

A CYTOARCHITECTURAL INVESTIGATION INTO THE BOUNDARIES OF CORTICAL AREAS 13 AND 14 IN THE HUMAN BRAIN

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INTRODUCTION

Walker (1940) has described two new areas in the posterior orbital surface of the macaque brain: area 13 in the posterior orbital gyrus and area 14 in the gyrus rectus beneath and medial to the olfactory tract. Both areas were essentially agranular. No corresponding investigations have been reported in the human brain, nor did Walker fully discuss the relationship of his two new areas to previously described cortical subdivisions in man. Von Bonin (1944), however, tried to correlate almost agranular zones in the posterior orbital surface of the human brain, described by von Economo & Koskinas (1925), with an 'area orbitalis agranularis' homologous in all mammals so far investigated. As will become apparent, however, this correlation does not seem to cover entirely the more complex conditions which appear to obtain in man. In the light of these considerations, and since the neurophysiology of this region has lately aroused much interest, re-examination of its cytoarchitecture seemed to be a matter of some urgency.

Bailey & Sweet (1940) stimulated the gyrus orbitalis posterior in monkeys and cats causing inhibition of respiration, rise of blood pressure and decrease in the tonus of the gastric musculature. Ruch & Shenkin (1943) ablated area 13 in a series of monkeys producing a marked degree of hyperactivity. Fulton (1947) mentioned that experiments carried out jointly with Livingston confirmed the results of Ruch & Shenkin in monkeys as far as area 13 was concerned. Small bilateral lesions of area 13 in one chimpanzee, however, did not cause hypermotility, from which Fulton concluded that the region may be larger than in the monkey and in man may be larger still. Ward & McCulloch (1947) recorded neuronographic evidence of strong projections in monkeys from posterior and medial portions of the orbital surface (areas 10, 47, 53 in Bailey's terminology) to the paraventricular nucleus of the hypothalamus and from area 47 and posterior area 45 to the posterior hypothalamic area. More recently, Delgado & Livingston (1948) published their results obtained by electrical excitation on monkeys and dogs, which showed that the active region concerned with respiratory and blood pressure changes coincides with area 13 and that in some animals its limits are sharp. After bilateral ablation of area 13 their monkeys showed elevated temperatures in the hind limbs.

That this region in man seems to be concerned with similar functions, has been shown in a paper by Meyer & McLardy (1948), dealing with posterior cuts in pre-frontal leucotomy; nine of their cases, with bilateral involvement of the central third

of the posterior half of the orbital region (liable to include the region corresponding to area 13 in monkeys), developed post-operative disturbances, many of which seemed to have an autonomic basis.

Although the precise delineation of the agranular orbital cortex in man was the object of this study, it has been necessary, for the understanding of the correct boundaries, to include a cytoarchitectonic description of adjacent areas.

MATERIAL AND METHODS

The cytoarchitectonic investigation of the orbital surface was carried out on nine hemispheres taken from seven different cases. Case 1, a normal male aged 40, was fully investigated in serial sections through the whole length of the left orbital region. Case 2, a normal male aged 20, was investigated in serial sections through the posterior half of the left orbital region, and through a sample block from the anterior half. Cases 3-7 were examined in serial sections through sample blocks from three different levels, chosen within the anterior, middle and posterior thirds of the orbital surface. This material (cases 3-7) was taken from four patients in whom prefrontal leucotomy had been performed without damaging the orbital region or its projections, and from one patient with an old arteriosclerotic softening around the Sylvian fissure.

The material, which was obtained approximately 24 hr. after death, was fixed in 10 % formalin and subsequently embedded in celloidin. Serial sections (30μ) were cut, of which every twenty-fifth was stained by the Nissl method. In these comparatively thick sections all the peculiarities of each region were emphasized, without obscuring finer details. Some myelin-stained sections (Heidenhain's modification of Weigert's method) were also examined to exclude the presence of any small lesion not obvious in the Nissl preparations. No lesions were found.

Owing to the convolitional characteristics of the orbital region, i.e. arrangement of sulci and gyri more or less parallel to the medial and lateral surfaces (Text-fig. 1*b*), only coronal sections were used. In this way the desired 'ideal plane' at right angles to the sulci and cortical surface was obtained and distortion of the cortical pattern due to obliquity of section was avoided.

The criteria employed for differentiation of the various areas were chosen with the greatest care, in order to avoid the criticism brought forward by Lashley & Clark (1946). Only striking alterations in the laminar pattern were regarded as a basis for subdivision and the characteristics of each area, as described below, could be recognized throughout the nine hemispheres. Minor differences of cell size, cell shape, or width of cortex, which could be interpreted as individual differences were noted, but never by themselves taken as an indication of a distinct cortical field. The above applies mainly to the criteria employed for parcellation in the medio-lateral axis; antero-posteriorly the subdivision was based on the presence or absence of an internal granular layer, a criterion which is valid beyond doubt.

