.6 per cent in Tonkinese) the two rami end on the medial side. It is more frequent for the superior than for the inferior ramus to encroach on the lateral side.

The course of the calcarine fissure in brain *Hl* is atypical. The hook mentioned a few times is not at Filimonoff's point φ' but within the course of the anterior calcarine and, at the point of inflection, a short "processus acuminis" *k* is given off dorsad. The posterior calcarine is wavy but ends in a typical bifurcation on the medial side of the hemisphere.

ce, the *central sulcus*. According to Broca, Leuret was the first to call the central sulcus the sulcus of Rolando. Symington and Crymble (1913) gave a detailed account of the course of the sulcus. It throws an interesting light on the variability of cerebral fissures that they found what they considered the typical form in only 55 ± 3.2 per cent of their 237 brains while they found a "fairly" typical form in another 18 ± 2.5 per cent. Roughly one out of four (27 ± 2.9 per cent) was therefore atypical.

The authors describe the typical central fissure (see Fig. 13) as harboring two buttresses in its anterior wall, causing two more or less pronounced concavities looking frontad. They indicated the relation of these buttresses to the parts of the motor area on the strength of Campbell's histological studies and Grünbaum and Sherrington's stimulations of the brains of anthropoid apes. Figure 13 should be compared with those given by Penfield and Boldrey (1937) or Scarff (1940) who stimulated human brains during operations.

The depth of the sulcus was measured in several places. There is a "fairly constant" (87 ± 2.8 per cent) elevation "between trunk and arm field." In the light of modern neurological results one might be inclined to shift this into the trunk field proper. This elevation may be considered as a *pli de passage*, and may oc-

Sulci and Fissures

Short, isolated dimples and sulci are given letters from *a* to *z*.		Sulcus occipitalis superior (Ecker)	*os*
Fissura lateralis (Sylvius)	*la*	Sulcus occipitalis transversus superior	*otrs*
ramus horizontalis	*lah*	Sulcus occipitalis transversus inferior	*otri*
ramus ascendens	*laa*	Sulcus temporalis superior	*ts*
Sulcus intraparietalis	*ip*	Sulcus temporalis medius anterior	*tma*
Sulcus centralis (Rolando)	*ce*	Sulcus temporalis medius posterior	*tmp*
Sulcus subcentralis anterior	*sca*	Sulcus temporalis inferior	*ti*
Sulcus subcentralis posterior	*scp*	Sulcus occipitotemporalis	*ot*
Fissura parieto-occipitalis	*po*	Fissura collateralis	*col*
pars medialis	*pom*	Fissura calcarina	*ca*
pars lateralis	*pol*	Sulcus rhinalis	*rh*
Sulcus praecentralis	*pre*	Sulcus intralimbicus	*il*
Sulcus praecentralis superior	*prcs*	Sulcus corporis callosi	*cc*
Sulcus praecentralis inferior	*prci*	Sulcus cinguli, sive supramarginalis	*ci*
Sulcus frontalis medius	*fm*	Sulcus cinguli, pars marginalis	*cim*
Sulcus frontalis superior	*fs*	Sulcus suprarostralis	*sro*
Sulcus frontalis superior anterior	*fsa*	Sulcus paracentralis	*pac*
Sulcus frontalis inferior	*fi*	Sulcus subparietalis	*sp*
Sulcus frontomarginalis (Wernicke)	*fma*	Sulcus cunei	*cu*
Incisura capitis	*ic*	Sulcus rostralis superior	*ros*
Sulcus orbitalis medialis	*orm*	Sulcus rostralis inferior	*roi*
Sulcus retrocentralis transversus	*rct*	Sulcus limitans operculi	*lo*
Sulcus olfactorius	*olf*	Sulcus supratemporalis transversus anterior	*stta*
Sulcus orbitalis lateralis	*orl*	Sulcus supratemporalis transversus medius	*sttm*
Sulcus orbitopolaris	*orp*	Sulcus supratemporalis transversus posterior	*sttp*
Sulcus orbitalis arcuatus	*ora*	Sulcus centralis insulae	*cins*
Sulcus marginalis anterior insulae	*mai*	Sulcus intraopercularis	*oper*
Sulcus marginalis superior insulae	*msi*	Sulcus arcus intercuneati	*aic*
Sulcus marginalis inferior insulae	*mii*	Sulcus radiatus	*ra*
Sulcus postcentralis superior	*pocs*	Sulcus occipitotemporalis accessorius	*ota*
Sulcus postcentralis inferior	*poci*	Sulcus temporopolaris	*tp*
Sulcus parietalis transversus (Brissaud)	*pt*	Sulcus polaris anterior	*pa*
Sulcus parietalis intermedius (Jensen)	*pj*	Sulcus polaris posterior	*pp*
ramus anterior	*pja*	Sulcus parainsularis	*pins*
ramus posterior	*pjp*	Fissura hippocampi	*h*
Sulcus praeoccipitalis (Meynert)	*ipo*		
Sulcus occipitalis anterior (Wernicke)	*oa*		

Gyri

Gyrus supramarginalis (Gratiolet)	*Sm*	Gyrus temporalis superior	*Ts*
Gyrus centralis anterior	*Ca*	Gyrus temporalis medius	*Tm*
Lobulus paracentralis	*Parc*	Gyrus temporalis inferior	*Ti*
Gyrus frontalis superior	*Fs*	Gyrus fusiformis	*Fus*
Gyrus frontalis medius	*Fm*	Uncus	*U*
Gyrus frontalis inferior	*Fi*	Gyrus orbitalis medialis	*Orm*
pars orbitalis	*Fiorb*	Gyrus orbitalis lateralis	*Orl*
pars triangularis (cap de Broca)	*Fit*	Gyrus rectus	*R*
pars opercularis sive pedalis (Broca)	*Fiop*	Gyrus limbicus (sive cinguli)	*L*
Gyrus centralis posterior	*Cp*	pars anterior	*La*
Lobulus parietalis superior	*Ps*	pars posterior	*Lp*
Praecuneus (Foville)	*Pc*	Area parolfactoria Broca	*AB*
Gyrus parietalis inferior intermedius	*Pim*	Gyrus temporopolaris	*Tp*
Gyrus angularis (Huxley)	*Ang*	Gyrus supratemporalis transversus primus (Heschl)	*Sttp*
Gyrus occipitalis superior	*Os*	Gyrus supratemporalis transversus secundus	*Stts*
Gyrus occipitalis medius	*Om*	Gyrus praecentralis insulae	*Ipr*
Gyrus occipitalis inferior	*Oi*	Gyrus postcentralis insulae	*Ipo*
Cuneus	*Cu*	Limen insulae	*Li*
Gyrus lingualis	*Lg*		

FIG. 8. Pattern of the sulci and gyri on the lateral surface of brain *Hl*. For legends see p. 28.

casionally even rise to the surface, thus leading to an interruption of the central sulcus. But we believe it is erroneous to base homologies of the central sulcus of primates with the corona-ansata system of carnivores on this rare variation.
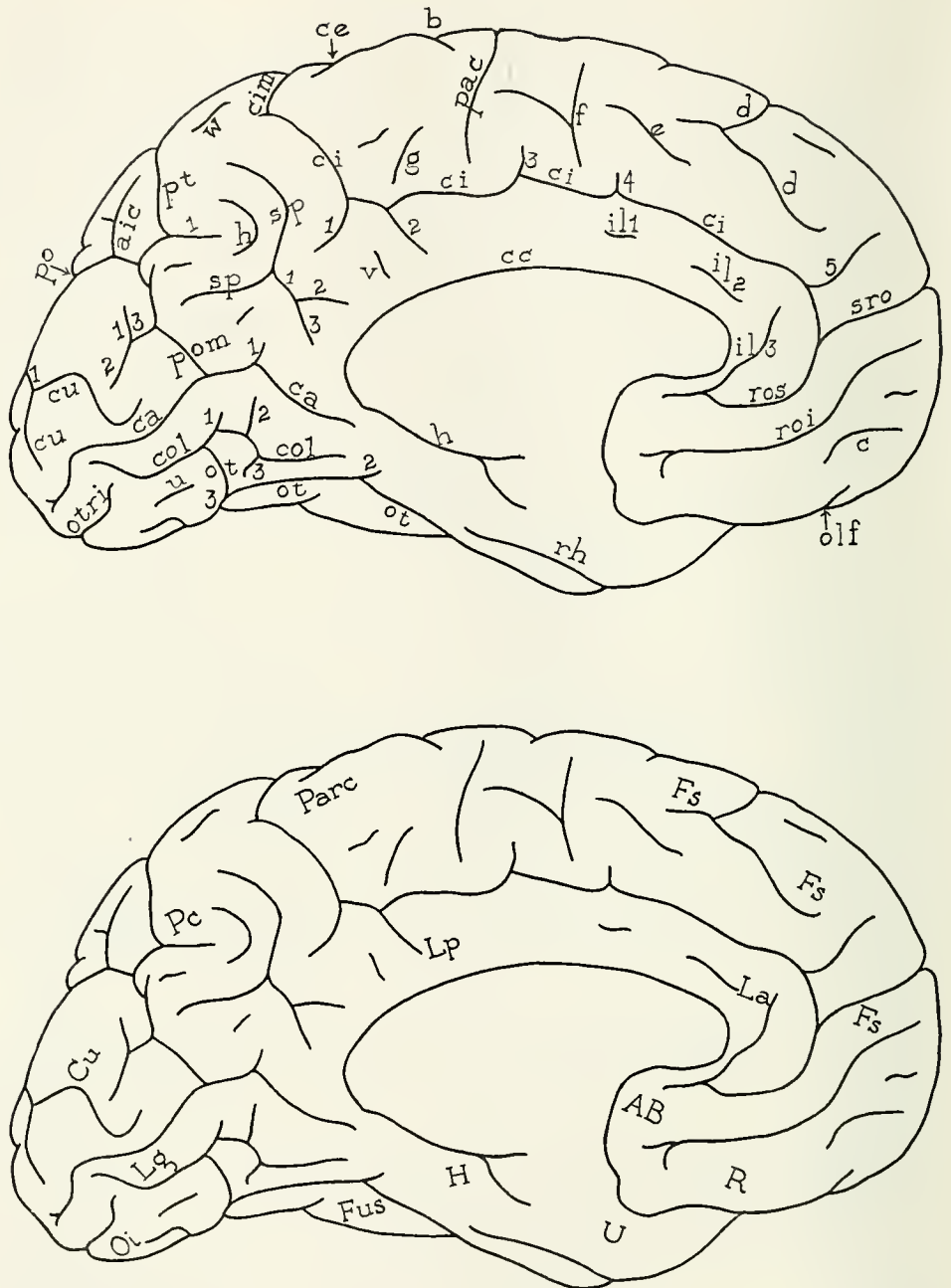
Fig. 9. Pattern of the sulci and gyri on the medial surface of brain *Hl*. For legends see p. 28.

Tricomi Allegra (1907) collected the data then available. An interruption occurs in 1.05 ± 0.2 per cent.

The upper end of the central sulcus (Table 3) may be either on the medial or

the lateral side of the hemisphere, or just at the margin. The first five lines of Table 3 are consistent with each other within the error of sampling. The last two lines show statistically significant differences. Are they due to the judgment of the observers or to actual differences in the material?
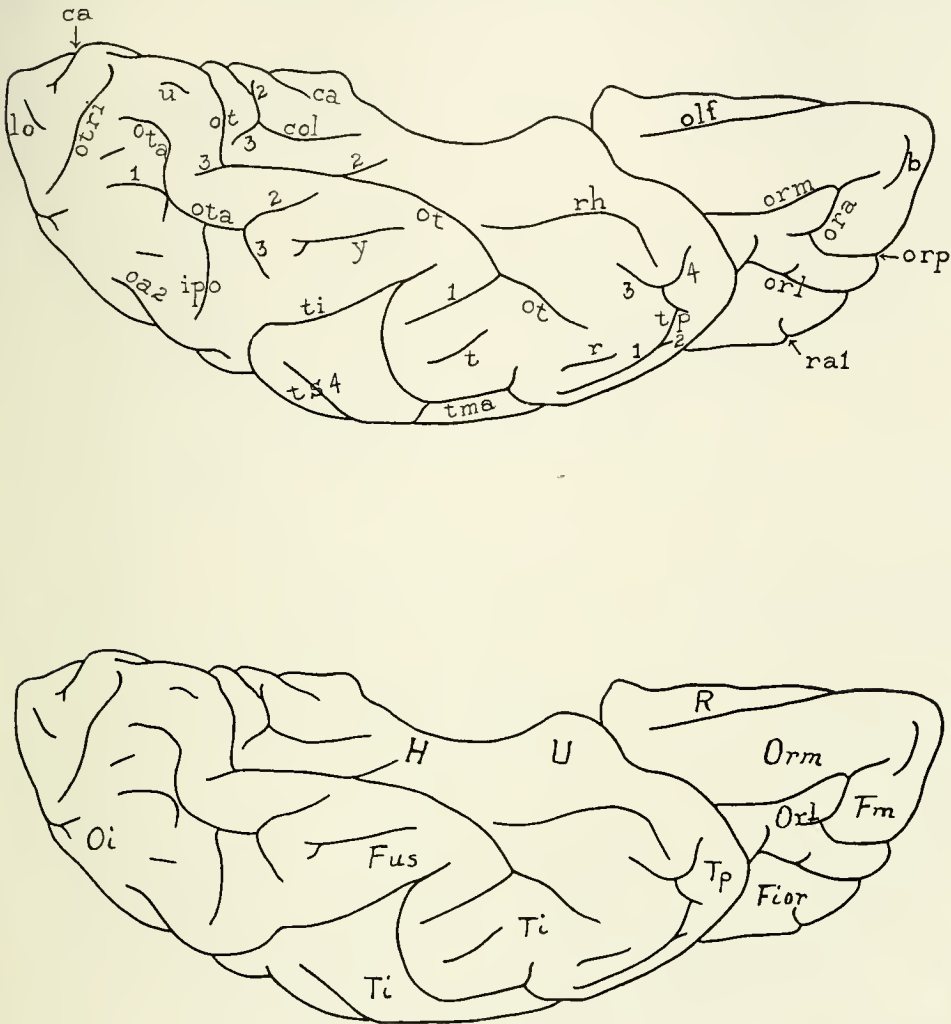

FIG. 10. Pattern of the sulci and gyri on the inferior surface of brain *Hl*. For legends see p. 28.

Anastomoses with other sulci—the subcentral, precentral, and postcentral (see p. 49)—are fairly frequent. Weinberg reports a frequency of 56 ± 7 per cent, Retzius of 59 ± 4.9 per cent of all his cases.

A connection with the Sylvian fissure, generally ascribed to an anastomosis of the central with the anterior or posterior subcentral sulcus, has been observed by Retzius in 23 ± 4.2 per cent, by Vint in 26 ± 4.4 per cent.

In brain *Hl* the central sulcus ends dorsally at the margin and shows the two

buttresses of Symington and Crymble very clearly. The sulcus has a short posterior processus acuminis (1) in the arm region, an anterior one (2) at the bend between arm and face, and another anterior one (3) within the face region. There is finally a spur (4) within the postcentral gyrus which connects the central with an accessory postcentral sulcus, *rct*. One might in the case of spur 4 be in doubt,
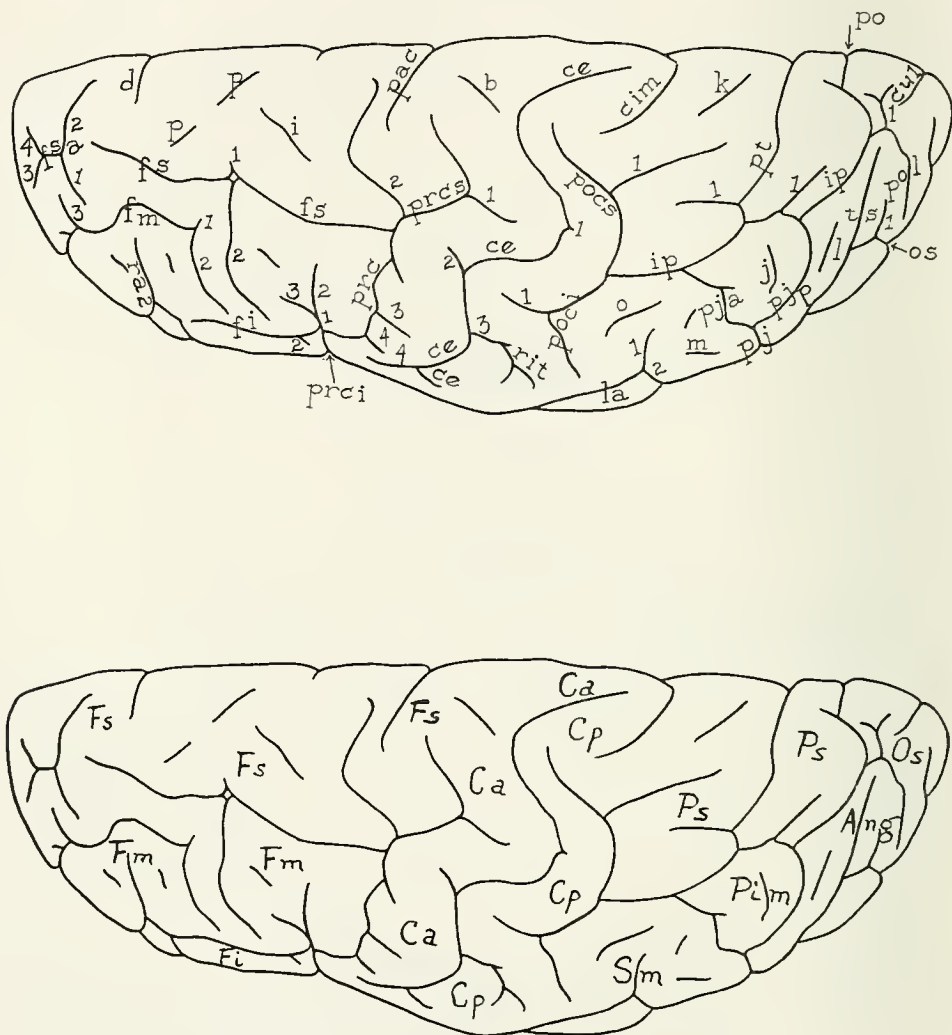

FIG. 11. Pattern of the sulci and gyri on the superior surface of brain *Hl*. For legends see p. 28.

when merely inspecting the hemisphere, which of the two branches represents the "true" central sulcus. We have taken the presence of giant cells of Betz in the anterior bank, and the presence of koniocortex in the posterior bank as our criterion (see p. 175).

ci, the *sulcus cinguli*. Few sulci have been given so many different names: fissura
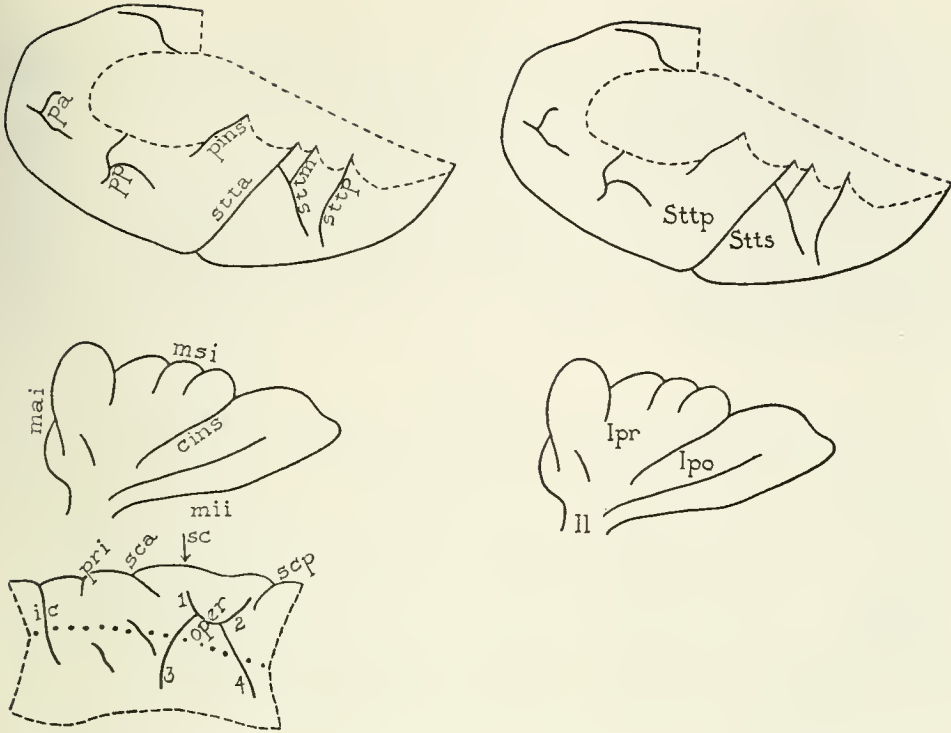
FIG. 12. Pattern of the sulci and gyri on the island, supratemporal plane and frontoparietal operculum of brain *Hl*. For legends see p. 28.
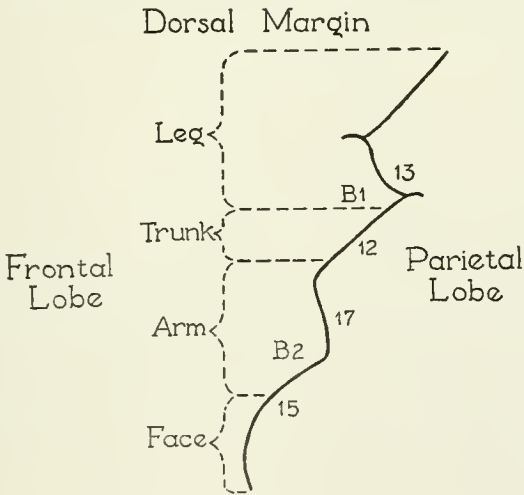

FIG. 13. Typical shape of left central sulcus. Redrawn after Symington and Crymble. B1, B2—buttresses. The figures indicate depth of sulcus in millimeters.

subfrontalis (Eberstaller, 1890), s. callosomarginalis (Huxley, 1861; W. Turner, 1891; Bischoff, 1868; Ecker, 1869; etc.), *scissure limbique* (Broca, 1878), to name

but a few. The sulcus courses on the medial side of the hemisphere, sweeping around
the rostrum of the corpus callosum, to end within the parietal lobe where it makes,
in a fairly sharp curve, for a point on the dorsal margin of the hemisphere about
8–12 mm. (Eberstaller) behind the central sulcus.

For few sulci can we point with such confidence to a factor responsible for their
formation. The sulcus cinguli reflects the pressure exerted by the growing corpus
callosum and the parieto-occipital lobe. The importance of the former factor is
proved by the cases of congenital absence of the corpus callosum (see Mingazzini,
1922); the importance of the latter factor is well illustrated by a comparison be-
tween the human brain and a brain which does not possess a posterior horn, e.g.,
that of an ungulate (Krueg, 1878).

TABLE 3
Sulcus Centralis Near Dorsal Margin, Frequencies in Percentage.

	I	II	III	References
Chinese	75 ± 6.0	17 ± 5.3	8 ± 3.7	v. Bork-Feltkamp, 1930
Swedes	64 ± 4.8	16 ± 3.7	20 ± 4.0	Retzius, 1896
Irish	60 ± 6.8	21 ± 5.7	19 ± 5.4	Cunningham, 1892
Dutch	55 ± 5.4	25 ± 4.7	20 ± 4.2	v. Bork-Feltkamp, 1930
Chinese	52 ± 5.0	40 ± 4.9	8 ± 2.7	Chi and Chang, 1941
Tonkinese	50 ± 5.6	43 ± 5.5	7 ± 2.6	Huard and Nguyen, 1938
Poles	44 ± 7.0	48 ± 7.1	8 ± 3.8	Weinberg, 1905
Kenya Negroes	14 ± 3.5	52 ± 5.0	34 ± 4.7	Vint, 1934

I: reaching medial side; II: just reaching margin; III: stopping on lateral side.

TABLE 4
Frequencies of No or One Interruption of Sulcus Cinguli on
Right and Left Sides, in Percentages.

	Eberstaller		Retzius	
	R	L	R	L
no	80 ± 3.0	56 ± 3.8	40 ± 7.1	41 ± 6.7
one	19 ± 3.0	42 ± 3.8	38 ± 5.8	49 ± 6.9

The fissure may be a single long furrow, or may be divided into two or more
fragments. The most frequent interruption occurs within the frontal lobe (Broca's
pli de passage fronto-limbique) well forward of the "upper Rolandic point." Eber-
staller (1890) as well as Retzius (1896) give the frequencies of this interruption
separately for right and left hemispheres. The standard errors of Eberstaller's
percentages as given in Table 4 have been computed on the assumption that he
had 169 pairs, as he states on his page 13 for the Sylvian fissure. While Eberstaller's
figures suggest a significant asymmetry, Retzius' observations point to symmetry.
Pooling both sides leads to a difference of 27 ± 5.6 per cent between Retzius'
Swedes and Eberstaller's Austrians, clearly a significant difference which may,
however, reflect a difference in interpretation rather than a racial one.

The caudodorsal hook impressed van Bork-Feltkamp (1930) as being frequently
much steeper in Chinese than in Dutch brains.

It is comparatively rare to find a bifurcation within the parietal lobe as is the rule in that of the chimpanzee.

The sulcus is sometimes doubled, particularly in its anterior part. Weinberg (1905) found such doubling in 32 ± 8.5 per cent on the right and in 68 ± 8.4 per cent on the left side. The difference (36 ± 12.1 per cent) indicates a probability of less than 1 per cent to have arisen merely by chance. As is well known, the anterior part of the sulcus cinguli is the limiting sulcus of the anterior limbic area in many primates. This seems to hold true in general of the human brain also (see frontispiece).

The brain *Hl* has an accessory intralimbic sulcus (*il*) between the main sulcus and the corpus callosum.

h, the *fissura hippocampi*, is a constant fissure. There is nothing to add to the textbook descriptions.

ip, the *intraparietal sulcus*. The sulcus was called interparietal by the Basle Commission, but it is within the parietal lobe, not between two lobes. A single fissure in some primates, it is frequently described as consisting in the human brain of four distinct elements: the superior and inferior postcentral, the pars horizontalis and the pars occipitalis (s. paroccipitalis of Wilder, 1886).

O. A. Turner (1948) described the intraparietal as continuous with the inferior postcentral sulcus (p. 49) in fetal brains, and showed a continuous postcentral sulcus in both early and late postuterine stages.

In most brains it is easy to distinguish between the pars horizontalis, i.e., the intraparietal in the stricter sense, and the postcentral sulcus. Between them there is a distinct angle even when they are continuous. The exact point where the pars occipitalis begins may be much more difficult to recognize.

The different relations between intraparietal *s. str.* and postcentral sulci were classified into five types by Cunningham (1892) whom most authors have followed. Figure 14 shows these types diagrammatically, and Table 5 gives the frequencies of these types in various series. A comparison between the various series shows one widely divergent one, namely that of Jefferson (1912–13) who worked in Manchester and examined "some eighty brains," presumably of Englishmen. The differences between Jefferson's series on the one side, and Cunningham and Retzius' series on the other (which belong to a presumably similar population) point, one may assume, more to a difference in judgment than to one of facts. Weinberg's Poles show a significantly greater frequency of type V than the other series. This, too, may be due to differences in judgment. For racially quite divergent series, such as Negroes and whites, or Australians and Chinese, when examined by the same observer show no significant differences. One can conclude only that racial differences for this character have not been demonstrated. A confluence of all three sulci—the intraparietal, the superior, and inferior postcentral sulcus (type IV)—is the most common occurrence; type III and II appear to follow, in that order while type I is fairly rare, and type V very rare.

The posterior part of the intraparietal, the pars occipitalis, was claimed as a "fissural integer" by Wilder (1886) who maintained that Ecker's (1869) original description of the intraparietal had included the true parietal and the pars occipitalis. Cunningham (1892) confirmed Wilder, for in older fetuses he saw the two sulci

fused in 33.3 ± 10 per cent, but in adult brains in 63.7 ± 5.5 per cent. Retzius found a fusion even in 95 ± 2.2 per cent of his hemispheres. In twenty-eight hemi-
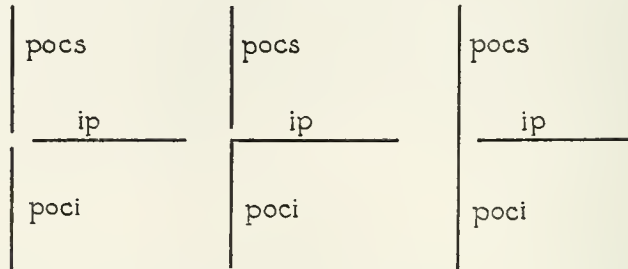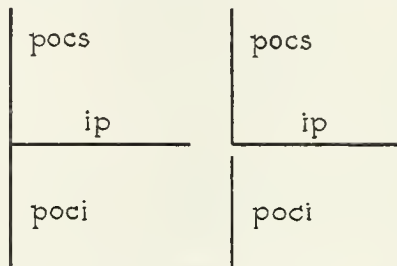

FIG. 14. Intraparietal and postcentral sulci (redrawn after Jefferson). Weighted means of Table 5 added.

TABLE 5

Relation of Intraparietal and Postcentral Sulci (Frequencies of types shown in Figure 14).

	I	II	III	IV	V
Irish	6 ± 2.2	19 ± 3.5	13 ± 2.8	60 ± 4.4	2 ± 1.2
Swedes	9 ± 2.8	11 ± 3.1	21 ± 4.1	55 ± 5.0	4 ± 2.0
English	35 ± 5.3	26 ± 4.9	25 ± 4.8	9 ± 3.2	5 ± 2.4
Poles	10 ± 4.2	16 ± 6.2	26 ± 6.2	26 ± 6.2	22 ± 5.9
Germans	7 ± 3.2	13 ± 4.4	25 ± 5.6	50 ± 6.4	5 ± 2.8
Negroes	8 ± 3.6	20 ± 5.1	28 ± 5.8	39 ± 6.3	5 ± 2.8
Australians	11 ± 4.8	11 ± 4.8	30 ± 6.9	41 ± 7.4	7 ± 3.9
Chinese (Southern)	9 ± 2.9	28 ± 4.5	27 ± 4.4	35 ± 4.8	1 ± 1.0
Chinese	16 ± 3.7	25 ± 4.3	17 ± 3.8	39 ± 4.9	3 ± 1.7

References: Irish: Cunningham, 1892; Swedes: Retzius, 1896; English: Jefferson, 1912–13; Poles: Weinberg, 1905; Germans: Connolly, 1950; Negroes: Connolly, 1950; Australians: Shellshear, 1937; Chinese (Southern): Shellshear, 1937; Chinese: Chi and Chang, 1941.

spheres Cunningham found a fusion in 87.5 ± 6.2 per cent on the right but only in 58.4 ± 9.4 per cent on the left side. The difference (29.1 ± 11.2 per cent) is significant.

In regard to intraparietal and postcentral sulci, brain *Hl* belongs to the most common type IV. It is exceptional, however, in exhibiting a wide gap between intraparietal proper and occipital part. The anastomosis between intraparietal and superior temporal sulcus seen in brain *Hl* appears to be rare. Shellshear's (1937) brain Q2788, however, and Retzius' (1896) Plate XLII, Figure 2 (to pick out two examples at random), show it.

la, the *lateral* or *Sylvian fissure*. This landmark, recognized as early as 1652 by François de le Boë Sylvius, is generally described as having several rami. There is the stem or vallecula Sylvii, seen on the ventral side between temporal and frontal lobe; there are the anterior rami of which classical anatomy recognizes two a, horizontal and an ascending one, and there is finally the long posterior ramus, marking the boundary between temporal and frontoparietal lobes. The way in

TABLE 6
Anterior Rami of Sylvian Fissure. Asymmetries.

	Negroes		Germans		Irish	
	R	L	R	L	R(46)	L(34)
I	27 ± 8.0	0	23 ± 7.7	6 ± 4.3	41 ± 7.3	15 ± 6.1
Y	13 ± 6.2	23 ± 7.7	30 ± 8.4	30 ± 8.4	26 ± 6.5	41 ± 8.4
U	47 ± 9.1	60 ± 9.0	23 ± 7.7	27 ± 8.0	0	44 ± 8.5
V	13 ± 6.2	17 ± 4.6	24 ± 7.7	37 ± 8.0	33 ± 6.9	0

References: Negroes and Germans: Connolly, 1950; Irish: Cunningham, 1892.

TABLE 7
Anterior Rami of Sylvian Fissure, Racial Data.

	I	Y	U, V or 3 branches	References
Germans	15 ± 4.6	30 ± 5.9	55 ± 6.4	Connolly, 1950
Dutch	18 ± 4.2	20 ± 4.3	62 ± 5.4	v. Bork-Feltkamp, 1930
Chinese	12 ± 3.1	16 ± 3.7	72 ± 4.5	Chi and Chang, 1941
Negroes	14 ± 4.5	18 ± 5.0	68 ± 6.4	Connolly, 1950

which the frontoparietal and temporal opercula grow over the insula and thus form the lateral fissure has been described so often (see especially Anthony, 1928) that we can forego a repetition. The anterior rami vary considerably. There may be only one ramus (*I*), there may be two, forming the shape of the letter V, U, or Y, and there occasionally may be three rami.

The information that could be gathered from the literature is assembled in tables 6 and 7. Table 6 shows that a single ramus is more frequent on the right than on the left hemisphere. In spite of the small samples, and the consequent large sampling errors, the difference is statistically significant for Negroes, while for the Germans the probability that the observed difference has been caused by chance is between 10 per cent and 5 per cent. For the Irish, too, the difference is not statistically significant. Table 7 compares the various races, both hemispheres having been pooled. A U- or V-shaped arrangement of the anterior sulci is sig-

nificantly more frequent in the Chinese than in the Dutch as well as in the German series (.05 > P > .02). That the behavior of the anterior rami is not an index for the "higher" or "lower" development of the brain has been stressed by G. Levin (1937).

The posterior ramus appears to be longer on the left than on the right side. Eberstaller (1890) gives as the means 58.2 and 51.8 mm., but no sampling errors can be computed from his data. The statistical significance of this asymmetry, however, can be estimated in a slightly different manner. Eberstaller states that of 169 brains the right Sylvian fissure was longer in 55 cases, the left in 107 cases. This leads to percentages of 32.5 ± 3.6 per cent and 63.3 ± 3.7 per cent, respectively, and the difference, 30.8 ± 5.2 per cent is very unlikely to have arisen by chance. Confirmation was provided by Cunningham and Shellshear. Cunningham (1892) measured twenty-eight right and twenty-three left adult hemispheres and convinced himself that Eberstaller's assertion "was fully borne out." No numerical data were provided. Shellshear (1937) measured on Australian brains the distance between the lower end of the central sulcus and the posterior end of the Sylvian fissure. He found 20.7 ± 1.0 mm. on the right, and 30.4 ± 1.1 mm. on the left side. The left Sylvian fissure is again significantly longer (by 9.7 ± 1.5 mm.).

The posterior ramus of the Sylvian fissure generally bifurcates near its end. Retzius found this in 70 ± 4.6 per cent of his cases.

The direction of the posterior ramus, i.e., "the angle which is formed by the posterior horizontal limb of the Sylvian fissure with a line drawn at right angles to the longest anteroposterior diameter of the hemisphere" was measured by Cunningham in sixteen right and fifteen left hemispheres. He found mean values of 66.3° and 70.3° respectively, but failed to give any data by which his sampling errors could be estimated. Whether the greater length of the left posterior ramus is correlated with a "flatter" course cannot be asserted with confidence.

In brain *Hl*, the anterior rami form the letter Y and the posterior ramus ends in a pronounced bifurcation. There are several small indentations on the posterior ramus. A fairly large sulcus cutting into the superior temporal gyrus is the continuation of the anterior transverse supratemporal sulcus (*stta*, see p. 56), two shorter ones on the dorsal side may be labeled anterior (*sca*) and posterior (*scp*) subcentral sulcus, respectively. Merely for purposes of orientation the end rami of the posterior ramus have been labeled *lapd* and *lapv* (dorsal and ventral branch of the posterior ramus of the lateral fissure).

olf, the *olfactory sulcus*. A meticulous description of this sulcus has been given by Kanai (1938).

In its course toward the frontal pole the sulcus (observed in 216 hemispheres) may veer mediad (69 ± 3.2 per cent), may run straight (24 ± 2.9 per cent), or it may veer laterad (7 ± 1.7 per cent). Of the two posterior rami, the lateral—generally about 7.2 mm. long—anastomoses occasionally (in 12 ± 2.2 per cent) with the sulcus orbitalis arcuatus, but fairly often (in 30 ± 3.1 per cent) with the Sylvian fissure. Kanai observed brains from northern Japan. We found no other data.

pom, the *medial parieto-occipital fissure*. The parieto-occipital fissure is as characteristic for the primate brain as the central sulcus. In man and in all higher an-

thropoids it shows a complicated system of submerged gyri and hidden secondary folds which have been studied and interpreted by many authors since Gratiolet (1854) first analyzed it.

Elliot Smith (1904) (see our Fig. 15) has described the parieto-occipital fissure as a fossa which contains in its depth an intercuneate arcus (i.e., gyrus), previously described by other authors, thrown into a semicircular shape by the parieto-occipital incisure. The postero-inferior border of this arcuate gyrus is given by the paracalcarine sulcus, the anterosuperior border by the sulcus limitans praecunei. The parieto-occipital fossa generally closes up completely so that the intercuneate arcus becomes buried and a continuous fissure appears to run from the parieto-occipital incisure to the stem of the calcarine fissure. Occasionally (in 5 ± 2.2 per cent in Retzius' material, in only 1 ± 0.9 per cent in Cunningham's material) the intercuneate arcus remains on the surface. Cunningham reports "the absence of the deep gyrus intercuneatus" in 47 ± 4.4 per cent of his cases.
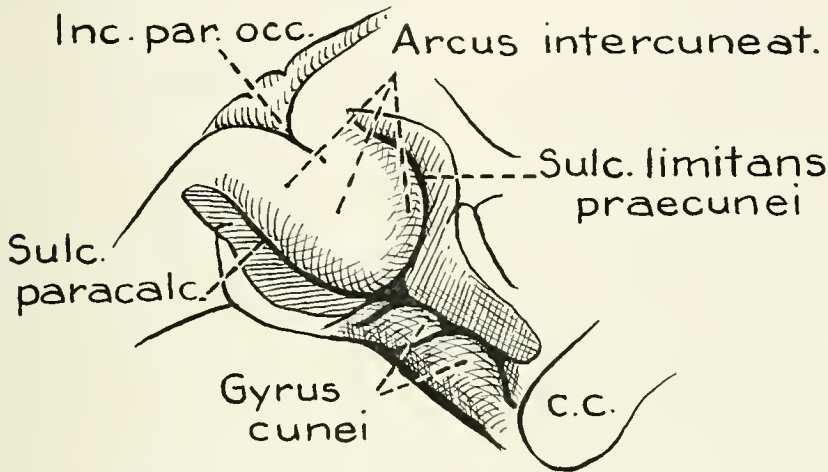

FIG. 15. Submerged gyri within the parieto-occipital fissure (after Elliot Smith).

Bianchi (1940) recognized five groups, exhibiting various degrees of development of the intercuneate gyrus. He examined 102 brains (i.e., 204 hemispheres). The standard errors of the percentages given by him have been added by us.

1. Parieto-occipital fissure not ramified, bordered laterally by the first lateral *pli de passage* (36.7 ± 3.4 per cent).
2. Parieto-occipital fissure ramified close to the dorsal margin of the hemisphere. Gyrus intercuneatus in the depth of the fissure (39.2 ± 3.4 per cent).
3. Gyrus intercuneatus largely on the surface, between two rami of the parieto-occipital fissure (11.7 ± 2.2 per cent).
4. Gyrus intercuneatus almost longitudinal, fused with the first lateral *pli de passage* of Gratiolet (6.8 ± 1.8 per cent).
5. Gyrus intercuneatus fused with adjacent gyri which do not properly belong to the system of the parieto-occipital fissure (5.3 ± 1.6 per cent).

Bianchi gives also the frequencies for right and left separately; the differences are not statistically significant (*non sono notevoli*) as the author himself points out.

Cases in which the gyrus cunei (a submerged gyrus just dorsal to the point where parieto-occipital and calcarine fissure merge) becomes superficial have been occasionally observed, but seem to have no racial significance.

On the lateral side, the parieto-occipital incisure may be continuous, at least superficially, with the intraparietal sulcus. Weinberg (1905) observed this in 32 ± 6.6 per cent in Poles and in 40 ± 9.8 per cent in Letts. The difference is clearly insignificant.

In brain *Hl* the parieto-occipital fissure represents a complicated pattern which almost defies analysis. The gyrus cunei near the point φ' of Filimonoff (see p. 26) is submerged. As the parieto-occipital fissure is followed dorsally, it merges with a sulcus on the cuneus. This has been labeled (3). Still nearer the dorsal margin, beyond a short unlabeled spur, the parieto-occipital fissure gives off a fairly large sulcus, which we take to be the superficial sulcus limitans precunei (see Fig. 15). On the lateral side of the hemisphere, this sulcus unites with the intraparietal. A short fold within the arcus intercuneatus might be called the sulcus arcus intercuneate.

rh, the *fissura rhinalis*. This is a small furrow on the lateral margin of the uncus marking the boundary between the allocortex and isocortex. For brain *Hl*, it is shown on the basal aspect (Fig. 10).

ts, the *sulcus temporalis superior*, *sulcus parallelis*. With Shellshear (1927) the parallel sulcus can be divided into an anterior and a posterior part. The former, one of the oldest furrows of the primate brain, runs in the temporal lobe; the latter, changing profoundly from macaque to man, runs in the parietal lobe. Near the temporal pole, the anterior end may be in line with the rest of the sulcus or may be bent ventrad so that the temporal pole appears as a continuation of the superior temporal gyrus. Occasionally, as Blinkow (1938) observed, this anterior hook may be an independent sulcus and the temporopolar region may be opercularized. Submerged bridging convolutions within the anterior part have been described by Blinkow. Within the angular gyrus the posterior part generally breaks up into three rami. Connections with the sulci of both occipital lobe and inferior parietal lobule are frequent. Shellshear reports that an interruption of the parallel sulcus between anterior and posterior part is not infrequent. No anthropological observations about this sulcus were found by us.

In brain *Hl* the anterior part of the parallel sulcus shows several longer branches labeled simply 1–4. The posterior part breaks up into two rami, an anterior one (*pj*) and a posterior one (*ts*). The anterior branch connects by two subbranches (*pja* and *pjb*) with the intraparietal sulcus. The posterior branch anastomoses with *os*.

II. THE SECONDARY SULCI AND GYRI

The secondary sulci are less constant than the primary ones and presumably genetically less fixed, as the studies of the brains of identical twins (see p. 23) indicate. It is at present not possible to define them further. Some of these sulci delimit gyri, others merely cut into a particular gyrus. We shall analyze them by regions, and indicate for each region the gyri which these sulci delimit. We shall adhere as closely as possible to the old subdivision of lobes, since this is still a convenient way to describe topographical relations.

FRONTAL LOBE

The frontal lobe of classical anatomy bears the precentral, the frontal, the orbital, and the rostral sulci, and contains the precentral gyrus, the three frontal convolutions and the gyrus rectus. Its fissures have been reviewed by Kononova (1938).

prc, the *precentral sulcus*. As a rule there is a superior and an inferior precentral sulcus. The two may be continuous, or there may be even three sulci. The frequencies of these configurations are given in Table 8. In all races, two sulci are most frequently found. The difference between the Chinese on the one side, and the Russians and Negroes on the other side is significant. Moreover, the Poles show one sulcus significantly more rarely than any other group, while three sulci are found more frequently in Negroes, Russians, and Poles than in Swedes or Chinese. These are erratic findings, and one is tempted to think of observational bias as much as of actual differences. A connection between the inferior precentral sulcus

TABLE 8

A. Frequencies of One, Two, or Three Precentral Sulci, in Percentage.
(Arranged in increasing frequency of two sulci)

Race	One	Two	Three	References
1. Kenya Negroes	14 ± 3.5	69 ± 4.6	17 ± 3.8	Vint, 1934
2. Russians	13 ± 2.3	72 ± 3.2	15 ± 2.6	Zernov, 1877
3. Swedes	23 ± 4.2	73 ± 4.4	4 ± 2.0	Retzius, 1896
4. Poles	4 ± 2.8	80 ± 5.5	16 ± 5.2	Weinberg, 1905
5. Chinese	17 ± 3.5	83 ± 3.5	0	Chi and Chang, 1941

B. Differences for Frequencies of Two Sulci.

	2	3	4	5
1.	3 ± 5.6	4 ± 6.3	11 ± 7.2	14 ± 5.7
2.	...	1 ± 5.5	8 ± 6.4	11 ± 4.7
3.		...	7 ± 7.1	10 ± 5.6
4.			...	3 ± 6.6

and the lateral fissure was stated to be frequent by Giacomini (1878). Eberstaller (1890) pointed out, however, that this connection was only indirect, namely by intervention of either the sulcus subcentralis anterior or the s. diagonalis. Cunningham and Retzius confirmed Eberstaller's conception.

In view of the variability of all secondary sulci, this argument may strike the modern reader as largely verbal and devoid of meaning. In any event, the connection in question is fairly frequent in both Irish and Swedes (see Table 9). A connection by means of the s. diagonalis appears to be more frequent in Swedes than in Irish. The difference is barely significant.

The sulcus precentralis inferior (*prci*) courses from a point near the Sylvian fissure dorsad and ends normally in front of, and a little below, the point at which the superior precentral sulcus begins. Cunningham (1892) pointed out that frequently the upper end of the inferior precentral sulcus branches and that the anterior branch courses for an appreciable distance in an almost horizontal direction.

This ramus horizontalis is found "in complete and uninterrupted union with the vertical stem" in 72 ± 6.3 per cent. Retzius confirmed Cunningham's observation; he found this condition in 73 ± 4.4 per cent.

The superior precentral sulcus (*prcs*) is generally smaller than the inferior one. In its simplest form it has the shape of a vertical furrow, to paraphrase Cunningham. Its variations—being broken up, connected with the superior frontal sulcus, exhibiting arciform shape—need not detain us here.

The sulcus precentralis medius when present may have become separated from either superior or inferior precentral sulcus by an annectent gyrus emerging from the depth. It is doubtful whether great stress is to be laid on its presence. O. A. Turner (1948) found it only in his late postuterine stage.

A small dimple may be found medial to the superior precentral sulcus. It was called s. precentralis marginalis by Cunningham. Another furrow, cutting into the dorsal margin a little anteriorly, is the s. precentralis medialis of Eberstaller. Both sulci were found in the early postuterine stage by Turner, but not in the fetal stage.

On the ventral part of the precentral gyrus there is the anterior subcentral sulcus (*sca*) normally a little behind the inferior precentral sulcus. Its length varies all the way from an appreciable sulcus to a small notch on the lateral fissure.

TABLE 9
Inferior Precentral Sulcus and Lateral Fissure in Percentage.

	Irish (50)	Swedes (100)	Δ
Unconnected	58 ± 7.0	53 ± 5.0	5 ± 8.6
Connected by s. diagonalis	22 ± 5.9	39 ± 4.8	16 ± 7.6
Connected by s. subcentr. ant.	20 ± 5.6	9 ± 2.9	11 ± 6.3

References: Irish: Cunningham, 1892; Swedes: Retzius, 1896.

f, the *frontal sulci*. Classical anatomy recognizes two longitudinal frontal sulci, the inferior and superior. We name them in this order, for the inferior appears to be the more constant and better developed of the two (see Retzius, 1896). One additional middle frontal sulcus is frequent; two additional middle sulci are but rare.

The inferior frontal sulcus (*fi*) arises in about three cases out of four (see Table 10) from the inferior precentral sulcus. This occurrence is, however, significantly rarer in American Negroes than in Swedes, Russians, or Austrians. No other differences are statistically significant. According to Eberstaller (1890), it rarely extends beyond about the middle of the pars triangularis; according to Weinberg (1905) it runs generally as far as the latero-orbital margin. At the junction with the precentral sulcus there is, as Eberstaller emphasized, almost always a submerged gyrus. When it comes occasionally to the surface it seemingly separates the inferior frontal from the precentral sulcus. Two other *plis de passage*, in the middle of the inferior frontal sulcus and a little more anteriorly, have been described, but in Retzius' material, at any rate, their frequency was not much greater than that of the posterior bridge.

The superior frontal sulcus (*fs*) arises frequently from the superior precentral sulcus (see Table 11), runs forward about two-thirds of the frontal lobe, gradually

nearing the dorsal margin of the hemisphere. The frequency of this behavior varies more widely from race to race and shows more significant differences than any other character thus far discussed. Within the errors of sampling, it appears to be of about equal frequency in Russians, Poles, and Chinese, but it is significantly more frequent in Swedes and significantly much less frequent in Tonkinese. Again,

TABLE 10
A. Frequency of Confluence of Inferior Precentral and Inferior Frontal Sulcus, in Percentage.

Race	Frequency	References
1. Swedes	77 ± 4.2	Retzius, 1896
2. Austrians	76 ± 2.6	Eberstaller, 1890
3. Russians	69 ± 3.3	Zernov, 1877
4. Germans	68 ± 6.0	Connolly, 1950
5. Poles	62 ± 6.9	Weinberg, 1905
6. Negroes (American)	53 ± 6.0	Connolly, 1950

B. Differences between Races.

	2	3	4	5	6
1.	1 ± 5.0	8 ± 5.3	9 ± 7.3	15 ± 8.0	24 ± 7.3
2.	...	7 ± 4.3	8 ± 6.6	14 ± 7.3	23 ± 6.6
3.			1 ± 6.9	7 ± 7.6	16 ± 6.9
4.			...	6 ± 9.2	15 ± 8.5
5.				...	9 ± 9.2

TABLE 11
A. Frequencies in Percentage of Confluence of Superior Precentral and Superior Frontal Sulcus.

Race	Frequency	References
1. Swedes	86 ± 3.5	Retzius, 1896
2. Poles	70 ± 6.5	Weinberg, 1905
3. Chinese	64 ± 4.8	Chi and Chang, 1941
4. Russians	63 ± 3.4	Zernov, 1877
5. Tonkinese	33 ± 5.3	Huard and Nguyen, 1938

B. Differences between Races.

	2	3	4	5
1.	16 ± 7.3	22 ± 5.9	23 ± 5.6	53 ± 6.3
2.	...	14 ± 8.1	13 ± 7.3	37 ± 8.4
3.		...	1 ± 5.8	31 ± 7.1
4.			...	30 ± 6.3

however, the grouping is queer. One would expect Russians, Swedes, and Poles to form one group, and Chinese and Tonkinese another. In any event, the wide variability in a region which is of recent phylogenetic origin is of more than passing interest. Often (according to Eberstaller in 44 per cent) it anastomoses with the middle frontal sulcus, to be mentioned presently.

The superior frontal sulcus is frequently interrupted in its course. The information gathered from the literature is tabulated in Table 12. In Negroes and Australians the sulcus is broken up into three parts more frequently than in Whites and Tonkinese. Several differences are statistically significant.

Within the middle frontal gyrus there is frequently a fairly long middle frontal sulcus (*fm*), roughly parallel to superior and inferior frontal sulci. This sulcus was considered as an important separate entity by Hervé (1888) and Eberstaller (1890). The latter described it as a sagittal furrow, beginning with a transverse bifurcation at about the middle between precentral gyrus and orbital margin, and ending

TABLE 12

A. Frequencies for Superior Frontal Sulcus Being in One, Two, or Three Parts.

Race	One	Two	Three	References
1. Germans	19 ± 5.0	54 ± 6.5	27 ± 5.7	Connolly, 1950
2. Irish	28 ± 6.1	49 ± 6.9	23 ± 5.7	Cunningham, 1892
3. Negroes	17 ± 4.8	40 ± 6.3	43 ± 6.4	Connolly, 1950
4. Tonkinese	42 ± 5.5	32 ± 5.2	16 ± 4.1	Huard and Nguyen, 1938
5. Australians	22 ± 6.2	27 ± 6.7	51 ± 7.5	Shellshear, 1937
6. Russians	66 ± 3.4	22 ± 2.6	12 ± 2.5	Zernov, 1877

B. Differences between Races for Sulcus to Be in Three Parts.

	2	3	4	5	6
1.	4 ± 8.1	16 ± 8.5	11 ± 7.0	24 ± 9.5	15 ± 6.2
2.	...	20 ± 8.5	7 ± 7.0	28 ± 9.5	11 ± 6.2
3.		...	27 ± 7.6	8 ± 9.9	31 ± 6.9
4.			...	35 ± 8.5	4 ± 4.8
5.				...	39 ± 9.5

TABLE 13

Middle Frontal Sulcus by Percentages.

	Frequency	Race	References
Absent	1 ± 1.0	Swedes	Retzius, 1896
Anastomosis with fronto-marginal sulcus	76 ± 4.2	Swedes	Retzius, 1896
In one part	33 ± 4.7	Swedes	Retzius, 1896
In two parts	37 ± 7.5	Australians	Shellshear, 1937
In two parts	33 ± 7.7	Chinese	Shellshear, 1937

frequently (see Table 13) near the orbitodorsal margin in a similar bifurcation, evidently a part of Wernicke's frontomarginal sulcus. Most subsequent observers (Cunningham, Retzius, Connolly, Shellshear, Kononova, etc.) commented upon the great variability of this sulcus. "There is," as Connolly (1950, p. 197) said, "every gradation between what is hardly more than a short stem of the frontomarginal and a highly developed and important sulcus." From Shellshear's (1937) tabulation it appears that in both Chinese and Australians the sulcus is commonly broken up into two parts and separated from the frontomarginal sulcus as well. Turner (1948) observed a rather striking elaboration during the postnatal phase.

fma, the *frontomarginal sulcus*. The frontomarginal sulcus was first described by

Wernicke (1876): "On the convexity above the orbital margin there is frequently a deep furrow which runs parallel to the orbital margin and is generally restricted to the second and third [nowadays, first and second] frontal gyrus. It is occasionally already present in the fetus and corresponds to the frontomarginal sulcus mentioned in the orang." It was discussed as *solco orbito-frontale* by Giacomini (1884). Eberstaller (1890) considered it as a "conglomeration of secondary sulci running roughly along the dorso-orbital margin," while Connolly (1950) states that the frontomarginal is "rather an important and constant sulcus." Shellshear (1937) mentions the sulcus only incidentally. Fusari (1910) pointed out that Retzius had observed the sulcus in six month-old fetuses, and called attention to the fact that the frontomarginal sulcus is generally much deeper than that frontal sulcus of which it might appear superficially to be a branch. On the other hand, O. A. Turner (1948) identified this sulcus only in his late postuterine phase.

On the opercular part there is "generally," according to Eberstaller (1890), the *diagonal sulcus*. Eberstaller himself gives no exact data about its frequency or its extent. "It may begin within the pars opercularis, separate from both precentral and inferior frontal sulcus or it may be in continuity with the one or the other of these sulci. The lower end of the diagonal sulcus may be separated from the Sylvian fissure by a superficial bridge, or may cut into the Sylvian fissure. . . . Sometimes the fissure may even go as far as the insula but never into the sulcus of Reil." Turner (1948) mentions the diagonal sulcus as a regular feature of the human brain. Our observations lead us to believe that the sulcus is by no means a constant feature of the human brain, but we have looked in vain for numerical data about its frequency.

Near the frontal pole a *radiate sulcus* is often present, according to Eberstaller in about one-third of all cases. It cuts into the triangular part of the third frontal convolution; its upper end may be united with the middle frontal sulcus. One branch of this sulcus has been called the *incisura capitis* (*ic*) because it cuts into the pars triangularis (*cap de Broca*); the other two branches are labeled in brain *Hl ra1* and *ra2*.

The orbital sulci have to be described together. Figure 16 sketches, after Kanai (1938), some of the more common types. The most conspicuous features of the orbital surface are three sulci which together form Broca's *incisure en H*. The transverse connecting link is the sulcus orbitalis arcuatus; the longitudinal fissures are the medial and lateral orbital sulci. Between these two there is generally, near the frontal pole, an intermediate orbital sulcus, and between the medial one and the olfactory sulcus (see p. 31) there is the variable sulcus orbitalis fragmentosus. In careful studies, Beccari (1911) and Kanai (1938) have collected data from the literature. Kanai compared them with his own findings in sixty-six male and forty-seven female Japanese brains. In what follows we draw mainly on that monograph; the sampling errors have been supplied by us.

ora, the *sulcus orbitalis arcuatus*, was called s. orbitalis transversus by Weisbach (1870); s. presylvius by Rauber (1886). Rauber considered it merely as the confluence of two apical processes, but most modern authors have recognized it as a definite entity. It was found by Kanai in 95.2 ± 1.4 per cent, and had in 90.5 ± 1.9 per cent the typical shape, namely convex toward the frontal pole.
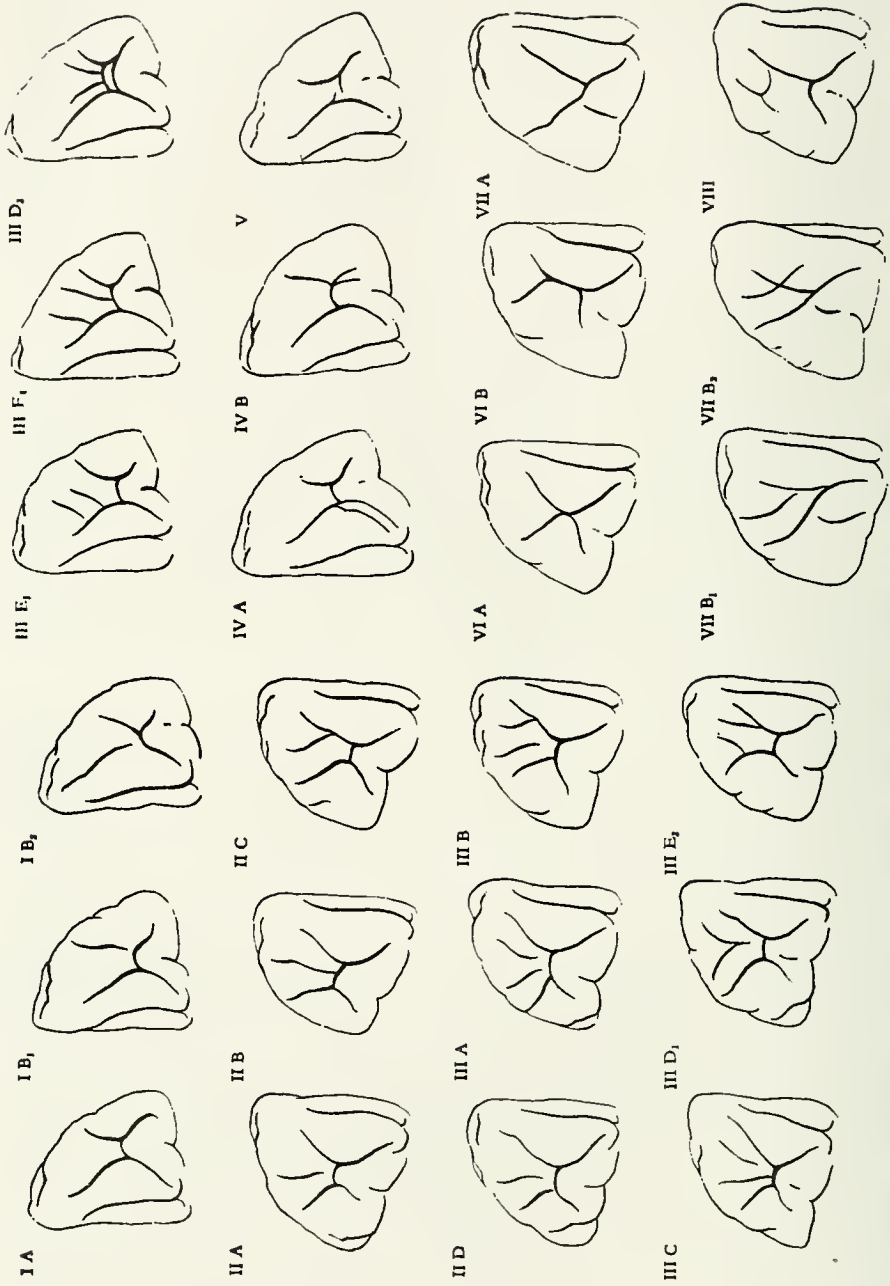
FIG. 16. Common configurations of the orbital sulci (after Kanai). Shows eight of his nine major types; the ninth type is a miscellaneous group.

Generally the sulcus anastomoses, as the term *incisure en H* indicates, with the lateral and medial orbital sulcus. In the Japanese the former anastomosis is a little more frequent than the latter (87 ± 2.2 per cent against 81.5 ± 2.5 per cent). Occasional anastomoses with the Sylvian fissure, or the olfactory or the intermediate orbital sulcus, have been described.

orf, the *sulcus orbitalis fragmentosus*, is generally a train of two (29.6 ± 3.0 per cent) or three (17.3 ± 2.5 per cent) fragments. It is present only in about three out of four cases (74.3 ± 2.9 per cent), and may anastomose with the medial orbital sulcus.

orl, orm, ori, the *lateral, medial*, and *intermediate orbital sulci*. These longitudinal furrows should be described together since the number of longitudinal orbital sulci varies between one and six. Three furrows are most frequently found, but four furrows are by no means rare (45.2 ± 3.3 per cent and 38.2 ± 3.2 per cent respectively). Two or five sulci occur each in less than 10 per cent of all cases.

Brain *Hl* shows the sulcus arcuatus to be connected only with the medial orbital sulcus and with a sulcus (*orp*) which extends over the frontal pole to connect with the frontomarginal sulcus.

ro, the *sulcus rostralis*. This sulcus, on the medial side of the hemisphere, runs in an anteroposterior direction, beginning near the *carrefour olfactif* of Broca and ending just short of the frontal pole. It was first described by Broca as *incisure sus-orbitaire*. Eberstaller felt that the sulcus had little or nothing to do with the orbital surface and adopted the name rostral sulcus which Krueg (1878) had given to a sulcus in the brain of nonprimates, adding that "the homologies were at once expressed."

The sulcus rostralis is almost invariably doubled in the human brain. Eberstaller described the lower one as shallower, and called it accessory rostral sulcus. Beccari (1911) merely called them superior and inferior. The relations between rostral sulci and sulcus cinguli are quite variable. Beccari constructed three major groups (see Fig. 17). The frequencies for sixty hemispheres are noted, after his data, in that figure.

Many brains, as Beccari's figures show, exhibit a transverse rostral sulcus which delimits Broca's *carrefour olfactif* from the gyrus rectus. In Beccari's material this sulcus was present in 65 ± 6.2 per cent. Eberstaller does not mention the sulcus; Retzius mentions it briefly, remarking that it could be considered as the endpiece of the s. cinguli. It is missing in brain *Hl*.

cr, the *cruciate sulcus*. Campbell (1905) called attention to a generally fairly small and quite variable "fissuret" on the medial side of the hemisphere, on the paracentral lobule, which coincided with remarkable constancy with the lower boundary of the gigantopyramidal area and which Campbell looked upon as the homologue of the cruciate sulcus of carnivores. While we cannot fully share this latter view, the relation of the cruciate sulcus to the motor area certainly deserves emphasis. In brain *Hl* the small dimple marked *g* might be this "fissuret."

The sulci mentioned thus far partition off the main gyri of the frontal lobe: the g. centralis anterior or precentralis, the superior, middle, and inferior frontal gyrus, the two orbital gyri, the gyrus rectus, the *carrefour olfactif* or subcallosal gyrus and the lobulus paracentralis. To repeat the usual textbook descriptions is unnecessary;
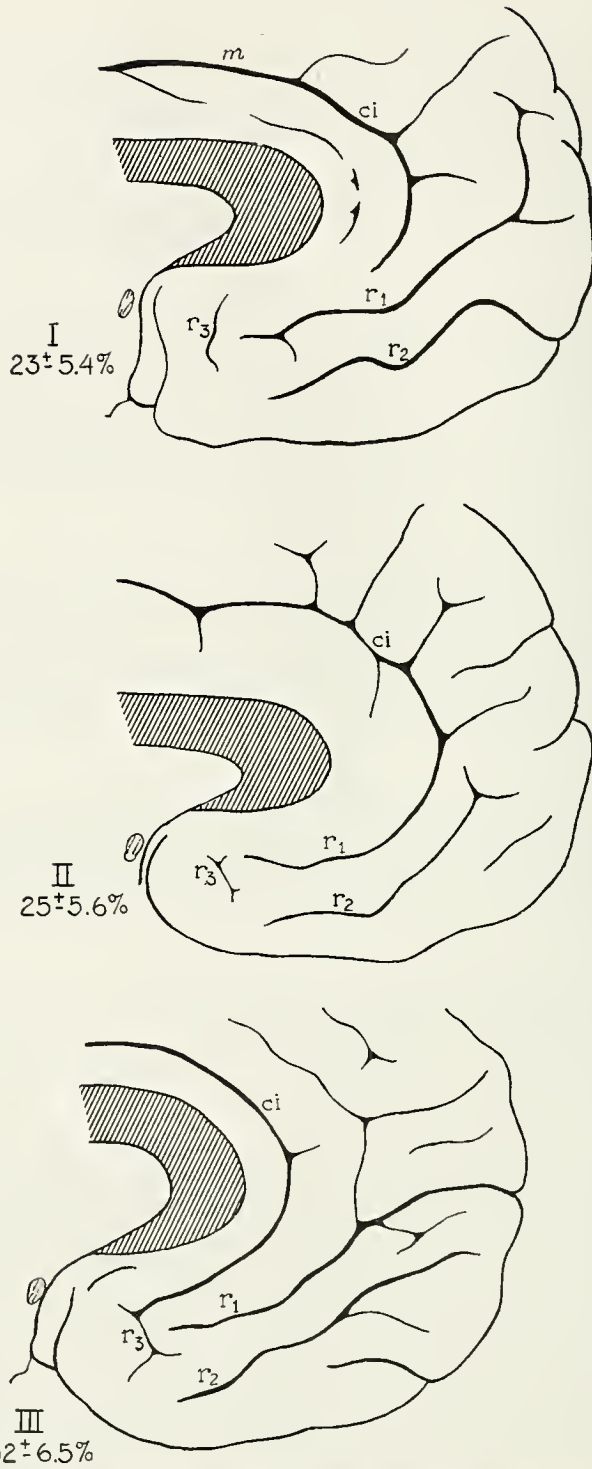
FIG. 17. Sulci around the rostrum of the corpus callosum (after Beccari).

their location is sufficiently indicated on our figures. The inferior frontal gyrus, it should be mentioned, is generally divided into a pars opercularis, triangularis, and orbitalis. A "postorbital limbus," caused by the sphenoid bone, was described by Spitzka (1903). Ariëns Kappers (1929) mentions its frequent occurrence in Chinese.

PARIETAL LOBE

More than three score years ago Eberstaller (1884) wrote that "the brain of man differs from that of the primates [sic!] not only by the large development of the third frontal convolution but also by that of the inferior parietal lobule." Yet the sulci of the parietal lobe have been studied much less thoroughly than those of the frontal lobe. The reason for this neglect may have been the bewildering variety of the sulcal patterns in this region, although it must be admitted that a similar state of affairs was no detriment in the case of the occipital lobe! Be that as it may, we must be content to note the definitions and descriptions of the secondary parietal sulci without benefit of statistics.

We begin in the postcentral region, gradually work our way toward the occipital lobe, and end up on the medial side, in the precuneus.

pocs, poci, the *superior* and *inferior postcentral sulci.* These two sulci, which run roughly parallel to the central sulcus, have been discussed with the intraparietal sulcus and the frequencies of their fusion with each other and with the intraparietal have been shown in Figure 14 and Table 5 (p. 36).

scp, the *sulcus subcentralis posterior* and *ret,* the *sulcus retrocentralis transversus.* The former was first described by Marchand (1895), the sulcus retrocentralis transversus by Eberstaller (1884). Retzius considered the two identical. Connolly (1950) pointed out, however, that both Eberstaller's retrocentralis transversus and Marchand's subcentralis posterior may be present in the same hemisphere, that the two are therefore distinct sulci and that there is, moreover, a compensatory relationship between them.

In brain *Hl* both sulci are present, but the posterior subcentral is no more than a small incision in the parietal operculum while the transverse retrocentral is a fairly large element fused, by means of a spur (*ce3*), with the central sulcus (see Fig. 8).

pt, the *sulcus parietalis transversus.* This sulcus was described by Brissaud (1893) as taking its origin on the medial side of the hemisphere, crossing the dorsal margin and ending on the lateral side. It thus divides the upper parietal lobule into an anterior and a posterior part. How constant the direction and configuration of this sulcus are, and whether it is the same as Retzius' sulcus parietalis superior (see Retzius' text, pp. 122–23!), is not quite clear. From the published figures one might assume it. Huard and Nguyen (1938) observed this sulcus in 65 ± 5.3 per cent of their Tonkinese brains.

pja, pjp, the *sulcus intermedius* (of Jensen), *anterior* and *posterior.* A short sulcus between lateral and parallel sulcus was first described by Jensen (1870). He gave schematic lateral views of the brain, drew on the left side an isolated furrow, and on the right side an intermediate sulcus fused with the intraparietal. Eberstaller (1884) who divided the inferior parietal lobule into three "arcs," namely the supramarginal and angular gyri and the posterior parietal arc, recognized two intermediate sulci, "borrowing the term from Jensen, but understanding by it

something quite different." Eberstaller pointed out that these sulci may anastomose with the lateral or the parallel sulcus respectively. The sulcal pattern on the inferior parietal lobule is so variable that hardly any two authors agree. Modern discussions, such as that of Ingalls (1914) are very much influenced by the cytoarchitectural maps of Brodmann (whom Economo and Koskinas followed) where two different areas *39* and *40* are shown divided by the sulcus of Jensen. That areas *39* and *40* (or *PG* and *PF*) are actually indistinguishable (see p. 215) was widely overlooked. Two intermediate sulci are shown by O. A. Turner (1948) during postnatal development.

sp, the *sulcus subparietalis*. The subparietal sulcus on the medial side is a very variable sulcus showing sometimes several radii, being in other brains a simple furrow in the prolongation of the mainstem of the sulcus cinguli. No data about frequencies of the various patterns are available.

We can be brief about the gyri of the parietal lobe: precuneus and a part of the paracentral lobule on the medial side, superior parietal lobule or gyrus, and the inferior parietal lobule, consisting of supramarginal and angular gyrus complete the list.

In brain *Hl* the two postcentral sulci are confluent. The transverse parietal sulcus has a fairly long anterior spur (*ptl*) running parallel to the intraparietal sulcus. Somewhat further occipitad, the sulcus limitans precunei (see below) joins the intraparietal. There are two intermediate sulci, *pja* and *pjp*, arising from the intraparietal, anastomosing further ventrad. The stem thus formed joins the parallel sulcus *ts*. Two lesser sulci have been labeled *m* and *o* respectively merely for identification in the sections.
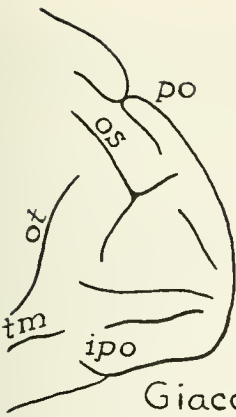
OCCIPITAL LOBE

Of all parts of the hemisphere, the so-called occipital lobe has been the most difficult to analyze morphologically. This is especially true of its lateral side which neither offers clear landmarks for its boundary nor exhibits an even tolerably constant pattern of fissures. To explain the very variable fissures, almost all authors have had recourse to comparative anatomy, and this led, naturally, to such concepts as higher and lower development, pithecoid and anthropine types, etc., etc. Since "lower," i.e., colored races, actually showed pithecoid characters with higher frequency than the "higher," i.e., the "white" race (whatever that may mean), there was no obstacle to accepting this line of reasoning.

But the way to evolutionistic synthesis leads through morphological analysis, i.e., through objective description. We shall, therefore, not discuss orangs, spider monkeys, or macaques, but confine ourselves to Swedes, Chinese, and Fellahin.

The schemes given by various authors and reproduced in Figure 18 illustrate that one can, perhaps with little justification, bring the pattern of the human occipital sulci into two types, frequently referred to as the pithecoid and the anthropine type. From what has just been said, the reader will understand that we do not quite approve of these terms. Let us, therefore, call the type given by Figure 18, left, the vertical, the one given by Figure 18, right, the longitudinal type.
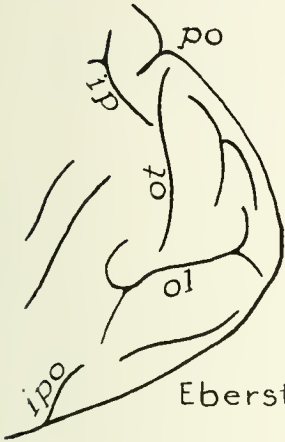
For both types, the anterior boundary of the occipital lobe is given at the dorsal margin by the parieto-occipital incisure, and on the ventral side by the inferior preoccipital (*ipo*) sulcus of Meynert, 1877 (Giacomini's lateral occipitotemporal).
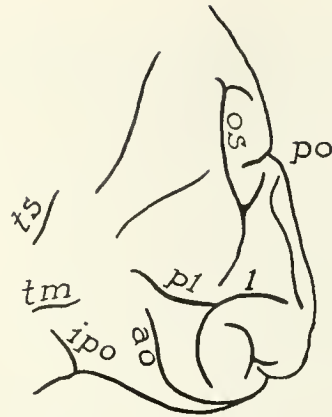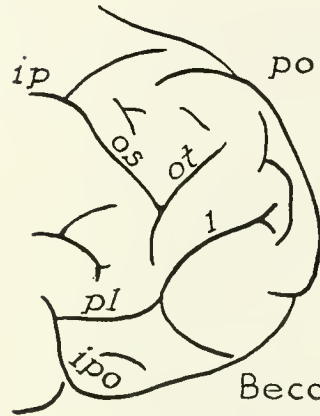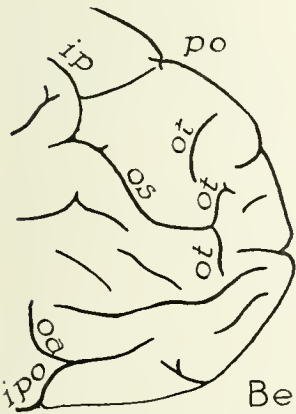
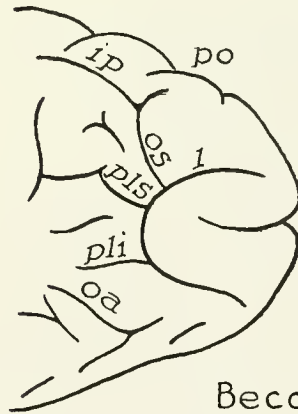FIG. 18. Sulcal patterns of lateral aspect of occipital lobe (after various authors). Left—vertical; right—horizontal types.

This fairly small, but evidently quite constant, sulcus was first used by Bischoff (1868) to delimit the occipital from the temporal lobe and, according to Meynert, was also discussed by Wernicke. "Since it cuts in anterior to the occipital lobe," so continues Meynert, "it deserves the name sulcus praeoccipitalis."

In the longitudinal type all authors recognize a transverse occipital sulcus, frequently represented as the accentuated two end-branches of Wilder's preoccipital sulcus. This sulcus lies roughly on a line connecting the dorsal notch of the medial parieto-occipital incisure with the ventral one of the inferior preoccipital sulcus of Meynert. It varies in length, but runs rarely for more than the dorsal half of the hemisphere and helps to mark the frontal boundary of the occipital lobe. Within the lateral aspect of the occipital lobe proper there are two or more longitudinal sulci. Giacomini (1878) distinguished between a shorter superior and a longer inferior one; Eberstaller (1884) called occipitalis lateralis what is obviously Giacomini's inferior occipital sulcus and sulcus triradialis what may be Giacomini's superior. Other authors have added to the confusion (see Economo, 1930, *loc. cit.* Fig. 27, p. 448). The occipitalis lateralis of Elliot Smith (1904) is Economo's occipitalis lateralis superior, while the lateral occipital of Zuckerkandl (1905) is Economo's occipitalis lateralis medius, and the lateral occipital of Holl (1907) is Economo's inferior lateralis occipitalis and Gratiolet and Broca's inferior occipital. But none of these is Giacomini's (1878) superior occipital, if its relation to the transverse occipital is taken as a criterion.

lo, the *sulcus limitans operculi.* The vertical type is characterized mainly by that much-debated furrow, the sulcus lunatus. An *Affenspalte* is, of course, an easily recognized landmark in the brains of monkeys. The question which the anatomists of the late nineteenth century attempted to answer was, in Mingazzini's (1893) words, whether there existed a sulcus in the human brain which could be considered as the equivalent of the so-called *Affenspalte.* Numerous writers, of whom Zuckerkandl (1905) and Holl (1907) are the last (and perhaps the most voluminous) ones, relied for the answer purely on gross morphological examination. They found an operculated sulcus describing a curve concave occipitad near the occipital pole. Its distance from the occipital pole, its length as well as its depth, may vary within wide limits. To Elliot Smith (1904a) belongs the credit for introducing a cytoarchitectural criterion. He (1904b) found in the brains of Egyptian Fellahin very frequently an operculated sulcus of semilunar shape which was the anterior limiting sulcus of the striate area. This he called, to avoid confusion, "sulcus lunatus," pointing at the same time to the presence of a homologous sulcus in the brains of anthropoid apes.

Economo's (1930) cytoarchitectural studies—unfortunately, of only three brains—showed, however, that an operculated transverse sulcus is not always a limiting sulcus of the striate area. Hence the Viennese author distinguished between a sulcus limitans operculi and a sulcus lunatus proper. Shellshear (1926) had previously described Chinese brains, in which the operculated sulcus is not invariably the limiting sulcus of the striate area (see Shellshear's Fig. 11). Since most of the statements in the literature concerning the sulcus lunatus are based merely on macroscopic inspection, they pertain, strictly speaking, to Economo's sulcus limitans operculi. As we understand it, a sulcus lunatus is always a sulcus limitans operculi, but a sulcus limitans operculi may or may not be a sulcus lunatus.

Turner (1948) found the sulcus limitans operculi fairly well developed in his early postuterine phase, but rudimentary in the later postuterine phase. The part of the cortex newly elevated from the fossa parieto-occipitalis is the dominant feature in the developmental changes occurring in this part of the brain, to paraphrase Turner.

The frequency with which the sulcus limitans operculi occurs in different races is given in Table 14. Most authors called it "sulcus lunatus," but not all observers may have understood that term in the same way, for there are borderline cases in which the sulcus is broken up by a gyrus translunatus, or in which its opercularization may be so poor, or its location so far forward, that it is hard to decide whether one has to deal with a "lunate sulcus" or not. It may be for such reasons that the information about the Chinese is so contradictory, or that Bianchi's (1936) Tuscans are so far out of line. The Northern Chinese of Shellshear agree with Chi and Chang's data, and Shellshear's Southern Chinese agree with van Bork-Feltkamp's data.

TABLE 14

Frequencies of Sulcus Limitans Operculi in Percentages, Computed for Hemispheres.

Race	Frequency	References
Germans	28 ± 5.9	Kuhlenbeck, 1928
Swedes	30 ± 4.4	Antoni, 1914
Chinese (Peking)	30 ± 4.6	Wen, 1933
Dutch	37 ± 5.3	v. Bork-Feltkamp, 1930
Chinese	37 ± 5.2	Shellshear, 1926
Chinese	50 ± 5.0	Chi and Chang, 1941
Chinese (Northern)	53 ± 5.4	Shellshear, 1937
Kenya Negroes ("A")	54 ± 5.0	Vint, 1934
Koreans	65 ± 6.8	Nagai, 1933
Australians ("B")	68 ± 6.6	Shellshear, 1937
Kenya Negroes ("B")	70 ± 4.6	Vint, 1934
Chinese ("A")	71 ± 6.3	v. Bork-Feltkamp, 1930
Chinese ("B")	73 ± 5.7	v. Bork-Feltkamp, 1930
Chinese (Southern)	79 ± 4.1	Shellshear, 1937
Tuscans	84 ± 5.2	Bianchi, 1936

But Wen's figures are far lower than any other. It appears justified, however, to state that a sulcus limitans operculi is found in one out of three or four Europeans, in about one out of two Northern Chinese, but in three out of four Southern Chinese, Australians, and Negroes.

Frequently the sulcus limitans operculi sends one or even two spurs toward the parietotemporal region which are known as prelunate sulcus, or superior and inferior prelunate sulcus, respectively. As Bianchi (1936) remarked, these prelunate sulci may be called lateral occipital sulci.

cu, the *sulcus cunei*. On the medial side, the cuneus, i.e., the region between medial parieto-occipital fissure, calcarine fissure and dorsal margin, bears a varying number of secondary sulci. Retzius described them as running predominantly in a sagittal direction; Shellshear, in his Australian brains observed frequently L-shaped or triradiate sulci. As Elliot Smith (1904c) first pointed out, it is generally possible to identify a usually rather shallow sulcus which runs approximately parallel to the calcarine fissure and at least part of which forms the dorsal boundary of the

striate area. He named it sulcus paracalcarinus or sulcus limitans areae striatae dorsalis (see Fig. 15, p. 39).

In the dorsal part of the cuneus the sulci are apt to run roughly parallel to the parieto-occipital fissure. Their behavior appears to be influenced by the gyrus intercuneatus (see again Fig. 15).

On the lingual lobe there is quite constantly a sulcus limitans areae striatae or sulcus paracalcarinus ventralis. The other fissures are best described in connection with the temporal lobe.

Brain *Hl* shows two well-developed transverse occipital sulci (*otrs* and *otri*). The irregular sulcus near the occipital pole (labeled *n*) is not a lunate sulcus as a glance at the cytoarchitectural map (frontispiece) will show. An anterior occipital sulcus (*oa*) with two long end-branches can be recognized, and Meynert's inferior pre-occipital sulcus (*ipo*) cuts into the ventral margin. The cuneus shows an irregular triradiate sulcus in its ventral part, which we called sulcus cunei (*cu*). Its anterior ramus corresponds to Elliot Smith's dorsal paracalcarine sulcus as another glance at the frontispiece will verify. The branches of the medial parieto-occipital fissure, 1, 2, and 3, which occupy the dorsal part of the cuneus are difficult to identify with

TABLE 15

Bean's data.

Anteroposterior diameter of basal plane of temporal lobe:

	(mm.)
Whites (53)	54.7 ± .79
Negroes (127)	51.8 ± .31
Δ:	2.9 ± .85
Transverse diameter:	
Whites (53)	49.3 ± .42
Negroes (127)	44.4 ± .26
Δ:	4.9 ± .49

(For definition of measurements, see Bean (1914)).

any other sulci. The ventral paracalcarine sulcus on the lingual lobe is the posterior part of the collateral fissure (*col*).

TEMPORAL LOBE

The temporal lobe is, as everybody knows, a relatively recent phylogenetic acquisition. As O. A. Turner (1948) has shown, a forward growth of the temporal pole is noticeable during postnatal development.

There appears to be some racial variation in the relative size of the lobe as a whole. Connolly (1950), adhering closely to Ariëns Kappers' encephalometry, measured the distance from temporal to occipital pole, projected onto the fronto-occipital diameter (= length of hemisphere), and expressed that distance as a percentage of the length of the hemisphere. His figures showed a small but statistically significant longer temporal lobe in whites than in Negroes. Several years previously Bean (1914) had stated that the temporal pole of the Negro brain was more pointed and smaller than that of whites. Using his data in conjunction with Pearson's tables of mean ranges of samples, the values shown in Table 15 can be computed.

Both differences are statistically significant. It is to be regretted that no more anthropometric data concerning the temporal lobe are available.

Turning to the sulci of the temporal lobe, we shall start on the inferomedial surface and proceed toward the first temporal sulcus which, it will be remembered, has been discussed as a primary fissure.

col, the *collateral sulcus*. The sulci on the basal aspect of the temporal lobe show a bewildering diversity (see, e.g., Retzius, Fig. XIII, p. 143). Yet in most brains it is possible to recognize a collateral fissure. When well developed this fissure runs over most of the inferior aspect of the temporo-occipital lobe. Posteriorly, it may fuse with the calcarine fissure. A deep connection between these two fissures—still marked, however, by a submerged gyrus rhinencephalo-lingualis—was seen by Retzius in 6 ± 2.4 per cent of his cases. Landau (1911) observed it in his brains of Esthonians in 13.3 ± 4.4 per cent. The difference is statistically not significant.

The collateral fissure is a continuous furrow about as often as it is interrupted. Landau (1911) found in Esthonians the former condition in 45 ± 6.4 per cent, the latter in 47 ± 6.5 per cent. The rest were irregular.

The posterior (i.e., occipital) end generally bifurcates. The two ends may assume the aspect of a transverse sulcus, described by Arkin (cited after Genna (1924–25)) as a separate entity, the transverse occipitotemporal sulcus. Connecting branches with the third temporal sulcus are present now and then. Landau found such furrows well developed in 13.3 ± 4.4 per cent of his cases. Adding seven cases in which only a very narrow gyrus intervened, a frequency of 25 ± 5.6 per cent might still be acceptable.

Near the temporal pole the collateral fissure may end in another transverse sulcus, called s. collateralis transversus by Elliot Smith (1931, pp. 661, 665). This sulcus had been described previously by Landau (1911).

When fully developed the collateral fissure divides the lingual lobe and the gyrus hippocampi, both of which lie medial to it, from the fusiform gyrus lateral to it. In the fusiform gyrus, i.e., between the collateral and the third temporal sulcus, there may be the sulcus sagittalis gyri fusiformis of Retzius. There may be one straight sulcus, or there may be several smaller sulci, often fusing by oblique or transverse branches with the collateral or the inferior temporal sulcus.

Concerning the inferior and middle temporal sulci we have found no utilizable data. Blinkow studied the basal (1936) surface and lateral (1938) surface of five brains but does not discuss the sulcal pattern systematically. The pattern of these two sulci is so inconstant that it has probably defied description. In brain *Hl* the sulcus which we have labeled inferior temporal (*ti*) runs a long irregular course from the basal surface posterolaterally to curve around the margin onto the lateral surface anterior to the inferior preoccipital sulcus. Between it and the parallel sulcus are two irregular configurations which we have labeled *tma* and *tmp* separated by a long descending spur (4) of the parallel sulcus (*ts*).

There is also an irregular configuration near the temporal pole which we have labeled *tp*.

The analysis of the supratemporal plane is more easily carried out by paying attention to the gyri than to the sulci. It was first brought to the attention of the scientific world by Heschl (1878). He described the anterior transverse temporal

convolution on the basis of 632 male and 455 female brains and pointed out that it formed an arch with the superior temporal convolution significantly more frequently on the left than on the right side (0.3 per cent right, 14.4 per cent left in males; 0.2 per cent right and 4.2 per cent left in females). He found in the cortex covering this convolution "only rather small ganglion cells. . . so that the cell shape suggests that this convolution belongs to the sensory parts of the brain." The earlier literature was reviewed and a detailed description added by Holl (1908). Flechsig (1908) realized that "Heschl's gyrus" was the cortical end-station of acoustic impulses, and he and his associates, among them Auerbach (1906–11), Klose (1920) and Pfeifer (1936), studied this region and its individual variations minutely. Economo and Horn (1930) also used both morphological and cytoarchitectonical methods in analyzing this region.

Following Holl, we can divide the supratemporal plane into a planum temporale and a planum polare. The latter, occupying the anterior part of the superior aspect was called limes temporalis by Holl (1908). He described three small gyri, separated by rather shallow sulci which so far have failed to evoke further interest. The planum temporale contains as the most conspicuous element the transverse supratemporal gyrus of Heschl. This is a slight misnomer for the gyrus runs always in an oblique direction, from medio-occipital to laterofrontal. It is bounded on either side by a sulcus. The frontal one was labeled by Holl the anterior limiting sulcus, the posterior one was called by him the transverse supratemporal sulcus. Not infrequently —we have no precise information—the gyrus of Heschl appears at least partly if not completely doubled by a sulcus intermedius. Either the intermediate or the transverse supratemporal sulcus may cut into the lateral aspect of the first temporal gyrus. Niessl von Mayendorf (1911, p. 293) appears to have used the term "s. acusticus" indiscriminately for any furrow cutting into the lateral aspect of the superior temporal gyrus. Heschl's gyrus may run more or less obliquely. Pfeifer (1936) speaks consequently of a steep or a gradually sloping type. The doubling of Heschl's gyrus appears to occur more frequently on the right than on the left side (Pfeifer, 1936).

<center>INSULA REILII</center>

The island of Reil has not received quite the same attention as the free surface of the cerebral hemisphere. Guldberg (1887) and Eberstaller (1887, 1888) laid the groundwork. Recently Kodama (1934) has made a detailed study of forty Japanese hemispheres, and Grzybowski (1938) followed this up with an analysis of brains of "Jews" [sic!] and Poles.

The insula forms a somewhat irregular quadrilateral pyramid with a generally quite pronounced apex, the monticulus. The anterior surface of the island is covered by the orbital operculum, its large laterosuperior surface by the frontoparietal operculum. The posterior surface lies beneath the temporal operculum; the basal side—the limen insulae—merges in the depth of the vallecula Sylvii with the frontal and temporal parts of the rhinencephalon.

On the laterosuperior surface, dividing it into a larger anterior and a smaller posterior moiety, there runs the sulcus centralis insulae. It begins dorsally almost always at the circular sulcus; it ends frequently beyond the monticulus on the

basal side of the insula (in Kodama's material in 60 ± 7.8 per cent, in "Jews" in 82 ± 5.4 per cent and in Poles in 64 ± 8.7 per cent). Retzius found this sulcus "well developed" in 94 out of 100 cases, i.e., in 94 ± 2.4 per cent.

The anterior part bears two sulci breves. Additional sulci, either between the two or in front of the anterior one, occur in Japanese in 60 ± 7.7 per cent, and in Jews in 32 ± 6.6 per cent. The posterior part bears a sulcus longus. Here, too, additional sulci may be found.

Whether the sulcus centralis or the sulcus longus was the "main" sulcus of the the insula, whether the insula was a *Bogenwindung* around the sulcus longus, as Marchand (1895) argued, or around the central sulcus as Retzius (1902) contended, has lost much of its scientific interest. It implies homologies between primates and other classes of mammals. Such questions are, as we saw, meaningless.

TABLE 16
Encephalometric Indexes (see Fig. 19).

	Zulu	Tuscans	Chinese A	Dutch	Sicilians	Sardin-ians
Callosal index	268 ± 5	349 ± 10	380 ± 8	302 ± 8	317 ± 5	328 ± 5
General index of height	467 ± 11	485 ± 6	537 ± 7	464 ± 6	447 ± 4	472 ± 9
Occipital index	1106 ± 45	1003 ± 40	1232 ± 45	1029 ± 28	1180 ± 13	1410 ± 43
Index of temporal depth	150 ± 6	172 ± 6	132 ± 5	144 ± 3	155 ± 2	181 ± 5
Index of temporal length	767 ± 6	741 ± 6	757 ± 4	751 ± 3	741 ± 2	772 ± 8
Index of frontal height	449 ± 12	470 ± 7	513 ± 6	448 ± 6	433 ± 3	434 ± 8
Index of frontal length	393 ± 4	383 ± 8	374 ± 5	364 ± 3	308 ± 1	299 ± 7
Index of rostral depth	89 ± 6	80 ± 5	64 ± 3	65 ± 2	64 ± 2	47 ± 3
Central index	439 ± 10	409 ± 12	398 ± 6	396 ± 8	425 ± 3	404 ± 10

References: Zulu: Bianchi, 1934; Tuscans: Castaldi, 1936; Chinese v. Bork-Feltkamp: 1930; Dutch: v. Bork-Feltkamp, 1930; Sicilians: Bianchi, 1939; Sardinians: Castaldi, 1936.

Kodama (1934) gives as the length of the insula—projected onto the sagittal plane—56.4 ± 0.64 mm. on the left and 52.8 ± 0.52 mm. on the right side, and for the height 38.1 ± 0.45 mm. on the left and 37.5 ± 0.38 mm. on the right. Obviously the left insula is significantly longer than the right one. The greater length of the left Sylvian fissure (see p. 37) appears as but another expression of the same fact.

ON RACIAL DIFFERENCES

The reader may well have despaired of scrutinizing all the tables informing him about the frequencies of this or that feature. Indeed, most of the significant differences seemed rather between the "personal equations" of the observers than between human races.

The superior frontal, the lunate sulcus, and the relative size of the temporal pole are almost the only characters for which racial differences may exist. But the
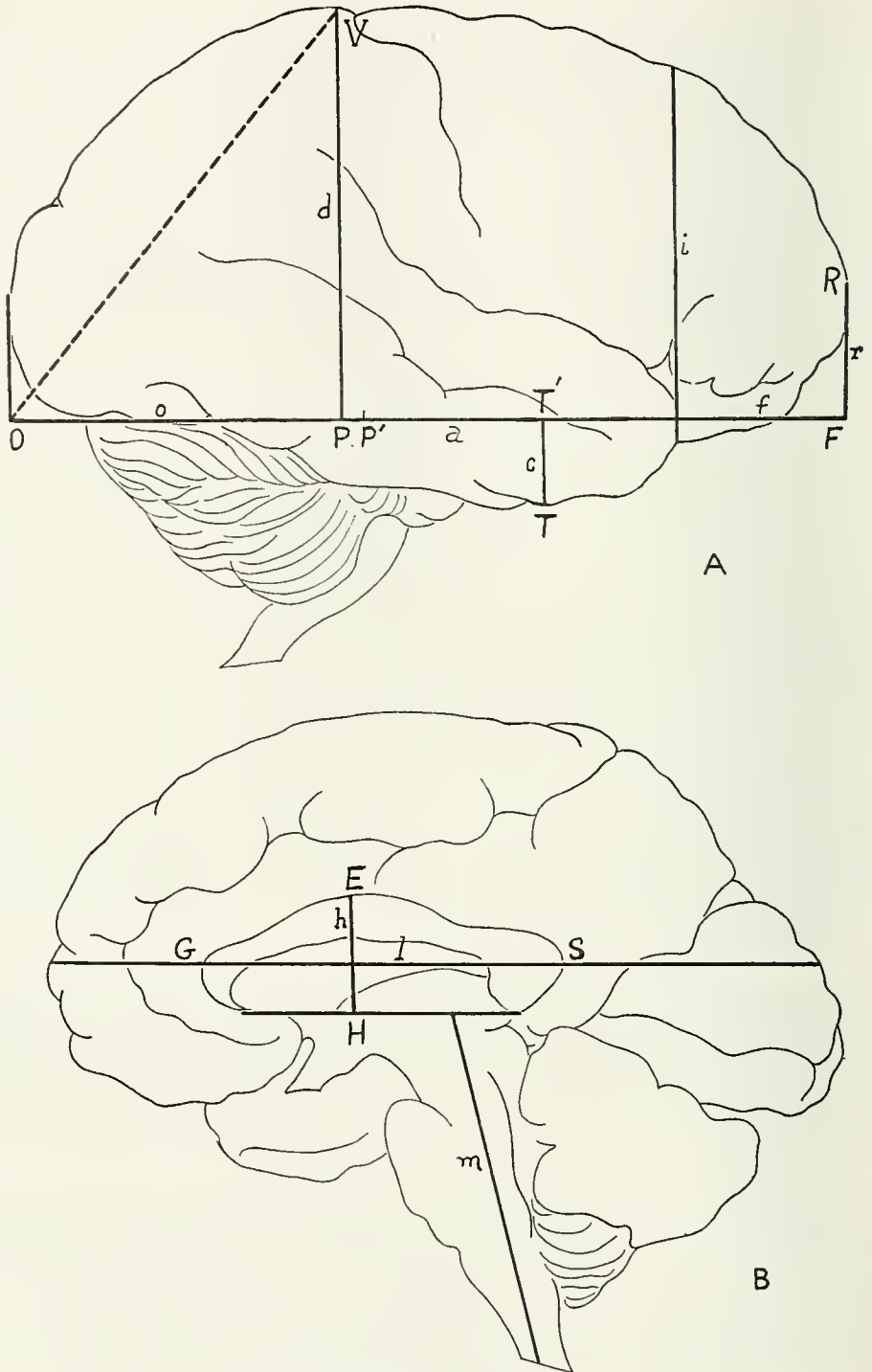
FIG. 19. For legend see opposite page.

last of these is not borne out by encephalometry (see below). The safest conclusion to be drawn appears, therefore, still to be that all human brains look essentially alike. This conclusion is neither startling nor new, as we learned in the introduction to this chapter. A few significant differences crop up here and there, but they fail to lead to any consistent grouping, and one is therefore led to suspect the methods of observation.

Sufficient data on the fissures of the brain have been amassed to convince us of the futility of further macroscopic examinations.

Several authors attempted to put the anthropology of the brain on the same precise numerical footing as the anthropology of the skull or other parts of the skeleton by devising systems of encephalometry. The method of Ariëns Kappers (1926) has been tried out in several instances, while that of Economo (1929b) has been employed by one of us in a short study of primate brains (Bonin, 1941).

Ariëns Kappers measures on photographs of the medial and lateral aspects of the hemisphere and computes several indexes. His technique is explained in the legends for Figure 19. Unfortunately most collections of brains are quite small so that there are but few series of even reasonable length available. What could be

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Fig. 19. Some encephalometric points according to Ariëns Kappers. Redrawn after Ariëns Kappers (unmodified except that the original was not lettered).

LATERAL SIDE: The *lateral horizontal a* = F O: a line drawn through the most ventral point of the orbital operculum and the base of the occipital lobe.

The *parietal perpendicular d* = V P: a line drawn perpendicularly to F O, from the highest point of the dorsal margin.

The *occipital length o* = O P.

The *temporal perpendicular c* = T T': the perpendicular from the lowest point of the temporal lobe to the line *a*.

The *temporal length t* = O T' (not lettered in figure).

The *chiasma perpendicular* (not shown in the figure): a line drawn through the optic chiasma at right angles to the line *a*. The distance from dorsal margin to the line *a* along this chiasma perpendicular is the *frontal height b*. The distance of the point *F* from the point at which the chiasma perpendicular crosses the line *a* is the *frontal length f*.

The *frontal perpendicular* is the line dropped from the most anterior point of the frontal pole to the line *a*. The distance *r* = R F: the rostral height.

The *central perpendicular p* (not shown in the figure) is the line dropped from the point at which the central fissure cuts into the dorsal margin onto the line *a*. It cuts the line *a* at the point P'.

The *insular perpendicular i* is the height measured along a line tangential to the temporal pole and at right angles to *a*.

MEDIAL SIDE: The *callosal length l* = G S: the distance from splenium S to genu G, measured parallel to the callosal base-line connecting the basis of the genu with the basis of the splenium.

The *callosal height h* is the perpendicular on the line G S dropped from the highest point of the dorsal contour of the corpus callosum.

The indices in Table 16 are defined thus:

Callosal index: 1,000 h/l
Occipital index: 1,000 d/o
Index of temporal depth: 1,000 c/a
Index of temporal length: 1,000 t/a
Index of frontal height: 1,000 b/a
Index of frontal length: 1,000 f/a
Index of rostral depth: 1,000 r/a
Central index: 1,000 p/a

The factor 1,000 has been introduced, contrary to the usage of Ariëns Kappers, to get rid of the zeros after the decimal point in the sampling errors.

found in the literature has been put into Table 16. The data of Huard and Nguyen (1938) had to be omitted since no sampling errors could be computed. Several of the indexes, such as the general height index and the frontal height index reflect, so one must assume, merely the varying configuration of the skull. Keenan's (1934) short note is not adequate for proving or refuting this assumption. Some other indexes such as the occipital index and the index of temporal length vary in an entirely haphazard manner and seem, therefore, rather unsuited to arrange the races in any intelligible order. We are left with five indexes, namely, the index of the corpus callosum, of temporal depth, of frontal length, of vertical depth and of the central fissure, for an arrangement of the various races. To visualize that arrangement is not easy. We can use the method of Pearson and Bell (1919). The interracial standard deviation for each index is determined, the deviation for each index of each race is computed in terms of the respective standard deviation and the sum for each race is found, once in absolute terms $A(n)$ and once having regard
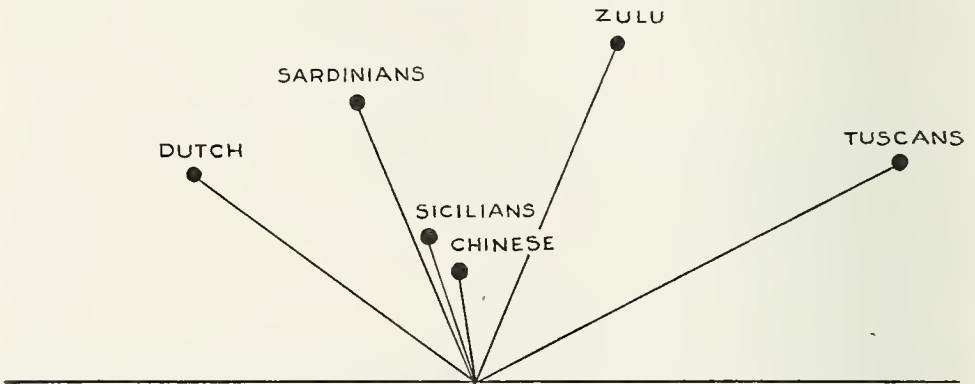
FIG. 20. Arrangement of races by encephalometry.

to the sign of the deviation $S(n)$. The value of $S(n)$ gives the distance from the point of origin, the quotient $\dfrac{S(n)}{A(n)}$ gives the cosine of the angle in a diagram of polar co-ordinates.

The races are then arranged as shown in Figure 20. It is certainly not what would be expected. The wide distance between the two Italian samples, the position of the Zulus between them, the close relation between Chinese and Sicilians are inexplicable features, hardly encouraging further laborious measurements and computations. The absence of racial peculiarities in the human brain remains still the most plausible hypothesis. We do not share Castaldi's (1936) hope for important results from this method.

