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Observations on some cortical areas of the Lesser Bush Baby (*Galago senegalensis senegalensis*)

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The cytoarchitecture of the brain of Strepsirhine primates has been the subject of several investigations. Brodmann (1908) studied the structure of the cerebral cortex of *Lemur macaco*, *Perodicticus potto*, *Propithecus coronatus* and *Nycticebus tardigradus* and Mott & Kelley (1908) have recorded their observations on the brains of *Lemur brunneus*, *L. mongoz* and *L. catta*. Le Gros Clark (1931) mapped out, in detail, the different areas of the cerebral cortex of *Microcebus murinus* and Bonin (1945) gave an extensive account of the cortex of *Galago demidovii*. By using electrophysiological methods, Mott & Halliburton (1908) localized the motor cortex of *Lemur macaco* and *L. catta* and Zuckerman & Fulton (1941) that of *Galago demidovii* and *Perodicticus potto*. No histological investigations have been made on the cortex of *Galago senegalensis senegalensis* except for a brief reference by Kanagasuntheram (1963). In the present paper an attempt is made to define some of the areas of the neocortex of this primate by the cytoarchitectural method and to correlate these findings with the functional subdivisions of the cortex obtained by electrophysiological studies.

MATERIALS AND METHODS

Three full brains and two hemispheres obtained from five adult specimens of *Galago senegalensis senegalensis* were examined. All brains, with the exception of one hemisphere which was fixed by immersion, were perfused with 10% formol saline after Nembutal anaesthesia. One full brain and a hemisphere were dehydrated and embedded in paraffin and serially sectioned at 15 μ thickness. Alternate sections of the full brain were stained by the Bodian technique for nerve fibres while the others were stained with cresyl violet. The sections from the hemisphere were stained variously with methylene blue, toluidine blue and gallocyanin. Ninety sections from this hemisphere were selected at approximately equal intervals, projected through an Edinger apparatus and drawn on sheets of paper at a magnification of 23 times. The various areas of the cortex were then demarcated and subsequently plotted proportionately on the figures.

Of the remaining material, two full brains and another hemisphere were all embedded in celloidin and serially sectioned at 25 μ thickness and stained with thionin or cresyl violet. One full brain was cut in the coronal and the other in the horizontal (transverse) plane, while the remaining hemisphere was sectioned in the sagittal plane. The various areas were then plotted on plastically reconstructed models of two hemispheres, one from each of the two full and brains the third from the

hemisphere which was sectioned in the sagittal plane. Thus three hemispheres cut in different planes were plastically reconstructed and the various areas were mapped out on the models using a 'Visopan' to identify the extent of any particular area of the cortex. The results thus obtained were compared with the graphically reconstructed figures. Except for minor differences which may be due to individual variations, modes of reconstruction or to differences in the plane of sectioning, the areas of the cortex showed a fairly consistent pattern. The general pattern obtained is shown in Fig. 1.