It proved extremely difficult to carry out parcellation by microscopical observation only. Therefore, in case 1 photomicrographs of every hundredth section of the gyrus rectus, of the orbital gyri and of the pars orbitalis of the inferior frontal gyrus were taken and were fixed to a board in their correct topographical position. In this way a reasonably representative sample of the microscopic structure of the entire

orbital surface could be viewed simultaneously; an invaluable help for parcellation. In addition, the surface outline of these sections was drawn by projection and the boundaries of the architectonic areas marked in under microscopic control. The chart (Text-fig. 1*a*), representing a reconstruction of the orbital surface of case 1, was based on these drawings. The level of each section has been shown by its corresponding serial number at the side of the chart; thus the exact location of photomicrographs (Pls. 1–3) can be easily determined. Where wide transitional zones between two areas occurred they have been indicated, using the symbols of both areas concerned simultaneously. The next charts (Text-fig. 2*a, b*) show the position of Brodmann's (1914, 1925) and von Economo & Koskinas' (1925) areas as they would appear, if projected on to the orbital surface of case 1. The thick lines in von Economo & Koskinas' chart indicate the location of their photographs.

Following Walker's example Brodmann's numerical nomenclature has been used as far as possible throughout the region investigated. It proved necessary, however, to introduce certain further terms: i.e. area recta anterior and posterior and area 47 anterior and posterior.* Reference to the most posterior extension of the orbital cortex—transition into insular and parolfactory regions—has been made in von Economo & Koskinas' terms *FJ* and *FL*, since, except for area 25, no terminology of Brodmann's is available. It seems likely that in future investigations von Economo & Koskinas' terminology will have to be introduced throughout as being more logical and more flexible.

RESULTS

The following areas have been recognized throughout the nine hemispheres; their position can be located from Text-fig. 1*a*.

Area recta anterior and area recta posterior (Text-fig. 1*a*)

Cytoarchitecture. Area recta anterior lies on the anterior half of gyrus rectus expanding laterally to cover the most medial part of the adjacent orbital gyrus. Anteriorly it terminates with the end of the olfactory sulcus; the subrostral sulcus forms its border on the medial surface.

Its main characteristics are: narrowness of the cortex as a whole; especially accentuated narrowness in layer III; cells of equal size throughout III; distinctly marked, though narrow internal granular layer and—in places—arrangement of the infragranular layers in vertical columns. None of the laminae is sufficiently well marked to give rise to horizontal striation (Pl. 1, fig. 1).

Area recta posterior covers the posterior half of gyrus rectus, and extends laterally into the most medial part of the adjacent orbital gyrus. Anteriorly it is bordered by area recta anterior, posteriorly it gradually merges into the parolfactory area of Broca (*FL* of von Economo & Koskinas). The sulcus subrostralis forms its boundary on the medial surface.

Area recta posterior may best be described as an agranular subdivision of area recta anterior, for it retains all its other characteristics (Pl. 1, fig. 2). The change from granular to agranular cortex is not a sudden one, but takes place over a fairly

* Brodmann already suggested a possible further subdivision of his area 11 into a medial area recta and a lateral area orbitalis interna on the strength of different cytoarchitecture. But he never actually executed this suggestion by drawing these areas separately on his chart.

extensive transitional zone in which the internal granular layer becomes gradually narrower, less dense and more intermingled with large cells from layers III and V. No difference in cortical structure could be noted between the crown of gyrus rectus and the walls of the olfactory sulcus.

Discussion. The position and structure of area recta anterior and area recta posterior—as described in this paper—seem to be identical with von Economo & Koskinas' description of their areas *FG* (their plate XXXV) and the orbital portion of *FH*, respectively.

Brodmann's* area 11 includes in its most medial portion the site of our areas recta anterior and posterior. Its architecture, however, described as being uniform for the entire area, resembles only the structure in our transitional zone, between areas recta anterior and posterior.

A cytoarchitectonic parcellation of gyrus rectus was undertaken by Ngowyang (1932), who confirms on the whole Vogt's (1910) myeloarchitectonic subdivisions. Ngowyang distinguishes between anterior granular and posterior dysgranular portions, the former being roughly identical with area recta anterior of the present writer. Only a small area in the depths of the olfactory sulcus is described as quite agranular but is assigned to the parolfactory region.

Walker, in the macaque, did not describe any area comparable to our area recta anterior. His area 14, however, occupies a position apparently similar to our area recta posterior; but the description and illustration of its architecture—taken from the walls of the olfactory sulcus—show it to be much more akin to the parolfactory cortex (*FL*) in man, although the latter is restricted to about the posterior tenth of gyrus rectus. It therefore seems probable that his area 14 is not homologous with our area recta posterior, a view which finds further support from von Bonin & Bailey (1947) who, adopting von Economo's terminology for their map of *Macaca mulatta*, assign the entire area equivalent to Walker's 14 to parolfactory *FL*.†

Areas 11 and 13 (Text-fig. 1a)

Cytoarchitecture. Area 11 represents the cortex of the anterior two-thirds of the medial orbital gyrus, forming the lateral boundary of area recta anterior. It curves round the anterior end of the olfactory sulcus, extending slightly on to the medial aspect of the hemisphere. Laterally it encroaches upon the middle orbital gyrus.