Chapter IV: Cortical Types

We recognize willingly that researches carried out with the aid of simple methods such as those of Nissl and Weigert have the appreciable result ... of demonstrating the existence of a large number of areas different in structure and function, as well in the cortex of projection as of association. But the progress is reduced to little more than that.

<div align="right">S. Ramón y Cajal (1911)</div>

The description of the cortical types, which is about to be given, follows Brodmann and Economo insofar as it is based primarily on the cell picture. This, as everybody knows, goes back to Nissl, who used material fixed in alcohol, cut without previous embedding, and stained in hot methylene blue solution. We no longer use his original method. We embed formalin-fixed material in celloidin, and stain with thionin, cresyl violet, toluidin blue, or still some other stain. But these are, after all, minor modifications. Nissl's original intention, to obtain an equivalent picture of the cell, holds good also for the architectural picture of the cortex as a whole and is achieved by any one of the stains just mentioned. Hence it seems only historically just to allude to the results of any of these methods as Nissl preparations.

We realize that Nissl preparations are incomplete and give no real insight into the intimate structure of the cortex. The Nissl method stains also the nuclei and a variable amount of the cytoplasm of the glial cells, but they all—neuroglia, oligodendroglia, and microglia—are evenly distributed throughout the thickness of the isocortex (O. H. Schroeder, 1935) and do not confuse the stratification as they may (Lorente de Nó, 1934) in the allocortex. This is revealed only by the Golgi method, which we could not use effectively (see p. ix). Of the results of the Golgi method we have at our disposal only the old studies of Ramón y Cajal (1911) on the brains of infants about one month old, and then only of the precentral, postcentral, and superior temporal gyri, and of the striate area. The recent description of Lorente de Nó (1949) is based on preparations of the mouse's cortex. The situation was clearly stated by Ramón y Cajal (1911, p. 598):

We recognize willingly that researches carried out with the aid of simple methods such as those of Nissl and Weigert have the appreciable result, already remarked by us, of demonstrating the existence of a large number of areas different in structure and function, as well in the cortex of projection as of association. But the progress is reduced to little more than that; since there cannot be any question of using such methods to reveal to us the very interesting details of the morphology of the cerebral cells, the course of their expansions, their connections in the various regions of the gray matter. The neurofibrillary methods, which we have used to fill these lacunae, have not given satisfaction, in spite of the works of Bethe, Cajal, Bielschowsky, Brodmann, van Gehuchten, Marinesco and others. They could not, because of the considerable number of the elements which they impregnate, the thinness of the sections which they necessitate, and their incapacity to disclose the ultimate terminations of dendrites coming from the pyramidal cells and the axial arborizations of the neurons with short axones. These defects, and many others also, more marked in the technic of Bielschowsky than in ours, oblige us to come back to the method of Golgi. So long as we have not found another technic capable of furnishing isolated and partial colorations of dendrites and the terminal ramifications of the axis cylinders, so long as we have not invented a more

faithful and reliable method, the method of Golgi remains, in spite of its inconstancy which has been erroneously exaggerated, the only one which can inform us concerning the morphological types of the cortical neurons and their intercellular connections, on condition, be it said, that we use as much as possible brains of men recently dead or of sacrificed animals. To do otherwise is to condemn ourselves to ignorance of all that is more interesting and typical in the structure of the gray cortex; it also is to retard, if not to arrest, the progress of our knowledge of the intimate mechanism of the organ of thought.

We have supplemented our studies by the examination of silver impregnations (Cajal's method for unmyelinated fibers, Conel, Bielschowsky, Bodian) and preparations stained for myelin (Kultschitsky), but did not find them of much assistance. Golgi preparations did not succeed, as is usual, for the adult brain. The modification of Bubenaite (1929), used by Bonin in previous studies, impregnates only dendrites but fails to show axones and their collaterals.

In the following pages there will be found many times such vague expressions as "about" (e.g. equal in size), "relatively," etc. Such vagueness has been, as we are well aware, the bugbear of the literature on cortical architecture. "About equal" refers to the impression one has under the low-power microscope. We have used routinely a binocular dissecting microscope, with a magnification of 32.5× as measured by ocular micrometer. (The manufacturer wants us to believe we work at 45×.) For finer work we used oil immersion at a magnification of 390×. "Relative" means relative to the typical isocortex (p. 69). "Dark" and "light" (band) refer to the appearance under the microscope or on the photograph. "Dark" does not necessarily mean rich in cells, since neurones are not stained equally heavily by thionin. The terms "thick" and "thin" refer to extensions perpendicular to the surface, "broad" and "narrow" to extensions parallel to the surface. It is to be regretted that other authors have used these terms interchangeably.

After the hemisphere had been cut into serial sections, over three hundred loci were chosen for photographs, without examining them under the microscope, taking care only that they were scattered fairly evenly over the exposed surface and were on the crests of gyri. An exception had to be made, however, for the supratemporal koniocortex which is nowhere to be found on the surface of the brain. These photographs were pasted on cardboards and shuffled like playing cards. Only those whose provenience we could recognize were retained. Of these, we chose for reproduction (see Plates) the photograph which was most nearly parallel to the radiation. We could easily have made photographs which would show more clearly characteristics of interest to us, but we preferred our random photographs as more accurately portraying the average structure.

We shall not always describe the layers in the orderly sequence from the surface down, but frequently turn to the most conspicuous or most important one first. As everyone knows, the fourth, or inner granular, layer (see Fig. 21) contains most of the outer stripe of Baillarger and receives the specific afferents when they exist. Layers $ii + iii$ will be referred to as the outer main layer, layers $v + via$ as the inner main layer, not quite in accord with the usual manner. We propose, in our descriptions, to follow the system first employed by Lewis (1878) and adopted by Brodmann and by Economo, which recognizes six fundamental layers in the isocortex. This means that we shall recognize one layer (vi) which includes $vi + vii$

of the Vogt school. There seems little to be gained by noting all the different numerations of the layers adopted by various authors; we might note, however, that Cajal (1911) makes two layers (3 and 4) of Economo's *III*, so that his internal granular layer is numbered 5. Lorente de Nó (1949) labels *iva* what Economo calls *IIIc*,
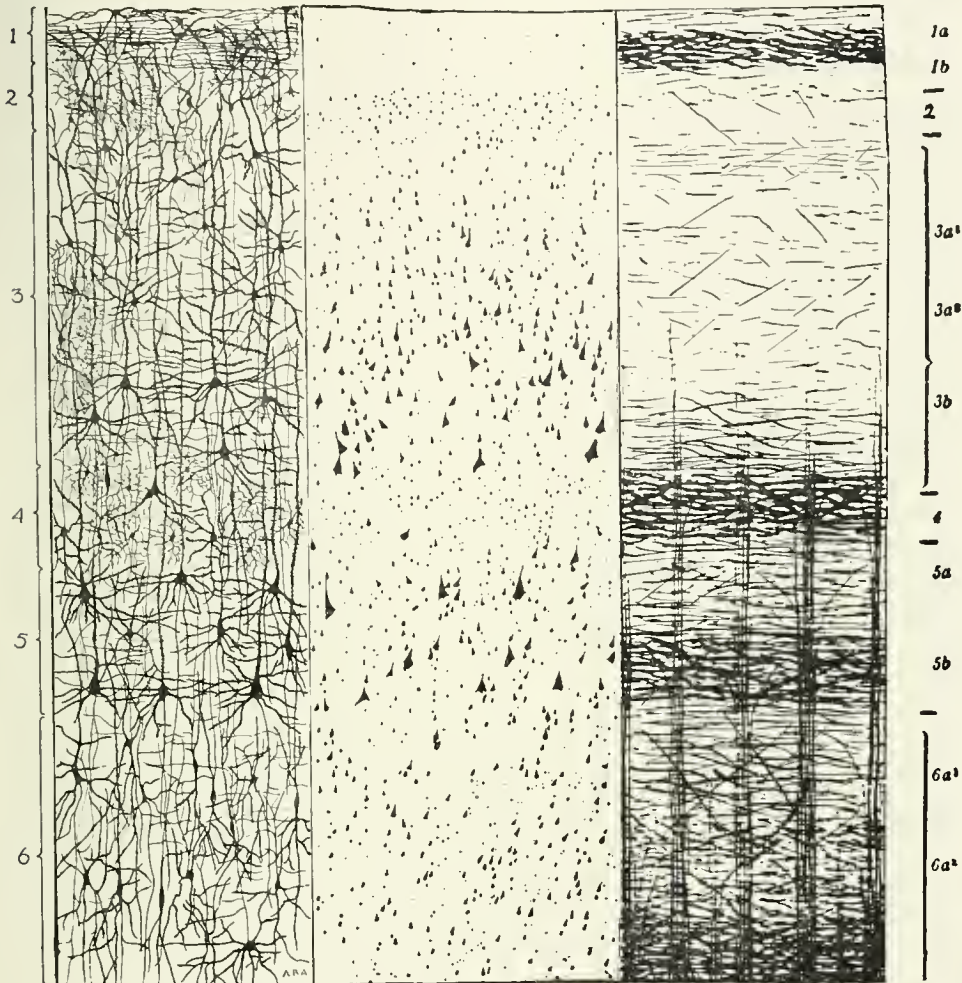

FIG. 21. Cross section of postcentral cortex stained by different methods. From left to right—Golgi, Nissl and Weigert: redrawn and modified after Cajal, Campbell, and Brodmann respectively.

Economo's *IV* becoming *ivb*. He does this because he believes that the afferent terminal plexus includes not only the granules of *IV* (which he calls star cells) but also the pyramids of *IIIc* (which he calls star pyramids).

The deeper boundary of layer *vib* is so vague in many regions as to make figures of the total thickness of the cortex very uncertain. The boundary between *via* and *vib* is much more evident. Even though Lorente de Nó states (1949) that the

boundary between *ivb* and *v* is the only sharp boundary in the cortex, we have found it possible to draw with reasonable accuracy the boundaries between *i* and *ii*, *iiic* and *iv*, *iv* and *v*, and between *via* and *vib*. We shall, therefore, give measurements of the outer main layer (*ii* + *iii*), and of the inner main layer (*v* + *via*) as defined above.

The correspondence of the layers of the typical isocortex, as shown by the various methods, is to be seen in Figure 21. All pictures were drawn from the postcentral gyrus. The Weigert picture is much too schematic; the inner stripe of Baillarger is too sharply outlined and the outer stripe should shade off more into the third layer; the stripe of Kaes-Bechterew is absent in many parts of the cortex, and the stripe in the first layer much less evident.

Numerous illustrations have been published of various parts of the cerebral cortex, both drawings and photographs, usually without accurate information of their exact location. Brodmann (1910, 1914) reproduced a few drawings; and a series of excellent drawings, presumably of Brodmann's areas, are given by Marinesco (1910b); one might note that his drawing of "area 22" looks suspiciously like parakoniocortex and should probably have been labeled *42*. Other drawings by van't Hoog are to be found in Ariëns Kappers, Huber, and Crosby (1936, vol. 2). In the great atlas of Economo and Koskinas (1927) the position of each photograph is carefully indicated. We have followed the same plan (see Fig. 120, p. 269).

In the present chapter we are concerned with the types of cortical architecture which we recognize, not with the number of areas which it is possible to distinguish. There are, e.g., several areas widely separated which belong to the parakoniocortical type, not to speak of the wide extent of the typical isocortex. To locate these areas will be the topic of the next chapters.

I. THE ALLOCORTEX (*A*)

To define the allocortex means also to define the isocortex. As is well known, "allocortex" is the term introduced by the Vogts (1919) for Brodmann's heterogenetic cortex. Brodmann (1909) had given merely a negative definition; the heterogenetic cortex comprised those parts which did not pass ontogenetically through a six-layered stage. The attempts to define the allocortex by its embryological history in a positive way, as M. Rose (1926) and Filimonoff (1929) had done, were sharply criticized by Eduard Beck (1940) and Lorente de Nó (1934) and we shall, therefore, not employ M. Rose's or Filimonoff's scheme (see p. 8).

The allocortex is roughly identical with Ariëns Kappers' (1909) archicortex and paleocortex. The former comprises the hippocampus and its related structures, such as the fascia dentata; the latter comprises the pyriform lobe. Both were considered as olfactory in function.

On the basis of Brodal's (1947) critical review, and M. Meyer and Allison's (1949) investigations, one might suggest a division of the "allocortex" into the prepyriform and the hippocampal region. The former contains, in its first layer, fibers from the olfactory tract and is, therefore, identical with Meynert's white cortex; the latter comprises the hippocampus and the adjacent subicular cortical areas among which the entorhinal area (Economo's *HD, HE*) appears to predominate. The hippocampal system has many other than olfactory afferents. To de-

scribe the histological characteristics of the hippocampus seems superfluous; the stratification of the subicular areas has been explained in detail by Lorente de Nó (1934). Perhaps one might add the retrosplenial areas (Economo's *LD, LE*) to the hippocampal system. The structure of these areas has recently been analyzed by Eduard Beck (1940). It is realized that this scheme leaves us entirely in the dark concerning the significance of the koniose and agranular cortices in the retrosplenial and presubicular regions which have always been thought to be the cortical centers for smell, perhaps also of taste. But this matter is not pertinent to our present theme. We shall give only one photograph of the allocortex to show the characteristics which we wish to mention in those parts of the isocortex which abut on the allocortex.

Plate I brings Economo's area *HA*, a part of the human prepyriform area (Allocortex praepiriformis, *Aprp*). The architecture of this area has been described in great detail by Ramón y Cajal (1900–03, 1911), where the older literature can be found. It can be divided into six layers, and thus resembles superficially the isocortex.

The first layer is, just as in the isocortex, a molecular layer, in Nissl preparations almost devoid of cells. Conel preparations show a wealth of fibers in this layer, while Weil preparations show a lesser number of thin or medium myelinated fibers. Most of the fibers course, at least approximately, parallel to the surface.

The second layer is thick, and contains the "islands of Calleja." These are clumps of densely packed cells, of about 0.5 mm. in diameter. Two types can be recognized; islands consisting of larger, and others of smaller cells. They contain, as Calleja and Cajal showed, cells of very different shape, preponderantly stellate in the islands of large cells, preponderantly fusiform or pyramidal in the islands of small cells. While there remains a vague impression that the long axes of the large cells are approximately parallel to each other and perpendicular to the surface, the small cells show no such regularity in their arrangement.

There follows a third layer, somewhat thicker than the second one, which contains a sparse population of not very large cells. Plate I shows them rather irregularly strewn about. In Economo's Figure 55 (1927), area *HA* exhibits (particularly toward the left) a columnar arrangement, the columns being slightly curved. There is no size gradient in this layer. Indeed, the cells in the lowest reaches of *iii* are perhaps a little smaller than those nearer to the islands of Calleja.

There follows a thin zone almost devoid of cells, except for a few scattered small or medium-sized pyramidal cells, which we may call layer *iv*.

Layer *v* is a little thicker than layer *iv*, and contains densely packed, medium-sized pyramidal cells. Most of them stain very darkly, but lighter ones are interspersed. The right-hand side of our Plate I exhibits traces of columnization.

The last layer (*vi*) can, just as in the isocortex, be broken up into two sublayers, a denser upper, and a scarcer lower one. The cells look pale in comparison with those of layer *v*, are of medium size, and show a fairly pronounced columnar arrangement. Between layer *via* and *vib* there is a barely discernible light zone, reminiscent of layer *iv*. The sixth layer blends fairly gradually into the white matter.

It is not possible to distinguish radii which are such a conspicuous feature of the isocortex. Instead, all the layers are filled fairly evenly by a feltwork of ground

fibers, which do not stain in Weigert or Weil preparations and appear uniformly thin in silver preparations.

The most important difference between the allocortex, just described, and the isocortex appears to be that the former receives its (olfactory) afferents through the tangential layer, while the latter, as we shall see in greater detail, receives its afferents, from a thalamic nucleus or elsewhere, through the white matter.

II. ISOCORTEX (*I*)

The isocortex, which covers the largest part of the human cerebral hemisphere, exhibits typically six layers. There are some areas in which this pattern is obscured in the adult, either by a lessened or by a more intense differentiation. This led Brodmann to speak of homotypical and heterotypical cortex. The latter comprised the agranular areas of the precentral motor cortex, as well as the striate area; the former comprised all the rest of the cortex. Economo and Koskinas, to whose scheme we shall return (see p. 229), emphasized that several "sensory" areas contain rather small cells in great density and coined for them the term koniocortex. They recognized the somesthetic area *PB*, the acoustic area *TC*, and the visual area *OC*. The first two were considered homotypical by Brodmann.

To elaborate slightly on these schemes, we shall call the "typical" cortex *eulaminate* (Fig. 22C), and distinguish from it two heterotypes: the agranular (Fig. 22A) on the one hand, and the koniocortex (Fig. 22B) on the other. We shall also describe three limitrophic variants, of which the juxtallocortex is represented in Fig. 22D. Within each type there are minor variants, but they resemble each other more closely than do the main types.

We will give names to the various types of cortex which we wish to recognize. In the illustrations, however, symbols are necessary, and we have adopted the following scheme: the allocortex is indicated by the heavy capital letter *A*, the isocortex by the similar letter *I*. The various histological types—such as agranular, koniose, eulaminate—are indicated by smaller capitals, thus A, K, E, etc.; lower case letters indicate merely positions.

In myelin preparations (see Fig. 21) the general pattern of the eulaminate cortex shows characteristically the two stripes of Baillarger, with a variable amount of myelinated fibers in the first layer and radii of myelinated fibers extending from the subcortex perpendicular to the stripes of Baillarger up to the outer zone of the third layer. In addition, one finds a less evident stripe of Kaes-Bechterew in the second layer and the outer part of the third layer. The ground fibers form a fairly uniform feltwork of fibers running in all directions. Heavy oblique fibers, generally believed to be either thalamocortical fibers or axons of cells of Martinotti, are found in varying numbers. The diagram of the myeloarchitecture, given by Vogt (see our Fig. 23) is excessively schematized; the inner stripe of Baillarger is too clearly drawn and the outer should spread diffusely upward to include *iiic*; the stripe of Kaes-Bechterew is rarely very definite; the tangential fibers of layer *i* are often almost imperceptible.

Cajal (1911) derived his account of the general structure from preparations of the posterior central gyrus which is covered by parakoniose cortex. We have chosen rather to base our description of the general eulaminate cortex, shown in Plate II,

Fig. 22. Cross sections of different areas of the isocortex. Drawn under the camera lucida from Nissl preparations at a magnification of 450× and reduced to 75×.

A. Simple precentral agranular cortex (*I*ʌx*prc*); *Hl*; block XI, section 990, posterosuperior wall of the superior frontal sulcus.

B. Postcentral koniose cortex (*I*ᴋ*poc*); *Hl*, block XI, section 100; posterior wall of the central sulcus.

C. Eulaminate parieto-temporo-occipital cortex (*I*ᴇ*pto*); *Hl*, block X, section 500; posterior wall of the superior temporal sulcus.

D. Temporal juxtallocortex (*I*ᴊ*t*); *Hl*, block XV, section 899; medial wall of the occipitotemporal sulcus.

on a preparation from the inferior parietal lobule. Economo and Koskinas' areas *FD*, *FE*, *PF*, *PG*, *TA* show so few and such small differences between one another that these are rather topographical designations than architectural distinctions.
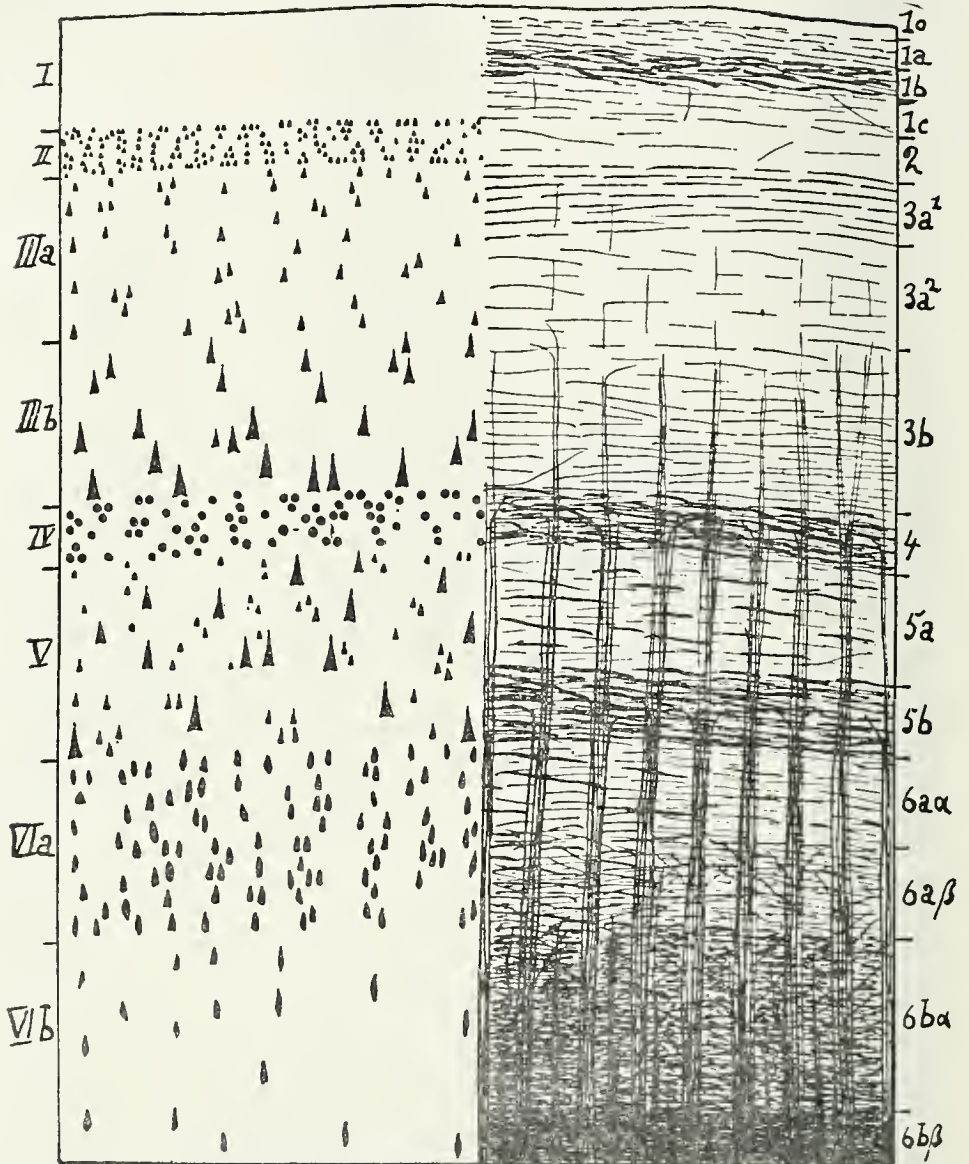
FIG. 23. Diagram of cross section of the isocortex: left, Nissl; right, Weigert (from O. Vogt).

The typical eulaminate cortex about to be described has been studied in preparations taken from the anterior half of the second frontal, inferior parietal, and posterior half of the first and second temporal convolutions. In our experience, any statements of differences to be found in these are true only statistically and are of no aid to the identification of any particular locus, since sections from various parts of any

given gyrus may differ from one another more than they do from sections of the other gyri. Any attempt to identify cortex removed from these regions at operation, such as was recently made by Mettler (1949), is doomed to failure.

Isocortex eulaminatus parietalis inferior (*IEpi*, Plate II).

The division into layers is clear, the cells of layers *vi*, *v*, *iv*, and *iii* are arranged in columns.

Layer *i* contains only a few cells, most of which are glial or mesenchymal.

The second layer has a slightly wavy upper boundary and contains a dense population of small cells. Many of them are pyramidal cells but "granules" of irregular spiny contour, in our silver preparations, appear to make up perhaps 30 or 40 per cent of the total cell population. The lower boundary of layer *ii* is fairly sharp.

The thick third layer contains mostly pyramidal cells which are the larger, the deeper their position. Those in the deepest reaches of layer *iii* dip, with their basal dendrites, into the fourth layer. These large cells are more conspicuous in some locations than in others, and similarly vary somewhat in size. Yet throughout they appear to be within the upper looser part of the outer stripe of Baillarger.

The fourth layer, broken up into "pleiades," as Economo expressed it, contains a wealth of small cells as well as some larger ones. The former are "granules," with irregular scanty cytoplasm; their exact shape can be recognized only in Golgi preparations. Among the latter, large star cells, as well as true pyramidal cells, are found.

The fifth layer contains a sparser population of medium-sized pyramidal cells, as well as small cells of other types. The pyramidal cells are relatively less numerous here than they are in layer *iii*.

The boundary between layer *v* and *vi* is not particularly conspicuous. Yet layer *vi* shows a more uniform cell size, somewhat below that of the large pyramidal cells of layer *v* and, as seen with higher magnification, exhibits fusiform cells which are absent in the higher layers.

The fibers form, in the lower strata, bundles which present, in optic cross section, 8 to 12 fibers and should, therefore, as a simple computation shows, be composed of from 50 to 110 fibers. Bodian or Conel preparations show a number of heavier oblique, frequently tortuous, fibers on a homogeneous background of fine fibers, running crisscross in every direction. Even in Kultschitsky preparations, the stripes of Kaes-Bechterew and of Baillarger fail to stand out clearly, so that O. Vogt (1911) calls this region divisio propeastriata.

Plate II, *IEpi*, is taken from Vogt's area *90*, Brodmann's *39*, Economo's *PG*.

A. THE EULAMINATE VARIANTS

Minor variants of this eulaminate type have been described and their number has reached a bewildering confusion. Many of them we have been unable to identify in our brain *Hl*, but four have seemed to us to have some validity, although even they are tenuous, inconstant, and difficult to recognize.

1. *Isocortex eulaminatus* parietalis superior. *IEps* (Plate III).

This variant is found principally on the superior parietal lobule, hence might be called superior parietal variant. Layer *iv* shows an elaboration. The large cells in *iiic* keep well above *iv* so that the inner granular layer exhibits two sublayers: an

upper lighter, and a lower darker one. On the other hand, many of the cells of layer *v*, particularly the pyramidal cells, are crowded against the lower border of *iv* so that layer *ivb + va* forms a conspicuous dark band, in contrast to the light band formed by layer *vb*. Hammarberg (1895) gives a drawing of our superior parietal variant (his Tafel II, Fig. 3), in which the relatively empty *iva* and the crowding of the layer *va* against *ivb* can be seen quite well, although Hammarberg's text does not mention these features explicitly.

Layer *via* is darker than layer *v* and contains cells of medium size which stain deeply; layer *vib* is thinner.

The outer main layer does not differ from that of the typical eulaminate cortex. Any differences are subtle and would hardly suffice by themselves to distinguish this type.

The myeloarchitectural picture (O. Vogt, 1911) is less characteristic. Vogt's area *85*, described as area subconjuncta bistriata is distinguished by a prominence of *5b* (the inner stripe of Baillarger). It shows, in his photograph, a thick outer Baillarger in which an inner denser part (Vogt's layer *4*) can be distinguished from an outer looser one (Vogt's layer *3b*). This latter is at the level of the large cells of our layer *iiic*.

Silver preparations show these cells to send their basal dendrites toward the fourth layer. Layer *ivb* contains, as our silver preparations show, scattered pyramidal cells, sometimes in nests of three or four cells. Crinis (1933) using a silver method of his own found peculiar "embracing" and "compass" cells in the superior parietal lobule, but these were present also in the postcentral gyrus and have not been sought for thoroughly elsewhere.

Economo and Koskinas remark (p. 558) on the similarity between their *PE* (our *IEps*) and *FDm* (*IEf*). The structure of *iv* and *v* affords, however, a precarious means of distinguishing the two. Plate III, *IEps*, is taken from Vogt's *85*, Brodmann's *7*, Economo's *PE*.

2. *Isocortex eulaminatus* praeoccipitalis. *IEpro* (Plate IV).

A rarefied fifth layer is found in the superior parietal lobule from the postcentral koniocortex posteriorly as far as the occipital region. It is not to be found in the inferior parietal lobule except in patchy fashion just below the intraparietal sulcus and on its walls. However, it spreads in the occipital region in a ring throughout the parastriate (*IPo*) cortex and extends forward a variable distance toward the parietal and temporal regions.

In this broad ring also, the cortex as a whole thins more and more as one goes posteriorly toward and into the parastriate cortex, to become thinnest near the striate margin. This thinning affects especially the fifth and sixth layers, and makes layer *iv* appear relatively thick, although it is not so by absolute measurement.

Within the rarefied fifth layer large pyramids appear here and there throughout this zone. Even more large pyramids are to be seen in the deeper reaches of *iii* and increase in number throughout the parakoniocortex as one approaches the striate margin. There they form a conspicuous band called the limes parastriatus gigantopyramidalis (*OBγ*) by Economo. (Elsewhere Economo used the symbol γ for giant cells in the fifth layer, for example *PEγ*, *PAγ*, *FAγ*, *PCγ*.)

Myeloarchitecturally, the preoccipital variant is, according to Lungwitz (1937),

bistriate and the outer stripe of Baillarger shows an inner denser and an outer looser zone. Even the difference between superior parietal and preoccipital variant is slight, but that has not prevented Lungwitz, a pupil of O. Vogt, from subdividing the preoccipital variant into several subvariants since, as he states, its fibrous structure is not uniform. According to O. Vogt (1911), the entire occipital cortex, apart from the striate area, is unitostriate.

Plate IV (*IEpro*) is taken from Brodmann's *19*, Economo's *OA*, Vogt's *Pro*.

The two variations from the eulaminate type we have just described are agreed upon by all authors, but they are the more tenuous the farther one progresses from the parastriate margin; and the anterior boundary of the preoccipital variant is impossible to fix, passing gradually over into the general eulaminate type. Moreover, as Economo insists, the structure within this zone does not show everywhere its characteristic features with the same distinctness.

3. *Isocortex eulaminatus* frontalis inferior. *IEfi* (Plate V).

This variant was first recognized by Betz (1881) (see p. 4). It is characterized by unusually large cells in layers *iii* and *v*. It covers the opercular and triangular parts of the inferior frontal convolution. The transition from the agranular type of the precentral sector to the granular eulaminate type of the frontal sector (see p. 207) occurs as gradually along the inferior as along the other frontal convolutions and it is, therefore, a matter of debate whether to put the cortex covering the Rolandic operculum into the inferior frontal eulaminate variant, or into the dysgranular limitrophic variant. However, on the triangular part, the fourth layer is definite and about 0.15 mm. in thickness. The fanlike striation to which Economo calls attention is due to the narrowness of the gyri in this region.

The unusual feature of the structure of the cortex in the inferior frontal gyrus is the presence of large pyramids in *iiic* (also found elsewhere in the frontal lobe) in association with less numerous very large cells in *v*, as shown in Plate V, which is taken from its foot.

Large cells are found also in the pars triangularis, i.e., in Economo's *FDΓ*, even in the posterior orbital cortex on the pars orbitalis of the third frontal convolution, especially in the walls of the posterior part of the lateral orbital sulcus. They are actually within the looser external stratum of the outer stripe of Baillarger, as the study of our Weil preparations and a comparison with Strasburger's (1937) illustrations of the myeloarchitecture show.

The fourth layer contains small cells, arranged in pleiades. Pyramids, some of which may be fairly large, are encountered here and there as Conel preparations show.

Bonin (1949) found that some at least of the large cells in layer *v* have asymmetrical basal dendrites and that one dendrite may ascend to branch out within layer *iv*, i.e., within the outer stripe of Baillarger.

Hammarberg (1895) gives a detailed description of *IEfi*. His Tafel I (Figs. 3 and 4) depicts the large pyramidal cells in *iiic* and in *v* behind and in front of the ascending ramus of the Sylvian fissure, respectively. The slight difference in cell size, which Hammarberg found between the cortex on either side of the ascending ramus, does not, in our opinion, necessitate the recognition of two different variants. The small pyramidal cells of layer *iv* are shown very clearly.

O. Vogt (1910) states that the inferior frontal gyrus is unitostriate except for the posterior half of Broca's convolution. Brodmann (1914) includes all of Broca's convolution in the unitostriate area.

Plate V is taken from Brodmann's *44a*, Economo's *FCBm*, Vogt's *56*.

4. *Isocortex eulaminatus* temporalis inferior. *Iεti* (Plate VI).

The inferior part of the temporal lobe, Economo's *TE₂*, shows a rather light outer main layer. The rarefication of layer *iii* impresses itself particularly, but layer *ii* shows also a patchy rarefication. Most of the cells of the outer main layer, even the pyramidal cells in the lower reaches of the third layer, are rather small.

The inner granular layer is not remarkable. Its cells are grouped in pleiades as in so many other parts of the isocortex.

The fifth layer is richer in cells than the third layer. The cells attain about the same size as the pyramidal cells in *iii*.

The sixth layer has smaller cells, but *via* shows about the same cell density as *v*. Layer *vib* shows a greater sparsity of cells and gradually fades into the white matter.

With the exception of the supratemporal plane a detailed myeloarchitectural analysis of the temporal lobe is lacking. Our preparations show two stripes of Baillarger, rather feebly developed and diffuse.

Plate VI, *Iεti*, is taken from Brodmann's *20*, Economo's *TE₂*.

We have not been able to identify in brain *Hl* any area which resembles Economo's *FDΔ*. Other such subdivisions in the frontal, temporal, parietal, and occipital regions have seemed to us too inconstant and uncertain to detain us here.

B. THE AGRANULAR VARIANTS

In the adult brain, this variant differs from the typical isocortex by the tendency of the granules to disappear and to be replaced by small pyramids. The cells of the agranular cortex are relatively large; the inner granular layer is attenuated and the laminar pattern is blurred. Brodmann stated that in embryonic life the agranular cortex shows the same six layers as the rest of the cortex, and that the fourth layer disappears only secondarily. What we know of the cortex of the newborn and the baby (Aldama, 1930; Conel, 1939, 1941, 1947) supports Brodmann's views.

The agranular cortex comprises two main variants, the precentral and the anterior limbic. In the precentral region are two subvarieties: the simple precentral cortex (Economo's *FB*) and the gigantopyramidal cortex (Economo's *FAγ*). The second agranular variant is found on the anterior part of the cingulate gyrus (Economo's *LA*).

1. *Isocortex agranularis simplex* praecentralis. *IΛxprc* (Plate VII).

The cortex as a whole is thick; its lamination is blurred and the inner granular layer (*iv*) consists of no more than a few lines of small cells, interrupted in several places by pyramidal cells.

Layer *ii* is thin, contains small pyramidal cells as well as a fair number of granules, and has a low cell density as compared with other parts of the cortex.

Layer *iiia* contains medium-sized pyramidal cells. Layer *iiib* contains larger pyramidal cells. The transition is rather abrupt; there is no gradient in the proper sense of the word.

Just beneath layer *iiib* there are occasionally found granules—the last remnant of layer *iv*. Silver preparations disclose also some short and medium pyramids. The pyramids of *iv* rarely reach the size of those in *iiic* or *v*.

Layer *v* contains a relatively dense population of medium-sized pyramidal cells throughout.

Layer *via* contains medium-sized fusiform cells. Its cell density is a little higher than that of *v*, but its cells are smaller. Layer *vib* is thick and light; it gradually fades into the white matter.

Columnization is, as always when the section is in the proper plane, well developed up to layer *iii*, but becomes indistinct in layer *ii*.

In spite of its indistinct cytoarchitectural stratification the precentral agranular cortex shows myeloarchitecturally two diffuse sparse stripes of Baillarger as Kawata (1927) maintained. O. Vogt (1910) described this variant as bistriate in its ventral and as propeunistriate in its dorsal part.

Plate VII, *I*A*xprc*, is taken from Vogt's *44*, Economo's *FB*, Brodmann's *6*.

2. *Isocortex agranularis gigantopyramidalis* praecentralis. *I*AG*prc* (Plate VIII).

This variant differs from the simple agranular cortex mainly by a lower cell density and by the presence of the giant pyramidal cells of Betz in the fifth layer.

The first layer is much as in the simple precentral agranular cortex.

The second layer forms not much more than a few lines of fairly evenly spaced small pyramidal and granular cells.

Layer *iii* shows an increase in cell size in its deeper part. It contains mostly pyramidal cells, which range up to about 50μ in length, but are slenderer than the giant cells of layer *v*.

In places, the inner granular layer is represented by a few lines of small cells (see left of Plate VIII). In other places (see middle and right of Plate VIII) there are wide lacunae. These cells are, as silver preparations show, mostly short or medium pyramids.

Layer *v* is very thick and contains, apart from small and medium-sized cells, the giant pyramidal cells, located at various depths of that layer. The tendency to form nests of Betz cells is not very pronounced in Plate VIII; elsewhere it can be seen quite clearly. The size of the cells of Betz varies within wide limits and is larger near the dorsal margin than toward the Sylvian fissure. Indeed, in the "face"-region of the motor area true giant cells are quite rare. They are most frequent in that part of the gigantopyramidal precentral cortex which covers the anterior bank of the central sulcus.

Layer *via* contains a relatively sparse population of fusiform cells; layer *vib* has a sharp boundary against the white matter in our Plate VIII, but elsewhere shows a much more gradual transition.

The myeloarchitecture of the gigantopyramidal precentral cortex shows a diffuse picture described by O. Vogt as astriate. According to him, the two stripes of Baillarger are embedded in a feltwork of ground fibers as dense as the stripes themselves, so that no distinction is possible. This is confirmed by Campbell (1905) and by Kawata (1927).

Cajal (1911) has published a detailed description of the cells of the precentral gyrus, based on Golgi preparations of the cortex of infants a month or so old.

Plate VIII, *I*AG*prc*, is taken from Vogt's *42*, Economo's *FA*γ, Brodmann's *4*.

3. *Isocortex agranularis juxtallocorticalis* limbicus. *I*AJl (Plate IX).

At first sight its strange appearance makes one doubt whether this is isocortex at all. Indeed, M. Rose (1927), who studied the region in a large number of mammals from monotremes to man, held that it was phylogenetically old, and was not true isocortex. He proposed the name mesocortex for it. But even the cytoarchitectural picture does not necessitate the assumption inherent in the term "mesocortex," as Bonin (1948) has previously argued.

The first (molecular) layer is of usual thickness.

The second layer is about as thick as layer *i* and contains pyramidal and other cells of about the same size as layer *iiia* but differs from that layer in its greater cell density and in its lack of columnization.

The third layer is filled with a homogeneous population of cells in its upper part *iiia* while its lower part *iiib* contains a dense population of somewhat larger, deeply staining, slender pyramidal cells. Many of them have, as silver preparations show, a remarkably rounded perikaryon and a rather slender apical dendrite. The band containing these cells is somewhat reminiscent of a similar band of large pyramids in the parakoniocortex (see Plate XIII).

There follows a very thin zone in which (see the right side of Plate IX) some small granules are found. Their density, however, is nowhere near that of the inner granular layer in other cortical types.

The inner main layer is fairly homogeneous in Nissl preparations. Silver preparations show clearly, however, a layer of large pyramidal cells and another of fusiform cells. The pyramidal cells are peculiarly "coarse" looking. Their perikarya are angular and prolonged, without sharp boundary, into a stout, frequently bent, apical dendrite gradually tapering off to "normal" caliber as it traverses the lower reaches of the third layer. Presumably these are the corkscrew cells of Economo and Koskinas. The boundary between *v* and *via* is barely visible on Plate IX. Layer *vib* is sparser and gradually fades into the white matter.

This is essentially the lamination described by Nikitin (1909) from Brodmann's laboratory. He noted that the fourth layer was inconstant and had been missed by many authors.

Myeloarchitectural studies have led M. Rose (1927) to call the anterior limbic area "infraradiate." The Vogts (1919) described the ventral part as infraradiate, the dorsal part as mesoradiate. The radii are described to end below or in the fourth layer. But whether the outer stripe of Baillarger is actually situated in that layer, which these authors labeled *iv*, was never made quite clear. "In (the anterior limbic area) the afferent messages play on a nerve net that is coarser and composed of larger neurons than in most other parts of the isocortex" (Bonin, 1948). It may also be important that the large pyramidal cells in layer *v*, considered to give rise to corticofugal fibers, are very close to the outer stripe of Baillarger.

C. THE KONIOSE VARIANTS

The general characteristics of the koniocortex are thick internal granular layer and small size of the cells. The three variants which we shall describe are known to be areas in which sensory radiations end. Of the three, the visual cortex varies

most widely from the general eulaminate type and the auditory cortex least. Moreover, the visual cortex is sharply circumscribed, whereas the somesthetic cortex has less sharp boundaries and the auditory cortex is found in patches with very vague boundaries. J. Rose (1949) protests the use of the term koniocortex for the somesthetic and auditory cortices.

1. *Isocortex koniosus striatus* occipitalis. *I*κs*o* (Plate X).

The occipital koniose cortex contains the stria Gennari and is, therefore, often referred to as the striate area or cortex. It is thin but, owing to further differentiation of some layers into sublayers, its appearance is more complicated than that of other cortical areas.

Layer *ii* shows nothing characteristic containing, as it does, mostly small pyramidal cells.

Layer *iii* shows very clearly a subdivision into a lighter *iiia* and a denser *iiib*. In the former, pyramidal cells prevail; the latter contains not only small pyramidal cells, but also a comparatively large number of granules.

The inner granular layer is almost as thick as the outer main layer, and shows an outer light and an inner dark sublayer. The former *iva* contains a sparse population of "granules" as well as scattered rather large star pyramids—the solitary cells of Meynert. Layer *ivb* is densely filled with granules. In brain *Hl* one can frequently (see left side of Plate X) observe a thin light band, suggesting a further subdivision into *ivbα + ivbβ*. This has never been described for man and may be an individual variation.

The fifth layer is poor in cells. In its upper part it contains small (medium and short ?) pyramidal cells which send their main axones in a sweeping half arch toward the surface (Cajal, 1911). In its lower reaches, close to the sixth layer, there are scattered fairly large pyramidal cells—the giant pyramidal cells of Meynert (not to be confused with Meynert's star pyramids of layer *iva*)—which send their axones, according to LeGros Clark (1942) to the roof of the midbrain.

The sixth layer consists of a dark *via*, rich in fairly large cells and containing a few displaced large pyramidal cells of Meynert, and a light *vib*, which has a remarkably sharp boundary with the white matter.

The myeloarchitecture of the striate area reveals a very broad outer stripe of Baillarger, known for a long time as the stripe of Gennari or Vicq d'Azyr. The stripe shows a sharp inner and outer boundary, in contrast to most other cortical areas where the outer boundary is indistinct. The inner stripe of Baillarger shows the same sharp outer boundary but is less dense than the stripe of Gennari.

Local differences in the structure of the striate area have been described by Ngowyang (1934a) on the basis of a survey of one brain, and by Eduard Beck (1934) who described such differences in detail for the macaque and promised a second monograph on man, the publication of which the war evidently hindered. We are not convinced by Ngowyang's subtle subdivisions nor have we attempted a similar survey in our own series.

The analysis of the layers, just given, is essentially that of Campbell (1905), of Cajal (1911), and was adopted by Bonin (1942). It differs from that given by Brodmann (1903), who considered our *iiib* as part of the fourth layer which he subdivided into *IVA*, *B*, and *C*. This scheme has found many adherents and Bárány

(1925) and Kleist (1926) even based an ingenious theory of binocular vision on it. The fact, however, that the outer stripe of Baillarger is found only in our layer *iva* and *b* makes Brodmann's conception unacceptable.

Plate X, *Iκso*, is taken from Brodmann's *17*, Economo's *OC*.

2. *Isocortex koniosus* postcentralis. *Iκpoc* (Plate XI).

The koniocortex in the posterior wall of the central sulcus, and on the paracentral lobule, shows a simpler lamination than the striate area, since neither layer *iv* nor layer *vi* has a conspicuous subdivision. On the other hand, columnization is much more pronounced than in the striate area.

Layers *ii* and *iiia* contain cells of about the same small size. They can be distinguished, however, by the greater cell density of layer *ii*. In layer *iiib* the cells are larger, the pyramidal cells stain more darkly, and the columnization is more pronounced.

The fourth layer is very broad and densely filled with cells. Most of these cells are granules. Medium or short pyramids have been occasionally observed in our silver preparations and there are, here and there, large pyramidal cells, as well as star pyramids. The prevailing columnization breaks up the layer into pleiades.

The inner main layer consists of a slight fifth and a somewhat heavier *via*. The fifth layer contains scattered large pyramidal cells.

Layer *via* contains relatively small but dark-staining fusiform cells. Layer *vib* can hardly be made out.

In myelin preparations it is difficult to distinguish the stripes of Baillarger. O. Vogt (1911) describes this area as "Area paradoxa internodensior," and calls attention to the unusually fiber-rich *5b* (internal stripe of Baillarger).

Plate XI, *Iκpoc*, is taken from Brodmann's *3*, Economo's *PB*, Vogt's *69*.

On the parietal operculum, near the island, Gerhardt (1940) described an isolated patch of koniocortex which she labeled *68IIgr*. In its cytoarchitecture it differs so little from the postcentral koniocortex that we see no reason to describe it separately.

3. *Isocortex koniosus* supratemporalis. *Iκst*. (Plate XII).

This is the least evolved of the koniocortical variants. Our plate does not show its most extreme form, for which Economo and Koskinas, Plate XCIV, should be consulted.

The inner granular layer is only fairly thick; the outer main layer shows the subdivision into layer *ii* and *iii* tolerably distinctly, but the inner main layer does not show the laminar pattern as clearly as the other koniocortices.

Layer *ii* is thin, densely filled with cells, but still exhibits a columnization, although not as clearly as layer *iii*.

Layer *iii*, as well as all deeper layers, shows the columns remarkably clearly, hence Economo called the supratemporal koniocortex "rainshower formation." The cells in layer *iii* are small but much sparser than in either occipital or postcentral koniocortex.

The fourth layer contains, of course, mostly granules but it has here and there larger cells displaced, as it were, from either *iii* or *v*.

The fifth layer contains a fair number of medium-sized cells, irregularly scattered over all levels of the layer, but always arranged in columns.

The sixth layer shows about the same cell density as layer v, but its cells are mostly fusiform and many of them stain less deeply than the pyramidal cells of layer v. Layer vib is blurred; it appears to be more a transition toward the white matter than a well-defined layer.

The supratemporal koniocortex is more thoroughly "mixed" with its parakoniocortex than any other koniocortex. Economo and Horn (1930) studied six hemispheres and showed this in detail. They set up numerous subtypes to analyze this phenomenon. Since these subtypes, and their arrangement, vary considerably from brain to brain, there seems little point to include them in a standard description.

Cajal (1911) described, in the acoustic cortex, giant fusiform cells which he thought to be characteristic. These cells were stated to be present in all the layers of the cortex, except the first. Their prolongations ran mainly horizontally. Crinis (1933) could find these cells only in the fourth layer. It is not certain, from their descriptions, that either was writing of the auditory koniocortex. Cajal says merely that he found them in all preparations of the first temporal convolution and of the insula and considers them important for "mental audition."

The myeloarchitecture of the supratemporal plane has been analyzed in great detail by Eduard Beck (1928). Beck states that over the transverse gyrus of Heschl (his subregio temporalis transversa prima) the cortex is characterized by an especially thick and fiber-rich inner stripe of Baillarger. He calls it an outspoken "internodensioren Typ," thus relating its structure to that of Vogt's area 69.

Plate XII, Iᴋst, is taken from Brodmann's 41, Economo's TC, Beck's $ttrI$.

D. THE LIMITROPHIC VARIANTS

Between any two regions of well-marked structure in the isocortex are to be found zones of transitional structure which have been described as limitrophic zones. Even between the agranular gigantopyramidal area and the postcentral koniose cortex there is such a zone which Brodmann called a "Mischzone" and Economo dignified as PA.

About each koniocortex there is a limitrophic zone, or parakoniocortex, characterized by unusually large pyramids in $iiic$. These cells are generally larger and more numerous near the koniose margin. They disappear gradually farther away from that margin.

We give, as an example of the parakoniocortices, the zone about the striate area.

1. *Isocortex parakoniocorticalis* occipitalis. Iᴘo (Plate XIII).

The whole inner main layer, not only layer v, is light and contains few cells.

The fourth layer is relatively thick; it contains mostly granules; only here and there is a star pyramid encountered. Sublayers cannot be distinguished.

The outer main layer is relatively thick. The upper boundary of layer ii is rather straight. The lower boundary of layer ii is a little difficult to distinguish because both layer ii and layer $iiia$ contain cells of about the same size. But the cell-density diminishes, and a columnar arrangement becomes more apparent as one enters $iiia$. Within layer iii, the cell size increases rather abruptly as one comes to layer $iiic$ which contains very large pyramidal cells, so large that Economo spoke of "giant cells." These large or "huge" pyramidal cells occur in irregular nests and

are situated immediately above or even within layer *iv*. They appear to be within the upper loose zone of the outer stripe of Baillarger.

Scattered, unusually large pyramids are found also in layer *v*.

Plate XIII, *I*po, is taken from Brodmann's *18*, Economo's *OB*.

The postcentral parakoniocortex (*I*ppoc) and the supratemporal parakoniocortex (*I*pst) are of similar structure. The dearth of cells in the fifth layer, the large pyramidal cells of layer *iiic*, the preponderance of small granules in *iv*, and the scarcity of pyramids in that layer are easily observed in all three variants, especially when silver preparations are studied.

Near the allocortex, a series of limitrophic zones or juxtallocortical variants may be seen and have been variously classified by different authors. We are concerned only with those modifications which occur in what is recognizable as isocortex. The distinguishing characteristics are usually a tendency of the cells of *ii* to be of relatively large size and to group in glomeruli and a densification of *v* with its cells crowding up toward *iv*.

We give, as an example of the juxtallocortical variants, the zone on the inferior surface of the temporal lobe (Economo's *TH*).

2. *Isocortex juxtallocorticalis* temporalis. *I*jt (Plate XIV).

Layer *ii* is very thin; its cells are relatively large. A few rows of pyramidal cells are arranged like palisades just beneath the first layer along a somewhat wavy front, with irregular breaks here and there. The cells comprising these palisades are no smaller than the pyramidal cells in layer *iii*. The cell size, and the breaks between the cell groups, reminiscent as they are of the gaps between the islands of Calleja, are almost sufficient in themselves to call this formation juxtallocortical.

The third layer shows an almost uniform size of its pyramidal cells. There is a faint columnar arrangement but the gaps appear to blur this pattern which, however, can be easily seen in the inner main layer.

The fourth layer is thin and contains some larger cells.

The fifth layer is the heaviest of all. Apart from interspersed granules, it contains numerous, fairly large, pyramidal cells which fill it with almost uniform density. Layer *v* is fairly thick and has a sharp lower boundary.

Layer *vi* is much lighter and is composed of much smaller cells than layer *v*. Layer *via* is compact; *vib* impresses the observer more as a transitional zone to the white matter than as a distinct layer.

Other juxtallocortical variants are found around the anterior limbic cortex, over the anterior wall of the island, spreading onto the inner side of the temporal tip, up to cover a part of the frontal operculum and anteriorly over the gyrus rectus (purple in the frontispiece).

Plate XIV, *I*jt, is taken from Brodmann's *36*, Economo's *TH*.

3. *Isocortex dysgranularis* frontalis. *I*df (Plate XV).

Anterior to the frontal agranular cortex is a zone of variable width which extends from the cingulate sulcus over the medial and dorsolateral surface onto the operculum, the posterior part of the orbital surface of the frontal lobe and the tip of the temporal lobe. In this zone the inner granular layer is very attenuated, hence it is generally referred to as dysgranular.

It varies somewhat in its various parts, merging into the juxtallocortex over the anterior part of the island, the orbital surface of the frontal lobe and the temporal pole; it also develops large cells in *iiic* and *v* over the inferior frontal gyrus.

On the inferior frontal convolution the isocortex dysgranularis thus overlaps, as it were, the horizontal zone of large cells in *iiic* and *v*, to which Betz called attention. This overlapped zone might be reckoned to belong either to the dysgranular or the inferior frontal eulaminate variant. Campbell looked upon this region as a part of his intermediate precentral cortex; Brodmann gave it the status of a separate type; Economo compromised by describing it as a transition between dysgranular and simple agranular cortex (*FCBm*).

The dysgranular cortex on the first and second frontal convolutions may be considered typical for this limitrophic variant. It shares with the simple agranular cortex a poor differentiation into laminae but it tends toward the eulaminate type by virtue of an inner granular layer, although a poorly developed one.

This limitrophic variant was not recognized by Strasburger (1937) in his myeloarchitectural studies. According to Kawata (1927), Vogt's areas *36*, *47*, and *46* are "very probably" identical with Economo's *FC*. It differs little, according to Kawata, in its myeloarchitecture from the simple agranular cortex. There are two horizontal strata (outer and inner stripes of Baillarger) but they vary within the "area" (*sit venia verbo*) in their wealth of fibers showing, on the whole, a looser texture. The radii are described as a little farther apart than in *FB*. Kawata's own figures hardly bear this out.

Plate XV, *I*Df, is taken from about Brodmann's *8*, Economo's *FC*, Vogt's *48*.

In spite of the variations we have just described, one fundamental pattern is readily identifiable throughout the isocortex even though we lack intimate knowledge of the intrinsic structure of the frontal regions (Lorente de Nó, 1949). The reasons for this arrangement of the cells in six layers are obscure. It is so constant, however, since the appearance of the cortex in the monotremes, that it is difficult to escape the conclusion that it has some fundamental significance.

Since the areas of the cortex to which specific sensations radiate (touch, sight, hearing) tend to become koniose, one could suspect that the granular layers (*ii* and *iv*) might be sensory end-stations and it is known that the specific thalamic afferents end principally in layer *iv* (see Chap. VIII); other afferents reach also layer *ii*. Since motor cells in the spinal cord and the large Betz cells of the motor cortex have prominent Nissl bodies, one could suspect that the corticofugal fibers might arise from the large pyramidal cells of layer *v*, and it is known that many of them do arise there (see Chap. VIII). Yet afferent fibers end also in other layers, and so do efferent fibers arise from other layers. The literature pertinent to this theme of the functional significance of the cortical layers has been collected by Ariëns Kappers, Huber, and Crosby (1937, pp. 1564–72); that the conclusions therein reached are too dogmatic has been pointed out by Lorente de Nó (1949) who concludes that "it is obvious that there is no basis for considering the cortex as composed of several layers with specific primordial functions: reception, association and projection." Nevertheless, Lorente de Nó makes a sharp distinction between an external lamina (*i − ivb*) and an internal lamina (*v + vi*) and calls attention to the

sharp boundary between them. He notes that, "The axons of the pyramids and star cells of LAYERS I to IV have their ramifications chiefly within the gray matter, although a number of axons of pyramids, especially of the large star pyramids, reach the white substance and form association and callosal fibers."

Although the structure of the cortex in six layers is probably functionally significant, in any attempt to understand its functioning the vertical arrangement of its cells in columns must also not be forgotten. "From the functional point of view it is a unitary system composed of vertical chains of neurons, among which anatomically the most important are those starting at the articulation of the specific afferents and the cells of the external lamina (Lorente de Nó)."

Much more information is necessary, especially concerning the intrinsic structure of the human cortex, before we can gain much insight into the relation of its structure to its manner of functioning. So far, only in the case of the striate cortex (O'Leary, 1949) has any systematic attempt been made with modern methods to study this problem.

However important the laminar structure of the cortex may be, there is ample evidence that it functions as a whole. Its intimate structure is compatible with such a conclusion. "Since the impulse conducted by a fiber necessarily passes into its collaterals, and branches of the descending axons are distributed in the same territories as the cortical afferents, there can be no doubt that the effect of the impulses entering the cortex depends largely upon the impulses at that moment circulating through the descending axons as a result of the existing cortical activity (Lorente de Nó, 1949)." O'Leary (1949) remarks also that the alpha-rhythm of the electroencephalographers is a function of the entire thickness of the cortex and not of its individual laminae and, moreover, this cortical mechanism has an intrinsic activity even when isolated from the rest of the organism (Bremer, 1950).

Chapter V: Serial Sections

I should not be surprised if some readers were, at the first glance, to think the subject recondite and its treatment heavy.

THUDICHUM (1884)

After photographing the brain from all aspects, we cut it, before embedding it in celloidin, into twenty-one blocks as shown in Figure 24. These blocks were sectioned at 24 μ and the sections stained with thionin. Every fifth section, without exception, was mounted. We have adopted a procedure intermediate between that of Vogt (1950), who sectioned whole hemispheres, and that of Economo and Koskinas (1925) who made numerous small blocks. We found, in our work on the macaque and chimpanzee, many advantages in having several gyri on the same slide, but large sections of whole hemispheres are unwieldy. The blocks were carefully planned to permit sectioning as nearly as possible perpendicular to the surface. The descriptions were written from inspection of the cross sections under a binocular microscope. Measurements of cortical thickness were made at a magnification of 32.5× with a micrometer scale in the ocular. These measurements are given for what they are worth—in our opinion very little. They vary greatly in different parts of the same gyrus as will be apparent. Also the measurements may vary greatly from one brain to another, of analogous loci of the precentral gyrus from 4.5 mm. to 3.6 mm., and of the gyrus supramarginalis from 3.7 mm. to 2.9 mm. (Economo and Koskinas, 1925, p. 40). Kraus, Davison, and Weil (1928) estimated that the brain changed insignificantly in size during fixation in 10 per cent formalin but shrank about 27 to 29 per cent during dehydration and embedding; the loss in volume was estimated at 12 to 13 per cent and the loss in surface area about 8 to 9 per cent. The size of cells was measured in the same manner under oil immersion at a magnification of 390×. The influence of fixation and embedding on cell size, studied by M. Rose (1929) and Sarkissov (1930), has not been taken into account. The actual dimensions are not of much importance for our theme. It is impossible, anyway, to measure accurately the size of cells as branched as nerve cells. The figures given are important only for comparative purposes.

Measurements of the total thickness of the cortex are made from the outer margin of the second layer to the inner margin of *via*, the inner boundary of *vib* often being too vague to determine. Even so, our measurements are often only rough approximations since these boundaries are not smooth lines. Since it is also often impossible to determine the limit between *ii* and *iiia*, the measurements will usually include only the outer main layer *ii + iii*, the inner granular layer *iv*, and the inner main layer *v + via*. Nonetheless our measurements are somewhat smaller than those given by Economo and Koskinas.

All measurements, unless otherwise stated, are made only from zones in which the section is parallel to the columns as nearly as possible. Unfortunately the columns do not always run perpendicular to the surface, nor do they always run in straight lines through the cortex but are variously curved; one may, therefore,

Fig. 24. Diagrams of the brain *Hl* showing blocks cut for sectioning.

see the columns well in the inner main layer only or in *iii*, *iv*, *v*, but not in *vi*. Nowhere in the isocortex are there no columns. When cut diagonally to the columns the cortex has a blotchy look; when cut parallel to them it is streaked.

The thickness of the cortex varies continuously, being usually, but not always, thicker over the crowns of the gyri and thinnest at the bottoms of sulci. Along the walls of sulci the cortex usually decreases in thickness as one progresses toward the depth. For this reason, whenever measurements are given from cortex within sulci, they have been made halfway down the wall.

On a narrow gyrus the thickness of the crown is exaggerated, usually also the thinness of the walls. It is advisable to make all measurements from the crowns of broad gyri. Even this has a disadvantage in that each gyrus, when it reaches a certain width, tends to buckle inward in the middle to form another sulcus. The first indication of this is a comparative thickening of *iii*. Such thickenings have sometimes been described by others as separate areas. The influence of these factors on cytoarchitecture and the exact way in which the cortex is bent over the inner granular layer, as it were, has been analyzed by Bok (1929).

On the crowns of narrow gyri the cells tend to be elongated. At the bottoms of sulci the cells are broader and shorter. At the bottoms of sulci the inner main layer is relatively thinned; over the crowns of the gyri the inner main layer is relatively thickened.

Whenever possible, photographs reproduced herein have been made from the crowns of flat broad gyri, or halfway down the walls of deep straight sulci.

Because of the impossibility of writing out in full the names of the various types of cortex distinguished, we have been obliged to use, in the accompanying illustrations, the symbols described on page 66. Since we are here interested only in the isocortex, the general symbol *I* for the isocortex is omitted. The capital letters refer to the type of cortex as follows:

A—agranular	K—koniose
D—dysgranular	P—parakoniose
E—eulaminate	S—striate
G—gigantopyramidal	X—simplex
J—juxtallocortical	

The lower case letters refer to topographic location as follows:

f—frontalis	poc—postcentralis
fi—frontalis inferior	pop—parietalis opercularis
fm—frontalis medialis	prc—praecentralis
fo—frontalis orbitalis	pro—praeoccipitalis
fop—frontalis opercularis	ps—parietalis superior
fs—frontalis superior	rs—retrosplenialis
i—insularis	st—supratemporalis
l—limbicus	t—temporalis
la—limbicus anterior	ti—temporalis inferior
o—occipitalis	tm—temporalis medialis
op—opercularis	to—temporo-occipitalis
p—parietalis	tp—temporopolaris
pi—parietalis inferior	ts—temporalis superior

All cross sections are drawn at a magnification of 2×.

BLOCK I (Fig. 25)

Section 100. Fig. 26.

The cortex of the cuneate sulcus is of parakoniose type (see Plate XIII), measuring 1.25 mm. on the posterior and 1.4 mm. on the anterior wall, and this type continues over the cuneus as far as *pom1*, after which it changes so that the cortex on the anterior wall of this posterior side-branch, although no thicker (1.4 mm.), has smaller pyramids in *iiic* and more cells in *v* and the large cells in *v* are scarcely larger than the others. On the crest of the small gyrus between *pom1* and *pom* the radiations are very broad and the cortex measures only 1.4 mm. but the cells of *iiic* are small and *v* fairly well filled. On the posterior wall of *pom* the cortex measures 1.7 mm., the pyramids of *iiic* are large, up to 29 x 18 μ; the outer main layer meas-
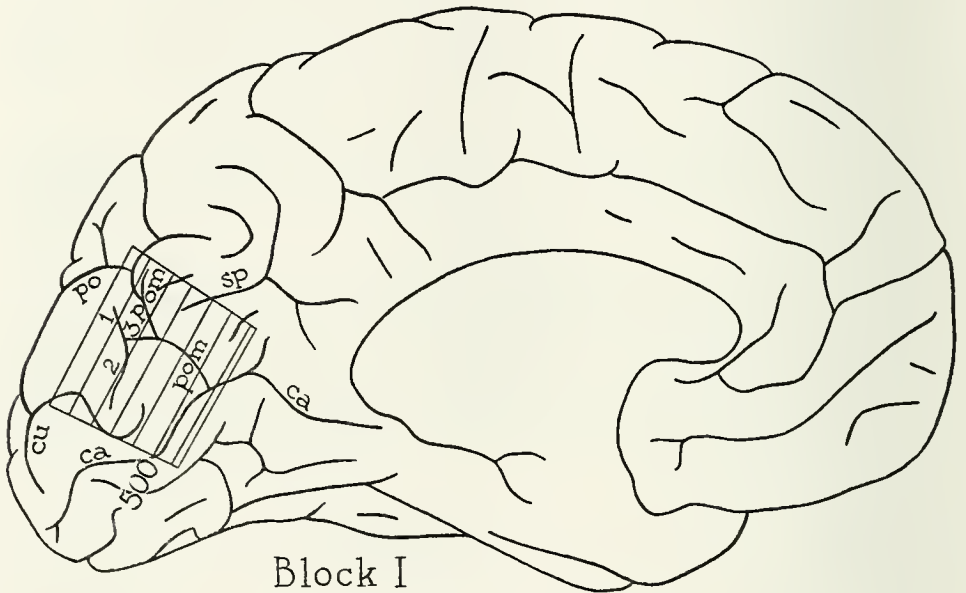
FIG. 25. Position of sections of Block I.

ures 0.84 mm., the inner 0.74 mm. This cortex thins in the depth of the sulcus to 1.1 mm., outer main layer 0.7 mm., inner 0.3 mm.; the radiations are very broad and the large pyramids in *iiic* very numerous, up to 39 x 24 μ, with equally large cells in *v*. Only on the crest of the small gyrus is this cortex not of parakoniose type.

On the anterior wall of *pom* the cortex is much thicker (1.9+ mm.), outer main layer 0.7 mm., inner 1.0+ mm. The thickness of the inner main layer is difficult to determine because the cells of *iv* are very small near *iiic* but become heavier in the deeper portion of the layer so that they are difficult to distinguish from the outer cells of *v*. The deeper part of *v* contains fewer cells so that the impression is of a dark band formed by *ivb* + *va* in which it is impossible to draw a boundary line between *iv* and *v*. The boundary of *vib* against the subcortex is very indefinite. The cells of *iiic* are pyramids measuring up to 34 x 18 μ. This cortex is clearly eulaminate of the type which we have called superior parietal (see Plate III).

The cortex over the surface anterior to *pom* cannot be read because it is cut tangentially.

Section 200. Fig. 26.
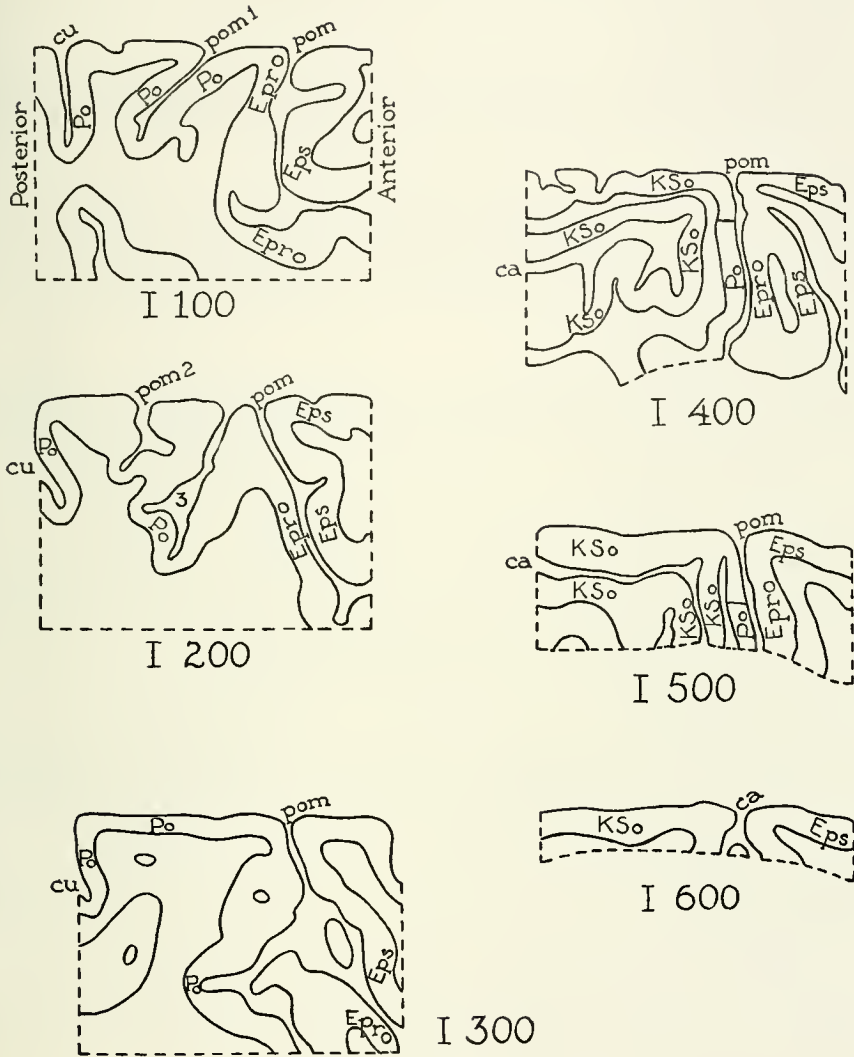
FIG. 26. Cross sections of Block I.

The cortex on the anterior wall of the cuneate sulcus (*cu*) is of parakoniose type measuring about 1.45 mm. It seems to be much the same in the depth of *pom3*, which is the only short stretch where it can be read until the posterior wall of *pom* is reached. Here the cortex varies from 1.4 mm. to 1.5 mm. in thickness. It contains many large cells in *iiic* and *v*, up to 32 x 18 μ, some of them in *iv* also. A typical measurement is outer main layer 0.6 mm., inner 0.8 mm.; the columns are broad,

the fifth layer fairly well filled. The cortex varies from typical parakoniocortex mainly in the thicker inner main layer and the relative filling of *v*.

The cortex on the anterior wall of *pom* is of the superior parietal type previously described in section 100. The same cortex can be seen on the surface anterior to *pom* where it measures 1.7 mm. and has the characteristic light *iva* and *vb*.

Section 300. Fig. 26.

The anterior wall of the cuneate sulcus (*cu*) is covered by cortex of parakoniose type, measuring 1.2 mm. The cortex of the cuneus is very similar, measuring 1.3 mm. The same cortex continues down the posterior wall of *pom* wherever it can be read.

The anterior wall of *pom* is covered by eulaminate superior parietal cortex, measuring 1.8 mm., with the characteristics already noted in section 100. This cortex continues over the surface anterior to *pom* but thins to 1.5 mm., outer main layer 0.65 mm., inner 0.75 mm., if measured from the outer margin of *ivb*. Layer *vb* is characteristically light.

Section 400. Fig. 26.

Although cut very irregularly, the cortex over the cuneus can be seen to be of parakoniose type to about its middle and then abruptly turns into striate cortex which continues into the posterior wall of *pom* only to become again of parakoniose type.

A deep dorsal shelf of the calcarine fissure is completely covered by striate cortex.

The cortex on the surface anterior to *pom* is characteristically eulaminate superior parietal, but that on the anterior wall of the fissure is not. It measures here 1.54 mm.; outer main layer 0.7 mm., inner 0.68 mm. The pyramids of *iiic* are small, not over 21 x 13 μ, and the heavy *ivb* + *va* is not very evident.

Section 500. Fig. 26.

The cuneus is entirely covered by striate cortex which extends a way down the posterior wall of the parieto-occipital fissure (*pom*). The superficial cortex anterior to *pom* is eulaminate superior parietal in type, but that on the anterior wall of the fissure is of the transitional character previously described in section 400.

Section 600. Fig. 26.

The cortex posterior to *ca* is all striate, that anterior is eulaminate superior parietal in type.

<div style="text-align:center">BLOCK II (Fig. 27)</div>

The description of this block begins at the tip of the occipital pole and progresses forward.

Section 700. Fig. 28.

The entire occipital pole is covered by striate koniocortex which is so characteristic that it can be recognized even when cut tangentially. In this section there is only one small segment, medial to the *lo* sulcus, which is covered by parakoniose cortex. Where it is cut perpendicularly in the extremity of the calcarine fissure the striate cortex measures 1.54 mm. in thickness. The parakoniose cortex measures approximately the same.

The striate koniocortex (cf. Plate X) has been so often described that it is unnecessary to do so here. The parakoniose cortex has an outer main layer which measures 0.65 mm., the inner granular layer 0.12 mm., and the inner main layer 0.77 mm. It is impossible to draw a line between *ii* and *iiia*. The outer margin of *ii*
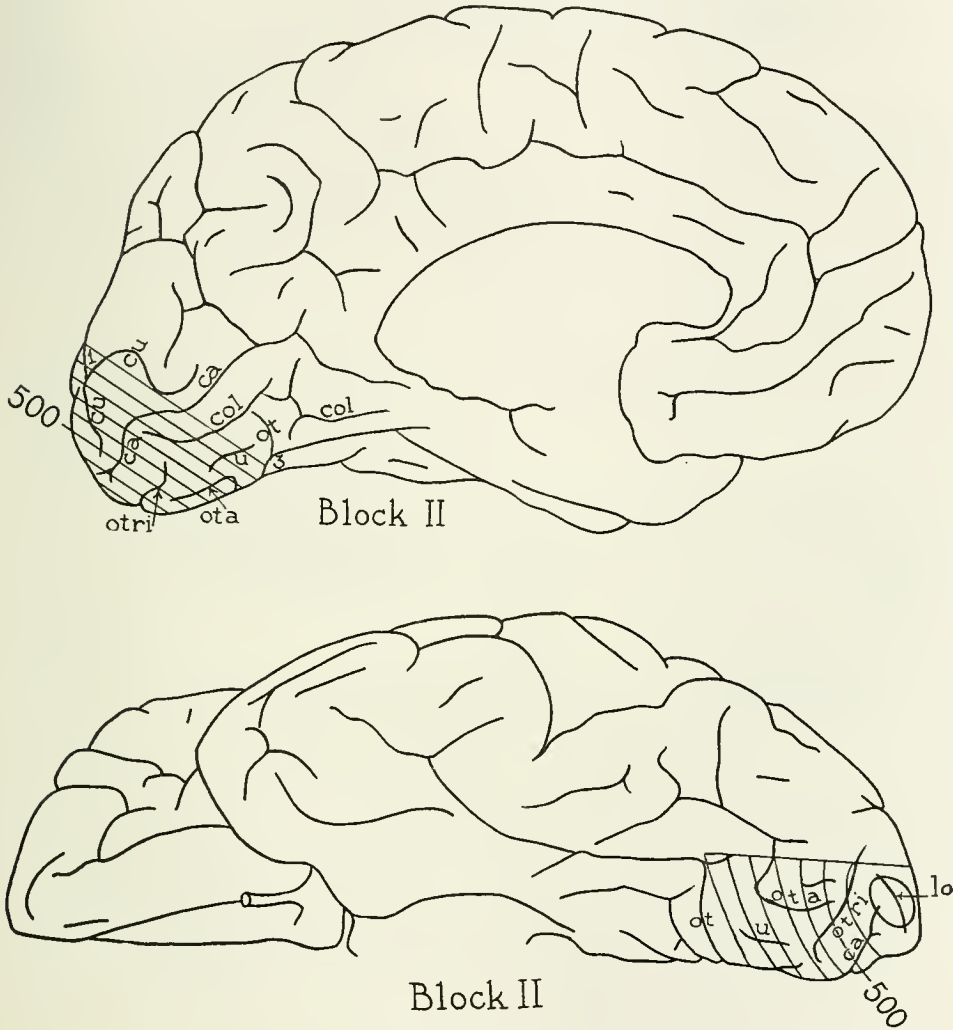
FIG. 27. Position of sections of Block II.

is quite smooth. The cells of *ii* + *iiia* are small and rather uniformly distributed although delicate radiations can be seen passing entirely through them in places. The cells of *iiib* are slightly larger pyramids and those of *iiic* reach as much as 26 x 18 μ. These large pyramids of *iiic* are numerous and are divided into columns by broad clear radiations which project from the subcortex through *vi*, *v*, and *iv*.
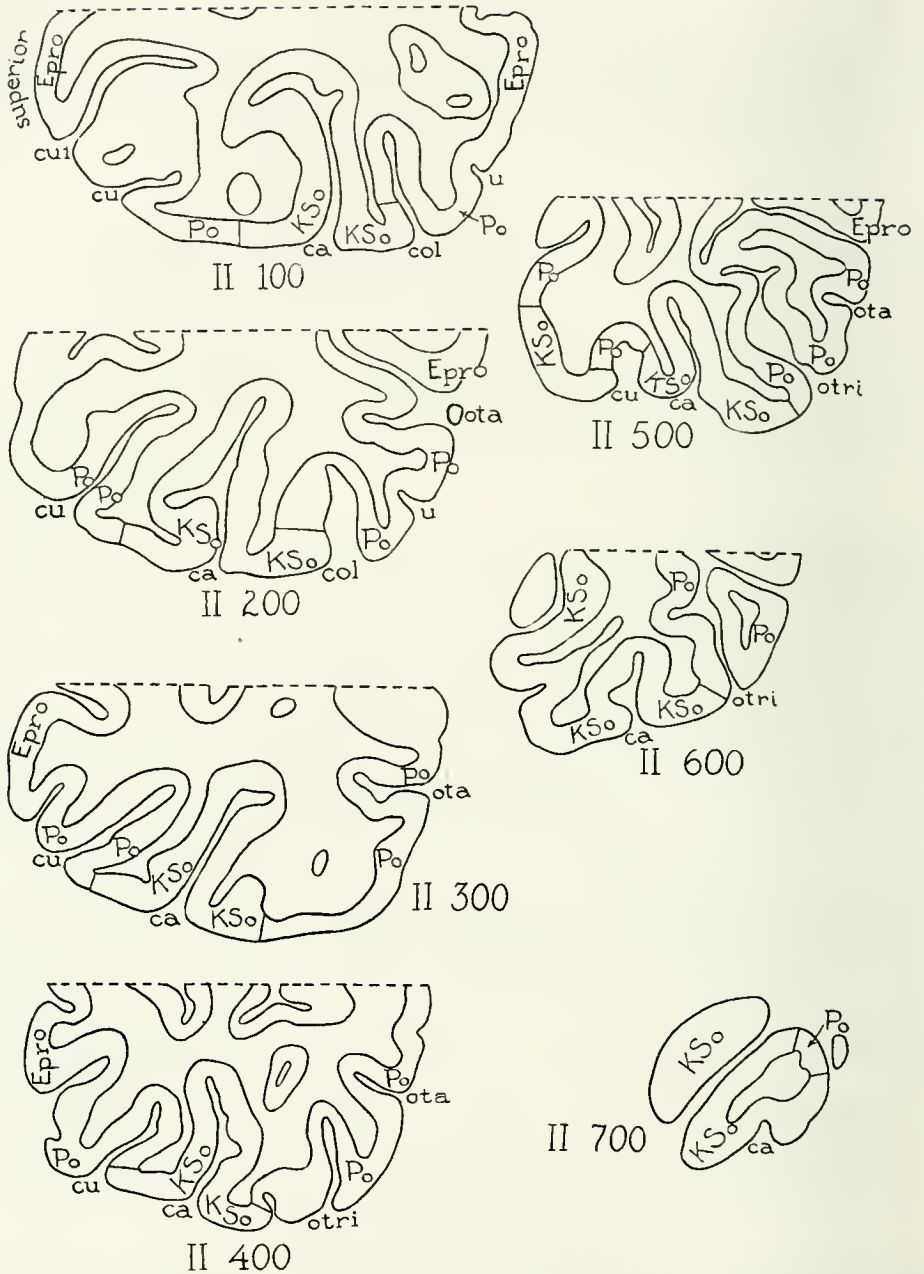
FIG. 28. Cross sections of Block II.

Layer *iv* has rather sharp limits and is uniformly filled with small granules arranged in broad columns; occasionally a medium-sized pyramid is seen in it. Layer *v* is relatively empty. It contains mostly small pyramids with scattered large cells, almost round, about 26 x 32 μ. Layer *vi* has an outer *via* with larger fusiform and

pyramidal cells and a thicker *vib* with smaller, more scattered fusiform cells. The boundary with the subcortex is, in this section, very diffuse. The limits of the parakoniose cortex against the striate are quite abrupt.

Section 600. Fig. 28.

The striate cortex covers the calcarine fissure (*ca*) and the cortex above it to the superior margin of the section; below the fissure it reaches to the upper lip of *otri* where it abruptly gives way to the parakoniose cortex. The latter extends to the inferior margin of the section.

The striate cortex varies in thickness on the crowns of the gyri from 1.3 to 1.8 mm. and in the depths of *ca* thins to 0.8 mm. The parakoniose cortex over the crown of the gyrus below *ca* is cut too diagonally to measure. On the walls of *otri* it varies from 1.7 mm. on the inferior lip to 1.0 mm. in the depth.

The cells of the parakoniose cortex vary in size somewhat in different parts but in general this cortex conforms to the description given for section 700.

Section 500. Fig. 28.

The striate cortex covers the calcarine fissure (*ca*) and extends below it to the upper lip of *otri*; above, it extends about halfway down the lower wall of the postero-inferior extremity of the cuneate sulcus (*cu*). It begins again at the upper lip and stretches onto the superior surface of the lobe.

Above and below the striate cortex (also in the depth of the cuneate sulcus) the cortex is typical parakoniose with the exception of the most inferior gyrus where the cortex contains smaller cells in *iiic* and no large cells in *v*. The radiations are also finer here and the cortex assumes the appearance of the preoccipital regions. There are here no pyramidal cells larger than 24 x 10 μ in *iiic* and most of them are much smaller.

Section 400. Fig. 28.

The striate cortex, as usual, covers the calcarine fissure (*ca*) and stretches upward to the lower lip of the cuneate sulcus (*cu*), where it gives place to typical parakoniose cortex as far as the last gyrus on the superior surface of the lobe. Over that gyrus the cortex measures 1.54 mm.; its radiations are finer and the cells of *iiic* smaller; there is one large cell in *v* but in general *v* is better filled than is typical for parakoniose cortex and the inner main layer measures 0.74 mm. The cortex between *otri* and *ota* is cut too diagonally to measure, but below *ota* its inner main layer measures only 0.46 mm., and continues as typical parakoniose cortex until it reaches the lateral part of the crown of the last gryus where the cortex thickens (1.7 mm.), inner main layer 0.77 mm., the cells of *iiic* are much smaller and *v* is better filled.

Section 300. Fig. 28.

The striate cortex covers the walls of the calcarine fissure. Above, it does not quite reach the lower lip of the cuneate sulcus; below, it reaches about an equal distance from the fissure where it abruptly assumes the parakoniose form. The striate cortex below the fissure measures 1.45 mm., above 1.54 mm. The parakoniose cortex near the striate measures about 1.4 mm., but its layer *vib* is so light that it looks much thinner. The cortex on the superior surface of the lobe measures 1.54 mm.; both *v* and *vib* are here much better filled and the cells of *iiic* smaller. The cortex on the inferior surface of the lobe is quite similar; there is no definite line where this change occurs.

Section 200. Fig. 28.

The calcarine fissure here has an accessory sulcus projecting into its upper wall; it is entirely covered by striate cortex which extends above, about halfway to the cuneate sulcus; below, it reaches into the upper wall of the collateral sulcus (*col*). Below the calcarine fissure, the striate cortex measures scarcely 1.54 mm.; above, it reaches 1.70 mm. The parakoniose cortex above the striate measures 1.40 mm.; below, about the same. It stretches in this section over the superior wall of *ota*; above, it gradually undergoes the changes noted in the previous section. However, in the depth of the sulcus on the lateral (*cu*) margin, the cortex, although it measures 1.60 mm. and its radiations are rather fine, has the typical numerous large pyramids in *iiic* and the empty *v* characteristic of the parakoniose zone. Below *ota*, the pyramids of *iiic* are smaller and *v* is better filled.

Section 100. Fig. 28.

The depth of the calcarine fissure spreads out to form an island. It is covered by striate cortex which extends, above, about halfway to the cuneate sulcus, below, onto the upper wall of the collateral sulcus (*col*). Above the fissure, the striate cortex measures 1.75 mm.; below, it thins to 1.3 mm. The parakoniose cortex above measures 1.6 mm.; below, 1.45 mm. On the inferior surface of the lobe, the cortex thickens to 1.75 mm.; the same is true of the superior surface. In both instances the radiations become finer, the cells of *iiic* smaller, but *v* remains relatively empty and the inner main layer measures about 0.6 mm. This has become eulaminate cortex of more generalized type and is labeled ɛ*pro*.

<div align="center">BLOCK III (Fig. 29)</div>

Section 100. Fig. 30.

The cortex over the superior surface, lateral to *aic*, measures 1.85 mm., outer main layer 1.0 mm., inner 0.7 mm. The margin between *i* and *ii* is irregular. The margin of *ii* and *iiia* is difficult to establish since many small pyramids are scattered among the granules. The pyramids of *iiib* are slightly larger and sparser. The pyramids of *iiic* are larger, ranging up to 39 x 26 μ. The granules of *ivb* are heavier and, with *va*, make a dark band. *vb* is lighter; *via* is well filled. This is superior parietal eulaminate cortex with unusually large cells in *iiic*.

Between *aic* and *pt* the cortex measures 1.85 mm.; also, outer main layer 0.7 mm., inner 1.0 mm. Although the ratio of outer to inner main layer is reversed, the cortex otherwise has the characteristics just described.

Between *pt* and *sp* the cortex is different. It measures 1.54 mm., outer main layer 0.83 mm., inner 0.53 mm. The border between *i* and *ii* is smoother, *iiib* is emptier, the pyramids of *iiic* do not surpass 24 x 16 μ. There are more cells in *vb* and *iv* is more uniform, but these changes are slight and do not warrant giving it a special designation. The adjacent cortex in Block I was labeled ɛ*ps*.

Just below *sp* the cortex is irregular but varies toward the cortex above *pt*.

The cortex below the small short sulcus again resembles the cortex between *pt* and *sp*. It measures 1.6 mm., outer main layer 0.7 mm., inner 0.68 mm.

The cortex above *cc* is retrosplenial allocortex, agranular above and granular below.

Section 200. Fig. 30.

The cortex over the dorsal surface resembles that described in section 100. There are numerous large cells in *iiic*, about 39 x 26 μ.
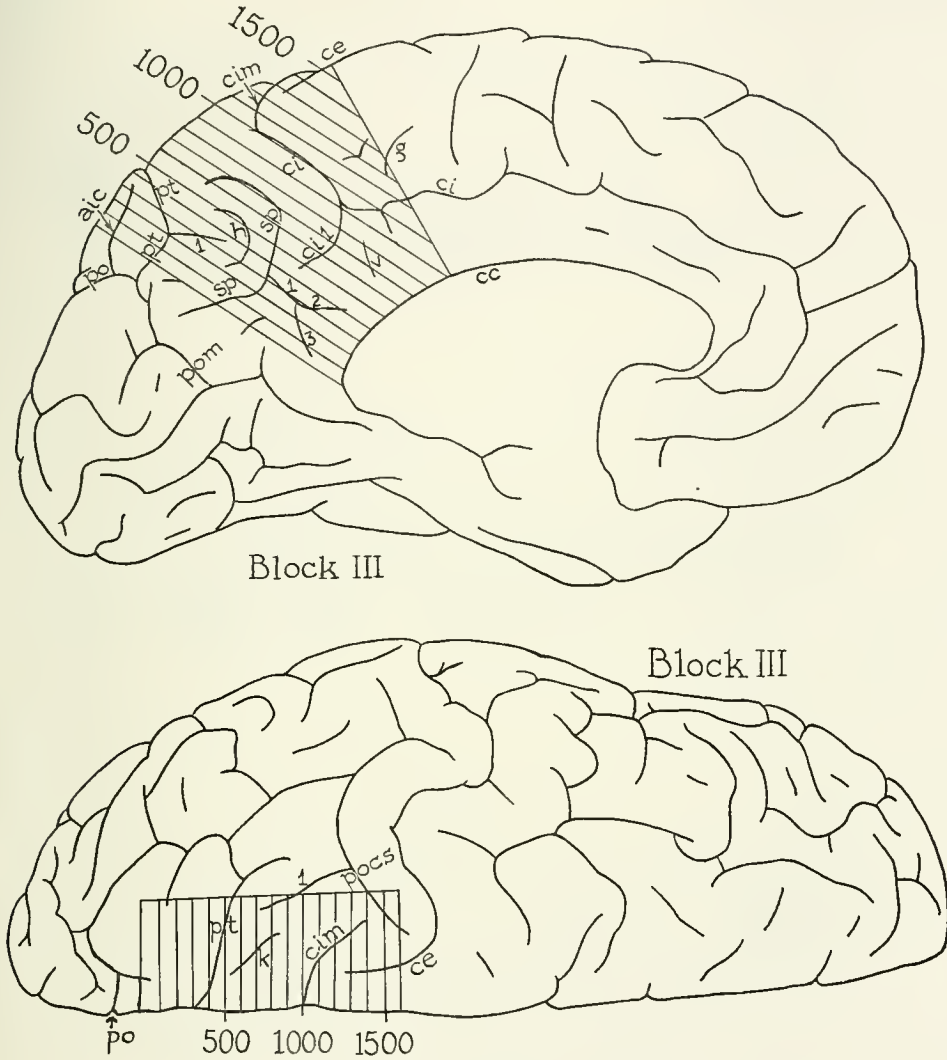
FIG. 29. Position of sections of Block III.

Between *aic* and *pt* the cortex is much the same as described in section 100 but the cells of *iiic* are slightly smaller.

Between *pt* and *sp* the cortex is as described in section 100 but has thickened from 1.5 mm. to 1.7 mm. and the dark band of *ivb* + *va* is much more distinct and the pyramids of *iiic* a little larger. This cortex is now clearly superior parietal eulaminate.

Between *sp* and *sp3* the cortex is irregularly constructed but averages about 1.7 mm. and looks much as it does above *sp*.

Above *cc* the cortex is retrosplenial in its lower part; the upper part is cut too diagonally to read.
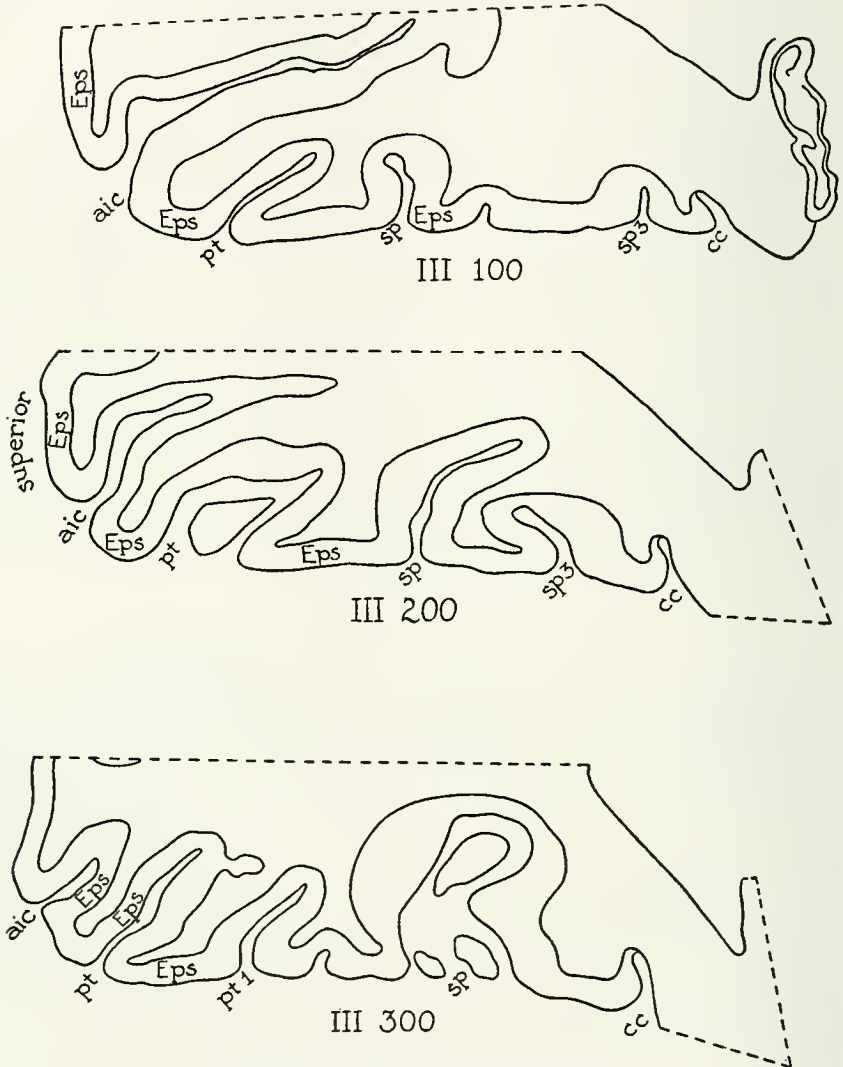
FIG. 30. Cross sections of Block III.

Section 300. Fig. 30.

The cortex lateral to *aic* is irregularly constructed but, in its medial wall, the cortex is superior parietal eulaminate with numerous large pyramids in *iiic* up to 39 x 26 μ in dimension and a few equally large ones in *va*.

Over the crown between *aic* and *pt* the pyramids of *iiic* and *va* are much smaller, but in the walls of *pt* they are again large and all this cortex is of superior parietal eulaminate type.

Below *pt* the cortex measures 1.54 mm., outer main layer 0.7 mm., inner 0.65 mm. The pyramids of *iiic* and *v* are not above 24 x 16 μ, but the heavy band of *ivb + va* is present.

Below *pt1* the cortex is irregularly cut but probably of the same type as the cortex above.
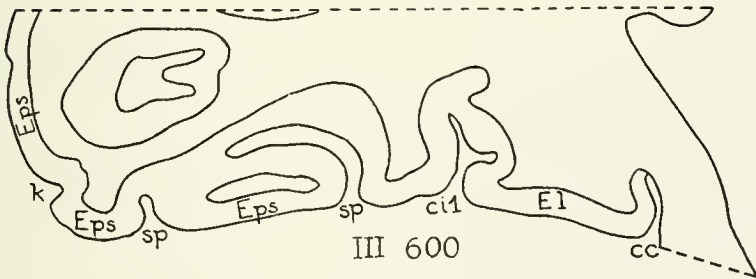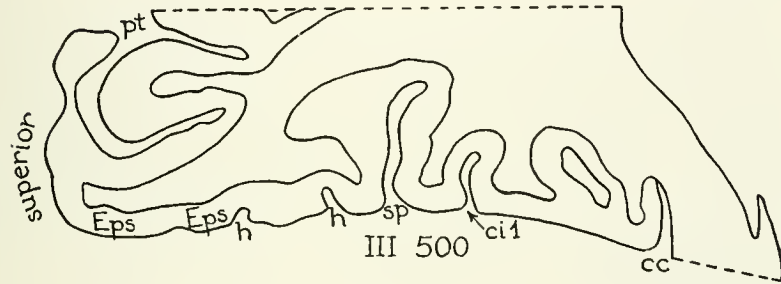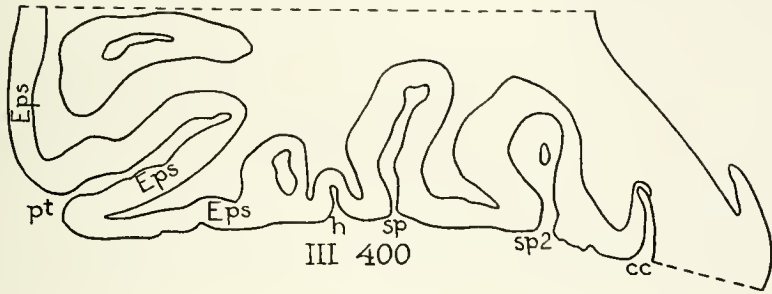
FIG. 31. Cross sections of Block III.

Above *cc* the retrosplenial formations reach about halfway to *sp* where they go over into eulaminate isocortex measuring 1.65 mm., outer main layer 0.77 mm., inner 0.74 mm., which is cut too diagonally to identify.

Section 400. Fig. 31.

The cortex on the dorsal surface is typically superior parietal eulaminate as

previously described, total thickness 1.7 mm., outer main layer 0.71 mm., inner 0.77 mm. This cortex continues to about the middle of the gyrus between *sp* and *sp2* where the dark band of *ivb* + *va* gradually fades out and *v* fills evenly with small and medium pyramids.

The retrosplenial formations scarcely extend out of *cc*.

Section 500. Fig. 31.

The cortex is typical eulaminate superior parietal all down the medial surface as far as *sp* wherever it can be read, but there are no very large cells in either *iiic* or *v*.

Just below *sp* the cortex is very much the same, total thickness 1.65 mm., outer main layer 0.68 mm., inner 0.74 mm. The pyramids of *iiic* are not above 21 x 13 μ, *iv* is thick and a darker *ivb* is visible, but the cells of *va* are sparse and dispersed so that a dark band is not very evident.

Just below *ci1* the cortex is very similar.

The retrosplenial formations are visible only within *cc*. Above *cc* the cortex cannot be read.

Section 600. Fig. 31.

On the dorsal surface the cortex is of superior parietal eulaminate type but there are no large pyramids in either *iiic* or *va*. This cortex continues on the medial surface as far as the ventral section of *sp*.

Between *sp* and *ci1* the cortex is irregularly built, *iiic*, *iv*, and *va* looking like a rail fence. On the upper lip of *ci1* the fourth layer is very thick (0.2 mm.).

Below *ci1* the cortex measures 1.85 mm. or more, outer main layer 0.77 mm., inner 0.8 mm. or more. The pyramids of *iiic* do not surpass 21 x 13 μ. The inner granular layer is very thick (0.25–0.3 mm.) and uniformly filled by granules. The pyramids of *v* are evenly distributed and about the size of those in *iiic* with an occasional slightly larger one. The cells of *via* are slightly smaller.

Section 700. Fig. 32.

The cortex on the dorsal surface is cut too diagonally to read. On the medial surface the cortex is of superior parietal eulaminate type at first, then cannot be read until one nears *ci1* where it has the irregular structure described in section 600.

Below *ci1* the cortex is cut too diagonally to read.

Section 800. Fig. 32.

On the dorsal surface the cortex is typically eulaminate superior parietal, the pyramids of *iiic* reaching 28 x 16 μ. This cortex continues down the medial surface, where one sees a few larger pyramids, as far as *ci1*.

Below *ci1* the cortex is not much different above the small abortive sulcus but, below it, the cortex measures 1.7 mm., outer main layer 0.7 mm., inner 0.9 mm. Layer *iv* is thin with no heavier *ivb*; layer *v* is thin and its cells well dispersed; layer *via* measures 0.55 mm. We have labeled this eulaminate limbic posterior (E*lp*).

On the upper lip of *cc* the inner granular layer disappears entirely.

Section 900. Fig. 32.

On the dorsal surface the cortex is eulaminate superior parietal, but only a few pyramids in *iiic* are above 26 x 16 μ. Total thickness 1.85 mm., outer main layer 0.9 mm., inner 0.77 mm.

On the medial surface the cortex is constructed in the same way but thinner (1.54 mm.), outer main layer 0.68 mm., inner 0.68 mm.

Just below *ci1* the structure is much more rugged. Throughout the cells are larger and those of *v* better dispersed. The remainder of the cortex cannot be read.

Section 1000. Fig. 33.

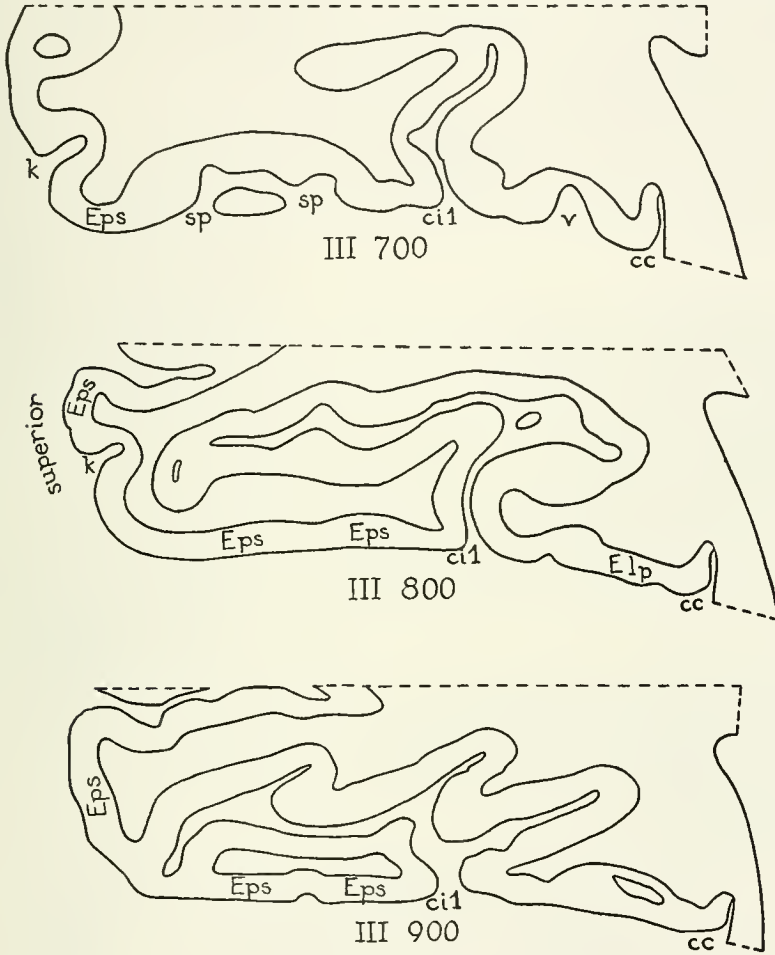The cortex on the dorsal surface is identical with that just described in section 900.

FIG. 32. Cross sections of Block III.

As one goes down the medial surface the cortex is cut diagonally but seems much the same until one gets into *cim* where one begins to see much larger pyramids in both *iiic* and *v*. This is evident also on the opposite wall of *cim* in spite of the diagonal section.

Below *cim* one encounters large numbers of very large cells in both *iiic* and *v* ranging from 37 x 26 μ to 45 x 32 μ. Throughout this region there is a prominent *iv*

measuring 0.2–0.3 mm., with often very large cells interspersed among the granules.