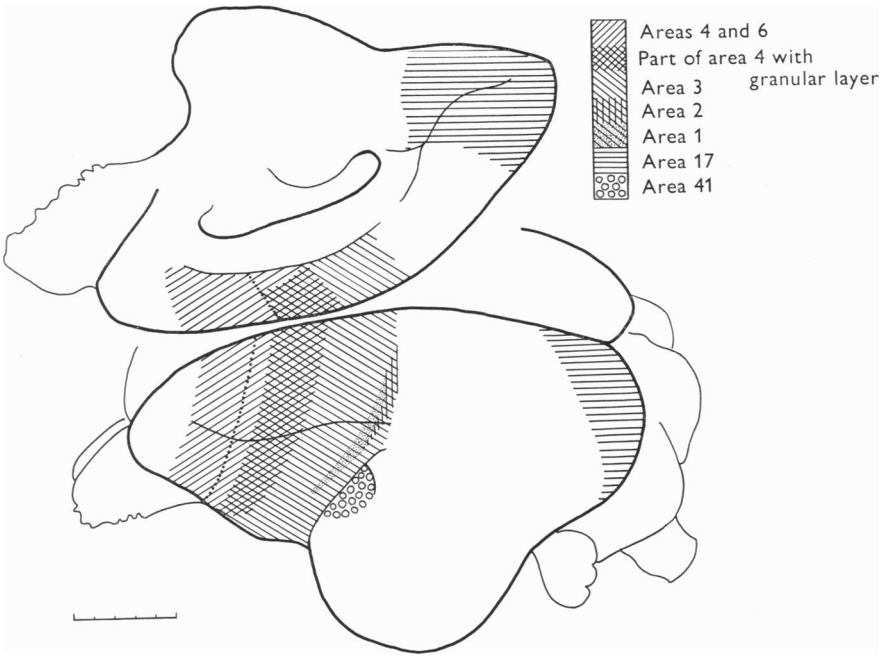

Fig. 1. An outline drawing of the brain (dorso-lateral and medial surfaces) showing the extent of the various cortical areas. Dotted line indicates the boundary between area 4 and area 6. Continuous line represents the groove running across areas 4, 6, 3, 1 and 2 on the lateral surface of the hemisphere. Scale is in mm.

In demarcating the various cortical areas we have taken into account the definition of a cortical field and its architectonic border given by Rose (1949) as well as by Powell & Mountcastle (1959*a*). These authors have observed that a cortical field is generally not morphologically uniform but presents consistent structural changes. Moreover, systematic variations which are said to occur within a field have been termed 'gradients' by Rose & Woolsey (1948) and Sanides (1964*a*, *b*). The latter author maintains that variations within a given cortical field occur abruptly or in steps, whereas the present observations tend to favour the view of Powell & Mountcastle (1959*a*) that changes within a cortical field or between different cortical areas are usually gradual. Therefore sharp lines are avoided in demarcating the borders of the different cortical areas. Moreover, the conventional subdivision of the cortex into six different laminae (Brodmann, 1908; Economo, 1929) was adopted

wherever possible. For the sake of convenience, the term *Galago* will hereafter be used to denote *Galago senegalensis senegalensis*.

In addition to the Nissl- and silver-stained sections, the present investigation also includes Golgi–Cox preparations of two hemispheres of an adult *Galago*. Our preparations are a modification of the method described by Sholl (1953) and, since they have the additional advantage of preserving the stain over a period of about 1 year without showing any signs of fading, it is proposed to describe the method briefly.

1. Fix parts of the brain at room temperature (25–28 °C) for 5–8 days in a volume of Golgi–Cox solution (Sholl, 1953) 10–15 times that of the material.

2. Wash and dehydrate for 16–24 h in two changes of equal parts of acetone and ethanol at 37 °C. Shorter times may be sufficient for small pieces like rat cerebrum cut coronally into two pieces.

3. Transfer to equal parts of ether and ethanol; embed in celloidin; cut and collect sections in 70 % ethanol.

4. Rinse the sections in two changes of distilled water.

5. Stain for 5 min in ammoniacal silver carbonate solution (Kubie & Davidson, 1928) diluted one part with two parts of distilled water and chilled to 0 °C before use.

6. Differentiate in 1 % sodium thiosulphate (A.R.) solution at 0 °C.

7. Wash for about 15 min in several changes of distilled water.

8. Intensify in 10 % formalin (A.R.) to which 0·5 ml of 5 % oxalic acid (A.R.) is added for every 100 ml of formalin. This step may be omitted.

9. Wash for about $\frac{1}{2}$ h in several changes of distilled water.

10. Counterstain with cresyl violet (G. T. Gurr), if desired.

11. Mount cover-slip with dammar xylol.

All glassware must be chemically clean; microtome knife must be grease free.

This modified Golgi–Cox method used in this investigation saves a lot of time and prevents formation of deposits and staining of blood vessels. It also renders cover-glassed preparations permanent.

Electro-physiological experiments were conducted on twelve adult specimens of *Galago* under Nembutal anaesthesia. The extent of the motor area was identified (Fig. 2) by marking out those portions of the cortex from which motor responses were elicited when the cortex was excited with a 60 cyc a.c. stimulator from which stimulus values could be read directly in milliamperes. Most stimulations were 2 s in duration and varied in intensity from 0·15 mA to 0·5 mA. Altogether four animals were used to localize the functional organizations within the motor cortex. The extent of the somatic sensory areas was explored by studying the evoked potential in six animals using a Tectronix amplification system and cathode ray oscilloscope. The stimulus was provided by hair movement or skin contact produced by a solenoid-driven brush. A steel electrode 300 μ in diameter was applied to the cortical surface with the aid of a vernier electrode carrier which permitted the plotting of the cortex in millimeter steps along rectangular co-ordinates. The auditory area of the cortex was defined by a similar technique but by substituting sound for touch as the stimulus (Fig. 3).