Its cytoarchitecture is similar to area recta anterior, the main differences being: gradual medio-lateral increase in total width, evenly distributed throughout the layers; a denser layer III with larger cells in its depths, which permit its subdivision into *IIIa* and *IIIb*; a more pronounced layer *Va* and layer *VIa* with lighter layer *Vb*,

* As the data on which Brodmann (1908, 1910, 1912, 1914 and 1925) based his cytoarchitectonic map of the human brain have never been published, Rose's (1935) detailed histological descriptions and photographs of Brodmann's areas have been used for the assessment of the architectonic characteristics.

† As far as can be seen from the literature no autonomic responses have so far been obtained from Walker's area 14 in animals. On the other hand, Fulton (1947) describes a human case in whom during the course of an operation for a pituitary tumour the most posterior portion of, what appears to be from his description, gyrus rectus was accidentally fixed bilaterally with Zenker's fluid. (This region would most likely include parolfactory as well as cortex from the posterior part of our area recta posterior.) The patient developed a condition similar to sham-rage in animals.

giving rise to distinct horizontal striation; and no columnar arrangement of the infragranular layers (Pl. 2, fig. 1).

Area 13 covers the posterior third of the medial orbital gyrus, or the posterior fifth only, if the transitional zone be excluded. Anteriorly it is bordered by area 11, posteriorly by von Economo & Koskinas' area 'fronto-insularis' (*FFJ*) in the gyrus transversus insulae.

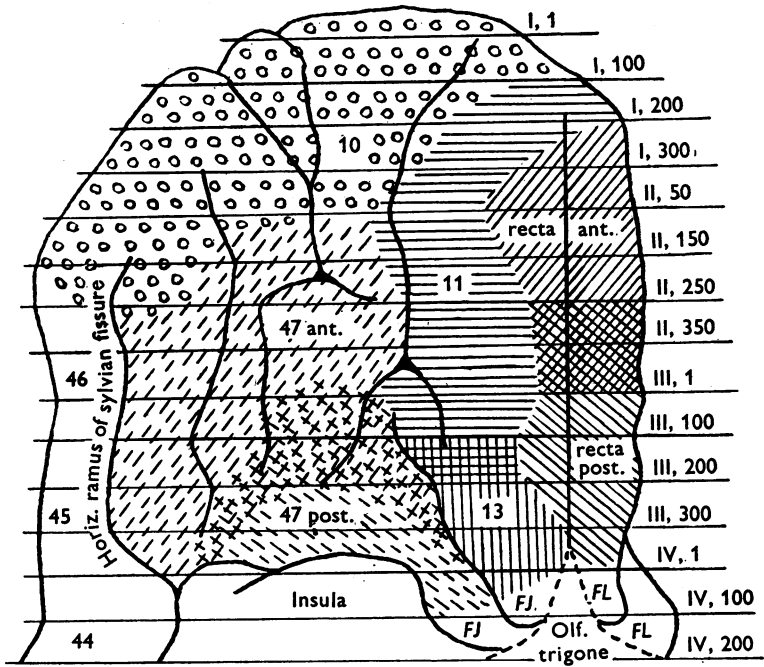
Just as I regard area recta posterior as an agranular subdivision of area recta anterior, so area 13 can be termed an agranular subdivision of area 11. It retains all the main characteristics of area 11, including a very marked layer *Va* with especially large cells towards the posterior end and a well-developed layer *VIa* (Pl. 2, fig. 2). The latter two features give rise to distinct horizontal striation, which also constitutes the main difference from area recta posterior. The transition from granular to agranular cortex is gradual, but extends only over 100 sections as compared with 200 on gyrus rectus.

Discussion. Neither Brodmann nor von Economo & Koskinas describe any area which is topographically or structurally identical with areas 11 and 13, as just defined. Topographically these areas fall within the lateral portion of Brodmann's area 11—i.e. his suggested area 'orbitalis interna'—for which, however, neither a separate structural description was given nor a further possible subdivision into granular and agranular parts considered.* With regard to von Economo & Koskinas' chart our areas 11 and 13 fall within the medial portion of their area *FF*. No part, however, of *FF* is described as similar to our 11 and 13, on the contrary representative photographs of the anterior granular and posterior agranular subdivisions (*FFg* and *FFa*), both taken from lateral portions, are identical in every detail with those of our areas 47 anterior and posterior, to be described later (Pl. 3, figs. 1 and 2). A comparison, however, of Pl. 2, figs. 1 and 2 with Pl. 3, figs. 1 and 2 will show the striking difference between our areas 11 and 13 on the one hand, and our 47 anterior and posterior on the other. Separation of areas 11 and 13 from the field *FF* seems therefore appropriate, and finds further support from Vogt's (1910) and Strasburger's (1937) description of the myeloarchitecture of this region; i.e. 'unistriär' corresponding to our areas 11 and 13, but 'bistriär' and 'unitostriär' to our areas 47 anterior and posterior, respectively.