Below *ci* the cortex measures 1.7 mm., outer main layer 0.7 mm., inner 0.86 mm. The pyramids of *iiic* and *v* are of moderate size up to 26 x 16 μ and well dispersed.
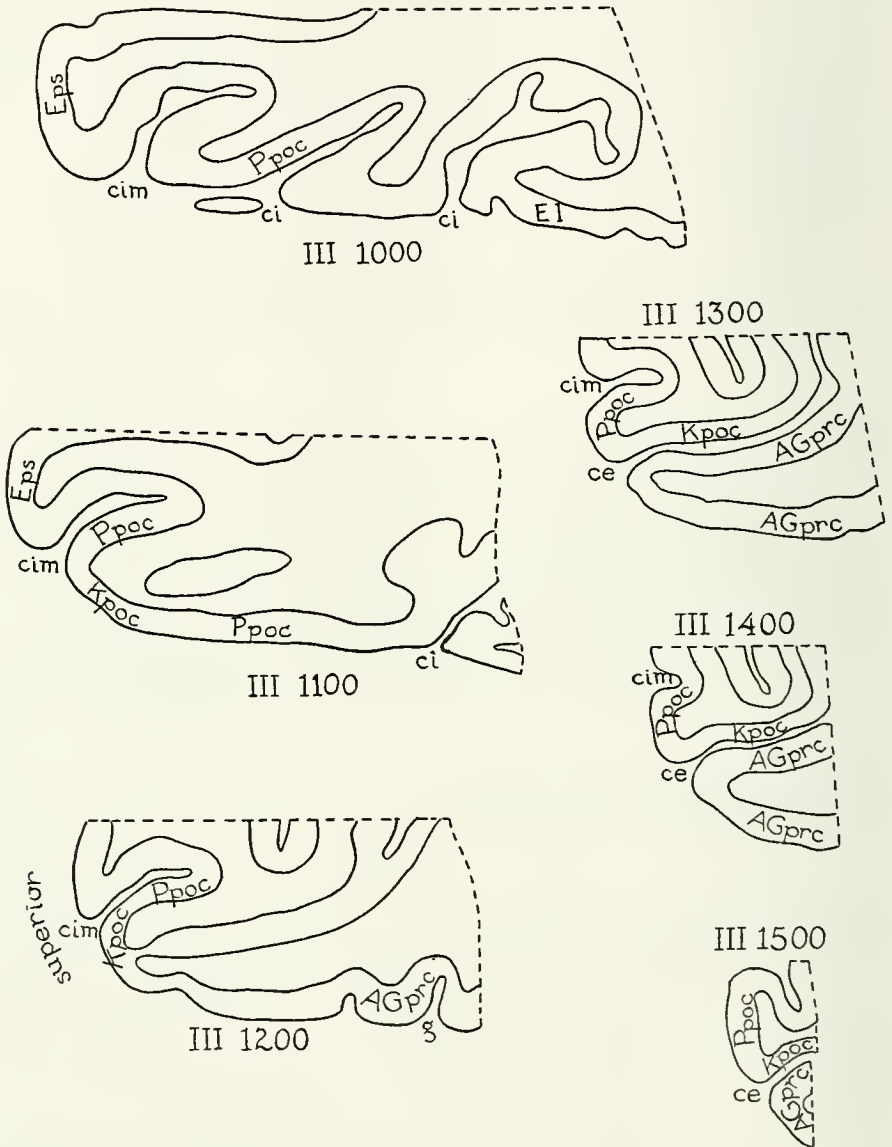
FIG. 33. Cross sections of Block III.

Section 1100. Fig. 33.

The cortex on the dorsal surface lateral to *cim* is of superior parietal eulaminate type with a few very large pyramids (39 x 26 μ) in *v*. The pyramids of *iiic* are mostly not larger than 23 x 13 μ but a few reach 32 x 21 μ.

On the medial wall of *cim* begins the formation ᴘ*poc* previously described in section 1000 containing huge pyramids in *iiic* and *v*.

Just as one passes over to the medial surface is a small patch of koniocortex, beyond which the parakoniocortex continues almost to *ci*. Near *ci* the internal granular layer disappears.

The cortex below *ci* cannot be read.

Section 1200. Fig. 33.

The cortex lateral to *cim* is cut too diagonally to read. It contains, however, no very large cells.

On the medial wall of *cim* can be seen the big-celled formation previously described.

On the crown, going over to the medial surface, the cortex becomes koniocortex and is followed by the eulaminate big-celled area again. The inner granular layer disappears just above the shallow short sulcus and is followed by typical precentral agranular cortex with Betz cells measuring 66 x 39 μ.

Section 1300. Fig. 33.

The cortex over this small section is quite variegated.

Lateral to *cim* it looks much like what has been seen over the dorsal surface posteriorly. Total thickness 1.7 mm., outer main layer 0.8 mm., inner 0.7 mm. There are some fairly large pyramids 26 x 16 μ in both *iiic* and *v*.

Between *cim* and *ce* the cortex over the crown and extending down the medial wall of *cim* measures only 1.4 mm., outer main layer 0.6 mm., inner 0.68 mm. Layer *vb* is relatively empty but there is no dark band of *ivb* + *va*. Many pyramids of both *iiic* and *v* reach 32 x 19 μ. This cortex looks like the postcentral parakoniocortex farther down the gyrus.

On the lateral wall of *ce* the cortex measures only 1.1 mm. and is granulose. This entire wall is koniocortex. One sees occasional large pyramids about 30 x 19 μ in the light band where layer *v* should be.

The lower part of the medial wall of *ce* is agranular cortex with huge Betz cells, but the outer part, over the crown and part way down the medial surface, is covered by cortex with very large cells in *iiic* and *v* not reaching the size of Betz cells, however. This looks very much like the cortex labeled ᴘ*poc* in section 1100 on the medial aspect; it soon loses its inner granular layer and becomes again agranular with Betz cells.

Section 1400. Fig. 33.

All of the cortex medial to *ce* is agranular with Betz cells.

The lateral wall of *ce* is koniocortex.

The crown of the postcentral gyrus is covered by parakoniocortex, total thickness 1.54 mm., outer main layer 0.68 mm., inner 0.71 mm. The pyramids of *iiic* are numerous, as big as 32 x 18 μ, occasionally larger ones up to 45 x 24 μ in the relatively empty *v*.

Lateral to *cim* the cortex measures 1.85 mm. and there is a huge pyramid 66 x 39 μ in *v*.

Section 1500. Fig. 33.

Medial to *ce* is only agranular cortex with Betz cells and occasional smaller pyramids in *iiic* about 36 x 24 μ.

On the lateral wall of *ce* is koniocortex.

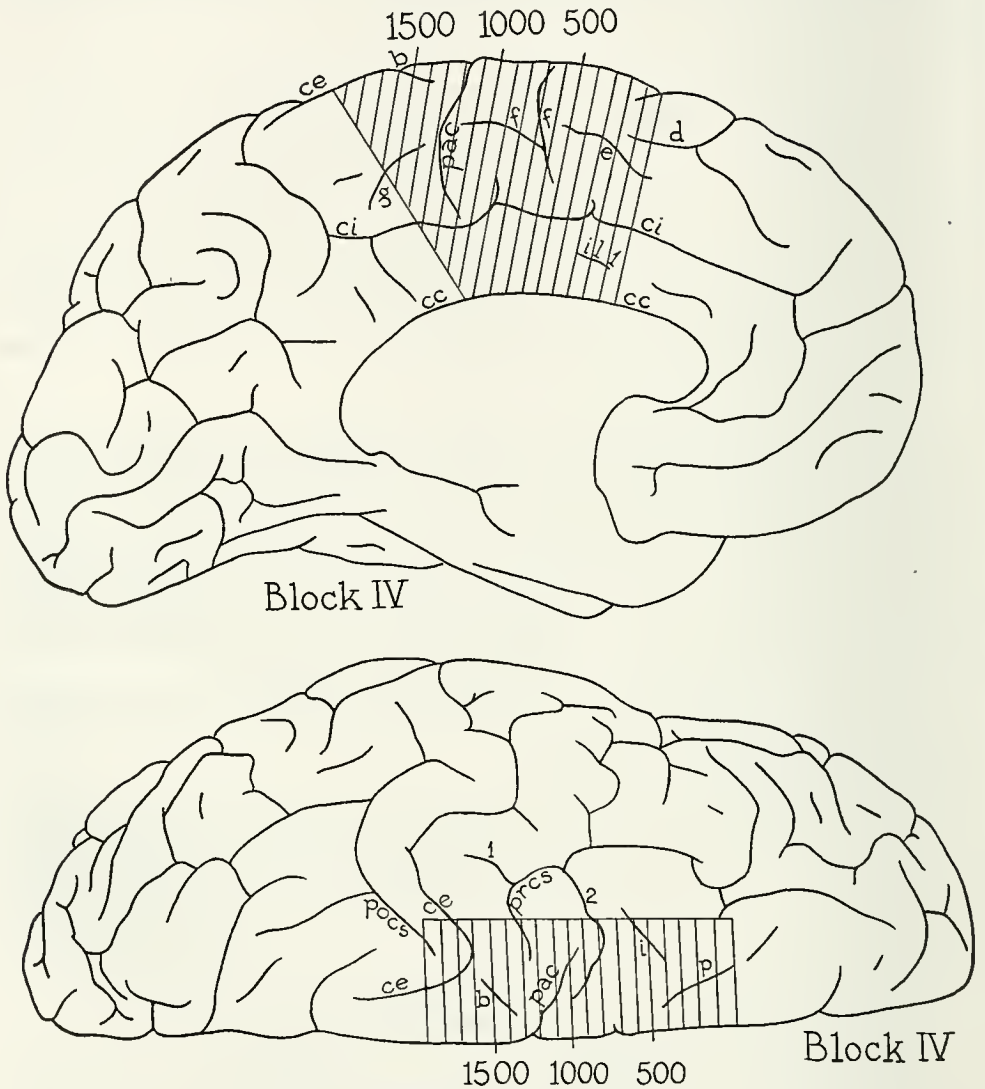On the crown of the postcentral gyrus is parakoniocortex as described for section 1400.

FIG. 34. Position of sections of Block IV.

BLOCK IV (Fig. 34)

We shall begin where we left off with block III and proceed anteriorly.

Section 1800. Fig. 35.

Medial to the central sulcus (*ce*) the cortex is thick (2.15+ mm., the inner boundary being very vague). It is agranular with numerous giant cells (about 63 x 39 μ) as well as numerous other large pyramids (up to 37 x 26 μ) at about the level of

what would be *v* in eulaminate cortex. There are also scattered large pyramids (39 x 26 μ) at about the level of *iiic*.

Lateral to *ce* the cortex is postcentral parakoniocortex on the surface. Within the sulcus, on its lateral wall, there is koniocortex measuring only 0.93 mm.

Section 1700. Fig. 35.
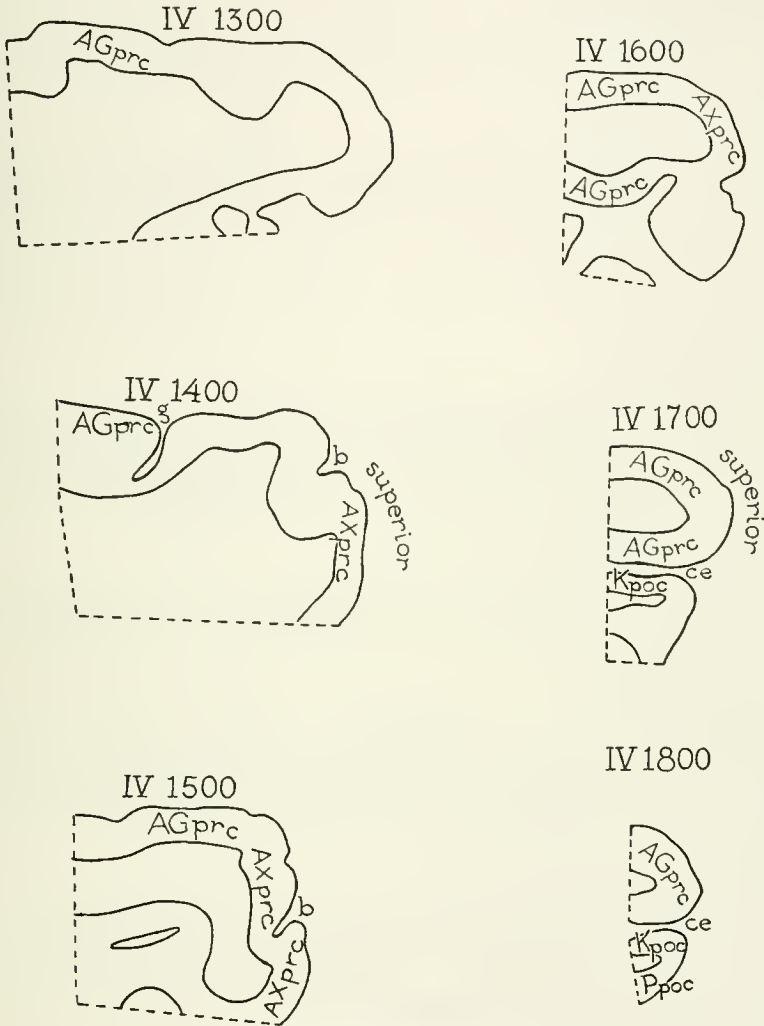
Fig. 35. Cross sections of Block IV.

Anterior to the central sulcus the cortex is agranular with Betz cells throughout and scattered pyramids about 36 x 22 μ at about the level of *iiic*.

Behind *ce* there is koniocortex on the posterior wall to the lip and then parakoniose cortex which is cut too diagonally to describe.

Section 1600. Fig. 35.

The precentral gyrus is covered by agranular cortex as described in the previous

sections which contains numerous Betz cells except on the crown, where there is none larger than 39 x 26 μ. Average thickness about 1.9 mm.

Section 1500. Fig. 35.

The cortex on the medial surface is agranular with numerous Betz cells, and pyramids in *iiic* about 39 x 24 μ. On the dorsal surface medial to the small sulcus (*b*) the large pyramidal cells are more elongated, about 58 x 26 μ, and the columniation of the cortex finer. Lateral to *b* the cortex is agranular, measures about 2.0 mm. and contains large pyramids in the medial regions of the cortex but none over 42 x 21 μ.

Section 1400. Fig. 35.

The cortex is all agranular. On the medial surface there are Betz cells below *g* only in the lower wall of the small sulcus. Just above *g* there are a few deep large pyramids, up to 60 x 39 μ in layer *v* but, in the remainder of the cortex between *g* and *b*, there is no pyramid above 39 x 26 μ in layer *v*. A few large pyramids, around 39 x 26 μ, are seen in *iiic*.

Lateral to *b* the cortex measures only 1.7 mm. It is agranular but there is only one large pyramid. It lies about the level of *v* and measures 39 x 26 μ.

Section 1300. Fig. 35.

The cortex on the medial surface measures 1.7 mm. There are a few large cells of the stature of Betz cells. Above them is a vague layer of very small pyramids which may correspond to *iv*. Above this are a few scattered large pyramids up to 39 x 26 μ. On the dorsal surface there is no pyramid of Betz caliber. Nor is there any in the walls of the sulcus.

Section 1200. Fig. 36.

The cortex below *ci* is eulaminate, measuring 1.17 mm., outer main layer 0.61 mm., inner 0.46 mm. There are a few medium pyramids in *iiic* and the larger pyramids of *v* are crowded against *iv* so that *vb* is very empty. Layer *vi* is well filled with small irregular cells.

The remainder of the cortex is agranular. On the dorsal wall of *ci* is seen a very large cell, deep in the cortex, measuring 52 x 45 μ. There is only one large cell, on the dorsal surface, which reaches 47 x 39 μ and seems to be in layer *v*. A few scattered cells reach 36 x 26 μ and seem to be in *iiic*. The cortex measures 2.0+ mm. on the dorsal surface.

Section 1100. Fig. 36.

On the dorsal surface there is one large cell, 39 x 32 μ, which seems to be in *v*. No other cell exceeds 32 x 24 μ. On the posterolateral wall of *pac* there are two large cells in *v*. On the superior wall of *ci* there are a few more. All of this cortex is agranular, but otherwise varies greatly as is customary in sulci. Total thickness 2.0 mm. on the dorsal surface.

On the medial surface, below *f*, there is nothing which could be called a Betz cell, nor is there on the anteromedial wall of *pac*. All this cortex is, however, cut very diagonally. Total thickness over 2.0 mm.

Section 1000. Fig. 36.

On the dorsal surface between *pac* and *prcs2* the cortex is cut parallel to the columns. They extend almost up to the *i* layer. The cortex is agranular, but the pyramids near *i* are very small and there is a faint layer deeper, near the middle,

of very small pyramids, above and below which lie the largest pyramids in the section, which do not, however, surpass 32 x 16 μ. The *vi* layer is distinct by the size and shape of its cells, measuring more than 0.62 mm. The total thickness is more than 1.85 mm.

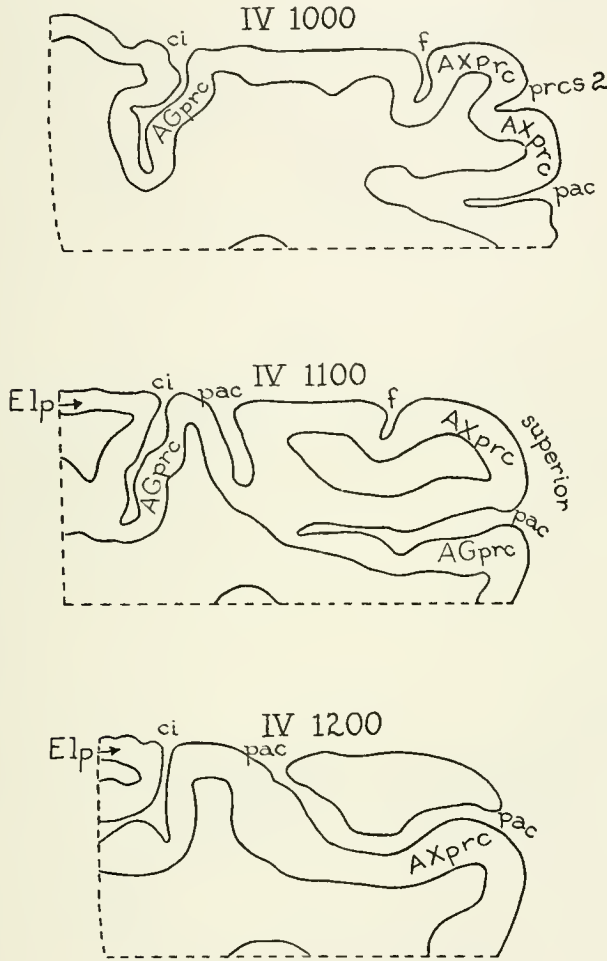The cortex on the medial surface between *prcs2* and *f* is similarly constructed

FIG. 36. Cross sections of Block IV.

but measures only 1.7 mm. The largest pyramids are about where one would expect *iiic* and they do not surpass 32 x 16 μ.

Below *f* the cortex is much the same until the upper wall of *ci* is reached, in which two cells are seen in *v* which reach a size of 53 x 37 μ.

Below *ci* the cortex has a faint internal granular layer and a dense band of cells in *va*, with a relatively empty *vb*.

Section 900. Fig. 37.

The cortex on the dorsal surface, lateral to *prcs2*, measures 1.85+ mm. It is agranular and contains no pyramids measuring above 34 x 18 μ. Above *f* on the medial surface the cortex is entirely similar.

Just below the small sulcus *f* on the medial surface is the same agranular cortex
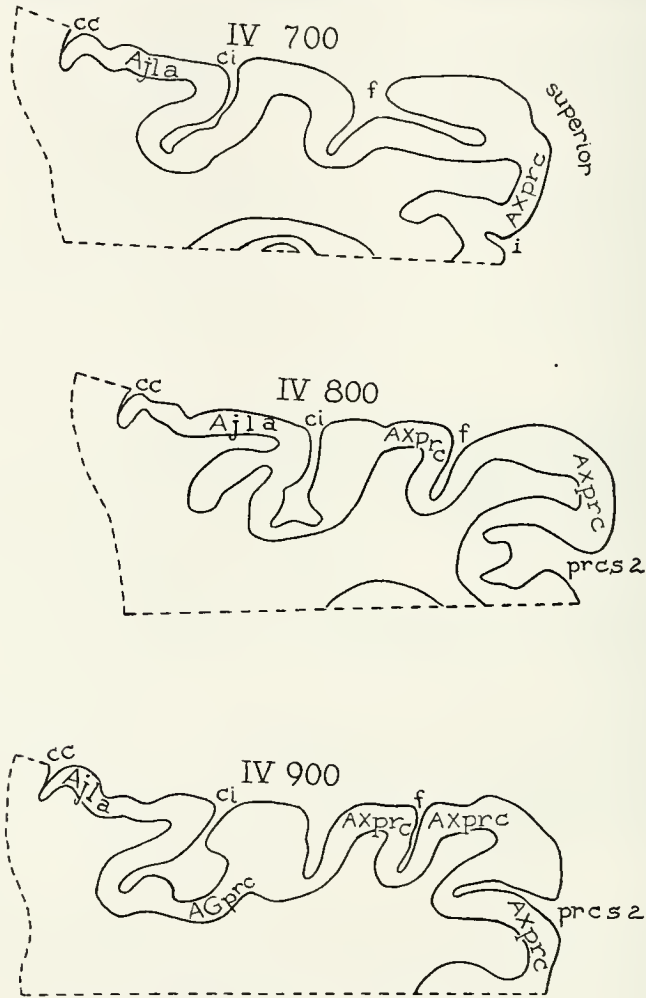
FIG. 37. Cross sections of Block IV.

but, in the depth of the dorsal spur of the cingulate sulcus, are a few deep-lying cells measuring about 53 x 47 μ.

On the lower wall of the cingulate sulcus *ci* there is a thin internal granular layer. The cortex measures 1.6 mm., outer main layer 0.65 mm., inner 0.8 mm. Layer *v* is divided into a dense *va*, which contains cells much larger than any in *iii*; layer *vb* is relatively very empty. Layer *vi* is filled with smaller cells, more lightly stained. There is scarcely any cell gradient in *iii*; none of its cells is above 26 x 16 μ.

The inner granular layer gradually fades until, before the callosal sulcus is reached, it entirely disappears.

Section 800. Fig. 37.

The cortex on the dorsal surface is identical with that described in section 900. It measures 2.0+ mm.
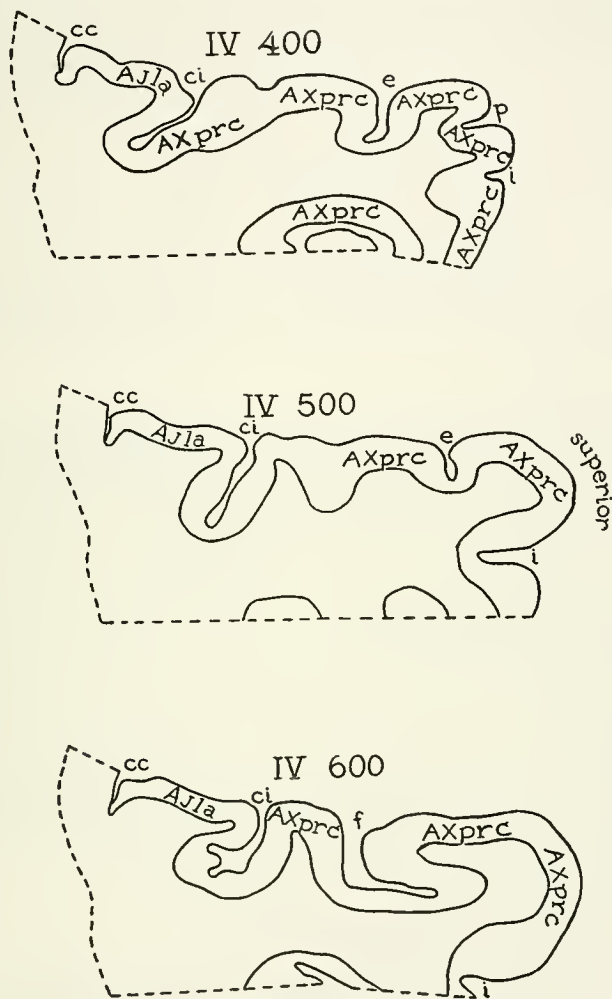
FIG. 38. Cross sections of Block IV.

The cortex just below *f* measures 1.85 mm. The largest pyramids, which do not exceed 26 x 16 μ, lie in the middle part of the cortex. The pyramids externally, and the fusiform cells internal to them, are smaller and more lightly stained. There is a faint, irregular stratum of small cells within the larger celled middle zone, but examination under high magnification shows them to be mostly small pyramids.

On the dorsal wall of *ci* no cell is seen large enough to be suspected of being a Betz cell.

The cortex in the ventral wall of ci is as described in section 900. Over the surface of the limbic gyrus the cortex is agranular. In thickness it measures only 1.25 mm. Most conspicuous is a band of medium pyramids, about 32 x 18 μ, closely packed together in its outer half, loosely scattered in its inner half. Beneath the loose streak is a band of about equal width, evenly filled with smaller irregular cells. Just outside the dense band of larger cells is another light streak containing scattered pyramids about 29 x 16 μ and mostly smaller irregular cells. Outside this light streak is a layer about 0.52 mm. thick containing evenly distributed smaller pyramids, growing slightly smaller and more numerous toward i. This agranular anterior limbic cortex we have labeled Aᴊla.

Section 700. Fig. 37.

The cortex above ci does not differ from that described in section 900. Thickness 1.85+ mm.

The cortex on the lower wall of ci and over the limbic gyrus is as described in section 800, except on the lower half where the outer light streak disappears and the inner one becomes much less evident. This is clearly agranular anterior limbic cortex Aᴊla.

Section 600. Fig. 38.

The cortex on the dorsal surface and on the medial surface above ci measures 1.7 mm. to 1.85 mm. It is typical agranular precentral cortex without Betz cells. There are many pyramids which are 29 x 21 μ and a few which reach even 39 x 26 μ. These pyramids lie in what should be the $iiic$. There are no very large cells which lie deeper.

The cortex below ci looks much as in section 700. There is still an inner granular layer in the lower wall of ci. The crown of the limbic gyrus is entirely covered by agranular anterior limbic cortex.

Section 500. Fig. 38.

The conditions in this section do not differ from those in section 600.

Section 400. Fig. 38.

The cortex on the dorsal surface and on the medial surface above ci is simple agranular precentral cortex without Betz cells as previously described. Total thickness 1.85+ mm.

Below ci the cortex is the same as in the previous section.

Section 300. Fig. 39.

The cortex is unchanged from the previous section.

Section 200. Fig. 39.

The cortex on the dorsal and medial surfaces is still simple agranular precentral down to ci. Thickness 1.7 mm. to 2.15 mm.

On the lower wall of ci there is still a thin light band filled mainly with very small pyramids with a few granules. This disappears on the surface of the limbic gyrus.

Section 100. Fig. 39.

The cortex over the dorsal surface and down the medial surface to ci looks much the same, but there is here and there a patchy, thin zone of granules in the middle of the cortex with the largest pyramids just external and internal to it. Thickness 1.55 mm. to 1.7 mm. This is the first appearance of dysgranular cortex.

The cortex over the limbic lobe is unchanged.

BLOCK V (Fig. 40)

We shall begin at the frontal pole, which is covered by general eulaminate cortex, and proceed posteriorly.

Section 1700. Fig. 41.

On the orbital surface the cortex measures 1.7 mm., outer main layer 0.7 mm., inner granular layer 0.15 mm., inner main layer 0.85 mm. The largest pyramids are
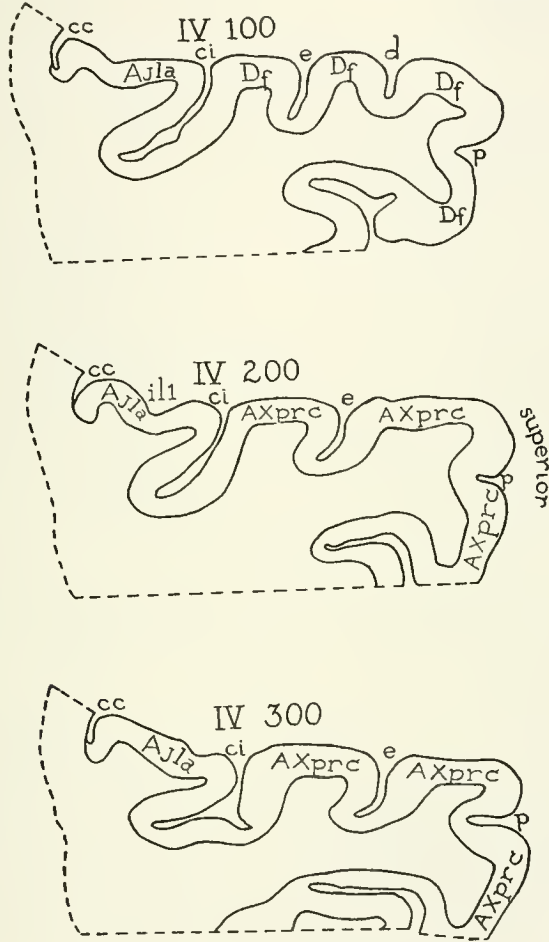

FIG. 39. Cross sections of Block IV.

in *iiic* and *v* but do not exceed 26 x 13 μ. Layers *iiib* and *vb* are relatively empty; layer *iv* is evenly filled with granules. Just within *i* many granules are mixed with small pyramids.

On the medial surface the cortex is of the same fundamental general eulaminate pattern.

Section 1600. Fig. 41.

On the crown of the narrow gyrus above *c* the cortex measures about 1.3 mm.

Below *c* it thickens to 1.4 mm., outer main layer 0.58 mm., inner granular 0.15 mm., inner main layer 0.65 mm.

On the orbital surface, medial to *orm*, the cortex measures 1.7 mm., outer main layer 0.95 mm., inner granular 0.15 mm., inner main layer 0.6 mm. The outer granular layer *ii* is definite, *iii* has scarcely any gradient, the cells of *iiic* rarely
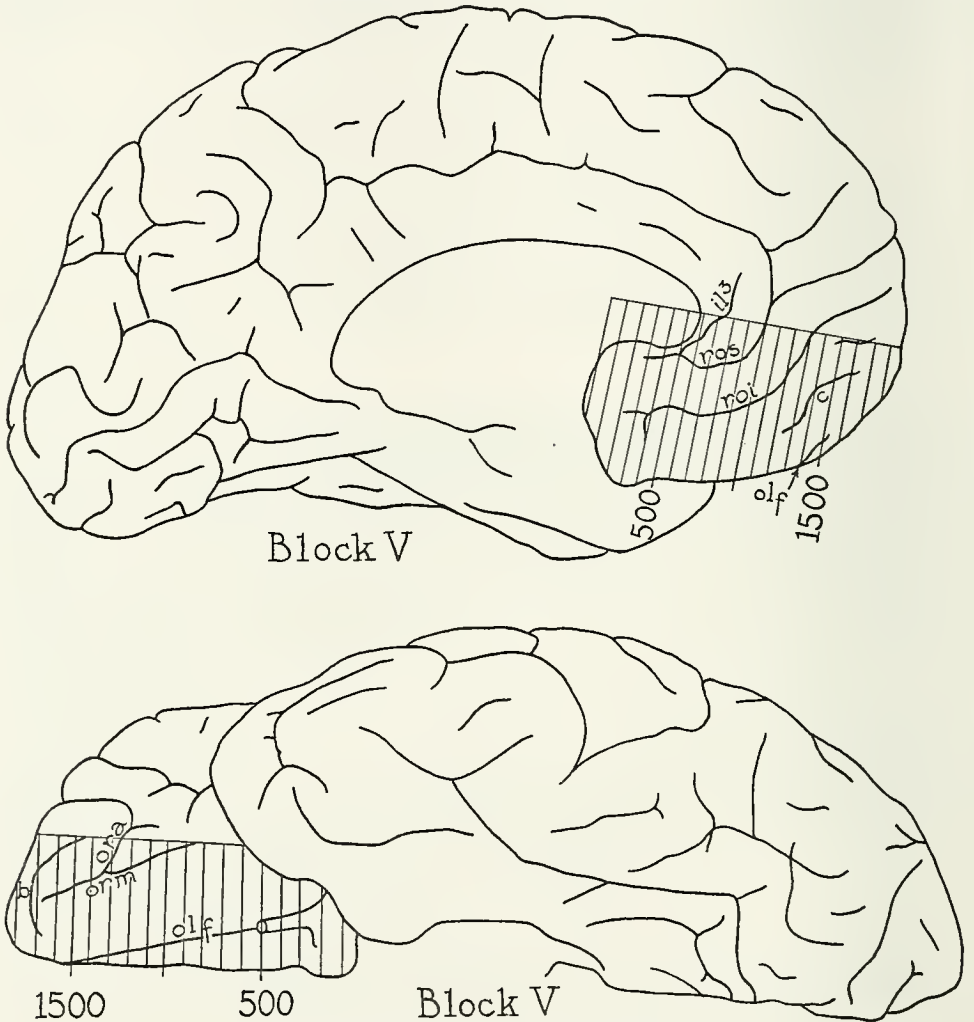
FIG. 40. Position of sections of Block V.

surpass 21 x 13 *μ*, the cells of *v* are slightly larger and more numerous. Layer *iiib* is fairly well filled so that *iii* has an even look throughout. This cortex shows juxtallocortical characteristics.

The cortex lateral to *orm* is of ordinary eulaminate generalized type.

Section 1500. Fig. 41.

Above *c* on the medial side, the cortex is of general eulaminate type measuring
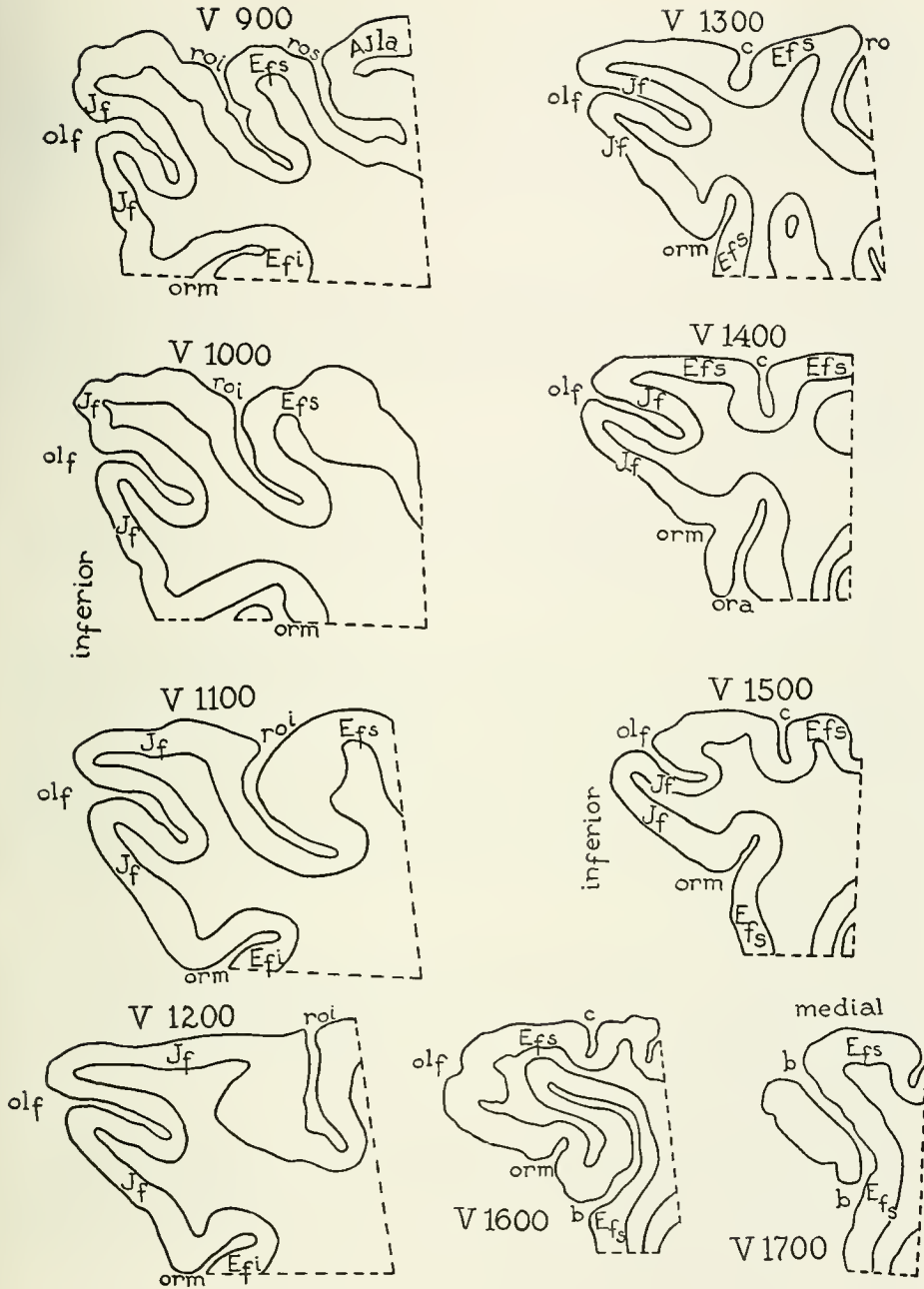
FIG. 41. Cross sections of Block V.

1.4 mm., outer main layer 0.55 mm., inner granular 0.15 mm., inner main layer 0.7 mm.

Between *c* and *olf* the cortex is cut diagonally but appears to be quite similar.

On the crown just at the orbitomedial margin the cortex thins to 1.2 mm., outer main layer 0.4 mm., inner granular 0.12 mm., inner main layer 0.68 mm.

Between *olf* and *orm* the cortex is as described in section 1600.

Lateral to *orm* the cortex is again of general eulaminate type, outer main layer 0.58 mm., inner granular 0.15 mm., inner main layer 0.62 mm., total thickness 1.35 mm. The pyramids of *iiic* and *va* are definitely larger than the cells of the other layers.

Section 1400. Fig. 41.

The cortex of this section does not differ from that of 1500. Above *c* on the medial surface it measures 1.4 mm. Below *c* it varies from 1.25 mm. to 1.54 mm.

Just lateral to *olf* on the orbital surface the cortex thins to 1.15 mm., but is constructed on the same model as more laterally where it measures 1.7 mm. The regularity of the border between *i* and *ii* is striking, reminding one of the parakoniose cortex.

Section 1300. Fig. 41.

The cortex does not differ from that of section 1400.

On both walls of *olf* and extending out of it on the orbital surface laterally, *vb* is very dense. This may be more apparent because of the thinness of the cortex.

Lateral to *orm* the cortex is of general eulaminate type.

Section 1200. Fig. 41.

On the medial surface the thickness varies from 1.2 mm. at the orbitomedial lip to 1.7 mm. near *roi.* It resembles now the cortex lateral to *olf* on the orbital surface in that it has a good outer granular layer and almost no gradient in *iii.* Also *va* is heavier. At about the middle between *roi* and *olf* the cortex measures 1.45 mm., outer main layer 0.83 mm., inner granular 0.15 mm., inner main layer 0.47 mm. At about the same distance lateral to *olf* the cortex measures 1.55 mm., outer main layer 0.75 mm., inner granular 0.19 mm., inner main layer 0.61 mm.

On the lateral wall of *orm* the cells of *iiic* are larger and *iv* is thinner, as in the inferior frontal gyrus.

Section 1100. Fig. 41.

The cortex above *roi* measures 1.54 mm. and is of general eulaminate type, outer main layer 0.58 mm., inner granular 0.15 mm., inner main layer 0.8 mm.

The cortex on both sides of *olf* is unchanged from section 1200 but is cut diagonally on the orbital surface.

The cortex lateral to *orm* is as described in section 1200.

Section 1000. Fig. 41.

The cortex just above *roi* is of general eulaminate type measuring 1.54 mm., outer main layer 0.7 mm., inner granular 0.15 mm., inner main layer 0.68 mm.

The remainder of the cortex is of the juxtallocortical type previously described with heavy *va*, empty *vb*, and no gradient in *iii.* It measures generally about 1.4 mm.

Lateral to *orm* the pyramids are again much larger in *iiic.*

Section 900. Fig. 41.

The cortex above *ros* has almost no granules and a heavy thick band of big cells in the middle. It is anterior agranular limbic cortex.

Between *roi* and *ros* the cortex measures 1.7 mm. It resembles the superior frontal cortex but has a heavier *va*. Outer main layer 0.75 mm., inner granular 0.15 mm., inner main layer 0.8 mm.
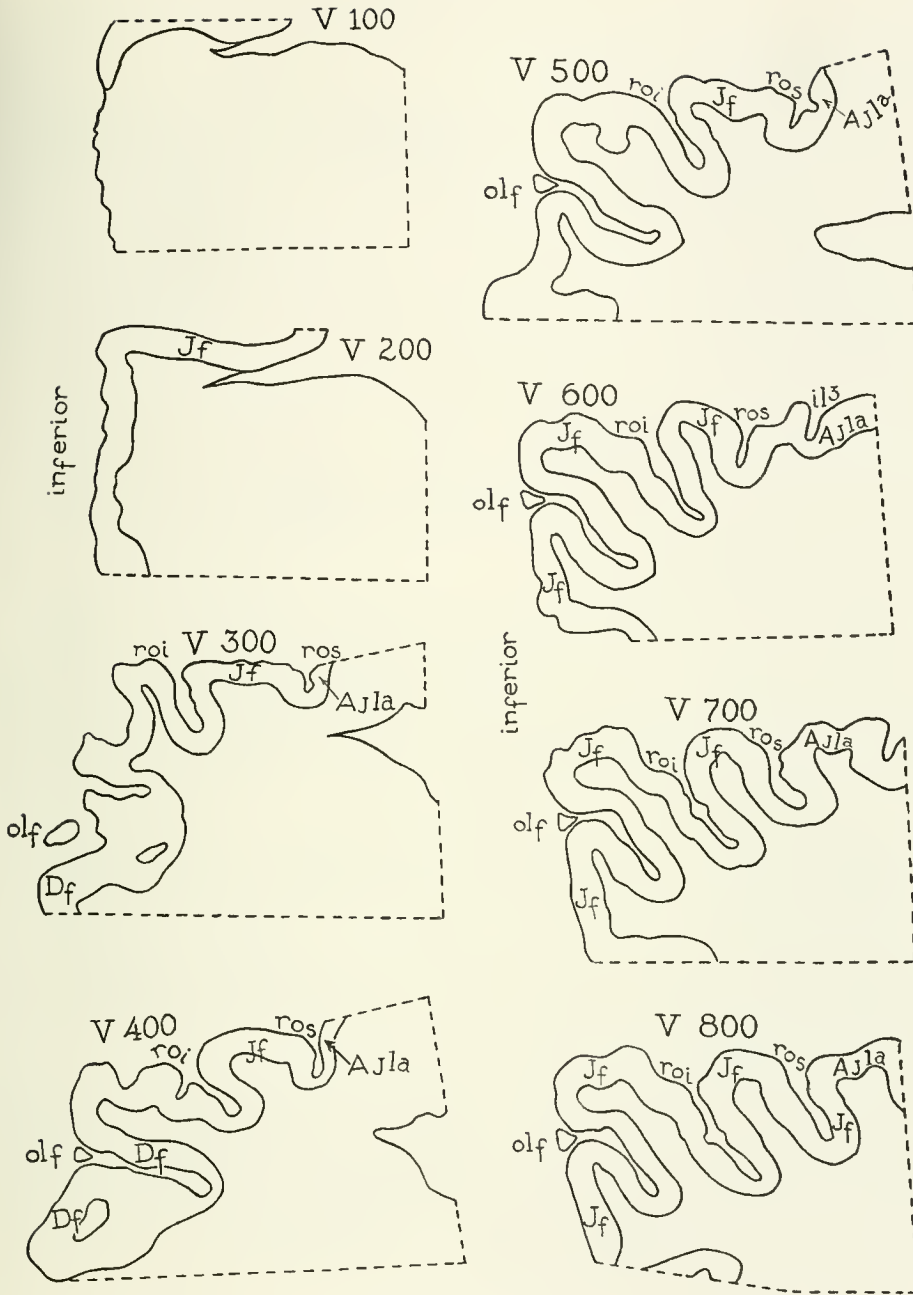
FIG. 42. Cross sections of Block V.

The cortex on the lip medial to *olf* measures 1.4 mm. and is of the juxtallocortical type, outer main layer 0.55 mm., inner granular 0.15 mm., inner main layer 0.7 mm. This cortex continues over the entire orbital surface but thickens laterally to 1.65 mm.

Lateral to *orm* the cells of *iiic* are much larger. The cortex is here clearly of inferior frontal type.

Section 800. Fig. 42.

Above *ros* is agranular limbic cortex which develops an inner granular layer as one follows into the upper wall of *ros*. The remainder of the cortex is all of the type we have called juxtallocortical, but below *roi* there is less distinction between *ii* and *iii* and somewhat smaller cells in *v*.

Section 700. Fig. 42.

Conditions in this section are identical with those in section 800.

Section 600. Fig. 42.

Identical with section 700.

Section 500. Fig. 42.

Above *ros* is agranular anterior limbic cortex.

Between *roi* and *ros* is juxtallocortex.

On the orbital surface medial to *olf* the cortex is irregularly constructed; particularly the cells of *v* are patchy, but otherwise as before.

Lateral to *olf* the internal granular layer is less conspicuous, the cells of *v* are smaller and better distributed.

Section 400. Fig. 42.

The cortex above *ros* is very thin and its cells irregularly distributed in patches.

Between *roi* and *ros* the cortex is of our juxtallocortical type, measuring 1.7 mm.

The cortex between *roi* and *olf* is very irregularly constructed but has a good internal granular layer everywhere until the medial wall of *olf* is reached, when it almost completely disappears and remains absent over the lateral wall also and lateral to *olf* on the surface. This is dysgranular cortex.

Section 300. Fig. 42.

The cortex between *roi* and *ros* is thinned, measures 1.5 mm., but is otherwise unchanged from section 400, except that *vb* is more filled.

The cortex beyond *roi* has no inner granular layer and is very irregularly constructed.

Lateral to *olf* the cortex is very thick, measuring more than 2.2 mm. Its cellular population is nearly uniform throughout so that it is difficult to recognize layers. There is a faint suggestion of an internal granular layer.

Section 200. Fig. 42.

The cortex on the medial surface measures only 1.15 mm. There are no granules under *i* and the cells here are bunched. There is scarcely any gradient in *iii*. Layer *iv* measures 0.15 mm. and is well filled with granules. Layers *v* and *vi* form a dense band measuring about 0.31 mm. which is very conspicuously darker than *iii*.

On the medial half of the orbital surface the cortex is agranular. The lateral half is anterior perforated substance.

Section 100. Fig. 42.

On the medial surface the cortex is still very thin and has lost its internal granular layer; unfortunately most of it has been cut off the section. In the intermediate sections it can be seen that the internal granular layer present in 200 rapidly disappeared.
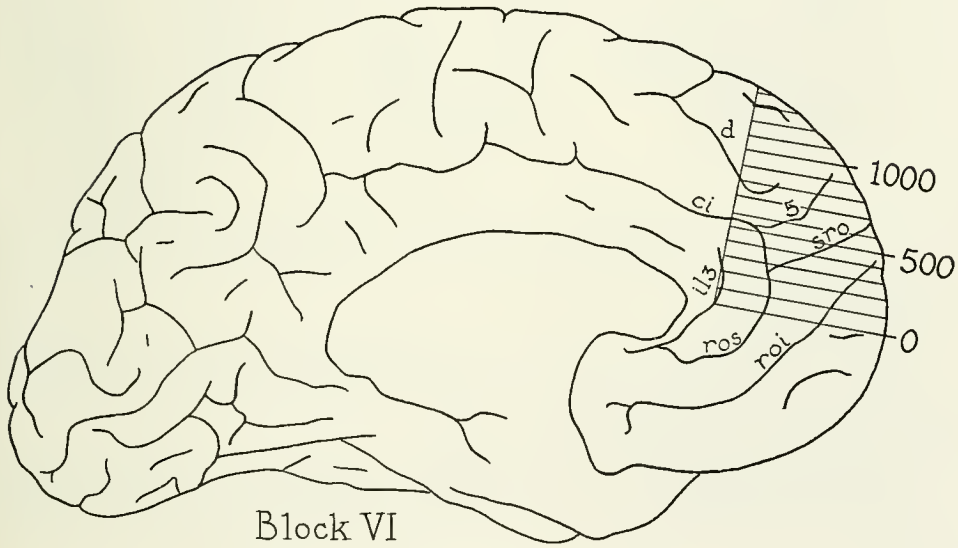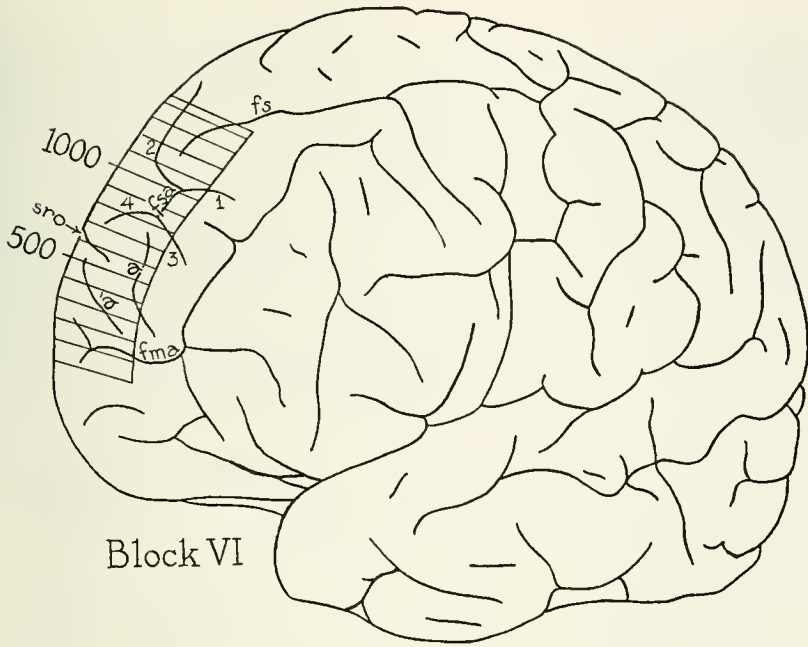
FIG. 43. Position of sections of Block VI.

BLOCK VI (Fig. 43)

Sections 1400, 1300, 1200, 1100.

These sections are cut too tangentially to read so they are not shown in the figures.

Section 1000. Fig. 44.

The cortex on the dorsal surface varies in thickness from 1.54 mm. to more than 1.85 mm. At a place where the total thickness is 1.7 mm., the outer main layer measures 0.95 mm., inner granular layer 0.15 mm., inner main layer 0.6+ mm. Under *i* is a band of small cells, mostly small pyramids with a few granules, measuring about 0.15 mm., in which the cells are relatively closely packed together. There is then a thick (0.8 mm.), lighter zone in which the pyramids gradually increase in size inward but rarely surpass 26 x 13 μ. Layer *iv* is uniformly filled with granules and an occasional pyramid. Layer *v* measures about 0.31 mm. and has two definite sublayers, an outer *va* containing numerous cells, slightly larger and fatter than those of *iiic*, and an inner *vb* which is relatively empty. Layer *vi* shades off gradually into the subcortex and is filled with fusiform and irregular cells. Delicate columns extend almost to *i*. This is eulaminate cortex of generalized type.

Section 900. Fig. 44.

The entire cortex of this section is essentially similar to that described in section 1000. It varies in thickness over the crowns from 1.54 mm. to more than 2.0 mm.
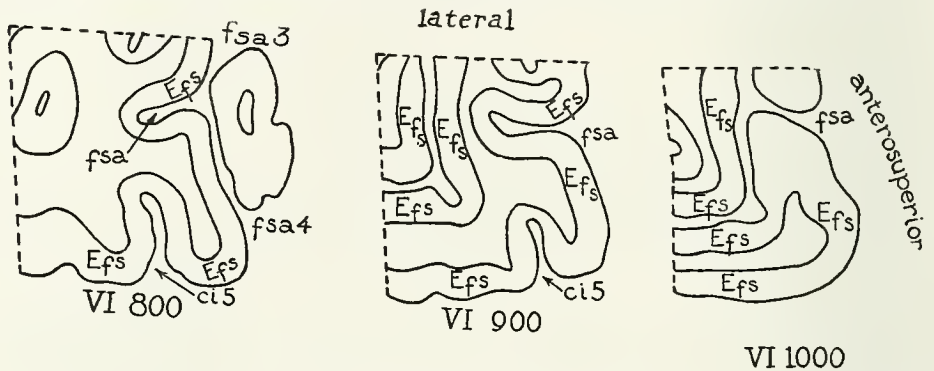
FIG. 44. Cross sections of Block VI.

In the depth of *fsa* are large cells on the border between *iiic* and *iv* measuring up to 45 x 32 μ.

Section 800. Fig. 44.

The cortex on the dorsal surface, where it can be read, is of the type described in section 1000. It measures about 1.7 mm. in cross section and continues without essential change over the medial surface.

There is an occasional very large pyramid in *iiic* or the outer part of *iv*. These are especially numerous in the superior frontal sulcus (*fsa*). They could almost qualify as giant cells, reaching 50 x 26 μ. There is even an occasional one 34 x 21 μ in *v*.

Section 700. Fig. 45.

The cortex of this section is all of the generalized type described in section 1000. The pyramids measure mostly about 26 x 13 μ with many larger ones in *iiic*, especially in the buried part of the superior frontal sulcus; those in *v* never exceeding 32 x 18 μ. Over the crowns, wherever cut parallel to the fine columns, the cortex measures about 1.7 mm.
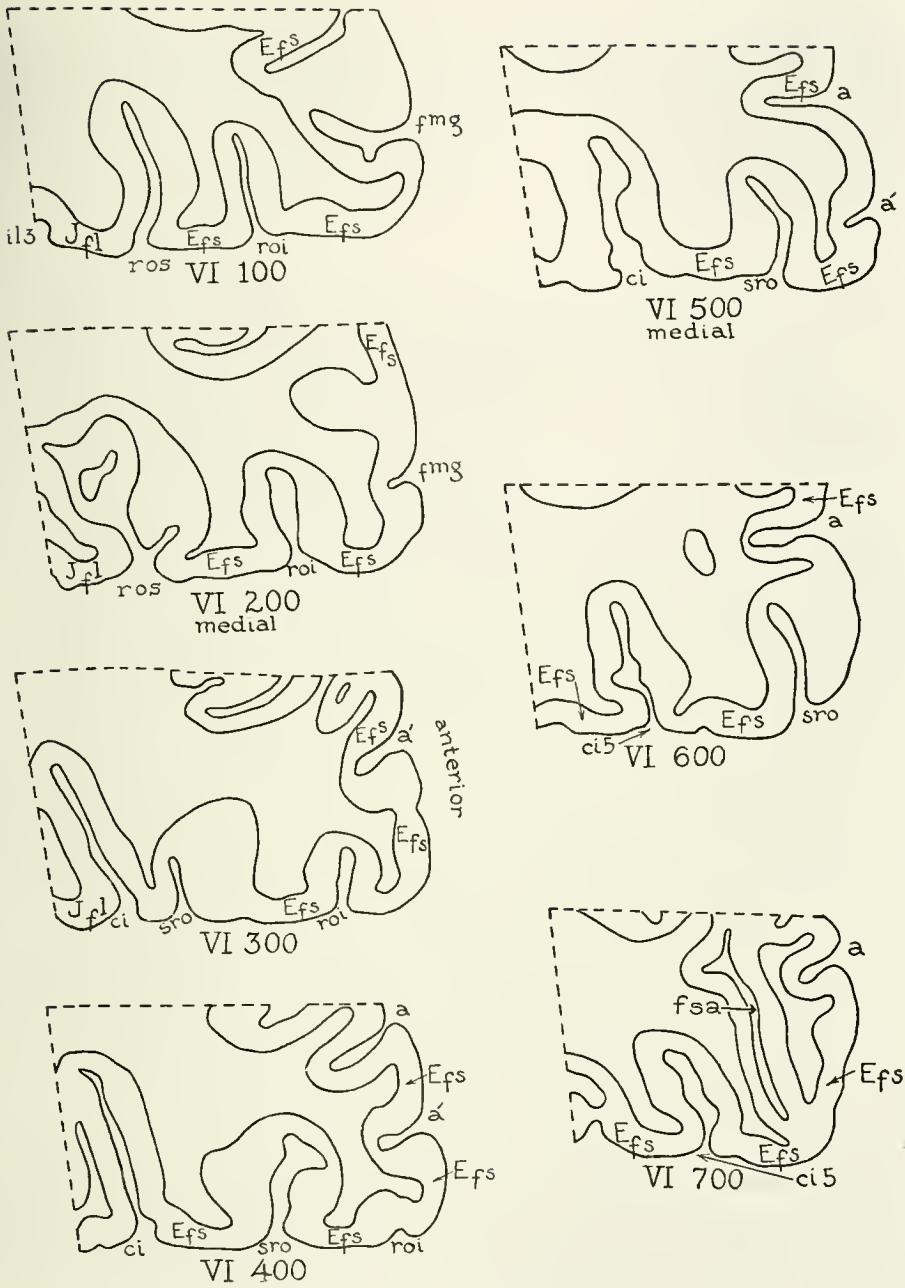
Section 600. Fig. 45.

FIG. 45. Cross sections of Block VI.

The cortex is identical in type with that of section 700. It varies in thickness over the surface from 1.4–1.8 mm.

Section 500. Fig. 45.

Same as in section 600, varying in thickness from 1.4–1.8 mm.

Section 400. Fig. 45.

Same as before, varying in thickness from 1.4–1.8 mm. Between *sro* and *roi* the cells are particularly small, but the relative size in the various layers is the same. Total thickness 1.4 mm., outer main layer 0.65 mm., inner granular 0.15 mm., inner main layer 0.6+ mm.

The cortex posterior to *ci* is cut too tangentially to read.

Section 300. Fig. 45.
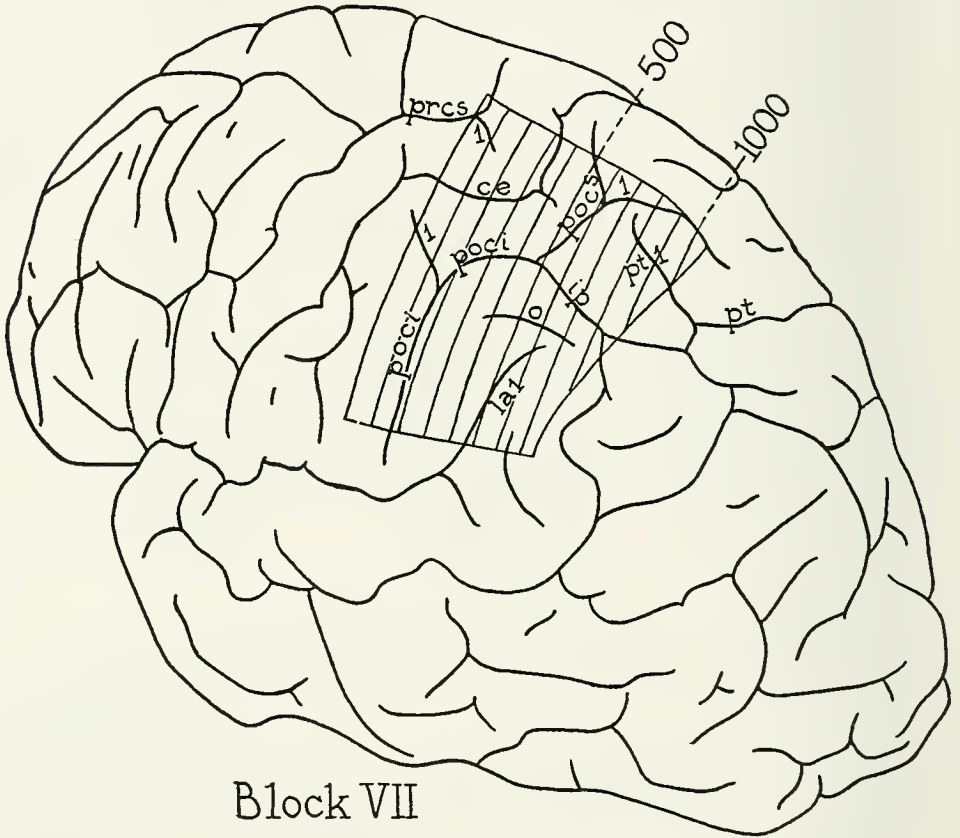
Block VII

FIG. 46. Position of sections of Block VII.

Cortex unchanged in type. Lateral to a^1 measures 1.54 mm., outer main layer 0.6 mm., inner granular 0.15 mm., inner main layer 0.8 mm. On the dorsomedial margin it measures 1.4 mm., outer main layer 0.62 mm., inner granular 0.15 mm., inner main layer 0.62 mm. Between *roi* and *sro* it measures 1.4 mm., outer main layer 0.65 mm., inner granular 0.15 mm., inner main layer 0.6 mm.

Medial to *ci* the cortex has a thinner *iv* and denser *va*. This is juxtallocortex (*jfl*).

Section 200. Fig. 45.

The cortex, wherever cut parallel to the columns, is identical with that of the section 300 anterior and lateral to *roi*.

Posterior to *roi* there are more and larger cells in *va*, and *iv* is thinner, measuring not more than 0.12 mm.

Posterior to *ros* the cortex has almost lost its internal granular layer. Although it approaches anterior limbic agranular cortex, it is still labeled *ıfl*.

Section 100. Fig. 45.

Identical with section 200.

<p style="text-align:center">BLOCK VII (Fig. 46)</p>

Section 100. Fig. 47.

The cortex above the posterior spur of the precentral sulcus (*prcs1*) is cut tangentially, but it can be seen that it is agranular and contains no giant cells.

Over the precentral gyrus the cortex measures 1.7 mm. in thickness. It is agranular, most of the cells of the *ii* layer being small pyramids. There are no small cells in the position of an inner granular layer. Over the crown there are no giant cells, the largest pyramid measuring 37 x 16 μ.

Beginning at the anterior lip of the central sulcus (*ce*) giant cells are numerous in the deeper parts of the cortex, measuring about 47 x 26 μ, which lie at approximately the same level in the cortex and extend to the depth of the sulcus.

As the cortex rounds the bottom of the sulcus it thins to 0.85 mm. and a thin internal granular layer can be seen, but occasional giant cells also in *v* and numerous large pyramids in *iii* up to 34 x 16 μ in dimension. This cortex soon changes rather rapidly, but without sharp margin, the large cells disappearing from *iii*, and *v* becoming empty, so that in the middle of the posterior wall of the central sulcus the cortex looks quite different.

Here the cortex measures 1.25 mm., outer main layer 0.6 mm., inner 0.5 mm. The outer main layer is almost of uniform appearance, consisting of granules and very small pyramids which are only slightly larger in *iiic*. Layer *iv* is thick and evenly filled with granules and a few small pyramids. Layer *v* consists of two sublayers, an outer *va* containing small pyramids about the size of those of *iiic*, measuring usually less than 18 x 13 μ, and an inner *vb* which is almost empty. Layer *via* contains small irregular and fusiform cells smaller than those of *iiic* and *va*, and *vib* is very thin and almost empty. This is evidently postcentral koniocortex (*κpoc*).

As one approaches the posterior lip of the central sulcus the cortex thickens to 1.4 mm. over the crown of the postcentral gyrus, outer main layer 0.63 mm., inner 0.63 mm. The pyramids in *iiic* become larger, up to 39 x 24 μ; *vb* remains empty. On the posterior wall of the postcentral gyrus the large cells in *iiic* seem more numerous and a few reach 48 x 26 μ, but it is cut here very diagonally. This is postcentral parakoniocortex (*ρpoc*).

Below the anterior spur of the inferior postcentral sulcus (*poci1*) the size of the cells in *iiic* decreases gradually until they reach scarcely 21 x 13 μ. The cortex also thickens to 1.54 mm. and *vb* fills. This has become generalized eulaminate cortex (*εpi*).

Section 200. Fig. 47.

The cortex above the central sulcus (*ce*) is agranular, measuring 2.0 mm. in total thickness, with giant cells extending upward to the incipient posterior spur from *prcs1* and down to the bottom of the central sulcus.

The deepest part of the posterior wall of *ce* is covered by the thin transitional cortex described in the preceding section 100. Then follows koniocortex (κ*poc*) also described in 100.

Just within the posterior lip of *ce* the koniocortex gives place to postcentral parakoniocortex which here measures 1.54 mm., outer main layer 0.6 mm., inner 0.6 mm. The pyramids of *iiic* reach as much as 42 x 26 μ. Layer *v* is relatively empty
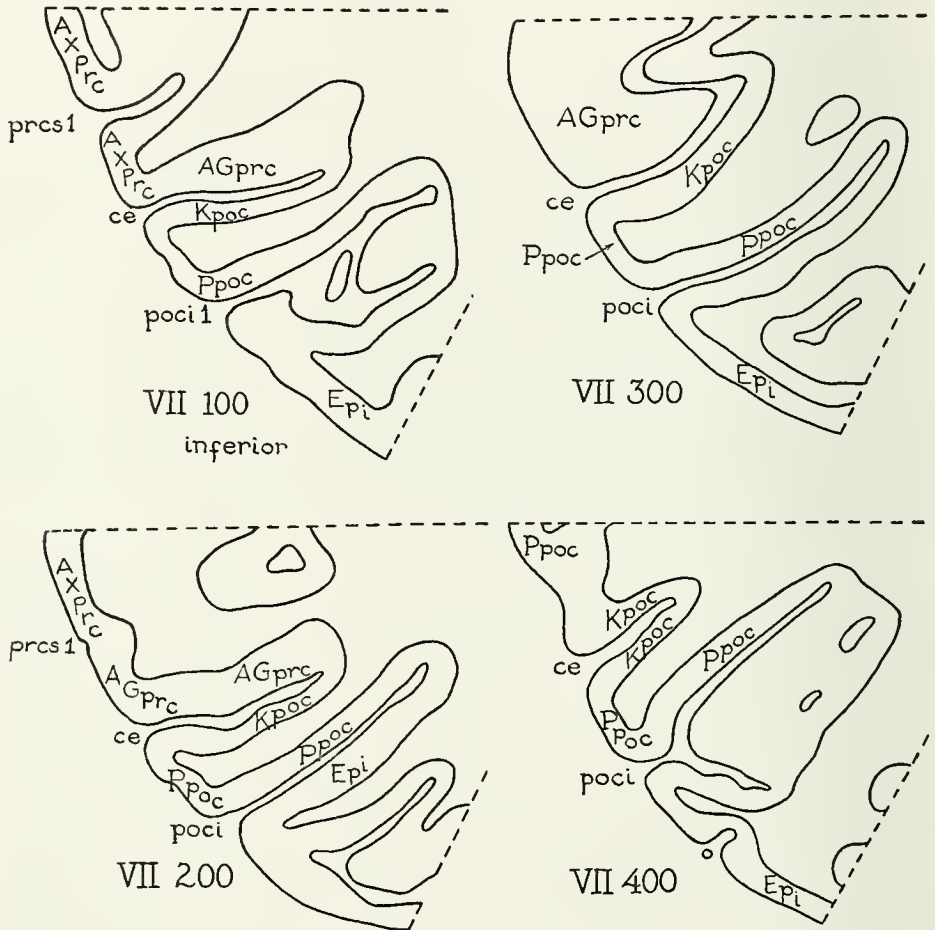

FIG. 47. Cross sections of Block VII.

and contains rarely a large pyramid; most of its cells are about the same size as those of *via*. Occasionally a very large pyramid may lie in the middle of *iv*. On the anterosuperior wall of *poci* the cortex is identical and measures 1.6 mm. The cells of *iiic* are neither larger nor more numerous than on the crown.

On the inferior wall of *poci* the cortex thickens to 1.8 mm. The pyramids of *iiic* are smaller and *v* fills with medium and small pyramids. The cortex here is of generalized type (ε*pi*).

Below *poci* the cortex is cut so diagonally it cannot be read.

Section 300. Fig. 47.

Above the central sulcus the cortex is cut very tangentially but giant cells can be seen throughout.

On the postero-inferior wall of *ce* lies koniocortex, also cut very tangentially.

On the crown of the postcentral gyrus and over its postero-inferior wall the cortex does not differ from that described in the preceding section.

Below *poci* the cortex measures 1.7 mm. in total thickness, outer main layer 0.7 mm., inner 0.85 mm. Layer *iiib* is relatively empty. The pyramids of *iiic* are not above medium size, about 24 x 13 μ on an average. The pyramids of *v* are about the same size, more numerous near *iv*. The cells of *via* are slightly smaller but more numerous. The boundary with the subcortex is vague. This is generalized eulaminate cortex except for the relatively empty *vb*.

Section 400. Fig. 47.

On the crown above *poci* the cortex is typical postcentral parakoniocortex in type, measuring 1.45 mm., outer main layer 0.6 mm., inner 0.68 mm.

The cortex in the posterior spur from *ce* is koniocortex on both walls.

At the upper extremity of the section the cortex is again postcentral (P*poc*).

On the upper wall of *poci* the cortex is cut diagonally but appears to be parakoniocortex. The inferior wall is cut too tangentially to read.

Just below *poci* the cortex measures only 1.3 mm. Layers *iiib* and *vb* are rather empty. The cells of *iiic* are not of more than moderate size.

At an inferior extremity of the section the cortex measures 1.85 mm. The cells of *iiic* measure about 21 x 13 μ. Layer *v* is well filled by cells of about the same dimensions.

Section 500. Fig. 48.

The cortex between the two branches of *pocs* is typical postcentral parakoniocortex (P*poc*). It measures 1.2 mm., outer main layer 0.46 mm., inner 0.6 mm. Large pyramids in *iiic*, empty *vb*, occasional large pyramid in *va*. This cortex covers also the anterior wall of *pocs* where it is thicker (1.4 mm.) but is cut diagonally.

On the postero-inferior wall of *pocs* the cortex thickens to 1.7 mm., outer main layer 0.83 mm., inner 0.7 mm. Layer *vb* is still rather light but the pyramids of *iiic* are smaller. This cortex continues to cover both *pocs* and *ip* and the cortex immediately below the latter. On the narrow gyri both above and below *ip* one can see a heavy band formed by the cells of the deeper part of *iv* and the outer part of *v*. This is characteristic of the superior parietal lobule.

Below *o* the cortex cannot be read.

Section 600. Fig. 48.

Between *pocs* and *ip* the cortex measures 1.54 mm., outer main layer 0.6 mm., inner 0.77 mm. It is difficult to separate *ivb* and *va* which, together, form a dense band between lighter *iva* and *vb*. This cortex covers also both walls of the gyrus.

Just below *ip* the cortex narrows to 1.23 mm., outer main layer 0.5 mm., inner 0.6 mm. Layer *v* is better filled and the dark band is not nearly as evident.

Below *la1* the cortex measures 1.6 mm., outer main layer 0.65 mm., inner 0.8 mm. Layer *v* is evenly filled with pyramids about 21 x 13 μ. Those of *iiic* are but little larger. Layer *iv* is evenly filled with uniform granules. This is generalized eulaminate cortex.
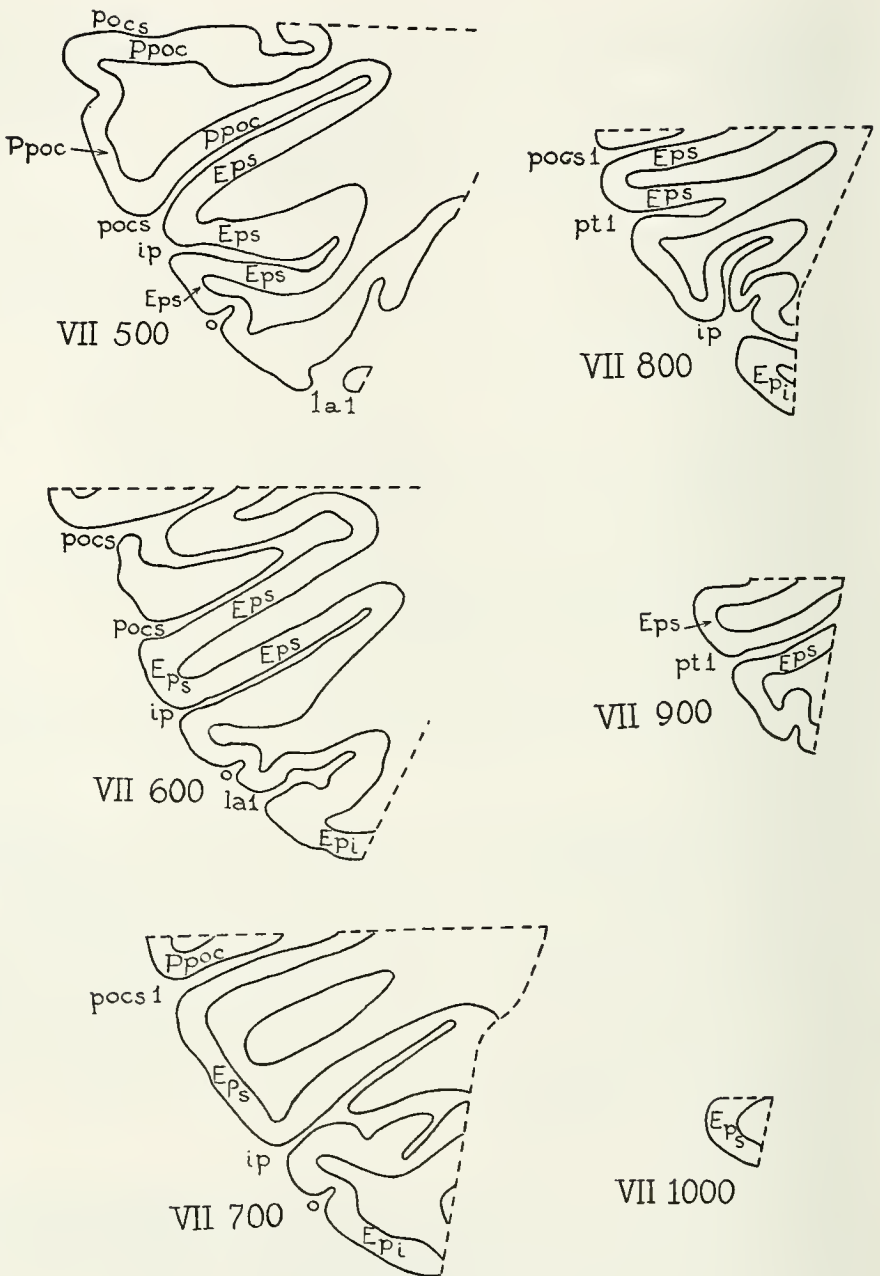
FIG. 48. Cross sections of Block VII.

Section 700. Fig. 48.

Above the posterior spur of the superior postcentral sulcus (*pocs1*) the cortex measures 1.4 mm., outer main layer 0.54 mm., inner 0.71 mm. The pyramids of *iiic* range up to 39 x 19 μ. In *v* are two huge pyramids, one 52 x 32 μ and the other 52 x 39 μ. Layer *v* is otherwise relatively empty. This is parakoniocortex.

Below *pocs1* the cortex is uniformly about 1.4 mm. There is a definite dark band formed by *ivb* and *va* beneath which is a light *vb*. But the pyramids of *iiic* are not above 26 x 16 μ in size and there are no large cells in *v*. Outer main layer 0.58 mm. This is eulaminate superior parietal cortex.

Just below *ip* the cortex measures 1.54 mm., outer main layer 0.58 mm. The dark band is not so evident and *v* is better filled. Farther down, the cortex measures 1.8 mm., outer main layer 0.7 mm., inner 0.9 mm. Layer *v* is evenly filled by pyramids very little larger than those of *vi*. The pyramids of *iiic* are slightly larger. The columns are quite fine. This is generalized eulaminate cortex.

Section 800. Fig. 48.

In the fragment of cortex above *pocs1* can be seen a huge pyramid in *v* measuring 47 x 39 μ.

On the gyrus below, the cortex is of eulaminate superior parietal type measuring 1.4 mm., outer main layer 0.5 mm., inner 0.75 mm.

Below *pt1* the cortex is irregular; below *ip* it is of the generalized eulaminate type described in section 700.

Section 900. Fig. 48.

Above *pt1* the cortex is of superior parietal eulaminate type, measuring 1.4 mm., outer main layer 0.6 mm., inner 0.6 mm. The same type covers both walls of *pt1*.

Below *pt1* the cortex is irregular and cut diagonally.

Section 1000. Fig. 48.

This fragment is of superior parietal eulaminate type, measuring 1.5 mm., outer main layer 0.65 mm.
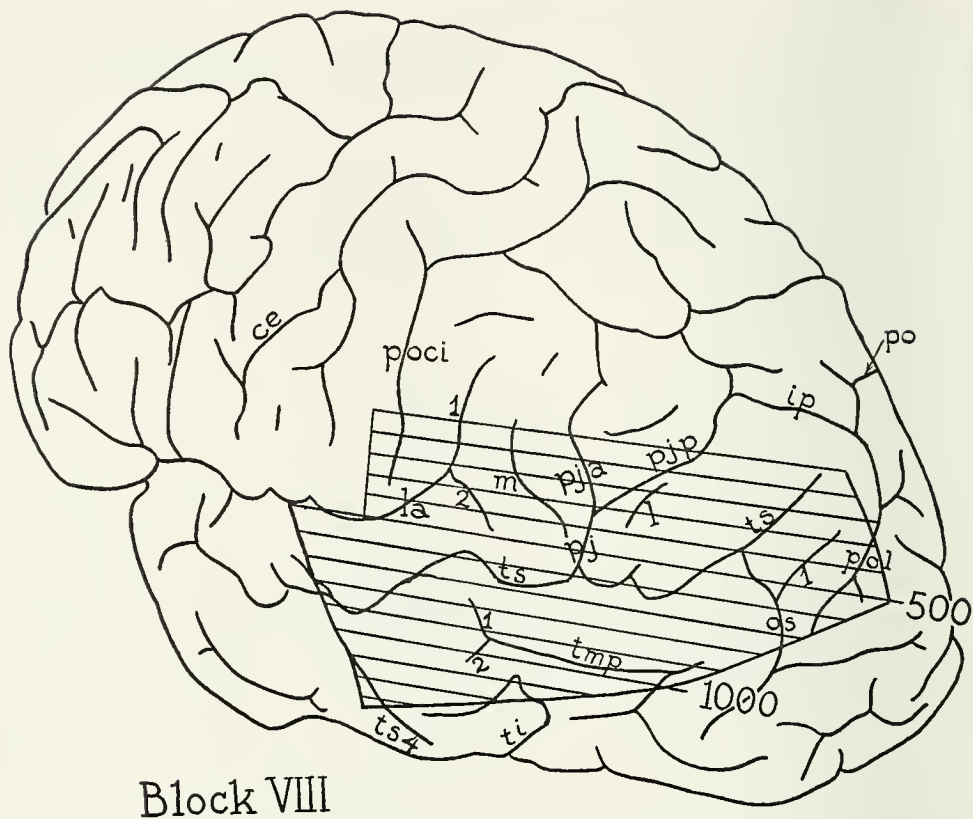
<div align="center">BLOCK VIII (Fig. 49)</div>

Section 100. Fig. 50.

The cortex posterior to *ts* measures 1.54 mm. in thickness, outer main layer 0.77 mm., inner 0.6 mm. The boundary between *i* and *ii* is smooth. It is difficult to distinguish *ii* from *iiia* except under higher magnification, since the pyramids of *iiia* are but little larger than granules; there are some pyramids also in *ii*. The pyramids of *iiib* are slightly larger but scarcer. The pyramids of *iiic* are still larger, mostly about 21 x 13 μ but some as large as 26 x 16 μ. Layer *v* has scattered medium pyramids. The cells of *vi* are distinctly smaller; a *vib* is hardly recognizable and the boundary with the subcortex is relatively sharp. The columns are moderately broad and extend up to *iiia*. This is eulaminate preoccipital cortex.

The cortex between *ts* and *pjp* is distinctly lighter and measures 1.7 mm. The border between *i* and *ii* is less regular. Layer *ii* is more clearly demarcated from *iiia* which contains sparser cells and is more like *iiib*. The cells of *iiic* are hardly ever larger than 21 x 13 μ. The pyramids of *v* are smaller than those of *iiic*. Layer *via* contains more cells than *v* and there is a distinct *vib*. This is eulaminate parietal inferior cortex. The outer main layer measures 0.77 mm., inner 0.77 mm., except in the middle of the gyrus, where one sees the phenomenon always found in the middle of a broad gyrus. Here the outer main layer thickens to 1.1 mm. and the inner thins to 0.6 mm. This is the sign of an incipient sulcus.

On the crown of the gyrus anterior to *pjp* the cortex cannot be read but, on the gyrus anterior to *pja*, the cortex is similar to that just described. Its thickness is 1.7 mm., outer main layer 0.74 mm., inner 0.8 mm. The cells of *iiic* and *v* are perhaps slightly larger.

Block VIII
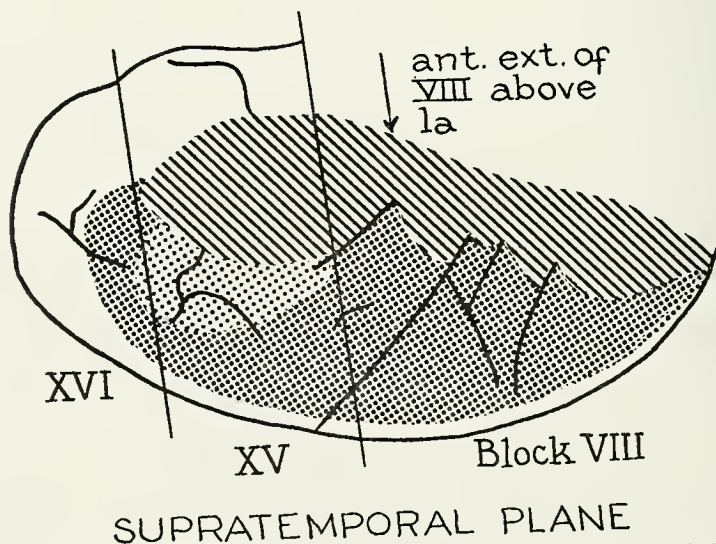
SUPRATEMPORAL PLANE

FIG. 49. Position of sections of Block VIII. Light dots—covered by island. Heavy dots—covered by frontoparietal operculum. Parallel lines—transected white substance.

On the gyrus just posterior to *la1* the cortex is cut diagonally but is thicker, outer main layer 0.68 mm., inner 1.0 mm., inner granular 0.18 mm. Layer *iiia* contains more and larger pyramids. The pyramids of *v* are larger also and *vib* is very thick.
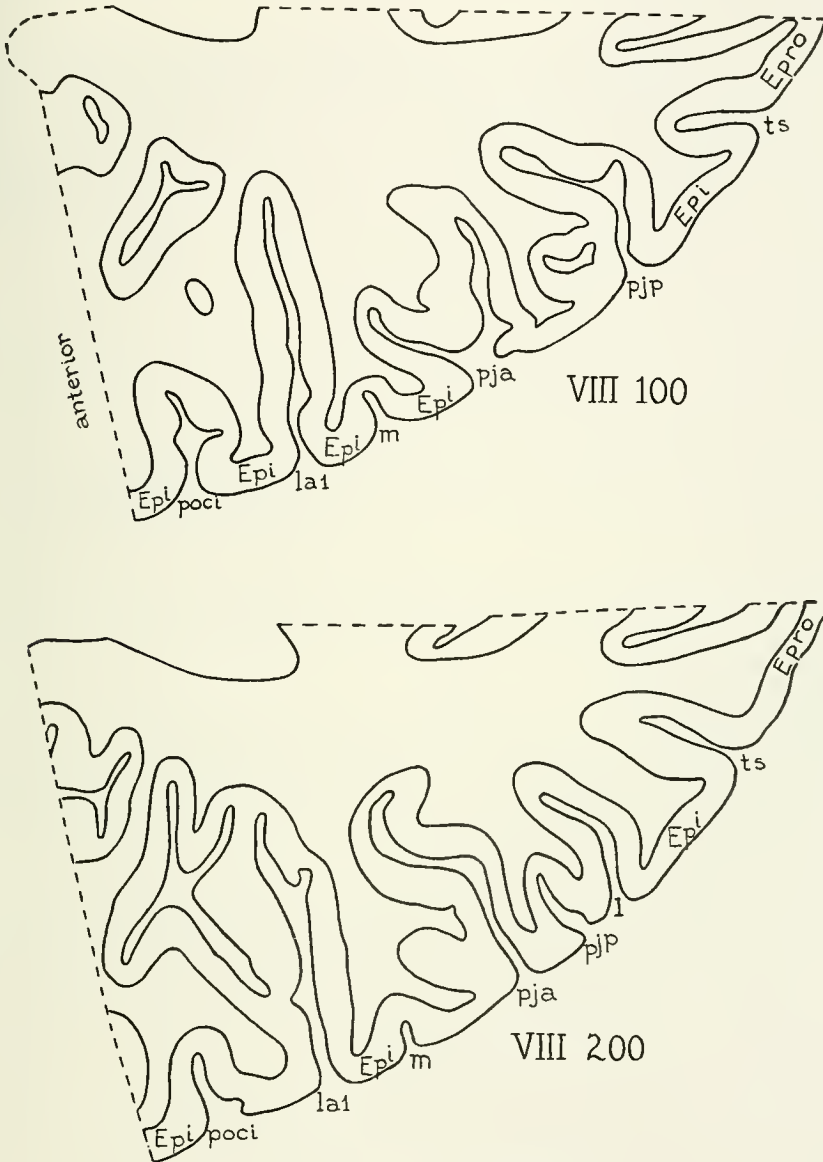

FIG. 50. Cross sections of Block VIII.

Anterior to *la1* the cortex is very similar, measuring 1.82 mm., outer layer 0.9 mm., inner 0.77 mm., inner granular 0.15 mm. Layer *iiib* seems a little less empty and *via* thinner.

Anterior to *poci* the cortex is still thicker (2.15 mm.), outer main layer 0.9 mm., inner 1.1 mm., the extra width being largely in *via*.

On the whole one has the impression that all the cortex represented in this section is essentially similar except for the most posterior gyrus whose cortex has some parakoniose traits.

Section 200. Fig. 50.

The cortex at the posterior extremity of the section is dense, thickness 1.62 mm., outer main layer 0.8 mm., inner 0.7 mm. The boundary between *i* and *ii* is smooth, *ii* and *iiia* form a rather homogeneous band. The pyramids of *iiic* often measure 26 x 16 μ. The pyramids of *v* are sometimes almost as large. Layer *via* is better filled and thicker than *v* and there is almost no *vib*. This is eulaminate preoccipital cortex.

Anterior to *ts* the cortex lightens; there is here a more definite *vib*, outer main layer 0.77 mm., inner 0.68 mm.

Anterior to *pjp* the cortex is cut diagonally and cannot be read.

Anterior to *pja* the cortex measures 1.65 mm., outer main layer 0.63 mm., inner 0.85 mm., of which *v* accounts for only 0.31 mm.

Just behind *la1* the cortex measures 2.16 mm., outer main layer 0.84 mm., inner 1.18 mm. Layer *iiib* is well filled with medium pyramids and *v* with pyramids of about the same size. Only a few pyramids of *iiic* reach 26 x 16 μ. Layer *vib* is very thick and *v* only 0.34 mm. or less. The columns are rather slender.

Anterior to *la1* the cortex is cut too diagonally to read, but, anterior to *poci*, it measures 2.0 mm. and is indistinguishable from the cortex just back of *la1*, outer main layer 0.83 mm., inner 1.1 mm. It gives the impression only of being somewhat denser.

Again the cortex of this section is essentially similar except for that over the posterior gyrus. The thinness of the cortex just anterior to *ts* seems without significance.

Section 300. Fig. 51.

The cortex posterior to *os1* measures 1.55 mm., outer main layer 0.77 mm., inner 0.63 mm. It looks very much as previously described for section 200.

Anterior to *ts* the cortex thickens to 1.7 mm. but is otherwise quite similar; outer main layer 0.85 mm., inner 0.7 mm.; *iiib* and *v* relatively light, almost no *vib*, boundary between *i* and *ii* smooth.

The cortex just anterior to *pj* is cut too diagonally to read. Just posterior to *la* it measures 1.95 mm., outer main layer 0.7 mm., inner 1.1 mm. Layers *iiia* and *ii* are with difficulty distinguished from each other and *v* from *via*.

The superficial cortex anterior to *la* is essentially similar, outer main layer 0.85 mm., inner 1.23 mm., inner granular layer 0.15 mm. The pyramids of *iiic* and *v* do not exceed 21 x 13 μ, the columns are rather narrow.

The cortex anterior to *poci* is a little denser but otherwise very much the same, measuring 1.92 mm., outer main layer 0.77 mm., inner 1.0 mm.

Within the lateral fissure, about halfway down the posterolateral wall (the more superficial portion is cut too diagonally to read) the cortex becomes thinner, total thickness 1.54 mm., outer main layer 0.74 mm., inner 0.68 mm. There are numerous very large pyramids in *iiic*, measuring up to 47 x 26 μ. This is supratemporal parakoniocortex *pst*.

The cortex over the buried isolated gyrus contains also the very large pyramids in *iiic*, total thickness 1.54 mm., outer main layer 0.9 mm., inner 0.46 mm., with a very light *v*. This is also supratemporal parakoniocortex.

Section 400. Fig. 51.

The cortex posterior to *ts* is of the type previously described for these gyri, total thickness 1.54 mm., outer main layer 0.62 mm., inner 0.68 mm.
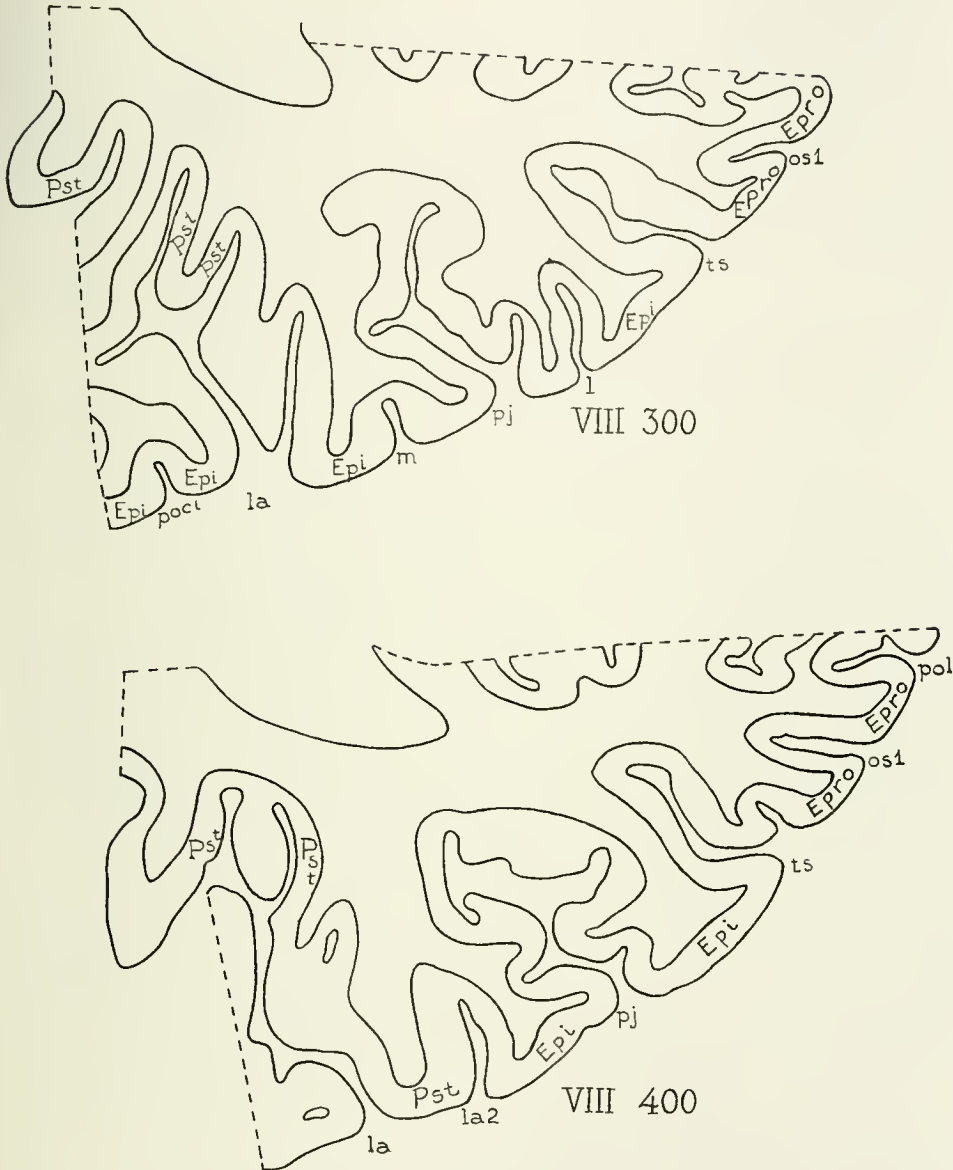

FIG. 51. Cross sections of Block VIII.

Anterior to *ts* the cortex thickens to 2.17 mm., outer main layer 1.05 mm., inner 0.95 mm., but *ii* + *iiia* form a dense band and *v* is still lighter than *vi*. The pyramids of *iiic* range up to 26 x 21 μ in size. A few pyramids in *v* are also of this size. Nevertheless it resembles more closely the generalized inferior parietal cortex.

Posterior to *la2* the cortex measures 1.95 mm. The cells of both *iiic* and *v* are smaller although larger than those of *iiib* and *vi*, measuring about 21 x 16 μ. Outer main layer 0.7 mm., inner 1.1 mm. Anterior to *la2* the outer main layer measures only 0.65 mm., the inner 1.23 mm. There are a few large pyramids (26 x 21 μ) in *iiic*. We shall return to this region presently.

As soon as the cortex passes into the postero-inferior wall of *la*, the large pyramids increase considerably in number and reach as much as 39 x 26 μ. These large pyramids continue to the depth of the fissure and over onto the buried gyrus. Over the posterior wall of this buried gyrus (the anterior is cut too diagonally to read) the cortex measures 2.0 mm., outer main layer 0.77 mm. Some of the large pyramids are displaced into *iv* and others lie considerably above the outer margin of *iv*. It is difficult to determine also the inner margin of *iv* since the cells of *v* are small and sparse. The cells of *via* are larger and more numerous than those of *v*, which looks empty in comparison. This cortex, which has the characteristics of the supratemporal parakoniocortex, extends outward over the postero-inferior lip of the lateral fissure onto the exposed surface of the superior temporal gyrus.

Section 500. Fig. 52.

The cortex on the crowns of the two small posterior gyri cannot be read, but on the walls of the intervening sulci it can be seen to be typically parakoniose, measuring 1.15 mm., outer main layer 0.55 mm., inner 0.46 mm.

Anterior to *pol* the cortex measures 1.54 mm., outer main layer 0.63 mm., inner 0.77 mm. The pyramids of *iiic* do not exceed 26 x 18 μ; the pyramids of *v* are generally smaller. Layers *v* and *iiib* are relatively empty and appear as light bands. Layer *vib* is thicker than *v*. The columns are only moderately broad.

On the posterior wall of *ts* the cortex measures 1.7 mm., outer main layer 0.65 mm., inner 0.9 mm. The boundary between *i* and *ii* is irregular. Layer *iiia* is lighter and rather easily distinguished from *ii*; layer *iiib* is relatively empty, containing mostly small pyramids. The pyramids of *iiic* measure mostly 21 x 13 μ, a few reaching 26 x 18 μ. Layer *v* is well filled with medium pyramids and is easily distinguishable from *via* which is about of equal density. There are a few scattered small cells in an indefinite *vib*. This is preoccipital eulaminate cortex.

Anterior to *ts* the cortex is cut too diagonally to read. Only in the deeper parts of the walls of *ts* and *pj* is the cortex cut parallel to the radiations. Here the cortex measures more than 2.15 mm., outer main layer 0.9 mm., inner granular layer 0.15 mm., inner main layer more than 1.1 mm. The pyramids of *iiic* are mostly of moderate size but a few are as much as 24 x 18 μ. The pyramids of *v* are well distributed, of moderate size, so that *v* can with difficulty be distinguished from *via* at low magnification. Layer *via* is as broad as *v*. This is generalized eulaminate cortex.

The cortex just anterior to *la2* is of generalized eulaminate type but, farther forward, in spite of its diagonal section, numerous large pyramids in *iiic* are seen.

Again in the depth of *la* the cortex is cut parallel to the radiations at two places. Here it measures 1.85 mm., outer main layer 0.83 mm., inner 0.77 mm. Layer *iiib* is better filled with medium pyramids. In *iiic* are many large pyramids up to 39 x 26 μ. The pyramids of *v* are very small, few of them more than 18 x 10 μ, smaller even than the cells of *via* and sparse so that *v* forms a band scarcely distinguishable at low magnification from *iv* and *via* except by the sparseness of its population. This cortex is clearly supratemporal parakoniocortex.

Section 600. Fig. 52.

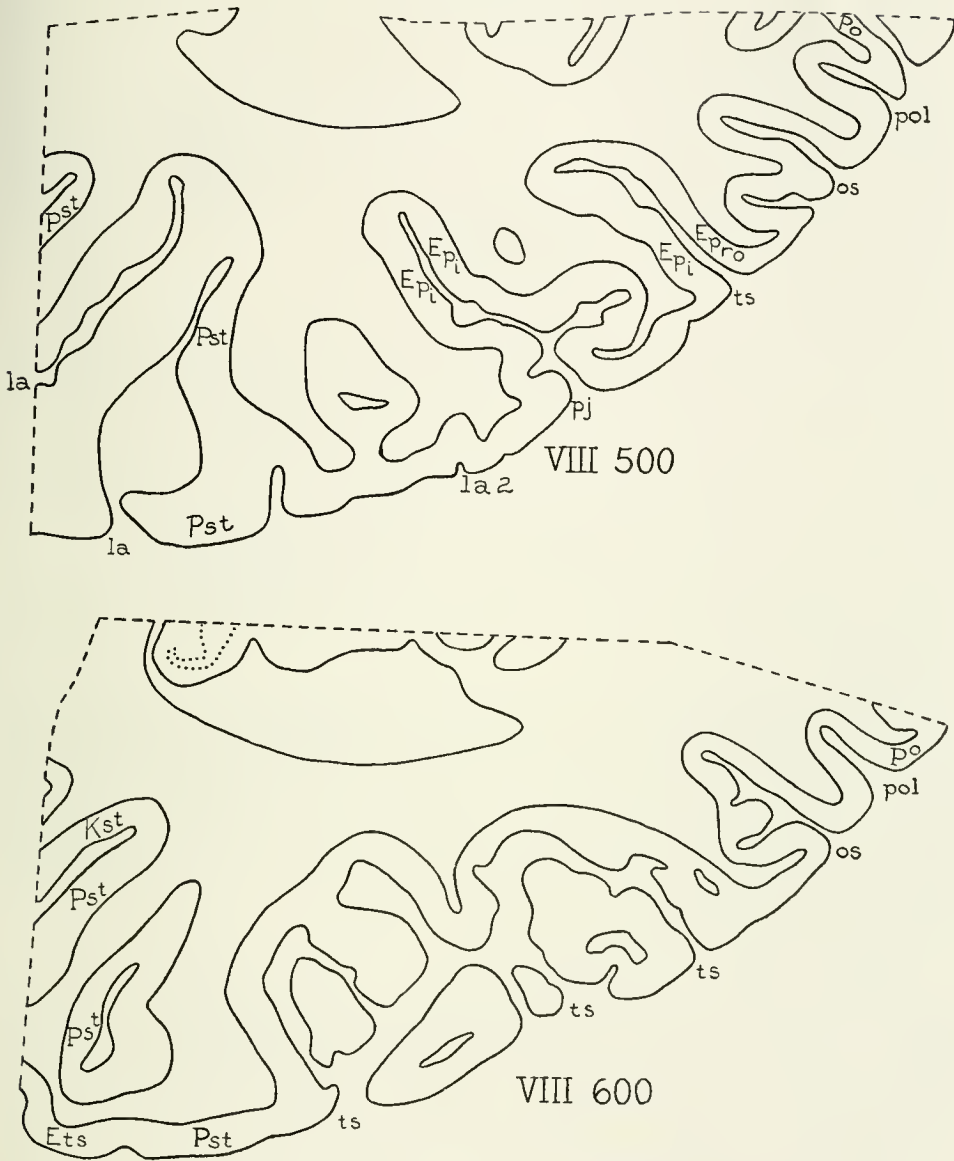The cortex occipitad to *pol* is of parakoniose type.

FIG. 52. Cross sections of Block VIII.

The cortex between *pol* and *os* measures 1.45 mm., outer main layer 0.55 mm., inner 0.68 mm. The boundary between *i* and *ii* is smooth, *ii* and *iiia* almost indistinguishable, *iiib* empty, *iiic* containing many large pyramids, the cells of *v* about the size of those of *iiib*, the columns broad all the way up to *iiia*. It differs from typical parastriate cortex largely by the thickness of the inner main layer and the filling of *v*.

Anterior to *os* the cortex thickens to 1.85 mm., outer main layer 0.93 mm., inner 0.77 mm. There are many more small pyramids in *iiib* so that it no longer looks so empty, and there are no large pyramids in *iiic*.

The cortex around the branches of *ts* is cut very irregularly. Where it can be read it is very thick, measuring more than 2.3 mm., outer main layer 0.9 mm., inner difficult to measure since the borders with *iv* and with *vib* are difficult to determine. Layer *iiia* and parts of *iiib* are well filled with small pyramids. Layer *iiic* contains almost exclusively medium pyramids with occasionally one as big as 24 x 21 μ. Layer *v* contains mostly medium pyramids about 21 x 13 μ, but there is an occasional huge pyramid measuring 47 x 29 μ.

Just anterior to *ts* there are very large pyramids in both *iiic* and *v*, reminding one of parakoniocortex.

At the anterior extremity of the section, the cortex over the superior temporal gyrus measures about 1.7 mm., it being difficult to determine the inner boundary of *via*. The outer main layer measures 0.63 mm. The boundary between *i* and *ii* is ragged. Layers *ii*, *iiia*, *iiib*, and *iiic* are clearly recognizable. *iiib* is fairly well filled with small pyramids. Those of *iiic* are of moderate size up to 24 x 16 μ. The pyramids of *v* are much smaller and evenly distributed so that from *iii* inward the impression is one of considerable uniformity in which the boundaries of the layers are blurred. This superior temporal cortex is of general eulaminate type.

At two places on the sulci which project into the supratemporal plane the cortex can be read. On the more lateral one the cortex is parakoniocortical as previously described with huge cells in *iiic*.

On the more medial one, its posterior wall, even though cut diagonally, can be recognized as parakoniocortex because of the very large cells of *iiic*. On its anterior wall the cortex narrows to 1.4 mm. The layers can, with difficulty, be distinguished. The cells of *iiic* are slightly larger. Measuring from the inner margin of these cells, the outer main layer measures 0.95 mm., inner main layer + *iv*, 0.43 mm. The cells of *v* are no larger than those of *iv* and sparser. The cells of *via* are also very small but more numerous. The cells of *ii*, *iiia* + *b* are almost the same size and uniformly distributed. This is evidently supratemporal koniocortex.