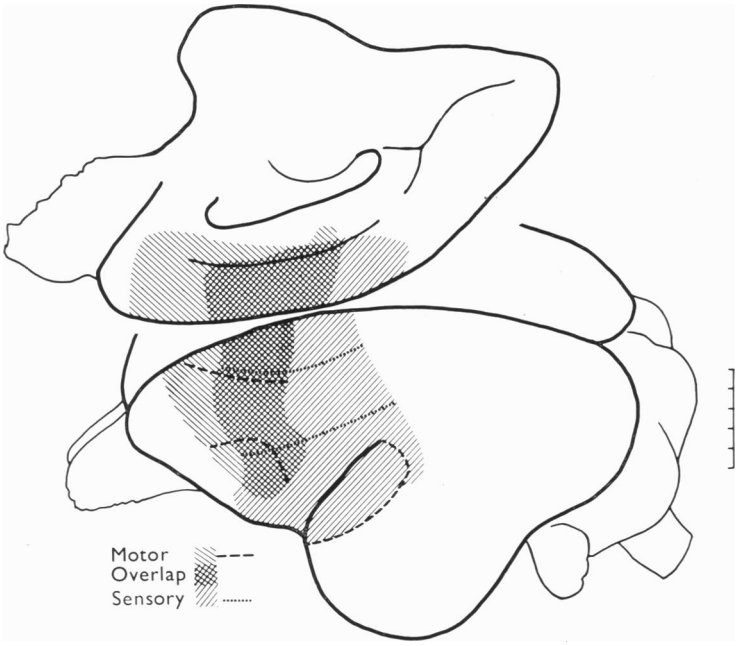

Fig. 2. An outline drawing of the brain (dorso-lateral and medial surfaces) showing the extent of the cortex from which tactile evoked potentials were recorded and the extent of the area (with the exception of the most anterior part of the medial surface) giving discrete movements when electrically stimulated. Interrupted and dotted lines indicate separation of fore-limb area from face and hind-limb areas. For details see text. Scale is in mm.

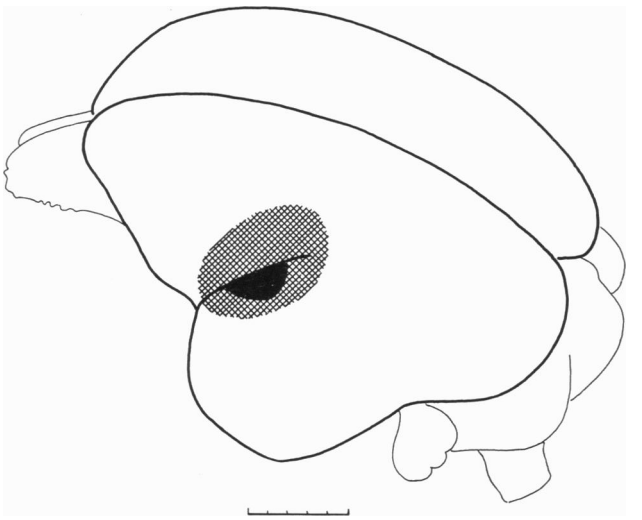

Fig. 3. Darkly shaded portion represents the area from which good auditory responses were obtained while checkered portion indicates weak responses. Scale is in mm.

OBSERVATIONS

The modified Golgi–Cox method

This does not produce a uniform staining of all regions of the brain or even the entire extent of a single area of the cerebral cortex. For instance, the cells of the cerebellar cortex do not take the stain at all while the hippocampus, dentate gyrus and the pyriform area give the best results. The other portions of the cortex give fairly good results, while the staining tends to be very intense within the fissures (e.g. at the depth of the calcarine and Sylvian fissures). This intense staining results in a blurring of the characteristics of individual cells. Moreover, sections counterstained with cresyl violet tend to show fewer cells than those by the pure modified Golgi–Cox technique. However, this may be due to differences in thickness of the sections since in our series the counterstained sections were only 120 μ in thickness while the others were 180 μ. Furthermore, the preparations stained over a period of 5 days have given better results than those over the longer 8-day period.