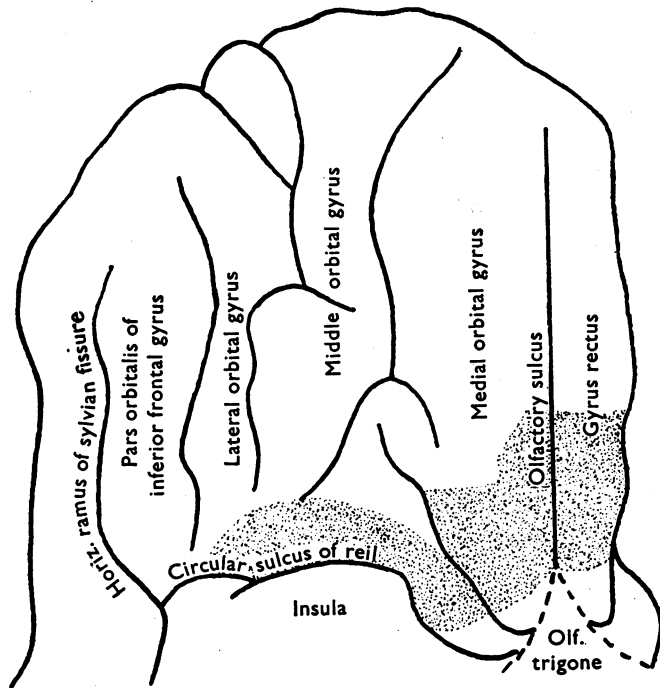
Walker's description and photographs of his areas 11 and 13 in the macaque show them to be homologous in topography and structure to those described in man in this paper. There exists only the difference in expanse, transition from areas 11 to 13 in the macaque occurring between the anterior and posterior half of the orbital gyrus, whilst in man it takes place between the middle and posterior third of the (medial) orbital gyrus. Thus area 13 in man is far more restricted.

In their charts of the macaque von Bonin (1944) and von Bonin & Bailey (1947) homologize Walker's area 13 with their areas 47 and *FF* respectively. It is not my intention to go into the often very contradictory evidence of homologies; in man, however, it must be stressed that investigation seems to show more complicated conditions, area 13 being by no means identical with area 47, even in the latter's most posterior agranular portion.

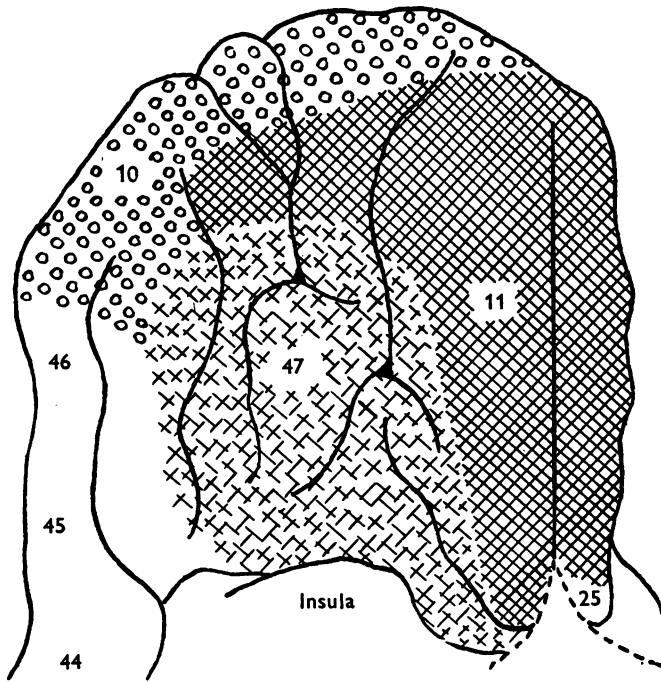
* Brodmann's original term 'area 11' has none the less been retained in this study on account of its customary usage in man and its homology to Walker's area 11 in the macaque.



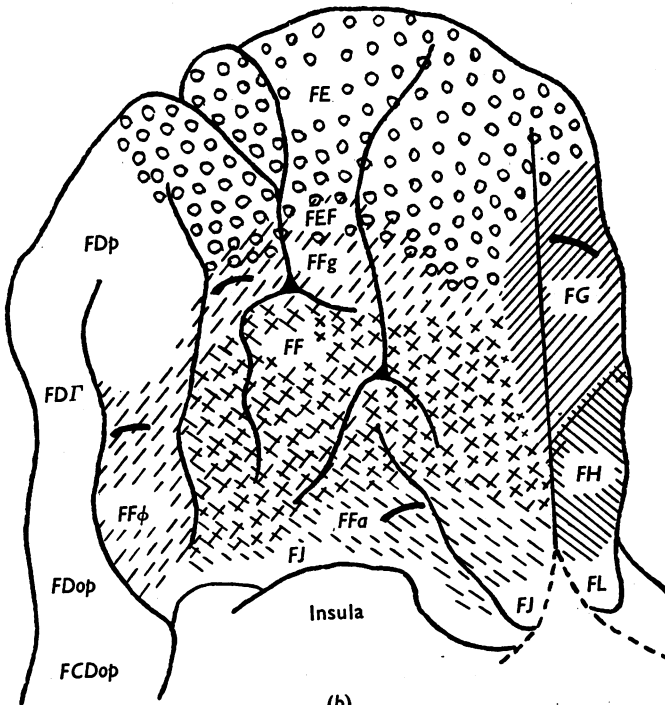
Text-fig. 1a. Parcellation of the orbital cortex in case 1, left; temporal pole removed. Reconstruction from diagrams of every hundredth section at a magnification of two (allowing 6 mm. for hundred sections of 30μ thickness). The curvature of the brain has been flattened out.