Section 700. Fig. 53.

Posterior to *os* are huge pyramids in *iiic*.

Anterior to *os* the cortex measures 1.6 mm., outer main layer 0.6 mm., inner 0.86 mm. There are numerous large pyramids in *iiic*, up to 39 x 26 μ. Layer *v* has mainly medium pyramids with an occasional large one, and is relatively empty. It is reminiscent of parastriate cortex but clearly cannot be so diagnosed, and is labeled ε*pro*.

Otherwise the cortex posterior to *ts* cannot be read. Only in one small stretch is it cut parallel to the radiations and even here the structure is disturbed by an incipient sulcus.

Anterior to *ts* the cortex is clearly legible. It is quite thick, measuring 1.85 mm. or more, outer main layer 0.95 mm., inner 0.7 mm. or more. There are numerous small pyramids in *iiia* which is of about the same density as *ii*. Layer *iiib* has pyramids only slightly larger but sparser than those of *iiia*. Among the cells of *iiic* are numerous large pyramids, 39 x 26 μ. The pyramids of *v* are small, up to 21 x 16 μ

at most, and sparse so that *v* looks empty. In *v* is an occasional larger pyramid, about 26 x 18 μ. Again this reminds one of parakoniocortex.

FIG. 53. Cross sections of Block VIII.

Section 800. Fig. 53.

At the posterior extremity of the section the cortex measures 1.85+ mm., outer main layer 0.65 mm., inner 1.05+ mm. The columns are of moderate thickness. The cells of *iiic* are mostly of moderate size but some reach as much as 47 x 21 μ.

The pyramids of *v* are nearly all small, even smaller than the cells of *via* and sparser but there is occasionally a very large one, 47 x 26 *μ*. This is not clearly parakonio-cortex.

Just posterior to *tmp1* the cortex measures 1.85 mm., outer main layer 0.7 mm., inner 0.95 mm. The cells of *iiic* are smaller with few large ones. The pyramids of *v* are larger than the cells of *via* and *v* is better filled. This temporo-occipital cortex is of generalized eulaminate type.

Between *tmp1* and *ts* the cortex cannot be read.

Anterior to *ts* the cortex measures more than 1.85 mm., outer main layer 0.83 mm., inner 0.93+ mm., it being difficult to determine the boundary between *via* and *vib*. Layer *v* is well filled with cells of practically the same size as those of *via* so that at low magnification it is difficult to distinguish *v* from *vi*. The cells of *iiic* are mostly of medium size with some reaching 39 x 24 *μ*. There are no large pyramids in *v*. This is generalized eulaminate cortex.

Section 900. Fig. 54.

The cortex posterior to *tmp1* cannot be read.

Anterior to *tmp1* the cortex measures 1.85 mm., outer main layer 0.93 mm., inner 0.74 mm. The outer boundary of *ii* is irregular. Layer *iiia* is evenly filled with small pyramids only slightly larger than the granules of *ii*. Layer *iiib* contains sparse pyramids very little larger than those of *iiia*. The pyramids of *iiic* are small or medium, not surpassing 26 x 18 *μ*. The pyramids of *v* are sparse and not above medium size, scarcely surpassing those of *via*. Layer *v* is not readily distinguished from *via* throughout this region, except by its lightness. This is generalized eulaminate cortex.

Section 1000. Fig. 54.

The cortex cannot be read, either behind *tmp2* or on its walls.

Anterior to *tmp2* the cortex measures 1.85 mm., outer main layer 0.74 mm., inner 0.96 mm. The boundary is irregular. Although *iiia* is about the same density as *ii*, it is readily distinguished from it by its small pyramids. The pyramids of *iiib* are slightly larger but sparser. The pyramids of *iiic* are of only medium size, not surpassing 26 x 18 *μ*. The pyramids of *v* are about the size of those in *iiic* and well distributed. *via* is slightly denser than *v*. Layer *iv* is well filled uniformly with granules and a few small pyramids. The columns are of moderate width. The boundary with the subcortex is blurred. This is eulaminate cortex of generalized type.

Section 1100. Fig. 54.

The cortex posterior to *ti* measures 1.85 mm., outer main layer 0.8 mm., inner 0.9 mm. It is practically identical in appearance with that described in section 1000 as eulaminate temporal. Layer *v* is of equal density with *via*, but its cells are more pyramidal so that they are readily distinguished.

Section 1200. Fig. 54.

The cortex on the surface is cut too diagonally to read but in the posterior wall of *ts4* it measures more than 2.15 mm., and is of the type described in section 1000. The outer main layer measures 0.86 mm., inner granular layer 0.18 mm. The boundary with the subcortex is vague.

Section 1300. Fig. 54.

The cortex anterior to *ts4* is of the type just described, outer main layer 0.8 mm., total thickness about 2.0 mm.
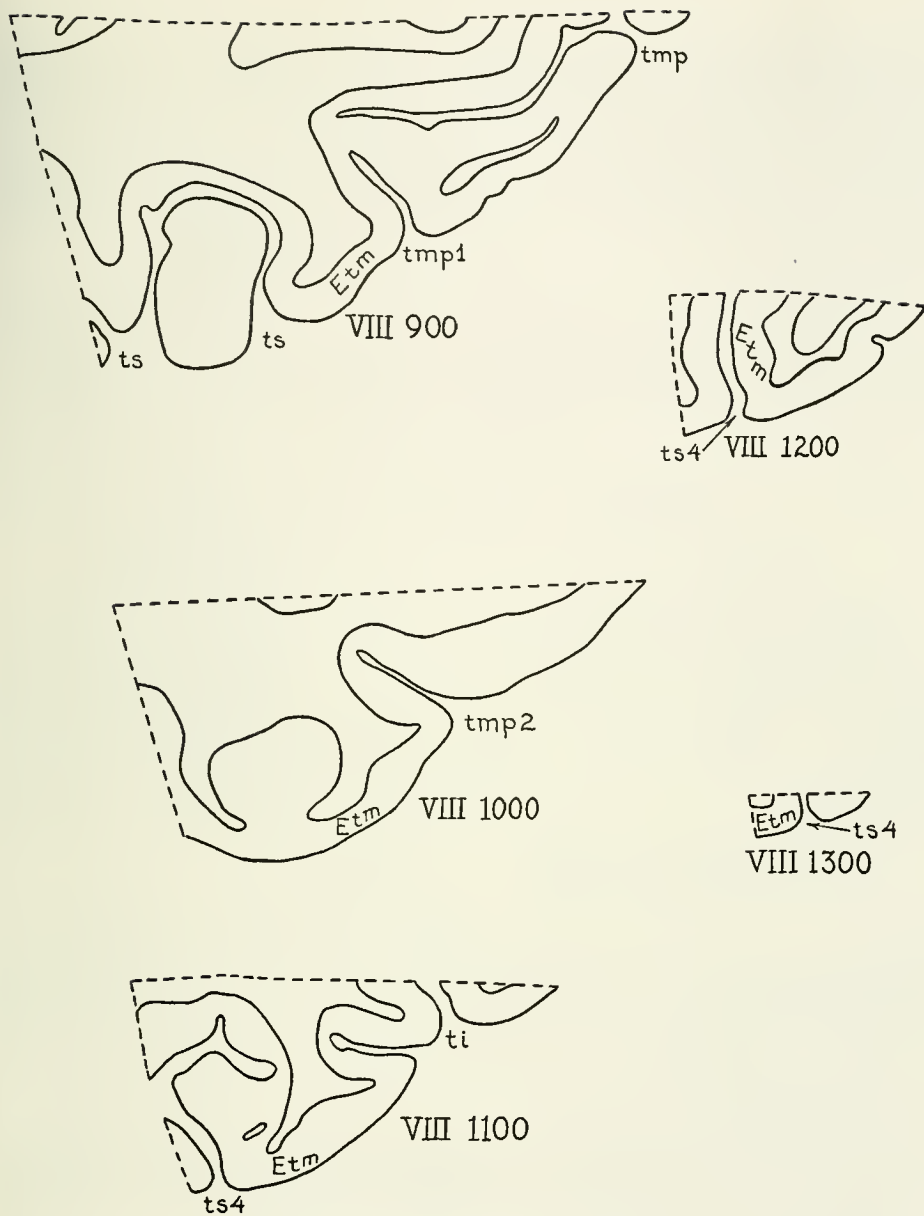
FIG. 54. Cross sections of Block VIII.

block ix (Fig. 55)

Section 1000. Fig. 56.

We will begin at the posterior extremity and move forward.

Medial to *ota* the cortex is irregular and cannot be read.

Just lateral to *ota* the cortex measures 2.1 mm., outer main layer 0.85 mm., inner 1.05 mm. The boundary between *i* and *ii* is irregular. *ii* contains small pyra-

mids as well as granules. Layer *iiia* is filled by very small pyramids. Layer *iiib* has slightly larger pyramids, sparse and scattered irregularly. The pyramids of *iiic* are still larger but do not surpass 24 x 16 μ. The granules are evenly distributed throughout a broad *iv* in thick columns. Layer *v* is evenly filled with pyramids about the size of those in *iiic*. The cells of *via* are slightly smaller, those of *vib* still smaller and scattered. The cortex is of this generalized type throughout the remainder of the section. There is nothing in it to remind one of the parastriate cortex. This temporo-occipital cortex (E*to*) is of generalized eulaminate type.

Section 900. Fig. 56.

The cortex medial to *ota* is a thin cortex (1.36 mm.). The outer main layer measures 0.68 mm., inner 0.55 mm. Layer *ii* + *iiia* measures 0.15 mm. The cells of *iiib* and *c* are larger, slightly scattered and sparse. The pyramids of *v* are also scattered
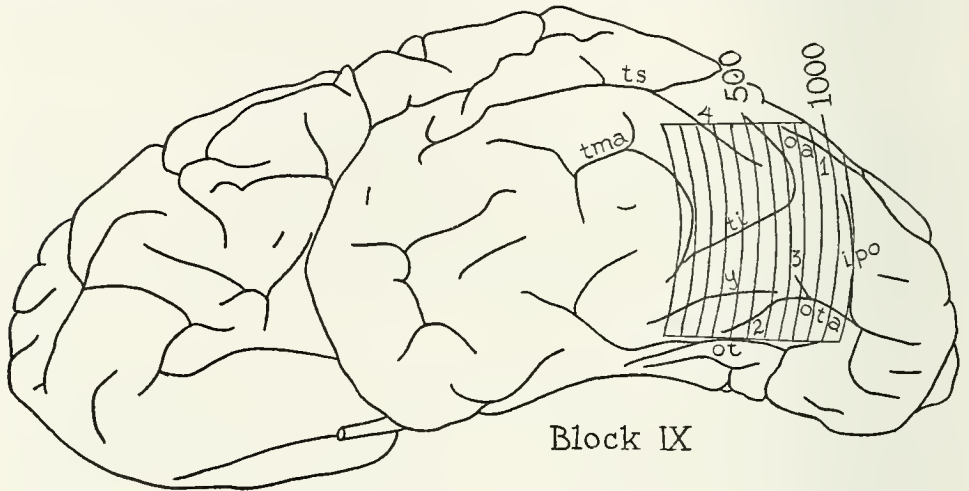

FIG. 55. Position of sections of Block IX.

and sparse, about the same size as those of *iiic*. The cells of *vi* are smaller. This cortex is eulaminate preoccipital in type (E*pro*).

Lateral to *ota* the cortex is of the type described in the preceding section 1000, but not quite so thick (1.9 mm.).

Section 800. Fig. 56.

The cortex medial to *ota* is thicker (1.54 mm.) but is cut so diagonally as to be unreadable. The same is true of all the rest of the cortex over the crowns of the gyri. On the medial wall of *oa1* the cortex can be seen to be eulaminate.

Section 700. Fig. 56.

The cortex medial to *ota2* still cannot be read. Lateral to *ota2* the cortex measures 1.7 mm. The clumps of cells distributed throughout give it a moth-eaten appearance. This appearance seems to be due to the fact that the cortex is cut diagonally through a region with very broad columns which extend through to *iiia*. Nevertheless, the larger pyramids seem to be shifted upward into *iiib* so that there is a clear zone above *iv* where ordinarily the larger pyramids form *iiic*. This cortex is very unusual.
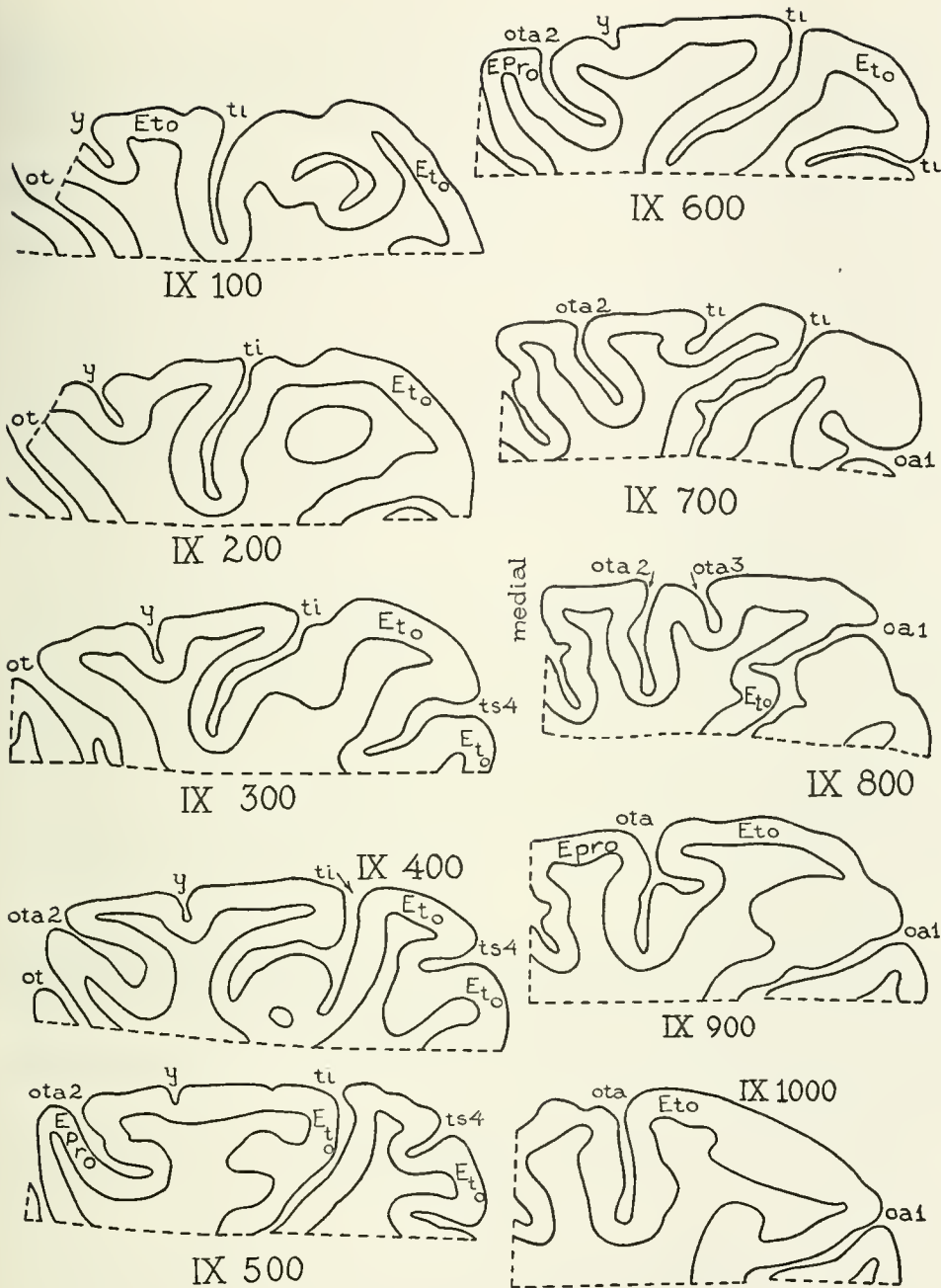
Section 600. Fig. 56.

Fig. 56. Cross sections of Block IX.

The cortex over the narrow gyrus medial to *ota2* measures only 1.2 mm. but, on the wall of the sulcus medial to it, it measures 1.45 mm. and is here cut parallel to the columns which are thick like those of the parastriate cortex. But the boundary

between i and ii is ragged, $ii + iiia$ measures 0.31 mm. The pyramids of $iiic$ are not above 21 x 16 μ. The boundary between $iiic$ and iv is ragged. There is a lighter iva and a darker ivb. Layer v is well filled with pyramids about the size of those in $iiic$, and measures 0.37 mm. in thickness. Layer vi is only about half as broad. This is eulaminate preoccipital cortex (Epro).

Between y and ti the cortex is thinner and has the moth-eaten appearance noted in section 700.

Between the two parts of ti the cortex is cut diagonally, but can be seen to be of general eulaminate type.

Section 500. Fig. 56.

The cortex of the narrow gyrus medial to $ota2$ is thin and looks as previously described in section 600.

Lateral to y the cortex has the moth-eaten appearance previously described and is cut irregularly as far lateral as the inferior temporal sulcus (ti). On the medial wall of ti the cortex is of the type described in section 1000. Over the lateral-most gyrus the cortex is similarly constructed and measures more than 1.85 mm.

Section 400. Fig. 56.

The cortex over the fusiform gyrus measures 1.54 mm.; it is the same on both sides of the intrafusiform sulcus (y). It has a patchy appearance. Layer iv is built like a rail fence with $iiic$ and v projecting alternately into it from either side. The border between i and ii is fairly smooth. Layer ii shades gradually off into $iiia$ and b with medium pyramids scanty and only in $iiic$ in patches. The cells of v are of the same size of those in $iiib$ and can, with difficulty, be distinguished from those of v except at a high magnification. There is almost no vib. The columns are thick. It is eulaminate generalized cortex, poorly constructed.

The cortex lateral to ti is of the type described in section 1000. It measures 1.85 mm., outer main layer 0.8 mm., inner 0.9 mm. The columns are of moderate thickness.

Section 300. Fig. 56.

The cortex on both sides of the intrafusiform sulcus (y) is the same as that described in section 400. In addition, one sees in places a tendency for the pyramids of v to arrange themselves in a dense layer in the middle of v. This cortex measures 1.6 mm., outer main layer 0.84 mm., inner 0.63 mm.

The cortex lateral to the inferior temporal sulcus (ti) measures 2.0 mm. and is of the type described in section 1000.

Section 200. Fig. 56.

The cortex over the fusiform gyrus remains as described before, but the appearance is more regular.

The cortex lateral to ti is unchanged from the previous section.

Section 100. Fig. 56.

The cortex over the fusiform gyrus has thickened and is cut irregularly. Its inner main layer has thickened to 0.93 mm. and its whole appearance is more regular, resembling that lateral to ti which is cut very obliquely but seems of the type previously described, measuring 2.0 mm. or more in thickness. Perhaps the columns are a bit broader and the whole structure looser.
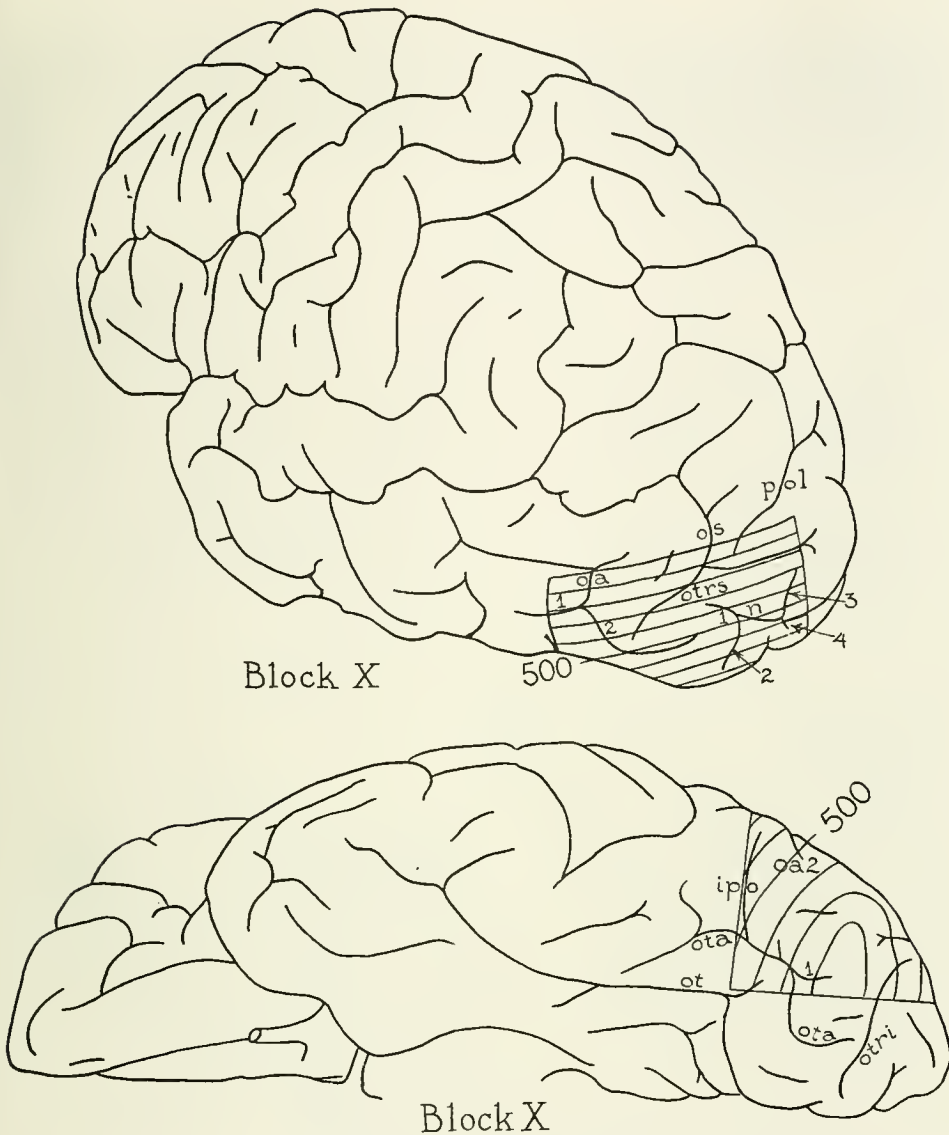
FIG. 57. Position of sections of Block X.

BLOCK X (Fig. 57)

Section 100. Fig. 58.

The cortex over the posterior part of the section is definitely parakoniose, measuring a scant 1.22 mm. in thickness, outer main layer 0.6 mm., inner main layer 0.5 mm. Between *os* and *oa* the cortex is thicker (1.7 mm.) but the cells of *iiic* are quite large, many of them 26 x 42 μ; the fifth layer is, however, better filled than posteriorly, with medium pyramids, and contains no large cells. This is eulaminate preoccipital cortex.

Anterior to the anterior occipital sulcus (*oa*) the cortex measures only 1.6 mm., outer main layer 0.63 mm., inner main layer 0.82 mm. The outer margin of *ii* is smooth, and *ii* cannot be demarcated from *iiia*. *v* is quite evenly filled with medium pyramids. This temporo-occipital cortex is of generalized eulaminate type.
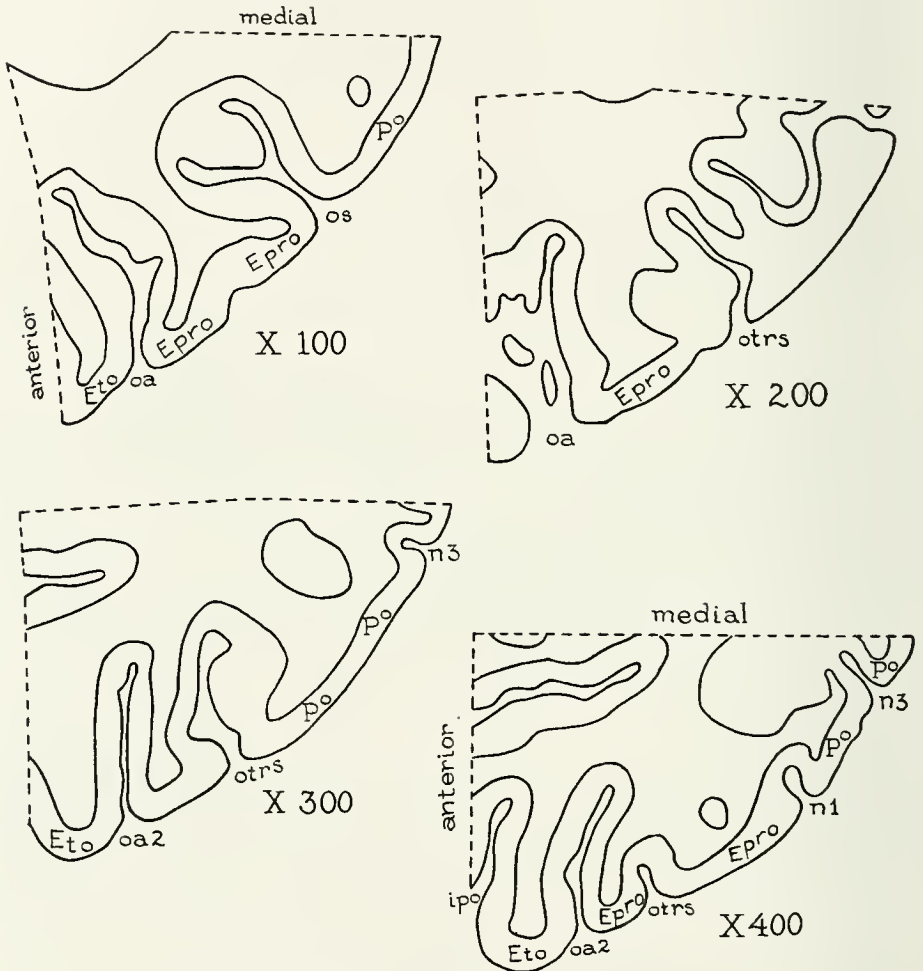
Section 200. Fig. 58.

FIG. 58. Cross sections of Block X.

Most of this section is cut too diagonally or tangentially to read but between *otrs* and *oa* the cortex is the same as the corresponding cortex in section 100 and measures full 1.85 mm. in thickness.

Section 300. Fig. 58.

This section is similar to section 100 and needs no special description. The cortex over the narrow gyrus between *otrs* and *oa2* resembles the parastriate type but the pyramids of *iiic* are rather small and *v* better filled. It is eulaminate preoccipital.

Section 400. Fig. 58.

The cortex at the posterior extremity of the section is definitely of parastriate type with very large pyramids in *iiic* and an occasional large cell in *v*. Over this posterior gyrus it measures 1.35 mm. in thickness. Over the next gyrus anteriorly between *n1* and *n3* the cortex is very similar and measures 1.4 mm., but beyond the shallow sulcus *n1* the cortex has changed. Here it measures 1.7 mm., the pyramidal cells of *iiic* are smaller and *v* is better filled. On the next small gyrus between
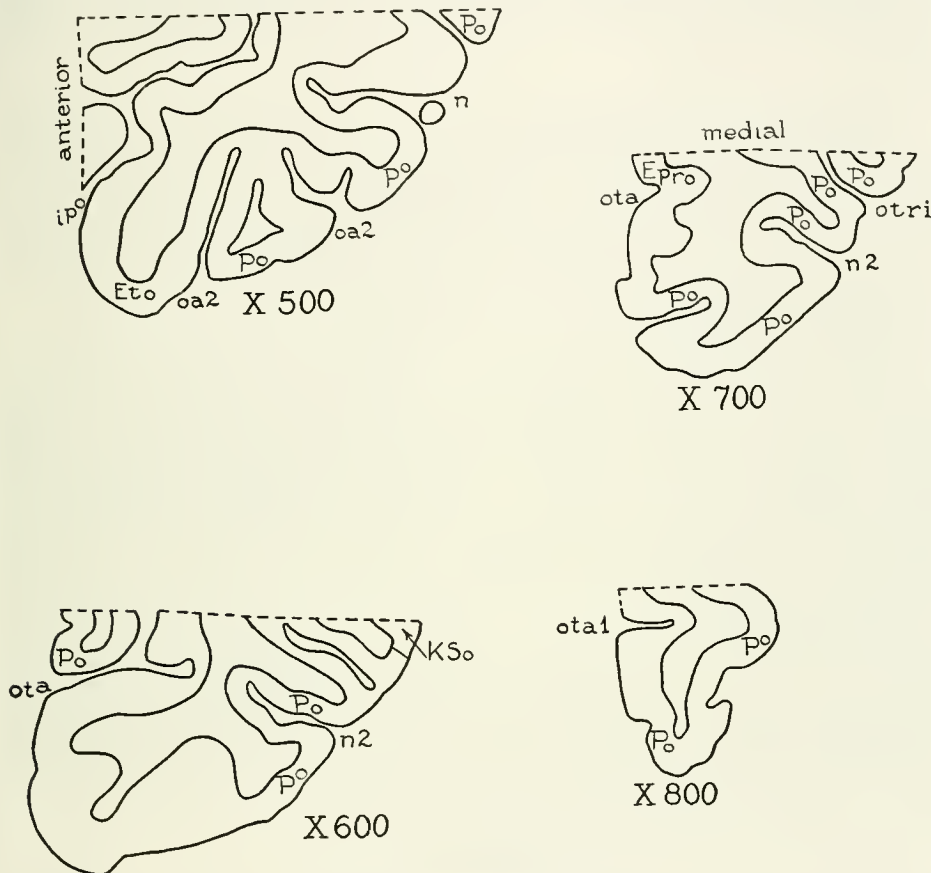

FIG. 59. Cross sections of Block X.

otrs and *oa2* the cortex is much similar but over the gyrus on the angle between the lateral and inferior surfaces of the lobe, just posterior to sulcus praeoccipitalis (*ipo*), the cortex is very thick (2.0 mm.) and has the characteristics described in the preceding section for the corresponding location.

Section 500. Fig. 59.

At the posteromedial extremity the cortex is of pronounced parastriate type, thickness 1.35 mm. On the second gyrus beyond it, between *n* and *oa2*, the cortex is still definitely parastriate and measures 1.45 mm. On the next gyrus it measures 1.54 mm. but is still parastriate, although the pyramids in *iiic* are smaller and *v*

has more cells but no large spheroidal ones. Over the gyrus at the angle between the inferior and lateral surfaces, between *oa2* and *ipo*, however, the cortex is quite different. It measures 2.0 mm. in thickness, outer main layer 0.7 mm., inner granular layer 0.1 mm., inner main layer 1.2 mm. The pyramids of *iiic* are larger than those of *iiia* and *b* but do not exceed 26 x 16 μ; most of them are about 21 x 13 μ. There are numerous pyramids of *v* of approximately the same size which tend to accumulate in the middle of *v*, giving it an appearance of three sublayers of which *va* and *c* are relatively empty. The fusiform cells of *via* are as large and numerous as the pyramids of *iiic* and *vb*. This is temporo-occipital cortex of general eulaminate type.

Section 600. Fig. 59.

At the posteromedial extremity of the cortex in this section is a small bit of unmistakable striate cortex. It gives way abruptly to cortex of pronounced parakoniose type measuring only 1.25 mm. in thickness. This cortex continues on the other gyri measuring at various places when cut parallel to the columns, 1.4, 1.2, 1.45, 1.6, 1.7, 1.4 mm. At both extremities of the section the cortex is clearly of parakoniose type. In the intermediate zone the cortex is cut rather diagonally or frankly tangentially and cannot be surely identified.

Section 700. Fig. 59.

Most of this cortex is clearly of parakoniose type but at the anteromedial extremity beyond *ota* the cortex measures 2.0 mm. in thickness, the pyramidal cells of *iiic* are small, the radiations are slender and *v* is better filled. This we have labeled ᴇ*pro*. Except for this gyrus, the cortex, wherever it is cut parallel to the radiations on the crowns, measures 1.54, 1.60, 1.70, 1.45 mm. In the sulci it measures 1.54, 1.30, 1.35, 1.60, 1.40 mm. The pyramidal cells of *iiic* are large, up to 42 x 26 μ and there are some large rounded cells also, 29 x 18 μ, in the relatively empty *v*.

Section 800. Fig. 59.

Most of this section is cut too tangentially to read but in places it can be seen that the cortex approaches parastriate type. At the posteromedial extremity it measures 1.52 mm. in thickness, the outer main layer 0.65 mm., the inner granular 0.12 mm., and the inner main layer 0.75 mm. The inner granular layer is sharply defined and filled by columns of granules of uniform size. There are occasional large cells in the rather empty *v*. The radiations are coarse up to *iiia*.

<div align="center">BLOCK XI (Fig. 60)</div>

Section 1000. Fig. 61.

The cortex posterior to *prcs2* is of simple agranular precentral type, measuring more than 2.45 mm. in total thickness. It contains pyramids measuring up to 39 x 21 μ. Some of these large pyramids are about where one would expect *iiic* and others lie deeper.

Between *prcs2* and *fs* the cortex is entirely similar, measuring more than 2.45 mm.

Over the gyrus between *fs* and *fs2* the cortex is cut diagonally but can be seen to have a faint internal granular layer about 1.0 mm. below *i*. It measures about 2.15 mm. in total thickness.

Anterior to *fs2* the cortex has a well-developed internal granular layer. Just anterior to this sulcus the cortex measures 1.85+ mm., outer main layer 0.77

mm., inner granular layer 0.15 mm. The boundary between *i* and *ii* is not sharp. There is no definite external granular layer but, just under *i*, there is a dense layer of small pyramids mingled with numerous granules. This we may call *ii* + *iiia*. Layer *iiib* and *iiic* contain more scattered larger pyramids, those of *iiic* being often as large as 32 x 18 μ. Layer *iv* is well filled with granules, plus scattered small pyramids and those near *v* are more heavily stained. In *v* the pyramids reach a size equal to those in *iiic* and are more numerous near *iv* which produces a light *vb* and a tendency to a dark band formed by *ivb* and *va*. This band is, however, not
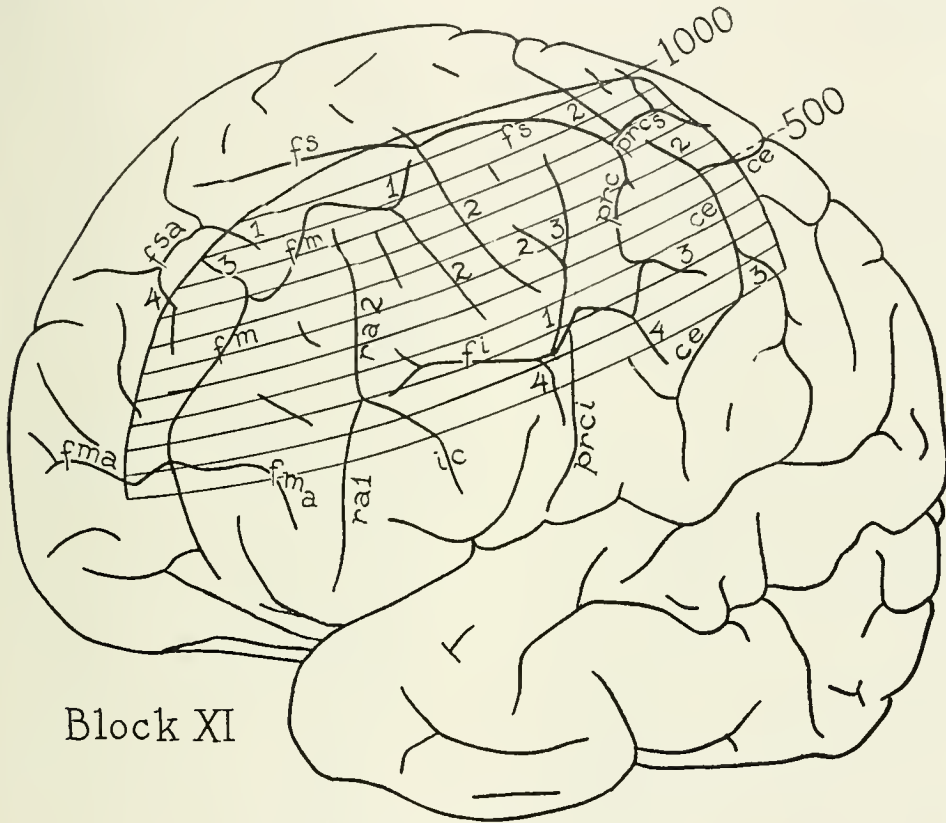

Fig. 60. Position of sections of Block XI.

so definite as in the superior parietal lobule. The cells of *vi* are smaller and more irregular than those of *v*. This is general eulaminate cortex (ε*fs*).

Further forward the inner granular layer is slightly thicker and the pyramids of *iiic* and *v* slightly smaller but the cortex still measures 2.0 mm. or more, outer main layer 0.8 mm.

Section 900. Fig. 61.

The cortex posterior to *fs* is of the simple agranular precentral type described in section 1000, except that, in the posterior wall of *fs* over the buried gyrus, there is a faint discontinuous inner granular layer.
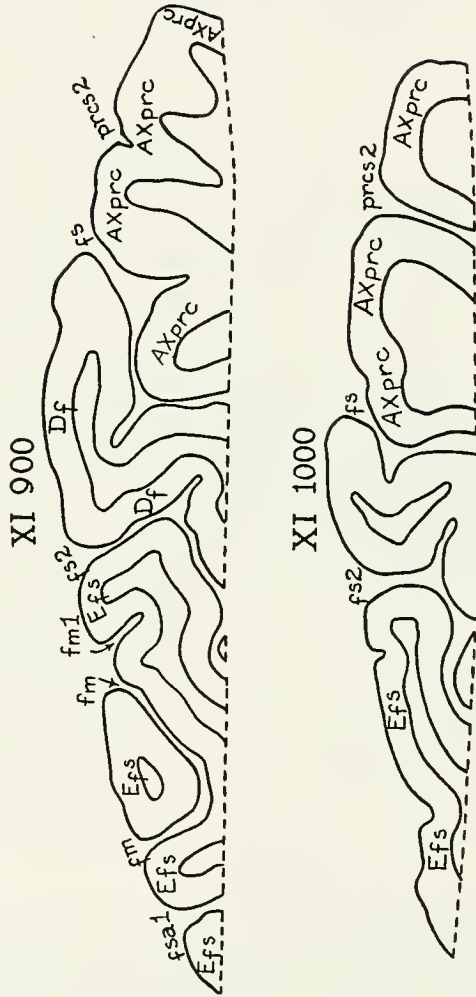
Fig. 61. Cross sections of Block XI.

Between *fs* and *fs2* the cortex is cut parallel to the columns in places. It measures about 1.85+ mm., outer main layer 0.9 mm., inner granular layer thin (0.06-0.1 mm.) but continuous, *v* in two sublayers, *va* with most of the cells and *vb* relatively empty, *vi* also in two layers with most of the cells in *via*, inner main layer 0.77+ mm. The inner margin of *vib* is vague. The largest pyramids are in *iiic*, many of them up to 29 x 16 μ, those of *v* generally slightly smaller. This is frontal dysgranular cortex (D*f*).

Between *fs2* and *fm1* on the narrow gyrus the cortex differs only in the slightly thicker *iv* (0.12-0.15 mm.).

Between *fm* and *fsa1* the cortex measures 1.7 mm., outer main layer 0.7 mm., inner granular layer 0.18-0.25 mm., otherwise unchanged.

All of the cortex anterior to *fs2* is of general eulaminate type (E*fs*).

Section 800. Fig. 62.

The cortex behind the tip of *fi3* is simple agranular precentral beyond which a faint internal granular layer begins and gradually increases in thickness until it measures 0.1 mm. on the posterior lip and wall of *fs2*. Anterior to *fs2*, *iv* thickens still more. Between *fs2* and *fm2* the inner granular layer measures 0.12 mm., total thickness 1.7 mm., outer main layer 0.86 mm.

Anterior to *fm2* the cortex is much the same. Between *fm* and *fm3* the total thickness is 1.54 mm., outer main layer 0.6 mm., inner granular layer 0.15.

All of this cortex anterior to *fs2* is of general eulaminate type but the thickness of *iv* increases anteriorly.

Section 700. Fig. 62.

Behind *fi3* the cortex is agranular precentral, measuring 2.5+ mm. There are occasional large cells at about the level of *iiic* measuring 47 x 24 μ and one deeper lying, measuring 66 x 24 μ, just back of *ce2*. On the anterior wall of *ce2* there are three large cells measuring 47 x 24, 47 x 31, and 45 x 24 μ at about the level of *iiic* and one deeper lying, measuring 53 x 26 μ. On the crown between *prc* and *fi3* there are no cells of this caliber but, on the posterior wall of *prc*, there are scattered big cells of this type. This is gigantopyramidal cortex (AG*prc*).

Anterior to *prc* the cortex measures 1.85+ mm. There is only one large cell, 47 x 34 μ on the anterior wall of *fi3* and another, about the same size in its anterior lip. Both appear to be about the level of *iiic*. The other pyramids, both of *iii* and *v*, do not surpass 34 x 24 μ. This is simple agranular precentral cortex (AX*prc*).

Between *fi3* and *fs2* the cortex is of the same type over the posterior half of the crown but anteriorly thins to about 1.7 mm. and develops a feeble internal granular layer which becomes more definite on the posterior wall of *fs2*. This is dysgranular cortex (D*f*).

On the anterior wall of *fs2* the cortex measures 1.85 mm., outer main layer 1.11 mm., inner granular layer 0.12 mm., inner main layer 0.62 mm. On the crown of the narrow gyrus between *fs2* and *fm2* the cortex measures 1.54 mm., outer main layer 0.65 mm., inner granular layer 0.15 mm., inner main layer 0.74 mm. The pyramids of *iiic* do not exceed 26 x 15 μ, those of *v* are generally smaller and sparse. Between *fm2* and *ra2* the cortex is identical. Between *ra2* and *fm* it is the same except that the pyramids of *iiic* and *v* seem slightly smaller. Between *fm3* and *fsa4* the cortex is practically identical except that *iv* is slightly thicker. This is all general eulaminate cortex (E*fs*).
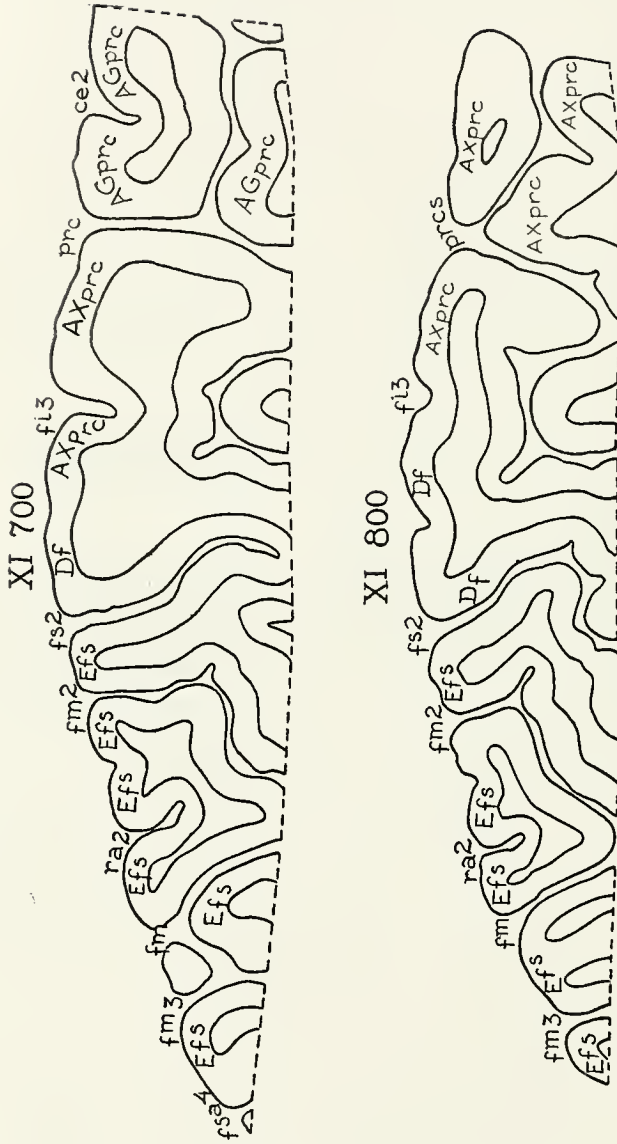
FIG. 62. Cross sections of Block XI.

Section 600. Fig. 63.

Posterior to *ce2* the cortex contains numerous deep lying giant cells of Betz. The thickness of the cortex varies from 3.1–1.4 mm. at the bottom of *ce2*. There is only one large pyramid on the anterior wall of *ce2* measuring 58 x 31 μ and none anterior to it until one reaches the posterior wall of *prc* where there is a solitary pyramid of about the same size.

Anterior to *prc* the agranular cortex continues to *fi3* with pyramids not exceeding 37 x 24 μ.

Anterior to *fi3* a thin discontinuous internal granular layer appears.

Anterior to *fi2* the internal granular layer is definite and continuous.

Between *fm2* and *ra2* the cortex is of the superior frontal type described in section 1000, total thickness 1.85+ mm., outer main layer 0.93 mm., inner granular layer 0.21 mm., inner main layer 0.7+ mm.

Between *fm* and *fsa4* the cortex thins to 1.54 mm. but is not otherwise different.

Section 500. Fig. 63.

The cortex posterior to *ce* is cut too tangentially to read.

Anterior to *ce* it is agranular as far forward as *fi3*. On the crown there is only one Betz cell about halfway between *ce* and *prc*. Numerous Betz cells are contained in the buried cortex under the postcentral blob but on the anterior wall of *ce*, there is only one and that near the bottom. On the anterior wall of *ce* are also the only two large pyramids about the level of *iiic*; they measure 47 x 32 μ.

Anterior to *fi3* a faint inner granular layer appears.

Anterior to *fs2* the cortex is of general eulaminate type. Between *fs2* and *fm2* it measures 1.4 mm., between *fm2* and *ra2* as much as 2.8 mm., but is cut diagonally; between *ra2* and *fm* it varies from 1.2–1.85 mm.; anterior to *fm* it measures 1.7 mm. Throughout this zone the cortex is of the same type but the cells are smaller and *iv* relatively thicker as one progresses anteriorly. The cortex is often thinner over the crowns than on the walls of the gyri.

Section 400. Fig. 64.

The superficial cortex behind *ce* is covered by parakoniocortex (P*poc*). It is cut diagonally over the crown which measures 1.66 mm., outer main layer 0.74 mm., inner granular 0.18 mm., inner main layer 0.74 mm. There are large pyramids in *iiic* and *v* measuring 43 x 32 μ.

The posterior wall of *ce* is covered by koniocortex (K*poc*) measuring 1.4 mm.

Anterior to *ce* is agranular precentral cortex with Betz cells in the anterior wall, numerous in the depth, scattered up to the anterior lip.

The simple agranular cortex extends as far forward as *prc*. Throughout this area there are scattered large pyramids, up to 47 x 32 μ, in both *iiic* and *v* but there is no zone in which large pyramids are conspicuous in *iiic*, nor is there any point where the cortex suddenly becomes thinner and the columns finer. The cortex measures 2.45 mm. on the crown of the gyrus.

Anterior to *prc* the cortex narrows to 1.6 mm. and a faint internal granular layer is present.

Anterior to *fi1* the cortex thins at one point to 1.4 mm. and the internal granular layer is more distinct.

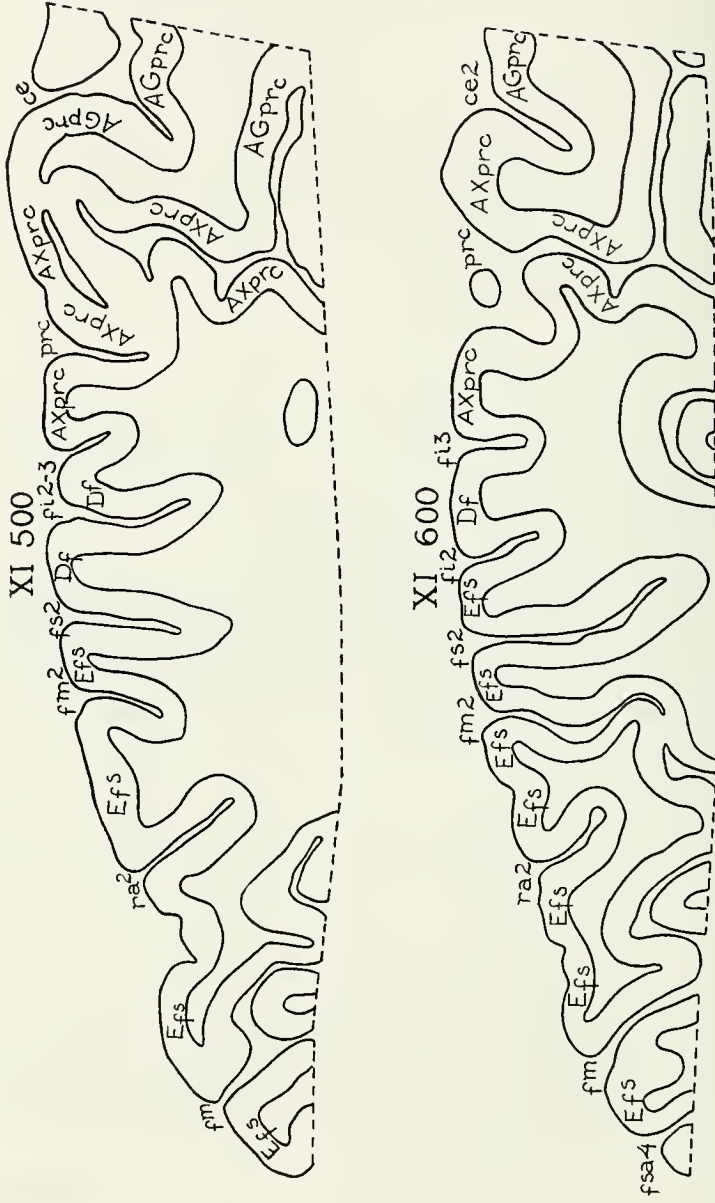Anterior to *fs2* the cortex is much the same and measures 1.54 mm.

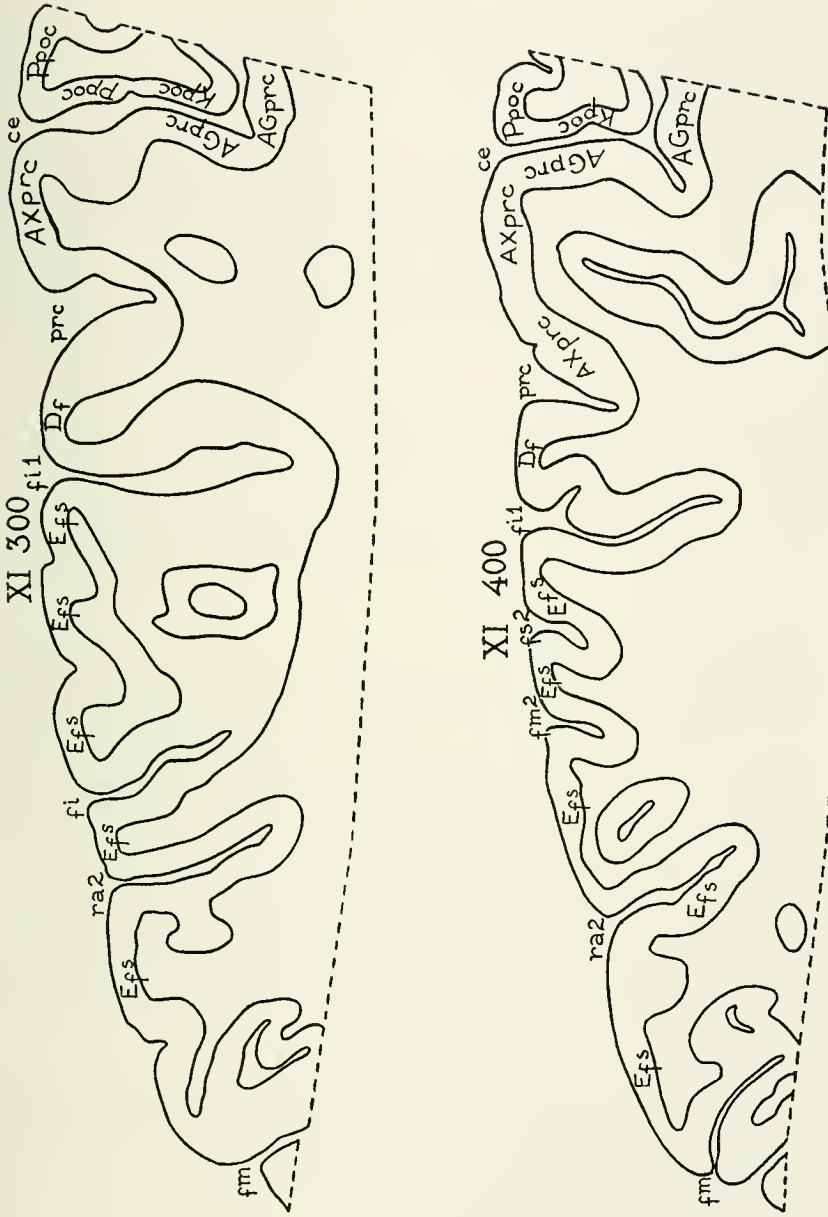FIG. 63. Cross sections of Block XI.

FIG. 64. Cross sections of Block XI.

Anterior to *fm2* the cortex varies in thickness from 1.2–1.85 mm. but is not otherwise different.

Anterior to *ra2* one sees the same variation in thickness from 1.4–2.0 mm.

Anterior to *fm* the cortex cannot be read.

Throughout this zone from *fi1* forward the only change seen is that the cells of *iiic* and *v* become somewhat smaller (39 x 26 μ, posteriorly; 26 x 18 μ anteriorly) and *iv* thicker (0.12 mm. posteriorly; 0.18 mm. anteriorly).

Section 300. Fig. 64.

On the posterior wall of *ce* the boundary between koniose and parakoniose cortex has shifted inward. In the depth of *ce* are numerous Betz cells which do not extend up to the tangentially cut thickening of the anterior wall. Deep in this thickening the cortex measures 2.3 mm. Over the crown of the precentral gyrus the cortex measures 2.15 mm. The simple agranular cortex extends to *prc*. Within the agranular zone are numerous large pyramids in *iiic* and *v* but none above 39 x 21 μ and there is no zone in which large pyramids in *iiic* are conspicuous either by their size or number.

Just behind *fi1* the cortex narrows to 1.6 mm. and a faint internal granular layer is seen. This is more distinct anterior to *fi1* (where the cortex measures barely 1.54 mm.), and grows thicker as one goes forward, measuring 0.1 mm. just posterior to *fi*. Between *fi* and *ra2* the cortex measures 1.4 mm. Anterior to *ra2* it measures 1.7 mm., outer main layer 0.74 mm., inner granular 0.12 mm., inner main layer 0.84 mm. The cortex here seems also more densely populated and *v* more evenly filled.

Section 200. Fig. 65.

Posteriorly conditions are essentially similar to those in section 300. Both the koniocortex and the Betz cells are entirely buried in *ce* and do not reach out to the lips. There are two conspicuously large pyramids in *iiic*, widely separated, about 39 x 21 μ, on the crown of the precentral gyrus. The simple agranular cortex extends as far forward as *prc4*. The internal granular layer develops gradually in the complicated irregular cortex between *prc4* and *fi1*. On the surface between *fi1* and *fi* the internal granular layer is well developed, also in all the cortex anteriorly.

Between *ra2* and *fm* the cortex is slightly different. Not only are the cells of *iiic* and *v* smaller but seem more numerous. Those in *v* are also better distributed. These changes give the cross section a more uniform and better populated appearance. Total thickness 1.85 mm., outer main layer 0.74 mm., inner granular layer 0.18 mm., inner main layer 0.93 mm. This is perhaps the vague variant which Economo called *FD∆*. We have still labeled it ᴇ*fs*.

Section 100. Fig. 65.

The koniocortex extends out to the posterior lip of *ce* as in section 400. The Betz cells fall just short of the anterior lip. The simple agranular cortex extends forward to *prc4*. Over the small gyrus between *prci* and *fi4* a faint internal granular layer is visible; it developed somewhere in the depths.

Just posterior to *ic* the cortex measures 1.4 mm., outer main layer 0.6 mm., inner granular 0.18 mm., inner main layer 0.62 mm. The pyramids of *iiic* and *v* do not exceed 26 x 16 μ; those of *v* tend to concentrate near *iv*. This is the typical eulaminate cortex.
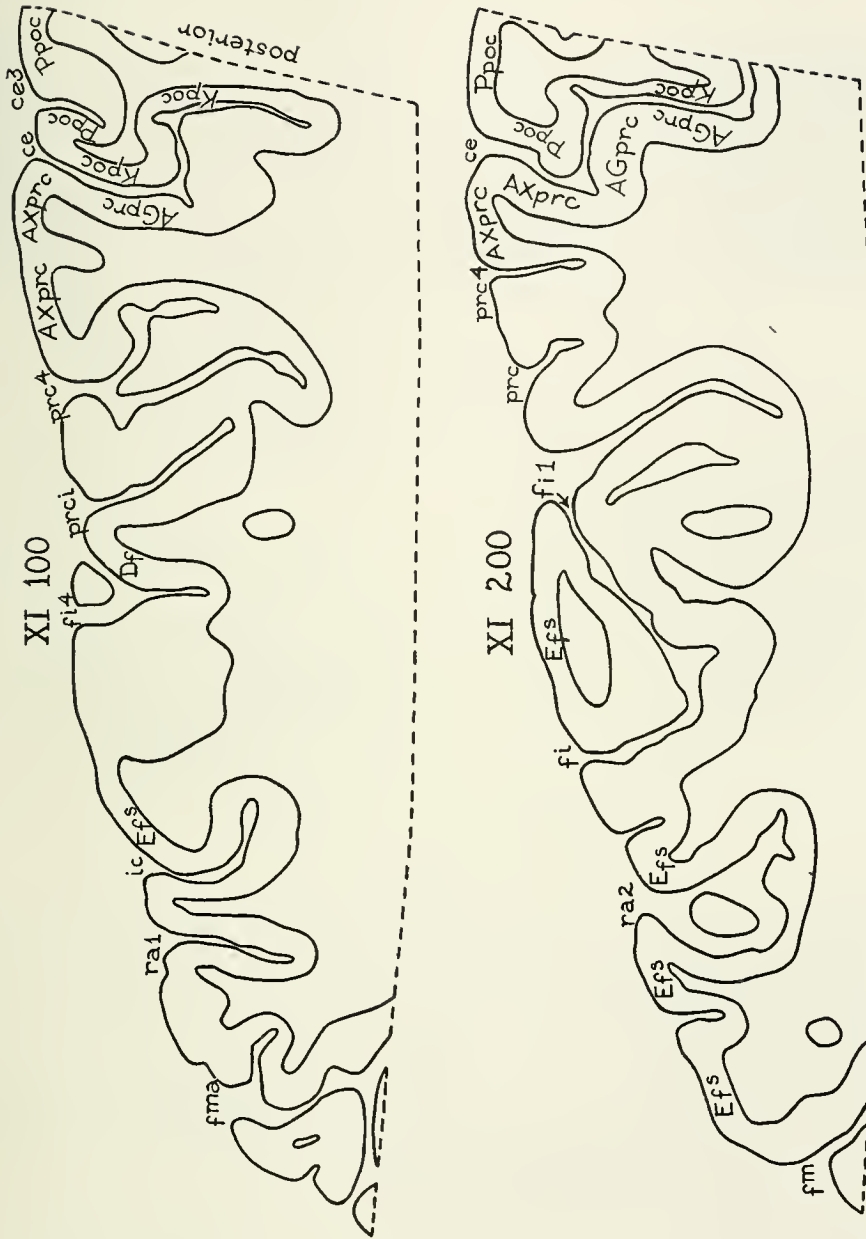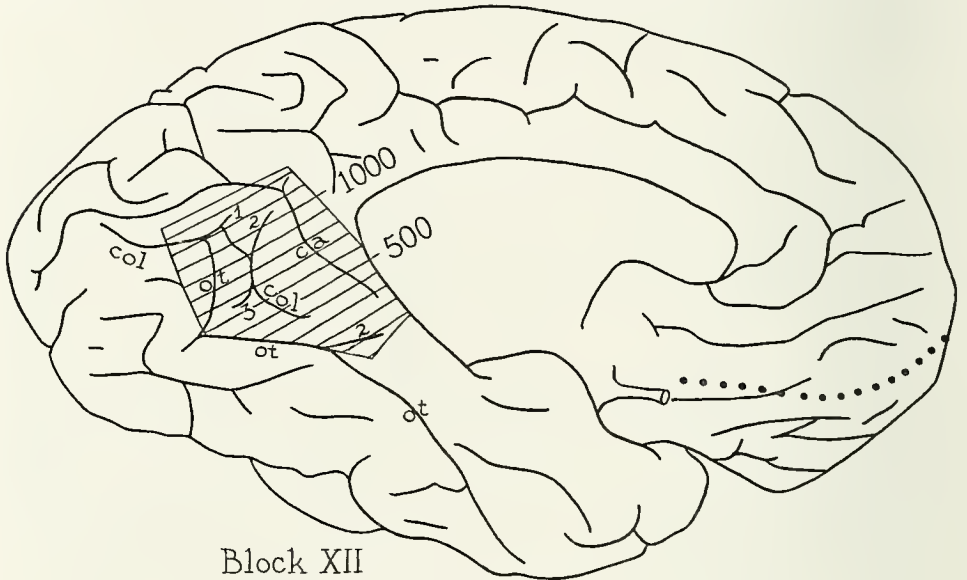
Fig. 65. Cross sections of Block XI.

Between *ic* and *ra1* the cortex is cut diagonally but seems to be of the same type.

Anterior to *ra1* the cortex is cut too irregularly to be read clearly but seems consistent with the description given for section 200.

BLOCK XII (Fig. 66)

Section 1200. Fig. 67.

All of the gyrus behind and below the calcarine fissure (*ca*) is covered with striate cortex measuring about 1.2 mm. in thickness; it covers also the posterior wall of the fissure but not the anterior.

The superficial cortex anteriorly is covered by a cortex 1.85 mm. in thickness, outer main layer 0.6 mm., inner 1.1 mm. The pyramids of *iiic* are only of moderate size (21 x 16 μ). Layer *v* is well filled with many pyramids equal to those of *iiic*.

FIG. 66. Position of sections of Block XII.

There is a lighter *iva* and darker *ivb* but not much tendency for *v* to subdivide. This is certainly not parastriate cortex, nor is it definitely superior parietal. It is called preoccipital (εpro).

Section 1100. Fig. 67.

The posterior gyrus is covered by cortex of parastriate type but quite thick (1.7 mm.), outer main layer 0.53 mm. There are many large pyramids in *iiic* and also in *v* which is unusually thick (0.32 mm.) and relatively empty. Anterior to *col* begins striate cortex which extends about halfway down the postero-inferior wall of *ca* where it gives way to parastriate cortex.

On the anterosuperior wall of the calcarine fissure the cortex is again quite thick (1.85 mm.), outer main layer 0.64 mm., inner 1.1 mm. The margin between *i* and *ii* is smooth, distinction between *ii* and *iiia* is impossible, the cells of *iiic* are small, there is a distinct *iva* and *ivb* but *iva* + *va* form a broad band (width 0.32 mm.) followed by a relatively empty *vb* and a better filled *iva*. The columns

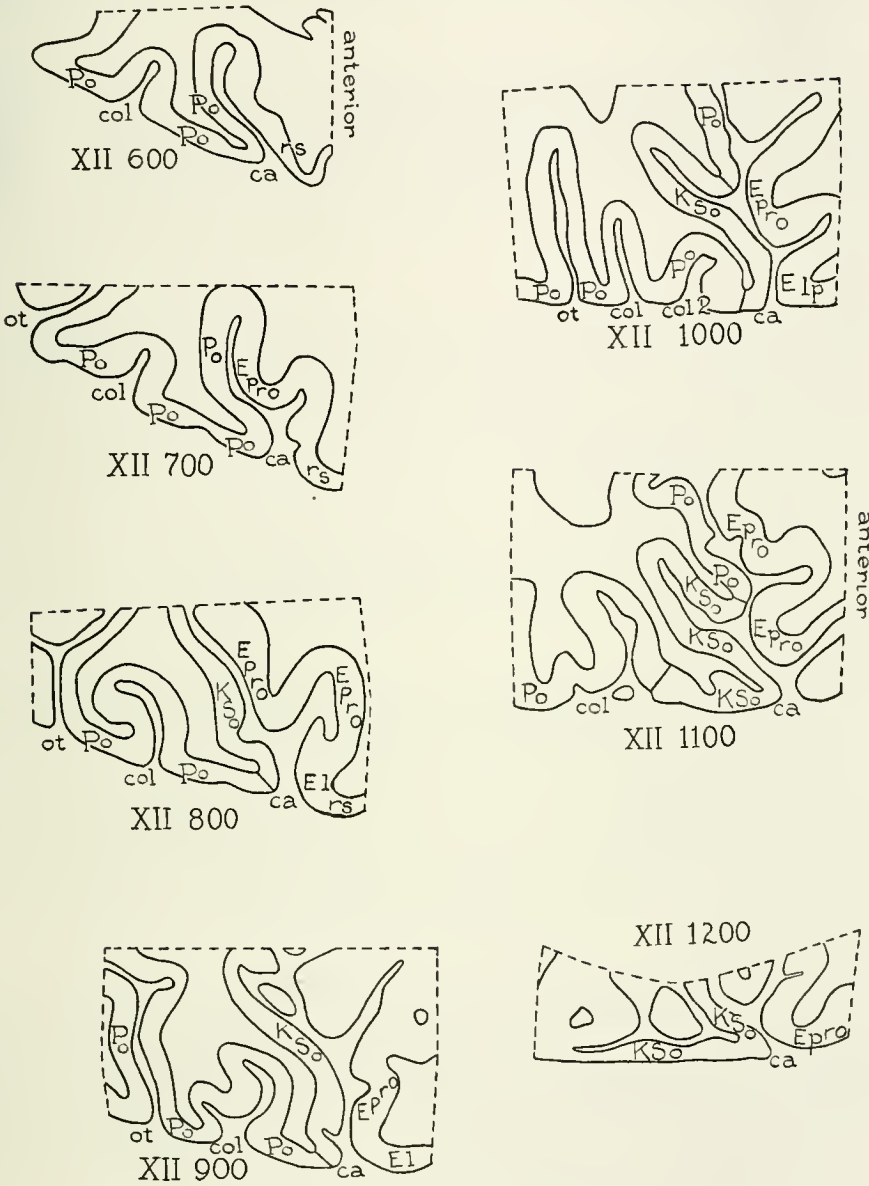are broad and the whole cortex gives one an impression of poverty. This is pre-occipital cortex (Epro).

FIG. 67. Cross sections of Block XII.

Section 1000. Fig. 67.

Between *ot* and the calcarine fissure (*ca*) there are three narrow gyri. The posterior is covered by cortex of parastriate type, measuring 1.08 outer main layer 0.4 mm., inner 0.56 mm. There are large pyramids in *iiic* and *v* and coarse columns. The cortex of the middle gyrus is cut obliquely but appears to be also parastriate, if one may

judge by the large cells of *iiic*. In the middle of the third gyrus the cortex changes to striate type which continues down the anterior wall around a posterior shelf and then goes over onto parastriate cortex at its deeper lip which latter continues into the depth.

The anterior wall of the calcarine fissure is covered by the cortex described in section 1100, thickness 1.85 mm. Shortly after the cortex emerges onto the surface anterior to *ca* it changes subtly, *iiib* becoming better filled, the cells of *iiic* still smaller so that a cell gradient is scarcely discernible and *v* fills evenly with small pyramids. This is posterior limbic eulaminate cortex (E*lp*).

Section 900. Fig. 67.

The cortex behind and on the posterior wall of *ot* is of parastriate type (thickness 1.4 mm.).

Between *ot* and the calcarine fissure (*ca*) are two gyri of which the posterior is covered by parastriate cortex (thickness averaging about 1.1 mm.) and the anterior with slightly thicker (1.3 mm.) parastriate cortex up to the posterior lip of *ca*.

The entire postero-inferior wall of the calcarine fissure (insofar as it is present in this section) is covered by striate cortex; the anterosuperior wall is covered by the cortex before described in section 1100 (at least in its more superficial portion where it can be read).

On the surface, as described in the preceding section, the cortex changes gradually, anteriorly becoming more uniform throughout, so that it is difficult to distinguish the layers, and very thick (2.0 mm.), but the thickness may be due to the obliquity of the section.

Section 800. Fig. 67.

The cortex in this section differs in no essential respect from that of the preceding section in its retrocalcarine region. The striate cortex begins at the postero-inferior lip of the calcarine fissure and extends to its depth.

The anterior wall of the calcarine fissure is covered by nondescript preoccipital cortex in its deeper portion. In its outer portion it is covered by posterior limbic cortex as described in section (1000). Over the surface anterior to *ca* the cortex changes rather rapidly to become agranular with a dense layer of larger cells about where *v* should be. This is now retrosplenial agranular cortex.

Section 700. Fig. 67.

Posterior to *ca* are two broad gyri, of which the posterior between *ot* and *col* is covered with cortex of parastriate type but with a rather thick inner main layer (0.77 mm.). The anterior gyrus is covered by thinner parastriate cortex (inner main layer 0.56 mm.). The posterior wall of *ca* is covered by parastriate cortex in which are huge cells in *iiic*. On the anterior wall of *ca* the cortex measures 1.7 mm., outer main layer 0.56 mm., inner 1.0 mm. Layer *v* is well filled and the pyramids of *iiic* are small. But *iiib* is relatively empty and there is a distinct cell gradient in *iii*. It cannot be called limbic cortex; we have labeled it E*pro*.

Anterior to *ca* are the retrosplenial formations, becoming granulous toward the splenium.

Section 600. Fig. 67.

The posterior wall of the calcarine fissure and all the retrocalcarine surface is covered by parastriate cortex. The cells of *iiic*, however, in the gyrus posterior to *col* are larger than those anteriorly.

If one begins at the splenium and goes backward the retrosplenial formations, first koniocortex and then agranular cortex, give way on the anterior wall of *ca* to nondescript cortex.

Section 500. Fig. 68.

The posterior wall of *ca* looks like parastriate cortex. The anterior wall is cut too diagonally in its deeper portion to be read, but its outer portion and the cortex anterior to it is covered by retrosplenial formations.

The superficial cortex behind *ca* looks somewhat like parastriate cortex but the cells of *iiic* are of only medium size and *v* is well filled. The cortex measures 1.4 mm., outer main layer 0.53 mm., inner 0.71 mm.
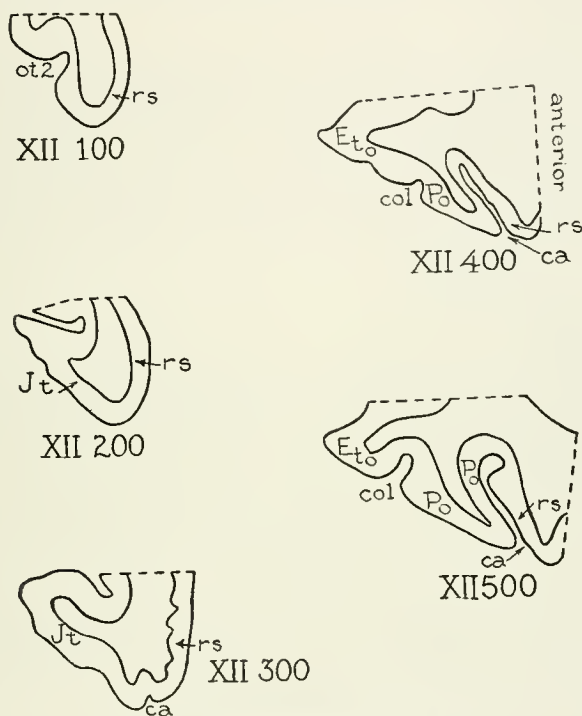

Fig. 68. Cross sections of Block XII.

On the most posterior gyrus the cortex is much thicker (1.54 mm.) with delicate columns and a well filled *v*. The cells of *v* and *vi* are about the same size but can be distinguished by shape. There is a cell gradient in *iii* but the cells of *iiic* reach only a medium size.

Section 400. Fig. 68.

Anterior to *ca* is retrosplenial formation, and on most of the anterior wall. On the posterior wall of *ca* and over the surface posteriorly is a cortex of parastriate type, very thin (0.77 mm.) with only medium sized pyramids in *iiic*.

The cortex posterior to *col* is as described in 500.

Section 300. Fig. 68.

The calcarine fissure ends. Anterior to it the cortex is retrosplenial. Posterior

to it the cortex is thin (1.02 mm.), inner main layer 0.31 mm., outer 0.62 mm. Layer *ii* is patchy and *iii* is rather empty. Layer *v* is pale with most of its cells near *iv*, which is poorly developed. Farther back the cortex is thicker (1.64 mm.) of the type described in section 500.

Section 200. Fig. 68.

The anterior surface is covered by retrosplenial formations, the inferior by a cortex which is thicker (1.4 mm.), outer main layer 0.58 mm. Layer *ii* is patchy, *iii* is lighter with scarcely any cell gradient. Layer *ivb* is darker and is combined with *va* to form a dark band followed by a light *vb*. Layer *via* contains closely packed cells larger and much more numerous than those of *iiic* forming another dark band. Layer *vib* is much lighter. This is juxtallocortex (*jt*).

Section 100. Fig. 68.

The anterosuperior surface and the medial portion of the latero-inferior surface almost as far as the spur of the fissura occip.-temp. (*ot2*) is covered by retrosplenial formations. Lateral to the spur the cortex measures 1.6 mm., outer main layer 0.62 mm., inner 0.9 mm. The boundary between *i* and *ii* is ragged. Layer *ii* is patchy. There is a cell gradient in *iii* but the cells of *iiic* do not exceed 26 x 16 μ. Layer *iiib* is rather empty. Layer *v* is filled with pyramids about the size of those in *iiic* and larger than the cells of *vi*.

<div align="center">BLOCK XIII (Fig. 69)</div>

Section 100. Fig. 70.

The cortex above the anterior spur of the transverse parietal sulcus (*pt1*) measures 1.6 mm. in thickness, outer main layer 0.68 mm., inner 0.77 mm., and is well laminated. The margin between *i* and *ii* is sharp and rather smooth. Layers *ii* and *iiia* are of about the same density but there are more pyramids in *iiia* and they are slightly larger than the granules of *ii*. Layer *iiib* contains sparse pyramids of slightly larger size. The pyramids of *iiic* are still larger, ranging up to 39 x 21 μ. Layer *iv* is clearly divided into *iva* with very small cells and a denser *ivb* containing many small pyramids. Layer *v* is also divided into two sublayers of which *va* contains more and larger pyramids about 24 x 13 μ, larger than the cells of *via* which are, however, much more numerous. This structure makes noticeable a dark band (*ivb* + *va*) bordered by two light streaks, characteristic of the superior parietal lobule.

Between *pt1* and the intraparietal sulcus (*ip*) the cortex is cut diagonally but appears to be of the same type. So are the walls of *pt1*. The walls of *ip* are also cut diagonally.

The sulcus below *ip* is also cut diagonally but the cortex on the upper wall of *pja* is cut parallel to the radiations. Here the cortex measures 1.64 mm., outer main layer 0.86 mm., inner 0.62 mm. Its only difference from that previously described above *ip* is that the band (*ivb* + *va*) is scarcely discernible. This band fades out somewhere on the upper wall of *ip*.

The cortex on the lower wall of *pja* is identical. The remainder of the section cannot be read.

Section 200. Fig. 70.

The cortex above *pt1* is of the eulaminate superior parietal type measuring 1.54

mm. The outer margin of *ii* is rather irregular. There is a thin layer of small pyramids just under *ii* and with difficulty can be separated from it so that there is a broad clear band between it and the big pyramids of *iiic* which are mostly about 24 x 13 μ, but one huge pyramid is seen between *iiib* and *iiic* measuring 42 x 26 μ. The dark band of *ivb* + *va* is definite and *vb* is clear, so it is labeled EPs.

Below *ip* the cortex is of the type previously described, measuring 1.9 mm. in total thickness, outer main layer 1.0 mm., inner 0.77 mm. *v* is evenly filled with medium pyramids.
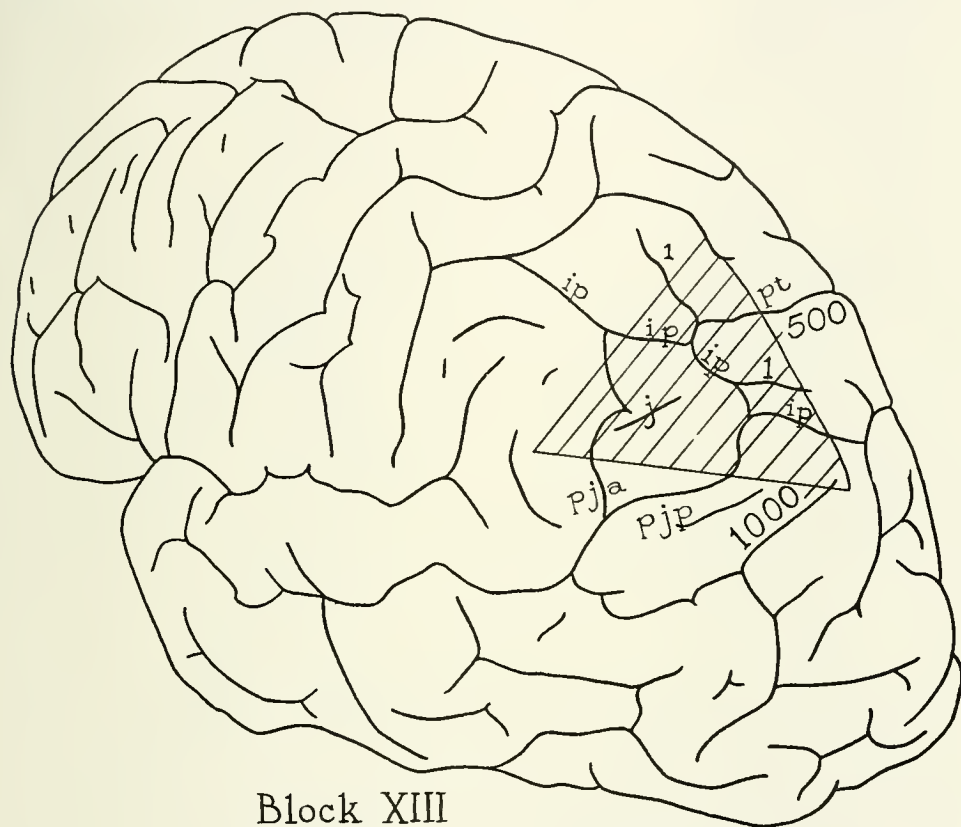
Block XIII

FIG. 69. Position of sections of Block XIII.

Below *pja* the cortex cannot be read.

Section 300. Fig. 70.

The cortex above *ip* cannot be read.

The cortex on the crown of the gyrus between *ip* and *j* is of the generalized eulaminate type but thinner than in the preceding section 200, measuring only 1.67 mm., outer main layer 0.77 mm., inner 0.74 mm.

On the gyrus below *j* the cortex is of the same type, total thickness 1.54 mm., outer main layer 0.65 mm., inner 0.74 mm. Layer *v* is evenly filled by small and medium pyramids. Those of *iiic* are larger, up to 26 x 16 μ.
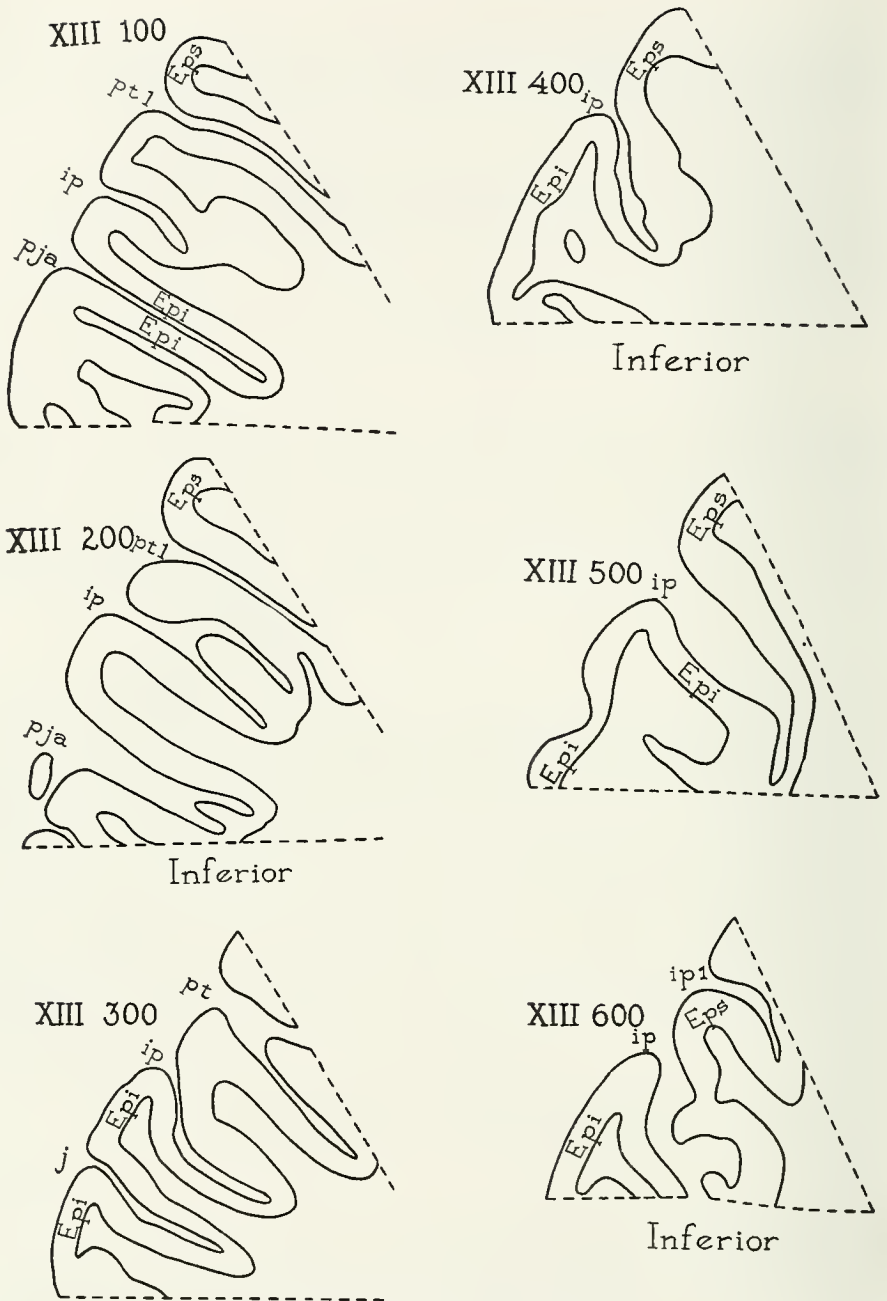
FIG. 70. Cross sections of Block XIII.

Section 400. Fig. 70.

Above *ip* the cortex is cut somewhat diagonally but the dark band characteristic of eulaminate superior parietal cortex can be seen. It measures 1.6 mm. in thickness.

Below *ip* the cortex does not differ from that of the preceding section 300, averaging about 1.54 mm. in thickness.

Section 500. Fig. 70.

Above *ip* the cortex measures 1.6 mm. and is of the eulaminate superior parietal type previously described.

Below *ip* the superficial cortex can be read only at the inferior extremity of the section. Here it measures 1.85 mm., outer main layer 0.86 mm., inner 0.86 mm. Layer *v* is evenly filled with small and medium pyramids. The pyramids of *iiic* range larger, up to 34 x 21 μ.

The cortex on the inferior wall of *ip* is identical.
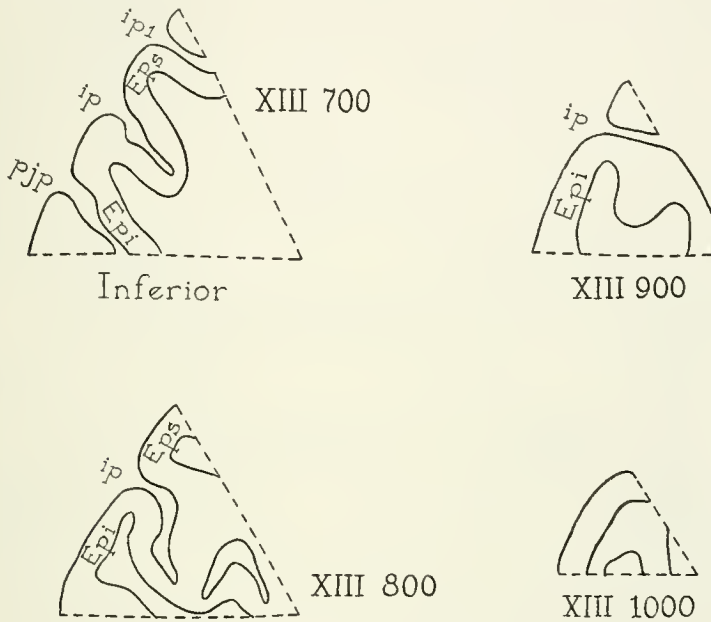
Section 600. Fig. 70.

FIG. 71. Cross sections of Block XIII.

Above *ip* the cortex measures 1.85 mm., outer main layer 0.77 mm., inner 0.93 mm. The band formed by *ivb* + *va* is very evident.

The cortex below *ip* measures 1.7 mm., outer main layer 0.71 mm., inner 0.83 mm. It is impossible to discover any difference from the cortex above *ip* except that the pyramids of *v* are a little smaller and better distributed.

Section 700. Fig. 71.

The cortex above *ip* measures about 1.5 mm., outer main layer 0.55 mm., inner 0.69 mm. The dark band of *ivb* + *va* is evident and *vb* is light.

On the crown of the gyrus below *ip* the cortex is cut too diagonally to read but on the upper wall of *pjp*, the cortex lacks the dark band.

Section 800. Fig. 71.

Conditions in this section are unchanged from 700. Above *ip* the cortex measures 1.5 mm. and is of eulaminate superior parietal type. Below *ip* the cortex measures

1.6 mm. and lacks the dark band of the superior region. Outer main layer 0.68 mm., inner 0.77 mm.
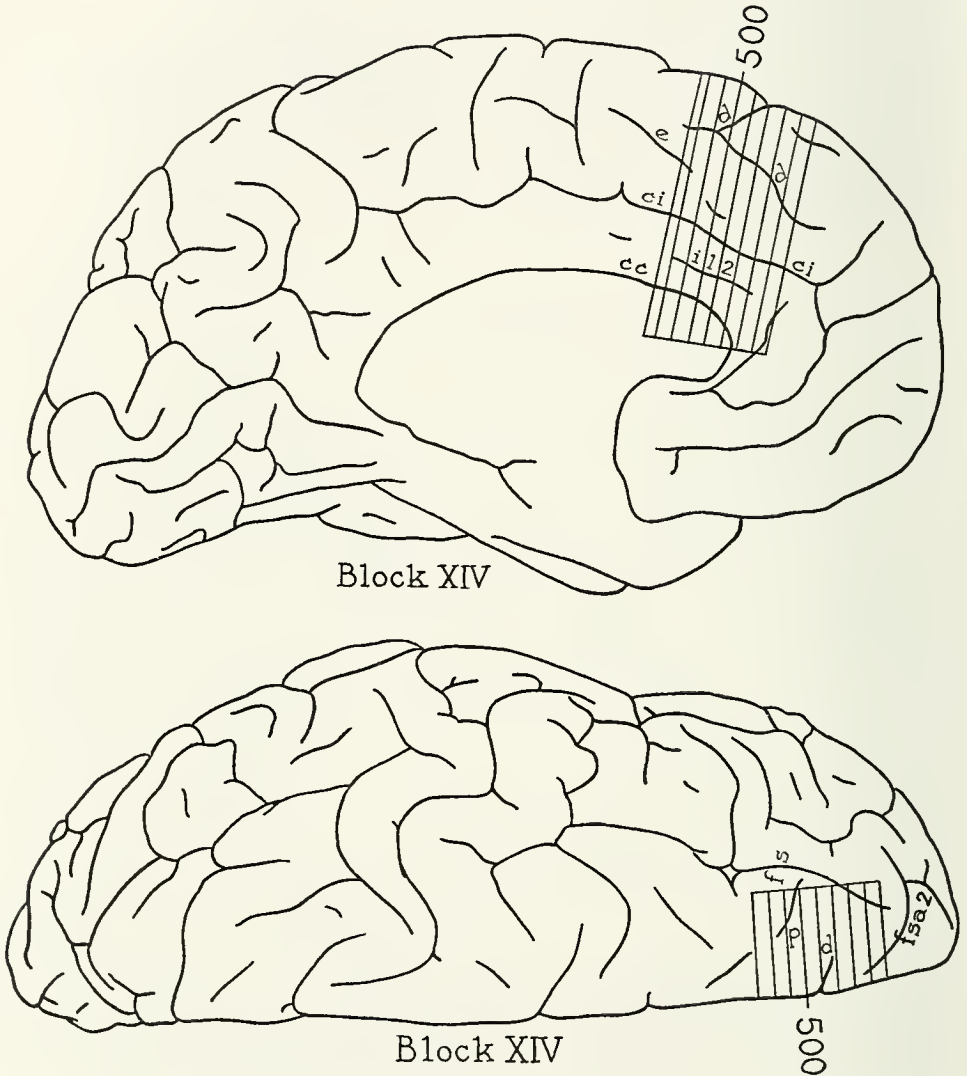
Section 900. Fig. 71.

FIG. 72. Position of sections of Block XIV.

The cortex below *ip* measures 1.74 mm., outer main layer 0.83 mm., inner 0.77 mm. It is of the generalized eulaminate type already described.

Section 1000. Fig. 71.

The cortex is cut too diagonally to read.

BLOCK XIV (Fig. 72)

We shall begin at the back and proceed forward.

Section 700. Fig. 73.
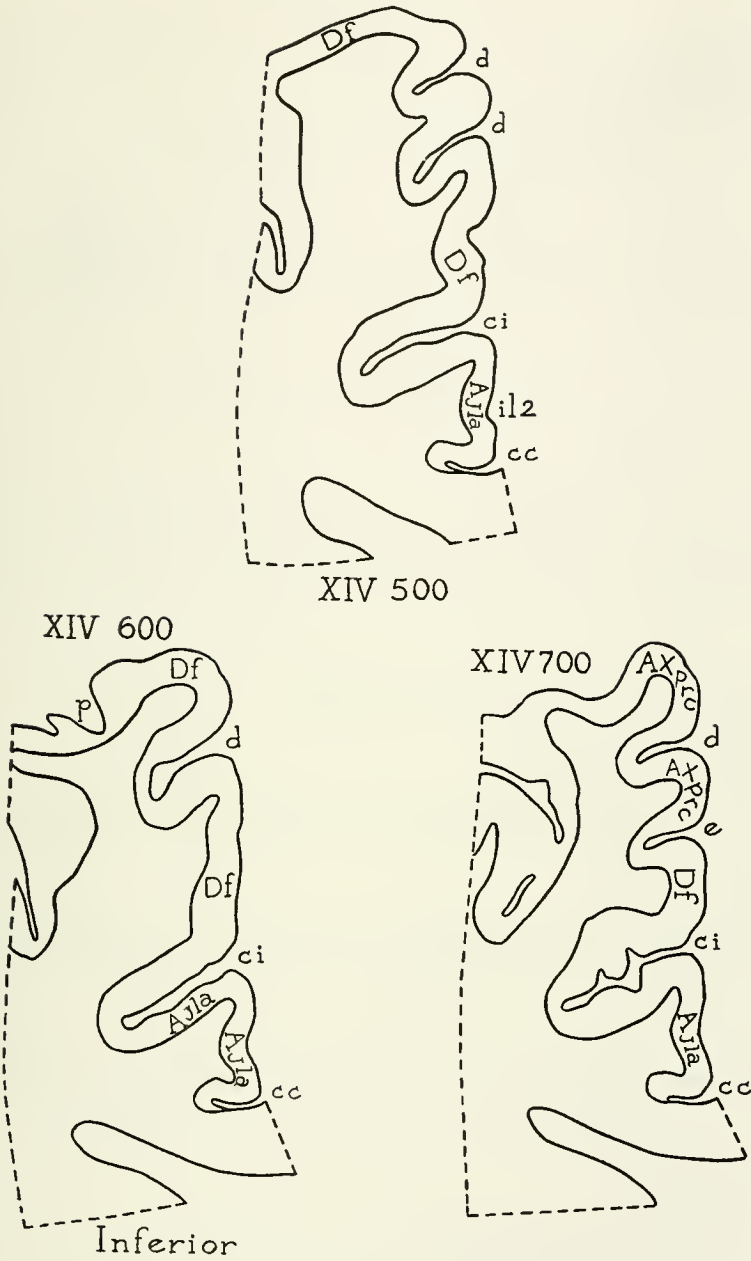
FIG. 73. Cross sections of Block XIV.

The cortex on the dorsal surface and extending on the medial surface to d measures 1.85+ mm. The largest pyramids, about 39 x 18 μ, lie about 0.8 mm. from the inner margin of i. Beneath i there are almost no granules. Beneath the layer of largest pyramids are a few scattered granules, but we have labeled it AXprc.

The cortex between d and e is identical; between e and ci are a few more granules (Df).

The cortex over the limbic gyrus is agranular anterior limbic (AJ*la*). That within the cingulate sulcus (ci) is cut too irregularly to read.

Section 600. Fig. 73.

The cortex on the dorsal and on the medial surface above ci is much the same. However, the thin internal granular layer is now distinct enough to justify labeling it D*f*.

On the dorsal wall of ci the cortex changes. Here the cells just beneath i are not so closely packed together and there is no deep layer of large pyramids so that the cross section has a more uniform appearance. There is also a thin, but definite and continuous internal granular layer. This cortex measures about 2.5 mm., outer main layer 0.93 mm.

The cortex on the lower wall of ci and over the surface of the limbic gyrus is agranular anterior limbic in type. It measures about 1.54 mm.

Section 500. Fig. 73.

In this section the cortex on the dorsal surface has a thin continuous internal granular layer. It measures about 1.85 mm., outer main layer 0.86 mm., inner granular layer 0.09 mm. The pyramids of v are larger than the cells of vi, more heavily stained and about the same size as those of *iiic* which measure around 32 x 21 μ. There is a denser zone just under i in which granules are mingled with small pyramids.

The remainder of the cortex above ci is much the same. Just above ci it measures about 2.15 mm. but is cut somewhat diagonally.

On the upper wall of ci the cortex resembles that described in section 600, and measures about 2.15 mm.

Over the crown of the limbic gyrus the cortex is anterior limbic agranular in type but in the lower wall of ci, there is a lighter layer of very small cells above the dense v.

Section 400. Fig. 74.

The cortex over the dorsal surface is of the same type as described in section 500, measuring about 1.85 mm. This type of cortex continues over the medial surface measuring, between the two branches of d, 1.7 mm., between d and ci, 1.85–2.0 mm.

In the lower wall of ci there are scattered larger pyramids up to 32 x 21 μ in *iiic*; the cells of v are larger and tend to concentrate just below iv. This is juxtallocortex J*fl*.

The cortex over the crown of the limbic gyrus does not differ from that described in section 500.

Section 300. Fig. 74.

The cortex of this section does not vary from that of section 400 except that the cortex described in the lower wall of ci now extends also over the dorsal half of the crown of the limbic gyrus, the agranular anterior limbic type occupying only the lower half. This tendency had begun already in section 400 but is here much clearer.

Section 200. Fig. 74.

In this section the cortex lateral to J*fs* can be seen clearly. It has a thick internal granular layer. This cortex measures about 1.85 mm., outer main layer 0.93 mm., inner granular layer 0.15 mm., inner main layer 0.77+ mm. The largest cells,

32 x 21 μ, are in *va* and there is a lighter, relatively empty *vb*. The cells of *vi* are smaller and more evenly distributed. Just beneath *i* are many granules mingled with
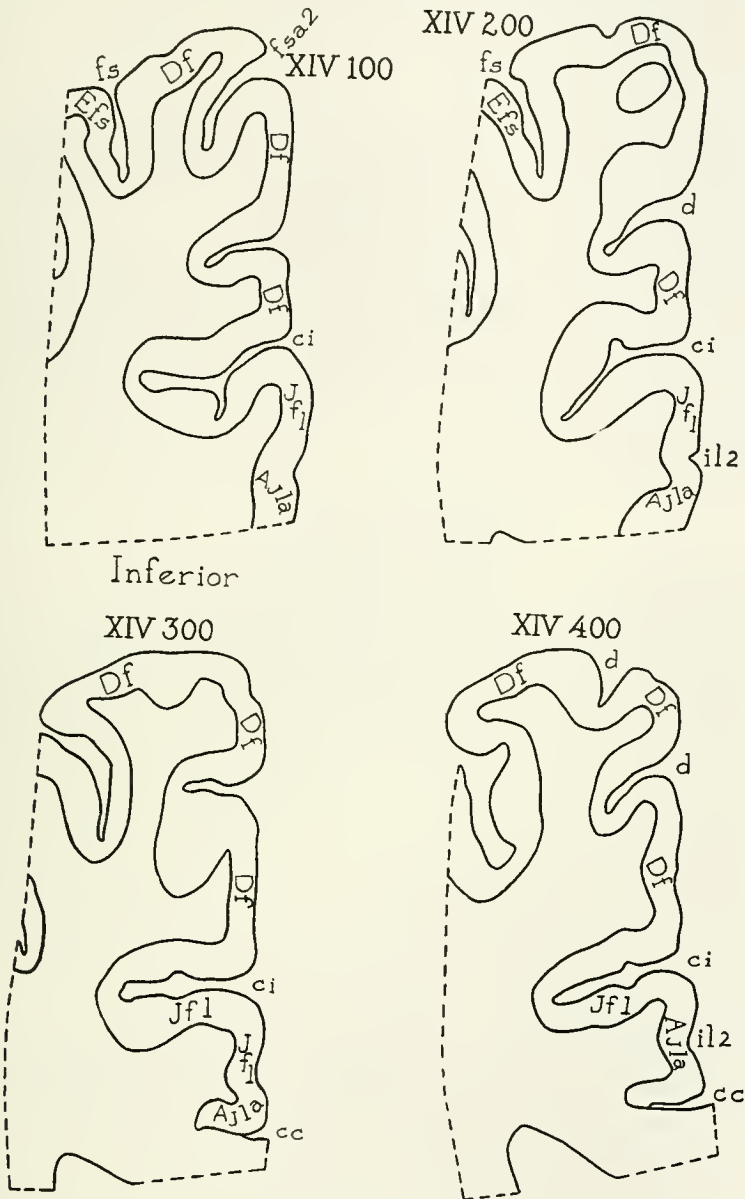

Fig. 74. Cross sections of Block XIV.

small pyramids. The pyramids of *iii* increase in size toward *iv* and those of *iiic* reach about 29 x 13 μ. This is generalized eulaminate cortex (E*fs*).

The remainder of the cortex on the dorsal and medial surface above *ci* is of the

type previously described with the inner granular slightly thicker. Its total thickness varies on the surface from 1.54–1.85 mm.

Below *ci* the anterior limbic agranular cortex is confined to the lower half of the limbic gyrus below the shallow sulcus *il2* and above it is the juxtallocortical variant previously described.

Section 100. Fig. 74.

The cortex lateral to *fs* is of the type described in section 200.

The cortex on the remainder of the dorsal and medial surface above *ci* is much the same, but the inner granular layer is thinner and the cells of *iiic* and *v* slightly larger. There are also fewer granules just under *i*.

The surface over the lower wall of *ci* and the upper half of the crown of the limbic gyrus is covered by cortex measuring about 1.85 mm., outer main layer 0.93 mm., inner granular layer 0.12 mm., inner main layer 0.8+ mm. The cells of *v* are about the size of those in *iiic* but crowded up against *iv* so as to leave a lighter emptier *vb*. The cells of *vi* are smaller and more evenly distributed. There is a tendency in *iv* to a lighter *iva* and a denser *ivb* which reminds one of the superior parietal lobule but is less clear because of the thinness of *iv*.

The lower part of the crown of the limbic gyrus is covered by agranular anterior limbic cortex.

BLOCK XV (Fig. 75)

Section 100. Fig. 76.

The supratemporal plane is missing from sections 100 and 200.

The cortex medial to *ts* is cut too diagonally to read but, in the superior wall of *ts*, it is cut parallel to the columns. Here it measures 1.64 mm., outer main layer 0.74 mm., inner 0.74 mm. Layer *ii* is clearly demarcated from *iiia*. The pyramids of *iiib* are only slightly larger and scarcer. Those of *iiic* do not surpass 21 x 13 μ. The pyramids of *v* are about as large as those of *iiib* and only slightly larger than the cells of *via*. Layer *v* is as well filled as *via*. Columns of moderate width extend up to *iiib*. The cortex on the inferior wall of *ts* is of identical width and appearance. This cortex is of general eulaminate type.

On the crown between *ts* and *tp1* the cortex is cut very diagonally. It measures 1.64 mm. On the superior wall of *tp1* it is of equal width and looks identical to that in the superior temporal sulcus.

On the crown between *tp1* and *r* the cortex is cut diagonally but measures only 1.7 mm. and looks no different.

Below *r* the cortex measures 1.8 mm., outer main layer 0.93 mm., inner 0.7 mm. The cells of *iiib* and *c* are sparser than usual and the columns coarser than above. The size of the cells is about the same.

Just lateral to *rh* the cells of *ii* become heavier and form a dark band. In the lateral wall of *rh* these cells begin to form clumps, a tendency which increases as one goes deeper in the sulcus. The internal granular layer thins and the cells of *v* become heavier. This is temporal juxtallocortex (*jt*).

On the medial wall of the sulcus the internal granular layer disappears and allocortex begins.