Cortical areas

Area frontalis agranularis and area gigantopyramidalis (areas 6 *and* 4 *of Brodmann)*

These two areas are considered together since they form the equivalent of the motor area as defined by the electro-physiological method (Figs. 1, 2). The principal features of these areas are a reduction in the thickness and clarity of the inner granular layer and a gradual increase in the size and number of pyramids within the ganglionic layers. Both these features become progressively more pronounced as the motor field is traced in the antero-posterior direction until they reach their zenith about the anterior portion of the area gigantopyramidalis. More posteriorly there is a decline in the size and number of ganglion cells within layer V and a progressive increase of the inner granular lamina until the anterior border of area 3 is reached. In Nissl preparations the plexiform layer in area 6 possesses no distinctive features, while the outer granular layer consisting of small darkly staining pyramids is ill-defined and merges with the underlying outer pyramidal layer. The latter lamina is broad and contains many small pyramids which stain less intensely than their counterparts in the outer granular layer. The inner granular layer comprising small granule cells is narrow and is moderately well defined from the adjacent layers. The ganglionic layer is divisible into two sublayers and contains a large number of small and medium-sized pyramids, the latter usually staining more intensely (Figs. 4, 5). The fusiform layer consists chiefly of small pyramids which show a reduction in their size as they approach the underlying white matter. The fusiform layer is not sharply demarcated from the underlying white matter. As the area frontalis agranularis is traced posteriorly it merges with the area gigantopyramidalis (area 4) without any sharp line of demarcation (Fig. 4). This portion of the cortex is distinguished from the area frontalis agranularis by the presence of the characteristically large pyramids in the ganglionic layer, which, in contrast to the same layer within area 6, is relatively thicker and is populated with medium- and large-sized pyramidal cells staining deeply and found in clusters (Fig. 6). However, the large pyramidal cells of Betz are few and infrequent. The pyramids in layer III

are thinly and evenly distributed over the anterior quarter of area 4, while in the posterior three-quarters layer III becomes gradually masked by invasion of granule cells. The inner granular lamina likewise shows a gradation in that it is almost totally absent over the anterior quarter of area 4, where granule cells are found

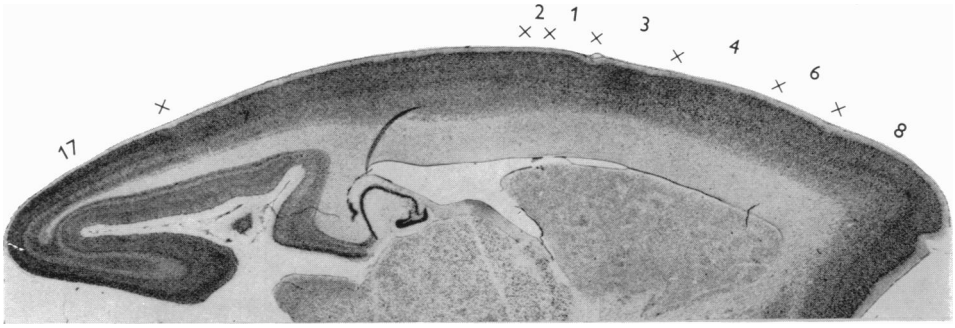

Fig. 4. Sagittal section of hemisphere with × indicating transition between areas. (Numbers represent Brodmann's cortical areas.) ×12.

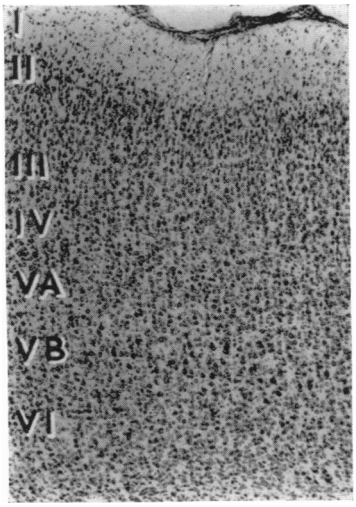

Fig. 5

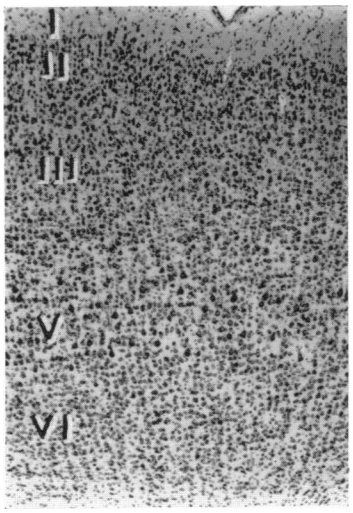

Fig. 6

Fig. 5. Area 6—Nissl preparation. Roman numerals denote cortical layers. ×50.