Text-fig. 1b. Diagram indicating the total amount of agranular orbital cortex (stippled area), and the terminology used for gyri and sulci.



(a)



(b)

Text-fig. 2. Brodmann's (a) and von Economo & Koskinas' (b) areas projected upon the orbital surface of case 1. The markings have been adapted to those of case 1, i.e. equal markings signify identically described cytoarchitecture.

Areas 47 anterior and posterior (Text-fig. 1a)

Cytoarchitecture. Area 47 anterior lies on the orbital portion of the inferior frontal convolution and extends medially to cover the lateral and middle orbital gyri. Anteriorly it is limited by the polar cortex (area 10); posteriorly by its agranular subdivision, area 47 posterior. The horizontal ramus of the Sylvian fissure provides its approximate lateral boundary, the medial orbital sulcus its medial one.

Area 47 anterior is differentiated from area 11, which it borders laterally, by a considerable increase in width and density of the cortex, especially marked in layers IV and VIa, the latter being far denser than in any of the previously described areas. The fifth layer also becomes wider but very light and cell-poor, especially Vb. This produces a very pronounced horizontal striation. There is also a tendency to arrangement of the cells in vertical columns (Pl. 3, fig. 1).

Area 47 posterior is a small zone which lies in the most posterior end of the lateral and middle orbital gyri. Anteriorly it is bordered by area 47 anterior, posteriorly by the anterior portion of the circular sulcus of Reil and von Economo & Koskinas' area fronto-insularis (FJ).

Area 47 posterior can best be regarded as an agranular subdivision of area 47 anterior whose main characteristics, i.e. emptiness of layer V and dense, well-developed layer VIa, are preserved. Horizontal striation, however, becomes indistinct owing to the lack of an internal granular layer; the arrangement in vertical columns becomes less marked; and the transition from fifth to sixth layer is in places difficult to assess (Pl. 3, fig. 2). In addition, the cortex becomes less dense and the individual cells larger as one progresses posteriorly. The increase in cell size applies mainly to layer Va, where indeed very large cells can be seen occasionally, nowhere, however, giving rise to distinct striation. This latter feature constitutes one of the main differences from area 13, which forms its medial boundary. The division of area 47 into granular and agranular cortex is less distinct than in previously described regions, the transitional zone—in some cases—being a much wider one, thus confining the completely agranular cortex to a narrow posterior strip in the lateral and middle orbital gyri. The cortex of the orbital portion of the inferior frontal convolution remains granular throughout its antero-posterior length.

Discussion. There seems to exist considerable confusion in the literature with regard to the topography and structure of area 47, which may be attributable to its apparently great variability. Brodmann's area 47—forming part of the 'infrafrontal region' in his revised terminology—occupies a similar topographical position to our areas 47 anterior and posterior, but does not reach the horizontal ramus of the Sylvian fissure at any point (the granular cortex of this region being assigned to his areas 45 and 46). The description of its architecture, however, with a feebly developed internal granular layer and wide infragranular layers renders it akin only to our transitional zone between areas 47 anterior and posterior.

Von Economo & Koskinas would include the site of our areas 47 anterior and posterior in the lateral two-thirds of their area FF, giving, in contradistinction to Brodmann, the horizontal ramus of the Sylvian fissure as its lateral boundary. They stress the fact that this region has no uniform character and that it is therefore impossible to give a description of its architecture equally applicable to every part.

They mention and illustrate besides an anterior granular portion, *FFg*, a posterior agranular *FFa* and a lateral granular *FFφ*. Apart from these they seem to have encountered considerable individual differences, *FF* showing in extreme cases a wide, dense internal granular layer throughout. Their representative photographs of *FFg* and *FFa*, both taken from lateral portions (their plates xxxii and xxxiii), are, as already mentioned, in every detail identical with those of our areas 47 anterior and posterior, respectively. A region corresponding in structure to *FFφ* could also be clearly seen in the present material.

Kreht (1936*a*) studied the cytoarchitecture of the region equivalent to our areas 47 anterior and posterior, using Vogt's (1910) terminology. His results with regard to anterior 'granularity' and posterior 'dysgranularity' are essentially in accordance with the findings in this study.

Walker, in the macaque, describes no area 47, nor any area homologous to our areas 47 anterior and posterior. The orbital portion of his area 12, which occupies a similar position to our area 47, displays a very different cytoarchitecture, and his area 13 has been shown in the present investigation to be homologous to area 13 in man.

Von Bonin (1944) emphasizes the presence of a homologous area 47 ('orbitalis agranularis'), in all mammals so far investigated (including man), and identifies it with Walker's area 13 in the macaque. In his joint publication with Bailey (1947) he terms it *FF* and gives a description of its architecture very similar indeed to that of Walker's 13. In his publication on Galago (1945), however, he describes area 47 as displaying a light fifth and a dense sixth layer, indicating a certain structural relationship to our area 47 posterior. The question of homology must therefore remain open.