Section 200. Fig. 76.
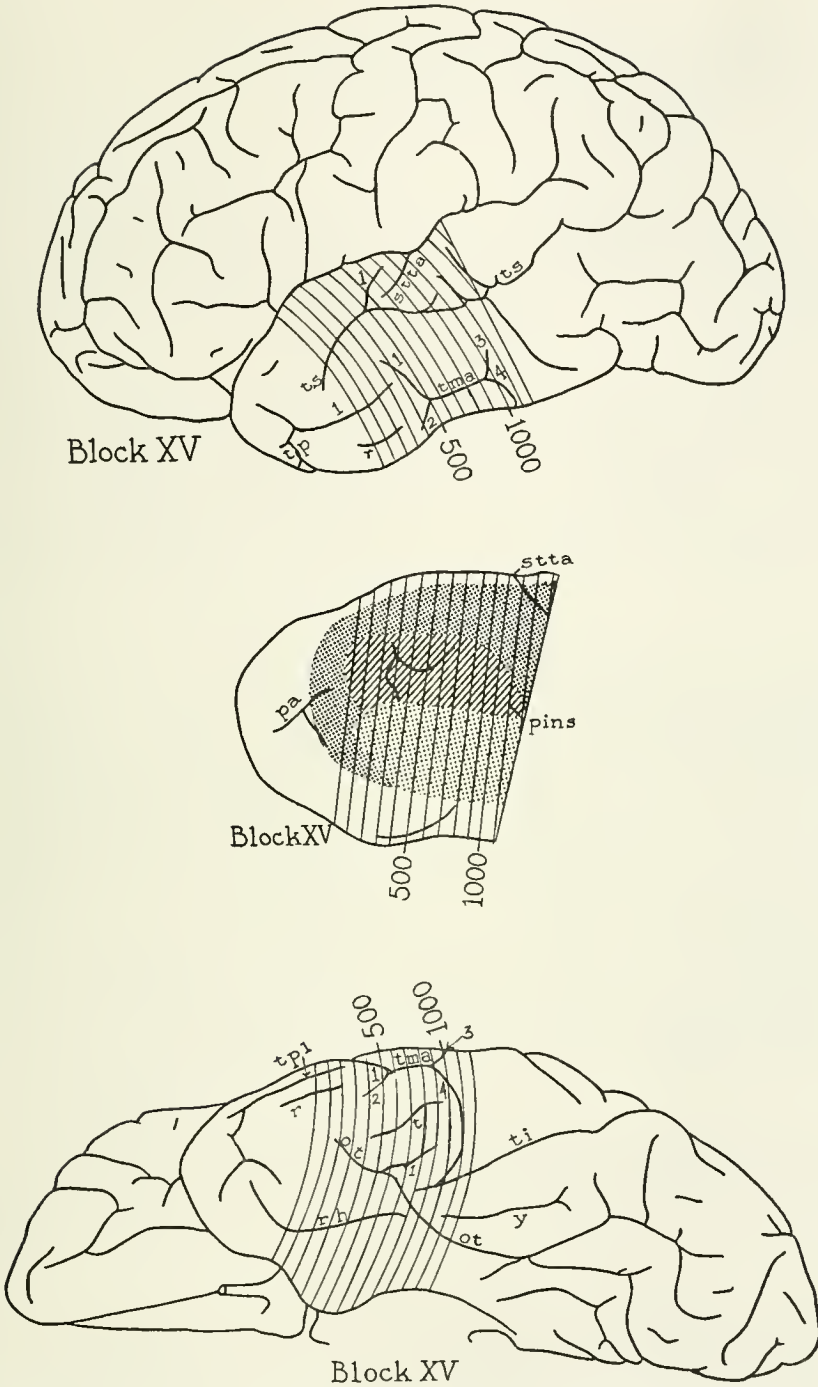
FIG. 75. Position of sections of Block XV. Heavy dots—covered by frontal operculum. Parallel lines—covered by island. Light dots—transected white substance. Superomedial surface as though seen through the lobe.

Medial and above *ts* the cortex measures 1.7 mm. and is of the type described in section 100. This cortex continues to the depth of *tp1*.
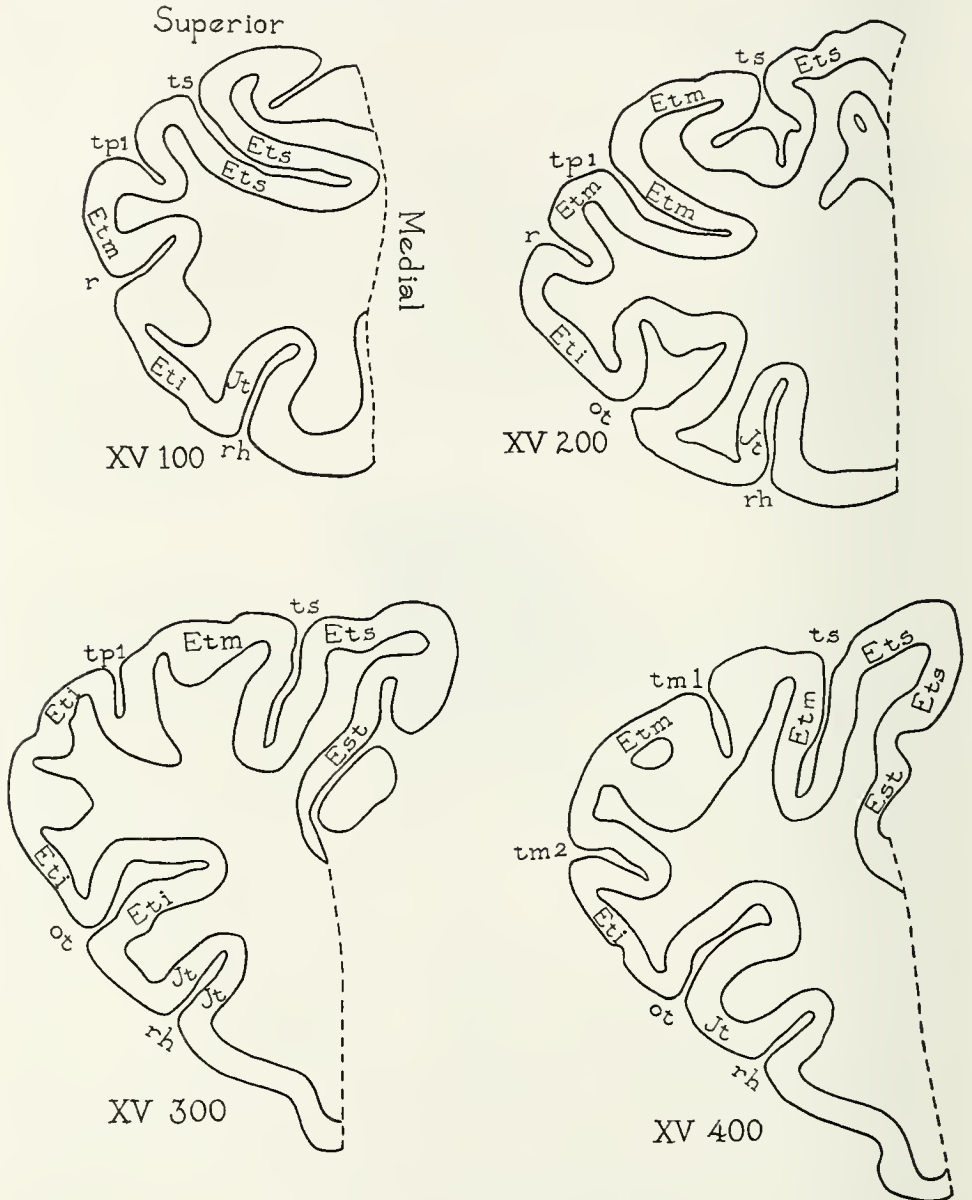
FIG. 76. Cross sections of Block XV.

On the crown of the gyrus below *tp1* the cortex is cut very diagonally but on its upper and lower walls it can be seen that the columns are very broad and the cells, particularly of *iii*, are sparse. The cortex below the small accessory sulcus (*r*) is similar, measuring 1.6+ mm. in total thickness, outer main layer 0.65 mm., inner granular layer 0.18 mm., inner main layer 0.8+ mm. Layer *ii* is easily sepa-

rated from *iiia* although the pyramids of *iiia* are scarcely larger than the granules of *ii*. The cells of *iiib* and *c* are sparse and those of *iiic* do not exceed 21 x 13 μ. Layer *v* is well filled with pyramids about the size of the cells of *via*. These two layers are about of the same thickness. The inner border of *vib* is indefinite. This cortex continues to the lip of *rh* where the alteration begins which was noted in section 100.

Section 300. Fig. 76.

On the supratemporal plane which here appears for the first time, the cortex measures only 1.5 mm., outer main layer 0.86 mm., inner granular layer 0.17 mm., inner main layer 0.46 mm. The cells of the outer main layer are scattered in patches with scarcely any cell gradient. It is difficult to distinguish *v* from *vi* at low magnification.

The cortex above *ts* is of the type previously described, total thickness 1.7 mm., outer main layer 0.68 mm., inner granular layer 0.18 mm. The outer boundary of *ii* is ragged. Layer *iiia* is distinguishable from *ii* although its pyramids are scarcely larger than the granules of *ii*. The pyramids of *iiib* are slightly larger and sparser. Those of *iiic* are more numerous and slightly larger still, but do not surpass 21 x 13 μ. Layer *v* is evenly filled with pyramids the size of those of *iiib*. Layer *via* is evenly filled by irregular and fusiform cells but slightly smaller than those of *v*. The boundary of *vib* against the subcortex is vague.

Between *ts* and *tp1* the cortex is slightly looser and its columns wider. It measures about 1.7 mm. on the crown below *ts*, outer main layer 0.68 mm., inner 0.83 mm.

Below *tp1* the cortex measures 1.54 mm., outer main layer 0.68 mm., inner 0.74 mm. Throughout there is a great poverty of cells but the layers are as readily distinguished as over the superior temporal convolution. The cells of *iiic* and *v* do not surpass 21 x 13 μ. The columns are very coarse. This is the eulaminate inferior temporal variant (see p. 72, Plate VI).

Between *ot* and *rh* the cortex is again different. The transformation occurs gradually on the inferior wall of *ot*. On the crown the cortex measures 1.85 mm., outer main layer 0.9 mm., inner 0.8 mm. The cells of *ii* tend to be grouped in clumps and are larger and denser than granules. The cells of *iiic* are fatter, up to 26 x 21 μ. The cells of *v* have the same fat appearance, are of about the same size and more numerous. Those of *vi* are distinctly smaller. These characteristics are accentuated on the lateral wall of *rh*. On the medial wall of *rh* the internal granules disappear and the uncinate type appears.

Section 400. Fig. 76.

The cortex on the inner part of the supratemporal plane is of the type described for section 300. Total thickness 1.54 mm., outer main layer 0.8 mm., inner 0.62 mm. Layer *iv* is thin and inconspicuous because of the smallness of the cells throughout. The cells of *v* and *vi* are very numerous, especially of *v*, so that these layers make a dense band.

The cortex over the outer half of the supratemporal plane, continuing over the crown of the superior temporal gyrus and the dorsal wall of the superior temporal sulcus is of the type previously described in this region. Total thickness 1.85 mm., outer main layer 0.77 mm., inner 0.93 mm. The pyramids of *iiib* and *c* are sparse, those of *iiic* being the largest in the section but not surpassing 21 x 13 μ. The cells of *v* and *vi* are more numerous than those of *iiib* + *c*.

On the lower wall of *ts* the cell population is perhaps somewhat sparser. On the

crown of the middle temporal gyrus the cortex cannot be read. The cortex between the two branches of *tm* is practically identical with that above *ts*, total thickness 1.7 mm., outer main layer 0.68 mm., inner 0.86 mm.

Between *tm2* and *ot* the cortex has a sparser cell population and the columns are coarser. Total thickness 1.64 mm., outer main layer 0.68 mm., inner 0.8 mm.

Below and medial to *ot* the cortex undergoes the transformation described in section 300.

On the medial wall of *rh* the cortex becomes definitely allocortex.

Section 500. Fig. 77.

On the inner portion of the supratemporal plane the cortex is of the type described in section 300. Total thickness 1.54 mm., outer main layer 0.77 mm., inner 0.65 mm., outer main layer patchy, inner denser, especially *v*.

On the outer part of the supratemporal plane and continuing over the crown and undersurface of the superior temporal gyrus, the cortex is as previously described, total thickness 1.85 mm., outer main layer 0.77 mm., inner 0.93 mm.

Below *ts* the total thickness is 1.85 mm., outer main layer 0.9 mm., inner 0.8 mm. The general appearance is practically identical with that above the sulcus.

Below *tma* the cortex measures 1.54 mm., outer main layer 0.83 mm., inner 0.55 mm. The cell population is sparse, the columns broad as before described.

Below and medial to *ot* is juxtallocortex as previously described, total thickness 1.85 mm., outer main layer 0.93 mm., inner 0.77 mm.

On the lateral wall of *rh* the cells of *iiic* and *v* become larger and the internal granular layer thinner to disappear at the depth of the sulcus.

Section 600. Fig. 77.

The entire supratemporal plane is covered by the thin patchy cortex previously described on the inner portion. It varies from 1.3–1.5 mm. in thickness. The outer main layer is consistently thicker than the inner; total thickness 1.4 mm., outer main layer 0.7 mm., inner 0.58 mm. The cells of the outer main layer are arranged in patches, those of *iiic* scarcely larger than those of the other layers. The pyramids of *v* are numerous, about 21 x 13 μ. The cells of *vi* are distinctly smaller.

Over the crowns of the two small superior gyri the cortex is of general eulaminate type; total thickness 1.54 mm., outer main layer 0.55 mm., inner 0.80 mm.

Over the crown of the second temporal gyrus, between *ts* and *tma*, the cortex measures 1.54 mm., outer main layer 0.63 mm., inner 0.77 mm. Its appearance is quite similar to that above *ts*.

Below *tma* the cortex measures also 1.54 mm., outer main layer 0.65 mm., inner 0.74 mm. The cell population is much sparser and the columns coarser.

Between *ot1* and *ot* the cortex cannot be read.

Between *ot* and *rh* the cortex measures 1.7 mm., outer main layer 0.83 mm., inner 0.74 mm. Layer *v* is broad and densely populated with pyramids as large as those of *iiic* which do not surpass 26 x 16 μ. This is juxtallocortex.

The internal granular layer is absent on the lateral wall of *rh*. The medial wall and the cortex remaining is allocortex.

Section 700. Fig. 77.

On the medial part of the supratemporal plane is the same patchy cortex pre-
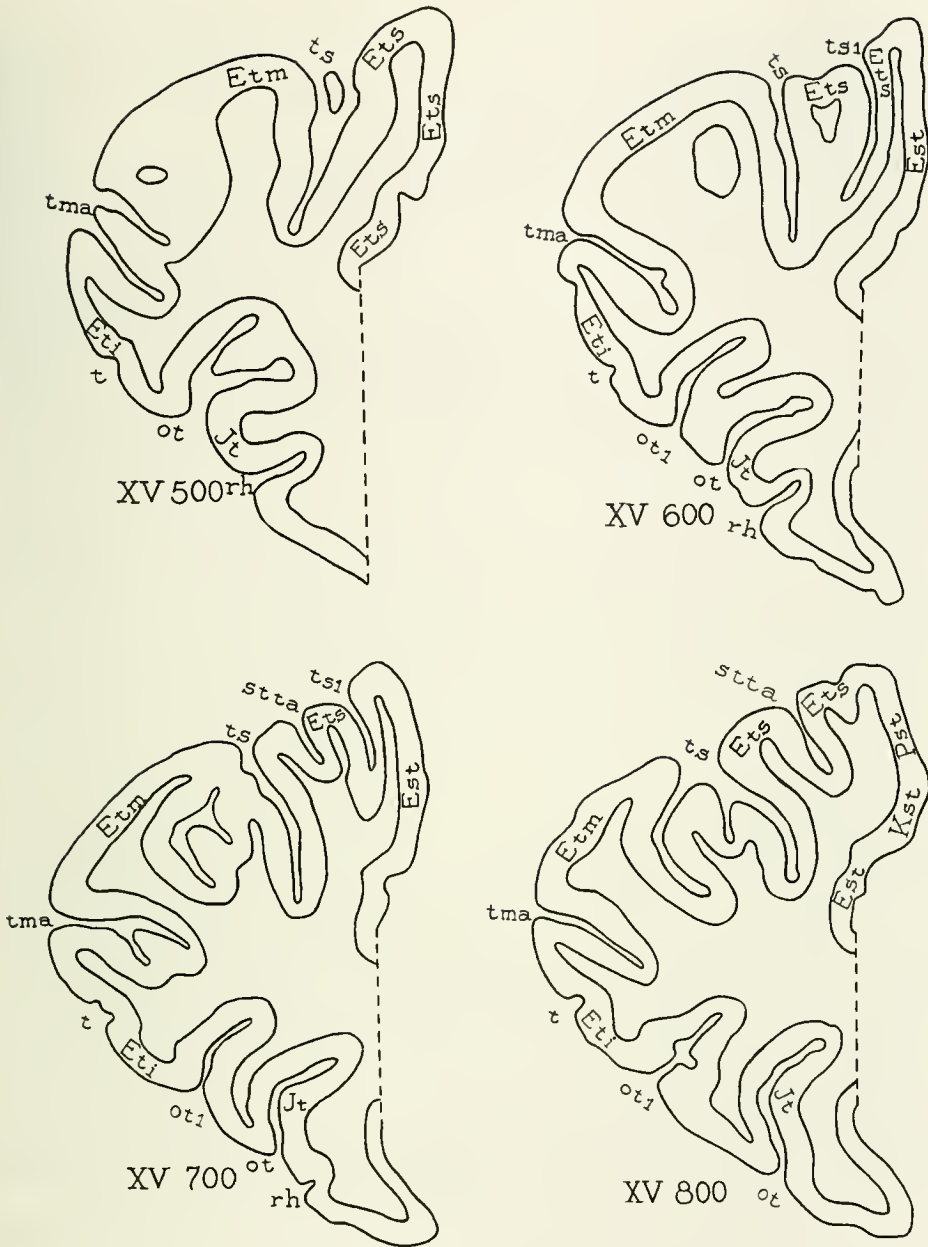
FIG. 77. Cross sections of Block XV.

viously described. Total thickness 1.4 mm., outer main layer 0.7 mm., inner 0.53 mm.

On the lateral half the cells begin to be larger in *iiic* and *v + vi* thickens until, on the crown above *ts1*, the cortex measures 1.54 mm., outer main layer 0.56 mm., inner 0.83 mm.

On the upper wall of *ts1* the cortex again thins to 1.1 mm., outer main layer 0.53 mm., inner 0.43 mm.

On the crown between *ts1* and *stta* the cortex again measures 1.54 mm., outer main layer 0.53 mm., inner 0.86 mm.

On the crown between *stta* and *ts* the measurements are the same.

On the upper wall of *ts* the cortex thins to 1.2 mm., outer main layer 0.6 mm., inner 0.5 mm. In all this stretch from the medial margin to *ts* the variations in this cortex seem to us haphazard.

Between *ts* and *tma* the cortex is cut parallel to the columns. It measures 1.95 mm., outer main layer 1.05 mm., inner 0.71 mm. Layers *iiib* and *c* are rather evenly populated with pyramids of which those in *iiic* reach 24 x 18 μ. Layer *v* contains pyramids of about the same size, more densely congregated, often in *va* so that an irregular light band appears in *vb*.

The cortex between *tma* and *ot1* is irregular but, above and below, it measures 1.6 mm., outer main layer 0.74 mm., inner 0.71 mm. The cell population is sparser and the columns broader.

The cortex between *ot1* and *ot* is cut diagonally and cannot be read. On the inferior wall of *ot1* the cortex measures 1.85 mm., outer main layer 0.8 mm., inner 0.9 mm. The pyramids of *iiic* do not exceed 21 x 13 μ. Those of *v* are smaller and evenly distributed; they are no larger than the cells of *vi*.

Over the medial wall of *ot* one sees the patchy *ii* and heavier *v* which signifies juxtallocortex.

The internal granular layer continues almost to the inferior lip of *ot* where allocortex begins.

Section 800. Fig. 77.

On the medial part of the supratemporal plane the cortex has the patchy appearance previously described but measures about 1.54 mm. in total thickness, outer main layer 1.0 mm., inner 0.4 mm.

In the middle of the supratemporal plane is an eminence where the cortex thickens to 1.85+ mm., the margin between *vi* and the subcortex being very vague. It is difficult to distinguish the layers in this region because all the cells are very small, those of *iiic* being largest, about 18 x 10 μ. Fine columns reach all the way up to *iiia*. Outer main layer 0.77 mm., internal granular layer 0.25 mm. This is supratemporal koniocortex (ĸ*st*).

Lateral to this patch the cortex thins again to 1.4 mm., outer main layer 0.57 mm., inner 0.68 mm., internal granular layer 0.15 mm. The cells of *iiic* are larger, up to 24 x 13 μ. Layer *v* is relatively empty and contains scattered large pyramids 26 x 18 μ. This is supratemporal parakoniocortex (ᴘ*st*).

On the crown of the two narrow gyri above *ts* the cortex is of generalized eulaminate type. Total thickness 1.54 mm., outer main layer 0.65 mm., inner 0.75 mm. on the upper gyrus; total thickness 1.62 mm., outer main layer 0.83 mm., inner 0.65 mm. on the lower.

The cortex between *ts* and *tma* measures 1.7 mm., outer main layer varies from 0.65–0.85 mm. and vice versa. Layer *v* is evenly filled with pyramids about the size of those in *iiic*.

The cortex between *tma* and *ot1* is irregular. The total thickness varies from 1.4–

1.7 mm. In general the outer main layer is thicker. The cell population is sparse and the columns thick.

Below and medial to *ot1* the cortex is cut too diagonally to read. On the lateral wall of *ot* the cortex measures 1.6 mm., outer main layer 0.86 mm., inner 0.58 mm. The pyramids of *iiib* and *c* are slightly larger than those of *iiia* and sparser. The pyramids of *v* are about the same size as those of *iiic* and evenly distributed.

On the medial wall of *ot* the cells of *ii* are bunched and larger; those of *v* more numerous. The internal granular layer disappears before the lower lip is reached to give place to allocortex.

Section 900. Fig. 78.

Now there are two eminences on the supratemporal plane covered by koniocortex with a narrow stretch between containing big pyramids in *iiic* measuring 29 x 21 μ. Lateral to the lateral eminence is a stretch of the same cortex measuring 1.6 mm. with big pyramids in *iiic*. Over the crown above *stta* the cortex is cut too diagonally to read. It thins again to 1.54 mm. in the superior wall of *stta*; there is good lamination and the pyramids of *iiic* are small. The lower wall of *stta* is quite similar, very thick (2.0+ mm.), outer main layer 0.86 mm., inner 1.0+ mm. Near the lip are nests of very large pyramids in *iiic*, up to 39 x 21 μ, as is so frequently seen near sulcal lips.

The cortex on the crown between *stta* and *ts* measures 1.7 mm., outer main layer 0.8 mm., inner 0.74 mm. The largest pyramids are in *iiic* but not above 26 x 18 μ. The cells of *v* are smaller, about the same size as those of *vi* and evenly distributed.

Between *ts* and *tma* the cortex measures 2.0 mm., outer main layer 1.0 mm., inner 0.8 mm. The cells of *iiic* are not above 21 x 13 μ.

Between *tma* and *ot1* the cortex measures 1.85 mm., outer main layer 0.68 mm., inner 1.0 mm. The cells of *iiic* reach 26 x 18 μ and those of *v* are also larger. Layer *v* is evenly filled.

The cortex immediately below *ot1* is cut too diagonally to read but just above *ot* the cortex measures 1.54 mm., outer main layer 0.77 mm., inner 0.62 mm. The cell population is less and the columns coarser.

In the deeper part of the lateral wall of *ot* the cortex measures 1.85 mm., outer main layer 1.0 mm., inner 0.71 mm. Layer *iii* has two sublayers, an outer with very small pyramids and an inner with slightly larger ones. Layer *v* is well filled with pyramids often larger than those of *iiic*, mainly in the deeper part of *v*.

On the medial wall of *ot* the cortex measures 1.54 mm., outer main layer 0.8 mm., inner 0.62 mm. The cells of *ii* are bunched and larger, those of *v* larger, more numerous and making a dense band of *v*.

Just before reaching the lip the inner granular layer disappears and the cortex goes over into allocortex.

Section 1000. Fig. 78.

The irregular patchy cortex now occupies only a short stretch near the medial border of the supratemporal plane. The cortex then thickens to 2.0 mm. and the cells become of almost uniform small size throughout but the layers are recognizable, outer main layer 1.05 mm., inner 0.74 mm., inner granular layer 0.21 mm. This is koniocortex. Lateral to this there is another less evident eminence, but mostly, the remainder of the supratemporal plane is covered by cortex measuring 1.6 mm. or

thinner, outer main layer about 0.8 mm., inner 0.65 mm. The cells of *iiic* range up to 26 x 18 μ. The cells of *v* are much smaller and sparse. Layer *vi* is better filled. This all looks more like parakoniocortex and continues on over the small gyrus and
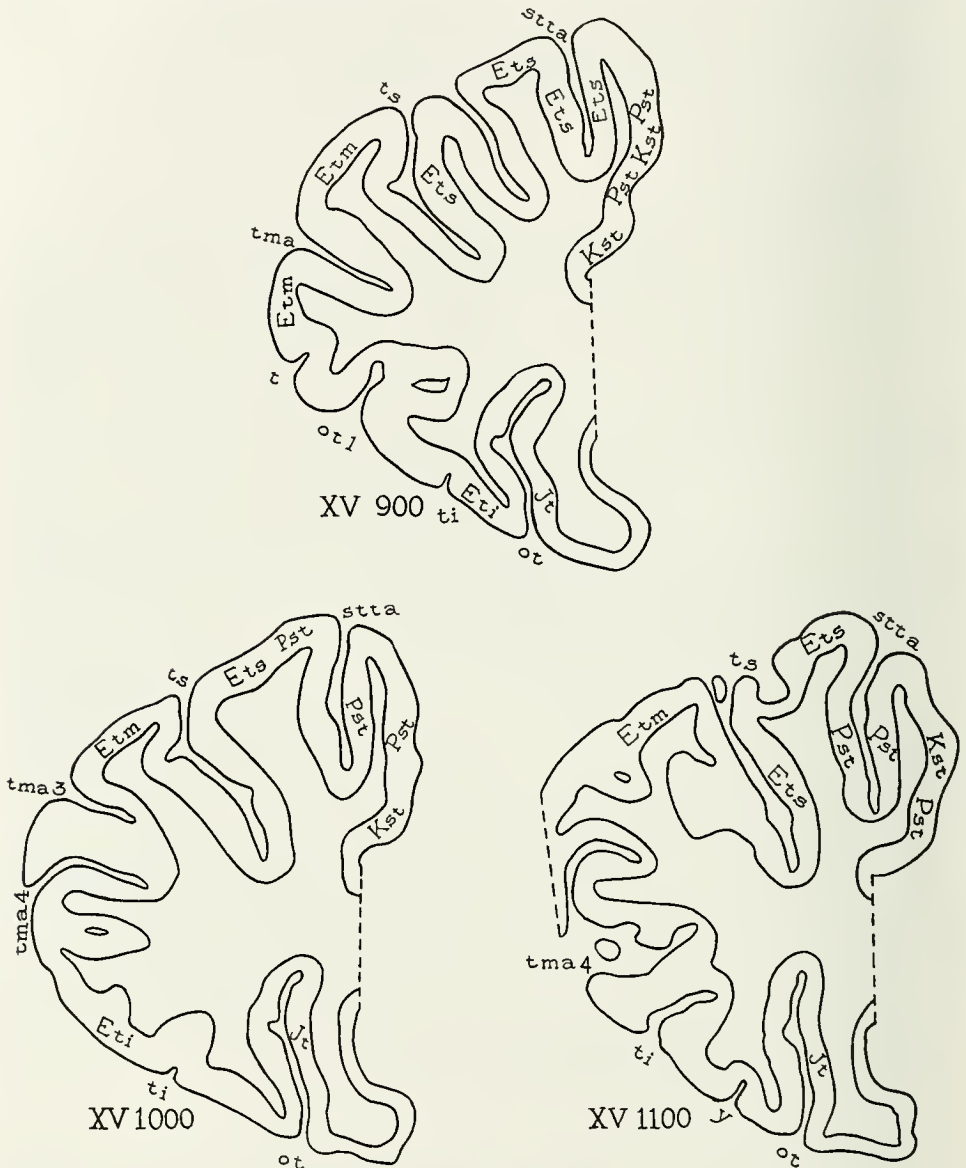

FIG. 78. Cross sections of Block XV.

down the superior wall of *stta*. Near the depth of this sulcus the large pyramids in *iiic* reach 36 x 26 μ. Such large pyramids are found scattered also on the lower wall and over the upper part of the crown between *stta* and *ts*.

    Below *ts* the cortex measures 2.0 mm., outer main layer 1.0 mm., inner 0.83 mm.

The pyramids of *iiic* do not surpass 26 x 16 μ. Those of *v* are smaller and well distributed. This is generalized eulaminate cortex.

Below *tma4* the cortex is irregular and difficult to read. Only just below *tma4* is the cell population sparse and the columns coarse. Farther down on either side of the beginning of *ti* the cortex measures 2.15 mm. The radiations are very fine. The inner granular layer is thin (0.1 mm.), outer main layer 0.77 mm. The pyramids of *iiic* reach 26 x 16 μ. Those of *v* are of equal size. Layer *v* is very thick (0.68 mm.) and its cells are more numerous in its outer half.

Below *ti* the cortex is equally thick; outer main layer 1.0 mm., inner 1.05 mm. Otherwise it is constructed much as above *ti*. This cortex continues down the lateral wall of *ot* to the depth where it becomes juxtallocortex.

The cortex medial to *ot* is all allocortex.

Section 1100. Fig. 78.

On the supratemporal plane there is only one eminence laterally with thick (2.0 mm.) cortex and nearly uniform cellular composition (*Kst*). Except for a short irregular stretch near the medial border, the plane is covered by cortex measuring about 1.45 mm., outer main layer 0.77 mm., inner 0.53 mm. Layer *iiic* contains large pyramids, up to 34 x 24 μ. Layer *v* contains mostly very small pyramids with a rare large one measuring about 32 x 21 μ. The cell population of *v* is also less than of *vi*. This cortex continues over the crown between *stta* and *ts* where the thickness increases to 2.0 mm., outer main layer 0.93 mm., inner 0.93 mm. The cells of *iiic* are more uniformly about 26 x 21 μ, those of *v* slightly smaller. Layer *v* is better filled. This cortex continues on the upper wall of *ts*, measuring here 1.85 mm. in total thickness, outer main layer 0.93 mm., inner 0.77 mm. The lower wall of *ts* is cut too irregularly to read.

On the crown below *ts* the cortex averages about 1.85 mm., outer main layer 0.9 mm., inner 0.8 mm. The cells of *iiic* are smaller.

On the buried gyrus above *tma4* the cortex measures 1.85 mm., outer main layer 0.68 mm., inner 1.08 mm. The cells of *iiic* are larger, those of *iiib* and *v* also. Layer *v* is very thick (0.68 mm.) and well filled.

Below *ti* the cortex measures 1.85 mm. and resembles that just described; outer main layer 0.77 mm., inner 1.0 mm. It is difficult to distinguish *v* from *vi*.

On the medial half of the fusiform gyrus, between *y* and *ot*, the cortex is thinner (1.54 mm.) but cut too diagonally to read. On the lateral wall of *ot* it measures 1.7 mm., outer main layer 0.77 mm., inner 0.77 mm.

On the medial wall of *ot* the cortex is thinner (1.1–1.2 mm.), outer main layer nearly twice as thick as the inner. Juxtallocortex begins about its middle and goes over into allocortex at the medial lip.

<p style="text-align:center">BLOCK XVI (Fig. 79)</p>

Section 100. Fig. 80.

Most of this section is cut too diagonally to read except on both sides of the temporopolar sulcus (*tp3*). Here the cortex measures 1.54 mm., outer main layer 0.62 mm., inner 0.86 mm. The inner granular layer is thin and inconstant. The cells of *ii* are large and tend to concentrate in clumps. Layer *v* is thick and densely filled with cells larger than those of *iiic*. This is juxtallocortex.

Section 200. Fig. 80.

The cortex on the walls of *rh* is of the type just described in section 100. That on the walls of *tp3* also. The cortex on the crowns is cut very diagonally but seems to be
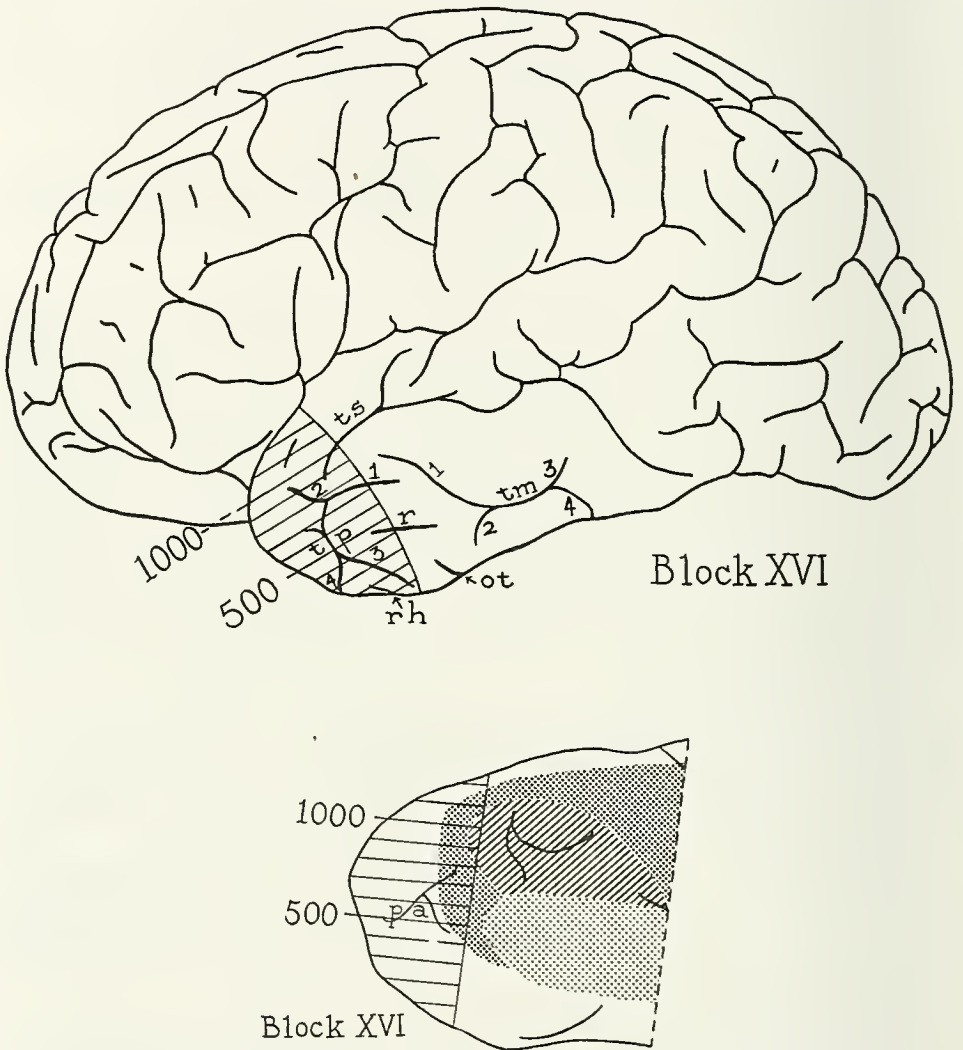
FIG. 79. Position of sections of Block XVI. Superomedial surface as though seen through the lobe.

of the same type. The cortex on the medial surface is agranular allocortex of uncinate type.

Section 300. Fig. 80.

The cortex posterior to *tp3* is cut too diagonally to read.

The cortex on both walls of *tp3* is of the type described in section 100.

The cortex on the crown anterior to *tp3* measures 1.7 mm., outer main layer 0.68 mm., inner 0.93 mm. Layer *ii* is distinct from *iiia* and is patchy. *iii* contains mostly

FIG. 80. Cross sections of Block XVI.

very small pyramids. Layers *iiib* and *c* contain scanty pyramids about 21 x 13 μ. Layer *iv* is thin. Layers *v* and *vi* are about equally filled with cells about the size of those in *iiib* + *c* but much more numerous. It is difficult to distinguish *v* from *via*

at low magnification. The inner border of *vib* is vague. This is dysgranular temporo-polar cortex (D*tp*).
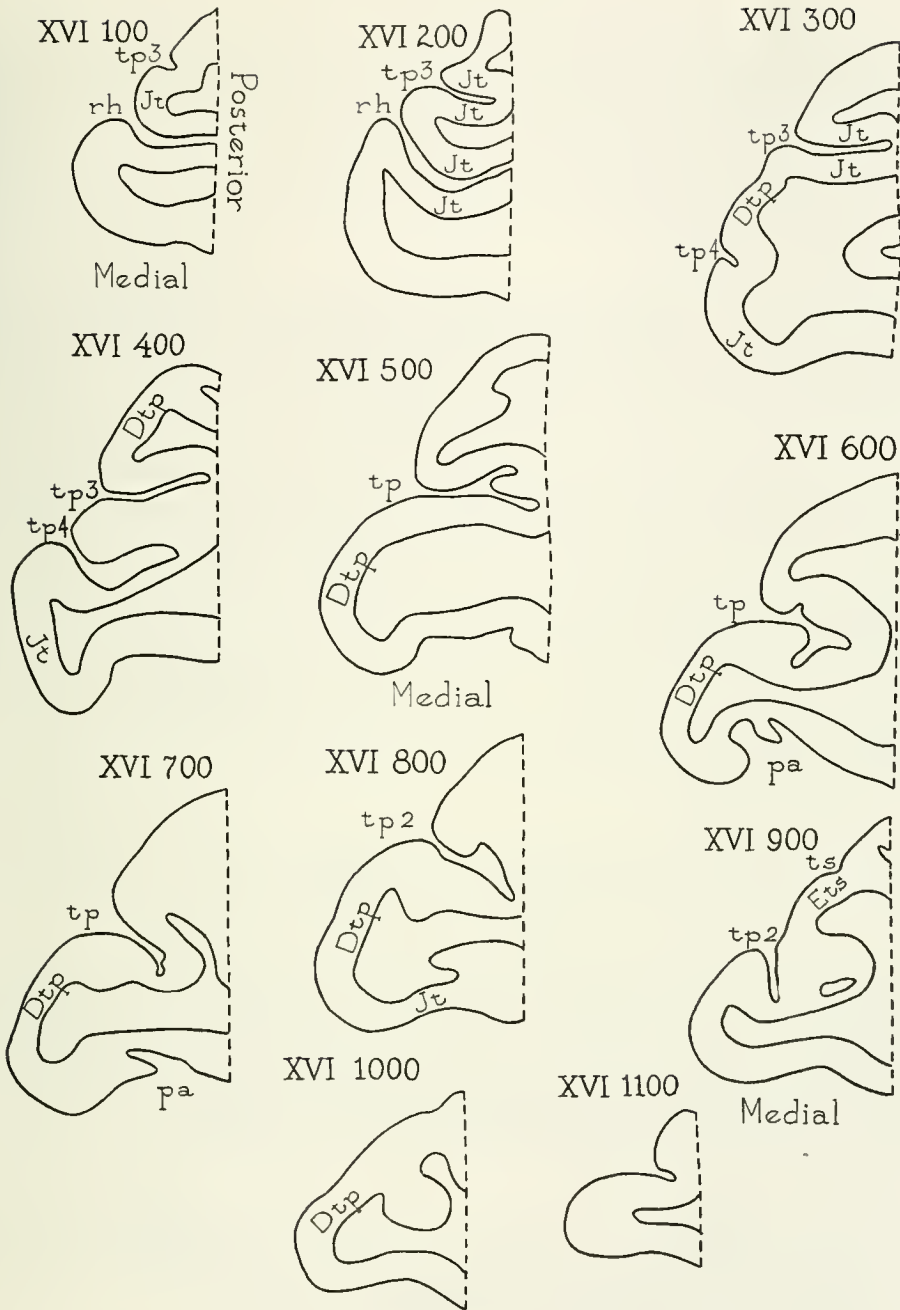
Medial to *tp4* the cortex measures 1.85 mm., outer main layer 0.86 mm., inner 0.93 mm. The inner granular layer is very thin. There is a very dense layer of cells in *vb*.

On the medial surface the inner granular layer disappears and the cortex becomes agranular allocortex.

Section 400. Fig. 80.

The cortex posterior to *tp3* measures 1.9 mm., outer main layer 0.86 mm., inner 0.96 mm. Layer *ii* is difficult to distinguish from *iiia* at low magnification. The pyramids of *iiib* are slightly larger and sparser. Those of *iiic* are still larger but do not surpass 21 x 13 μ. Layer *iv* is thin. Layers *v* and *via* are evenly filled with cells about the size of those in *iiib* but more numerous.

The cortex on the lateral wall of *tp3* measures 1.85 mm., outer main layer 0.93 mm., inner 0.8 mm. It is very difficult to distinguish *ii* from *iiia*. The cells of *iiia* are only slightly larger than the granules of *iv*. The pyramids of *iiib* are larger and sparser. Those of *iiic* are slightly larger but do not exceed 21 x 13 μ. The cells of *v* and *via* are about the size of those of *iiib* but more numerous and evenly distributed.

The cortex anterior to *tp4* measures 1.85 mm., outer main layer 0.86 mm., inner granular layer 0.12 mm. Layer *v* measures 0.55 mm. and contains closely-packed cells as large as those of *iiic* in its deeper half, which forms a dark band.

Shortly after the cortex passes onto the medial surface the inner granular layer disappears and agranular allocortex begins.

Section 500. Fig. 80.

The cortex posterior to *tp* measures 1.62 mm., outer main layer 0.9 mm., inner 0.65 mm. Layer *ii* is irregular and patchy. The cells of *iiib* + *c* are sparse with a slight cell gradient. The pyramids of *iiic* do not surpass 24 x 16 μ. Layer *iv* is thin (0.12 mm.) and divided into columns. Layer *v* is less dense than *via*.

The cortex anterior to *tp* is thicker, measuring more than 2.0 mm., outer main layer 0.8 mm., inner granular thin and irregularly developed, varying from 0.03–0.1 mm. in thickness, inner main layer consisting of a light *va* with small pyramids followed by a broader denser *vb* with medium pyramids, then a varying *via* with slightly smaller cells not clearly separated from *v*. The margin of *vib* with the subcortex is vague. This is the temporopolar dysgranular formation.

Shortly after rounding the tip onto the medial surface, the inner granular layer disappears and allocortex begins.

Section 600. Fig. 80.

The cortex just posterior to *tp* measures 1.6 mm. and resembles that described above *tp* in section 500, outer main layer 0.59 mm., inner 0.93 mm.

Anterior to *tp* the conditions are as described in section 500.

Section 700. Fig. 80.

The cortex posterior to *tp* is cut so tangentially that it cannot be read.

Anterior to *tp* the cortex is as described in section 500.

Section 800. Fig. 80.

The cortex posterior to *tp2* cannot be read.

Anterior to *tp2* the cortex is of the polar type described in section 500, very thick, measuring more than 2.3 mm., outer main layer 0.93 mm., inner granular layer very scanty and irregular, with fine radiations clearly visible through *vi*, *v*, and *iv*.

On the medial surface the cortex thins to 1.54 mm., or less, and has an internal granular layer throughout. Layer *ii* is bunchy and *v* is thick and dense. This is juxtallocortex.

Section 900. Fig. 80.

Between *ts* and *tp2* the cortex measures 1.85 mm., outer main layer 0.7 mm., inner granular 0.12 mm. and regular, inner main layer 1.0 mm. The cortex here is of general eulaminate type.

Anterior to *tp2* the cortex measures also 1.85 mm., outer main layer 0.93 mm., inner granular layer 0.15 mm., inner main layer 0.77 mm. There is here a tendency for *v* to have a dense inner sublayer.

Section 1000. Fig. 80.

The cortex on the lateral surface of the tip is cut diagonally but seems of the dysgranular polar type with a slight and irregular *iv*.

On the medial surface the cortex measures 1.7 mm., outer main layer 1.02 mm., inner 0.53 mm. The inner granular layer is regular and well formed (0.15 mm.). It is difficult to distinguish *v* and *via*. The cells of *iiia* are very small and often cannot be distinguished from those of *ii* even with high magnification. There are very few granules in either layer.

Section 1100. Fig. 80.

The cortex on the medial surface is of the type just described. The remainder cannot be read.

Section 1200. Fig. 80.

This section is too tangential to read, and therefore not sketched.

BLOCK XVII (Fig. 81)

Section 100. Fig. 82.

The cortex is cut too tangentially to read until the lip of the sulcus *rct* is reached. Here it measures 1.54 mm., outer main layer 0.65 mm., inner 0.75 mm. The cortex has medium columns. The pyramids of *iiic* do not surpass 24 x 16 μ. Those of *v*, which is well filled, are about the same size. This is general eulaminate cortex.

The cortex in the lower wall of *rct*, although cut diagonally, seems to be of the same type. On the infraparietal plane the cortex can be read at a couple of spots and seems essentially identical.

Section 200. Fig. 82.

The cortex above *rct* measures 1.4 mm., outer main layer 0.5 mm., inner 0.74 mm. The pyramids of *iiic* reach 32 x 21 μ. Layer *v* is rather empty but contains some large cells as big as those in *iiic*. This looks like postcentral parakoniocortex.

Below *rct* the cortex is cut too irregularly to read until just above *scp*. Here the cortex measures 1.85+ mm., outer main layer 0.74 mm., inner granular layer 0.15 mm. Layer *ii* is clearly differentiated from *iiia*. *iiib* is relatively empty. Layer *iiic* contains mostly small pyramids which do not exceed 21 x 13 μ. Layer *v* is uniformly

filled with pyramids about the same size. The boundary of *vi* against the subcortex is blurred. This is general eulaminate cortex (E*pi*).

At two points on the opercular surface, where the cortex can be read, it seems to be of the same type.

Section 300. Fig. 82.
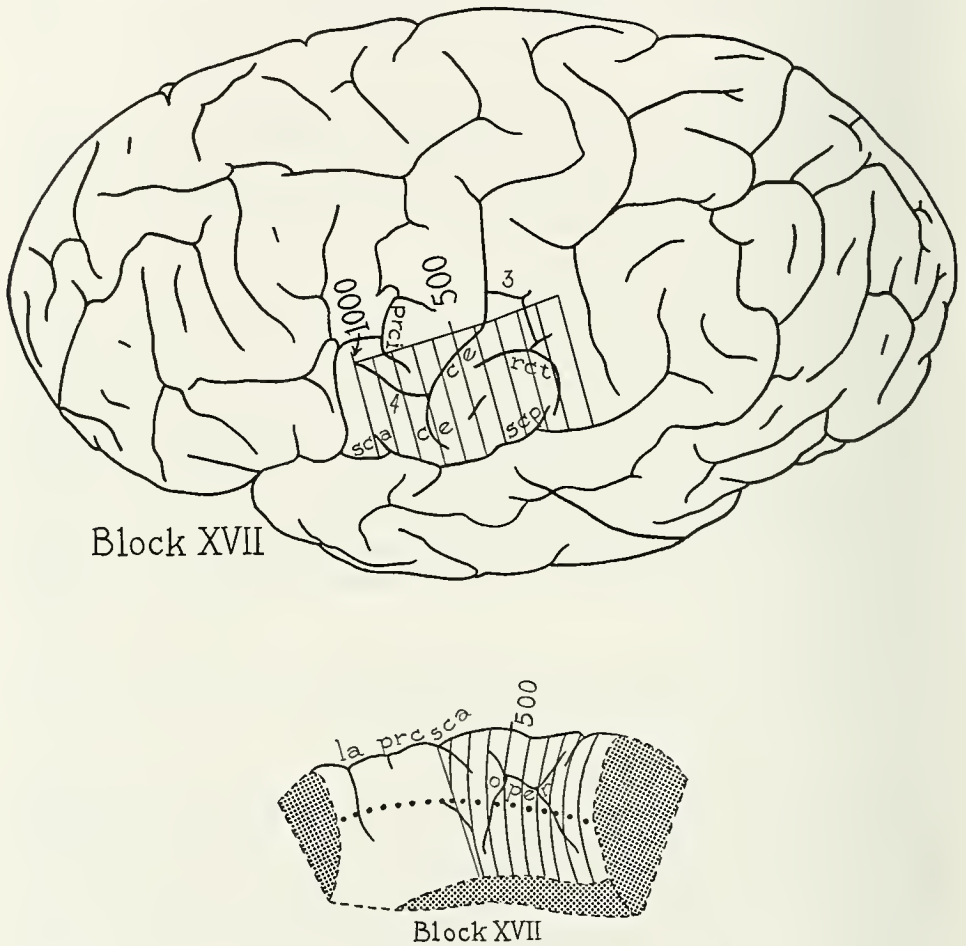
FIG. 81. Position of sections of Block XVII. Dotted—transected white substance. Row of heavy dots—limit covered by temporal lobe.

The upper margin of the section passes through the central sulcus *ce*, on the postero-inferior wall of which can be seen koniocortex. Anterosuperior to *ce* the cortex is cut tangentially but seems to be agranular.

The cortex between *ce* and *rct* is of the postcentral type described already in section 200. The pyramids of *iiic* reach even larger dimensions. Total thickness 1.2 mm., outer main layer 0.6 mm., inner 0.46 mm.

Below *rct* the cortex measures 1.54 mm., outer main layer 0.68 mm., inner 0.71 mm. The pyramids of *iiic* are quite small and almost disappear as the lip is approached.

Near the medial margin of the infraparietal plane the cortex is again cut parallel to the columns. Here it measures 1.54 mm. *iiic*, *iv*, and *v* zigzag like a rail fence but the outer main layer is relatively thin, about 0.5 mm. on an average. The most striking characteristic of this region is the numerous large pyramids in *iiic* measuring about 39 x 26 μ. This looks like parakoniocortex (see section 500).

Section 400. Fig. 82.
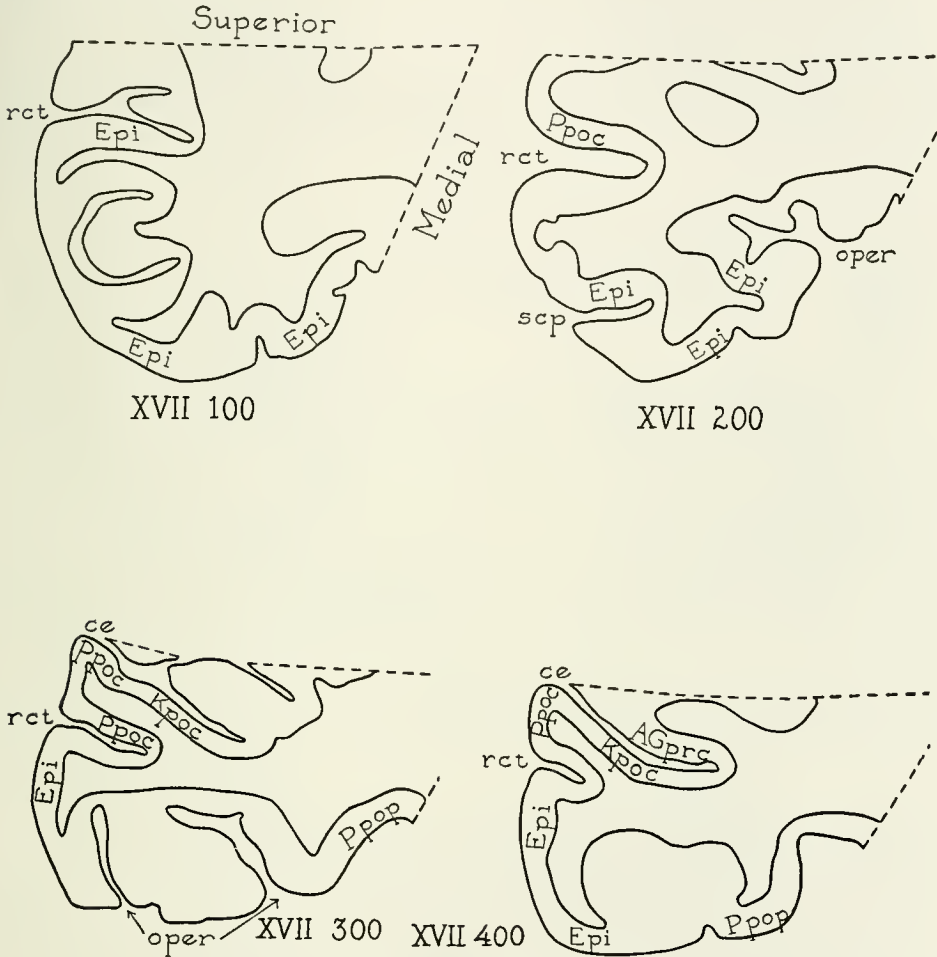
FIG. 82. Cross sections of Block XVII.

This section is essentially similar to section 300.

Anterior to *ce* the cortex measures at least 2.15 mm. There is no internal granular layer. In the deeper regions of the cortex are numerous very large cells reaching 66 x 39 μ. This is precentral agranular cortex with Betz cells. Broad columns can be clearly seen in the layers above the Betz cells.

After a narrow transitional zone in the depth, the posterior wall of *ce* is covered by koniocortex measuring about 1.1 mm., almost to the lip of the postcentral gyrus.

The crown of the postcentral gyrus is covered by parakoniocortex previously

FIG. 83. Cross sections of Block XVII.

described, measuring 1.4 mm., outer main layer 0.62 mm., inner 0.62 mm., *v* relatively empty. Many big pyramids in *iiic*.

Below *rct* the cortex is of general eulaminate type varying in thickness from 1.54–1.85 mm.

Near the medial margin of the opercular surface can be seen the formation before described with the zigzag layers and big pyramids in *iiic* (P*pop*).

Section 500. Fig. 83.

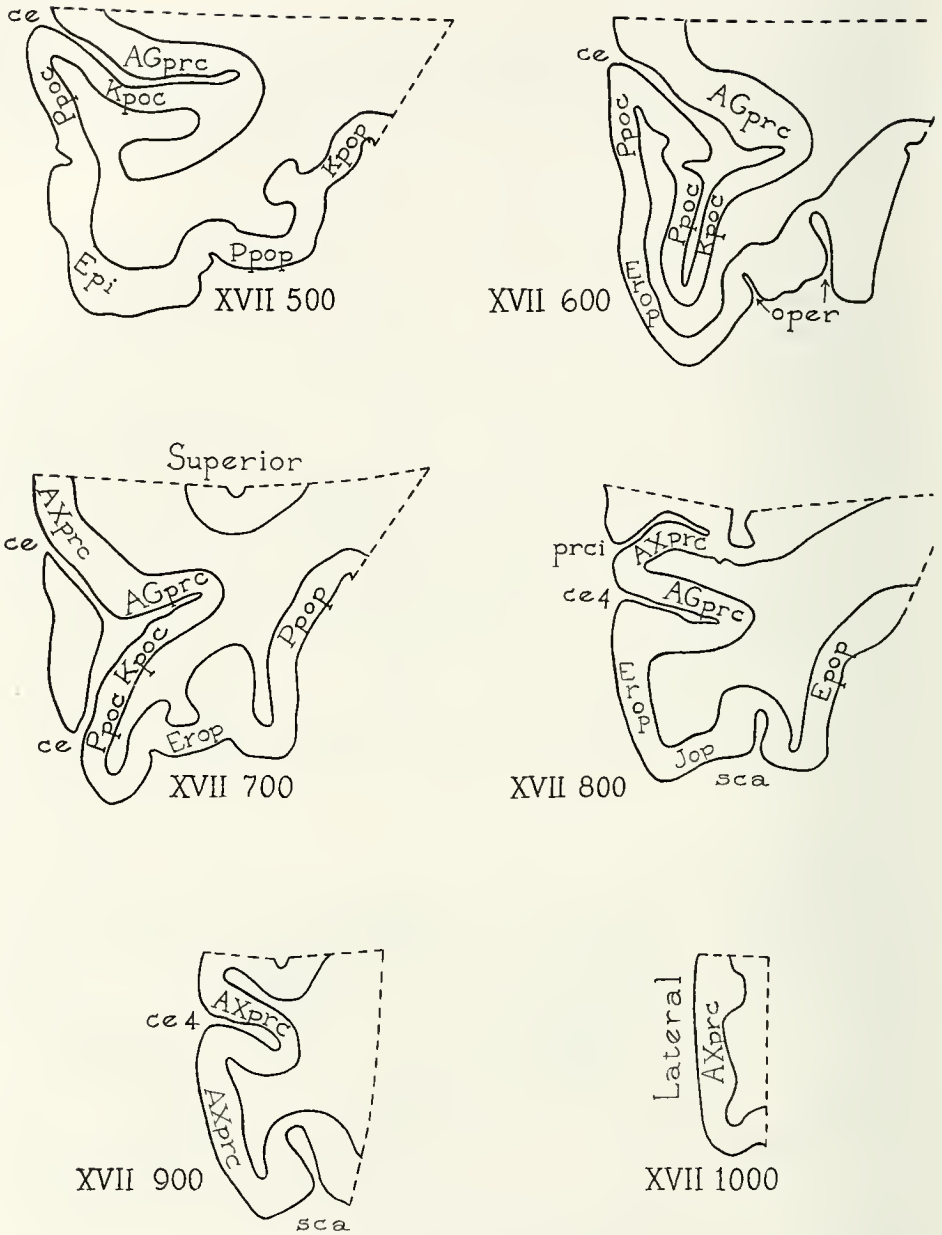Essentially similar to section 400, except that on the opercular surface near the medial margin is an area which is relatively uniform throughout the cross section. The cortex measures 1.54 mm. The pyramids of *iiic* and *v* are scarcely larger than granules. Layers *iiib* + *c* and *v* can be recognized by their lightness and *iv* is very thick (0.28 mm.). This cortex is obviously differentiated toward koniocortex (κ*pop*).

Section 600. Fig. 83.

The cortex anterior to *ce* is cut very tangentially but contains Betz cells reaching 58 x 34 μ.

There is now only a small patch of koniocortex on the operculated depth of the central sulcus. On both sides it is surrounded by cortex with large pyramids in both *iiic* and *v*. This cortex covers the postero-inferior wall of *ce* and extends a short distance over the surface.

The remainder of the external surface is covered by general eulaminate cortex measuring 1.54 mm., outer main layer 0.74 mm., inner 0.68 mm. The pyramids of *iiic* and *v* rarely exceed 24 x 16 μ. This cortex rounds the lip to the opercular surface, most of which is cut too tangentially to read.

Section 700. Fig. 83.

Anterior and above *ce* is agranular cortex measuring more than 2.5 mm. but containing no Betz cells until the operculated depth of the sulcus is reached.

There is a very small patch of koniocortex on the floor, which is covered otherwise by parakoniocortex. This cortex extends out on the lip and there changes subtly.

The cortex of the lip measures 1.4 mm., outer main layer 0.5 mm., inner 0.77 mm. The pyramids of *iiic* and *v* are smaller but yet larger than is customary in general eulaminate cortex. Layer *v* is better filled than in typical parakoniocortex and the inner main layer is relatively thicker.

On the undersurface of the operculum the cortex thickens to 1.85 mm. and has the characteristic structure of the inferior parietal region, except near the medial border where it measures 1.7 mm. and has the irregular construction and big cells in *iiic* before mentioned.

Section 800. Fig. 83.

The cortex above the inferior extremity of the precentral sulcus (*prci*) cannot be read. Over the gyrus between *prci* and *ce4* the cortex is agranular with Betz cells only near the depth of *ce4*. The cortex on the inferior wall of *ce4* is cut very diagonally but can be seen to contain an internal granular layer. It is not koniocortex but appears to be of postcentral type (ρ*poc*).

On the lip of the operculum the structure of the cortex is of general eulaminate type (ε*vop*), but on the superior wall of the lateral fissure the cells of *v* become larger and more numerous, forming a conspicuous dark band in *va*. This is a juxtallocortical characteristic (*jop*).

Internal to *sca* the cortex is again of general eulaminate type (ε*pop*).

Section 900. Fig. 83.

The cortex above *ce4* is agranular without Betz cells.

Below *ce4* the cortex over the external surface measures 2.0 mm. It has only a very thin and inconstant inner granular layer until it rounds the lip when the inner

granular layer becomes continuous but thin (0.09 mm.). The pyramids of *iiic* and *v* are also smaller. The superficial cortex might be essentially precentral agranular but does not extend below the lip.

The cortex on the superior wall of the lateral fissure is cut too diagonally to read. *Section 1000.* Fig. 83.

Block XVIII
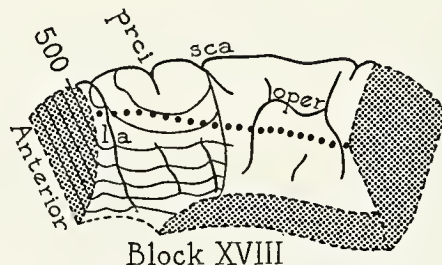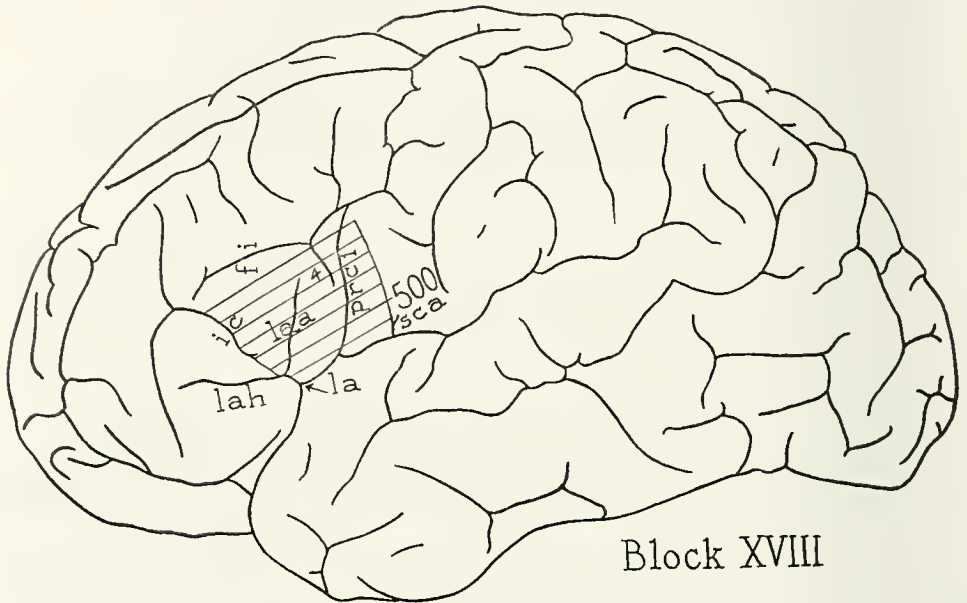
Block XVIII

Fig. 84. Position of sections of Block XVIII. Dotted—transected white substance. Row of heavy dots—limit covered by temporal lobe.

This is all essentially agranular cortex without Betz cells, measuring 2.0 mm. Below the lip an inner granular layer is present.

<div align="center">BLOCK XVIII (Fig. 84)</div>

Section 100. Fig. 85.

The cortex posterior to *prci* is simple agranular precentral cortex without Betz cells. In the posterior wall of *prci* it varies from 1.85–2.8 mm. in total thickness. It contains no pyramids larger than 45 x 26 μ. On the anterior wall of *prci* the cortex is thinner, 1.2–1.85 mm. Again there are no pyramids larger than 42 x 26 μ.
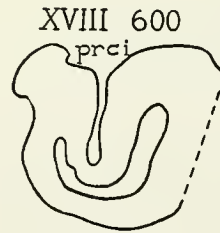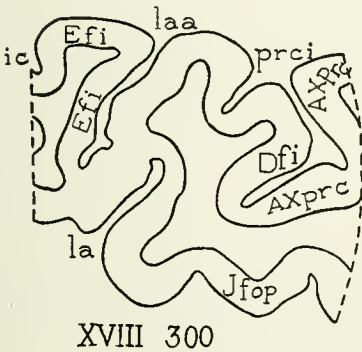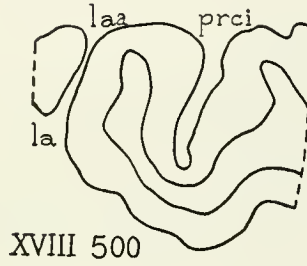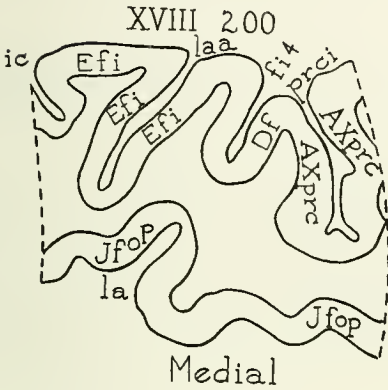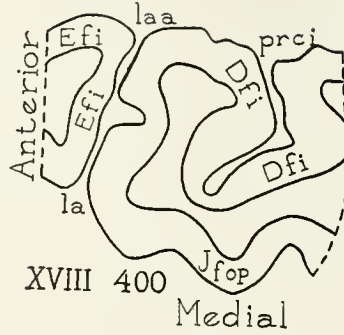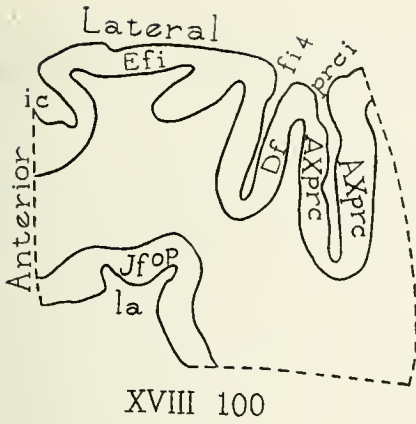
FIG. 85. Cross sections of Block XVIII.

On the posterior wall of *fi4* the cortex measures about 1.85 mm., the pyramids of *iiic* range up to 47 x 24 μ, and one sees only a few scattered granules at the level of the internal granular layer.

On the anterior wall of *fi4* the cortex measures about 1.7 mm., outer main layer 0.93 mm., inner granular 0.09 mm., inner main layer 0.68 mm. *ii* + *iiia* form a

dense band measuring about 0.3 mm. There are only a few granules in *ii*. The largest pyramids are just above *iv* measuring about 37 x 21 μ. The pyramids of *v* are grouped in patches. Layer *via* is filled with smaller cells about the size of those in *iiib*. Layer *vib* has much fewer cells and an indefinite inner boundary. This is the inferior frontal variant of the eulaminate cortex.

The cortex over the surface anterior to *fi4* measures 1.7 mm., outer main layer 0.87 mm., inner granular 0.15 mm., inner main layer 0.68 mm. The pyramids of *iiic* do not surpass 37 x 21 μ. It looks much like the anterior wall of *fi4* except for the thicker internal granular layer.

On the posterior wall of *ic* there are larger pyramids in *iiic* measuring 47 x 32 μ.

On the opercular surface the cortex measures 1.7 mm., outer main layer 0.77 mm., inner granular 0.09 mm., inner main layer 0.84 mm. The margin between *i* and *ii* is sharp. There is a definite *ii* with many granules, very little cell gradient in *iii* with a few slightly larger pyramids in *iiic*, a very dense *va* and a relatively empty *vb*. This is juxtallocortex (*jfop*).

Section 200. Fig. 85.

The cortex on the posterior wall of *prci* is agranular precentral cortex without Betz cells and no large pyramids. On the anterior wall of *prci* the cortex is the same except that a thin irregular internal granular layer begins near the crown of the narrow gyrus.

On the posterior wall of *fi4* the cortex has a thin but continuous internal granular layer. On the anterior wall of *fi4* this is slightly thicker. Over the crown between *fi4* and *laa* the cortex measures 1.54 mm. and looks much the same, except that the internal granular thickens to 0.15 mm. This continues unchanged down the posterior wall of *laa* up the anterior wall and across the crown to *ic*. Throughout this extent *iiic* contains numerous pyramids measuring 39 x 24 μ. Since the cells of *v* are much smaller this *iiic* is very conspicuous in the section. This is the inferior frontal variant of the eulaminate cortex.

On the walls of *ic* the pyramids of *iiic*, although no larger, are more conspicuous because of the generally smaller size of the other cells of *iii* and *v*.

On the opercular surface the cortex is as described in section 100 but, as one passes posteriorly, the heavy *va* becomes more evident and the cells of *iiic* smaller.

Section 300. Fig. 85.

The cortex behind *prci* is agranular precentral without Betz cells, measuring 2.15 mm.

Over the anterior wall of *prci* the cortex measures not more than 1.85 mm. It contains a faint internal granular layer.

On the crown of the gyrus between *prci* and *laa* the cortex measures more than 2.0 mm. It not only contains a thin internal granular layer but numerous large pyramidal cells in all layers from *iiia* to *via*. The cell in *via* measures 47 x 32 μ. There are numerous cells of equal size in all the layers, being most numerous in *iii*.

The cortex anterior to *laa* does not differ from the preceding section 200.

The cortex on the opercular surface is identical with that described in section 200.

Section 400. Fig. 85.

The cortex behind *prci* has now a thin internal granular layer (0.09 mm.) and beneath it the cells of *v* are heaped in a dense band of small heavily stained cells.

On the operculated bottom of the sulcus there is almost no *iv* and the large cells of *v* are where one would expect *iv*. This appearance continues to the anterior wall of *prci* where the *iv* is very scanty and discontinuous. On the crown of the gyrus just behind *laa* there are numerous large pyramids in *iiic*, a few in *v* and one large one in *via* and a distinct *iv*.

On the posterior wall of *laa* there is a thin internal granular layer. Just outside it is a row of large pyramids measuring about 39 x 26 μ. The other pyramids of *iii* are much smaller, as are those of *v* which are crowded up towards *iv*.

On the anterior wall of *laa* the cortex is much the same, although the pyramids of *iiic* do not form so definite a line, and the internal granular layer is thicker (0.12 mm.).

Anterior to *laa* the cortex measures 1.85 mm. and is of general eulaminate type, outer main layer 0.74 mm., inner granular 0.15 mm., inner main layer 0.96 mm. The pyramids of *iiic* do not exceed 24 x 13 μ.

The opercular cortex is of the type previously described. The heavy *va* grows less conspicuous as one passes outward over the posterior wall of *laa* and the pyramids of *iiic* larger.

Section 500. Fig. 85.

The cortex posterior to *prci* measures about 1.85 mm. It contains the same dense band in *v* noted in section 400. This band continues anterior to *prci*, down the posterior wall of *laa* and across the opercular surface, everywhere lying just beneath a faint internal granular layer. Anterior to *laa* the cortex cannot be read. The cortex on the opercular surface differs only in a lesser cell gradient in *iii*, a more distinct *ii* with more granules and a sharper margin between *i* and *ii* as previously described. This entire section seems to be on the margin between the juxtallocortex of the opercular surface and the dysgranular cortex of the lateral surface.

Section 600. Fig. 85.

The cortex cannot be read.

<center>BLOCK XIX (Fig. 86)</center>

Section 100. Fig. 87.

Anterior to *orp* the cortex is of general eulaminate type, total thickness 1.7 mm., outer main layer 0.82 mm., inner granular layer 0.18 mm., inner main layer 0.7 mm.

Just posterior to *ora* the cortex is of the same type but measures only 1.54 mm. The cortex is then cut too diagonally to read until one reaches the plica falciformis (*pf*), where it measures 1.85 mm., outer main layer 0.62 mm., inner granular 0.09 mm., inner main layer 1.14 mm. There is an irregular outer boundary between *i* and *ii*. There is a definite outer granular layer *ii* which contains also some small pyramids. The cells of *iii* are rather evenly distributed but the size varies in patches; in places there is a gradient, at others the larger pyramids extend out to *ii*, none, however, exceeds 26 x 16 μ. Layer *iv* is thin and irregular. The pyramids of *v* reach about the same size as those of *vi* and are thickest nearer *iv*. *vi* is very thick. This is dysgranular cortex.

On the opercular surface the cortex has a thin granular layer below, which becomes almost imperceptible above, but this cortex is cut too diagonally to read clearly.

Section 200. Fig. 87.

The cortex anterior to *orp* is now cut too diagonally to read. Between *orp* and *ora* it measures about 1.54 mm., where cut parallel to the columns, and can be seen to be of general eulaminate type. In the depths of *ora* there are numero s large pyramids in *iiic* which reach as much as 39 x 26 μ.

As one passes backward from *ora* the internal granular layer decreases in thickness gradually.
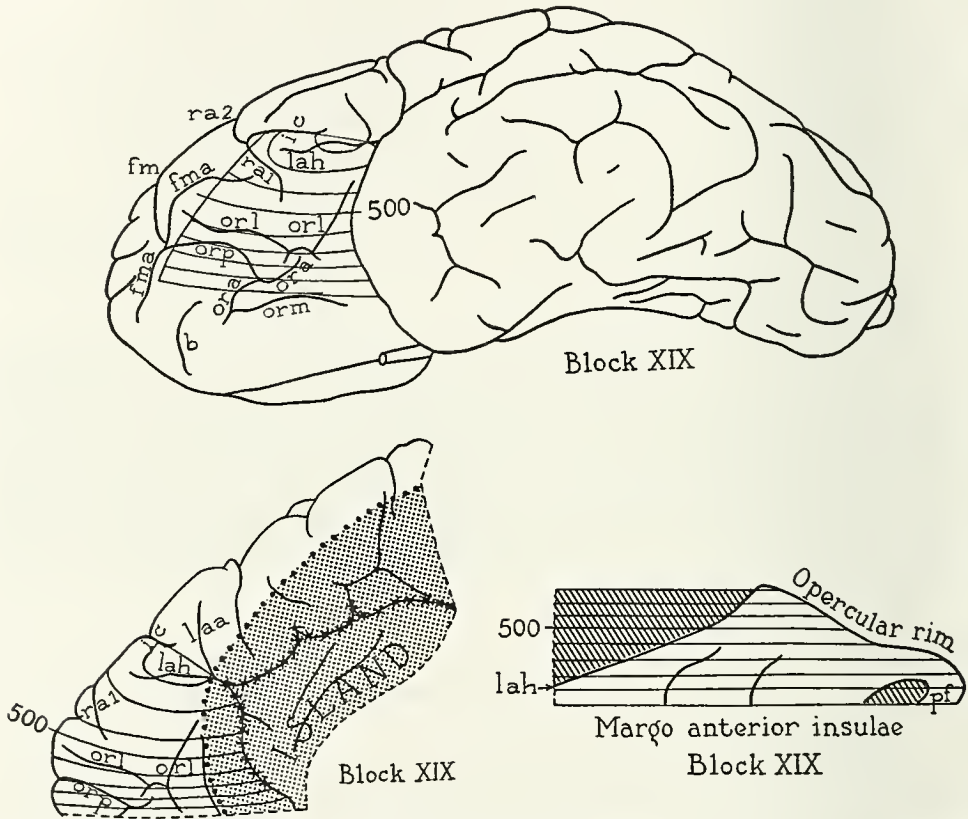
FIG. 86. Position of sections of Block XIX. Lines—transected white matter. Dotted—area covered by temporal lobe. Row of crosses—margin of island.

Above the plica falciformis, on the opercular surface, the cortex measures 1.85 mm. and is of the dysgranular type described in section 100. Cortex of this type covers the entire opercular surface.

Section 300. Fig. 87.

The cortex anterior to *orl* is cut too diagonally to read except just anterior to *orl* where it measures 1.7 mm. and is of general eulaminate type. Again in the depths of *orl* can be seen the big pyramids of *iiic* measuring up to 39 x 26 μ. This cortex is of inferior frontal type.

Posterior to *orl* the internal granular layer thins and the cells of *v* are larger and more numerous. This type of cortex is continuous over the opercular surface.
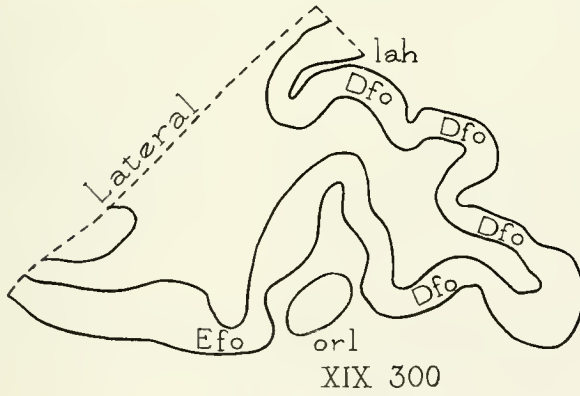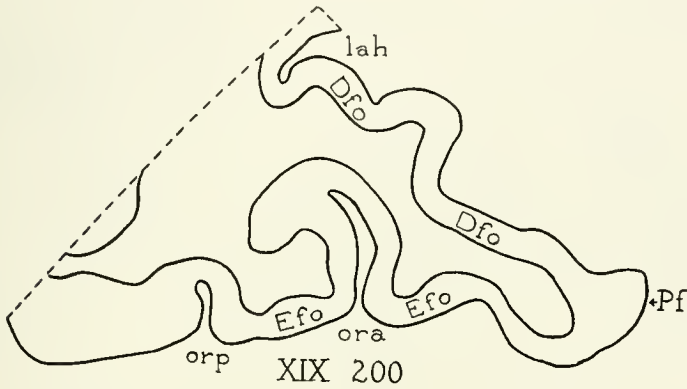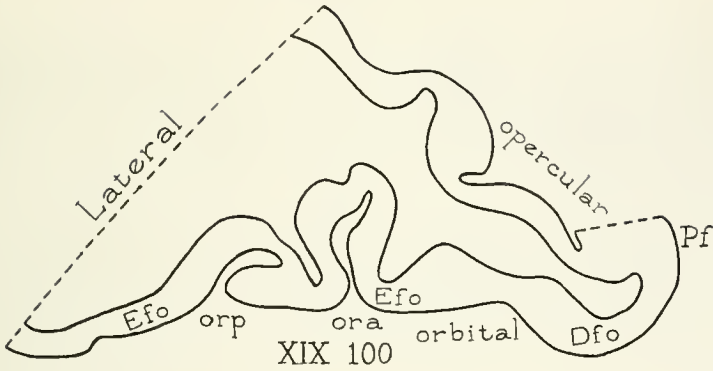
FIG. 87. Cross sections of Block XIX.

Section 400. Fig. 88.

The cortex anterior to *orl* is still cut too tangentially to read. In the depth of the posterior ramus of *orl* are the large pyramids in *iiic* before mentioned.

Posterior to *orl* the cortex is thin, measuring less than 1.54 mm. and is cut diagonally. One can see, however, that *iv* is thin and *va* heavy.
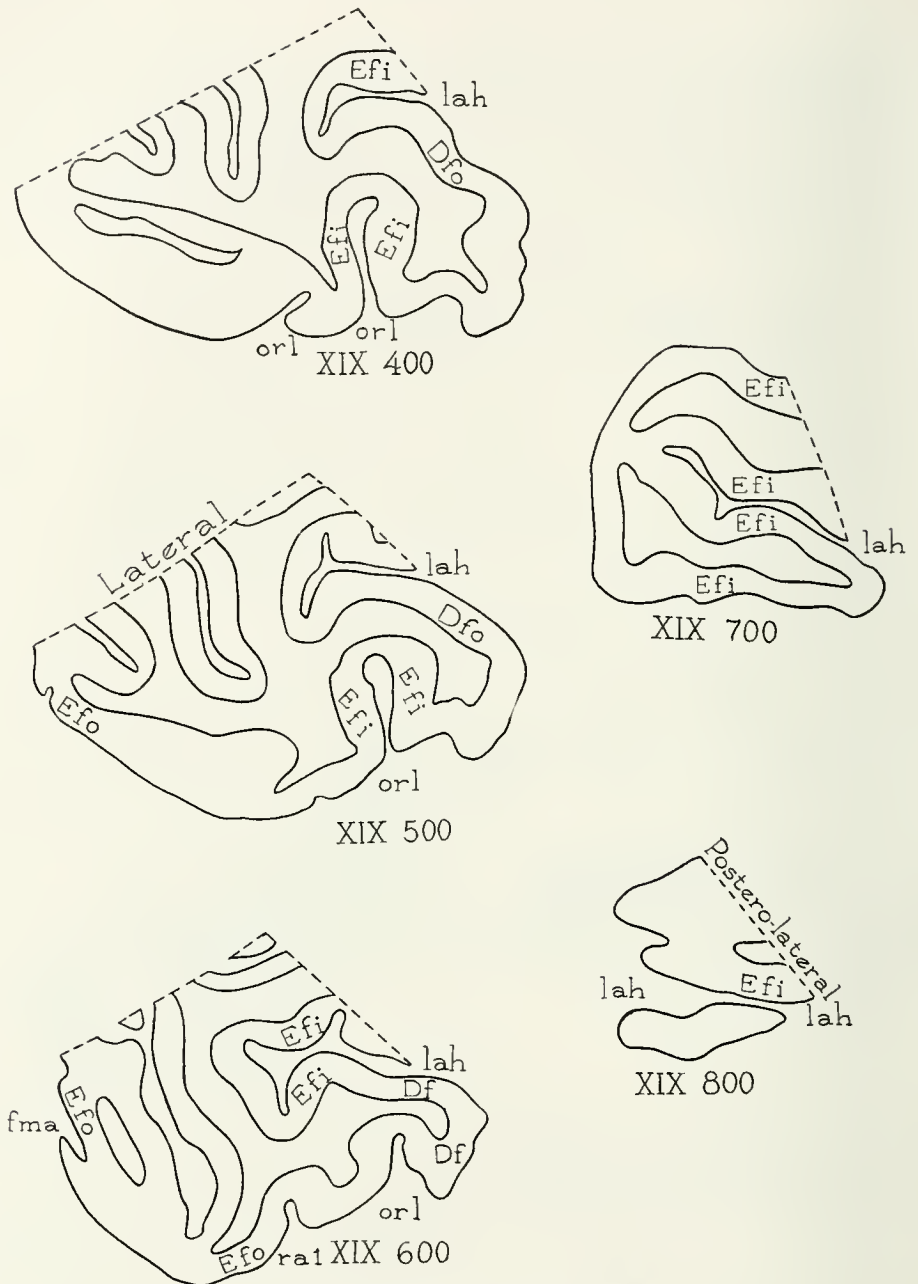
FIG. 88. Cross sections of Block XIX.

On the opercular surface the cortex measures about 1.7 mm. and is of the dys-granular type described in section 100, except above the deep sulcus *lah* where there are numerous large pyramids in *iiic* up to 42 x 26 μ, and those of *v* are much smaller and sparser. Layer *iv* is also thicker and evenly filled with granules.

Section 500. Fig. 88.

Near the anterior margin of the section the cortex at one short stretch is cut parallel to the columns. It measures 1.85 mm. and is of general eulaminate type. Just anterior to *orl* it is somewhat irregular but definitely of the same type. In the depth of *orl* one sees again the big pyramids in *iiic*. There are none in *v* but occasionally one is dislocated into *iv*.

Posterior to *orl* on the orbital surface the cortex is too irregular to read.

On the opercular surface the cortex is of the dysgranular type already described up to the deep sulcus *lah*. In its depth are large pyramids in *iiic* but, above, the pyramids of *iiic* do not exceed 21 x 13 μ and the cortex is of general eulaminate type.

Section 600. Fig. 88.

Anterior to *fma* the cortex measures 1.7 mm. and is of general eulaminate type. Anterior to *ra1* it is cut diagonally but measures 1.85 mm. and seems to be of the same type. Between *ra1* and *orl* the cortex looks much the same except that the inner granular layer is a little thinner. In the depth of *orl* the cells of *iiic* are distinctly larger, ranging up to 39 x 26 μ.
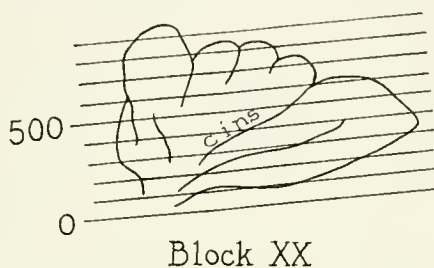
FIG. 89. Position of cross section of Block XX.

Over the opercular lip the cells of *iiic* are not above 24 x 16 μ but in the depth and upper wall of *lah* the large pyramids of *iiic* again become numerous. This cortex is of inferior frontal type.

Section 700. Fig. 88.

This section is covered entirely by eulaminate frontal cortex which varies only in the size of the cells of *iiic*. On the anterior surface they are small, not exceeding 24 x 16 μ. Over all the rest of the cortex the cells of *iiic* are much larger, ranging up to 42 x 26 μ.

Section 800. Fig. 88.

In the one short stretch where the cortex can be read it is of frontal inferior type with well developed inner granular layer and large pyramids in *iiic*.

BLOCK XX (Fig. 89)

Section 100. This section is not figured.

Over the limen insulae (*li*) is allocortex (*A*) with no trace of lamination.

Posterior to the limen is a narrow bit of cortex with a very poor lamination, no definite *iv* and bunchy *ii* which might be called juxtallocortex.

Section 200. Fig. 90.

Anteriorly there is some sketchy indication of lamination but the cortex is cut very diagonally for the most part.

Above there is a thin stretch of nondescript cortex which has no lamination and the cells under the plexiform layer are collected in large bunches.

Behind this thin stretch begins a cortex well laminated with definite inner and outer granular layers, measuring about 1.85 mm. in total thickness, outer main
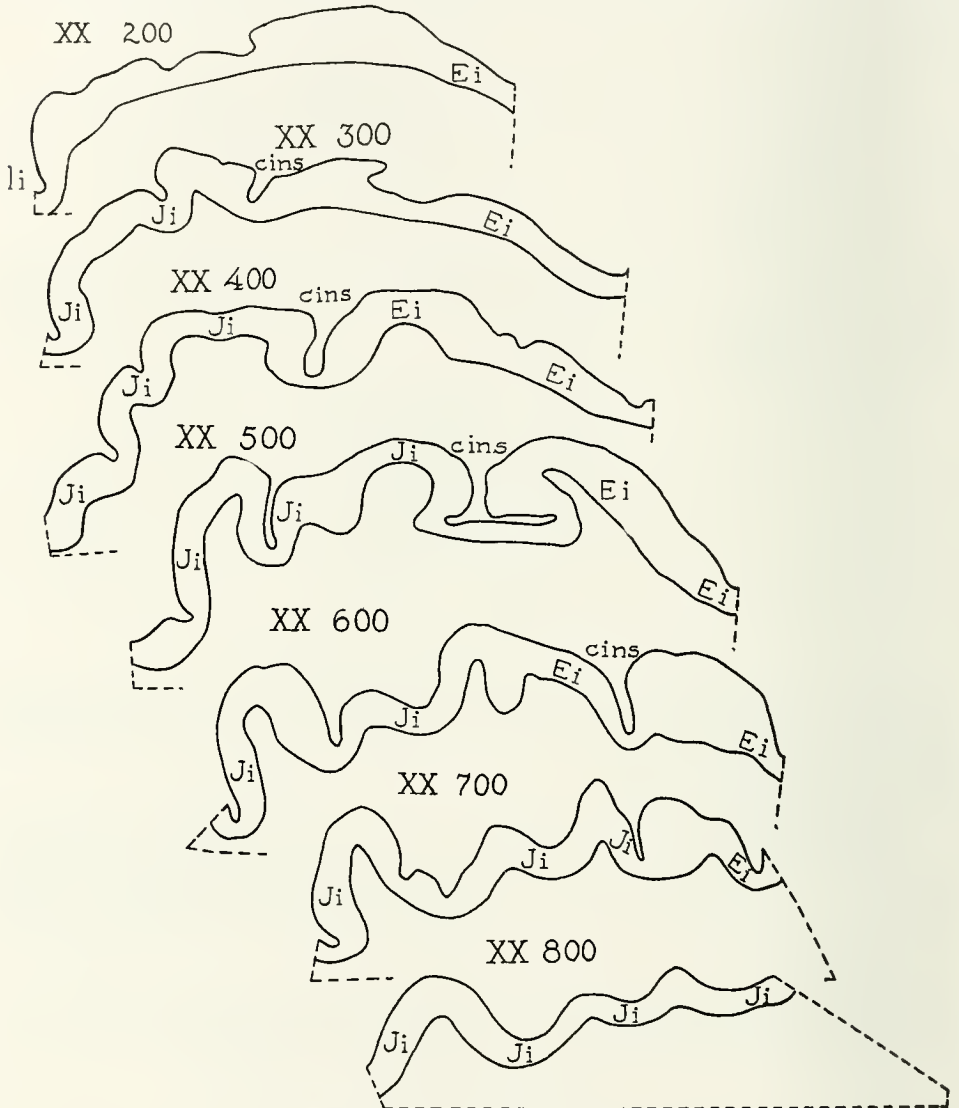
FIG. 90. Cross sections of Block XX:

layer 0.93 mm., inner granular 0.15 mm., inner main layer 0.77 mm. The outer granular layer is distinct from *iii*, which has a definite cell gradient although the largest pyramids in *iiic* do not exceed 24 x 16 μ. The pyramids of *v* are about the same size as those of *iiic*. Layer *iv* is well filled with granules; there is a slight tendency for those in the deeper sublayer to be more deeply stained.

Section 300. Fig. 90.

Anteriorly the cortex is cut most diagonally but where it can be read, it has an irregular *ii*, a thin inner granular layer and very little cell gradient in *iii*. It is of juxtallocortical type. There is a tendency for the cells of *v* to accumulate just below the scanty *iv*.

There is a narrow thin stretch of nondescript isocortex behind *cins* followed posteriorly by the eulaminate cortex previously described in section 200.

Section 400. Fig. 90.

The juxtallocortex extends from the anterior extremity posteriorly to the posterior lip of the sulcus centralis insulae (*cins*) before giving way to the eulaminate cortex previously described.

Section 500. Fig. 90.

Juxtallocortex anterior to *cins*, eulaminate cortex posteriorly.

Section 600. Fig. 90.

Same as before, except that the eulaminate cortex now extends anterior to *cins*. The anterior cortex contains throughout the thin *iv* and heavy *va* before described.

Section 700. Fig. 90.

Only the posterior short gyrus is covered by eulaminate cortex.

Section 800. Fig. 90.

There is no good eulaminate cortex anywhere on this section. On the anterior wall the cortex is thicker, has a thicker internal granular layer and the cells of *v* are better distributed.

Section 900.

Cannot be read, and so is not figured.

BLOCK XXI (Fig. 91)

Section 100. Fig. 92.

Anterior to the intraparietal sulcus (*ip*) the cortex measures 1.8 mm. It is cut slightly diagonally to the columns but it can be seen to be of the superior parietal type. The outer main layer measures 0.8 mm., the inner main layer about the same. the *iv* layer is about 0.15 mm. and one can distinguish a lighter *iva* from a darker *ivb* which merges with *va*. Layer *vb* contains fewer and smaller cells. The pyramids of *va* are about the same size as those of *iiic* which do not surpass 26 x 16 μ.

The angular gyrus between *ip* and *pol* is cut too tangentially to read but in the depth of the lateral parieto-occipital fissure (*pol*), the cortex is reminiscent of the parastriate type on the anterior wall. The cortex measures here 1.43 mm., outer main layer 0.8 mm., inner 0.46 mm. *ii* cannot be separated from *iiia*, the pyramids of *iiic* are larger (up to 37 x 24 μ), *iv* is quite distinct and uniform, *v* is relatively empty, *vi* is thin and sharply bounded against the subcortex, the columns are broad and extend through *iiib*.

There is a buried gyrus which is cut tangentially but seems to be covered by similar cortex.

The cortex over the two narrow gyri posterior to *pol* also resembles the parakoniose type. It measures 1.3 mm. over the anterior and 1.24 over the posterior gyrus. Both contain very large pyramids in *iiic*, up to 34 x 21 μ but scattered in patchy fashion.

Section 200. Fig. 92.

The cortex anterior to *po* is of superior parietal type measuring 1.64 mm. The cortex over the next gyrus posteriorly measures 1.85 mm., being cut diagonally to the columns but resembles superior parietal cortex, outer main layer 0.68 mm., inner 1.0 mm.; the dark band made by *ivb* + *va* is, however, not very evident, and the pyramids of *iiic* are large. On the anterior lip of *pol1* the cells of *iiic* are very large, many of them measuring as much as 58 x 31 μ; some in *v* are 39 x 13 μ.
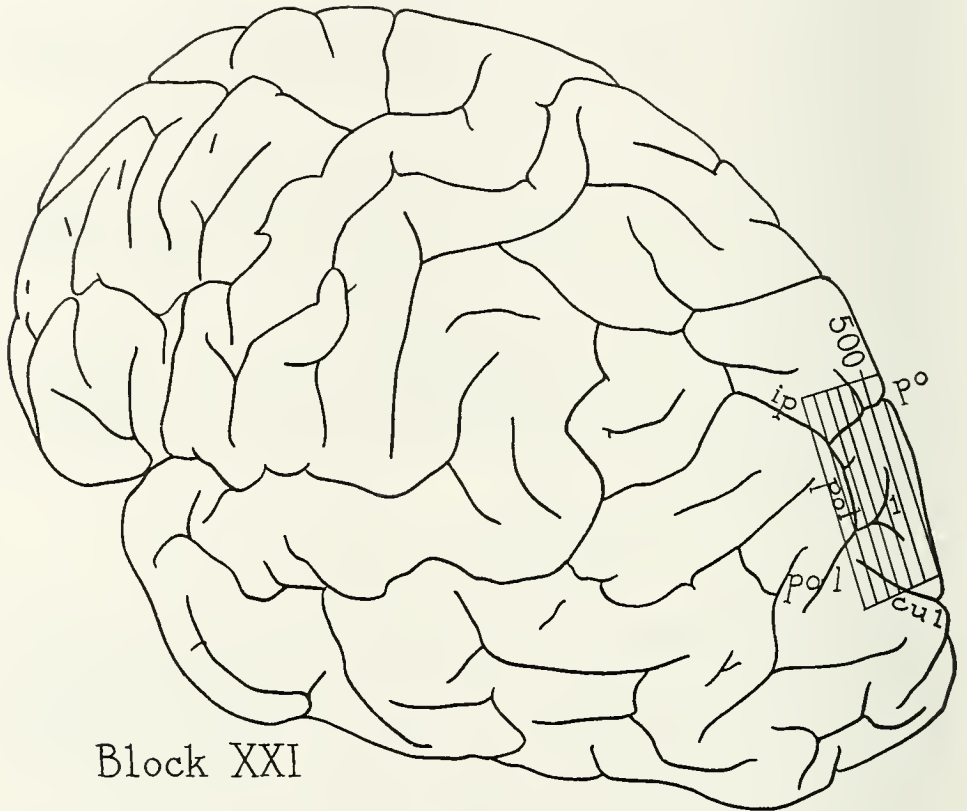
Fɪɢ. 91. Position of sections of Block XXI.

Posterior to *pol1* the cortex thins to 1.49 mm., outer main layer 0.83 mm., inner 0.55 mm. The boundary between *ii* and *i* is smoother than it is anterior to *po*, the cells of *iiic* are larger, the columns broader, *v* emptier, *vi* thinner and more sharply separated from the subcortex.

All of the cortex behind *pol1* is of parakoniose type. The transition occurs on the anterior lip through a zone of thicker cortex with huge cells in *iiic* and *v*.

Section 300. Fig. 92.

Anterior to *po* the cortex, measuring 1.85 mm., is very unusual. The cells of *iv*, *v*, and *vi* are almost of a uniformly small size so that the layers must be distinguished largely by their density, *va* and *via* being recognizable in this way because they are more dense than *vb* and *vib*. Even the pyramids of *iiic* are unusually small and slen-

der, scarcely reaching 31 x 13 μ. The lamination is quite evident in spite of the generally small size of the cells.

Posterior to *po* the cortex thins greatly to 1.08 mm., the transition occurring in the depth of *po*. Here the cortex has an outer main layer of 0.46 mm., inner 0.49 mm., the columns broad, the pyramids of *iiic* larger (up to 34 x 31 μ). The only character reminiscent of the parietal cortex is the faintly evident band of *ivb* + *va*.
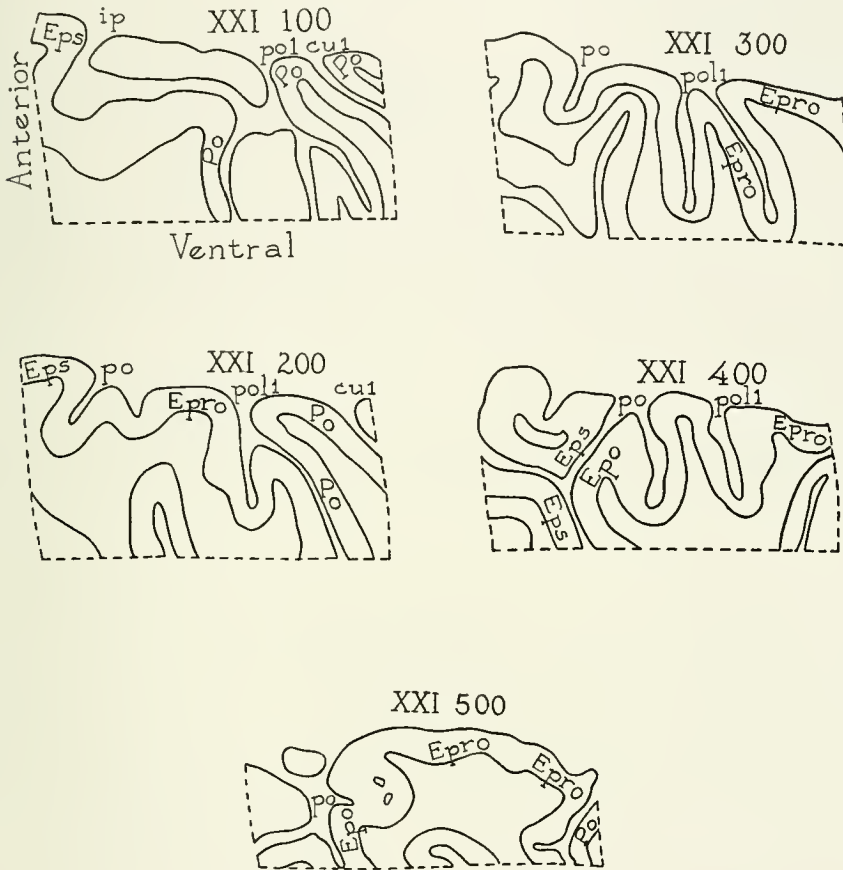
Fig. 92. Cross sections of Block XXI.

The cortex over the posterior gyri measures about 1.5 mm., outer main layer 0.62 mm., inner 0.71 mm. The pyramids of *iiic* are smaller, as a rule, the columns are thinner and *v* is better filled. There are occasional larger pyramids. The cortex here is of eulaminate occipital type.

Section 400. Fig. 92.

The cortex over the posterior gyrus is of eulaminate occipital type, measuring 1.4 mm. in thickness.

The cortex of the narrow gyrus is less typical; it measures 1.54 mm., outer main layer 0.53 mm. It is difficult to draw a boundary between *vi* and *v* which is well

filled with very small pyramids, much smaller than those of *iiic*. Even the boundary between *iv* and *v* is not clear.

The remainder of the cortex in the posterior wall of *po* is similar to that just described but in the depth the cells of *iiic* become again very large as previously described for section 200 in the anterior lip of *po1*.

The cortex in the anterior wall of *po* measures 1.54 mm. also, but differs from that of the posterior wall in the definite heavy band made by *ivb* and *va*. The cortex here is of superior parietal type.

Section 500. Fig. 92.

The cortex anterior to *po* is cut too tangentially to read.

In the posterior wall of *po* it measures 1.3 mm., outer main layer 0.58 mm., inner 0.56 mm. The pyramids of *iiic* are mostly small with a few of medium size. Layer *v* is rather well filled.

Over the top of the broad gyrus the cortex is similarly constructed but measures 1.54 mm. It does not become definitely occipital in type until one reaches the posterior small fragment of gyrus. Here the cortex measures only 1.3 mm., outer main layer 0.56 mm., inner 0.58 mm. Layer *v* is relatively empty, the cells of *iiic* large and *vi* rather abruptly bounded from the subcortex.

Section 600.

The cortex is cut too tangentially to read, and so is not reproduced.

The frontispiece and figures 95 and 96 have been drawn on the basis of data contained in this chapter.

Chapter VI: The Brain Map

Unless the criteria are clearly stated and objectively verifiable . . . architectonic charts of the cortex represent little more than the whim of the individual student.

<div align="right">

LASHLEY AND CLARK (1946)

</div>

After long and careful study of the human isocortex the main impression we have retained is that vast areas are so closely similar in structure as to make any attempt at subdivision unprofitable, if not impossible. We have, in the frontispiece, summarized the main facts of cortical differentiation in such a manner as to show not only the extent of certain structural peculiarities but also their nature. In this map each color represents a definite feature. *Blue* is used for the allocortex and *red* represents granules in the isocortex. Usually at the boundary between isocortex and allocortex we find juxtallocortical transitions which are represented in *purple*—a mixture of red and blue. Granulose areas, called by Economo koniocortices, are *deep red* and the eulaminate isocortex, which contains fewer granules, is *pink*. The agranular cortex is *yellow* and the dysgranular becomes *orange*, since it contains a tenuous inner granular layer. The anterior limbic area, which is agranular but has allocortical traits, becomes *green*. Areas containing large pyramids in *iiic* add *black* to the *pink* of the eulaminate cortex and become *brown*. Since the gigantopyramidal area of the precentral agranular cortex contains also large pyramids in *iiic*, it becomes *grayish*. Minute variations in the eulaminate isocortex are ignored; not only are they so tenuous as to defy recognition but any significance that they might have is totally unknown.