Some difficulties were encountered in delimiting area 47 anterior from area 10. For this reason no transitional zone has been drawn in on the chart (Text-fig. 1*a*) and the boundary given should be regarded only as a rough indication.

Individual differences

The fact that the main characteristics of each region could be recognized in all nine hemispheres by no means excludes the presence of distinct individual differences. Width of cortex, cell size, structure and density and above all granularity varied greatly from case to case. It therefore seems possible that the discrepancies between the various findings of different observers may be largely due to their considering such individual differences too much as a basis for parcellation, as indeed has been pointed out by Lashley & Clark (1946). Whether individual differences also exist with regard to the extent of granular and agranular orbital cortex in antero-posterior direction, or with regard to the size of the architectonic areas as a whole—such as Kreht (1936*b*) actually demonstrated for the 'wider area of Broca'—cannot be established from the present material. This question will have to be investigated later in serial sections throughout the length of the orbital surface in a large number of brains.

CONCLUSIONS AND SUMMARY

The most striking fact brought out by this study is that in all the cases a granular area recta anterior and area 11 could be subdivided from an agranular area recta posterior and area 13. The difference between a granular and an agranular area 47 was not so distinct, because in some cases the transitional zone was wide and complete agranularity was reached only in the most posterior levels. The cortex on the orbital portion of the inferior frontal gyrus was granular throughout its entire length in all cases.

The new terms, area recta anterior and posterior and area 47 anterior and posterior, have been introduced to signify the division into granular and agranular cortex.

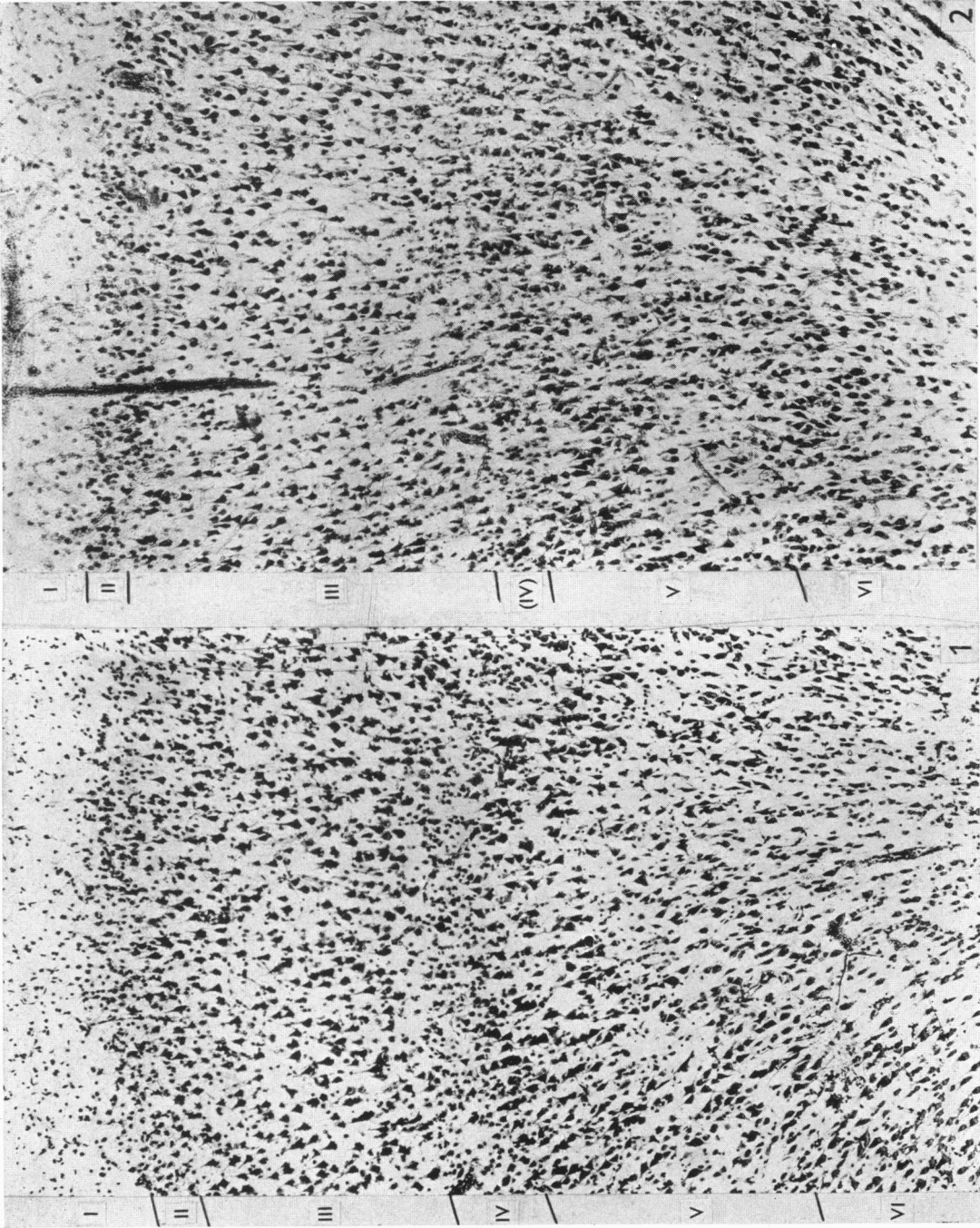
Homology of Walker's area 13 in the macaque to area 13 in man could be established, while homology of his area 14 in the macaque to area recta posterior in man seemed extremely doubtful. A different terminology, i.e. area recta posterior, was therefore chosen for the latter.

As compared with Walker's (1940) findings in the macaque the agranular portion of the orbital cortex in man seems to be proportionately much smaller. It is difficult to say where the exact anterior boundary should be drawn, as all these areas show a comparatively wide transitional zone with gradually decreasing internal granular layer in antero-posterior direction. This problem, however, might be solved if a more accurate functional boundary were determined. Meanwhile, it is interesting to note that this region belongs to the agranular type of cortex and is therefore more akin to premotor (area 6) than to prefrontal cortex.

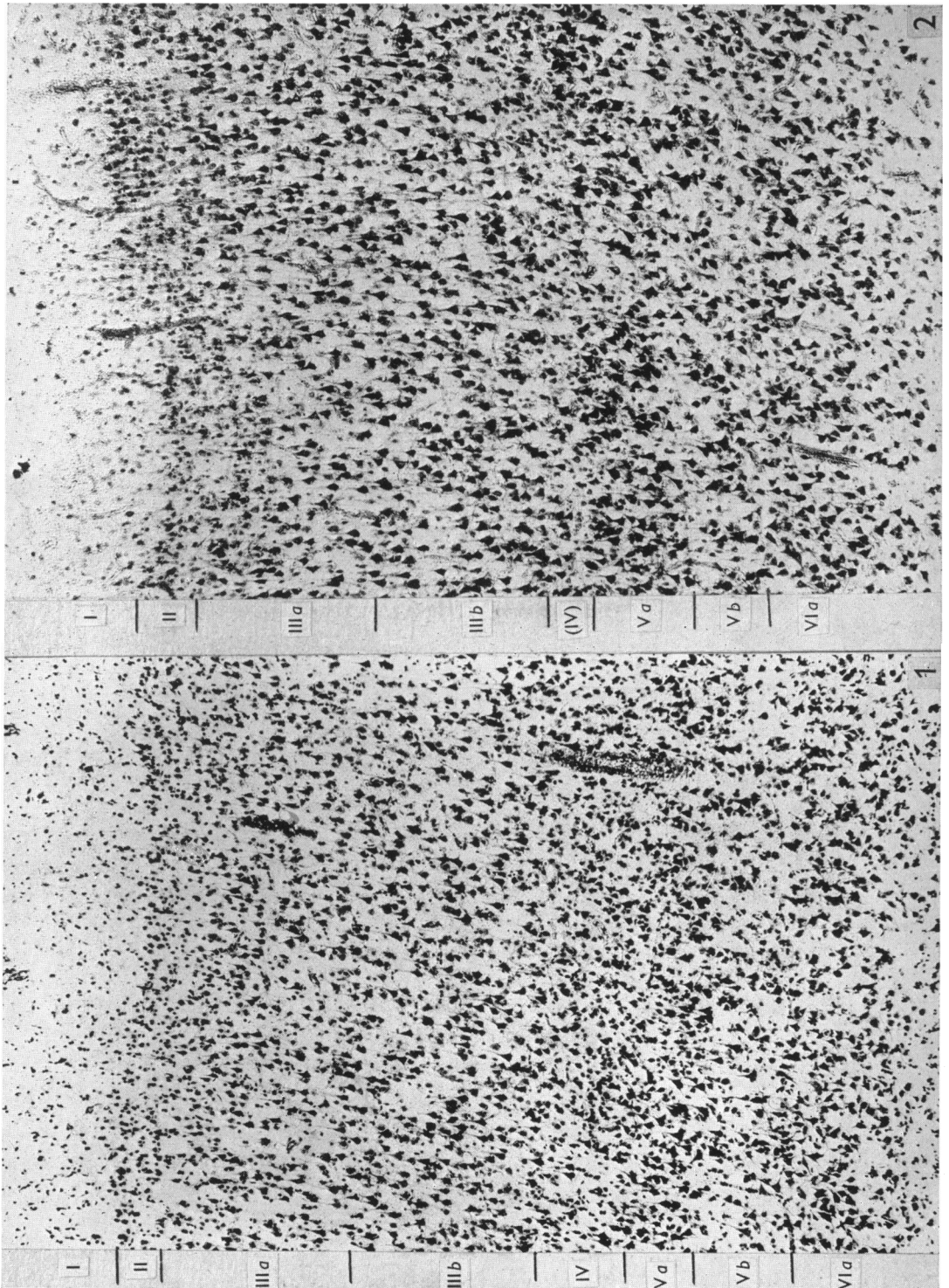
I wish to express my gratitude to Dr A. Meyer, at whose instigation this study was undertaken, for his criticism throughout.