The drawing of sharp areal boundaries, on the basis of many structural peculiarities of varying distinctiveness and significance, is the fundamental defect of most maps and has been carried to absurd lengths by the Vogt school. Another defect of all published black-and-white maps, which attempt to combine the delineation of many structural features, is the failure to represent transitional areas. The result is that such maps as those of Campbell (our Fig. 2), Brodmann (our Fig. 93), and Economo (our Fig. 94) give a false impression of sharpness of areal boundaries and fail to distinguish subdivisions, based on important and distinct differences, from tenuous and inconstant variations.

Areas recognized early by Meynert, Betz, and others as having distinctive structure had proven also to be related to different functions. Brodmann (1914) lists them as: (1) *regio praecentralis*, (2) *regio postcentralis*, (3) *area striata*, (4) *regio supratemporalis*, (5) *regio hippocampica*, (6) *regio insularis*, (7) *regio infrafrontalis*, and (8) *regio retrosplenialis*. He called them the physiologically most important (*wichtigste*) areas, although it is evident that he did not know what function the insular and retrosplenial regions might subserve. But that must have left students of cytoarchitectonics, operating (as pointed out in the Introduction) on the hypothesis that the cortex is a mosaic of discrete organs, distressed at the vast unsubdivided territories in the frontal, temporal, parietal, and occipital regions.

Hence they attempted to isolate, in the remaining cortex, areas of distinctive structure which might also prove to be organs of special function. Unfortunately

FIG. 93. Map of the cytoarchitectonic areas of the human cerebral cortex (from Brodmann).
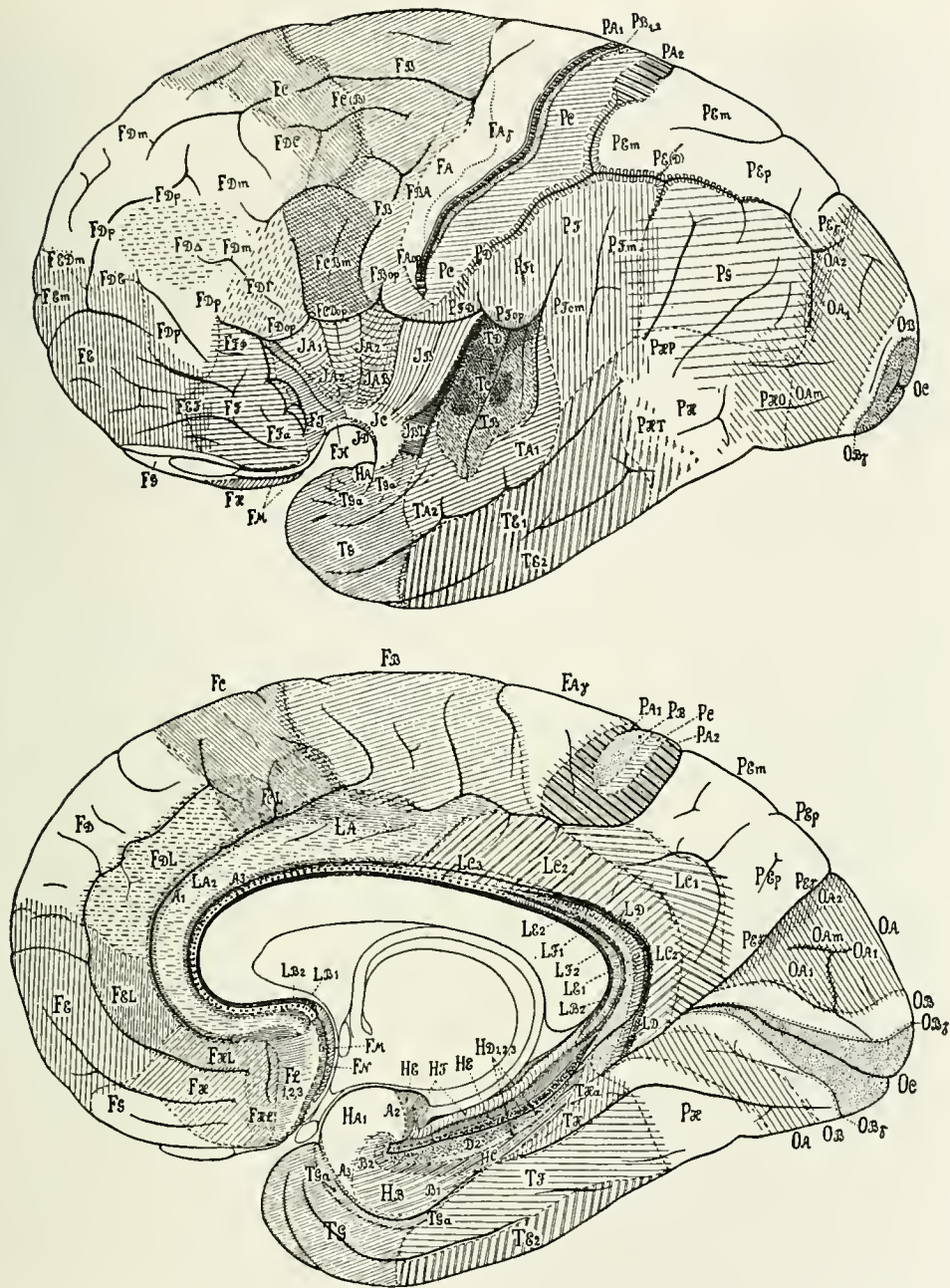
FIG. 94. Map of the cytoarchitectonic areas of the human cerebral cortex (from Economo).

the remainder of the cortex was of such uniform structure that the results, as Brodmann says (1905), were somewhat gratuitous (*etwas willkürlich*). Unfortunately the purely tentative results of Brodmann (for the human brain he never published

his data so that it is impossible to check them) have been accepted by physiologists as of divine authority and a vast superstructure has been built on this shaky foundation which is now being extended to the human brain by the neurosurgeons.

We shall now attempt to describe the distribution of the isocortex and its structural variations as they were defined in chapters IV and V.

The larger portion of the cerebral cortex has the typical eulaminate structure (IE) to be seen in Plate II. This cortex covers vast areas of the frontal, parietal, and temporal regions, proportionately a larger area of the cortex than in either the monkey or chimpanzee. We told (p. 62) how we made photographs from divers parts of this vast expanse, pasted them onto cards, and then shuffled them like playing cards. It is true that, if any two photographs are placed side by side, differences can be described between them but these differences are rarely greater than those to be found on different parts of the same gyrus. Only when we were able to teach ourselves to recognize differences, without knowing the provenience of any section, have we taken such distinctions seriously. The following pages will give examples showing how previous authors have struggled with tenuous differences. Let us begin with the frontal lobe.

We have never been able to find any account of the data on which Brodmann (1907) established his subdivisions and only brief descriptions of areas *1, 3, 4, 6, 17,* and *18* (Brodmann, 1914). We may note, therefore, the general resemblance of his map to that of Economo and confine our attention to the latter's account. Economo distinguishes many areas denoted by the capital letter F followed by other alphabetic signs as follows: FA, FB, etc., up to FM. He designates areas of intermediate structure thus: FBA, $FC(B)$, FDC, FHL, etc. Further subareas are denoted by adding small letters thus: FDm, $FCBm$, $FAop$, or capital Greek letters as in $FD\Gamma$ or $FD\Delta$.

All authors agree that, within the frontal lobe of classical anatomy, two regions can be distinguished: an agranular precentral and a granular frontal or, as some authors prefer to say, "prefrontal" region. These two regions differ not only in their intrinsic structure but also in their afferent connections (see Chap. VIII, especially Fig. 115) and can therefore be considered as belonging to two different "sectors."

The precentral region was divided by Economo into three or four areas. Beginning at the central sulcus these were $FA\gamma$, FA, $FA(B)$, and FB. Bonin (1949) followed him and, adopting Brodmann's numerical system, called these areas *4γ, 4a, 4s,* and *6.* In area *4s* Bonin described particularly large pyramidal cells in layer *iii*. He identified this area with the suppressor area of Hines (1936) and of Dusser de Barenne and McCulloch (1941). Economo and Koskinas (1925) had previously published a map (their Fig. 74, p. 131) showing a band of large cells in *iii* at the anterior margin of their FA. This we cannot find in brain Hl and it seems unlikely that such a conspicuous band could have been missed by Betz, Campbell, Brodmann, Ngowyang, and Kononova.

The criteria used for distinguishing the two major areas FB and FA (not $FA\gamma$) are:[1] (Economo, 1929a, p. 34) "FB shows, as compared with FA, (1) a general

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[1] All quotations from Economo are from the English translation by Dr. S. Parker (Economo, 1929a) unless otherwise noted but, after comparison with the original German text, we have sometimes changed the wording of Parker's translation.

narrowing of the cortex, (2) a finer more regularly radiate arrangement, and (3) an abrupt [*sic!*] thickening of layer III." One may object that the layers are not distinct so that measurement of their thickness is dubious and that it is not clear whether what Economo calls *III* (*II*) and *III* (*IV*) are included; if they are, then on his figures 11 and 13 the thickness of *III* is identical. His own figures show neither this thickening of *III* nor the general thinning of the cortex as a whole; if both are true, *III* should be comparatively much thicker in *FB*. All these criteria should make a conspicuous boundary which we cannot find in brain *Hl*.

We see no reason, therefore, to distinguish an *FA* free of Betz cells from the rest of the simple frontal agranular cortex (*FB*). We are left, therefore, for the moment with an area containing Betz cells and a simple agranular area in front of it. The former is our isocortex agranularis gigantopyramidalis—*I*AG*prc*—(see Chap. IV, p. 73, Plate VIII), the latter our isocortex agranularis simplex—*I*AX*prc*—(see Chap. IV, p. 72, Plate VII).

If, now, we attempt to define the boundaries of the isocortex agranularis giganto-pyramidalis praecentralis (*I*AG*prc*, Plate VIII), we become aware that there is no generally accepted definition of a Betz cell. The largest cells in layer *v* of the pre-central cortex are situated on the medial surface of the hemisphere and they de-crease in size as one passes over onto the superior and down the lateral surface of the hemisphere until, near the inferior extremity of the central sulcus, one finds cells which, although larger than their neighbors, would scarcely qualify if situated in the paracentral lobule. Again, if one depends on the fact that these cells are con-spicuously larger than their neighbors, then one finds such cells in layer *v* of the postcentral, occipital, and inferior frontal regions. These last were described also by Betz (1881). Economo (1929a, p. 62) attributes their discovery to Hervé, but the latter merely refers to Betz in a footnote; there is nothing in his thesis to indicate that he himself had ever seen them. We must restrict the term Betz cells to con-spicuously large pyramids in layer *v* of the precentral agranular cortex. As such their area of distribution is broadest on the medial surface of the hemisphere and rapidly narrows as one passes over the lateral surface until, in the region which can be shown by electrical stimulation to serve the arm, it does not cover the entire precentral gyrus and, in the "face" area, it is entirely hidden on the anterior wall of the central sulcus.

Since, by definition, the anterior margin of the gigantopyramidal area is marked by the most anterior Betz cells, one must conclude that this margin is very irregular since isolated, conspicuously large, pyramids are often found far forward of the others; there is no neat anterior boundary. One can establish this boundary only for the particular section which is being examined. But any accurate boundary drawn on the map of the brain would be very irregular and, if one is to judge from the maps of Brodmann (1903a), Economo (1929a), Campbell (1905), and others, would vary for each individual brain. There is, however, general agreement that the area is broadest on the medial aspect of the hemisphere and gradually recedes into the central sulcus as one passes lateral and inferior (Fig. 95).

Within the gigantopyramidal area one finds conspicuously large pyramids also in *iiic*. In the map given by Economo and Koskinas (their Figs. 74 and 75), these cells are represented only in the posterior zone of what in their figures 92 and 93
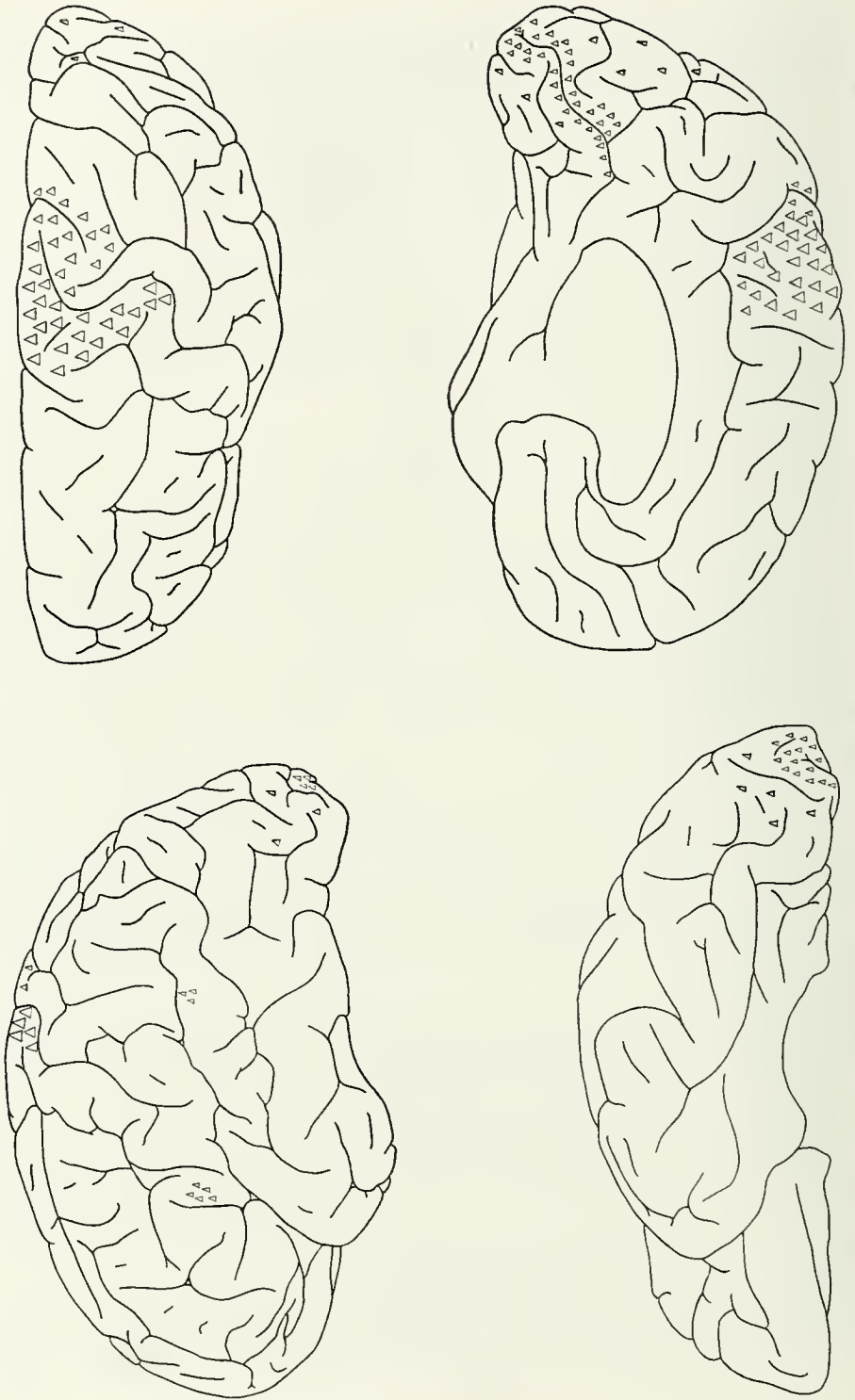
Fig. 95. Distribution of cells conspicuously larger than their neighbors in layer v of brain Hl; those in the buried cortex are not shown.

is labeled *FB* but, in the text, they state that such cells are more numerous in the anterior parts of *FA*. Economo (1929a, p. 29) mentions these cells only in his description of *FA*. In brain *Hl* we have found them throughout the gigantopyramidal area. Their anterior extent differs little from that of the Betz cells. Where there are no Betz cells they are more conspicuous but they are equally distributed throughout the gigantopyramidal area (Fig. 96). The map of Economo and Koskinas, therefore, gives a false impression of the distribution of these cells and one, moreover, in contradiction with their own description. From what has just been said about the large pyramidal cells in *iiic*, it should be clear that an "area 4s" can no more be recognized.

Medially the gigantopyramidal area extends almost to the cingulate sulcus. Large pyramids are found within layer *v* in the walls of the posterior portion of the cingulate sulcus but always accompanied by an internal granular layer. The posterior margin of the area corresponds closely with the depth of the central sulcus, throughout most of its course. At the mediosuperior extremity the boundary leaves the sulcus and runs anterior to it; at the latero-inferior extremity the boundary ends on the anterior wall.

Anterior to the gigantopyramidal area is, therefore, only the simple agranular frontal cortex (*IAxprc*) which Campbell (1905) called intermediate precentral. Just as the gigantopyramidal area, it is broader on the medial aspect of the hemisphere and narrows laterally and inferiorly. Its posterior margin, in its boundary with the gigantopyramidal area, is irregular; this has been described with sufficient length. This simple agranular cortex extends medially to the depth of the cingulate sulcus and latero-inferiorly to the opercular lip. In brain *Hl* it does not extend onto the upper wall of the lateral fissure but in others, according to Economo (1930b), it may do so.

The inferior boundary of the frontal agranular cortex is vague and so is its anterior border. As one passes anteriorly, granules become progressively more numerous until they form a distinct inner granular layer. At no point does this begin abruptly. The zone with indistinct tenuous internal granular layer is by definition Economo's *FC*. It extends from the upper lip of the cingulate sulcus to the frontal operculum but has no definite anterior or posterior margin. Not only does the number of granules vary continually in this dysgranular zone but it has other local variants. Near the cingulate sulcus, the number of cells in *v* increases, hence Economo calls this region *FCL*. Over the inferior frontal gyrus there are larger cells in *iiic*, also often in *v*, to produce a variant which was recognized by Betz, Hammarberg and practically all later authors and which we have called *IDfi*. The dysgranular zone continues over the operculum onto the anterior part of the island (Economo's *IA*) and the posterior portion of the orbital surface of the frontal lobe, i.e., the pars orbitalis of the inferior frontal convolution where it is called *FF* by Economo.

Ngowyang (1934b) says of this dysgranular zone, "Brodmann has not extended these weakly granular formations far enough below; for, as we could determine in our case and as Riegele had already seen in another brain, not only our area *55* (the lower part of Brodmann's area *9*) is weakly granular, but also the area *56* (homologous with the posterior part of his *44*) and the area *41* (the lowest part of
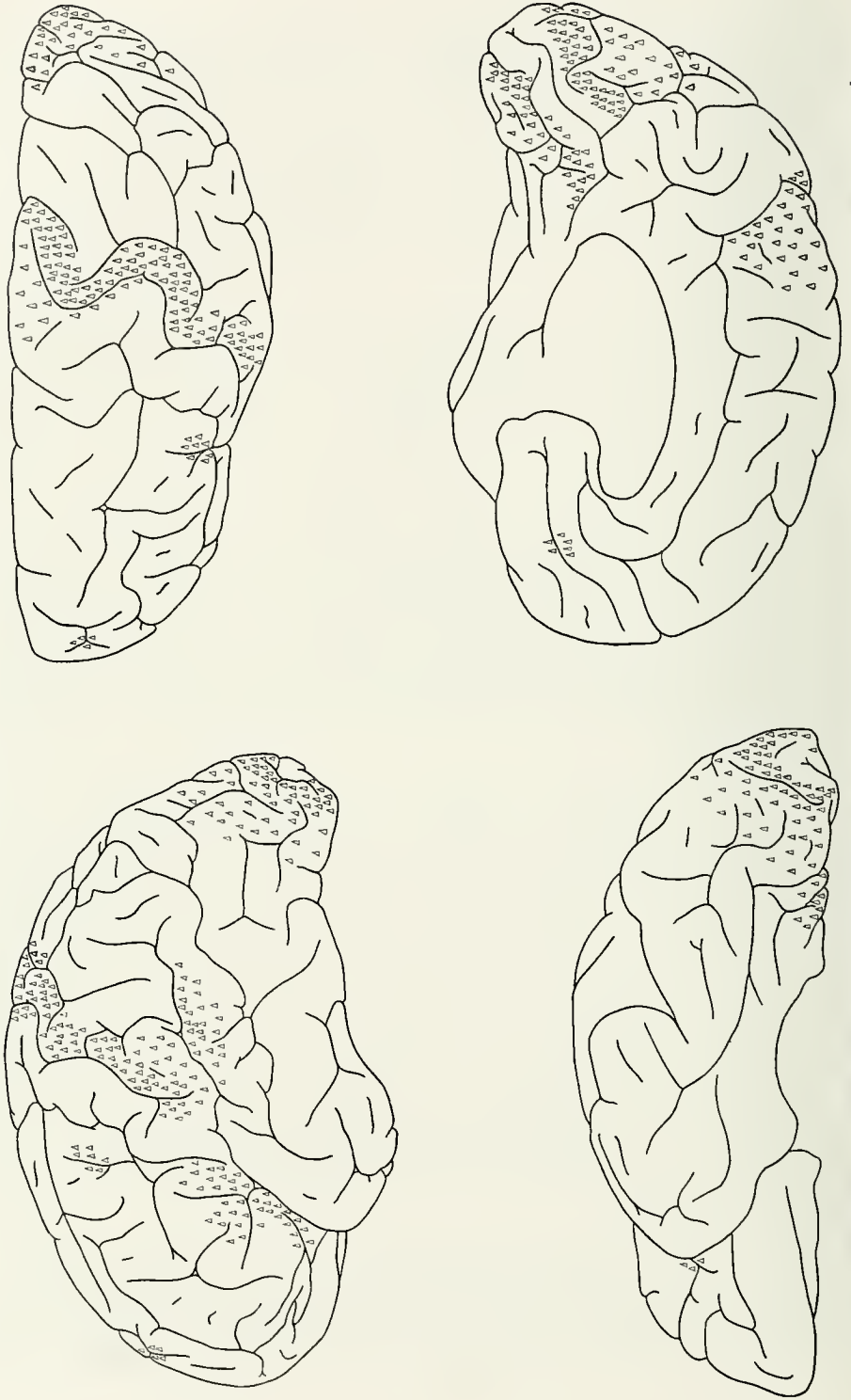
Fig. 96. Distribution of cells conspicuously larger than their neighbors in layer *iiic* of brain *Hl*; those in the buried cortex are not shown.

his area *6*) or the ventral parts of *FB* of Economo and Koskinas. This difference may be only caused by individual variation." (See Fig. 97).

Beyond this transitional zone, to which we shall have to revert later, we enter the frontal or "prefrontal" sector. We shall begin with its lateral aspect. A comparison of the map in our frontispiece with the map of Campbell (1905, our Fig. 2), will reveal a marked resemblance, especially in regard to the large undifferentiated areas of the frontal, parietal, and temporal lobes; the original description of Betz (1881) is not much different. Campbell subdivided the frontal cortex into "frontal" and "prefrontal" but, as he remarks, their structural differences are of a "subtle description." Economo (1929a) states that the structure of the frontal pole differs essentially only in its greater thinness and the smaller size of its cells, and this is a gradual change which progresses from the precentral cortex to the frontal pole, a statement with which Campbell agrees. Jakob (1943) says that the frontal lobe, anterior to the precentral region, is of "perfectly uniform" structure. It is obvious that the distinction made between "frontal" and "prefrontal" rests upon structural differences of an entirely different order from those used to distinguish "frontal" from "precentral."

In the frontal cortex anterior to the dysgranular zone Economo recognized *FD* and *FE* as major types. Of *FD* he says (p. 39), "The structure of the area changes frequently." He distinguishes *FDm*, *FDp*, *FDΔ*, *FDop*, *FDΓ*, *FDL*, and *FDE*. He met the same difficulty in *FE* (p. 40). "The structure of FE is not the same everywhere." Consequently he distinguishes *FEL*, *FEm*, *FEDm*, and *FEF*. But even the distinction between *FD* and *FE* is not very clear. In his own words: (p. 39) "the typical frontal attenuation of the cortex becomes more pronounced in FE, the reduction of cell size becomes more evident, the sharp distinction from the white matter gets more striking, and II and IV become gradually more evident. But the transition between the two is only gradual. The extension of FE and the breadth of the gyri seem to have a connection in the sense that this area covers only the quite narrow types of gyri." Economo notes (p. 40), "the marked [*deutliche*] radiate striation just at the pole" although he had previously stated (p. 14) that "In the frontal lobe there is almost no striation, traces of such an arrangement being most easily found in the pars triangularis, and faintly at the base of all three frontal gyri, occasionally also at the frontal pole." It has been our experience that the cortex over narrow gyri is usually thinner and the radiations more evident. Quite apart from the extreme variability of the pattern and size of the frontal gyri, it is evident that the distinction between *FD* and *FE* is very precarious and based on no feature which would seem from any viewpoint to be important.

The distinction of most of the subvariants of *FE* and *FD* seems to us even less important. Economo (1929a) distinguishes an *FDm* from an *FDp* on the basis of cell size. Since the cortex of the frontal pole differs little except in the small size of its cells, he could just as well have written *FDe* instead of *FE* and the entire "prefrontal" region would have been *FD*.

In the recent neurosurgical literature (Mettler, 1949) much is made of the results of extirpating Brodmann's area *9*. The term area *9* appears to be no more than a topographical designation and corresponds roughly to Economo's *FDm*. Ngowyang and Jakob were unable to find any such area. On the other hand, Kononova's (1934) area *9* assumes even more bizarre shape than Brodmann's (Fig. 98).

Economo distinguishes also a variant $FD\Delta$, described as follows (p. 62): "In its circumscribed area the frontal granular cortex becomes thicker and distinctly
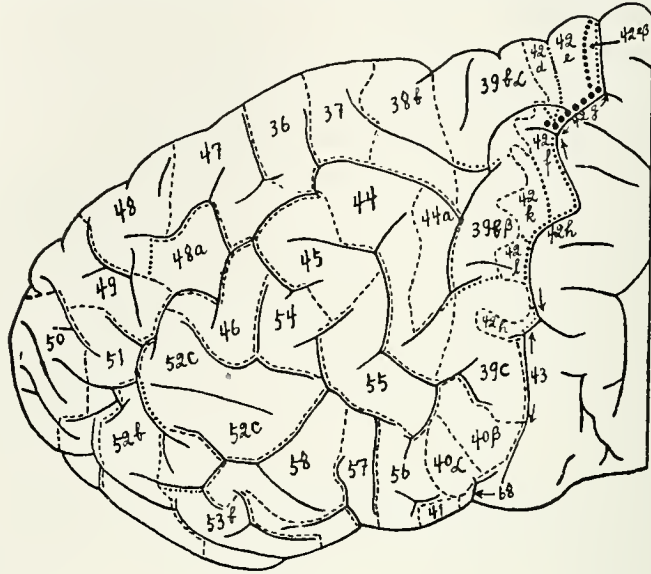
Abb. 1
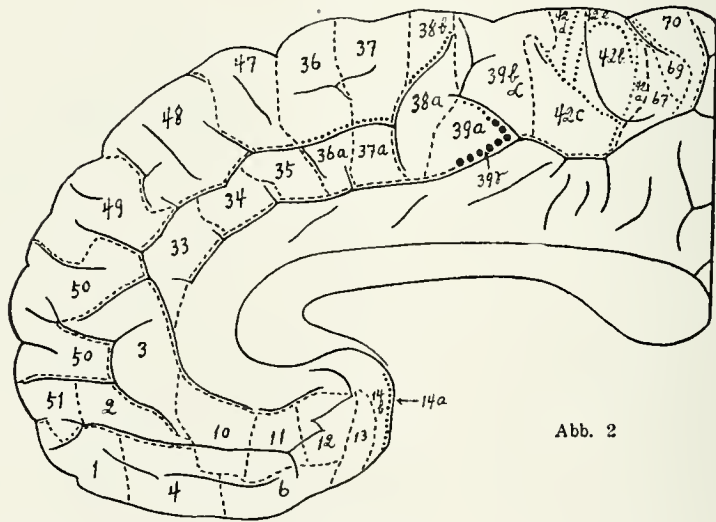
Abb. 2

FIG. 97A

FIG. 97 (Above and on opposite page). Ngowyang's map of the architectonic areas of the frontal lobe.

richer in smaller, more compactly arranged cells. II and IV become considerably broader and more densely supplied with cells than anywhere else in the frontal brain. The pyramidal cells of III are moderately large, at best, but they are more
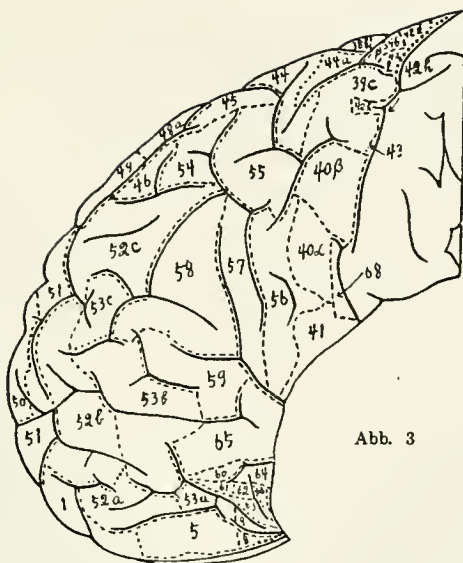
Abb. 3
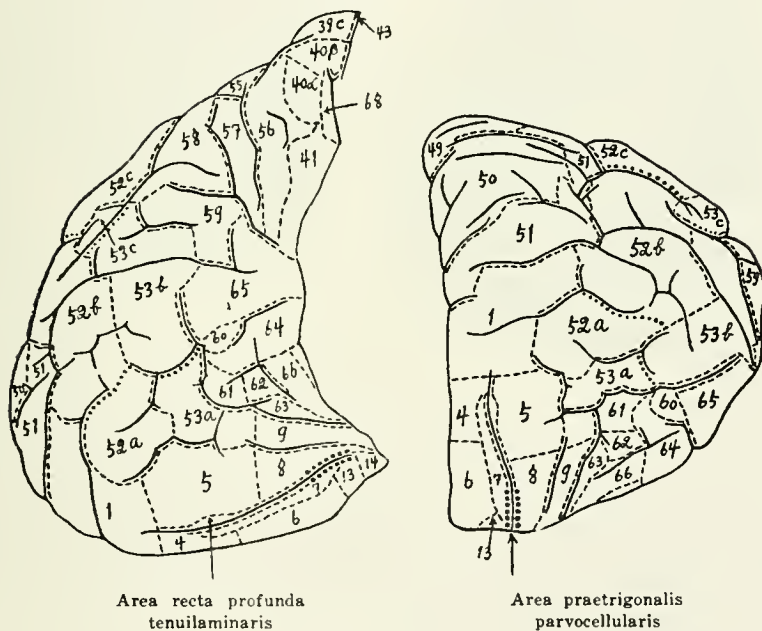
Area recta profunda
tenuilaminaris

Area praetrigonalis
parvocellularis

FIG. 97B

numerous and densely placed than elsewhere, without forming a substratum IIIc. V is also regularly and densely packed, and does not show two subdivisions as in FD elsewhere. The border between V and VI is indistinct."

This variant $FD\Delta$ appears, on Economo's map, to occupy approximately the same location as Brodmann's *46*. Brodmann, as previously noted, never described the

structure of his area *46*, but Kononova (1938) has outlined on several frontal lobes an area of bizarre and varying shape which she implies is Brodmann's area by numbering it *46* (see Fig. 98). Her description follows: "It is characterized by its width (3.22 mm.) mainly due to the III layer. Both strata are approximately equally wide. The cells are of average size, more or less uniform. Their number is very great. Fine radial markings, due to the regular orientation and arrangement of cells, is found in all layers. The II and IV layers are well developed. The horizontal striation is distinct. The boundary between the VII layer and the white matter is not sharp."

Ngowyang (1934b) describes in great detail the regio frontalis granularis, compares his description with that of Economo and Koskinas and tries to relate it also
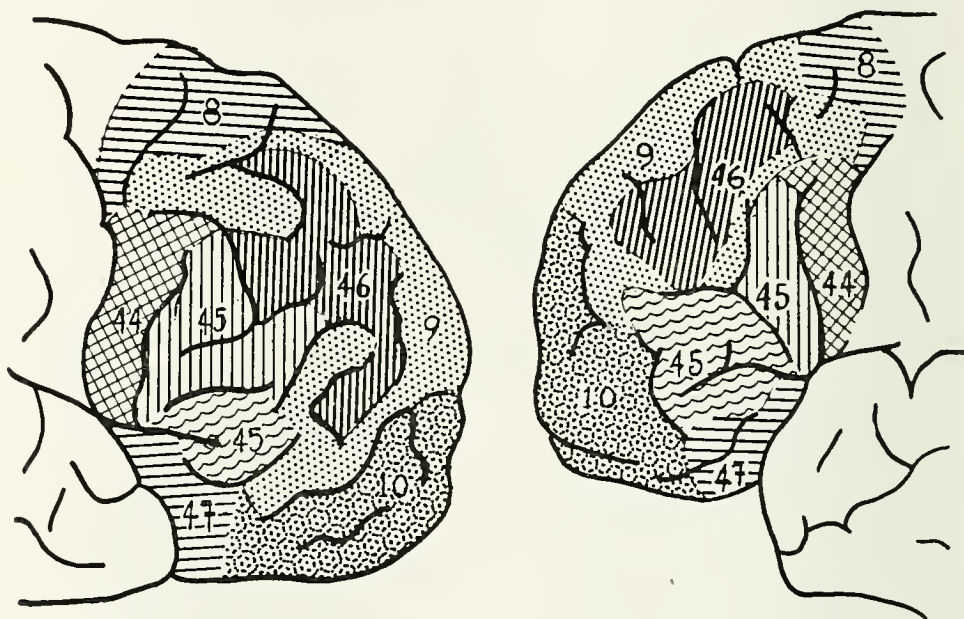
FIG. 98. Kononova's map of the cytoarchitectonic areas of the frontal lobes of brain A32 (redrawn).

with the map of Brodmann (see Fig. 97). But he does not discuss *FDΔ* (Brodmann *46*). It would seem that such an area should lie about in the situation of Ngowyang's area *53c*. If one reads the description of his area *53c* and of the surrounding areas *51*, *52b*, *52c*, and *53b* and examines the photographs of them, one finds nothing resembling Economo's description of *FDΔ*.

We have sought in vain for something resembling *FDΔ* in brain *Hl*. There is, at most, a very small spot in this general neighborhood which varies perceptibly in the sense of *FDΔ*.

Let us turn for a moment to the medial and orbital surfaces. Economo makes a series of distinctions of *FF, FH, FHL, FFa, FI, FL, FM*. Although he states that *FF* and *FH* are very similar in structure, their "gradual metamorphoses . . . make it impossible to give a general description." In other words, they are not fields but

zones of transition to the allocortex lying posteriorly. The same is true of *FFa*, *FI*, *FL*, and *FHL*. *FM* is allocortex.

If we turn for help to the studies from the Vogt school we fare no better. The frontal regions have been studied by Ngowyang (1934b, Vogt's areas *4*, *6*, and *7*), M. Rose (1932b, areas *10–14*), M. Rose (1927, areas *15–32*), Ngowyang (1932b, areas *1*, *2*, *3*, *5*, *8*, *9*, *44–55*), Ngowyang (areas *33–43*, see Ngowyang, 1934b, footnote on page 9 of reprint, never published to our knowledge), while Riegele (1931) and Kreht (1936) studied areas *56–66*. These studies describe the cytoarchitecture of the areas distinguished by O. Vogt (1910) on the basis of myeloarchitecture. Given any two parcels of the cortex it is always possible to describe differences between them but, when these descriptions are analyzed, no clear distinguishing characteristics emerge by which one can recognize them. This is not true, of course, as between granular and agranular cortex, or as between limbic cortex and eulaminate isocortex, but, in the vast zone which Economo calls *FD* and *FE*, the descriptions which Ngowyang (1932b, 1934b) gives of (Vogt's!) areas *1*, *2*, *3*, *5*, *46*, *49*, *50*, *51*, *52*, and *53* are to us mere paraphrases of identical findings. We might conclude, from the authors cited above: that Vogt's areas *36*, *37*, *38b*, *39b*, *39c*, *40*, *42*, *43*, and *44* are agranular; that *41*, *45*, *47*, *48*, *54*, *55*, perhaps *57* (although there is no photograph of this area) and *8* on the orbital surface are dysgranular. If these are plotted on the frontal lobe the result is approximately Economo's *FA + FB*, *FC + FF*, and *FD + FE*. Areas *4*, *6*, *7*, *8*, *9*, *10*, *11*, *12*, *13*, *14*, *33*, *34*, *35*, *36*, *37a*, *39a* are juxtallocortex and *15–32* anterior limbic which does not here concern us. Ngowyang (1934b) himself has subdivided the frontal lobe, with the exception of the gyrus limbicus anterior (areas *15–32*) into four principal regions. The regio frontalis agranularis contains areas *36–40*, *42*, and *43*. The regio frontalis dysgranularis contains areas *44*, *44a*, *45*, *47*, *48*, *48a*, and *55* as well as areas *41* and *56*, while the regio frontalis paralimbica contains only the areas *3*, *33*, *34*, *35*, and *36a*. All the other fields (areas *1*, *2*, *4–12*, *46*, *49–54*, and *57–65*) belong to the regio frontalis granularis. Area *14* is an allocortical field, and area *13* is a transitional field to allocortex. Area *66* is a transition to the agranular anterior insular cortex. Ngowyang states that the affinities of areas *56–66* are given in accord with the studies of Kreht (1936).

Economo distinguished, on his orbital region (see Fig. 99C), an *FF* and an *FH* which he says (p. 44), "would have formed a single and common field had not the area FG separated them from front to back like a peg." Is this a sufficient reason for increasing the number of areas? This *FG*, he goes on, is very similar to *FE* but shows a less distinct separation of *IIIa* and *b*. Moreover, the cells of the fifth lamina are "exceptionally crowded, almost bandlike in the walls of the gyrus—a circumstance which points to the proximity of the olfactory brain."

The last phrase is important. As Economo notes, and as is evident also in brain *Hl*, in the frontal and temporal lobes, the fifth layer becomes denser wherever the allocortex is approached. This zone we have called juxtallocortical. Economo gives it numerous designations—*FCL*, *FDL*, *FEL*, *FHL*. Logically he should have written also *FEL* instead of *FG* but did not, we suppose, because he would then have had *FH* intervening like "a laurel leaf" between the two parts of *FEL*.

The latest study of the orbital surface is that of Elisabeth Beck (1949). Her

photographs show clearly those structural modifications on which there is general agreement, namely the gradual disappearance of the inner granular layer, as the posterior margin of the orbital surface is approached, and the gradual appearance of allocortical characteristics as the gyrus rectus is approached. The overlapping of these two tendencies makes possible numerous subdivisions. The resulting map (Fig. 99A) looks more different from the maps of Brodmann and of Economo and Koskinas than is really the case, since the alterations described have no sharp boundaries. The great differences in the surface map introduced by the very varied

Fig. 99. Maps of orbital surface of the frontal lobe. A—after Beck. B—after Campbell. C—after Economo.

gyral pattern on the orbital surfaces is evident from the maps of Knauer (1909), Kreht (1936), Ngowyang (1934b), and O. Vogt (1910). Moreover, because the gyral pattern of the orbital surface is so variable (see Chap. III, p. 45) it is not permissible to transfer Brodmann's and Economo's maps to the gyral pattern of another brain, as Beck has done. It might be pointed out that she has used Brodmann's number *11* for an area which is not identical with his but that she has some justification for extending Brodmann's area *13*, which that author recognized in Hapale and Lemur, to the posterior zone of the orbital cortex.

The situation over the inferior frontal gyrus is somewhat different. If we super-impose, on the general frontal agranular-dysgranular-granular series, a horizontal band over the inferior frontal gyrus containing large pyramids in *iiic* we get the *FCBm*, *FDΓ*, of Economo or *44*, *45* of Brodmann, or even the *44*, *44a*, and *45* of Brodmann's later map (1914). Is this important? Actually we do not know. At any rate it is a little more striking than the *FDm*, *FDp*, *FE* sequence in the superior frontal gyrus. In brain *Hl* these large cells in *iiic* continue over the frontal oper-culum onto the orbital part of the inferior frontal convolution. The same large-celled area in the posterior orbital region was seen by Riegele (1931) and numbered *64*. It might be noted here that there is also an area buried in the superior frontal sulcus of brain *Hl* (Fig. 96) with equally large pyramids in *iiic*.

The inferior frontal gyrus, covered by Vogt's areas *56–66*, has been studied in great detail by Riegele (1931) and by Kreht (1936). Riegele studied brain *A43r* (Fig. 100A) and noted that areas *61*, *62*, and *63* on the posterior orbital surface had scarcely any internal granular layer; they lie about in the position of Economo's *FF*, stated by Economo to be dysgranular. He noted also that fields *60* and *64* had a good internal granular layer and big pyramids in *iiic*; these would correspond to Economo's description of *FDΓ* although the situation of this area in Economo's brain would rather seem to correspond to Riegele's *59*. We might add that such large cells are found in brain *Hl* also on the orbital surface in a situation closely analogous to Riegele's *60* and *64*. Kreht (1936) made an elaborate study of the left hemispheres of brains *A58*, *61*, *64*, and *65* (see Fig. 100C and D). His photographs are all at a low magnification (20×) and taken at what he claims are boundary lines between fields; no field is, therefore, shown clearly. He found the largest cells in Vogt's area *65*.

Although we are, in general, suspicious of the validity of myeloarchitectural studies, we must mention the statement of Knauer (1909) (see Fig. 100B), repeated by Brodmann (1914), by O. Vogt (1910) and by Strasburger (1938), that the in-ferior frontal convolution is "unitostriate," i.e., that the outer and inner stripes of Baillarger are united into one horizontal band of fibers (see Fig. 111). Brod-mann (1914) states that this structure covers the entire inferior frontal gyrus and also the posterior half of the middle orbital gyrus. He adds that otherwise this cortex has the usual six-layered structure and that it is much better characterized by its myeloarchitecture than by its cytoarchitecture. Nevertheless, this is the zone of large pyramids in *iiic* noted first by Betz (1881, see p. 4).

Betz (1881) divided the inferior frontal convolution into three parts, the posterior extending from the lower extremity of the precentral sulcus to the ascending branch of the Sylvian fissure, the middle extending to the beginning of the orbital surface, and the third lying anterior to the pole of the insula. His account of the large cells is as follows: "The first part sometimes shows, in its third layer, pyramidal cells larger than those of the other convolutions of the frontal lobe. Here and there, especially in the brains of older subjects, are found cells almost gigantic in size which sometimes extend to the inferior extremity of the anterior central convolution. In some brains they occupy a considerable part of that extremity, but this I have never encountered in the brains of young subjects." The presence of these large cells has been confirmed, as we said, by Economo and Koskinas (1925, cf. their
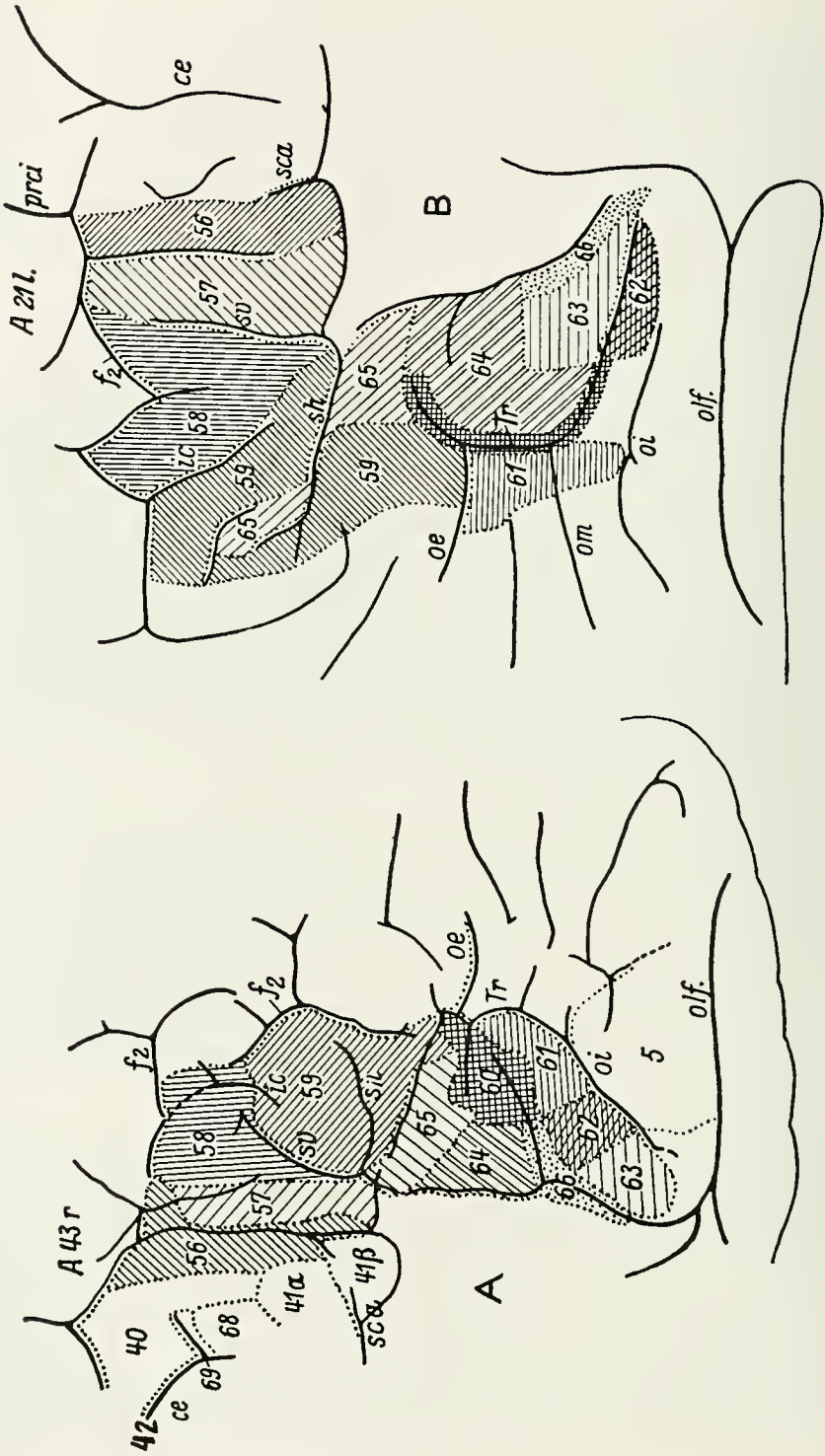
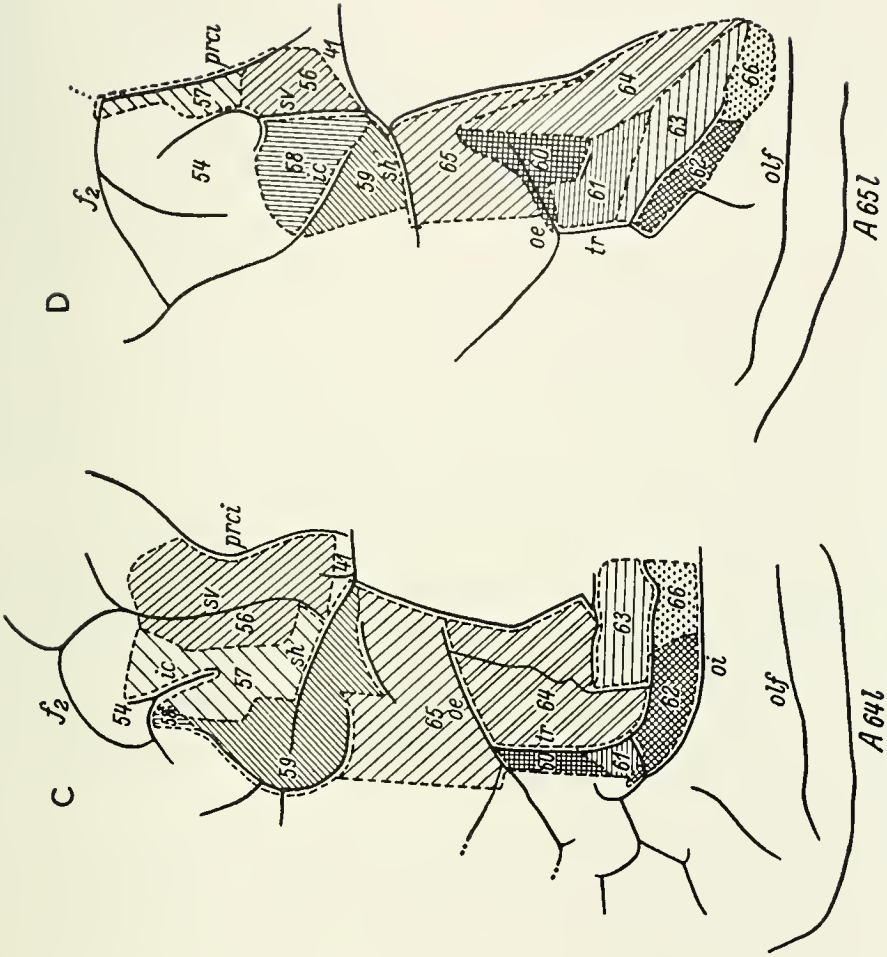FIG. 100A. Maps of the inferior frontal convolution. A—after Riegele. B—after Knauer.

Fig. 100B. Maps of the inferior frontal convolution. C and D—after Kreht.

Fig. 74), by Riegele (1931), by Krcht (1936) and also by the examination of brain *Hl.* We cannot, therefore, agree entirely with Jakob (1943) that the intimate structure of the three frontal convolutions is perfectly uniform. As we have already noted, if we superimpose this horizontal zone of large cells on the frontal series of agranular, dysgranular, and granular cortex, we get something resembling Brodmann's *6, 44, 45* or Economo's *FBop, FCBm, FDΓ.*

Kononova (1935) accepts the division of the inferior frontal gyrus into three parts which she calls, following Brodmann, *44, 45,* and *47.* Area *44* covers the opercular part and area *45* covers the triangular part, while area *47* is almost totally situated on the orbital part of the inferior frontal gyrus (Fig. 98). "The common characteristics of all areas of the inferior frontal gyrus are a medium breadth of cells, prevalence of medium sized cells, indistinctly marked radial striation (most clearly pronounced in area *45*) and especially horizontal striation; the division of layer III into three sublayers according to the size of the cells, the innermost of the sublayers possessing the largest cells. The fifth layer is divided into two sublayers as to the number of cells, an outer richer in cells and an inner forming a pale band. The sixth layer has many cells of diverse shape, of medium size, and gradually passes into the white matter of the gyrus." It is obvious that this description would apply to a large part of the eulaminate isocortex.

How, now, does she distinguish the three parts from each other? For area *44* she notes the large pyramids in *iiic* and the weak development of *iv.* This area *44* she states extends over the upper wall of the lateral fissure as far as the sulcus marginalis superior insulae. Posteriorly it is bounded by the agranular cortex *6* and above by the richly granular cortex *9.* Anteriorly it reaches to area *45.*

Area *45* is said to cover the whole free surface of the pars triangularis and the walls of the adjoining sulci, the upper wall of the horizontal branch of the sulcus Sylvii and the lower wall of the inferior frontal sulcus. "Area *44* differs from it in being thicker but less rich in cells. Its radial striation is weaker. Layer IV is less developed. The large cells of IIIc are a little smaller. Layer VI is considerably thicker; all the other layers differ only in the number of cells, which is larger in area *45.*" One wonders how much of the difference is due to the fact that *45* covers mainly sulci and narrow gyri. Of the long and detailed account of the variation in structure in different parts of area *44* and *45* very little remains except the increase in granules of layer *IV.*

"The area *47,* as to its cytoarchitectonic structure, separates into five formations, which differ from each other in their microscopical structure." Only *47³* is said to have very large pyramids in *iii.* The subareas *1* and *2* lie on the posterior orbital region, called by Economo *FF,* and are said to have a poorly developed inner granular layer.

The study of Kononova is based on eighteen hemispheres and contains a vast amount of detail concerning the extent and location of the areas and their cellular constitution and variation in the individual hemispheres and a comparison of the conditions in the two hemispheres of each brain. Such a study, of course, can yield useful results only if it is possible to identify sharply the limits of the areas studied. By the avowal of the author herself, this is not possible and she draws one valid conclusion, namely, that "there is great variability in the structure of the inferior

frontal convolution, not only in different brains, but also in both hemispheres of the same brain. This variability shows not only macroscopically—in the shape, size, and distribution of the sulci and gyri—but also microscopically in the cytoarchitectonic expansion of areas, their dimensions and correlation. Between two different areas there is a variable zone of limiting adaptation, which may be quite large and almost seems to be a new area or subarea." These conclusions apply not only to the inferior frontal but to the entire frontal region (Kononova, 1938). "The cortex of the frontal region has a very complex structure consisting of a great number of areas. To determine their borders is very difficult, due to the vague limits, presence of borderline adaptation and the vague differences in their structures. The shapes of these areas vary greatly as one might expect from the exceedingly varied sulcal pattern of the frontal lobe. Its exact dimensions, how far it will reach forwards, upwards, backwards, its exact boundaries with the neighboring areas— all these questions cannot be answered without careful investigation." Microscopical investigation is meant.

Concerning the frontal cortex in general, Ngowyang (1934b, p. 193), states: "The thickness of the cortex diminishes gradually forwards from the central sulcus as does also the size of the pyramidal cells of III and the ganglion cells of V. Conversely the number of cells, especially the granule cells of IV, increases progressively as one goes forward. In general the size and the number of cells for all layers are inversely proportional; the relationship of cell size and thickness of cortex is about the same. In other words: in the thicker cortex one finds larger but fewer cells than in the thinner fields, yet exceptionally one finds large-celled thin cortical layers."

When one reads through this long and laborious work, and the equally long and laborious studies of the Russian school, one finds oneself agreeing with Jakob (1943) that a precise cytoarchitectural map of the frontal lobe is impossible.

As Kononova (1938) puts it, "This variability in the size and disposition of the fields (of the frontal region) makes it impossible to construct a cytoarchitectonic map which will be applicable to each individual case." We cannot follow Jakob, however, in denying any and all differentiations within the frontal lobe.

Betz's description of the third frontal convolution is valid, although the subdivisions of this convolution are again to be rejected. These distinctions of minimal differences in the inferior frontal convolution are due, so it would seem, merely to the fascination of Broca and his speech center. Except for the limbic lobe there are no precise limits anywhere, but only a gradual passage from the agranular cortex posteriorly to the granular tip of the frontal pole. Even the anterior limbic area is bounded by a transitional zone of varying width.

In the light of the preceding we may perhaps venture to describe the frontal lobe as follows (see frontispiece): The frontal pole is covered by typical eulaminate isocortex with a thick internal granular layer which thins gradually, as one passes posteriorly, and finally disappears. But, even as far back as the central sulcus, its position is marked by a layer of pyramids which are smaller than those above and below. Next to the central sulcus this agranular cortex contains scattered very large pyramids in the deeper part of layer *iii* and gigantic cells in *v*. This gigantopyramidal zone is broader above than below and extends onto the medial surface of the hemisphere almost as far as the cingulate sulcus; over the lateral surface it

narrows until, in its lowest portion, it is confined to the anterior wall of the central sulcus which it does not depass. Anterior to the gigantopyramidal zone the simple agranular cortex, without giant pyramids or very large pyramids in *iii*, extends forward, much broader above than below; it extends also onto the medial surface to the depth of the cingulate sulcus. Over the lateral surface it also narrows markedly until it is about a centimeter in width anterior to the lower extremity of the central sulcus which it depasses usually to extend even, in some brains, onto the upper wall of the lateral fissure to a variable extent. As one passes anteriorly from the agranular cortex (marked in yellow), at first scattered thin patches of granules appear and then a continuous sheet which progressively thickens anteriorly (marked in pink.) The zone with poorly developed internal granular layer (marked in orange) we called the frontal dysgranular variant *I*ʙ*f* (Chap. IV, p. 79, Plate XV); it has no definite anterior or posterior border and extends as a band from the cingulate sulcus on the medial surface over the superior and lateral surfaces of the hemisphere onto the upper wall of the lateral fissure and the orbital operculum to cover also the posterior part of the orbital surface. Anterior to this dysgranular zone the frontal cortex stretches without notable variation to the pole.

This progressive change affects all three frontal convolutions alike, but the cortex of the inferior frontal convolution differs from that of most of the other two in having larger pyramids in *iiic* (and sometimes in *v*) which occasionally reach gigantic size. Principally for this reason the lower segments of the bands were described by us as a slight modification of the eulaminate cortex (Chap. IV, p. 71) and labeled *I*ʙ*fi* (Plate V).

In addition, all around the posteromedial and inferior border of the frontal cortex, where it borders on the allocortex, lies a narrow limitrophic zone (shown in purple) in which the inner granular layer becomes attenuated and the cells of *v* more numerous. Its main characteristics were described in Chapter IV, page 78; its location in the frontal lobe is shown in detail in blocks V, VI, XIV (Chap. V).

Is it possible to distinguish the frontal eulaminate cortex from that in the parietal and temporal regions? Economo begins his description of the frontal lobe as follows (p. 40): "In general, the frontal brain has a broad well-developed cortex which is not specially rich in cells." This statement would be equally true of the inferior parietal lobule or the superior temporal gyrus. It gives us no clue to identify the frontal cortex. He proceeds: "The typical feature of this region of the cortex is the presence of large well-formed and well-arranged pyramidal cells in the IIIrd and Vth laminae, as they are hardly to be found anywhere else in the brain." By this feature the frontal pole cannot be distinguished from the inferior parietal lobule or superior temporal gyrus. He has this to say about the inner main layer: "The VIth layer is also well developed and reveals rather large and well-arranged spindle cells, oriented perpendicularly, that is, in the direction of the incoming medullated fibers." This is a good description of the VIth layer of the inferior parietal lobule or of the superior temporal gyrus. About the granular layers he says: "The IInd and IVth layers are less well developed as a rule; their cells are usually small and triangular, and are sometimes altogether missing." This statement is applicable only to the precentral subsector. It gives one no suggestion of the important fact that the thickness of the IVth layer increases steadily from 0.0 to 0.3 mm. as one progresses from the central sulcus toward the tip of the frontal pole.

The entire first paragraph of Economo is misleading and too general to have meaning. It illustrates well the futility of trying to make general statements concerning the cortex of an entire traditional lobe of the brain. The lobes of the brain were originally named from their relations with the bones of the calvaria and it is time this terminology was abandoned.

Other authors are no more helpful. Kononova (1938) states (p. 271): "The cortex of the frontal region is characterized by the presence of (1) the internal and external layers (II and IV), (2) the clear zone in the depth of the Vth layer, (3) the large pyramidal cells in the IIIrd and Vth layers." Not very helpful, when one remembers that v is very clear in the superior parietal lobule and that there are large pyramidal cells in the postcentral cortex.

There is no characteristic of the eulaminate frontal cortex which will permit it certainly to be distinguished from the eulaminate cortex of the other lobes.

At the posterior margin of the agranular frontal cortex the internal granular layer again appears near the depth of the central sulcus, sometimes on its anterior wall, at others on the posterior, but the giant cells of layer v persist for a variable distance posteriorly to the granular margin to form a limitrophic zone which Brodmann calls a *Mischzone* and Economo dignifies by the term *PA*. It is important to note that, even between two areas of such different functional and structural characteristics as the precentral gigantopyramidal and postcentral koniocortex, there is no sharp boundary.

Posterior to this limitrophic zone, just described, the cortex of the posterior wall of the central sulcus becomes granulose; the giant cells of v disappear, the cells of iii become smaller and v becomes nearly empty excepting an occasional big pyramid. This is the postcentral koniocortex marked κpoc in the sections, denoted by *red* on the frontispiece. It is almost entirely buried in the central sulcus. Only at the dorsal margin of the hemisphere, where the central sulcus bends backward, it passes onto the anterior wall of the sulcus and for a short distance then over the medial surface of the hemisphere. Brodmann's *Mischzone* also comes to lie on the free surface near the hemispheric margin and thereby suffers some changes in its architecture. Economo states (1929a, p. 72): "In consequence of these differences between the area in the valley of the central sulcus and the area on the paracentral lobule one may call the latter PA_2 and the former PA_1." On the same basis one would have to scatter such subscripts all over the brain. We do not see much excuse for all the complications Economo makes around the upper medial end of the central sulcus. Eulaminate cortex surrounds the postcentral koniocortex which he subdivides (1929a, Figs. 1a and b) into PA_1, PA_2, PC, and $PC\gamma$. The differences which he notes between these various subdivisions are very tenuous and probably of no functional significance. At least PC and PB are both end-stations for incoming somesthetic impulses (see Chap. VIII, p. 246), and their differences in structure are greater than these around the end of the sulcus. It seems probable to us that PA, PB, and PC constitute the somesthetic cortex of which only the central portion (PB) is differentiated into koniocortex. We see in brain Hl the eulaminate cortex with big cells in the fifth layer surrounding the medial end of the central sulcus but cannot distinguish the finer differentiations which Economo makes. Possibly there are variations in this region of different brains as there are around the inferior lateral extremity of the sulcus. We have contented ourselves with carrying PA

around back of the sulcus as far as we can see giant cells in layer *v*. At the lower extremity of the central sulcus the koniocortex usually ends on the posterior wall but, depending on the configuration of the sulcus, it may encroach on the anterior wall or may appear on the surface when the lower end of the sulcus is very shallow. These variations around the lower end of the central sulcus have been studied in a number of brains by Economo and Koskinas (1925) (see also Economo, 1930b).

Behind the postcentral koniocortex a parakoniocortical variant of the eulaminate cortex begins. Over the crown and posterior wall of the postcentral gyrus layer *v* is still somewhat pale but there are large cells in *iiic* and sometimes near the interhemispheric fissure in *v*, which are also found, to a limited and variable extent, over the superior margin of the superior parietal lobule, extending along the walls of the cingulate sulcus onto the medial surface of the hemisphere. It is in this region that Brodmann distinguished his areas *1*, *2*, and *5* and Economo *PCγ*, *PA₂*, and *PD*. The giant cells in this region were seen already by Betz (1881). We see no purpose to be served by these distinctions which are scarcely greater than those generally found around narrow gyri and sulci. Especially is this true of Economo's *PD*. His description follows (p. 78):

"In the posterior wall of the postcentral convolution, the cortex, which was broad at the crown of the gyrus, thins once more markedly. This attenuation exceeds that which is usual elsewhere between the crown and the wall; so that, considering also certain other structural changes in the posterior wall of the postcentral gyrus, we may consider it also as a separate striated area PD." This exaggerated attenuation is not present in brain *Hl*. What are the "other structural changes?" He goes on to say: "In contrast with the anterior wall of this convolution [But this is not the point. The point is to differentiate it from the adjacent area *PC* on the crown] the posterior wall is characterized by its large cells, especially by the dense, band-like and multi-laminated stratum of pyramidal cells in IIIc." In brain *Hl* the cells of *iiic* on the posterior wall of the postcentral gyrus are no larger or more numerous than on the crown anterior to the postcentral sulcus. If they seem so, it is because of the fanning out of the cortex over the crown of the narrow postcentral gyrus. To hear Economo again: "This row of large cells also differentiates PD from all other regions of the superior parietal lobe, which are in other respects similarly constructed in their walls." This is not true of brain *Hl*. In the anterior wall of the cingulate sulcus, and to a lesser extent in many parts of the intraparietal sulcus, one finds as numerous and large cells in *iiic* as in the posterior wall of the postcentral gyrus. In the intraparietal sulcus they were seen also by Economo (p. 78) who remarks, "In this caudal prolongation [of *PD*] the area does not retain its pure type, but shows an admixture of the type of the neighboring area." It was not pure to begin with. We can see no valid reason for making such an area as Economo's *PD* and wonder whether he was not subconsciously influenced by Brodmann's map and by Elliot Smith's (1907) visuosensory band *β*. We see nothing in the postcentral sulcus which cannot be explained by the customary changes which occur when passing from the crown of a gyrus into a sulcus.

Behind the postcentral parakoniocortex there stretches out a vast zone of typical eulaminate isocortex. The authors entangle themselves inextricably trying to

describe how this expanse differs from the similar one in the frontal region. Economo (p. 69) gives a general description in these terms: "Both granule layers, II and IV, usually consist of true granule cells, are especially distinct, broad and rich in cells; so that the cortex here is much more markedly laminated than it generally is in the frontal brain." As any silver preparation shows, the outer granular layer contains just as many small pyramidal cells in the parietal as in the frontal lobe. Economo's statement concerning this layer is simply not true (see quotation from Gerhardt below). A marked lamination, moreover, does not serve to differentiate parietal cortex from the frontal pole. Economo then goes on: "A further important characteristic is a fine, perpendicular striation which passes through all the laminae of the cortex, and is most distinct in the IIIrd layer." This is by Economo's own words (p. 40) characteristic of the frontal pole but is incorrect in any case since lamina *ii* never shows perpendicular striation. "This type possesses more, but smaller, cells than the frontal brain." This is not true of the frontal area called by Economo *FDΔ*.

Other authors are just as disappointing. M. Rose (1935, p. 687) fails to give any general description of the regio parietalis. He merely discusses the boundaries of this undefined type. Gerhardt (1940, p. 385) writes (see Fig. 101):

All parietal fields (78–90) are more or less (the latter is especially true for marginal fields) characterized in fiber preparations and in cell preparations by certain typical features: Medium broad to broad cortex, accentuated horizontal demarcation, the radii being tolerably distinct, of average breadth or fine; characteristic structure of II + III^1. The latter always has a dense population of nerve cells, contains very small corpuscles, is well delimited against the neighboring strata while its boundaries are nonetheless relatively soft. The second layer shows an admixture of small pyramidal cells, the layer III^1 an admixture of corpuscles, hence the two layers are strongly welded into a unit; II is always narrower than III^1; the rest of the third layer shows a more diffuse arrangement of nerve cells, and can be subdivided only with uncertainty or with great difficulty into III^2 and III^3. The latter contains pyramidal cells not above medium size, and always has a layer III$^{3\beta}$.

The fourth layer is very characteristic, with its very small granules. It is distinctly bipartite in the fields on the precuneus and at least noticeably so in the fields on the convexity. The granular layer, comprising III$^{3\beta}$–V$^{1\alpha}$ often becomes remarkably dense in the dense IV^2 and V$^{1\alpha}$; layer V is of monotonous structure, broad to medium broad. V$^{1\alpha}$ is always present, generally quite dense, often bipartite, V$^{1\beta}$ with medium sized pyramidal cells arranged in more or less irregular groups. V^2 is more or less light, but generally hardly more so than III^{2+3}; VI is of very characteristic breadth and density, especially VI^1; it is divided into several sublayers. VII is also broad, gradually changing over into the white matter.

Let whoever will wade through this verbiage and then try to recognize the parietal lobe. Perhaps such statements may have in the average some validity (this has never been proven) but, in the identification of any particular section, they have been of no assistance to us.

When it comes to distinguishing the various parts of the parietal lobe we are on equally unsure ground. Gerhardt (1940, p. 385–86) writes:

"The fields of the upper parietal lobule are distinguished from the postcentral fields (the marginal fields are 71, 75) by a greater scarcity of cells throughout, especially in III^{2+3}, by a broader and looser arrangement of the radii, by a more even, almost diffuse distribution of the nerve cells in III^{2+3}, by very constant ac-

centuation of II + III¹, IV and VI which, with little variation, impose themselves
as very dense bands of nerve cells. The VI is broader, especially the dense VI¹
and VII. There is a dense V¹ᵃ hardly to be divided off from IV; V¹ᵝ and V² are as
light as III² and III³, not as easily subdivisible, well delimitable from the dense
VI. The IV has a tendency to be bipartite. Cell laminae can be well delimited and
there is a far reaching evenness of the cross section as regards size, staining and
arrangement of the nerve cells." How can it be both ways?
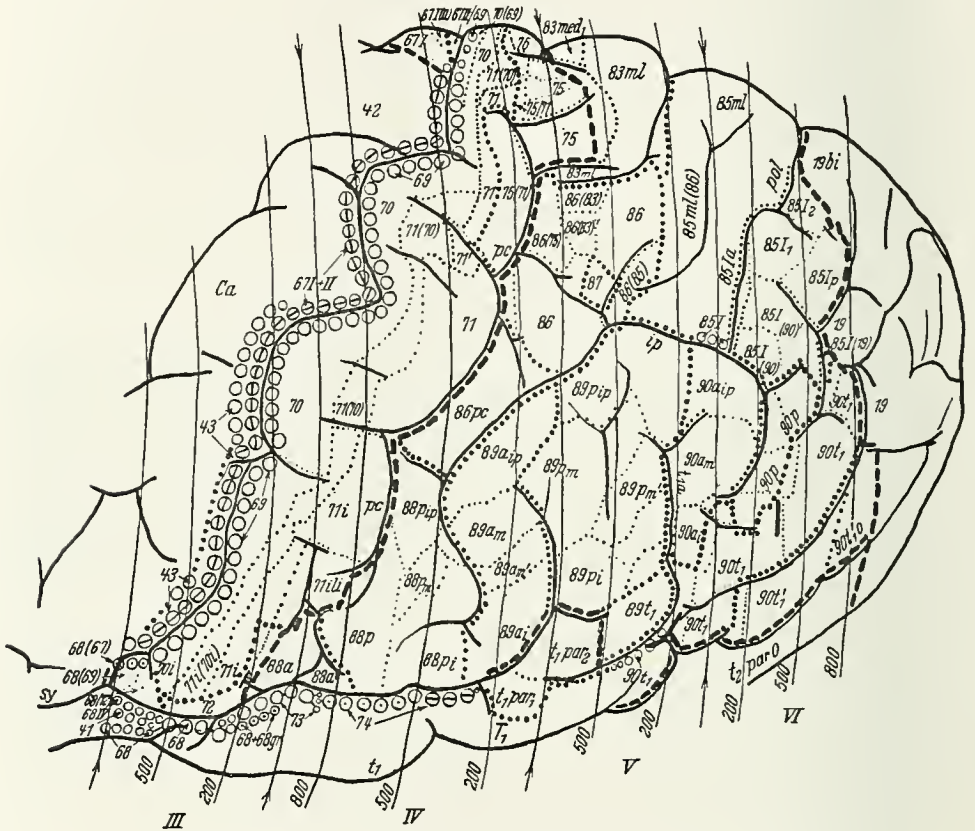
FIG. 101. Gerhardt's architectural map of the parietal lobe, outer surface.

Gurewitsch and Khatchaturian (1938) write that "Microscopically the cortex
of the superior parietal region is of average thickness, possesses large enough cells
in layers III and V with a lighter band in layer V and has distinct radial stria-
tions." This is scarcely illuminating. They go on to say: "Thus it appears that, at
any rate, the architectonic structure of the regio parietalis superior is uniform
enough." Elsewhere they note the band formed by the heavier *IVb* and *Va* and
remark also that it is much less evident as the limbic gyrus is approached. They
study at great length a limitrophic band between the preoccipital (Brodmann's
19) and parietal cortices (Brodmann *7, 39, 37*) which they call *PEO* and subdivide
into *PEOs*, *PEOα*, and *PEOγ* (Fig. 102); the first subdivision is buried in the

intraparietal sulcus and corresponds to Elliot Smith's visuosensory band β, the last to Economo's $PE\gamma$. This limitrophic zone is said to have cytological characteristics intermediate between the parietal and preoccipital formations.

Economo says (1929a, p. 80): "The entire superior parietal lobule is occupied by a single area; within its extent it shows regional differences in thickness and cell
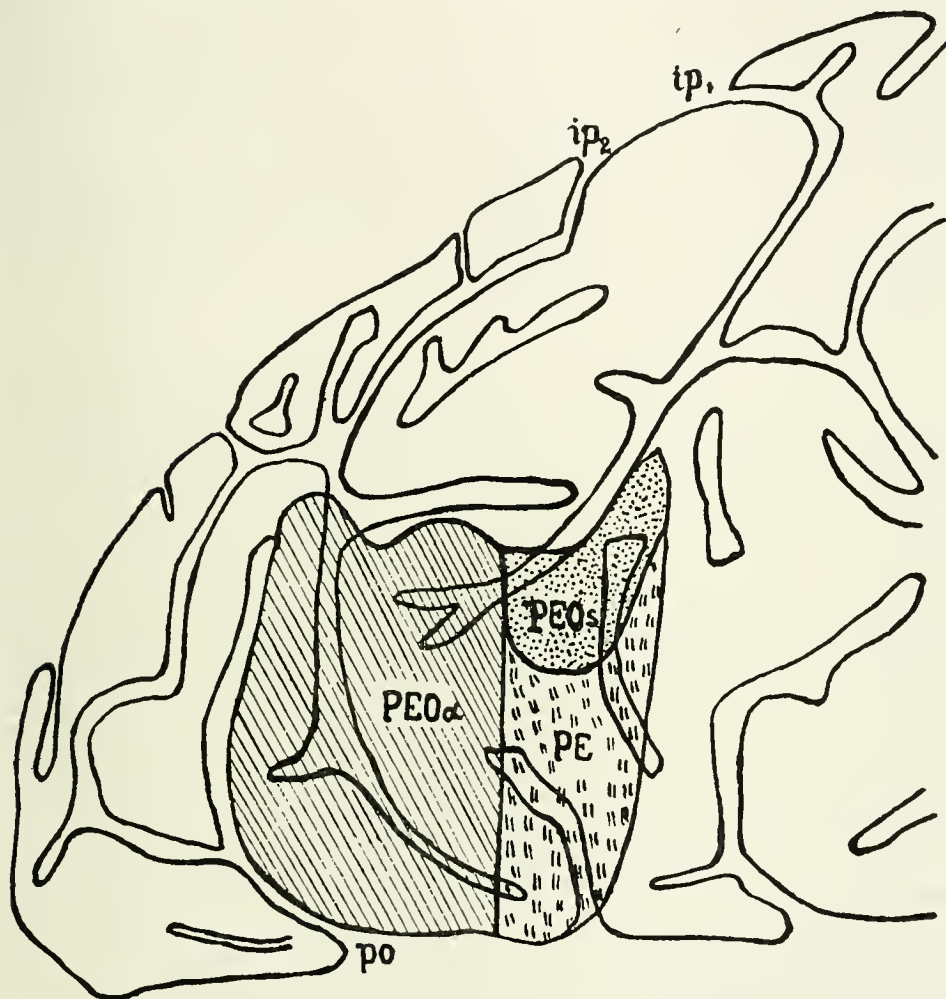
Fig. 102. Gurewitsch and Khatchaturian's map of the superior parietal lobule. Orthogonal projection of the dorsal surface of brain A29.

size." What is the difference between a single area with regional differences and several areas he states nowhere. "PE is further characterized by the breadth of the granule layers and a strikingly pale band in V which is visible to the naked eye." This does not differentiate it from PC. As Economo states further on (p. 80): "It (IV) divides into an upper IVa stratum of less compactly placed round granules ... and a deeper IVb stratum of more densely laid and usually triangular

cells . . . V . . . is divided into an upper stratum, Va, containing more and larger cells, and a deeper and paler Vb, which possesses smaller and fewer cells. This latter stratum appears typically as a pale band in the cell picture under a very low power."

Although not uniformly conspicuous throughout the superior parietal lobule, this dark band made by $ivb + va$ is at its outstanding characteristic, and has been described as a eulaminate variant in Chapter IV (p. 69, Plate III). As we shall see (p. 218) this agrees with Campbell's (1905) findings. In brain Hl, tendencies to form a band $iva + ivb$ are observed here and there near the frontal pole, in the inferior parietal lobule, and in the preoccipital regions so that, if poorly developed, it does not serve certainly to identify the superior parietal cortex.

The cortex of the inferior parietal lobule has caused difficulties to all observers. We turn again to Gerhardt and to Economo. We have mentioned the rarity of the dark band $ivb + va$ in the inferior lobule. That it may be present, however, is evident from the description of Gerhardt.

Gerhardt says (1940, p. 393):

The fields of the lower parietal lobule, especially 88 and 89 can be distinguished from the fields of the upper parietal lobule and of the postcentral gyrus by a tendency to greater thickness—a clearer, although still medium broad, but a little finer radial arrangement of the nerve cells, often up to III^2 by a horizontal lamination which is only a little accentuated by the denser and a little broader $II + III^1$ on which often there follows a dense III^2, especially on flat surfaces and on the walls of sulci, by the somewhat broader III, the less lighter III^2, by a III^3, containing larger pyramidal cells in a little greater number, the $III^{3\beta}$ of which shows a medium wealth of granules and hardly any gaps, by a dense generally bipartite IV, a broad, often bipartite $V^{1\alpha}$, the outer sublayer of which contains very dense granules and was considered as a third sublayer of IV by Economo and Koskinas, by a broader V–VII, a much less lighted V^2, the somewhat denser, not so well set-off, better subdivisible VI, the somewhat broader VII, a $II + III^1$ and $IV + V^{1\alpha}$ quite prominent in cross section while the VI is less prominent because of the denser V. This basic type is realized in 89, to a certain degree also in 88 and 90. $90t_1$ and its subfields group themselves around a type similar in many respects, which however can also be deduced from the structure of the posterior part of the superior temporal convolution: horizontal lamination recedes in favor of a stricter, often denser columnization and a generally much looser arrangement of the nerve cells; $II + III^1$ is narrower and more clearly set off against III^2; $III^{2 + 3}$ is a little denser in nerve cells, IV does not contain as many nerve cells, just as $II + III^1$ is not so accentuated, but still bipartite. $V^{1\alpha}$ does not belong quite so much to IV, is not so dense in cells, and loses in distinctness caudally. V as a whole contains less cells, is not easily subdivisible, VI–VII are also less dense in cells, but can be well distinguished. $90t_1 + 90t'_i$ takes over the transition to the occipital structures which are characterized in fiber preparations by the caliber of their fibers, their astriate character, and in the cell picture by their greater cell density, the deeper staining of their nerve cells, the much coarser, rigid arrangement of their radii, a slight narrowing of the cortex, a broader more compact IV and a denser VI.

Economo (1929a, p. 83) characterizes the inferior parietal cortex as follows: "All this inferior parietal lobule is clothed by a typical [of what?] broad, distinctly laminated cortex, which is characterized not only by the two outstanding granule layers II and IV, but also by the great development of III, while V and VI lose much of their importance in the cell picture." Certainly V is much better filled with cells, as Gerhardt stated correctly, than either in the occipital cortex or the superior parietal cortex. This is another instance of Economo's inaccuracy in his general

statements. "Another typical character of this cortex is a very fine, radiate, i.e., perpendicular striation." Again one might ask: typical of what? In any event, this does not serve to differentiate this cortex from that of the frontal pole or superior temporal convolution.

Economo's statement (p. 84): "V [in *PF*] is neither subdivided into two distinct sublaminae nor is it lighter stained as in the superior parietal lobe and in the post-central gyrus," is usually true. But places can be found in the inferior lobule in which this feature is present. When Economo goes on to say "Just as in IV of the superior parietal lobe, although not so distinctly, we can discern more characteristic granule cells in the superficial stratum IVa and numerous triangular cells in the lower stratum, IVb," he seems unintentionally to demolish a distinction between superior and inferior parietal lobule previously laboriously elaborated.

Of the inferior parietal lobule Economo states (p. 83), "The division of this extensive district into areas is far more difficult than in the frontal brain." Heaven help us then! (p. 84) "The delimitation of the areas is thus somewhat more arbitrary, and has to depend more on the macroscopic anatomical boundaries." Shades of Brodmann's *etwas willkürlich*! The gyral pattern, moreover, is so varied as to be useless.

But let us hear more from Economo! (p. 86): "The cell structure [of *PG*] is very similar to that of PF, with the exception that the deeper layers of III, which is somewhat narrowed, become again larger celled, and there is also a tendency to pallor of lamina V." In brain *Hl* the cells of *iiic* are perhaps a little larger anteriorly, but there is not much to choose between the anterior and posterior inferior parietal region. Whether the lamination is better pronounced in the anterior or posterior part of the inferior parietal lobule is not clear from Economo. When describing his area *PH* he says (p. 88): "This field (PH) reveals much the same structure as the area PF, i.e., in contrast to PG, a more distinct lamination...." But, on page 86, he had stated: "The columnar arrangement of the cells [in *PG*] is somewhat broader than that of PF, as a result of which the horizontal lamination is somewhat more clearly visible." Since Economo himself cannot remember for the space of two pages, we feel that this characteristic is not sufficiently clear to be important.

The inferior parietal lobule was studied in great detail by Stankewitsch and Schewchenko (1935). They state, "The characteristics which separate the cortex of the inferior parietal region from the neighboring regions are: The breadth of the cortex, comparative density and small size of cells, regular fine radial striation going throughout all the layers frequently even II, regular orientation of the basic mass of cells pointing with their major axis towards the surface in fine long regular streaks which gives a sharply marked regularity to the cortex, broad compact inner strata, the V layer passing without sharp limit into VI layer, medium size of cells of V layer, absence of pallor in V, broad VI and VII and vague transition to white matter." They accept a subdivision into areas *40* and *39* but describe numerous intervening subareas (Fig. 103) and state, "because of the fact that the portions occupied by these interareal modifications are quite large and that they are more or less regularly found in a series of hemispheres, we separated them as special subareas." Concerning area *40*, they write, "This compact character of the inner-most layers together with the comparative uniformity in size and density of cells is

the characteristic feature of the area *40*." It might be remarked here that these are essentially the features given by Economo as characteristic of his area *PH* (Brodmann's 37).

FIG. 103. Map of the inferior parietal lobule (redrawn after Stankewitsch). Brain АД147. Horizontal lines—area 40; regular dots—area 39; groups of dots and cross-hatchings—subareas.

Concerning area *39* Stankewitsch and Schewchenko go into a long account of its differences from area *40* as follows:

Whereas in area *40* the radial striation almost completely supersedes the horizontal lamination; in area *39* the horizontal stratification is a little more distinct. The longitudinal radii are wider and coarser. The III layer in area *40* is distinguished by its very great uniformity of cell size, but the increase in cell size from III¹ to III³ is so gradual, that notwithstanding the considerable size of the cells in III³ they do not stand out from the mass of cells. In area *39* the III³ with its very large pyramids stands out quite distinctly The merging together of the V and VI layers is characteristic of the cortex of the whole inferior parietal region, only area *40* possesses it completely. In area *39* this solidity is somewhat lost. The V layer has larger cells than in area *40*, but less dense, and so the limit with the VI layer is more distinct. The

II layer of area *39* is broad, but little narrower than that of area *40*; also more loose. Its superior limit is less straight than in area *40*. The inferior limit with the III layer is clearer. There is less implantation of the granules of the II layer into the III layer. The broad III layer is more clearly subdivided into three sublayers, than in area *40*. III^2 is paler than that of the area *40*. III^3 has larger cells. The gradual increase in cell size, characteristic for area *40*, is not so gradual in area *39*, and so the cells of III^3 are standing out by their size over cells of the III^2. The cellular columns several cells deep are separated from each other by wider spaces than in area *40*. The radial striation of the III layer is less fine than in area *40*; the radii do not reach II layer at all. The limits of III layer with the IV in area *39* are much more distinct due to lesser implantation of cells from IV layer into the III and vice versa. The IV layer is narrower in area *39*. Its cells are arranged into separate columns of equal width; connected with radii of the III layer. There are less pyramids in the lower portion of the IV layer as compared with area *40*. The limit between IV and V is clearer than in area *40*. In the V layer the area *39* possesses larger ganglia, but there are no especially large cells here. Lesser cell density of the V layer gives it more pallor. The limit with the VI layer is more distinct. The VI + VII layers consist mainly of spindle-shaped cells. In their mass they are regularly oriented. The cells of the VII layer reach deeply into the white matter and so their boundary is even more transgradient than in area *40*. The structure of area *39* shows considerable local changes, just as area *40*, according to its position on the surface or inside the sulci. There are also many focal modifications.

After this verbose comparison they say:

Notwithstanding the fact that in the inferior parietal cortex we distinguish two areas *40* and *39* differing from each other and even separate some variants inside their limits, still the basic features characteristic of the inferior parietal formation are retained in the whole inferior parietal region and so we can, on the basis of the complex of these characteristics, always correctly distinguish areas limiting with the inferior parietal region and its neighboring regions. [We admit our inability to do so.] The basic differences of the superior parietal formation are: Absence of regular striation, absence of regular orientation of cells, which are specific of the inferior parietal cortex, attenuation of the whole cortex, prevalence of the outermost strata over the innermost strata, larger cells in III and V layers, distinctness of the limit between V and VI layers due to the pale band in the lower portion of V. All of these characteristics give the basis for the establishment of the boundary between the superior and the inferior parietal formation.

We should like to add that the intraparietal sulcus is a big help!

Out of all this we may salvage again the clear band in *Vb*, which, although it is present also in the postcentral and the occipital parakoniocortex, is generally less evident in the inferior than in the superior parietal lobule. Regular striation and orientation of the cells is not at all peculiar to the inferior parietal lobule. In direct contradiction to Stankewitsch and Schewchenko, Economo states (1929a, p. 80) of the superior parietal cortex, "There is also a distinct radiate striation." In fact we know of no part of the eulaminate isocortex in which there is not a distinct radiate striation. It may be more or less evident, depending on the plane of section.

The region ventral to the inferior parietal lobule was considered by Economo as a part of the parietal lobe, but he differentiated it from the rest stating (p. 89) that, "The chief characteristic of PH is thus the fusion of V and VI into one single lamina." To our eyes it is just as difficult to distinguish V from VI in the inferior parietal lobule. The distinction of this basal region between parietal, occipital, and temporal lobes is exceedingly precarious. When Economo states (p. 90), "this area basalis reaches beyond the temporo-occipital fissure on the basal surface of the

brain as far as the calcarine trunk. There, however, the area can no longer be clearly distinguished from the area fusiformis of the temporal lobe, into which it passes," he depends here again on the macroscopical anatomical boundaries.

The eulaminate cortex of the inferior parietal region continues over the parietal operculum and the posterior portion of the island. At the junction of island and operculum is a small area of koniose cortex (called by Gerhardt, 1948, *68IIgr.*), surrounded by a narrow zone with large cells in *iiic*. This has been thought to be the cortical center for taste (Ruch and Patton, 1946; Gerebtzoff, 1941) (see Chap. VIII, p. 246).

After long study of the verbose literature concerning the parietal region we still cannot consistently identify photographs taken from various parts of it. In general, the cortex of the superior parietal lobule shows the dark band *ivb* + *va* and, with it, a bipartition of the inner granular layer, distinctly enough. Moreover, the cortex of the superior and inferior parietal lobules is generally thicker than that of the preoccipital and postcentral regions but over many small gyri this is not true and photographs from such gyri cannot be distinguished from others taken of the postcentral gyrus. While it is true that, over the inferior parietal lobule, layer *v* is generally better filled than in the superior parietal lobule, this is often not so in its anterior and posterior parts. In the inferior part of the medial surface of the superior parietal lobule, near the limbic gyrus, layer *v* becomes better filled and photographs from this region cannot be distinguished from others taken of the inferior parietal lobule. The laborious studies of the parietal cortex seem to us to result in very little which is verifiable and constant. The structure of most of this cortex is practically identical and practically identical also with that of the eulaminate frontal cortex.

How is it with the temporal cortex? Most authors agree that it is practically impossible to determine the boundary between the parietal and temporal cortices. Campbell (1905, p. 159) states of his temporal type III "in its upper part this area of the cortex is contiguous with the field which I shall describe later under the designation 'parietal' and the dividing line between the two areas corresponds approximately but not absolutely with the disposition of the horizontal and occipital rami of the intraparietal fissure."

A glance at Campbell's map (Fig. 104) will show that we are brought by this definition into the inferior parietal lobule. The parietal type of Campbell is obviously our variant *IEps*. He made no attempt to distinguish between inferior parietal and temporal types. He continues: "The relation to the ramus occipitalis appears to be more definite than that to the ramus horizontalis, for while temporal characters usually reach up as far as the ramus occipitalis (so covering the angular gyrus) they exhibit an inclination to stop some distance short of the ramus horizontalis; at the same time I must mention that, all along the line, the change in type from temporal to parietal cortex takes place gradually. The only points to be relied on in deciding the transition are the appearance of fibers and cells of greater size than those usually present in the common temporal cortex, and it is really impossible to lay down a sharp line of demarcation.

"The anterior boundary is also an unsatisfactory one, but it to some extent follows the sulcus postcentralis inferior and along this line the temporal gradually passes into the postcentral arrangement."

We might add that his Figure 15 (Fig. 104) shows the posterior half of the island also to be covered by his Type III temporal cortex.

Brodmann strained hard at further subdivisions. He expresses his difficulties in 1907: "Slighter differential development is shown by the parietal and temporal types; they are, therefore, more difficult to distinguish from each other and show also less sharp localizing subdivisions." Nevertheless in 1909 he stated, "The regio temporalis is a well circumscribed and uniform region which, apart from its posterior border, is fairly well delimited on all sides." This is exactly the border which Campbell said is readily defined.

Brodmann's discussion, moreover, is empty of concrete architectural data and cannot be considered as anything but a revelation from on high. O. Vogt also
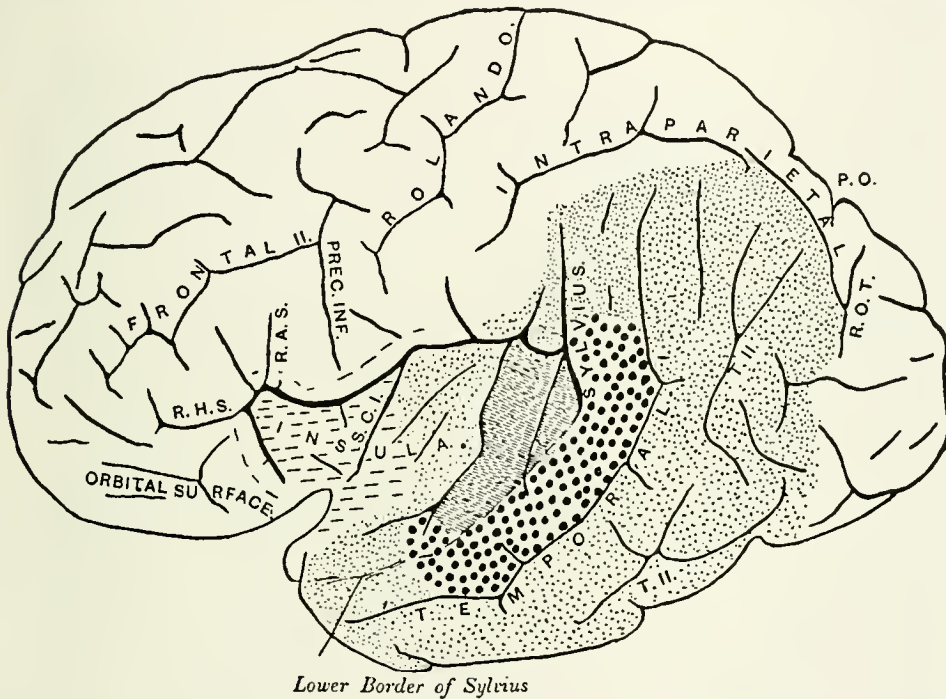

Lower Border of Sylvius

FIG. 104. Campbell's map showing the region around the island.

(1911, p. 383) states, "From an architectonic standpoint it seems much more natural to unite fields 88, 89 and 90 [the inferior parietal lobule] with certain parts of the temporal lobe."

Economo (1929a, p. 111) makes at least an attempt to be of help and gives a general statement concerning the temporal cortex (which we annotate in square brackets). "The most striking characters of the temporal type are, shortly, the following: The general thickness of the cortex [no thicker than the inferior parietal region or the middle frontal gyrus], a peculiarly shredded or irregularly interrupted appearance of II." [No more so than in the frontal region in brain *Hl.*] "A strikingly columniated appearance of the cells of IV." [No more so than in the occipital region.] "The IIIrd layer of the temporal lobe is larger celled in general, but less rich in

cells and thinner than in the parietal lobule." [This will certainly not hold for the superior parietal lobule.] "This layer has also the peculiar character of becoming not only relatively but also absolutely, thinner on the crowns than in the walls of the convolutions." [This is not true of brain *Hl* except over broad gyri within any lobe.] "Laminae V and VI, on the other hand, increase remarkably, especially in comparison with the same layers in the parietal and occipital lobes, where they had lost much of their importance; so that in thickness, development and wealth of cells, the Vth and VIth laminae here excel the upper layers, and show most prominently in the cell picture, a circumstance which immediately differentiates the temporal cortex from the granular formations of the frontal brain." This remarkable statement, in which frontal, parietal, temporal, and occipital are inextricably confused is simply not true for brain *Hl*, nor is it true of the brain of Economo and Koskinas, as anyone can convince himself by consulting the photographs of their atlas.

Stankewitsch and Schewchenko (1935), after noting that "there are difficulties according to Campbell, Brodmann and Economo, in establishing boundaries with the temporal cortex," go on to say that they do not share this opinion. They give as characteristic of the temporal cortex "distinct division into columns, separated by spaces, which go through all the layers; eroded II layer possessing empty spaces having the character of nests; larger cells in III layer; sharp splitting of columns of the IV layer, separated from each other by wide spaces; paler V with a distinct inferior boundary and the absence of a continuous character of the innermost strata (characteristic of the inferior parietal formation) give a possibility of an accurate establishing of the areal limits." Note the "possibility." None of the characters given is confined to the temporal cortex, and the nests in *II* occur only on the boundary of the allocortex.

We might add also the following statements of Economo (p. 111), "The cortex of *TA* is . . . very similar in its formation to the cortex of the inferior parietal region; but the radiate striation in *TA* is somewhat coarser and more striking than in *PF*, for example." We cannot see this in brain *Hl*. Page 112, "Posteriorly, the area *TA* gradually passes into . . . the area *PF* which it resembled to begin with." In fact the two resemble each other so closely that we are unable to distinguish them. The columnization of the "IVth into perpendicular little columns" is seen equally clearly in Economo's *OH*, *PH*, *PF*, and *PE* (p. 112). The rather uniform middle size of the pyramids in the third layer "so that no IIIc is recognizable," is not true for brain *Hl*, nor is it true for Economo's brain as he, himself, admits, since he labels *iiic* clearly enough (see his Fig. 42). The cells in layer *v* are "Of distinct pyramidal form, however, in contrast with the cells of the fifth layer of the inferior parietal brain." In brain *Hl* the cells of *v* in the inferior parietal brain are equally distinctly pyramidal (see Plate II).

We may conclude that the cortex of most of the superior temporal convolution and, as we have seen previously, of the posterior portions of the middle and inferior temporal convolutions resembles that of the inferior parietal region so closely as to be impossible of certain recognition. Campbell (1905) reckons all this territory to his type III temporal cortex, as we have seen. Is this true of the remainder of the temporal cortex?

Blinkow (1938) distinguishes within the temporal cortex a regio temporalis superior (*RTS*), regio temporalis media (*RTM*), regio temporalis basalis (*RTB*) and regio temporo-parieto-occipitalis (*RTPO*). He states that the regio temporalis media is the most typical of the temporal lobe. His figures show it to be situated in the same general region as Economo's TE_1, but his *RTM* spreads also over a portion of the polar region of Economo or of Brodmann. Blinkow states that "it is impossible to find just one portion of *RTM* which would be representative of all the other portions of this region." Nevertheless he ventures that "the structure of *RTM* possesses individual characteristic features: the border of I with II looks 'fringy,' the transition of II into III is gradual, the larger cells of III are arranged in groups, the radial striation goes throughout the whole lower stratum to the IV
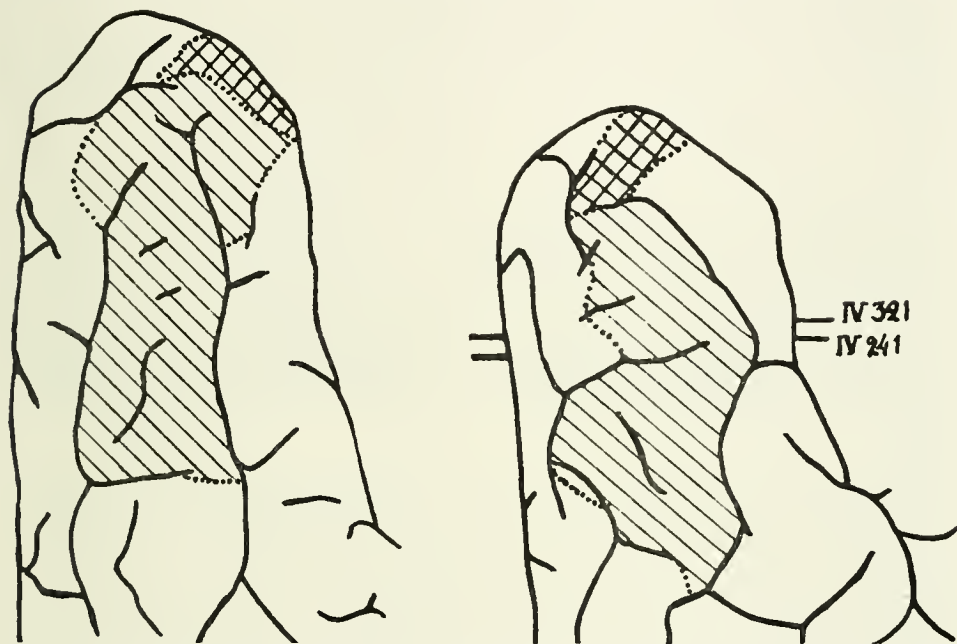

FIG. 105. Blinkow's map of the regio temporalis media of brain A27. Right hemisphere (left) drawn in mirror image.

layer inclusive, the V layer is very thick." Blinkow gives a long and detailed justification of his extension of *RTM* (Fig. 105) further over the temporal pole than did Brodmann and Economo. We agree, from our study, that the characteristics of Economo's temporopolar formation *TG* are found most clearly on the medial side of the temporal pole. Economo states, moreover (p. 125), "The transition of this area *TG* to the other areas of the various temporal convolutions is always a gradual one, and not at all distinctly marked."

Concerning the differences between *RTM* and *RTPO* Blinkow says that in the latter, "The II and IV layers are very distinct as dark bands, sharply demarcated against the neighboring layers and sharply pronounced because of paler III² and V layers; in the V layer the largest cells are still smaller than the corresponding

cells of RTM (especially in comparison with the largest cells of III) and are distributed more loosely." Later he says, "In our investigations the most persistent characteristic of RTPO as compared with RTM was the distinct demarcation of II and IV layers in RTPO." We would call attention to the absence of such statement in Economo's description of his area *PH* concerning the *II* and *IV* layers and the absence in Blinkow's description of any mention of fusion of *V* and *VI* which, according to Economo, is the chief characteristic of *PH*.

Economo states (p. 120), "A very striking feature is the fine formation of the pyramids in V of TE as compared with their irregular shape and small size in the same layer of the neighboring parietal region, PH." This distinction is not evident in our brain *Hl*; in the zone which Economo calls *PH* the pyramidal cells of *v* are well formed and larger than those farther forward.

Speaking of the region anterior to *PH*, which he calls *TE*, Economo says (1929a, p. 119), "In this region the cortex is very thick (3.5 mm.). [Not true of brain *Hl*.] III is thin, rather poor in cells, but these are large in size. [True only of IIIc and there not very large.] V and VI are enormously thick. [Not true of brain *Hl*.] (p. 120) "In TE the cells are also collected in perpendicular columns throughout the thickness of the cortex. This fact, and the preponderant thickness and cell wealth of the lowest laminae, V and VI, serve, however, to differentiate TE from the frontal formations. [But the perpendicular columns will not differentiate it from *OA* or the thickness and cell wealth of V and VI from *PH*. These are not distinguishing features]. A typical characteristic of TE is the fact that this IIIrd lamina is often not only relatively, but also absolutely, thicker in the walls of gyri than at the crowns, i.e., an inverted relationship from that usually observed in other convolutions." This characteristic is "often" observed elsewhere, "usually" over broad gyri.

Page 122: "This preponderance of V and VI in the cell picture as against the relatively slight development and paucity of cells in III, and the weak development of II and IV are striking features of the true temporal formation." The weak development of II and IV is not confined to *TE* and hence does not serve to identify it. We cannot find a preponderance of V and VI in brain *Hl*. The inner main layer is not absolutely better developed than in the frontal or inferior parietal regions, but only appears so in contrast to the poorly developed layer III. Indeed, this seems to us the only distinctive feature of this relatively small region over the middle portion of the second temporal gyrus.

We have the impression, from the examination of brain *Hl*, that there is a region about where Brodmann puts *20*, Economo puts *TE₂*, or Blinkow *RTM*, which is slightly different from the surrounding cortex in that layer *iii* is relatively thin and usually scarce of cells, but the region is vague and, as Blinkow says, not constant in structure. We have given in Plate VI a photograph of this region, there labeled Isocortex eulaminatus temporalis inferior (*IEti*, see Chap. IV, p. 72).

On the basal surface of the temporal lobe Economo distinguishes an area *TF*. He states (p. 123), "The difference between TF and the latter [*PH*], however, lies chiefly in the relatively good development of the Vth lamina, which shows beautiful pyramidal cells in contrast to the stunted ones in the basal parietal region." The "marked development of the efferent laminae, V and VI" was said (p. 122) to be

typical of *TE*. We cannot see in our sections any difference in size of the pyramids of *v* over the fusiform gyrus and over the temporo-occipital zone which Economo calls PH. (p. 124), "Vb appears distinctly lighter than the above stratum [Va], and thus differentiates the area TF from the other surrounding temporal formations." (p. 122) "Both its granule layers are somewhat more distinct than in the two middle temporal convolutions, and this makes horizontal laminations more distinct. The perpendicular striation is again quite narrow, resembling that of the first temporal convolution, and the parietal formation posteriorly annectent." Neither of these two characteristics is either prominent or constant in brain *Hl*. The distinctness of II and IV was given by Blinkow as characteristic of his *RTPO* (Economo's *PH*).

Blinkow (1936) has studied this basal temporal region in detail (Fig. 106). His regio temporalis basalis, *RTB*, includes Economo's *TE₂*, *TF*, *TH*, and a part of *TG*. He divides this region into thirteen subfields. He states that, "The peculiar morphological features of the basal temporal lobe are condensation of the ganglion
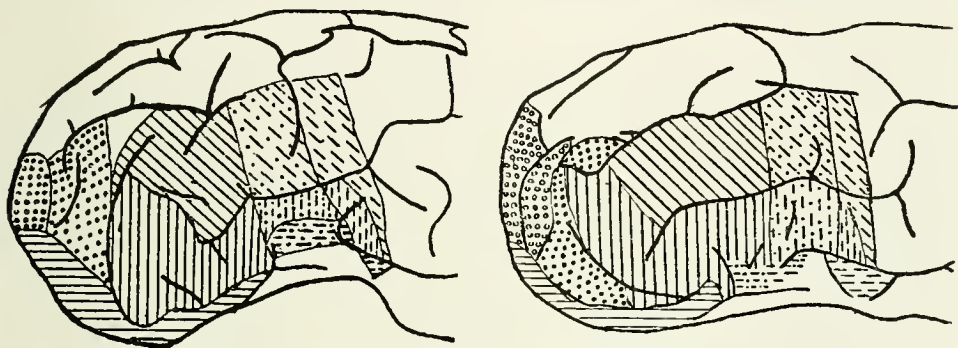

FIG. 106. Blinkow's map of the basal temporal regions of brain Ap18. The right hemisphere has been drawn in mirror image.

cells of the IInd layer, a light stripe in the middle of III, and massive dark lower layers." The light *iii* is given by Economo as characteristic of his proper temporal area *TE* and the heavy *v* as characteristic of *TH* whose (p. 125) "V also discloses a very distinct horizontal cell-band consisting of some few rows of very compactly arranged pyramidal elements. This is the structure which we have found typical for all formations in the vicinity of the olfactory brain." In brain *Hl* the cortex of the basal temporal surface shows these changes in layer *v* on the medial side and a lighter *iii* and *v* where it approaches the middle temporal convolution. We can see no reason to distinguish a separate area *TF* over the fusiform gyrus.

There remains the upper surface of the temporal lobe, on which Brodmann located the koniocortex, although he doubted (1914, p. 236) its connection with hearing, because he could not see it in the brains of lower primates. There is general agreement now that this is the auditory sensory cortex. Economo (p. 116) describes this cortex as follows: "This area TC is characterized by the smallness of the majority of its cells . . . by the thickness of the true granule layers, as well as by the narrow perpendicular arrangement of its granule elements in fine narrow striae which we have chosen to call rain-shower formation. The cortex is about 3.0 mm. thick, a

little too thick for koniocortex. Other peculiarities, however, such as the pallor of layer *v* characterize this area sufficiently as koniocortex." (p. 118) "It is strange that the area TC does not form a completely closed territory of its own as, for instance, the area striata does, but that frequent bands and islets of the surrounding area TB reach over its boundaries far into its territory; many of these bands show all degrees of transition from the granular structure of *TB* to the granulous structure of TC." This description was confirmed by the examination with Horn of a number of brains.

Around and amongst the patches of koniocortex is a zone of parakoniocortex, characterized as always by unusually large pyramids of *iiic*. This parakoniocortex extends outward on the lateral surface of the superior temporal gyrus to a variable extent. Medial to the auditory cortex is a narrow zone whose cells are, to quote Economo, "strikingly irregular, as already noted in other opercular formations . . . This cortex may be considered either as a less well differentiated granulous, but cell-poor type, or else as a part of the cortex whose development has lagged behind." In either case we see no reason to distinguish it, with Economo, as a separate area *TD*.

The maps of the supratemporal plane given by Campbell, Brodmann, Economo and Horn (1930), Kakeshita (1925) (see Fig. 107), Blinkow (1935), and Marinesco and Goldstein (1910), differ only in details; the general plan is agreed, and the examination of brain *Hl* adds nothing new. The infinite myeloarchitectonic parcellation of this region by Eduard Beek (1928) leaves us completely cold.

Toward the tip of the temporal lobe the fourth layer becomes thinner, the second layer becomes bunchy, the columns less distinct and the fifth layer denser. Over the tip, the cortex is quite thick. But these changes, as we saw, are very gradual and become well marked only on the medial surface as the allocortex is approached.

In general we may say that the cortex of the temporal lobe, as a whole, differs only in minute ways from that of the other lobes. It has a koniocortical area, a parakonicortical zone about it, and juxtallocortical zones near the allocortex. For the rest we can distinguish only a vague territory (see Plate VI) over the anterior half of the middle temporal gyrus which has characteristics, however slight, which enable it, in its extreme form, to be recognized, namely the thin and relatively empty *iii* together with a relatively thick *v* + *vi*.

We have already noted the zone posterior to this proper temporal cortex which Economo calls *PH* and Blinkow *RTPO*. It may be a part of the band, lying all around the occipital pole, to which Stankewitsch and Schewchenko (1935) called attention. The occipital cortex they characterized as follows: "Thinner and denser cortex with wide and coarse radial striation; considerable size of cells in III³; thin compact IV layer; pale small-celled V, sharply delimited from VI, which appears as a dark distinct band due to its dense and large-sized cells and sharp limit with the white matter." This is a fairly good description of Brodmann's *18* (Economo's *OB*), which is a parakoniocortical zone immediately adjacent to the striate cortex. As one passes anteriorly, however, the cortex loses these characteristics gradually to form a vague zone which is called by Brodmann *19* and by Economo *OA*. Of this zone (*OA*) Economo says (p. 98), "The broader external area, which resembles the parietal cortex in many respects, lies all along the posterior border of the parietal

lobe." Of *OB*, Economo says (p. 100): "the border against the latter (*OA*) generally cannot be drawn very precisely." If anything, this is an understatement.

Economo describes *OA* in detail thus: "At the boundary towards lamina IV one sees rarely single examples of larger pyramidal cells, here and there sporadically
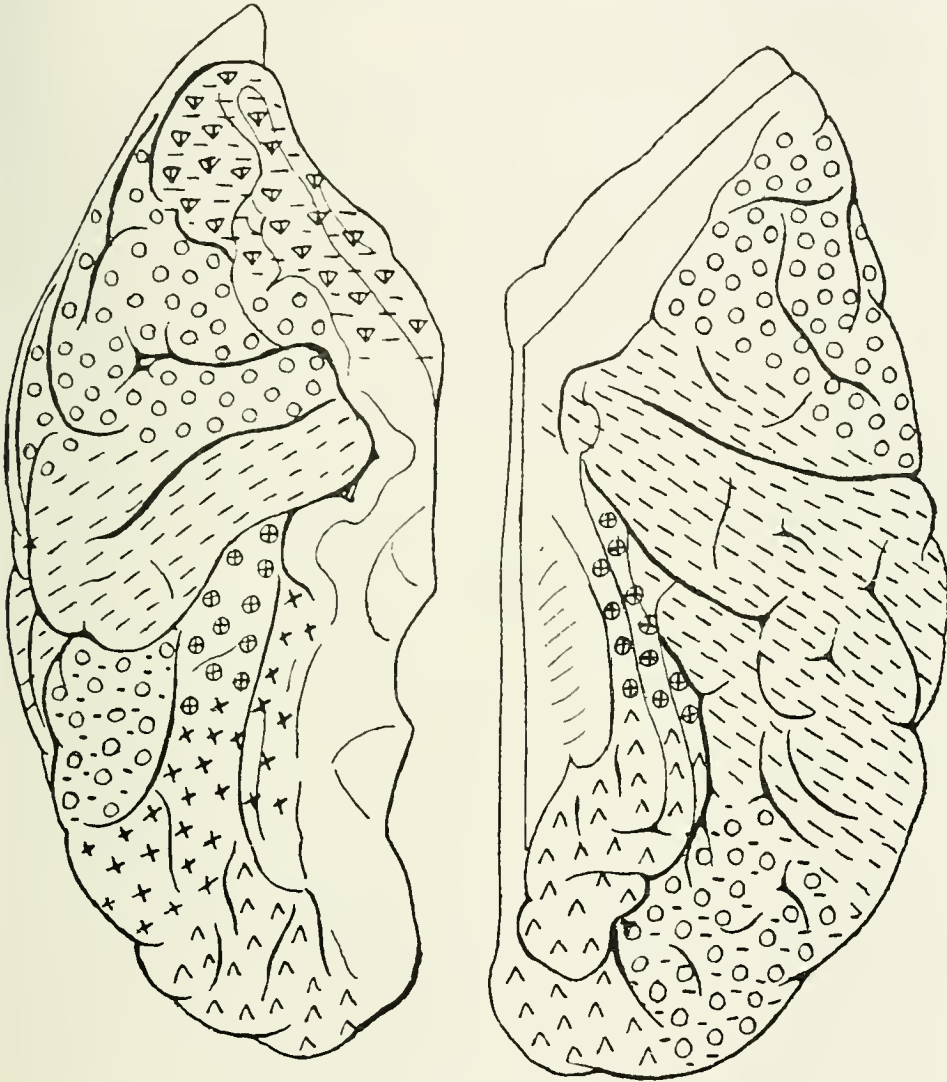
FIG. 107. Kakeshita's map of the supratemporal planes of the same brain. Acoustic koniocortex represented by dashes.

even very large pyramidal cells, but these are so few that they make up no actual substratum; so that there is no IIIc in fact." There is, as everywhere else, a size gradient in *III*, the cells near *IV* being largest, yet they are smaller than the corresponding cells in the parakoniocortex or near the parieto-occipital fissure at the

interhemispheric margin. Economo then remarks (p. 100), "The great pallor of V in the occipital lobe is one of its characteristic features, as compared with the structure of the inferior parietal lobe [but not of the superior parietal lobe] and the cytoarchitectonic limits of the parietal and occipital lobe can be determined on this basis." This is not true for brain *Hl*; V fills gradually and in patchy fashion as one goes forward from the striate margin.

Economo's discussions abound with statements like these: "This picture of *OA* is not everywhere precisely the same." "Nevertheless the structure of *OA* varies from gyrus to gyrus." Precisely. And the differences are minimal in any case. As Bianchi (1940, p. 371) states: "Examining the series of characters of the cellular architecture of the two areas [*OA* and *PE* of Economo] it is easy to see how some of them are so little typical that they are unable to be a precise guide for the recognition of one or the other of these areas. Such, for example, as the thickness of the first layer, the slight difference in thickness and concentration of cells in the second layer, the thickness of the third, and such things; characters so slightly different in the two cases as to be easily within the limits of individual variation." (p. 422) "The characteristics of the zone of transition are, therefore, represented by a gradual transformation, within the limits of individual variation. . . ." (p. 420) "In general the vast area of transition corresponds to the walls, the depth and all the immediate vicinity of the superior part of the parieto-occipital fissure. The gyrus intercuneatus is covered by it, at least in large part, since it is constituted by the emergence of the deeper, superior part of the fissure itself." Bianchi could find the large-celled patch called by Economo *PEγ* in only a few brains and says (p. 423): "At any rate these large cells are not characteristic of this transitional zone."

Gerhardt (1940), p. 390, says of this zone: "The delimitation against the occipital structures, against Brodmann's area *19*, is difficult because area *19* is not a homogeneous field but consists of several areas (Eduard Beck, 1934; Lungwitz, 1937). Moreover, there are here, at the transition between the two zones, as always, numerous limitrophic adaptations. I have put them with the parietal or occipital region according to the preponderance of their characters and in addition in such a way that the most important boundaries are chosen for the construction of the boundaries between regions. Boundaries perpendicular to the plane of section are surprisingly sharp and noticeable. Toward the occipital pole the cortex becomes suddenly thinner as compared with the parietal field; IV and VI become more prominent, the boundaries between the laminae become harder, the radii broader, coarser III² and III³ can be better distinguished; V¹ characterized by small pyramidal cells vanishes or is quite weakly and thinly sketched; V contains smaller and fewer nerve cells but shows in certain parts isolated very conspicuous large pyramidal cells, can be better separated into V¹ and V²; VII is thinner, more sharply set off from the white matter." Lungwitz's (1937) subdivisions of area *19* are based on myeloarchitecture. In spite of his elaborate table (pp. 632–33) we remain unimpressed.

Although on the outer surface of the hemisphere we have found it impossible to determine where the occipital parakoniocortex ends, or where one may properly speak of parietal or temporal cortex; on the medial surface one is greatly aided by

the medial occipitoparietal fissure. One can see that the cortex anterior and posterior to that fissure is different and, if one wishes to call the one parietal and the other occipital, one can see that in general the cortex behind the fissure is thinner, has a sharper division between i and ii, less distinction between ii and $iiia$, smaller cells in $iiic$, and denser vi. Much in the same way, in the chimpanzee and macaque monkey, if one defines OB as the cortex posterior to the lunate sulcus, and OA as the cortex anterior thereto, it is possible to describe their differences; unfortunately the human brain has rarely a sufficiently definite lunate sulcus to help us (see p. 52). Attempts such as those of M. Vogt (1929) to state the differences between the occipital parakoniocortex and preoccipital cortex in words leave us unimpressed since they deal with nuances which vary from place to place in both regions. Under the circumstances we would rather resign ourselves to stating that there is a gradual transformation of the cortex anterior to the striate area during which it gradually loses the parakoniocortical characteristics. Our description of the preoccipital variant (Chap. IV, p. 70, Plate IV) will have made it clear that the differences between I_{Epo} and I_{Eps} are slight indeed and that no sharp boundaries can be shown. It is interesting to note that Betz (1881) stated that "the structure of the lobulus quadratus (praecuneus internus) is the same as that of the parietal lobe."

On the medial surface the extent of the distinct parakoniocortical zone about the striate area varies in width. Because of the impossibility of defining this zone accurately, comparative measurements such as are given in the studies of Filimonoff (1932) are futile as pointed out by Bonin, Garol, and McCulloch (1942). In brain Hl the parakoniocortex seems to end anteriorly in the depth of the calcarine fissure and does not emerge on the upper lip anteriorly to the medial parieto-occipital fissure. Around the anterior extremity of the calcarine fissure the cortex is thin, badly formed, of nondescript character, impossible to assign to parietal, occipital, or temporal lobe. Anteriorly this ill-defined region merges into the retrosplenial formations.

The extent of the striate cortex is easy to determine and we have many maps at our disposal. Its relationship to the calcarine fissure is constant (Fig. 108) but its extent on the surface varies from brain to brain (Elliot Smith, 1904a; Campbell, 1905; Brodmann, 1903b, 1909, 1912; Economo, 1930a; and Filimonoff, 1932). Attempts to divide it into subareas such as those of Ngowyang (1934a) seem fruitless. Anteriorly, it extends in the bottom of the calcarine fissure roughly as far as the point where medial parieto-occipital fissure and calcarine fissure meet (Filimonoff point φ'', see Chap. III, p. 26) but covers generally more of the ventral than of the dorsal lip. In the opposite direction, it covers the occipital pole. Its extent on the lateral aspect of the hemisphere varies. Its relations to the "sulcus lunatus" were discussed in chapter III. Wen (1933) distinguished between an anthropine and pithecoid type. The surface covered by the striate area was given by Economo as about 24.5 cm.[2] From Filimonoff's data, Bonin, Garol and McCulloch computed an area of 21.1 ± 0.3 cm.[2], for the human brain. Popoff (1927) gives 45 cm.[2] for one, and 20.4 cm.[2] for another brain and states that Brodmann found in seven hemispheres an extent between 44 and 29.5 cm.[2] M. Rose (1935) gives for the volume of the striate area 4.9 cm.[3] or 3.2 per cent of the whole cortex.

On the posterior part of the cingulate gyrus is an extension of eulaminate cortex

of the parietal region. Economo divides it into LC_1 and LC_2 but admits that they are sufficiently alike to be described together (p. 135):

The area LC_1 which borders on the region of the superior parietal lobule at the level of the sulcus subparietalis, may be distinguished from the latter [LC_2] by the somewhat slighter development of III, as well as by the lack of the fine, radiate striation which characterizes the parietal cortex.

The striation is visible when cut in the proper plane (p. 136):

IV. . .shows the characteristic division of the parietal lobe, which is a special feature of the superior parietal lobule, i.e., an upper, looser IVa stratum and lower, denser IVb consisting of compactly placed pyramidal cells. . . . V. . .is divided, although not very clearly, into a Va and Vb substratum. . . . In the dorsal region [LC_1] the larger pyramidal cells are found compactly placed directly beneath IV.
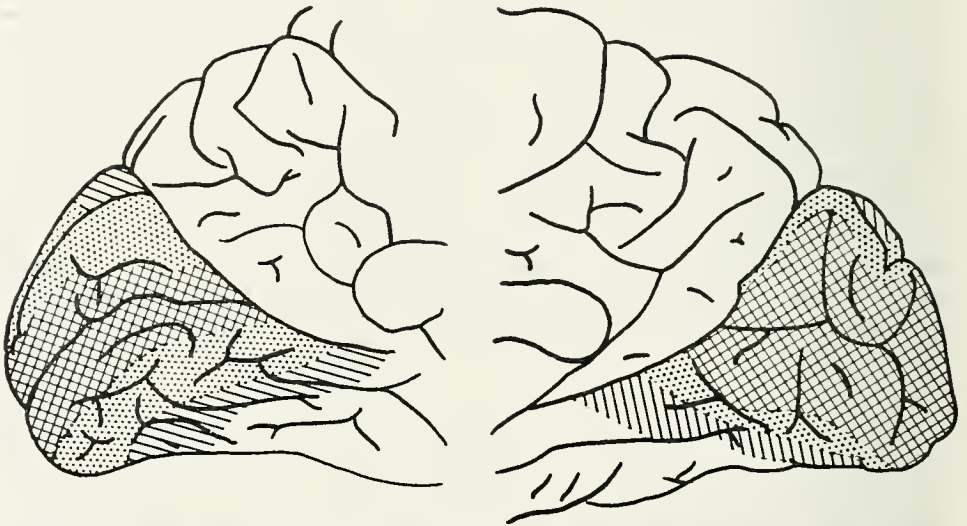

FIG. 108. Maps of the striate area on the medial surfaces of the two hemispheres of the same brain (redrawn after Filimonoff). Striate area cross-hatched; parakoniocortex dotted.

The differences from the eulaminate superior parietal cortex are so tenuous that we see no cytoarchitectonic reason to emphasize them. We also agree with M. Rose (1927) that there is no good reason to reckon the posterior limbic region with the anterior limbic and retrosplenial formations. The posterior limbic area is typical parietal cortex as Betz (1881) already remarked. The elaborate subdivisions of Gerhardt (1940) we are unable to confirm.

The anterior limbic region is covered by an agranular cortex which, because of its peculiar structure has been called mesocortex. It has been studied in detail and minutely subdivided, especially near the sulcus corporis callosi, by M. Rose (1927) to no purpose so far as we can see. Around it and its subcallosal allocortical extension, called by Economo FM, there is a variable juxtallocortical zone (Economo's FL, FCL, FDL, FEL, FHL) to which we have, referred. It extends along the cingulate sulcus as far back as the agranular precentral cortex.

We have discussed the inferior wall of the lateral fissure (see p. 224). On its superior wall the cortex is eulaminate and resembles that of the inferior parietal lobule as far forward as the lower end of the central sulcus; this cortex extends over the posterior part of the island of Reil. About this region, Economo states (p. 91), "The posterior part of the island . . . recalls the small-celled, compact structure of the parietal type, with its characteristically broad granule layers." We agree. Since identical cortex covers also a large part of the superior temporal gyrus there seems no reason to make of it a separate area. Campbell (1905) reckoned it with his type III temporal cortex (our Fig. 104). Finer cytological studies seem of little help. Cajal (1911) found his characteristic auditory cells in the insular cortex. Ngowyang (1932a), Crinis (1933), and Brockhaus (1940) have also described peculiar "forked cells" (Gabelzellen). Before any conclusion can be drawn about the insular cortex, the effects of post mortem autolysis must be ruled out.

Anteriorly the simple agranular cortex of the convexity may extend on to the operculum whose anterior portion is dysgranular and resembles the cortex of the anterior half of the island. According to Economo this is IA and is characterized by "the density and the strikingly fine cell formation of the Vth layer, often so marked as to appear even to the naked eye as a blue band in the stained preparation." The cortex of the island has been analyzed in detail by Brockhaus (1940). There is clearly an anterior agranular and a posterior eulaminate part (Fig. 109) divided by the sulcus centralis insulae (see Chap. III, p. 33). Its only unity lies in the fact that it is underlain by the claustrum, which Brodmann (1914) calls its VIc.

The limen insulae is covered by allocortex (Fig. 109). Surrounding this focus, juxtallocortical zones can be recognized over the orbital operculum, the posterior orbital surface, the inner surface of the temporal pole, as well as over the island anterior to the sulcus centralis insulae and up onto the frontal operculum almost to the lip of the lateral fissure. Throughout this zone the layer iv becomes more attenuated and the layer v denser and better filled with large cells, as one approaches the limen insulae. This zone bears various designations in Economo's text—FH, FHL, FL, FG, FI, FIH, IA, TG_a.

It seems unprofitable to divide the isocortex into the five fundamental types of Economo (1926c, see our Fig. 110). The koniocortex (type 5) is, of course, clearly enough defined. It always covers areas of primary sensory radiation. The agranular cortex (type 1) varies considerably in structure from $FA\gamma$ to LA and probably also in function. Nevertheless, it contains the area FA which, when stimulated electrically, gives movements of various kinds. But when one comes to Economo's types 2, 3, and 4 one is on much more dubious ground. Type 4 seems to have been separated because of its thinness, but the frontal and occipital regions of type 4 (see his Fig. 9, a and b, 1929a) are very different otherwise; the frontal type 4 is juxtallocortical and characterized by a heavy v, whereas the occipital type 4 has a light v and big cells in $iiic$. The occipital type 4 resembles, in fact, closely the postcentral part of type 2 and is parakoniocortex in our sense. The differences between Economo's types 2 and 3 are still more tenuous.

The same remarks might be made concerning the fundamental myeloarchitectural variants of O. Vogt. They seem to have no more intimate association with any func-
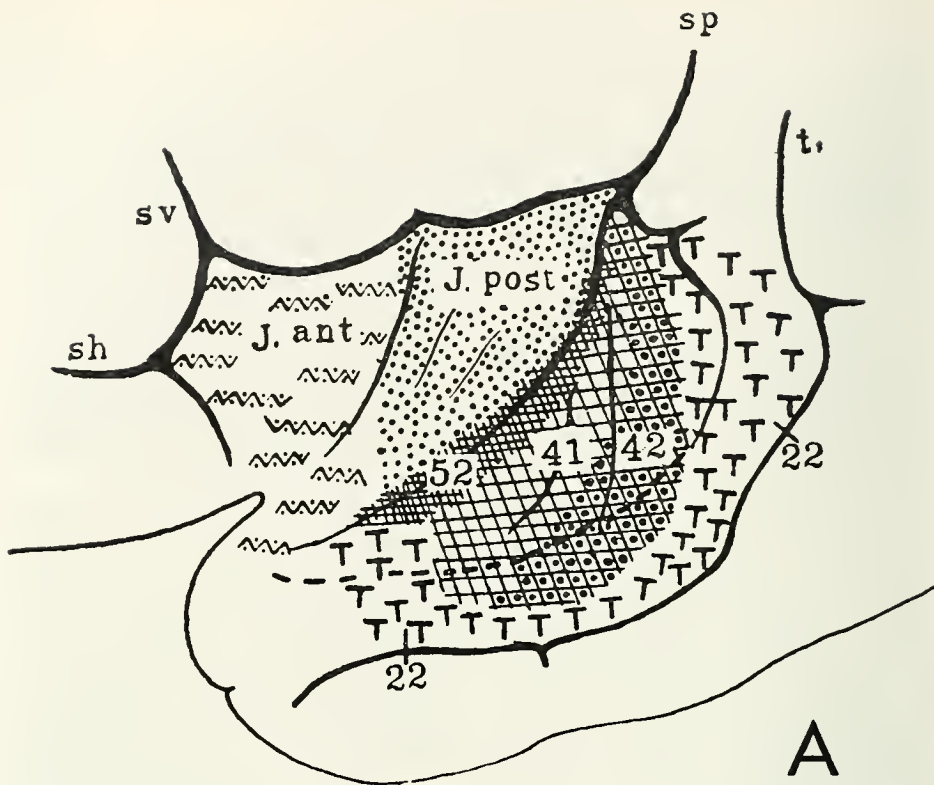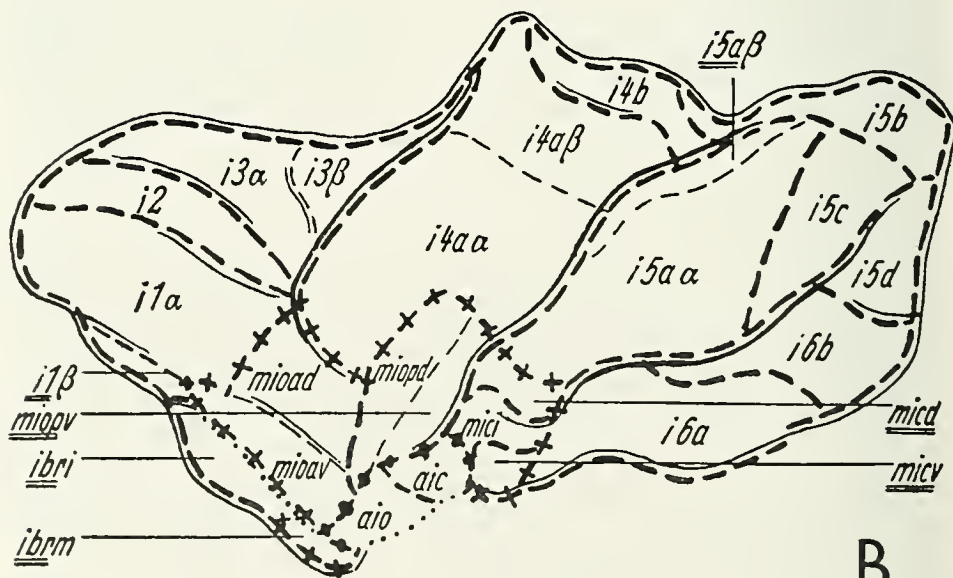
FIG. 109. Maps of the island of Reil. A—after Brodmann: J. ant.—anterior area of island, J. post.—posterior area. B—after Brockhaus: *aio, aic*—allocortex; all *mi* ... labels indicate mesocortex.

tional distinctions which might be related to internal cortical structure. Moreover, the system used is illogical and inconsistent. For example, O. Vogt (1910, Fig. 2) gives as fundamental variations of the myeloarchitectural pattern 4 types—bistriate, unistriate, unitostriate and astriate (Fig. 111). In discussing the frontal lobe, however, he lists six fundamental regions: I, Regio unistriata euradiata tenuifibrosa; II, Regio unistriata infraradiata; III, Regio unistriata euradiata grossofibrosa;
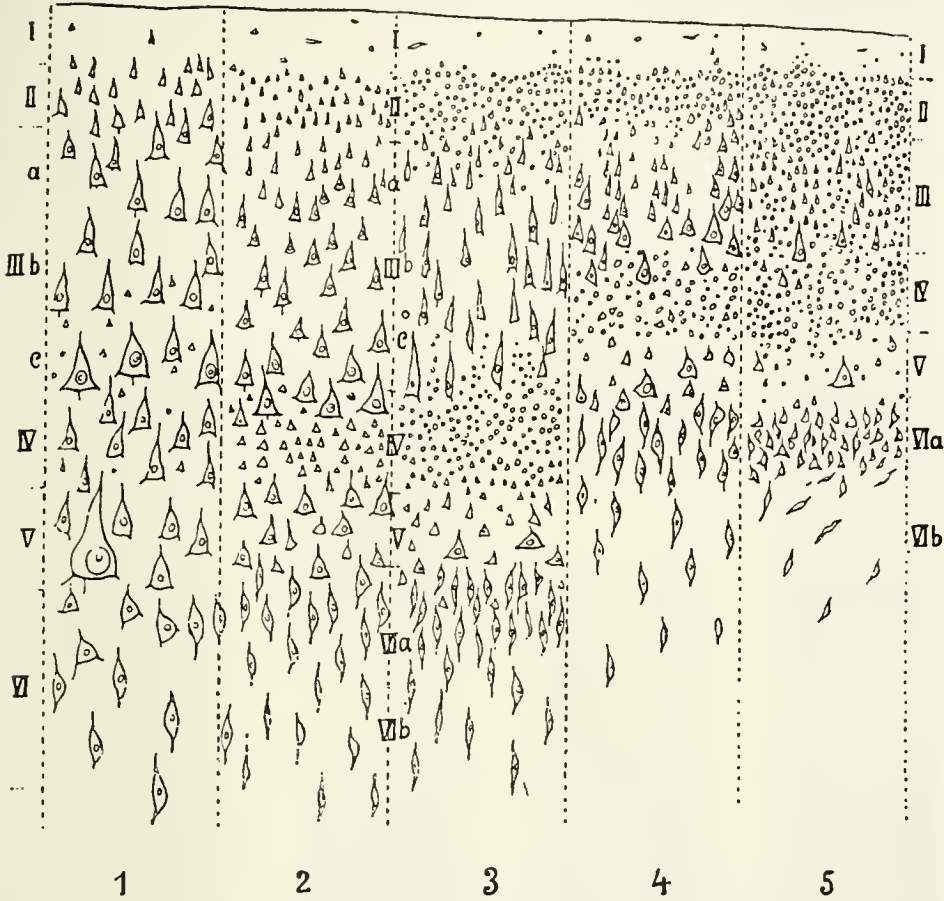
FIG. 110. The five fundamental types of the isocortex according to Economo.

IV, Regio propeunistriata; V, Regio bistriata; VI, Regio unitostriata. The astriate type appears only as a minor subregion under III.

The distribution of all these types, however, serves to emphasize a point to which we have repeatedly recurred, namely, the practical impossibility of distinguishing vast regions of the frontal, inferior parietal, parieto-occipital, occipitotemporal, basal temporal, and superior temporal regions. If we take once more our photographs of these regions without identifying marks and shuffle them, we are still unable to sort them by region. We are unable to distinguish surely a photograph

of *FDm* from one of *PG* or *TA*, a photograph of *PC* from one of *PEγ*, a photograph of *FDΓ* from one of *OA*, a photograph of *PF* fom one of *TF*, etc . It is easyo take the photographs, place them side by side, and describe differences between any two
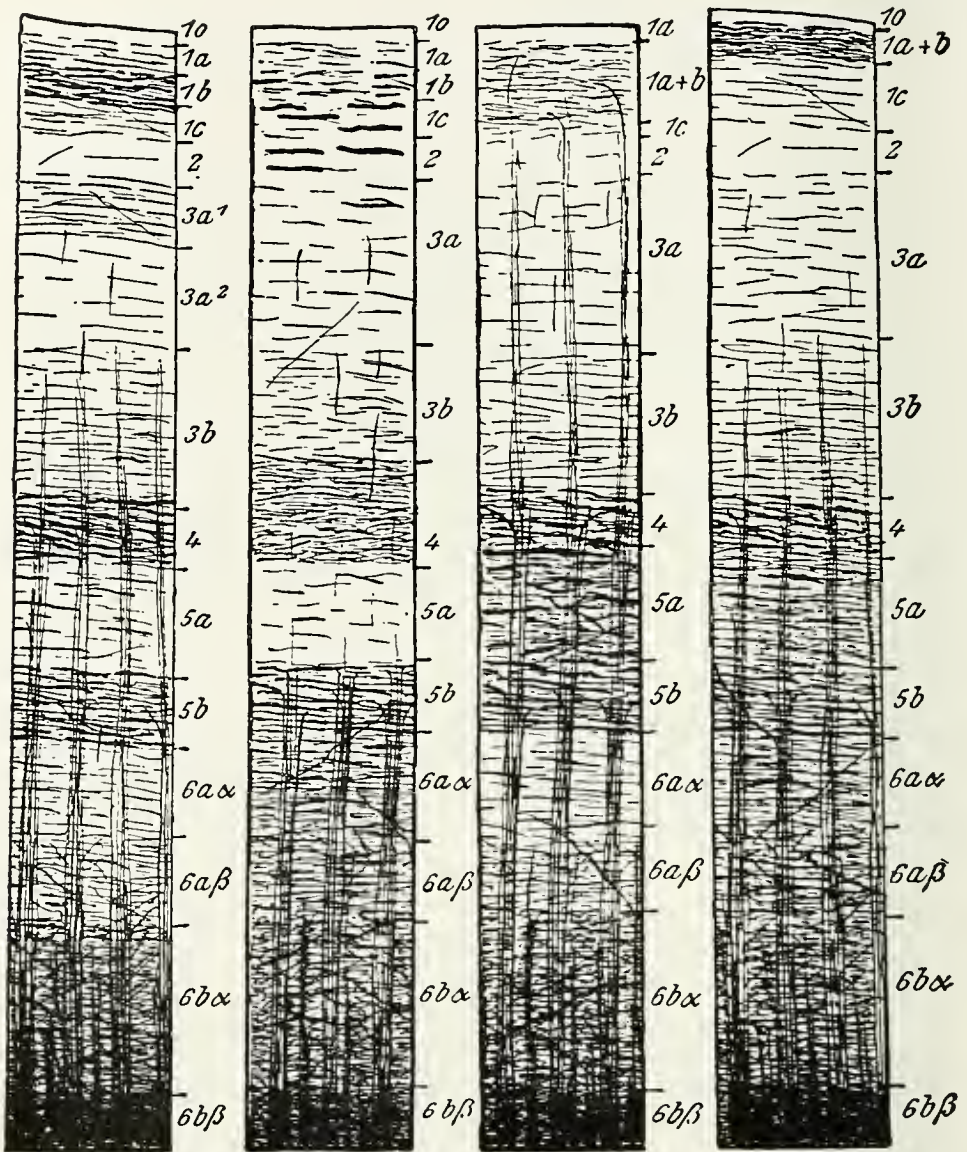
FIG. 111. The four fundamental types of isocortex according to Vogt (see p. 231).

of them, just as it is easy to take two photographs of the inferior parietal lobule 200μ apart and describe differences between them, but that these differences are either constant or important we do not believe. For this reason we reject the ex-

cessive parcellations of the Vogt, Economo, and Filimonoff schools as misleading and insignificant. As one reads through their prolix descriptions, and has the misfortune to remember what he has read, one is either repeatedly shocked by contradictions or suffers from what the French psychiatrists call *le phénomène du déjà-vu*, description after description sounding merely like paraphrases of the preceding one.

The structural peculiarities which we have been able consistently to distinguish, and which seem to us possibly important, are summarized in the frontispiece to which reference was made at the beginning of this chapter.

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Chapter VII: Intercortical Connections

During the process of differentiation of these more specific tracts they retain collateral connections along the entire course, so that they continue to perform integrative functions similar to those of the less specialized ancestral pattern.

C. Judson Herrick (1948)

Cortical function depends not only on the intrinsic structure, but also on cortico-cortical and extrinsic connections of the various areas. Nervous activity is the transmission of signals from one set of neurons to other sets. These signals are trains of impulses varying in frequency, in regularity, and in their distribution over the available pathways. The exact values of these parameters are, so we assume, a function of the "cytoarchitecture" of the set of neurons emitting signals, the set receiving any train of impulses is determined by the course of the pathways and the effect which the signals have on the receiver set is a function of its cytoarchitecture.

While we do not subscribe to Meynert's *Elementarorgane* as they appear to have been originally conceived, there is yet ample justification to look upon the cerebral cortex as a multitude of sets of neurons distinguishable by their connections and/or by their architecture. To treat cortical areas as separate entities is almost unavoidable if we wish to analyze the connections which tie them together, yet the development of modern neurophysiology has revealed that such an enormous extent of cortex is involved in almost any cortical functioning as to deprive an analysis on this basis of any correlation with functional data.

Neurology, urged by the important task to define the *sedes morbi* to plan the proper therapeutic measures, is apt to forget that "mind" or, for the matter of that, "soul" is merely the totality of all judgments or statements and that, linguistically as well as epistemologically, such judgments consist of relations between words or concepts. The neurological correlate of the mind can, therefore, not be this or that center but only the pattern of the connections between these centers. When Wernicke (1906) defined mental diseases as diseases of the association system he was right, in a very modern sense, although he worked out details in a manner that appears to us decidedly old-fashioned.

A critical appraisal of what we know about the corticocortical (association) fibers should be included in any monograph on the isocortex. This is all the more timely because Dusser de Barenne and McCulloch's method of physiological neuronography has furnished experimental evidence not yet checked against the earlier anatomical and pathological observations.

Scientific interest in the white matter can be traced back as far as Descartes. The plates illustrating his essay, *L'Homme*, show schematic pathways from the "conarium" (pineal gland) to certain parts of the brain, and Descartes refers to them as tubes (*tuyaux*). Vieussens (cited after Soury, 1899), whose name was connected until quite recently with the term centrum ovale, stated that "the white substance consists of innumerable fibrillae, connected in several bundles, as can be clearly seen when they are boiled in oil." However, failure to appreciate the active

role of the cerebral cortex led Vieussens and the other anatomists of the century of enlightment to regard the white matter as the seat of some faculty or other, and not as a structure relating centers with each other.

It is surprising that, in spite of their obvious inability to understand, even in the most general way, the function of the centrum ovale, much information was added by anatomists who lived during the Napoleonic period. Among them Reil (see Neuburger, 1913), who mentions Franz Joseph Gall with admiration, showed by careful and methodical gross dissections several of the fiber tracts of the white matter. Burdach (1822), in his famous book on the structure and the life of the brain, frequently refers in his text to Reil's plates.

The modern period, made possible by Gall but ushered in by Baillarger's (1840) demonstration that white and gray matter are in intimate contact with each other, began seriously with Meynert (1884, 1892). Yet the number of workers trying to disentangle the crisscross of fibers in the centrum ovale has never been very large. The lack of suitable methods must have discouraged many students. Macroscopic dissection, as it was used by Reil and by Burdach, was resorted to again and again, in spite of the obvious fact that its possibilities must have been exhausted long ago. Even in the twentieth century Elze (1929), Hultkrantz (1929), and Klingler (1935) still took up forceps and orangewood stick. A better demonstration of the association fibers was tried by "automatic internal dissection" (Rosett, 1933), but this method appears more suited for the study of the short U fibers than for the deeper long association tracts. The microscopical study of pathological material, of immature brains (Niessl-Mayendorf, 1919), of nonhuman mammals (Redlich, 1903 and 1905), as well as of experiments on primates (Mettler, 1935), was pursued. The schematic drawings given by such men as Monakow (1905) and Dejerine (1895) have ever since gone from textbook to textbook without serious alterations or improvements.

The method of physiological neuronography offered for the first time a check on the anatomist's work by observing—under controlled conditions—the behavior of the living brain. Applicable in principle to the human brain during neurosurgical operations, it has so far been systematically employed only in experiments on the cat (Garol, 1942) and on two primates, the macaque (McCulloch, 1944b; Bonin and Bailey, 1947) and the chimpanzee (Bailey, Bonin, and McCulloch, 1950). The patterns in these two primates are remarkably similar, hence it appears permissible to draw tentative conclusions about the human brain—verifiable by the neurosurgeon. What follows is essentially a summary of the human association systems, as they were anatomically described, discussed in the light of these experimental findings on nonhuman primates.

Many authors, such as Schnopfhagen (1890) and Rosett (1933) expressed with some emphasis that association fibers end in the valleys or walls but not on the crests of the gyri. Strychninizations, however, have shown time and again that association fibers certainly emerge from that part of the cortex which is on the free surface of the hemisphere. The more recent experiments by Chusid, Sugar, and French (1948) have made it equally clear, of course, that fibers also arise from the parts of the cortex buried within the cerebral folds. The view that the valley of a sulcus has a preponderantly receptive function and the crest of a gyrus a prepon-

derantly effective one was put forward on cytoarchitectural grounds by Economo (1926a); a few years later Bok (1929) showed the fallacy of his argument. For, while the inner main layer is indeed thinner in a valley than on a crest, as Economo observed, the volume of a cortical unit is the same in both locations.

The detailed descriptions of the association bundles vary little from author to author. We follow mainly Monakow (1905) and Dejerine (1895), who appear to have been the last to write a "classical" account on the basis of personal observations.

Perhaps the least disputed is the *uncinate tract* which connects the orbital surface of the frontal lobe with the temporal pole. Schnopfhagen (1890), after gross dissection, stated that it arose from the internal and external basal frontal gyrus, "but not from that part which has been described as the basal part of the middle frontal gyrus." The bundle runs, according to Schnopfhagen and other authors, partly through the anterobasal part of the external capsule, and partly through the adjacent corner of the claustrum which it breaks up into cell islands. Landau (1919) states that it also runs through the *capsula extrema*. Monakow (1905) gives the *Hakenwindung* (Temporal) as the other end-station of the uncinate bundle. The term *Hakenwindung* is nowhere explained. Did Monakow mean the uncus? Anton and Zingerle (1902) deduced from pathological cases (destruction of the orbital gyrus) that many of the fibers of the uncinate bundle end in the lower part of the insula. It is impossible to decide whether olfactory fibers (of the lateral root, toward limen insulae and uncus) were involved or not.

The *arcuate fasciculus* consists of fine fibers which curve around the dorsal and posterior margin of the insula. They are separated from the uncinate fascicle by commissural (callosal?) fibers (Monakow, Schnopfhagen). Rosett devoted considerable labor to its investigation. He found a bundle between frontal and temporal cortex, of varying thickness, best developed in the temporoparietal region.

Physiological neuronography presents evidence for both uncinate and arcuate bundles. That for the uncinate fascicle is particularly strong; orbital cortex and temporal pole are connected with each other in both macaque and chimpanzee. The firing between areas *47* and *38* in the macaque (McCulloch, 1944b) and between *FF* and *TG* in the chimpanzee (Bailey, Bonin, and McCulloch, 1950) has been observed in several experiments. Whether the firing of the inferior frontal gyrus and the parietal operculum by strychninization of the first temporal convolution, that of the inferior frontal gyrus from the second and of the middle frontal gyrus from the inferior temporal gyrus (Petr, Holden, and Jirout, 1949) is due to conductions in the arcuate or uncinate fascicle cannot be decided at present; that the last, if not the latter two, observations should be ascribed to the arcuate fascicle seems more plausible. The firing of the middle temporal gyrus from the inferior parietal lobule as well as the firings of the inferior parietal lobule from the inferior frontal gyrus can be taken as further evidence for "arcuate" fibers.

A *fronto-occipital* bundle, running in the angle between corpus callosum and ventricular ependyma, was described in a case of agenesis of the corpus callosum by Onufrowicz (1887) who worked in Forel's laboratory, by Kaufmann (1887) and subsequently by many other authors. The presence of long fibers in the stratum subcallosum was confirmed by Muratoff (1893) in dogs by means of Marchi prepara-

tions. But whether the impressive bundle of fibers present in malformed human brains is homologous to the sparse and slender band of fibers seen in normal brains or whether it is a heterotopic bundle has not yet been definitely decided. Mingazzini (1922), after weighing the pros and cons, ended with the remark that "we are still far from having reached a satisfactory result."

The question of the *subcallosal fasciculus* became further complicated when Dejerine (1895) described an occipitofrontal fasciculus and identified it with the bundle which Onufrowicz found in malformed brains. Monakow expressed his doubts about this identification. Niessl-Mayendorf (1919) went even further and denied altogether the existence of long fronto-occipital (or occipitofrontal) fibers, calling Dejerine's bundle "merely an arbitrary pooling of some fragments of different tracts." Mettler (1935) also does not consider Dejerine's bundle identical with that of Forel-Onufrowicz, but admits the possibility of slight intermingling. Several authors, among them Wernicke, considered the subcallosal bundle as an association system of the caudate nucleus. This enigmatic bundle has gained in interest since McLardy (1950) showed that it had been severed in cases of delayed death after frontal lobotomy.

Strychninizations merely show, of course, the presence of fibers, their beginnings and their endings but not their courses. Thus far the involved questions about the subcallosal fibers just sketched have been brought no nearer their solution. Experiments by Chusid, Sugar, and French (1948), however, show beyond any doubt the existence of long association fibers between frontal and occipital cortex and should definitely rule out the opinion of Niessl-Mayendorf (1919).

The *cingulum* is readily observed in frontal sections of the hemisphere as a bundle of fibers cut in cross section just above the corpus callosum and just below the cortex of the cingulate gyrus. Beevor (1890) divided the cingulum of the marmoset into a horizontal part, just dorsad to the corpus callosum, an anterior part sweeping around the genu of the corpus callosum and a posterior part extending beyond the splenium. The difficulties ever since have been to determine the exact origin and/or destination of the cingular fibers in the anterior and posterior parts and to unveil the composition of the horizontal part, whether composed of association fibers or of radiation fibers; whether, if the former were true, composed of shorter interlaced fibers or of long fibers. Ramón y Cajal (1911, p. 810), after studying the brains of small mammals, stated that the anterior part of the cingulum descended not to the olfactory region but into the corona radiata, that the cingulum, therefore, is a projection pathway (*une voie de projection*), that the posterior part ends in the subiculum and cornu ammonis and that it contains, apart from shorter fibers, also very long ones (*une voie fort longue*). In support of these views could be cited Flechsig (1896) who depicted fibers from the internal capsule going far frontad and then turning sharply mediad and occipitad to reach the cingulum (see his Fig. 9, fiber η and δ). Valkenburg's (1908) statement that the fibers in the cingulum run fronto-caudally in the lateral portion of the horizontal part of the cingulum gives additional support. Recently Krieg (1946) stated that, in the rat, fibers from the anterior thalamic nuclei "form the ventral end of the cingulum." However, all authors, including Cajal, agree that the cingulum contains also association fibers. Most older authors, probably under the spell of Broca's conception of the *grand lobe*

limbique, thought of the fibers of the cingulum as rounding the splenium of the corpus callosum to reach the subiculum or even the cornu ammonis. Only Elze (1929) states that the precuneus receives the greatest part of the cingulum and adds that the cuneus is almost completely devoid of cingular fibers. That the firing within the "cingular belt" (Bailey *et al.*, 1944) occurs through fibers of the cingulum has not been proven. The observations made thus far would support Elze's statement of fibers from cingulum to precuneus (*LC* fires *OA*!). Firing into the subiculum and the cornu ammonis has thus far been observed only from the retrosplenial region (Pribram, Lennox, and Dunsmore, 1950).

The *inferior longitudinal fasciculus*, known ever since Burdach dissected it out, has been interpreted sometimes (e.g., Rosett) as an association bundle, and sometimes (e.g., Probst, 1901, or Niessl-Mayendorf, 1919) as but another—rather superfluous—name for the optic radiation. Most authors, however, such as Monakow, Redlich (1905), Archambault (1906), Valkenburg (1908), and Davis (1921) considered the inferior longitudinal bundle as composed of both association and radiation fibers. This problem is intimately connected with that of the *strata sagittalia*, found in the lateral wall of the posterior horn of the lateral ventricle (see Bonin, Garol, and McCulloch, 1942). Whether in these strata optic radiation and association bundle are clearly separated cannot be decided by physiological neuronography and appears to be at present of purely academic interest in any case. Physiological neuronography proves, in any event, that there are association fibers which run in the direction of the inferior longitudinal bundle and shows that some of these fibers are, contrary to the opinion of Rosett, fairly long, although never as long as the whole bundle. These authors, who assumed association fibers in the inferior longitudinal fasciculus, generally looked upon them as connections between the visual and acoustic parts of the cortex. There is no proof for that, but there is good reason to believe that the connections of the temporal with the optic sector subserve some of the higher visual functions (see Pötzl, 1928).

Some dorsoventral bundles have been described in the occipital lobe: the *fasciculus transversus lobi lingualis* of Vialet (1893), the *stratum transversum cunei* of Sachs (1892), and the *fasciculus occipitalis lateralis verticalis* of Wernicke (1881). The last one was first demonstrated in the brain of the macaque and later identified in the human brain as the *stratum verticale convexitatis* by Sachs (1892). All three of them have been verified by strychninization (Bonin, Garol, and McCulloch, 1942).

Apart from the systems thus far discussed, physiological neuronography has demonstrated further connections (Fig. 112). The vertical fibers under both occipital and parietal lobe appear to be richer than could be expected from purely anatomical studies. Some of them should undoubtedly be considered to be the temporoparietal fascicle of Monakow (1905). The connections between first and second motor area found in the macaque by French, Sugar, and Chusid (1948) have never been demonstrated by anatomists. The rich corticocortical afferents to the first motor area, from postcentral, parietal, and frontal (or premotor?) region might have been suspected from the varying topography of lesions which caused apraxia. Yet Monakow's centroparietal fascicle (see also Katzenstein, 1930) was the only one discovered by anatomists.

Commissural fibers between the isocortex of the two hemispheres course through
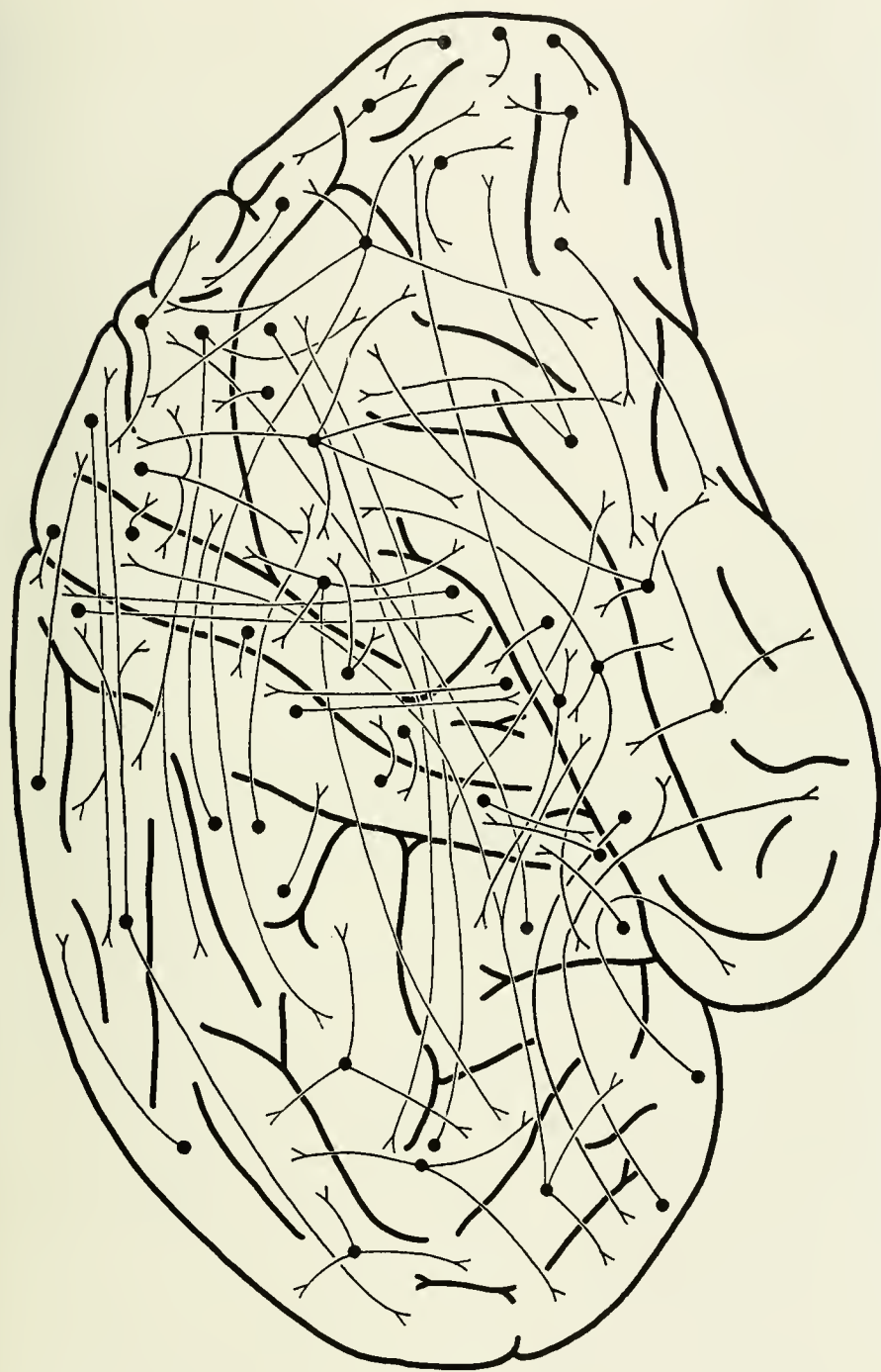
FIG. 112. Corticocortical connections as revealed by physiological neuronography in the chimpanzee (after Bonin, modified).

the corpus callosum or the anterior commissure. The latter provides a pathway for fibers connecting the two temporal lobes which appear to be restricted, if the macaque and chimpanzee represent indeed small-scale models of man, to the second temporal gyrus. The corpus callosum provides a pathway for all other fibers. We have very little direct information about the origin and the distribution of the commissural fibers in man. Ramón y Cajal (1911) and Villaverde (1932), who studied the brains of bats and rabbits respectively, considered the majority of callosal fibers as collaterals of those axons which form the systems of projection. Pines and Maimun (1939), who were the last to investigate the origin of the callosal fibers, found, after lesions of one hemisphere, retrograde degeneration of scattered cells in the third, fifth, and sixth layers. These were always found in homotopic fields; the question of heterotopic fields was left undecided. Lorente de Nó (1949) states that the fibers end in the inner stripe of Baillarger and the stripe of Kaes-Bechterew. Ariëns Kappers' (1947, p. 315) statement that the callosal fibers end principally in the second and third layer is hardly borne out by Lorente de Nó's figures. That the commissural fibers are not equally densely distributed over the whole isocortex is obvious. The lack of such fibers for most of the first and third temporal convolutions has just been mentioned. From our knowledge of the brain of the macaque and chimpanzee, one would infer that the area striata (Bonin, Garol, and McCulloch, 1942), the fields for the extremities in the sensory and motor cortex, and fairly large parts of the frontal region are also without callosal connections (Bonin and Bailey, 1947; Bailey, Bonin, and McCulloch, 1950). The fusion of the two halves of the visual field, in spite of the absence of callosal fibers, is remarkable and suggests a very close "collaboration" between striate and at least parastriate areas. It should be remembered, however, that Gengerelli (1948) found Wertheimer's φ phenomenon to occur more readily within one-half of the visual field than across the midline.

Sakurai (1939) has given the area of cross section of the corpus callosum in forty-one Japanese. His mean, with the standard error added by computing the necessary statistics from his data, is 6.1 ± 0.2 cm.² Schepers (1938) gives a mean sectional area of 6.8 ± 0.5 cm.² for Negroes of South Africa. If the average diameter of the fibers is assumed to be 10 μ, and the fibers are assumed to be densely packed, one arrives at an estimate of 1.21 x 10⁶ or 1.3 x 10⁶ fibers in the corpus callosum. The anterior commissure will add no more than a small percentage to this figure. The fiber diameter may be smaller, but the fibers are not densely packed since there is neuroglia and some mesenchymal tissue between them. It may be safe to assume that the human brain contains about 10^6 commissural fibers. This should be compared with Economo's estimate of 10^{10} cells in the human isocortex.

Ariëns Kappers (1926) and his followers computed a "callosal index" from its height and length. This index is correlated, of course, with the general shape of the brain (see p. 59). It varies between 380 (Northern Chinese of Bork-Feltkamp (1930) and 280 (South African Negroes of Schepers, 1938). More interesting is the shape of the corpus callosum. It is far from being of uniform thickness as some textbooks and atlases like to portray it but is quite slim in its posterior third. It ends, however, in a very massive splenium. This peculiar shape of the human corpus callosum may be due to the scarcity of callosal fibers between the two pre- and postcentral areas.

The origin and termination of the corticocortical fibers in the cortex are not

certainly known. Ariëns Kappers, Huber, and Crosby (1936) state (p. 1571) that, "the higher associative and receptive character of the supragranular layers is indicated by the fact that the corpus callosum fibers terminate in the supragranular layers, although, as has been seen, they arise from the infragranular layers." We do not quite follow this argument which seems to involve as much the infragranular as the supragranular layers. At any rate, it seems too dogmatic. This thesis had been elaborated by van't Hoog (1920) who concluded that $ii + iii + iv$ are receptive and associational and $v + vi$ are efferent and commissural. Lorente de Nó (1949) found, in the mouse, that the callosal fibers arose from the star pyramids of $iiic$ as well as from the short pyramids of v and the upper stratum of layer vi. He stated also that (p. 301), "the association fibers give off collaterals in the deep layers, especially VI; but their main territory of distribution is in the layers I to IV, and especially II and III."

The experimental approach to this problem of the origin and termination of the callosal fibers has not been very fruitful (deVries, 1912; Valkenburg, 1913; Pines and Maimun, 1939). We have repeatedly transected the corpus callosum in adult macaque monkeys without finding sufficiently evident degenerations to justify definite conclusions; perhaps experiments on newborn animals may give clearer results.

In an attempt to evaluate the functional role of the association fibers, it must not be forgotten that they are not the only means for conducting signals from one part of the cortex to another. In physiological neuronography, Dial narcosis suppresses the transmitter system of the intracortical feltwork, and makes the signals coming in over the association fibers stand out more clearly, thus creating quite artificial conditions. Physiological neuronography, as employed heretofore, tells, therefore, only a part of the story (Rosenblueth and Cannon, 1942).

In Figure 112 we have drawn upon a schematic human brain some of the cortico-cortical connections which have been demonstrated in the brain of the chimpanzee by the method of physiological neuronography. For other details see Bailey, Bonin, and McCulloch (1950).

Chapter VIII: Afferent and Efferent Connections

The normal functions of a gray mass . . . depend first and foremost on the afferent and efferent long pathways.

C. AND O. VOGT (1928)

A. AFFERENT CONNECTIONS

The cerebral cortex receives afferents or "radiations" from diencephalic nuclei. Afferents from other parts of the brain, such as the "direct lemniscus" or the rubro-cortical tract (Monakow, 1905) have not been confirmed. Indeed, Monakow himself considered the rubrocortical tract which he described as "not quite certain." Recently, however, Moruzzi (1949) found that the electrical activity of the cortex is influenced by stimuli applied to the reticular substance of the brain stem. But whether direct tracts exist has not been established. Most of the corticopetal fibers arise in the dorsal thalamus, but the geniculate bodies ("metathalamus" of some authors) certainly have to be included and the zona incerta of the subthalamus, as well as some nuclei of the hypothalamus, may also send afferents to the cortex. Anatomical (see Rose and Woolsey, 1949) and experimental (see Jasper, 1949) work makes it clear that we have to distinguish between at least three types of afferent impulses. The first two are "specific," i.e., they arrive from a specific thalamic nucleus and go to a specific region of the cortex. They show, moreover, a subordinate spatial organization. One class of specific impulses arises from extrinsic thalamic nuclei (Rose and Woolsey, 1949), i.e., from nuclei which receive impulses from "lower" centers in the cord, in the brainstem or in the retina. A second class of specific impulses arises from intrinsic thalamic nuclei, i.e., from nuclei thought to receive messages from the extrinsic thalamic nuclei but perhaps also from the striate body. These two types of afferents go to different parts of the cortex. A third class of impulses arrives over the "diffuse" system or, as Lorente de Nó (1949) called it, the nonspecific afferents. These fibers, still insufficiently studied in man and other primates reach by way of collaterals fairly large regions of the cortex.

Specific and unspecific afferents of thalamic origin were described histologically by Lorente de Nó (1949) in the mouse (Fig. 113). The former run a wavy, oblique course in the inner main layer to split up into telodendria within the outer stripe of Baillarger, the latter enter the cortex within the radii to end by means of collaterals mainly in the sixth layer; anatomically these unspecific afferents of thalamic origin have not been demonstrated in the primate cortex.

Most of our knowledge of these systems has been gained experimentally on animals. The scanty observations on human material fall into three classes: (1) It is possible to trace the radiations from the extrinsic thalamic nuclei in immature brains where they are myelinated earlier than those from the intrinsic nuclei. This myelogenetic method has been employed by Flechsig, Pfeifer and others. (2) The study of retrograde degenerations which follow cortical lesions was begun by Monakow (1895) and Dejerine (1901) but has not been very actively pursued since. The pit-

falls inherent in the study of pathological material are indeed numerous. In vascular insults or in porencephalic defects it is never certain beyond doubt that the primary lesion was strictly confined to the cortex or the white matter, nor can in cases
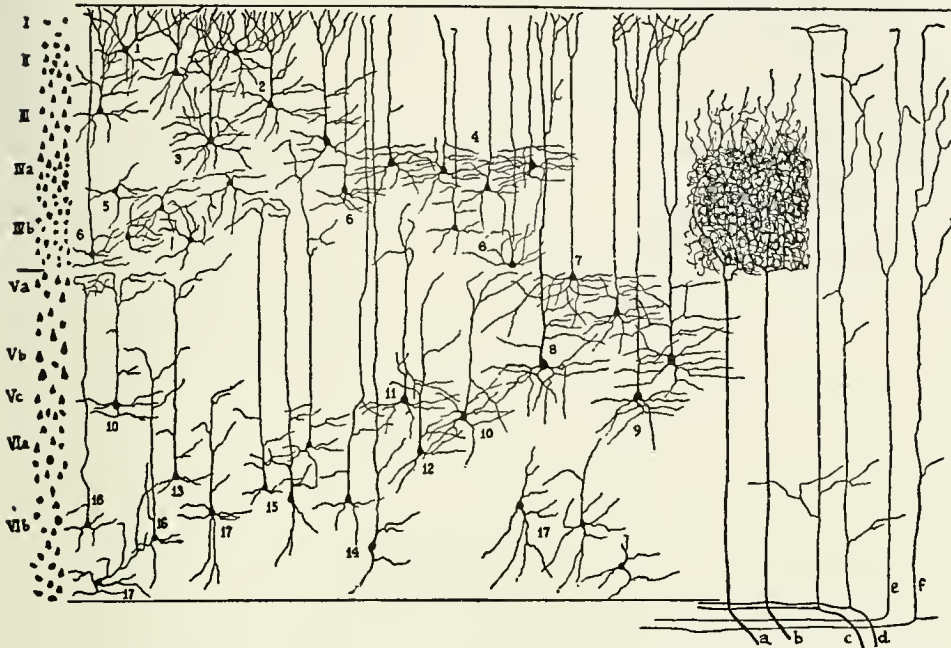

FIG. 113. Cortical afferents (from Lorente de Nó). At left side a diagrammatic Nissl picture of parietal cortex of adult mouse stained after Nissl. Cell layers are marked with Roman numerals. Except between IVb and Va there is no sharp boundary between layers. At the center, bodies and dendrites of representative types of cells with descending axons; to avoid complication of drawing, axons have not been included. At right the main types of cortical afferent fibers. 1, pyramids of layer II; 2 and 3, pyramids of layer III; 4, large star pyramids; 5, star cells; 6, small star pyramids; 7, 8, 9, long deep pyramids; 10, short pyramids; 11, medium pyramids; 12, 13, short pyramids of layer VIa; 14, long spindles; 15, medium spindles; 16, short spindles; 17, deep star cells; a, b, specific thalamic afferents; c, d, unspecific or pluriareal afferents; e, f, association fibers. Cells have been reproduced from two consecutive sections through the brain of an adult mouse, stained after Golgi-Cox, and the fibers from section through brains of 11-day-old mice stained after Golgi. In examining this drawing, it must be considered that cells of each type appear at the same level at more or less regular intervals, so that dendrites of all cells form a dense plexus, articulated with fibrillar plexuses such as that formed in layer IV and lower part of layer III by afferent fibers a and b. It must be noted that dendrites of cells of each type are distributed only through special zones of cortex, e.g., cells 5 have dendrites only in layer IV, cells 10 only in layer V, and cells 17 only in layer VI, while other cells like 14 have dendrites in all layers. Cells with dendrites in several layers have a number of dendrites concentrated in one layer, e.g., the side branches of shaft and basilar dendrites of cells 4 are located in layer IV, those of cells 7, 8, and 9 in layer V, etc.

of Pick's disease the cortical defect be always precisely delimited. (3) Only quite recently, the introduction of frontal lobotomy or leucotomy by Moniz (1936) made it possible to examine now and then retrograde degeneration after well defined surgical lesions in the frontal lobe of otherwise "normal" brains. However, these lesions are usually made by section of the centrum ovale so that it is often uncertain

which areas of the cortex have been disconnected (Meyer and McLardy, 1948). Very few brains have been examined after removal of restricted portions of the cerebral cortex (gyrectomy, topectomy) (Mettler, 1949).

The pattern of the specific thalamocortical radiation from the extrinsic nuclei is fairly well known for the two geniculate bodies. The optic radiation emerges from the lateral geniculate body, streams through Wernicke's field into the internal capsule, curves around the "stalk" of the inferior horn of the lateral ventricle, then spreads out into a thin lamella in the lateral wall of the posterior horn and ends in the striate area, mostly on the medial aspect of the hemisphere. Pfeifer's myelogenetic studies (1925) form the basis of this description. The relation of the optic radiation to the strata sagittalia and the inferior longitudinal fasciculus have been a matter of much debate (see p. 238).

The topological correspondence of retina, lateral geniculate body and striate area has been worked out experimentally in the macaque (see Marshall and Talbot, 1942) and is known from clinical observations (Brouwer, 1936; Holmes, 1918; Chacko, 1948) to be the same in man, at least in broad outlines. Brouwer's figure suggests a little larger representation of the macula in man than in the monkey.

The acoustic radiation goes from the medial geniculate body into the posterior part of the internal capsule, then swings lateral and a little ventral to clear the lentiform nucleus and moves finally dorsal into the supratemporal plane. Its close relation to the fibers of the anterior commissure and to the inferior insular sulcus has been demonstrated by Pfeifer (1936). On the basis of his myelogenetical studies, Flechsig (1908) emphasized that the acoustic radiation ends preponderantly in the medial two-thirds of the supratemporal convolution. There is a point-to-point correspondence between cochlea, thalamic nucleus, and cortical area in the monkey, probably also in man, with the result that the low tones are conveyed to the lateroanterior, and the high tones to the medioposterior part of Heschl's gyrus. Nothing is known in man about a second acoustic area. The statement of Monakow that there are two acoustic radiations, one arising in the external geniculate body, the other in the posterior quadrigeminal body, was refuted by Henschen (1917) and by Pfeifer (1936).

The somatic radiation forms part of the radiation of the ventral thalamic nucleus. The afferent fiber systems to this nucleus will, therefore, have to be discussed first.

Following Walker (1938), Papez, Bull, and Stotler (1940), and Hassler (1949b), we include among them the spinothalamic tract, the medial lemniscus, the two trigeminal lemnisci, the brachium conjunctivum and the pallidothalamic fibers (Fig. 114). Both spinothalamic tract and medial lemniscus end in the posterior part of the ventral nucleus of the thalamus. The spinothalamic tract could be studied in a few cases of cordotomy by the Marchi method (Foerster and Gagel, 1932; Walker, 1940). Walker felt that no statement could be made regarding the topical ending of the tract. In the monkey, Walker (1938) had found that the fibers from the leg end near the external medullary lamina, those from the arm in an intermediate region and those from the spinal nucleus of the trigeminal nerve in the medially located arcuate nucleus (ventralis posteromedialis).

The medial lemniscus has not been well studied in human material. From the

available scanty observations, generally made on the basis of staining methods which would now be considered antiquated, one gathers that the lemniscal fibers and those emerging from the main sensory nucleus of the trigeminus end respectively in the same nuclei in which the spinothalamic, and the fibers from the spinal nucleus of the trigeminus, end. This is in any event what is found in the macaque (Walker, 1938).

The brachium conjunctivum was studied in the human brain by Uemura (1917) and Környey (1926). It ends at least partly in the thalamus. Its other ending in the small-celled part of the nucleus ruber and in the reticular substance does not concern us here directly. The fibers destined for the thalamus stream past the red
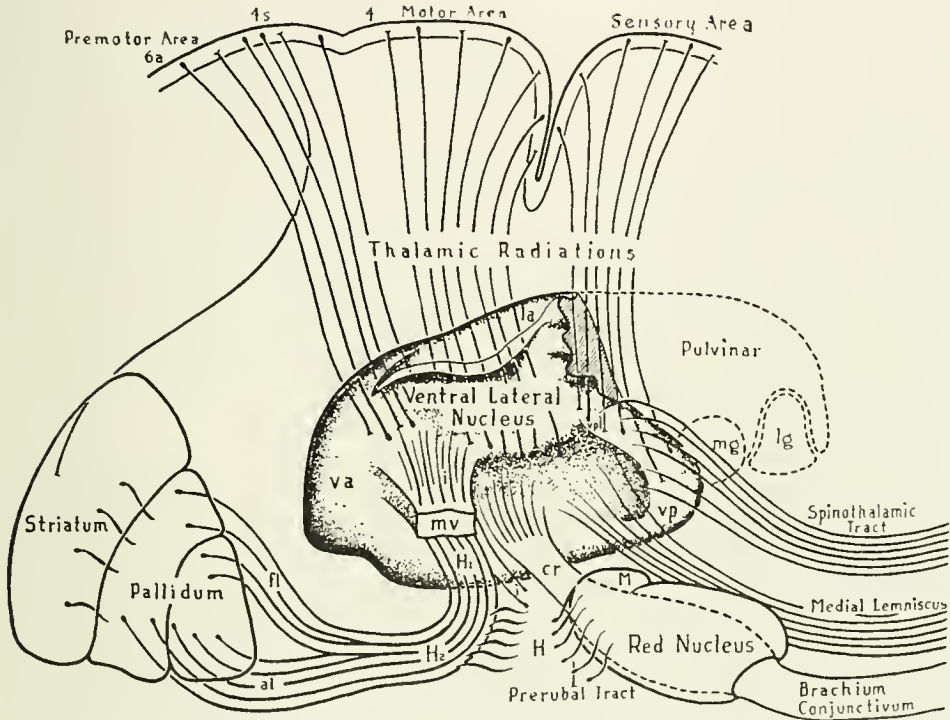

Fig. 114. Schematic representation of the ventral thalamic nucleus and its connections (after Papez, Bull, and Stotler).

nucleus, in its capsule or perhaps even straight through the nucleus, into Forel's fields H and H_1, to reach the ventral nucleus and the median center of Luys. This tract consists in man of both gross and fine fibers. Környey (1926) considered the former to be fibers from the brachium conjunctivum, the latter to be axons of the small cells in the neorubrum. The ventral nucleus relays messages to the agranular areas of the cerebral cortex through the prelemniscal radiation.

The pallidothalamic fibers were described by Hassler (1949b) and by Papez, Bull, and Stotler (1940). Through fields H_2 and H_1 axons of pallidal cells reach the anterior part of the ventral thalamic nucleus. Another system which, according to Hassler, breaks through the internal capsule to end in the oral part of the reticular

zone of the thalamus will be alluded to presently. Direct thalamostriatal connections have been described in lower mammals (Gerebtzoff, 1940) but remain to be proven for man (Clark and Russell, 1940).

The three systems, i.e., the somesthetic tracts in the narrower sense (from both spinal cord and brainstem), the cerebellothalamic and the pallidothalamic systems, appear to end in different parts of the ventral nucleus. Hassler (1949b), a pupil of C. and O. Vogt, distinguishes them as ventrocaudal, ventro-intermediary and ventro-oral parts. Sheps (1945) enumerates ventralis anterior, ventralis lateralis, and ventralis posterior and states that in respect to the ventral nuclei, the scheme of Walker (1938) which he adopted and that of the Vogts "agree in general."

It does not seem to be feasible, however, to subdivide these nuclei much further. The somesthetic nucleus proper may perhaps be divided in a mediolateral sequence into ventralis posterolateralis and ventralis posteromedialis, but the elaborate scheme of Hassler, a part of his endeavor to match the 150-odd cortical fields with 150-odd thalamic regions is, in our opinion, too ambitious. That there is a topographical correspondence between cortical regions and thalamic regions does not mean that there must be a microscopically distinguishable cortical area for each microscopically distinguishable thalamic area or vice versa. Meyer, Beck, and McLardy (1947, footnote p. 25) are careful to point out that they "distinguish nucleus anteromedialis from nucleus anteroventralis not in virtue of any cytoarchitectural differences but simply in accordance with the topographical description of Sheps."

The radiation from the ventral nucleus enters the internal capsule and makes for the post- and precentral convolutions as well as, one must assume, the parietal operculum. But only the former has been studied anatomically.

The distinction into three systems, which we recognized earlier, remains valid for the thalamocortical radiation: the somesthetic impulses are relayed to the postcentral gyrus, in the macaque monkey to the entire breadth of the postcentral gyrus (see Woolsey, Marshall, and Bard, 1942) and, according to Foerster, to the superior parietal lobule; the cerebellar impulses are relayed to the precentral agranular cortex; the pallidal impulses reach the simple agranular and, according to Freeman and Watts (1947), the dysgranular cortex. The precise manner of ending of the somesthetic fibers is not known (Walker, 1940). In spite of its importance for the understanding of sensation in the cerebral cortex even such an astute critic as Walshe (1948) deals almost exclusively with the lower levels.

It should at least be noted in passing that the secondary pathways for taste are generally assumed to end also in the ventral nucleus of the thalamus. They appear to run with the trigeminal lemniscus, and to be relayed to the ventral part of the postcentral convolution or to the parietal operculum (Gerhardt's area *68IIgr*?, see p. 218). These problems have been discussed with great thoroughness by Gerebtzoff (1939–40) who based his conclusions about the human brain mainly on the cases of Adler (1934) and Strauss (1925). The location of the radiation of gustatory impulses to the cortex is still undetermined. Logically one would look for it in the allocortex. One might suppose, however, by analogy with the somesthetic system (Woolsey, 1947) that there might be a second receiving area (*68IIgr*?) in the isocortex.

Three intrinsic nuclei send their radiations to the cortex: the dorsomedial, the anterior, and the pulvinar. The radiation from the dorsomedial nucleus has been

studied in cases which died at various intervals after frontal lobotomies and in which a retrograde degeneration had set in. Freeman and Watts (1947) and Meyer, Beck, and McLardy (1947) have contributed most to our knowledge. The older studies of Fukuda (1919), Hartmann (1943), and others who found changes following upon vascular insults or Pick's disease were not only confirmed to a large extent but were also put on a much surer footing.

The dorsomedial (Sheps, 1945) nucleus (medial of Toncray and Krieg, 1946) consists of a voluminous small-celled part, but bears in its dorsomedial corner a nest, as it were, of large cells. According to Meyer, Beck, and McLardy (1947), the large-celled part projects to the orbital region, the small-celled part to the cortex covering the lateral aspect of the frontal region. Meyer, Beck, and McLardy, as well as Freeman and Watts, have tried to establish a correspondence between Brodmann's areas and the different parts of the dorsomedial nucleus. Hassler (1948) states: "The oldest, oromedial part of this nucleus projects to the gyrus rectus of the orbital region; its neighboring lateral part to the lateral orbital gyri (area 47 and parts of area 11 Brodmann); the middle inner moiety of the medial part projects to the frontal pole (about area 10), the middle outer moiety to the region around the anterior end of the third frontal convolution (about area 46), the caudal inner moiety of the medial part to the region bordering on the precentral motor region (corresponding about to area 9) and the caudal outer moiety of the medial part to Broca's region in its narrow sense." At any rate, the exact boundary of that part of the cortex which receives radiations from the dorsomedial nucleus is not yet known. Freeman and Watts would put Brodmann's area 8, our dysgranular cortex, into the sector of the ventral nucleus; Meyer, Beck, and McLardy (1947) and LeGros Clark (1948) feel that this is unjustified. There may be a zone without thalamic radiation between the sectors of the ventral and the dorsomedial nucleus.

The exact course of the radiation from the dorsomedial nucleus is similarly not known. It certainly occupies a rather small region in the anterior part of the internal capsule, but whether it is intermixed there with other fibers (radiation from the anterior nucleus, the frontopontine bundle) is not quite clear.

The anterior nucleus was divided by Sheps (1945) into three parts. The bulk of the nucleus is formed by the anterior ventralis and anterior medialis; a thin cap of cells was distinguished as anterior dorsalis (shown by Sheps on the ventral side of the anterior nucleus of his Plate 1). Toncray and Krieg (1946) could not see any cytoarchitectural differences between Sheps's medial and ventral parts. Freeman and Watts (1947) state that the anterior nucleus (by which they mean the ventromedial part) sends its radiations to "areas 24 and 32." Their material, namely frontal lobotomies, did not permit them to investigate whether the anterior nucleus has connections with the posterior limbic area. Meyer, McLardy, and Beck (1948) conclude that it "remains to be seen whether area 23 or part of it receives some fibers from the anterior complex." Meyer, Beck, and McLardy (1947) found that the "anteromedial nucleus projects at least to the precallosal part of the cingulate gyrus; the anteroventral nucleus to more posterior parts of the cingulate gyrus." Experiments have demonstrated such connections in primates (Bonin, 1948) as well as lower mammals (J. Rose and Woolsey, 1948). After extensive destruction of the human cortex the anterior nucleus is degenerated (see Sheps, 1945).

The posterolateral nucleus and its large outgrowth, the pulvinar, send radiations

through the posterior limb of the internal capsule to the parietal lobe. Localized destructions, particularly of the inferior parietal lobule, have been examined several times (Monakow, 1895; Dejerine, 1901) but they are not sufficient to delimit the sector of the pulvinar precisely. There is some evidence that the pulvinar projects into at least a part of the occipital lobe, roughly that area which Brodmann called *19* and Economo *OA* (Dejerine's cases Bras, Heudebert, and Seguillon; Monakow's cases 1–3, and his cases Pfister and Montgenet) but whether the parakoniocortex receives any radiation from the pulvinar is not known. Monakow's last case (Montgenet), who had a lesion of the occipitotemporal gyrus, suggests that the ventral border of the sector of the pulvinar is quite low, so as to include most of Economo's *PH*, but one would welcome further confirmation. Walker's experiments on monkeys (1938) as well as those of Clark and Boggon (1936) indicate that the extension of the field of the pulvinar to the intermediate occipitotemporal region is correct. The anterior extent of the sector of the pulvinar is equally uncertain.

The eulaminate isocortex of the temporal lobe and of the insula are generally believed to be devoid of thalamic radiation as a result of experiments on monkeys and chimpanzees (Walker, 1938; Bucy and Klüver, 1940), but more recent studies indicate that the lateral surface of the temporal lobe has connections with the pulvinar (Chow, 1950). Observations on human brains (Dejerine, cases Bras and Neumann; Monakow, case 11) are few and of dubious value. The study of Papez (1939) leaves much to be desired, but the involvement of the parietal region in his case seems surely too restricted to account for the severe degeneration of the pulvinar; the major lesion was of the lateral and superior surfaces of the temporal lobe, so far as one can judge from the photograph and meager description. The connections of the cornu ammonis and the uncus are not strictly within the province of this monograph. Monakow's observations, however, that the corpus mamillare showed degeneration after necrosis of the uncus due to compression may be noticed in passing.

The specific afferents discussed on the previous pages form the most logical basis for a rational subdivision of the cerebral cortex (Fig. 115). One is led to recognize a frontal "sector" of the dorsomedial nucleus, a central sector of the ventral nucleus, a parietotemporal sector of the posterolateral nucleus and its large expansion— the pulvinar, an occipital sector of the lateral geniculate body, a supratemporal sector of the medial geniculate body, and a limbic sector of the anterior nucleus. To these may be added, temporarily, a temporal sector whose thalamic connections (if any) are at present in question, a perifalciform sector which has dysgranular, largely juxtallocortex, and important relations to respiration (Kaada, Pribram, and Epstein, 1949). But a strict adherence to the principle of afferent connections would tear asunder koniocortex and parakoniocortex, and would put some areas which we know to be closely related into different sectors. Thus it seems advisable to define occipital and supratemporal sectors as consisting not only of the two koniocortices but of the surrounding parakoniocortices as well. To draw sharp boundaries from cytoarchitectural observations alone we would not dare. Physiological neuronography allows us to determine how far association fibers from the koniocortices are distributed and that might, perhaps, be considered the outer boundary of the parakoniocortex. A tentative sectoral map is given in Figure 115. It is understood that the boundaries given are very roughly approximate; much more detailed in-

vestigation is necessary to draw accurate limits to the individual sectors. More-over, the density of radiation is not uniform throughout the sectors shown. Never-theless, such a subdivision seems to us more logical than the usual division into
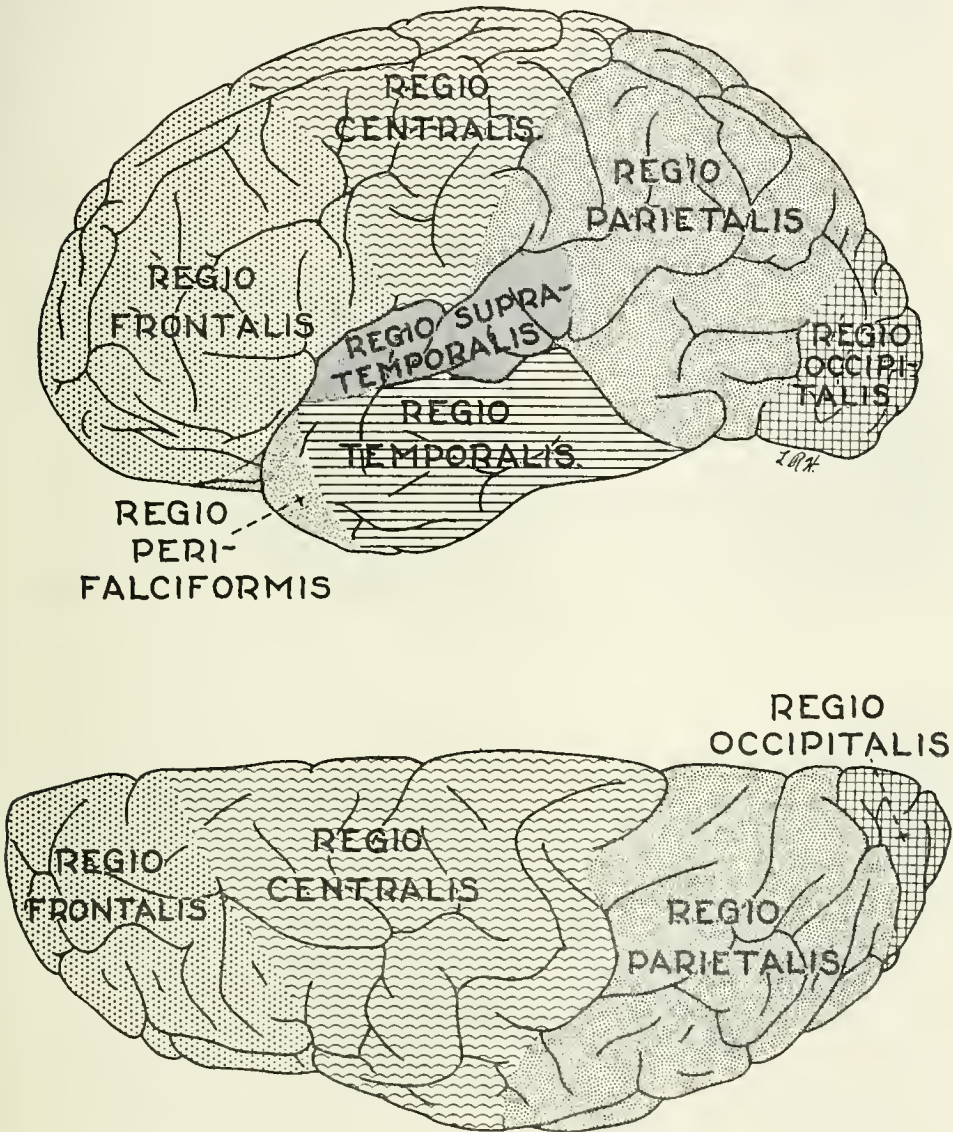

FIG. 115A. Sectoral map of the cerebral cortex (Bailey). (See Figs. 115B and 115C.)

lobes, and promises to be a more useful guide to further studies than the cyto-architectural maps previously utilized.

"Unspecific" afferents have been seen, as mentioned above, in the brain of the mouse by Lorente de Nó. By stimulating, in the cat, the medial part of the thalamus

and observing the ensuing changes in the electrical activity of the cortex, Morison and Dempsey (1943), and quite recently Jasper (1949), deduced the existence of a similar system in the brain of that carnivore. Jasper states that he has observed the same phenomena in the macaque. There is no direct evidence for the human brain. However, it should be noted that, in widespread destruction of the cortex, LeGros
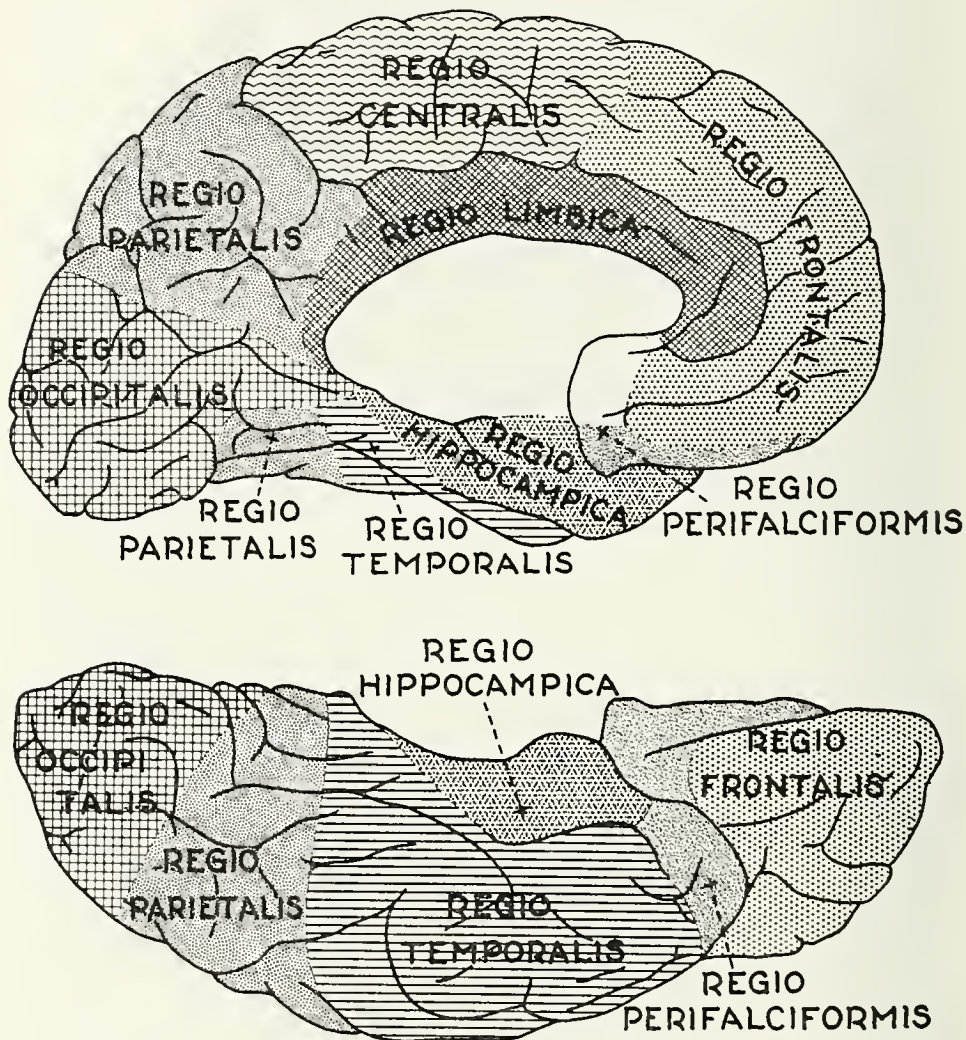

FIG. 115B. Sectoral map of the cerebral cortex (Bailey). (See Figs. 115A and 115C.)

Clark and Russell (1940) observed a degeneration of the intralaminar nuclei, which presumably give origin to the unspecific afferents, as well as of most of the reticular zone. Sheps (1945) observed a similar case, according to his own words, but found the intralaminar nuclei intact. Fukuda (1919) observed (his case iv) a retrograde degeneration of the reticular zone in a child with idiocy and microcephaly. Fickler

(1913), who examined Weigert-Pal, van Gieson, and carmine preparations, does not mention the intralaminar nuclei but noticed degenerations in the corpus mamillare

Regio perifalci-formis

Regio supratemporalis

Supratemporal plane

Regio perifalci-formis

Regio parietalis

Island

Regio centralis

Regio frontalis

ce

Regio parietalis

Regio perifalci-formis
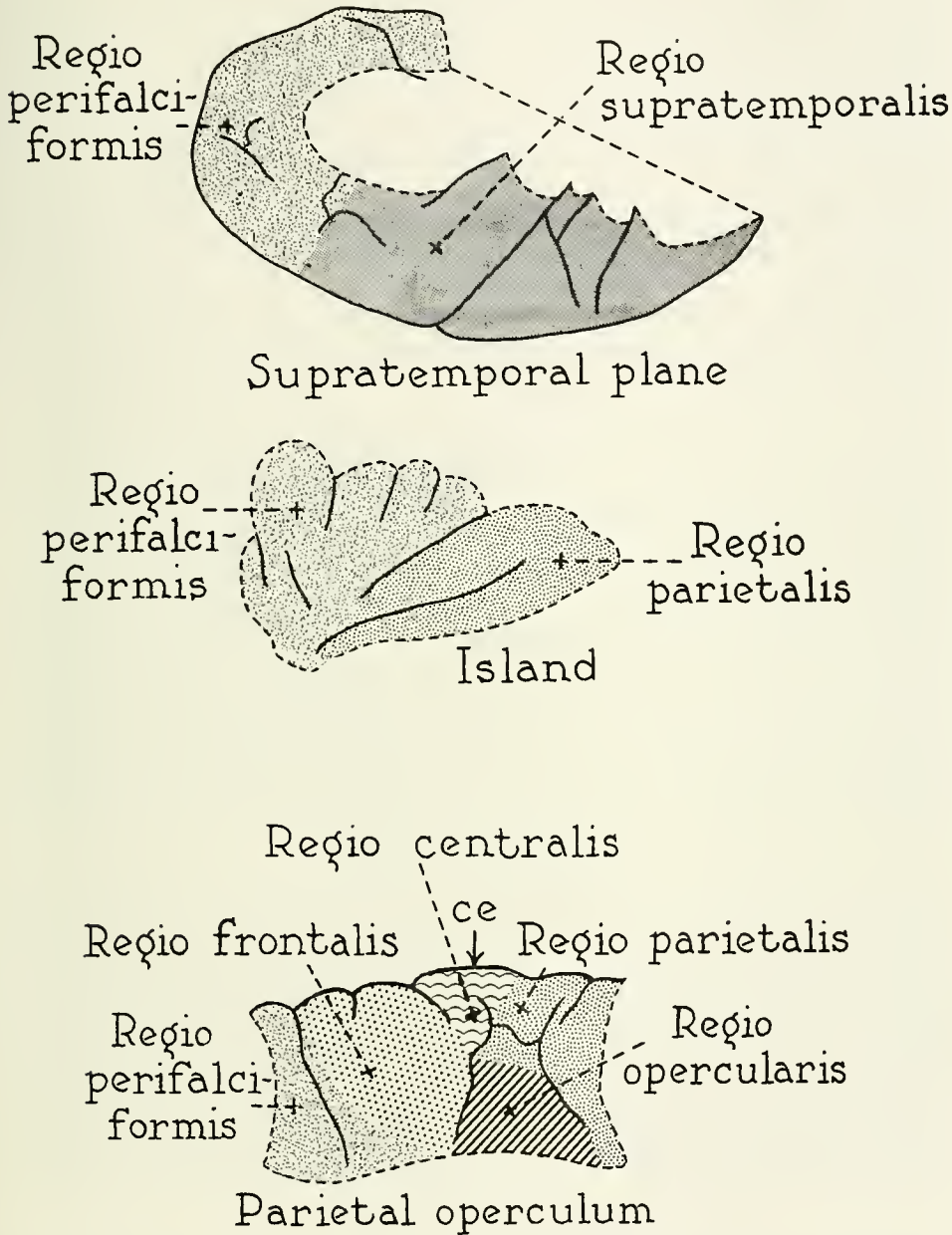
Regio opercularis

Parietal operculum

Fig. 115C. Sectoral map of the cerebral cortex (Bailey) (See Figs. 115A and 115B.)

and the zona incerta. The question of the existence of "unspecific" thalamic afferents is by no means settled but enough is known to make further investigation desirable.

Just as in the case of the cortical afferents, most of our information on the cortical efferents or "projections" is based on the study of animals. The founders of modern neuroanatomy—von Monakow (1914), van Gehuchten (1907), Winkler (1918–33), Bechterew (1908–11)—to name but a few, used largely rabbits, cats and other nonprimates. The experiments of Nissl (1908, 1911) are often quoted as showing that the projection fibers of the cerebral cortex arise in layers *v* and *vi* but, so far as one can judge from the brief notes which he published, the brains of his rabbits were so maltreated as to make any conclusions drawn from them very questionable. Modern workers have generally been more careful and secured at least monkeys. But the number of human brains which have been thoroughly investigated is still amazingly small—much too small when the difficulties of interpretation inherent in pathological material are taken into account. To conclude from animals to man concerning matters of cortical projection is particularly dangerous, as the classical study of Fulton and Keller (1932) of the Babinski reflex convincingly demonstrates. The most superficial observer will be struck by the dramatic consequences of a cortical lesion in man, but even the trained neurologist may find it difficult to detect any alteration in a monkey with a similar lesion. "Progressive corticalization" has become a byword in comparative neurology, but it is still too readily brushed aside when it comes to a discussion of the finer structure of the human brain.

The anatomical data from the human brain are very limited and derived mainly from the study of pathological lesions by the older neuropathologists (Dejerine, Monakow, Winkler). Many of these cases are very complicated and difficult to interpret; even the cautious conclusions which have been drawn from them are questionable. Lately even more limited data, as in the case of the afferent connections, are beginning to accumulate from the study of lobotomies. Also the results of electrical stimulation of the human cortex (Penfield and Rasmussen, 1950) by neurosurgeons can be taken as corroborative evidence of the presence in the human brain of tracts demonstrated anatomically in lower primates.

Corticothalamic System

Corticothalamic fibers have long been known in the macaque (see Walker, 1938, p. 249) but have been proven for the human brain only in the case of the frontal lobe, and even here only quite recently. M. Meyer (1949) investigated the degenerated end-buttons by Glees's ammoniacal silver method and found projections from the frontal eulaminate cortex to the dorsomedial nucleus of the thalamus, although "surprisingly few in number," and from the agranular precentral areas to the ventrolateral nucleus. Whether in the human brain the closed circuits formed by these fibers in conjunction with the thalamocortical fibers play the important role which McCulloch (1944b) assigned to them requires further confirmation.

The Oculomotor Apparatus

The oculomotor apparatus is frequently treated as a part of the somatomotor system. Indeed, a dyed-in-the-wool anatomist could point to the mesodermal origin of the extraocular muscles and the "somatomotor" character of the third, fourth, and sixth cranial nerves. Yet, as Sherrington's description (1906) made quite clear, and

as Holmes (1938) emphasized once more, the type of control that the cortex exerts over the movements of the eyes (and, perhaps, of the eyelids) differs from that which it exerts on the other muscles of the body. The slow movements elicited after a long latency by relatively strong stimuli in the former case are in sharp contrast to the immediate, almost twitchlike, response to relatively weak stimuli in the latter case.

From observations in the operating room (Foerster, 1936; Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950) we know that, in the human brain just as in that of the other primates which have been investigated, there are two cortical regions which control eye movements, a frontal and an occipitoparietal one. In Holmes's (1938) opinion, the frontal field essentially controls the voluntary movements, and the parieto-occipital field is primarily concerned with the adjustment of the gaze toward the stimulus of greatest interest (the phrase is ours). But Best (1942) argued that to distinguish between *spähen* and *blicken* (viewing and looking) was unimportant (*unwesentlich*), since in all eye movements environmental stimuli induce the shift of the gaze, repeating the gist of what Roux (1899) had said in his classical discussion.

In the monkey, Crosby and Henderson (1948) found that the upper part of "area 19" and the lower occipital region project to the rostromedial part of the superior colliculus and that the lower part of "area 19" and the upper occipital region project to the caudolateral part of the superior colliculus. That in the macaque the striate area gives rise to oculomotor pathways was shown by Walker and Weaver's (1940) experiment on the effect of electrical stimulation and by LeGros Clark's (1942) anatomical studies, also on monkeys, which demonstrated by the method of retrograde degeneration that the solitary pyramidal cells of Meynert send their axons to the anterior quadrigeminal body.

Foerster (1936), however, was unable to obtain eye movements in his patients by stimulating the occipital pole, that is to say, presumably the striate area. It can be argued, of course, that only that part of the striate area was exposed by the surgeon which corresponds to the macula lutea and that, therefore, no shifting of the eyes could be expected. The existence of corticotectal fibers in the human brain was inferred by Edinger and Fischer (1913, see especially their Fig. 4) from their examinations of the malformed brain of a child. Juba (1939) reported two cases in which softenings on the medial side of both occipital lobes had partially destroyed striate and parastriate areas; Marchi preparations showed degenerating fibers in the zonal and superficial medullary strata of the anterior quadrigeminal bodies. Monakow (1905) and Winkler (1918–1933, vol. 4) had previously found that, after old lesions of the occipital cortex, the medial medullary stratum of the superior colliculus was affected. Both Best (1942) and Kleist (1934) reported transitory paralysis of ocular movements after lesions of the striate area in about 20 per cent of their cases. It is difficult, in view of these observations, to deny that the striate area controls the position and movements of the eyes.

The Somatic Apparatus

It has become almost traditional to group the somatic efferents into pyramidal and extrapyramidal pathways. For classical anatomy the pyramidal tracts are the corticospinal tracts. The terms just used are, therefore, a little narrow, for somatic

efferents should include most of the corticobulbar pathways, namely those to the *v*, *vii*, *ix*, *x*, *xi*, and *xii* nerves whether morphologically viscero- or somatomotor nerves.

The corticospinal and corticobulbar tracts are known to arise from the precentral agranular cortex. It may be safe to assume that the second motor area and that part of the parietal cortex which is between the two motor areas sends off corticospinal and corticobulbar fibers. Woolsey and Chang (1948) demonstrated them in the macaque by recording antidromic impulses from the pyramidal tract, confirming older anatomical work by Minkowski (1923–24) and others done before the second motor area was recognized. The extirpation of this region, it should be noted, is said by Penfield and Rasmussen (1950) to cause "no evidence of either sensory or motor paralysis of either arm or leg after the first few days of postoperative convalescence have passed." That the simple agranular cortex gives origin to pyramidal fibers was demonstrated (Minckler, Klemme, and Minckler, 1944) in Weigert and Swank-Davenport preparations of the brain of a patient whose "premotor" cortex had been removed nine months before death. They were able to trace degenerating fibers from the "premotor" cortex through the brainstem into the anterior funiculus of the spinal cord; at least this is the conclusion they drew from examination of the "lowermost" level of the medulla oblongata.

It has been argued by Lassek (1948) that the cells of Betz can account for no more than 2 to 3 per cent of all pyramidal fibers, if one assumes at least that each fiber in this tract comes from a separate cell. The exact origin of the pyramidal tract is not yet clear. Do its fibers arise solely from (large or giant) pyramidal cells in layer *v* as Lorente de Nó thinks or do the large pyramidal cells in layer *iiic* contribute to the tract as Cajal, and Economo and Koskinas held? P. Schroeder (1914) found a gliosis (pseudogranular layer) only in layer *v*, and Bielschowsky (1916) concluded that the corticofugal fibers arose from cells in layer *v*. Marinesco's (1910a) and Wohlfahrt's (1932) conclusion that the Betz cells are the sole origin of the pyramidal tract is no more accepted.

We need not discuss the details of the somatotopic organization of the motor cortex; the reader is referred to the recent authoritative monograph by Penfield and Rasmussen (1950). That the chapter is not entirely closed, however, is apparent from the work of Woolsey and Settlage (1950).

The course of the corticospinal and corticobulbar tracts through the white matter of the hemisphere, the internal capsule, the pes pedunculi and farther caudad has been so often described as to need no repetition. The "twist" from cortex to pes pedunculi, the orderly arrangement of the fibers which tend, as far as we know, to keep their relative position to each other throughout the brainstem, deserve brief mention. The decussation of about 80 to 92 per cent, the course of these crossed fibers in the lateral pyramidal tract and the further course of the uncrossed ones in the lateral and anterior tracts are also well known. The lateral tract appears to end in the internuncial part of the posterior horn. This is, in any event, the interpretation which Lloyd (1941) gives of his experiments on cats; actual observations in the human spinal cord do not seem to have been made. The precise ending of the anterior tract was investigated in Golgi preparations by Lenhossek, Kölliker, and Ziehen (q.v., 1899). While Lenhossek reported endings in the homolateral, and Kölliker in the contralateral anterior horn, Ziehen (p. 271) stated that he found

collaterals to both anterior horns. Since the motoneurons on which these collaterals end innervate the axial musculatures, a bilateral ending appears perfectly intelligible. Whether the fibers of the anterior tract end directly on motoneurons or on intercalated neurons has, so far as we are aware, never been investigated.

Weil and Lassek (1929) counted fibers in the pyramidal tract and determined the mass of the musculature controlled by the pyramidal tract. They stated that the muscles of the hand are not better supplied than those of the arm or shoulder, but that the neurons for the upper extremity receive approximately twice as many pyramidal fibers as those for the lower extremities. The number of fibers, their caliber (and their velocity of conduction) has occupied the attention of numerous scholars. Blocq and Ozanoff (1892) reported, after careful comparison of a sound and diseased side, 79,000 fibers in the lateral pyramidal tract; 49,000 of them to the cervical, and 30,000 to the lumbosacral enlargement. Later estimates revised this figure upwards; Weil and Lassek (1929) counted 250,000; van den Bruggen (1930) counted the pyramidal fibers on one side "at the level of the olive" in nine cases. The average number of fibers was found to be $150,600 \pm 1,410$ (S.D. = 11,280). Lassek and Rasmussen (1939) stated that there are "about 1,000,000 axons located in the pyramids of man." Since there are only about 25,000 (Campbell, 1905) to 34,000 (Lassek, 1948) Betz cells in the human precentral cortex, it was argued, as we have just noted, that only a relatively small number of fibers arise from the giant cells of Betz.