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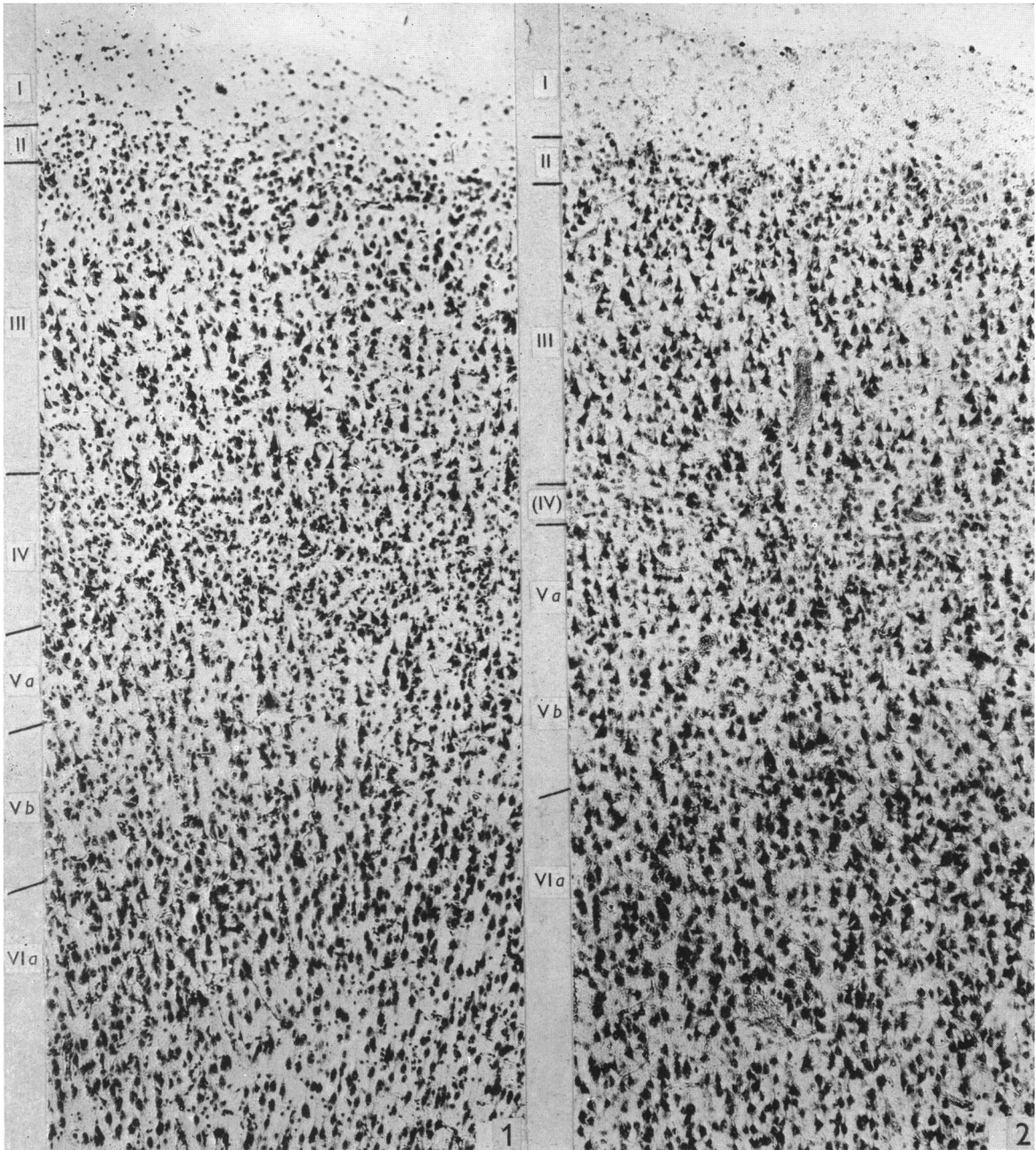
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EXPLANATION OF PLATES

All the photomicrographs are taken from Nissl preparations at a magnification of $\times 85$. The '(IV)' in Pls. 1, 2 and 3, fig. 2, which illustrate agranular cortex, indicates the position of the outer stripe of Baillarger as seen in myelin-stained sections.

PLATE 1

- Fig. 1. Case 1, left. Bl. II, 150. Photomicrograph of area recta anterior, on the crown of gyrius rectus.
- Fig. 2. Case 1, left. Bl. III, 200. Photomicrograph of area recta posterior, on the crown of gyrius rectus.

PLATE 2

- Fig. 1. Case 1, left. Bl. II, 150. Photomicrograph of area 11, in the centre of the medial orbital gyrius.
- Fig. 2. Case 1, left. Bl. III, 275. Photomicrograph of area 13, in the centre of the medial orbital gyrius.

PLATE 3

- Fig. 1. Case 1, left. Bl. II, 150. Photomicrograph of area 47 anterior, on the crown of the lateral orbital gyrius.
- Fig. 2. Case 1, left. Bl. III, 275. Photomicrograph of area 47 posterior, in the centre of the middle orbital gyrius.