The diameter of the fibers has been determined by Häggquist (1936) by comparing a healthy and a degenerated side. The lateral pyramidal tract "probably contains fibers between 5 and 21 μ diameter." There appear to be two favored frequencies: namely, 5–6 μ and 10–11 μ. Häggquist felt that the area of the lateral pyramidal tract contained numerous fibers not of cortical origin and that he had not sufficient material on which to base a numerical estimate of the corticospinal fibers. The area of the anterior tract contains (at the level of T_3), according to Häggquist, preponderantly fine fibers of 1–4 μ but the "fiber-spectrum" showed again a relative maximum at 10–11 μ. These data are in fairly good agreement with Woolsey and Chang (1948) who found, for the macaque, both fast and slow fibers; the former conducted with a velocity of about 70 m sec,$^{-1}$ the latter of about 15 m sec^{-1}.

The cerebral cortex sends fibers to most of the "extrapyramidal" servomechanisms. Since the functional organization of this system is imperfectly understood, it is at present difficult to arrange these projections in anything approaching logical order. However, a valiant attempt, on the basis of present knowledge, has recently been made by Bucy (1942) (see Fig. 116). We take the extrapyramidal mechanisms to include the basal ganglia of the endbrain, the derivatives of the ventral thalamus (corpus subthalamicum of Luys and zona incerta), the red nucleus and the substantia nigra of the midbrain, the pontine nuclei and tracts, the cerebellum and its ganglia, the inferior olive and the reticular substance of the brainstem, the role of which has been so brilliantly demonstrated by Magoun and Rhines (1947).

Of the basal ganglia of the endbrain, the caudate nucleus has been shown in the monkey to receive fibers from all "suppressor" areas. The details of the corticostriatal connections, as revealed by physiological neuronography, have been recorded by Dusser de Barenne, Garol, and McCulloch (1941) for the macaque monkey; those of the chimpanzee by Garol and McCulloch (1944) and need not be re-

capitulated here. In man, however, M. Meyer (1949) failed to find any degenerated end-buttons in the caudate nucleus after leucotomy which, in some at least of her cases, must have cut the efferent fibers from "area 8," known to be a suppressor area in macaque and chimpanzee. M. Meyer has shown, on the other hand, that the simple agranular precentral area sends a "considerable" number of fibers to the globus pallidus. The exact origin and ending of these corticopallidal fibers were left undecided.
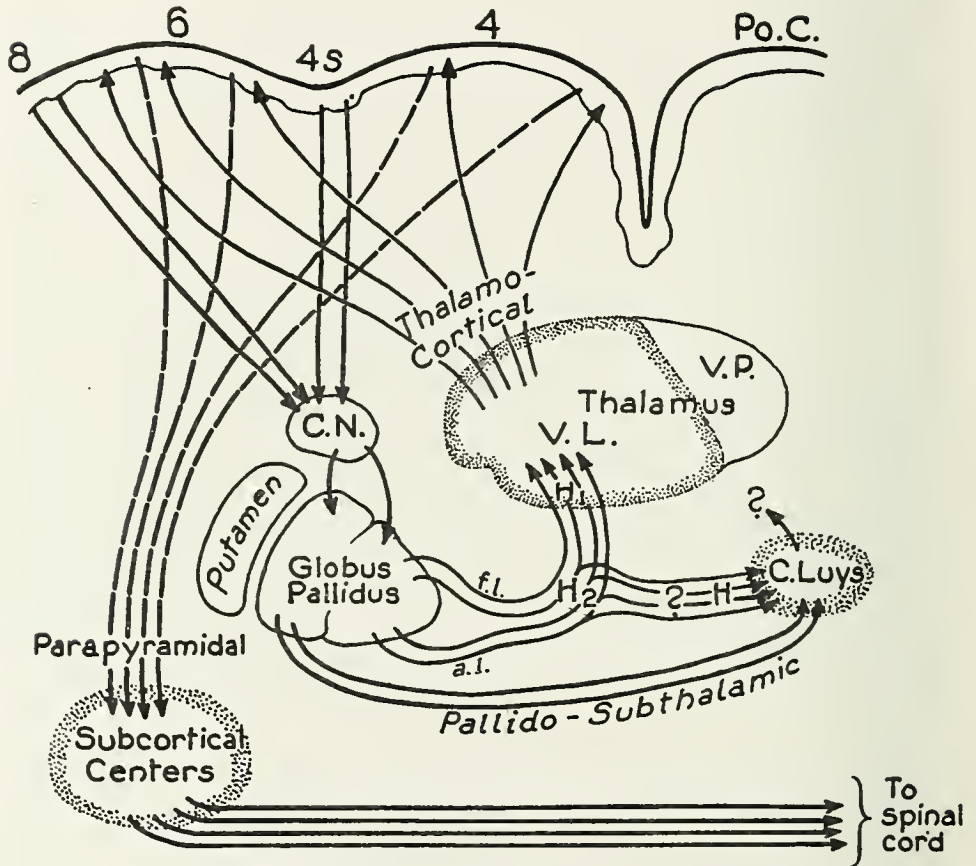

FIG. 116. The neural mechanism of choreoathetosis (after Bucy).

Corticosubthalamic connections were described by Mahaim (1893) in the brain of a thirteen-year-old girl who had suffered since she was nine months old from paresis with epileptic attacks. A large focus of long standing involved the supramarginal, angular, and superior temporal gyri but also the anterior part of the internal capsule and the head of the caudate nucleus. Whether the corticosubthalamic fibers arise from frontal or parietotemporal region could, therefore, not be decided. Monakow's (1895) case 7, which showed a partial degeneration in the subthalamic nucleus, is similarly unsuited for information about the exact origin of the corticosubthalamic path (defect in F_3, operculum insulae, T_1, and putamen). Winkler

(1919–1932, vol. 4) describes a bundle breaking off from the internal capsule, to pierce the subthalamic nucleus and to become gradually smaller toward substantia nigra and pontine gray. He thought that connections between frontal cortex and the body of Luys might thus be established. Material from leucotomy was studied by Meyer, Beck, and McLardy (1947) and by M. Meyer (1949). Both papers find degeneration in the subthalamic nucleus. The former concludes that only the agranular precentral cortex sends fibers to the subthalamic body; the latter finds some partial degeneration in the lateral part of Luys's body when only the eulaminate frontal cortex was involved. It is noteworthy that the recent study on the connection of the subthalamic body by Whittier and Mettler (1949) does not list cortico-subthalamic fibers as a separate paragraph and that experiments in animals have led most modern authors to deny such connections (see M. Meyer, 1949).

Cortico-incertal or, as P. M. Levin (1949) called them, corticozonal connections were described by Monakow (1895). Though evidence was again insufficient to determine their exact origin, the modern study of M. Meyer implicates the agranular precentral cortex. The eulaminate frontal cortex may be ruled out; no evidence is available for the rest of the brain.

Corticorubral fibers were studed by Monakow, Dejerine, LaSalle Archambault (1914), Winkler, and many others. They agree that the corticorubral fibers arise from the frontal lobe and some authors, notably Winkler, have gone so far as to say "plus exactement, des circonvolutions basales de ce lobe." In conjunction with M. Meyer's recent statement that only the agranular precentral cortex sends fibers to the red nucleus one would conclude that the corticorubral tract arises from the pars opercularis of the third frontal convolution. The course of this tract through the internal capsule and into the nucleus ruber has been followed by Winkler in the brain of a four-month-old child where it is unmyelinated and bordered laterally by striorubral and medially by rubrothalamic and (according to Winkler) rubro-cortical fibers. It runs through the anterior limb of the internal capsule to gain the red nucleus via Forel's field H_2 and H dorsal to the pallidorubral fibers.

Corticonigral fibers have generally been assumed to issue from the precentral gyrus (see P. M. Levin, 1949). In the human brain they were described by Dejerine (1901) to arise "surtout des régions rolandiques supérieures" (*loc. cit.*, vol. II, p. 81) after having stated a few pages previously (p. 73) that the majority of the fibers arise from the motor zone of the face. Meyer (1949) saw some degenerations in the ventromedial part of the substantia nigra but considers her findings merely suggestive. Minckler, Klemme, and Minckler (1944) described corticonigral fibers coming from the "premotor" region. Winkler discusses temporoparieto- and fronto-nigral fibers; the first run from cortex to midbrain with Türck's bundle, previously denied by Dejerine; the second run from the frontal part of the parietal operculum; the last from the frontal operculum—one is tempted, of course, to think of the second motor area. Winkler bases his assertion on the study of pathological material; corroboration seems badly needed.

The cerebral cortex sends, as everyone knows, messages to the cerebellum by way of the corticopontine tracts of which there are two: a frontal and a parietotemporal one. The custom to attach the names of Arnold and Türck to these tracts appears to be based on a suggestion by Meynert (1879). He wrote in part: "from the anterior

part of the hemisphere a mass of bundles enters the pes pedunculi which deserves the name of Arnold's bundles [*sic*!] since this author demonstrated in an indubitable manner their course by dissection. The bundles of the pes pedunculi which enter it from the cortex of the occipital and temporal lobes deserve the name of Türck's bundles [*sic*!] because he was the first to analyze this region of the mass of the pes pedunculi by pathological-anatomical observations."[1]

The former, frequently named (a little too flatteringly) after Arnold, occupies the most medial fifth of the pes pedunculi; the latter, known as the bundle of Türck, occupies the most lateral fifth of the pes pedunculi and arises, according to Dejerine (1901), from the second and third temporal convolutions. The frontopontine tract arises, again according to Dejerine, in the motor zone for face, pharynx and larynx. It runs through the knee of the internal capsule and ends in the anterior part of the pontine gray as well as, be it remembered, in the substantia nigra. Verhaart (1948) found in two human cases evidence that the frontopontine tract contributed fine fibers to the pyramid. Monakow (1905) stated that the frontopontine tract became conspicuously (*in prägnanter Weise*) myelinated only in the fourth and fifth week after birth and that it originated from the anterior part of the first and second frontal convolutions (see his Fig. 82); in other words from what we defined as the frontal sector. It is not clear from his description precisely where the tract ends.

According to Quensel (1910) the fibers in Arnold's bundle have the following origins (Fig. 117):

I. The medial third of Arnold's bundle in the cerebral peduncle, in the anterior limit of the internal capsule in its basal third, belongs to the basal and frontal parts of F_1 and the gyrus fornicatus in front of the genu corporis callosi, perhaps also to the pars orbitalis of F_3.

II. The middle part of Arnold's bundle, middle segment of the anterior internal capsule, belongs to the parts of F_1 on the medial cortex of the hemisphere including the gyrus fornicatus in the region of the genu corporis callosi and immediately adjoining it. After the general arrangement of the fibers of the internal capsule comes again into account the anterior part of the pars triangularis of F_3. Uncertain are fiber connections with the posterior half of the pars triangularis, as well as the entire pars opercularis of F_3.

III. The lateral part of Arnold's bundle, dorsal third of the anterior limb of the internal capsule, belongs predominantly to the foot of F_1 and the adjacent gyrus fornicatus. In this part of the internal capsule appear, laterodorsal and behind the knee of the internal capsule, the fibers from the operculum Rolandii. As a rule, they leave the *pes pedunculi* to run variously in the *Fussschleife*.

Papez and Vonderahe (1947) describe a brain from which area *4* (α and γ) of Bonin was missing from one hemisphere. The patient had a contralateral flaccid hemiplegia since childhood. Examination of the nervous system revealed the corresponding corticospinal tract to be missing but there was a well developed frontopontine tract.

Kirschbaum and Bonin (1947) examined a brain in which the "pre-" frontal regions had been severely damaged twenty-three years previously. There was no

[1] Die aus der Rinde entsprungen en Bündel des Hirnschenkelfusses gehen theils aus dem vorderen Antheile der Hemisphäre als eine Bündelmasse ein, welche den Namen der Arnold'schen Bündel verdient, indem dieser Autor ihren Verlauf in unzweifelhafter Weise durch freie Präparation dargestellt hat. Die Bündel des Hirnschenkelfusses die aus der Rinde des Hinterhauptes und Schläfenlappens eintreten, verdienen den Namen der Türck'schen Bündel, weil er die Region dieser Hirnschenkelmassen durch pathologisch-anatomische Erfahrungen zuerst aufgewiesen hat.
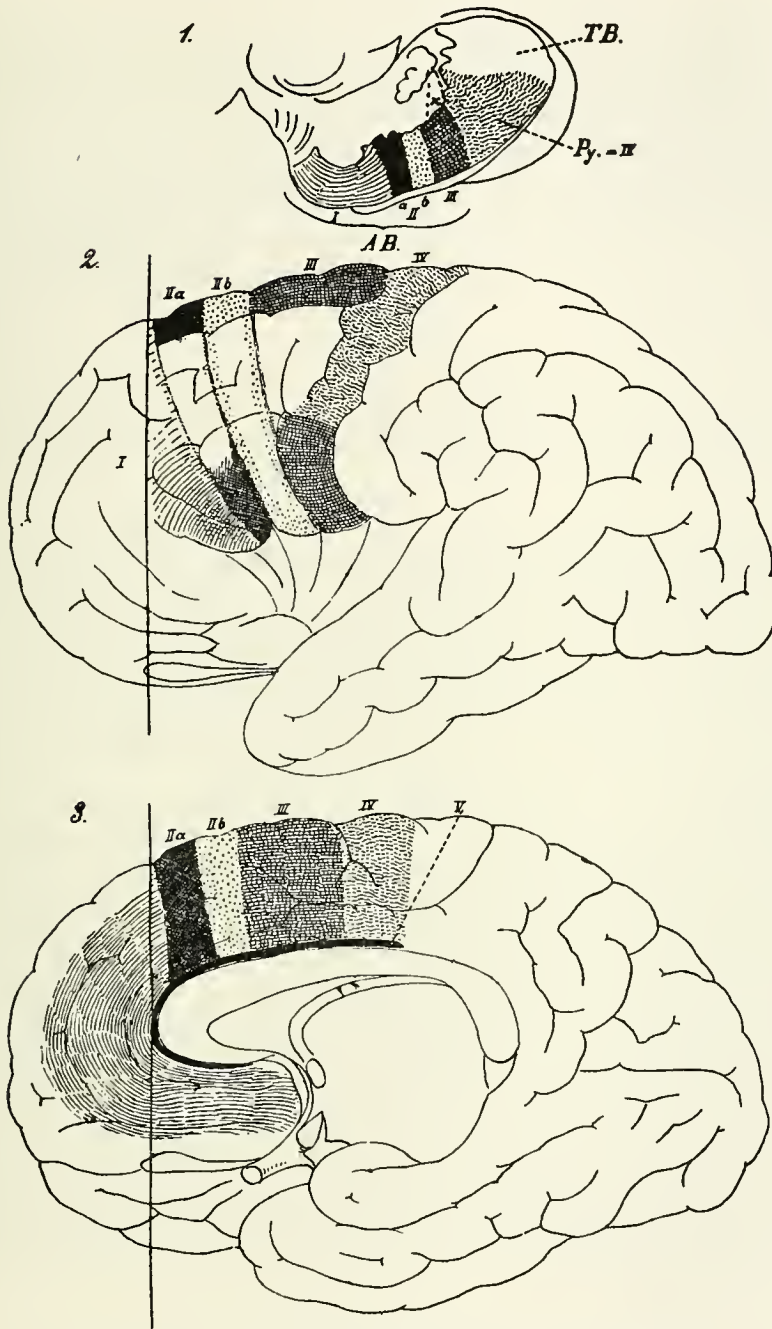
Fig. 117. Sources of Arnold's bundle according to Quensel.

1. Cross section of the peduncle (after Dejerine). TB—Türck's bundle; AB—Arnold's bundle; Py = IV—pyramidal tract; X—position of the *Fusschleife* (dorsal F).

2 and 3. Surface of the hemispheres (scheme of Flechsig) with schematic indication of the areas in relation to the parts of the peduncle.

Fibers in the peduncle and sources of these fibers similarly marked.

degeneration of Arnold's bundle. Meyer, McLardy, and Beck (1948) state that "there is some evidence in favour of a prefrontal origin of fibres going into the peduncle and pons, but further clarification is necessary." The frontopontine tract is not clearly degenerated after frontal lobotomy, but Meyer, Beck, and McLardy (1947) said their findings tended to point to area *10*. M. Meyer (1950) thinks she has found a few end-buttons degenerated in the pontine nuclei after leucotomy, but it should be remembered that the exact origin of degenerated fibers is difficult to establish in such cases and the method of Glees is equally uncertain when used on human brains removed several hours postmortem and fixed by immersion in formalin. Yakovlev, Hamlin, and Sweet (1950), from the study of two brains after lobotomy, conclude

The inference is close at hand [whatever that may mean] that the fronto-pontine tracts, at least in Cases 5 and 6, were bilaterally and symmetrically degenerated as a result of their surgical section close to the areas of their origin in the frontal lobe—areas 10 (*FE*), mesial 9 (*FD*) and 8 (*FC*).

The experimental evidence is equally inconclusive. Using the Marchi technic on macaque monkeys, Mettler (1935) derived the frontopontine tract from area *9*, Levin (1936) from area *10*, and Sunderland (1940) from area *6* of Brodmann. In spite of the assertions of LeGros Clark (1948) and Bonin (1950) the origin of the frontopontine tract is not established. Perhaps the studies of brains on which topectomies have been performed will decide the argument. So far the evidence seems to us to indicate that the bulk of the fibers in the frontopontine tract arise about where Brodmann located his area *6*; there may be some fibers from further forward.

The temporal or, as it might be called, lateral corticopontine tract is even more uncertain. Dejerine saw it degenerated after lesions in the second and third temporal convolutions. Monakow agrees in general but adds that he also observed an occipito-temporal origin which he indicated in his Figure 82. Marie and Guillain (1903), on the other hand, found indubitable proof only for an origin from the third temporal convolution, and Rhein (1922) restricts the origin of Türck's bundle still further to the posterior part of the third temporal convolution. These statements were contradicted by Flechsig (1908) who denied an origin of Türck's bundle from the third temporal convolution but emphasized, on the other hand, that he had seen complete degeneration of this tract only in cases which had involved the primary acoustic area. The literature up to 1917 has been collected and discussed by Henschen (1917) who, on the basis of a case of his own, concluded that the fibers of Türck's bundle do not arise from the primary sensory areas but from the "psychic areas." In the macaque monkey it must arise, according to the results of Bucy and Klüver (1940), from that part of the temporal lobe posterior to the lower extremity of the central sulcus.

Visceral Efferents

Visceromotor control by the cortex appears to be achieved by pathways which project from the frontal and precentral sectors to the hypothalamus. The method of physiological neuronography was employed by Ward and McCulloch (1947) to

investigate these connections in the monkey. Projections from "area 6" to the posterior hypothalamic region had been traced anatomically by Mettler (1948) in the macaque. Bonin and Green (1949) found fibers going from the orbital surface of the macaque to the hypothalamus. For the human we have at present only the report by M. Meyer (1949) who found degenerated end-buttons in the mamillary body in two cases where the lobotomy cut had removed part of the simple agranular precentral cortex. The possibility that these fibers arise from the anterior limbic cortex was, however, not definitely ruled out.

Chapter IX: Functional Significance

Only by continual modification of its ancestral powers to suit the present can (a creature) fulfil that which its destiny, if it is to succeed, requires from it as its life's purpose, namely, the extension of its dominance over its environment. For this conquest its cerebrum is its best weapon. It is then around the cerebrum, its physiological and psychological attributes, that the main interest of biology must ultimately turn.

C. S. SHERRINGTON (1906)

Investigators have labored so diligently over the structure of the cerebral cortex because of a conviction that in this way they might gain some understanding of the manner of its functioning. As Hughlings Jackson put it: "Differentiation of structure of necessity implies difference in function." Otherwise it is not likely that their curiosity would have led them so far since, as Flourens remarked in 1842, an anatomy without physiology is an anatomy without purpose. As physicians we are further interested in the utilization of this understanding for the relief of suffering caused by perversions of its functioning.

It is now well established that certain structural peculiarities of the cerebral cortex are coextensive with areas of specialized functioning. We need mention only the striate area and the agranular precentral area, although it is unknown how these structural peculiarities are necessary to that special function. As this fact became clearly established it was logical to seek for other similar areas of specialized structure which might be supposed to have peculiar functions. In doing so two factors seem to have been often forgotten: (1) the corollary of the underlying hypothesis is also probably true, namely, that areas having a very similar structure are likely to have similar functions, insofar as their functioning depends on their intrinsic structure, and (2) the cortex being a part of a communications system, its functioning is not dependent solely on its intrinsic structure but, in large part, on its external connections. This is very evident for exactly those areas first distinguished because of their unusually variant structure—the striate area and the motor—the former coinciding with the radiation of visual impulses to the cortex and the latter with the most powerful projection system.

At any rate, anatomists proceeded on the assumption, explicitly stated by Brodmann, that the cerebral cortex consisted of a mosaic of juxtaposed organs. Vogt added that the boundaries between these organs were "hair-sharp." The problem then became, for an anatomist, to identify these organs and trace their boundaries, leaving to the physiologists later to determine their functions. Perhaps there was, in all this, the influence of a subconscious recollection of Gall and his phrenological charts. However that may be, anatomists began to outline ever more supposed organs, the functions of which physiologists labored as diligently to discover.

This pursuit was not too illogical so long as we possessed only the relatively simple charts of Brodmann, and this is doubtless the reason that physiologists still cling to them, but became quite absurd when guided by the exceedingly complicated charts of the Vogt school. Even Hassler (1948), a pupil of Vogt, when discussing

the thalamocortical relationships uses Brodmann's subdivisions. It is too great a strain on the credulity of the most convinced believer in cerebral localization to suppose that there are in the cerebral cortex as many as one hundred fifty separate and distinct organs. Vogt, as early as 1903, insisted that (p. 161) for each physiological center there must be at least one special specific fiber connection.

In the preceding chapters we have analyzed the cytoarchitectonic lore and outlined our convictions concerning its reliability and usefulness. We have distinguished a considerably smaller number of "areas" than Brodmann or his successors. The vogue of Brodmann's chart is a remarkable instance of the credulous acceptance by the scientific world of a construct, the factual basis of which was never published. Whether our map is more "correct" than the current ones, depends partly on what is meant by "correct." It does not mirror the functional organization of the cerebral cortex, which depends as much on input and output signals and on "long distance" corticocortical signals as on the local variation of cortical architecture, the only variable which the map is meant to portray. But, even when this is clearly understood, the exact criteria by which "areas" are to be distinguished remain to be defined. So far the definition of what constitutes a histological area, what is a variant or a subarea, have been more intuitive than quantitative. The Vogts have built up an imposing vocabulary in which—characteristically enough—comparatives abound. What is needed are measurements, but of what? Thickness of layers, size and density of cells suggest themselves. But that is, with our present facilities, an exasperatingly slow business. Better, so it seemed to us, to err on the side of caution and to distinguish only those areas which can be intuitively recognized without difficulty. Further subdivisions are undoubtedly possible. To make them at present, without sufficiently precise definitions, serves no useful purpose.

The term "functional organization" has been, we fear, badly misused by us in former years. It has become equivalent to the arrangement of corticocortical association fibers whereas it should mean the spatial distribution of nervous processes in the cortex. To show how and to what extent the structure of the cortex (not only its architecture) determines its "functional organization," thus defined, must be our aim. We are far from having achieved it. But to reach it, a subdivision of the cortex has always been considered as the first step. After Gall and Spurzheim had proposed an elaborate and rather mythological subdivision, their saner successors proposed a division into lobes based, it is true, on rather fortuitous relations between brain and bones. Then came the subtle parcellation into areas more bewildering and confusing than clarifying. We propose to go back to a simpler scheme of "sectors" based on corticothalamic afferents and to supplement it by an architectonic map based on easily recognizable distinctions.

If we suppose that the conditions in man follow the pattern which has been worked out in some detail for the macaque, and less extensively for the chimpanzee, we may subdivide the isocortex in the manner indicated in Figure 115 by using the corticothalamic relationships as a basis. This results in what Bonin (1950) has called a sectoral map, and is justified by the fact that nearly every larger thalamic nucleus has its individual sector of the cortex with which it is connected by fibers going in both directions. Each sector has, therefore, one of the features pointed out by Vogt (1903) as necessary to a functionally individual area, namely, a unique

fiber connection. The median center of Luys and the intralaminar nuclei are exceptions to the rule.

It is at once apparent, however, that such a sectoral map gives as false an impression as the usual cytoarchitectonic map. In the first place, the radiation of each nucleus seems to be concentrated more or less in the central part of each sector which includes the closely related parakoniocortex. The sectors, therefore, do not have uniform intrinsic structure. Moreover, the thalamic nuclei, if judged by their other connections, are not of uniform functional significance. Some—for example the external and internal geniculate bodies—are obviously relay stations for sensory stimulation coming from the periphery; others—such as the dorsomedial nucleus and the pulvinar—have no such direct relationship to the incoming sensory streams. It is evident that, if such a sectoral map be drawn, the sectors are not of uniform functional significance. This fact invalidates Vogt's (1906) criticism of the work of Flechsig. It is doubtless true that Flechsig made many statements which subsequent investigation has not substantiated, and that he delimited his areas too sharply, yet the general resemblance of his map to that of the Vogts (Fig. 118) is too obvious to be fortuitous. In its general lines the concept of Flechsig holds fast. It is interesting to remark that Vogt fell into the same error for which he criticizes Flechsig, stated his myeloarchitectural findings dogmatically and drew the boundaries of his areas with even more improbable sharpness. If now we scrutinize this sectoral map more closely, we find that those sectors which are related to the thalamic nuclei not directly in the pathway of the incoming sensory impulses, such as the pulvinar (parietal sector) and dorsomedial nucleus (frontal sector), are covered by generalized eulaminate cortex. The same is true of what we have called the temporal sector which, recent experiments (Chow, 1950) indicate, may also be related to the pulvinar; much of the generalized frontal, parietal, occipital, and temporal cortex seems to have only scanty thalamic connections in any case. A comparison of figures 1, 112, and 118 shows that it is just the cortical regions most tardily myelinated which develop intimate connections with each other by means of long fiber tracts and were called by Flechsig, in terms habitual to the psychology of his day, the associational areas. All that we know of their intrinsic structure and connections indicates that they must have some function in common and, most probably, of greater complexity than simple reflex activity after the pattern of the spinal cord.

What is this generalized function common to these cortical sectors of generalized structure? Beritoff stated (1924), on the basis of experimentation carried out by Pavlov's school, that this function was to make transitory connections. Many illustrations have been given of the manner in which conditioned reflexes can be built up, torn down, reconstructed or altered under experimental conditions; such reflexes are formed in the cerebral cortex. Hughlings Jackson had something of the same idea when he wrote: "if the centers of the highest level ('mental centers') were not little organized, and therefore very modifiable, we could only with difficulty adjust ourselves to new circumstances and should make few new acquirements." These suggestions still consider cortical activity as tantamount to reflex activity. Even Pavlov and Sherrington thought almost exclusively about reflexes. With that mode of thinking went hand in hand Brodmann's conception of cortical areas as elementary organs.

Meanwhile Gestalt psychology was led to consider fields in the sense in which that concept had been developed in physics. Indeed, Köhler (1924) demonstrated that the physicist's concept of fields was essentially a gestalt in the technical sense of the psychologist. From that Köhler (1938) developed his theory of isomorphism.
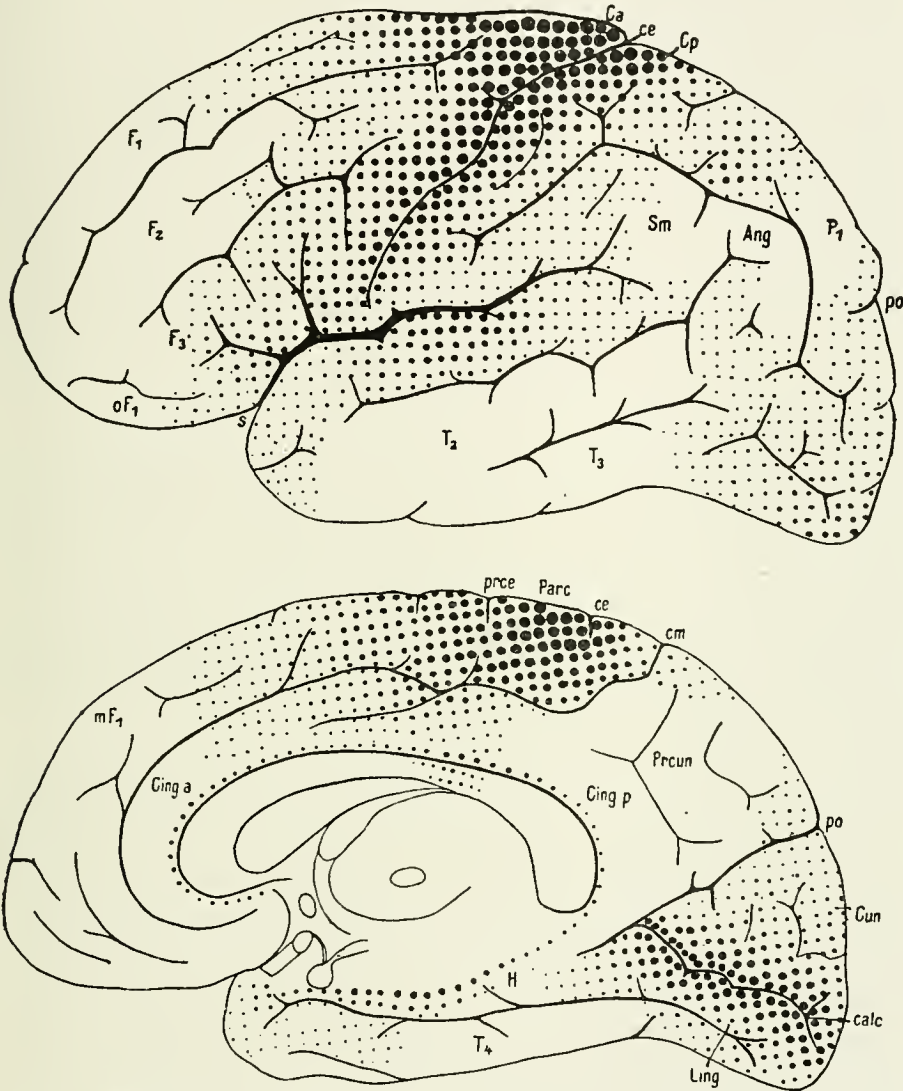

FIG. 118. Myelinization of the cerebral cortex (the extent of the myelinization is indicated by the size of the dots) of a nineteen-day-old child (after C. and O. Vogt).

Whether it can be upheld in precisely that sense which Köhler gave it, with its assumption of cortical fields (see Köhler and Wallach, 1944), is not for us to decide. Its success in explaining sensory phenomena does not guarantee its ability to explain everything. But isomorphism, in the abstract sense in which the mathematician uses the term, between mental and neural processes, is exactly what Craik (1943)

states by the phrase "thought models or parallels reality," and is at the base of the theory of Pitts and McCulloch (1947). In this general form it leaves, of course, undefined the nature of the processes.

Thurstone's factor-analysis, used among others by Halstead (1947) in his study of impaired brains and their functions, and Wiener's *Cybernetics* (1948) have given us new viewpoints for the analysis of cerebral functions. It is clear to most students that the cortex can be likened to a calculating machine (Craik, 1943; McCulloch, 1949) with greater justification than to a slot machine, although even this simile breaks down eventually. For, in spite of Ashby's (1949) or Grey Walter's (1950b) visions, no machine has been constructed that can outwit a human brain in choosing goals and Lady Lovelace, Lord Byron's daughter, has put it on record that this will never happen (see Hartree, 1949). Be that as it may, to consider memory, recognition, and forecasting as fundamental properties of the brain appears now necessary. Whether this is a complete list is, however, not certain. If volition can be defined as a forecasting and a comparison of the result with an established set of (ethical) values, and if comparison and recognition can be considered to be two aspects of the neuron as coincidence detector, we may be well on the way to a theory of cortical function.

In any event, Wiener has made it clear that order as against mere noise is the important characteristic of nervous functions. It is not always sufficiently realized that the cortex has, as every electroencephalographer knows, a high level of "noise" of a random background activity. This activity, whether aroused from deeper nervous centers or inherent in the cortex itself (Bremer, 1947), serves perhaps to keep the cortex alert and ready to receive stimuli. The histologist is apt to construct his firing diagrams without much regard to this noise. Indeed, it has to be admitted that we are unable at the moment to state with sufficient generality what distinguishes "meaningful" signals from random noise. "Order" is a very vague term; there is an infinity of types of order.

There is a spatial order in cortical events, mirrored inadequately in the areal maps which adorn the literature on cortical architecture. We understand fairly well the functional organization of the input signals—where visual, tactile, and acoustic messages arrive, how their subordinate spatial arrangement subserves topographical discrimination in the first two, and pitch discrimination in the last case. We also know that output signals emerge from the "motor" area, e.g., the agranular gigantopyramidal area, and we know something of its type of order. That is, however, certainly not the whole story; oculomotor output signals, e.g., can be traced from other areas. In any event, there is a wide gap between input and output. That gap is Hughlings Jackson's highest level; psychologically it contains almost everything that is in our consciousness. The ordering principle within the highest level is still largely a mystery. Spatial organization does not seem to be the clue. The studies of aphasia (Head, 1926; Alajouanine and Mozziconacci, 1947), of apraxia and agnosia (Lange, 1936) as well as the modern tests of clinical psychologists have never led far beyond a very general localization (Goldstein, 1946); every attempt at detailed subdivision has failed. One can only conclude that the important type of order is that of the mutual relations of vast numbers of neurons within a given, somewhat vaguely circumscribed, region. Kubie (1930), Lorente de Nó (1938), Dusser de

Barenne and McCulloch (1938), and others talk about hypothetical reverberating electrical circuits and Adrian (1947) talks vaguely about still vaguer electrical phenomena. There is physiological evidence to support these speculations, such as the long-lasting traveling effects of cerebellar stimulation (Clark, 1938), the phenomenon of the spread of suppression (Garol, 1940), the spreading depression of Leão (1944), or the figural aftereffects of Köhler and Wallach (1944).

Anatomists have shown that sensory input, and much of motor output, are handled by cortical areas which differ markedly from eulaminate cortex and differ, as might be expected, in opposite directions, namely in that of a koniocortex in the former and in that of an agranular cortex in the latter instance. It is also clear that a koniocortical input area renders the eulaminate cortex in its immediate vicinity into a parakoniocortex. But, beyond that, areal differentiations of the human cerebral cortex become hazardous. We were able to point to a few local peculiarities —on the inferior frontal convolution, the superior parietal lobule, within the temporal lobe, etc.—but these are all minor. The human isocortex is more remarkable for its uniformity than for multifarious differentiations.

It may well be, and some theories (Lashley, 1942; H. v. Foerster, 1948) explicitly assume it, that higher mental functions are based on a statistical interplay of neurons. Such processes would be favored by a relative homogeneity of wide cortical fields. These theories have been greatly strengthened by the revelations of electroencephalography. By this method we can observe the cortex in action, albeit indirectly. One of the fundamental discoveries is that there is a regular rhythmical fluctuation of the electrical potential of the cortex, at a rate of about 10 c/s, which was called by Berger (1929) the alpha rhythm. It is best seen when the cortex is receiving as little as possible of sensory stimulation and the cortex is in other ways nearly at rest. Under such conditions we find that the alpha rhythm (Jasper and Penfield, 1950) is distributed over all the generalized eulaminate regions of the cortex (Fig. 119) but is absent from the agranular regions. There is now a tendency to identify the alpha rhythm with a scanning mechanism such as is used in television (Craik, 1943; Pitts and McCulloch, 1947; Walter, 1947). In this case it should be operative also in the koniocortices but we lack direct observational data.

Later studies (Walter, 1950a) have shown that the rhythm is plural. In normal subjects there are two or three components in the band of frequencies from 8–13 c/s. These rhythms may be disturbed by external stimulation or by mental effort (for example by opening the eyes or by visual imagination) and a change provoked in their form and harmonic content. Such harmonics may appear not only in the visual area but almost anywhere in the cortex. If a sensory area is activated at an appropriate rate it can be forced to communicate with other regions. A stimulation of the visual area at 12 f/s can evoke a component at 6 c/s in the temporal and at 24 c/s in the frontal region. It is characteristic of these transactivation effects that the rate is different from that of the primary activating stimulus (Livanov, 1938). These secondary transactivations are most easily provoked in the temporal lobes, usually in the theta band (6–7 c/s).

We do not wish to pursue these electrical studies further. Enough has been said to show that vast areas of the cerebral cortex are functioning during mental processes. It is not surprising that large quantities of the general eulaminate cortex

can be removed without too obvious a defect. As Walter remarks (p. 30), "In the sort of experiments I have been describing, the activity of single units seems to us of no greater relevance than the behaviour of a single ion in a chemical reaction; the removal or destruction of great numbers of units seems to have a negligible effect upon function. The study of brain function can only be statistical in this sense because the brain can only function statistically in relation to the environment."

The cerebral cortex does not normally function in isolation. We have endeavored
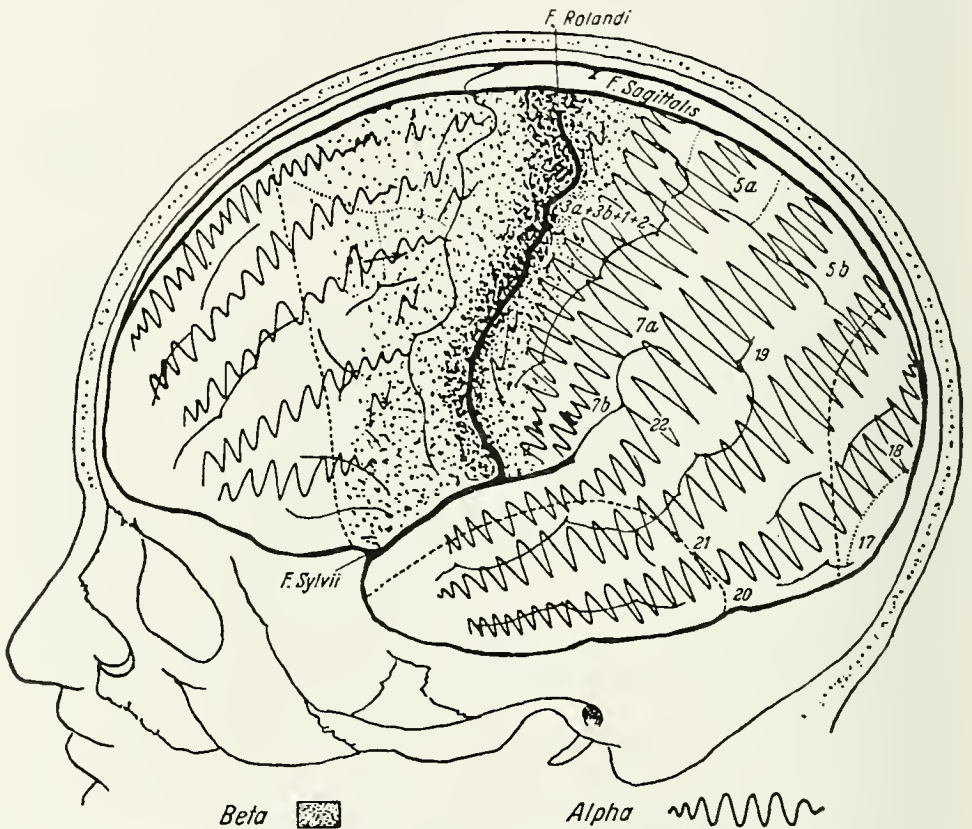
Fig. 119. Diagrammatic representation of cortical areas giving rise to *alpha* rhythm as opposed to those showing *beta* rhythm (stippled). From Jasper and Penfield.

to collect the evidence for corticopetal and corticofugal pathways, so far as it is derived from the human brain. While we have doubtless overlooked scattered papers, we believe that we have at least cited a fair sample. The observations are few and usually inconclusive. Indeed, it is perhaps not too much to say that, before the advent of leucotomy, only two authors were really interested in these questions—Dejerine and Monakow. Pathological lesions are, of course, very unsuitable material in most instances but, for many parts of the brain, they will remain for long the only source available. Recently surgical lesions of the frontal lobe have been available for study. Precisely because interpretations are precarious, investigation of
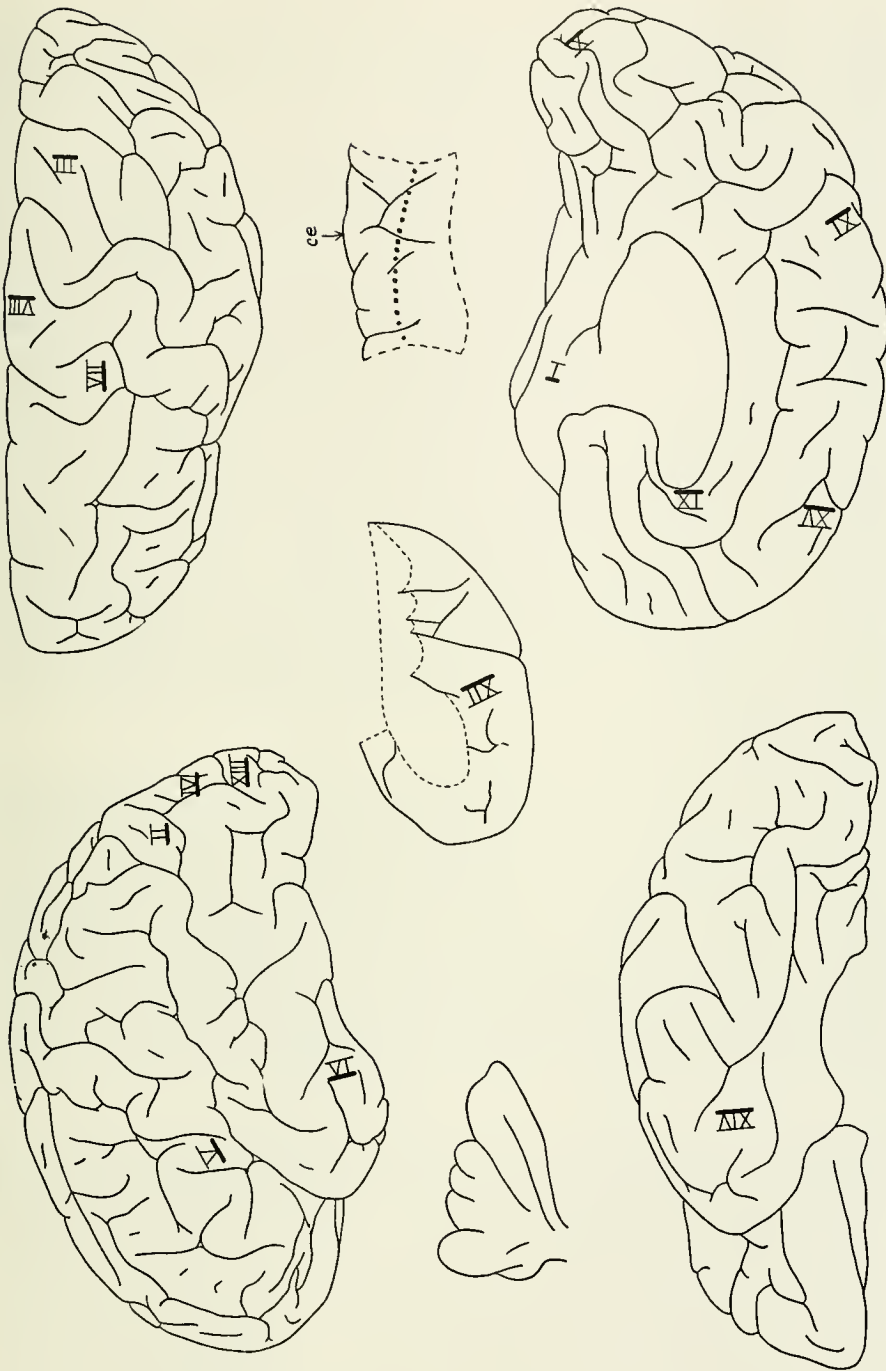
Fig. 120. Schemas of brain *Hl* showing location of plates.

numerous brains is desirable. This is not a glamorous task; no oscilloscope flashes, no Geiger counter clicks, but the "wiring diagram" of the brain is as interesting and important as it ever was. We have seen how the specific afferents may form the basis of a fruitful subdivision of the cortex.

In an attempt to evaluate the functional role of the association fibers, it must not be forgotten that they are not the only means for conducting signals from one part of the cortex to another. In fact, Wiener (1948) believes that, when compared to the brain of a lower mammal, the human brain is "quite defective in the matter of long-distance trunk lines." In physiological neuronography, Dial narcosis suppresses the transmitter system of the intracortical feltwork, and makes the signals coming in over the association fibers stand out the more clearly, thus creating quite artificial conditions. As employed heretofore physiological neuronography tells, therefore, only a part of the story. Yet a few generalizations can be made.

On the sensory side, it has been shown for optic and acoustic impulses that the primary sensory areas, i.e., the koniocortices, stand in close connection with the parakoniocortices; the concept of parakoniocortex, originally advanced by Economo and retained in our study, receives support from physiological neuronography. The primary sensory areas do not send messages very far into the surrounding cortex and receive cortical impulses almost exclusively from the parasensory areas; the parasensory areas, on the other hand, receive afferents from several other cortical areas and send their corticocortical efferents much farther away. But the longest corticocortical pathways connect the generalized eulaminate areas which Flechsig called the associational areas.

As Flechsig (1901) long ago pointed out:

The areas (of the cortex) differ with respect to the corona radiata and they also differ in a most extraordinary manner with respect to the long association systems. The terminal zones are the richest in them; they are the endings of the long association systems. On the other hand, no long association system is known which connects two primordial zones that are to be regarded as sensory centers. . . . If a visual and an auditory impression meet one another anywhere in the cortex of the cerebrum, this can only happen through the instrumentality of the intermediate and terminal zones. If the mutual interference of the stimuli is a preliminary condition of the association of their mnemonic impressions, the cortex of the intermediary and the terminal zones will be indispensable for this purpose also. They are, therefore, association centers; and this view is strongly confirmed by the clinical observation that in lesions of the region lying between the visual and tactile spheres it is association troubles that occur, the best known of which is sensory alexia.

Somatomotor events can easily be traced up the pyramidal tracts to the precentral gyrus, to the second motor area on the infrafrontal and infraparietal plane and to the region between these two branches of the "V." But motor impulses do not arise spontaneously in the giant cells of Betz (Hassler, 1949). During life they are obviously under the influence of frontal, premotor, and parietal regions as well as under those from the thalamocortical afferents which Hassler (1949) studied. The loss of either frontal or parietal signals will cause a dysfunction clinically noticeable as apraxia (see Lange, 1936). It is tempting to think of the parietal influx as somehow regulating motor activity in the light of information given the parietal lobe as "bodyscheme," in the widest and most "dynamic" sense of the word, and of
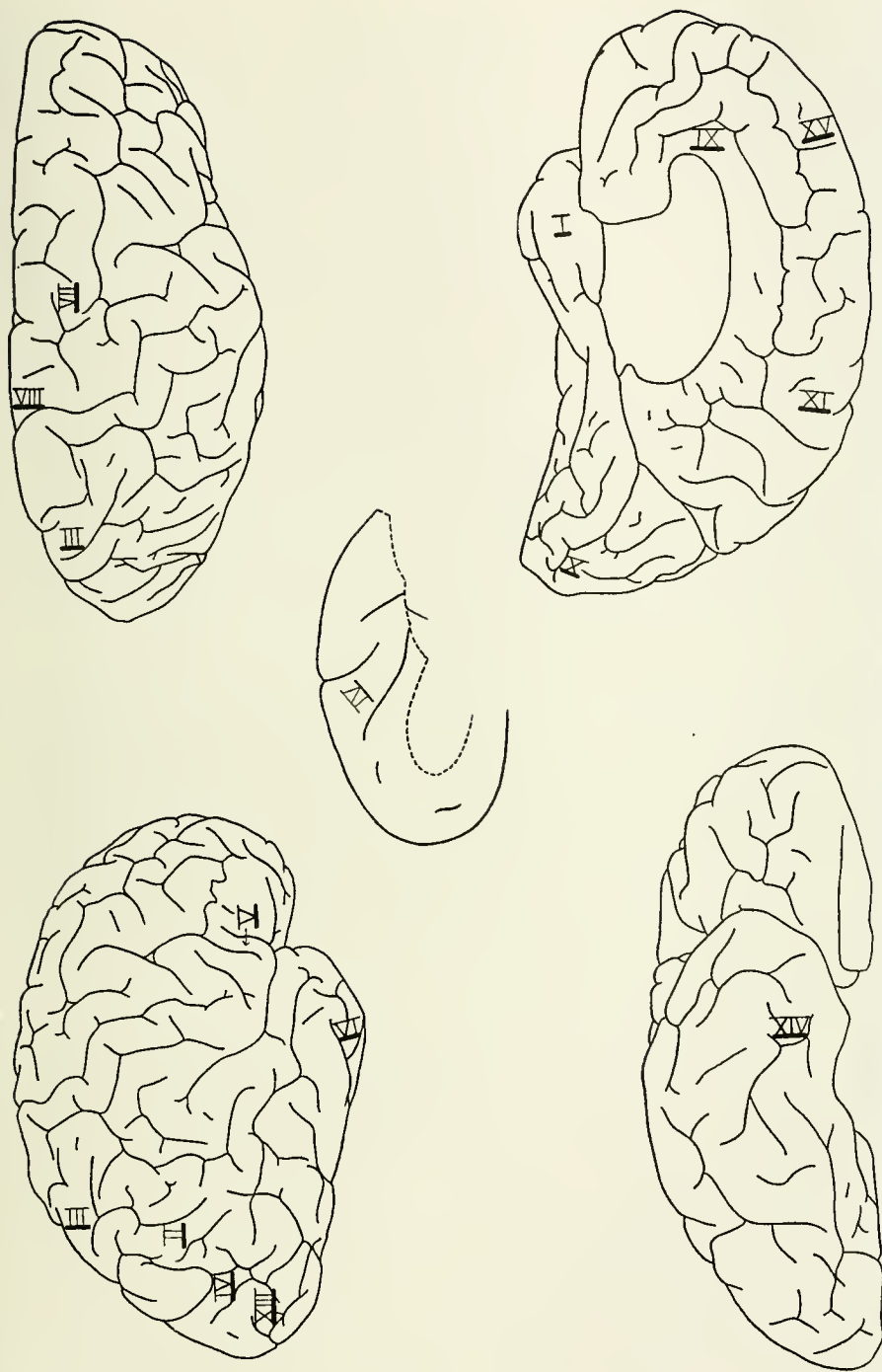
FIG. 121. Schemas of brain Hr showing approximate location of plates (from the regions indicated, preparations were made by other histological methods for comparison with the Nissl preparations of the left hemisphere, Hl).

the frontal influx as related to Liepmann's *Bewegungsentwurf*, a sort of forecast of future movements by the prefrontal field.

Disturbances of associations of images with symbols, or of symbols with each other, should be expected to cause aphasia and related disorders. Indeed, who would not think of transcortical aphasia? But it appears useless to give rein to further speculation; we begin to indulge in armchair philosophy.

The question of the functional dignity of the commissural fibers is particularly vexing since, from the meticulous studies by Akelaitis (1944) of patients whose commissures had been sectioned by van Wagenen, it is clear that the impairment following sectioning of the corpus callosum is astonishingly slight. We pointed out (p. 240) that the number of commissural fibers is small, as compared with the total number of cells in one hemisphere, of the order of less than 1 per cent. Morin and Goldring's (1950) observation that, in the opossum, transmission of excitation from one hemisphere to the other is not abolished after cutting all commissures of the forebrain, is of interest. Jasper (1950) observes that section of the corpus callosum does not abolish the effect of the bilateral recruiting response from thalamic nuclei. It is known also that callosal activity modifies the brain waves in the cerebral cortex (O'Leary, 1949). It is incredible that such a vast tract of nervous fibers should be functionless but we have no clear idea of its significance. The theoretical considerations of Nielsen (1937) and the cases of Trescher and Ford (1937) and of Maspes (1948) indicate that more ingenious examination may discern very useful material for our understanding of cerebral functioning.

Preparatory to the study of cortical architecture we have passed in review the information on racial differences which have accumulated over the years. We discovered a lamentable amount of prejudice and biased thinking. The first task was to root out a rank growth of misstatements and irresponsible distortions. When properly evaluated by statistical methods, very few racial characteristics can be shown to exist in the configuration of the sulci. Even in the few cases where racial peculiarities can be asserted, as e.g., in the dorsal part of the frontal lobe or in that of the lunate sulcus, it is merely a matter of different frequencies and not of clear dichotomies. Estimates of brain weight and metrical characters have also shown racial differences but they are so erratic that one is, at present, forced to look upon them as entirely fortuitous.

The few notes on racial differences in cytoarchitecture by Vint (1934), Stefko (1926), Loo (1933–35), and van Noort (1918) are even more disappointing. One wonders whether they show much more than the rapidity with which postmortem changes appear in cadavers kept under what must have been primitive conditions and fairly warm weather. Vint's measurements of the thickness of the cortex can be duplicated by many of our own recorded in Chapter V. Whether or not the Chinese and the orang have sprung from the same stem as Klaatsch (1911) and Kurz (1924) believe, cytoarchitectonic study led Loo (1933–35) to conclude "that histologically the cerebral cortex of the Chinese brain is neither lower in organization, nor more anthropoid, nor fetalized." van Noort's statement that large pyramidal cells are absent in the acoustic koniocortex of his two Madurese brains would merely indicate, so one could argue, that the Madurese were more highly differentiated than the "Whites." To save the self-esteem of the white man, and help

him carry his burden, we hasten to add that we would not consider this argument any more cogent than van Noort's own conclusions.

When we remember that man is born with a very immature cortex, that even his pyramidal tracts remain unmyelinated for almost a year, it should be clear that culture in its widest sense is not innate but learnt by the individual during infancy. That is true of language, of skills, of everything that follows. That genotypes are not the same throughout the world we know from the distribution of blood groups; that different environments and different cultural patterns have led to different trends in Natural Selection (or should we say Cultural Selection?) must also be admitted, and may suffice to explain those psychological and mental differences which have been reported; but anatomical racial differences in the brain have yet to be found.

Our knowledge of the structure of the cerebral cortex is so incomplete, and our methods of study so crude, as to make any attempt to identify structural peculiarities characteristic of the brains of unusually intelligent persons entirely fruitless (Riese and Goldstein, 1950). What dubious information we have, especially from the Russian school, indicates that the normal range of variation is so great as to invalidate, for a long time to come, any such attempt. The same reasoning applies to studies (Eduard Beck, 1950) of differences in structure to be found between the two hemispheres of the same brain, and even more so to studies of racial differences (Loo, 1933–35). We are quite incapable of identifying anatomical correlates of race, intelligence, or genius.

It is possible that the more efficient functioning of the brain of a genius is a matter of quality rather than of structure but, at the present time, our knowledge even of its structure is so rudimentary that we can formulate only the crudest hypotheses (Pavlov, 1928) concerning the manner of functioning of the cerebral cortex. When all is said and done we are most impressed by the limited use made, even by the most civilized peoples, of the possibilities which our vaunted "best weapon" offers us. It remains to be seen whether we shall not fly into the atom bomb as helplessly as moths into a candle.

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PLATES
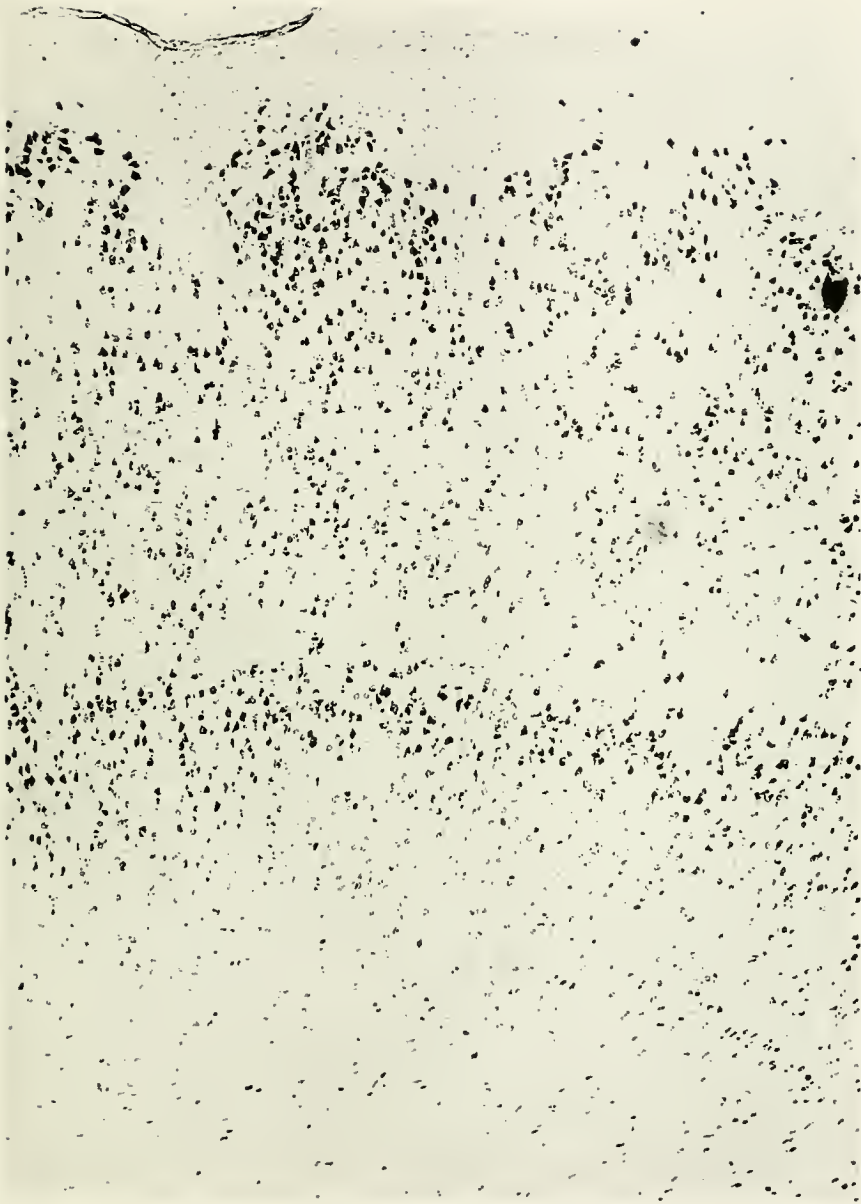
Plate I. *Allocortex* praepiriformis *A prp.*
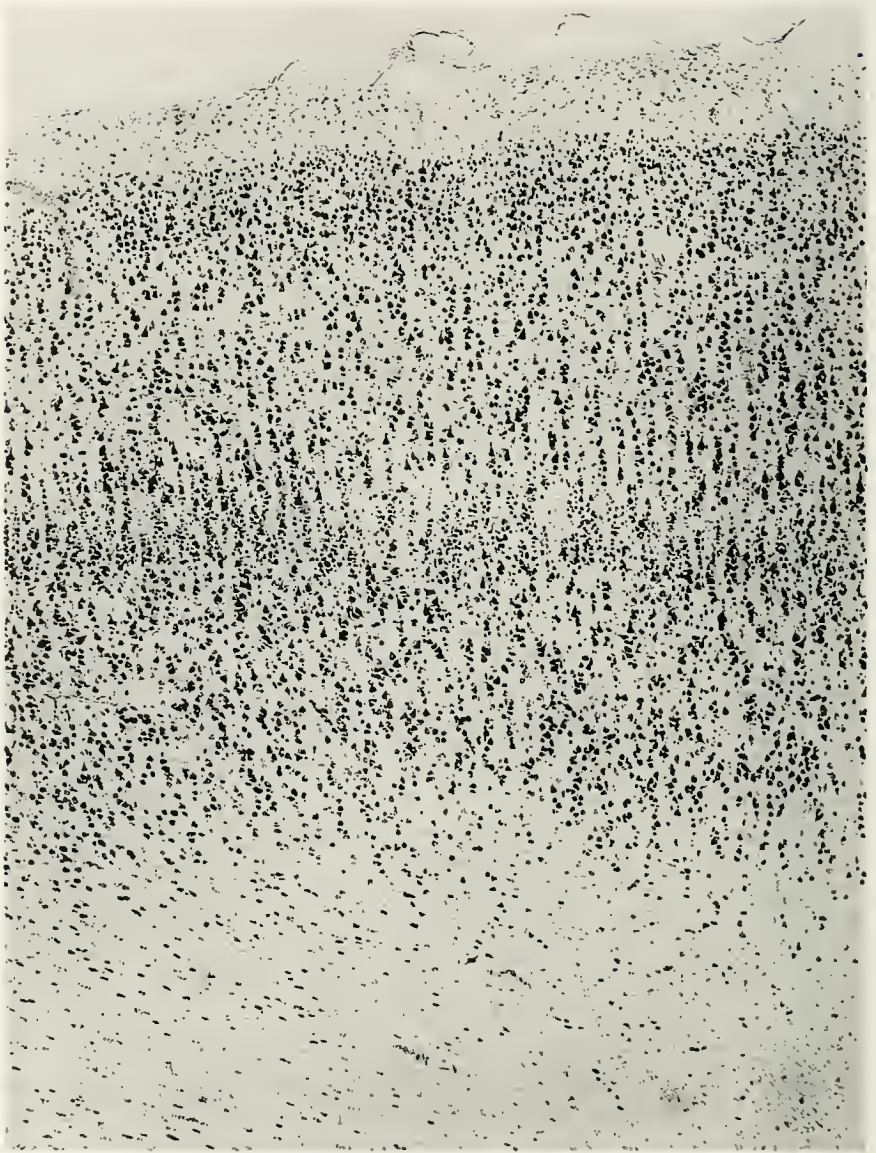
Plate II. *Isocortex eulaminatus* parietalis inferior *IEpi.*
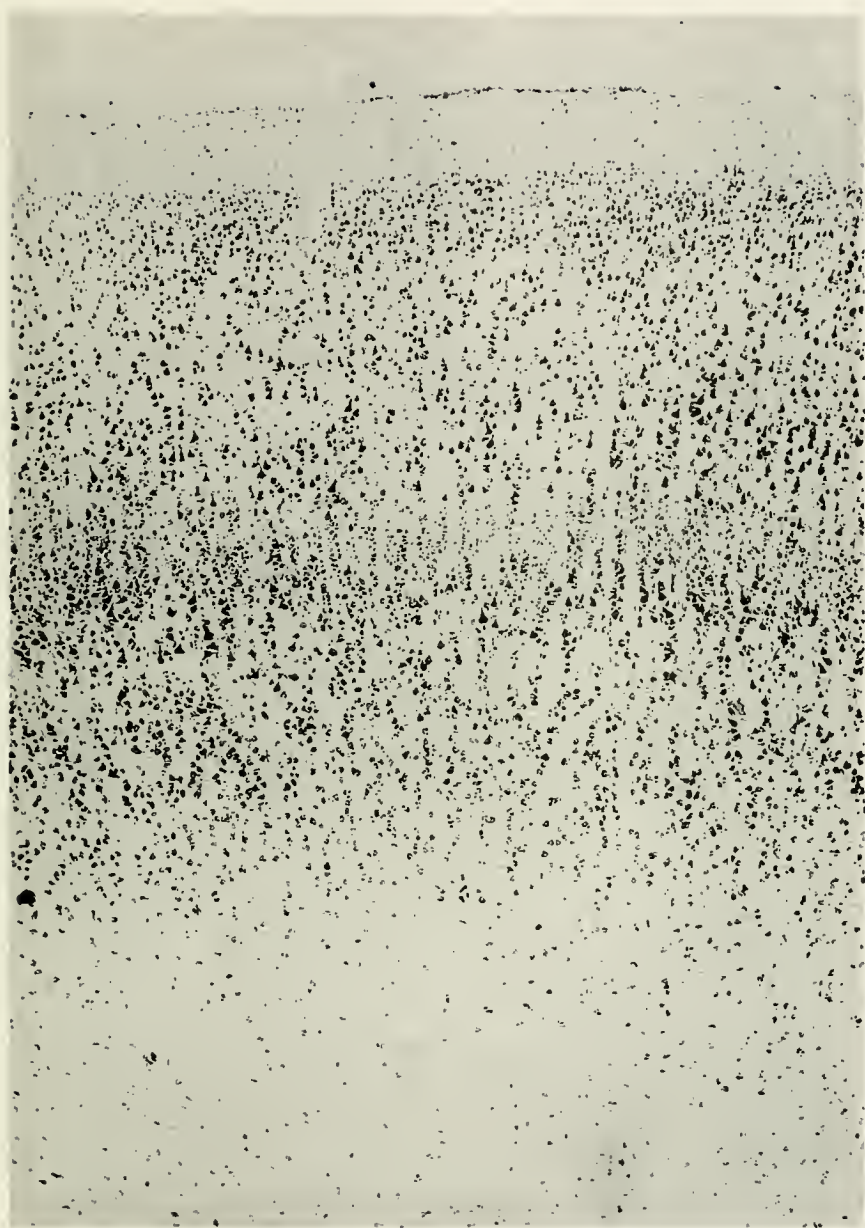
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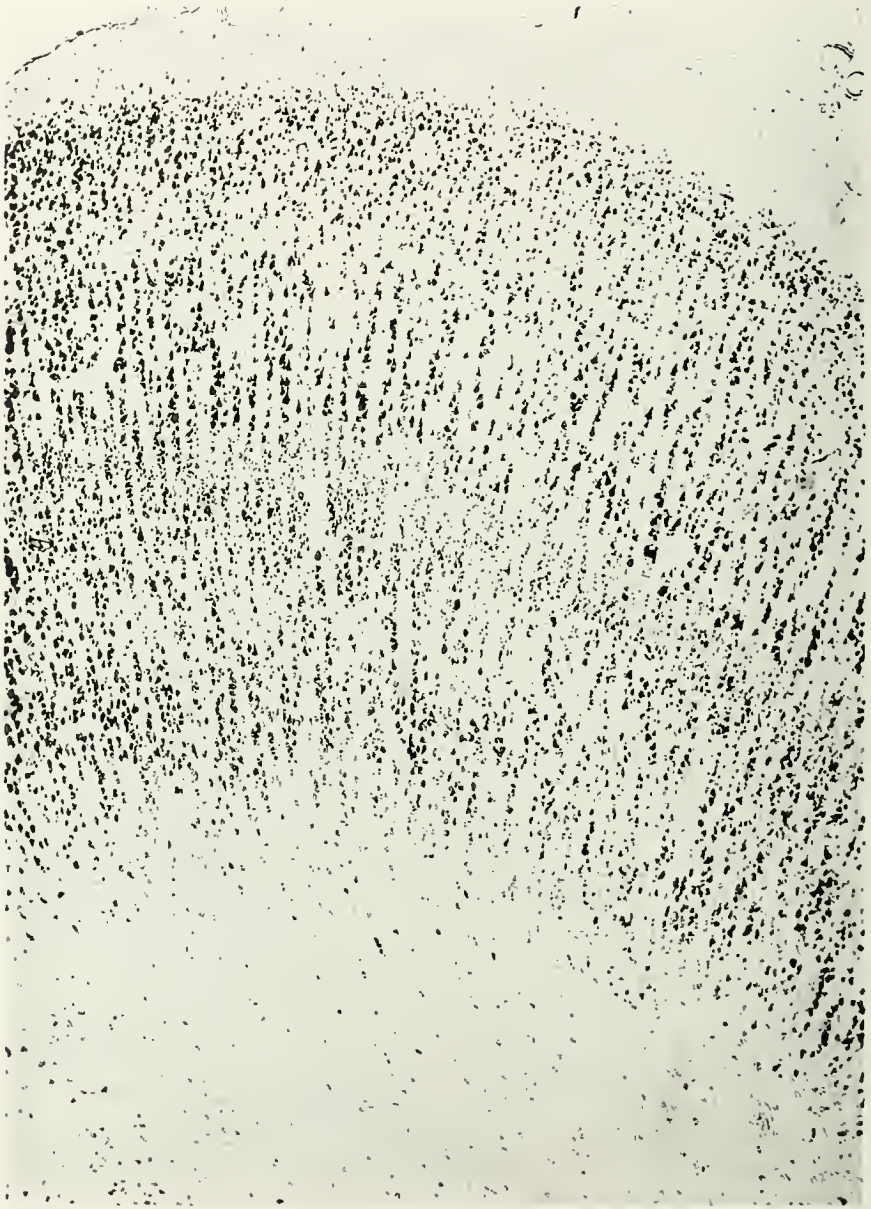
Plate IV. *Isocortex eulaminatus* praeoccipitalis *IEpro*.
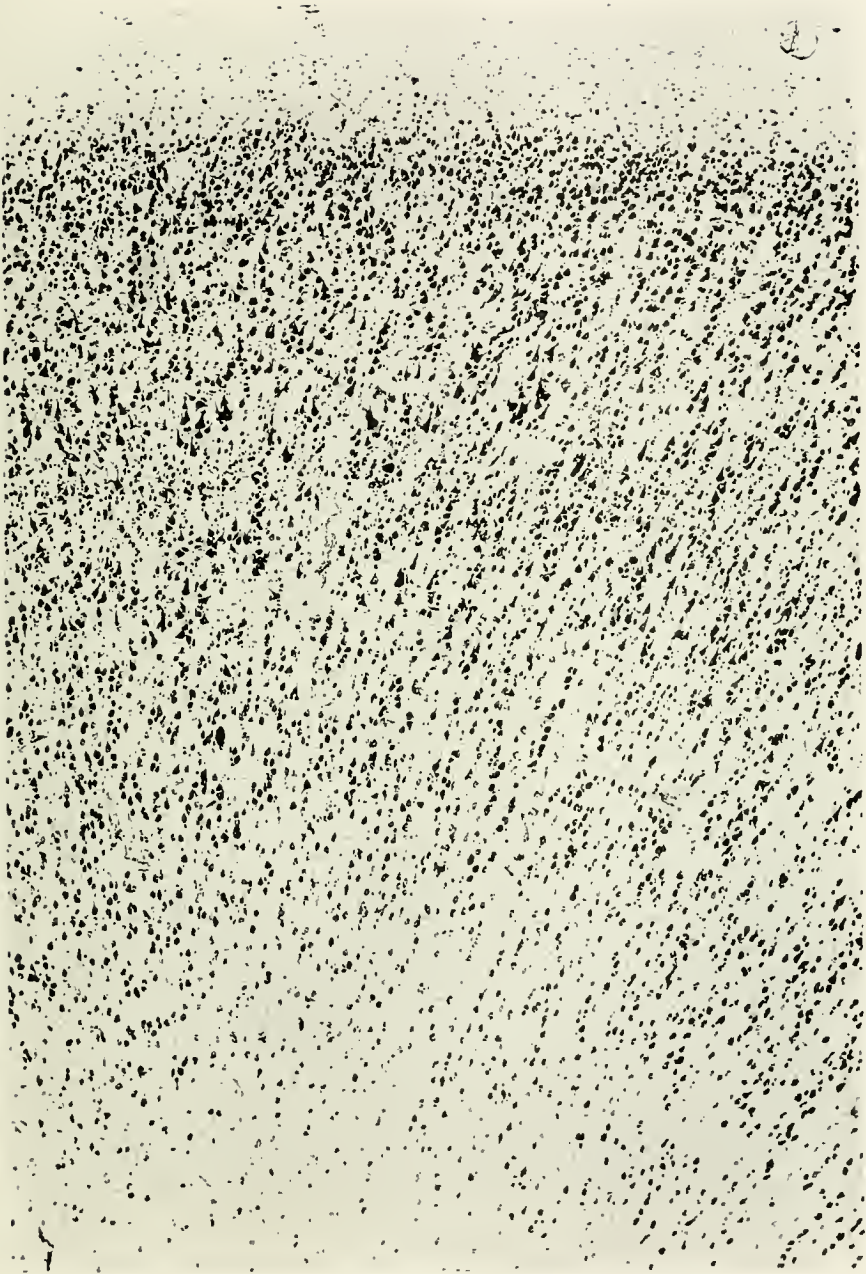
Plate V. *Isocortex eulaminatus* frontalis inferior *IEfi*.
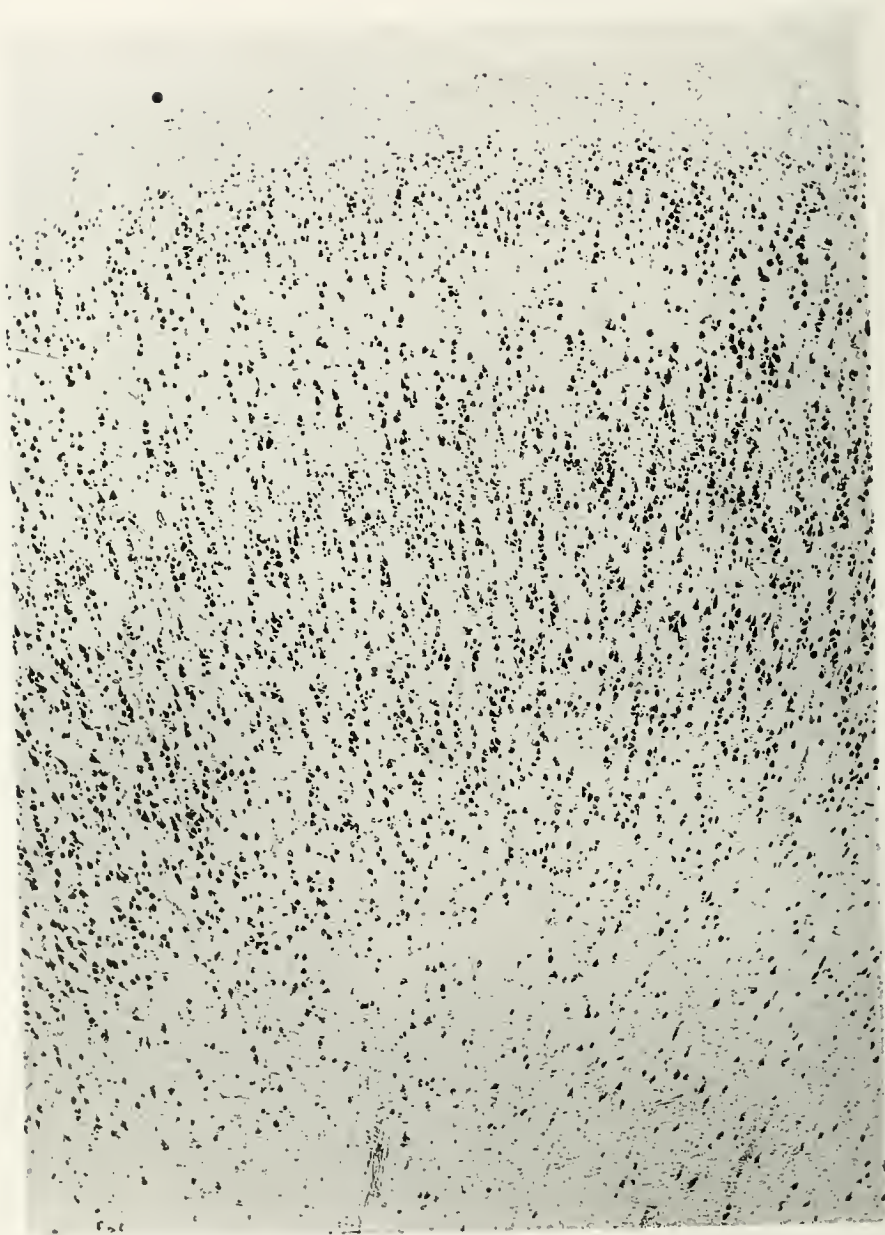
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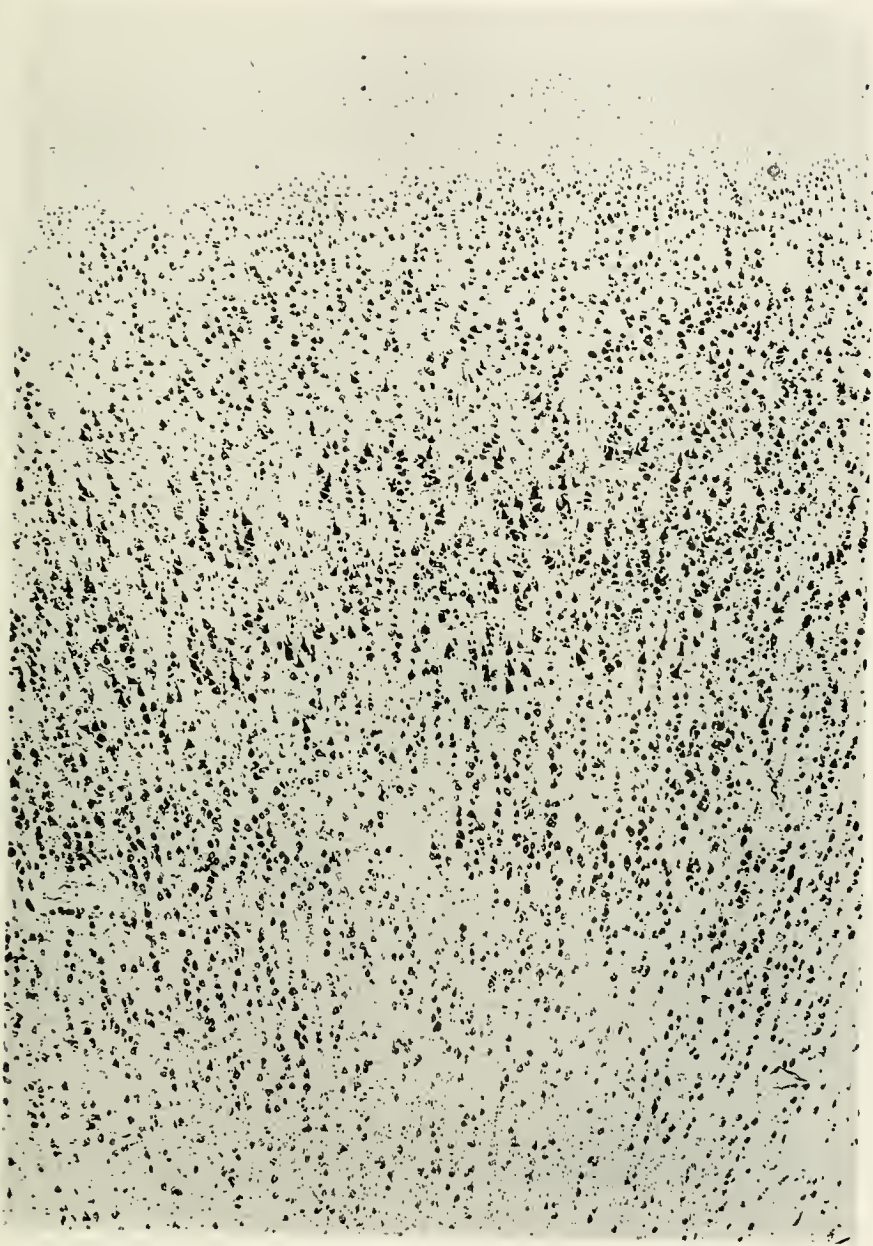
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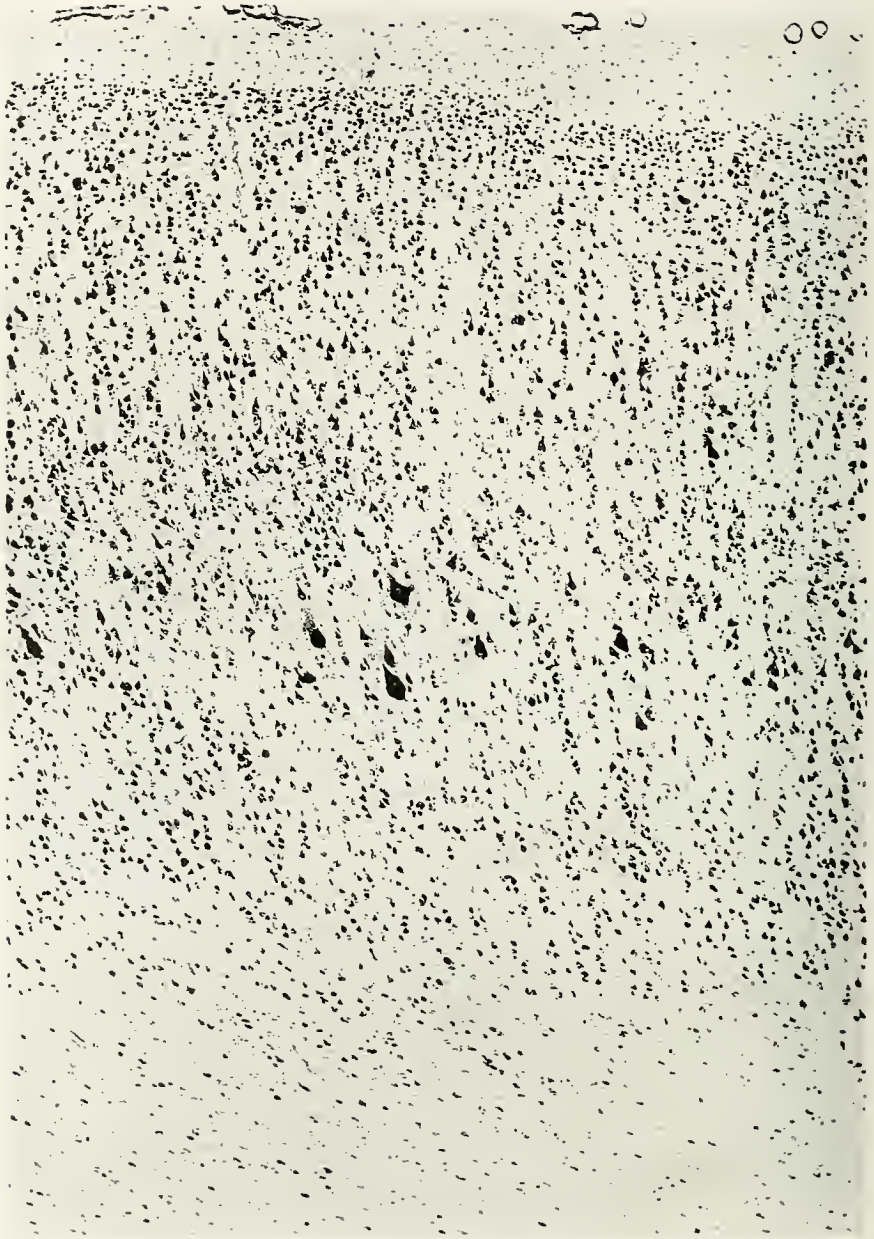
Plate VIII. *Isocortex agranularis* gigantopyramidalis praecentralis *IAGprc*.
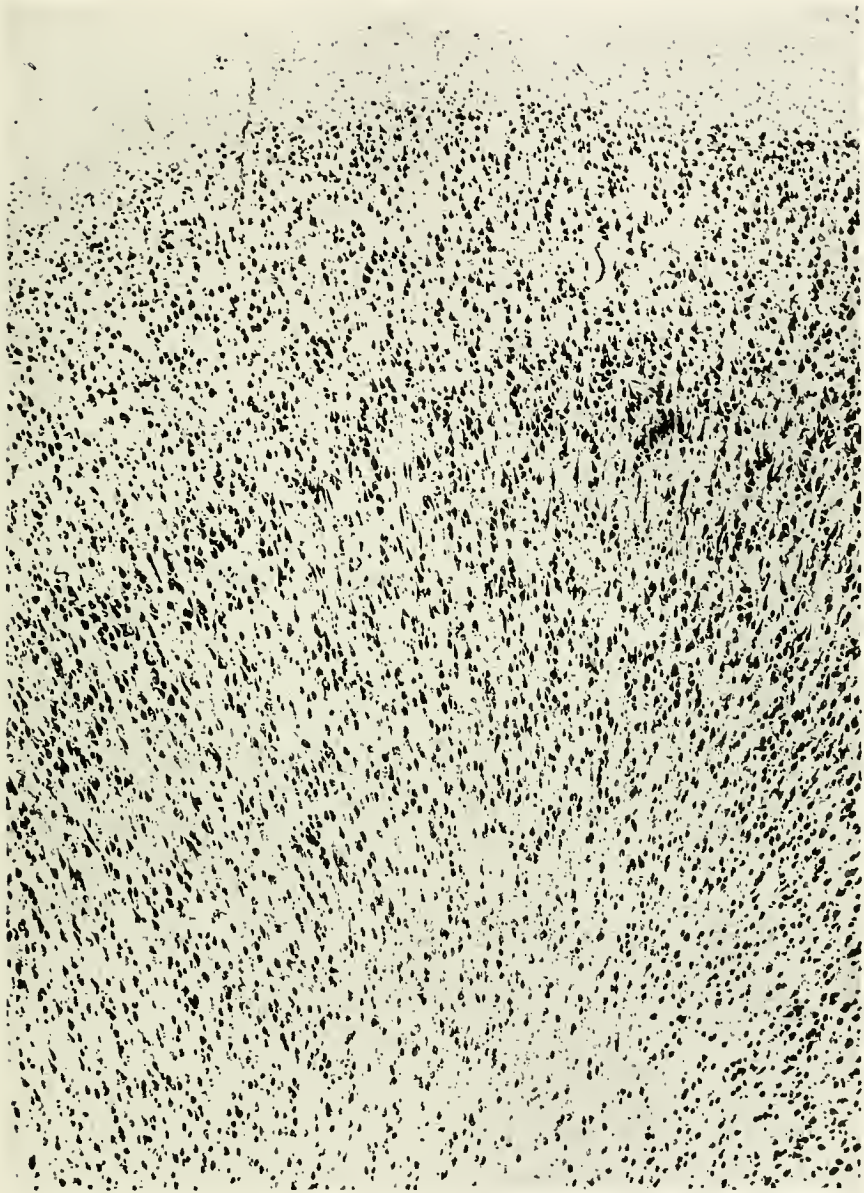
Plate IX. *Isocortex agranularis* juxtallocorticalis limbicus *IAJl*.
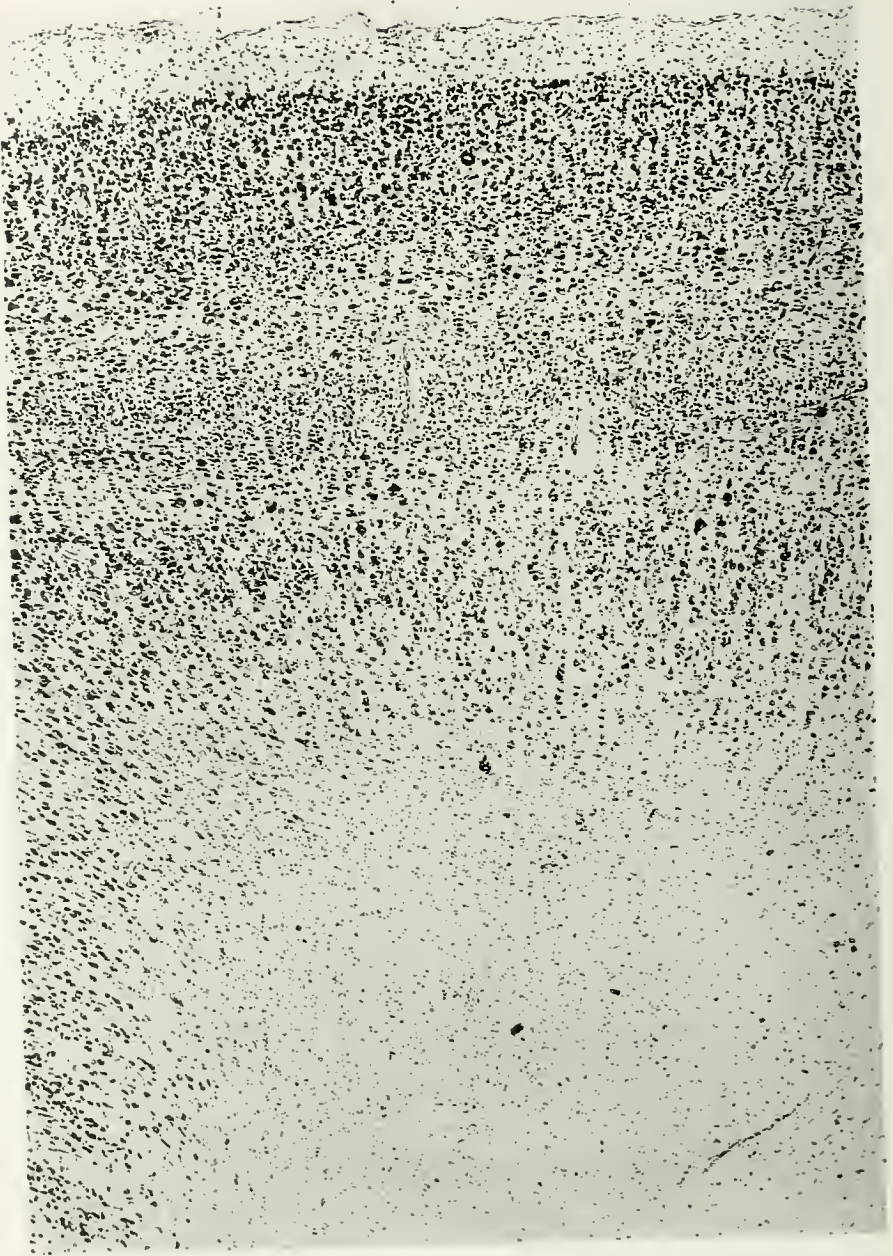
Plate X. *Isocortex koniosus striatus* occipitalis *IKSo*.
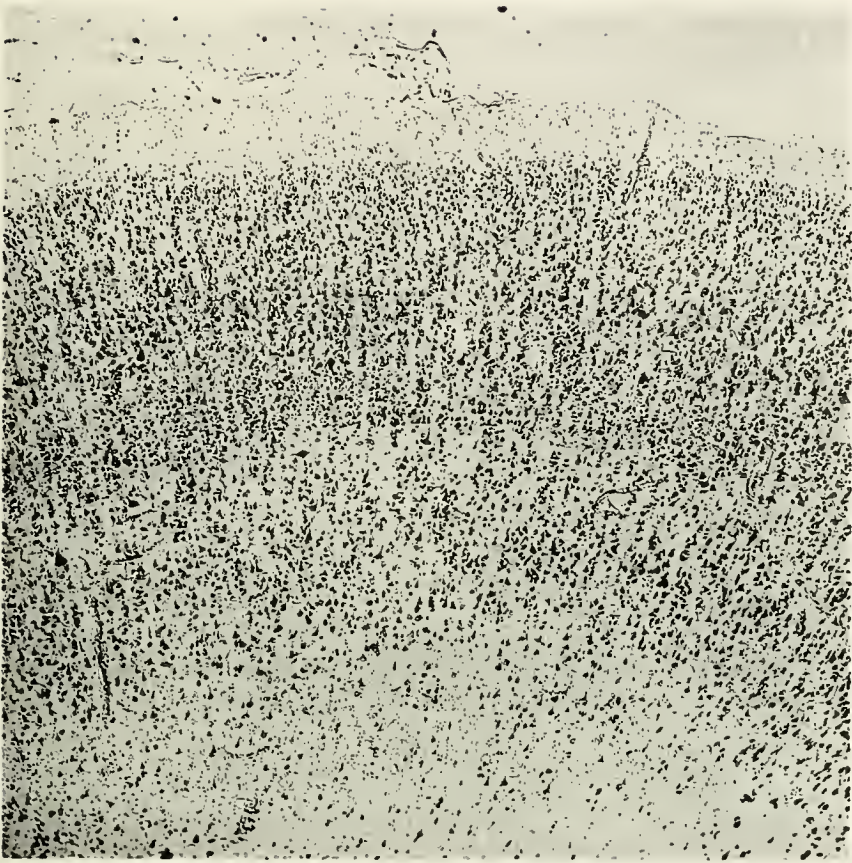
Plate XI. *Isocortex koniosus* postcentralis *IKpoc.*
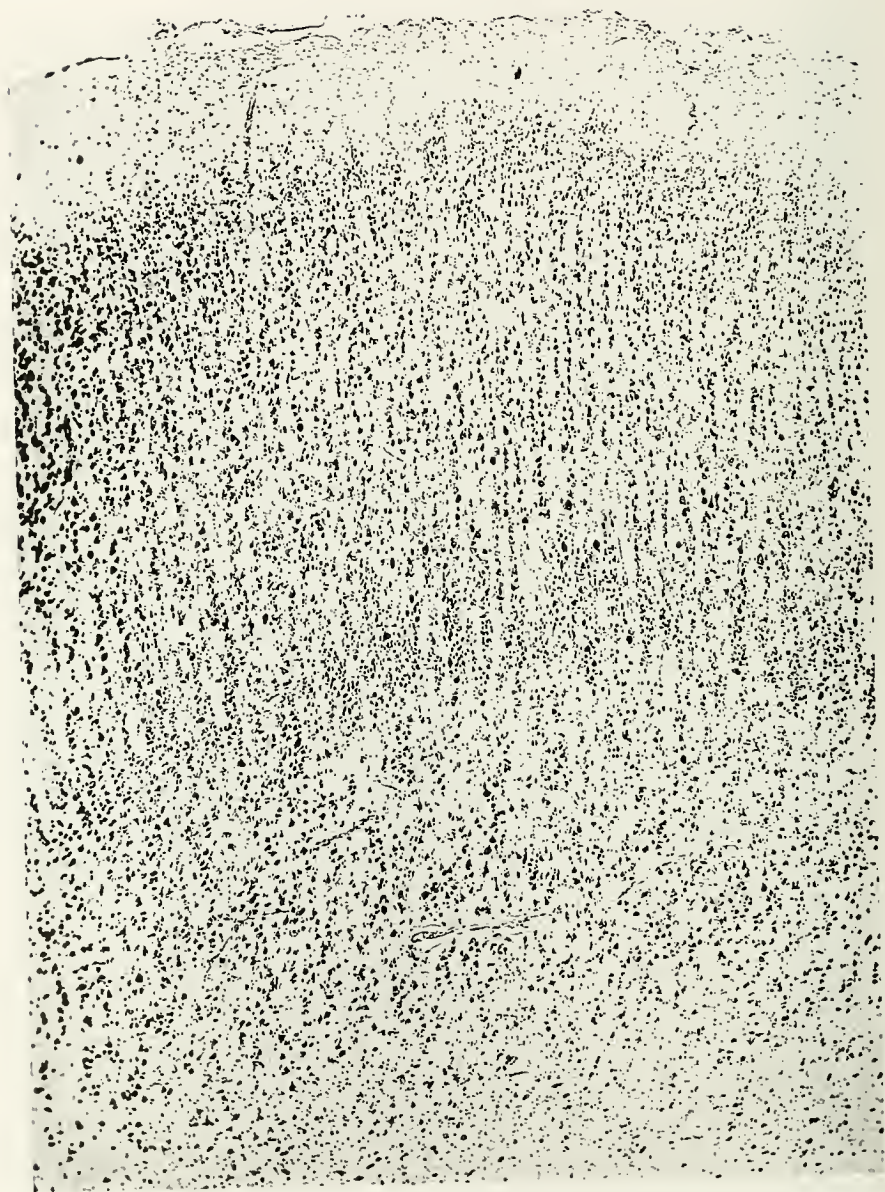
Plate XII. *Isocortex koniosus* supratemporalis *IKst.*
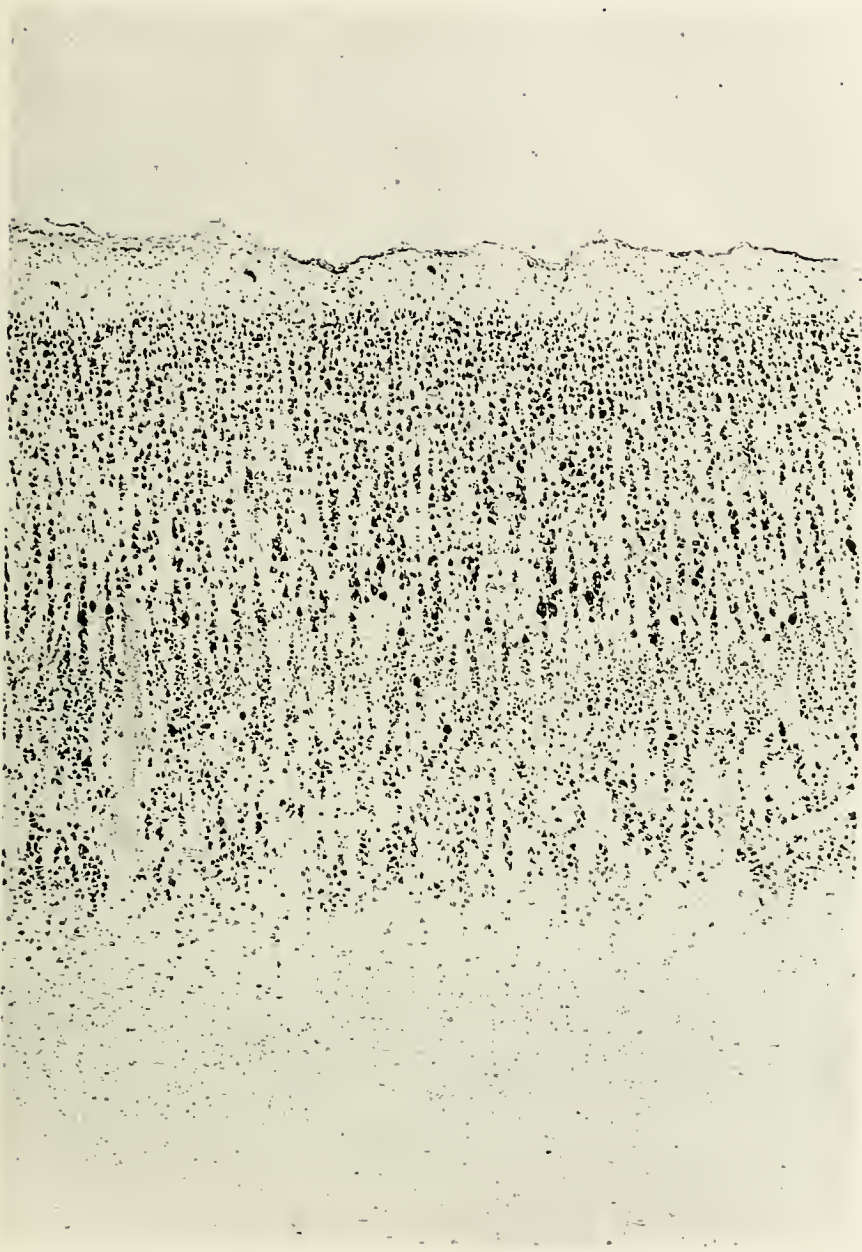
Plate XIII. *Isocortex parakoniocorticalis* occipitalis *IPo*.

Plate XIV. *Isocortex juxtallocorticalis* temporalis *IJt*.
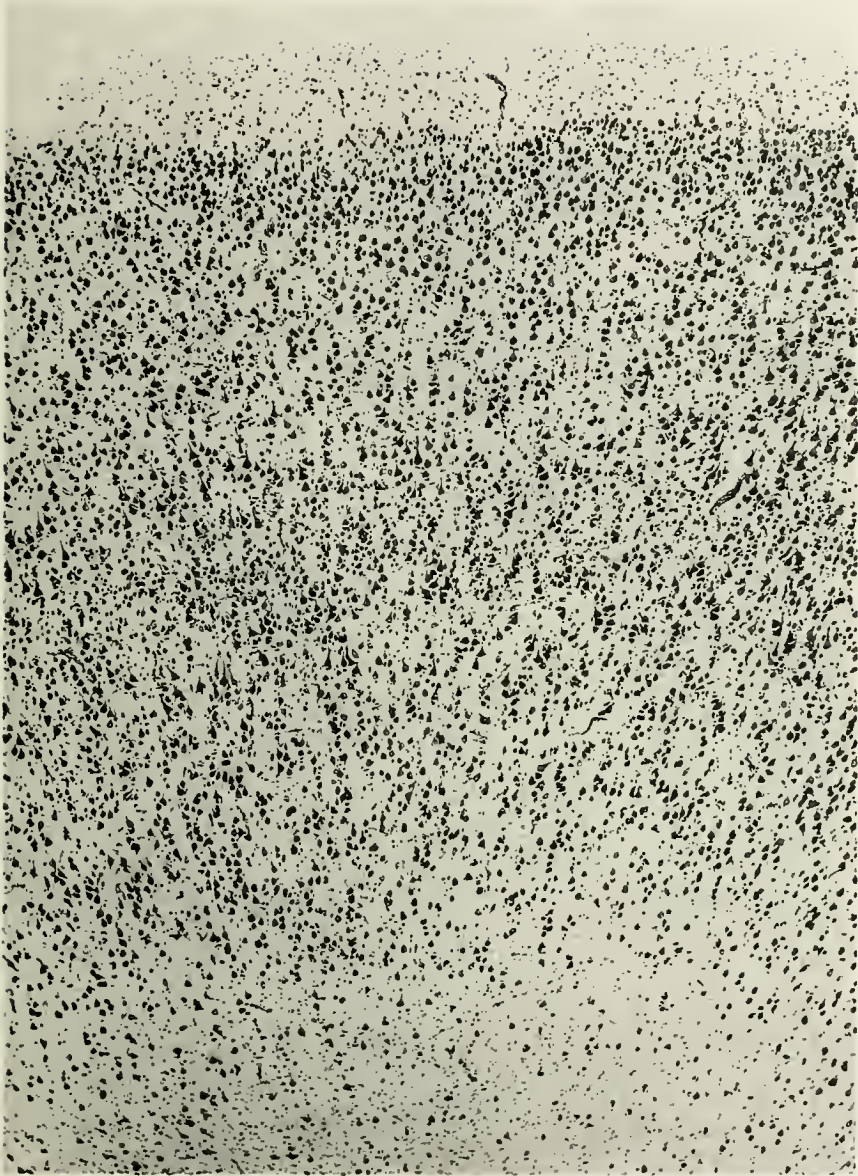
Plate XV. *Isocortex dysgranularis* frontalis *IDf*.

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