Fig. 6. Area 4—Nissl preparation. Note concentration of large pyramids in layer V and absence of inner granular layer. ×50.

scattered amongst the pyramids of layer III. However, granule cells are more frequently seen and form an indefinite layer over the posterior three-quarters of the area. Thus there are gradients within the motor field (areas 4 and 6) with reference to the outer pyramidal, inner granular and ganglionic layers.

Since no accurate reconstruction of the sections prepared by the modified Golgi–Cox technique is possible only some of the salient features of the various areas are

given below. In areas 4 and 6 four layers are generally recognizable: (1) a molecular layer which is usually cell-free; (2) an outer pyramidal zone corresponding to layers II, III and IV of Brodmann; (3) a ganglionic layer; and (4) a fusiform layer.

The horizontal cells of Cajal which are said to be present in layer I are practically absent in our preparations. Even the horizontal plexus, though clearly visible in Bodian preparations, is hardly seen, although vertical and obliquely running fibres originating from cells of the underlying cortical layers and passing into the molecular layer are abundant. The pyramidal zone consists chiefly of pyramids which show a

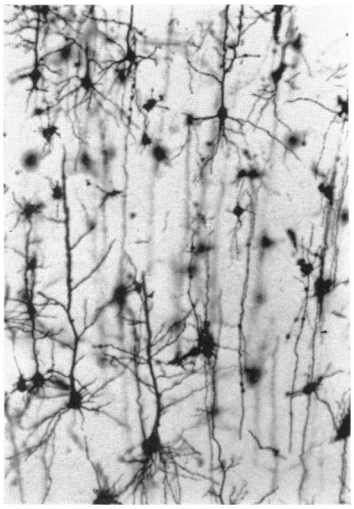

Fig. 7

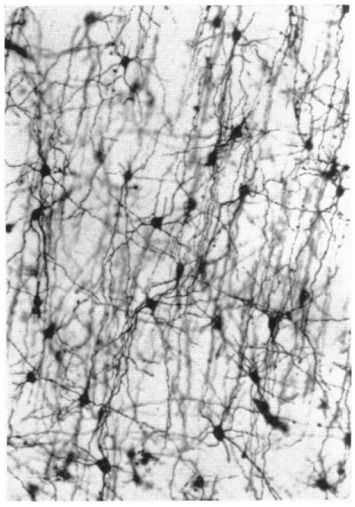

Fig. 8

Fig. 7. Modified Golgi–Cox preparation showing ganglionic and part of outer pyramidal zone in area 4. × 100.

Fig. 8. Modified Golgi–Cox preparation from the posterior part of area 4 showing stellate neurons in layers V and VI. Note plexus formation which is not always evident in Golgi–Cox preparations. × 100.

gradual increase in their size from the superficial towards the deeper portions of the zone (Fig. 7). These pyramids are of various shapes and quite frequently their dendrites are seen to arise beyond the basal half of the cell body. Few stellate cells are scattered within the pyramidal zone while they are practically absent within the ganglionic and fusiform layers. The ganglionic layer has a few scattered large pyramids while the fusiform layer has a number of inverted pyramids in addition to small pyramids and spindle cells. Fibre plexuses representing the inner and outer bands of Baillarger are not evident. Towards the posterior part of the motor area a number of stellate cells make their appearance not only within the pyramidal zone but also within the ganglionic and fusiform layers (Fig. 8). However, this feature is not constantly seen beyond the transitional zone.

A groove runs across the entire antero-posterior length of areas 4 and 6 and extends posteriorly up to the posterior limit of the postcentral area (Fig. 1). The significance of this groove will be discussed later.

Areas 3, 1 *and* 2

These areas are characterized by a significant reduction in their cortical thickness as seen in coronal and sagittal sections. Area 3 is the most well-defined and easily recognizable portion of this entire region. However, the transition from the area gigantopyramidalis (area 4) to area 3 is gradual and this feature is clearly brought out in sagittal sections (Fig. 4).

The essential features of area 3 are the fusion of supra-ganglionic layers II, III and IV and the presence of a clear band within the ganglionic layer (Fig. 9). The outer granular layer is ill-defined and narrow and merges with the outer pyramidal

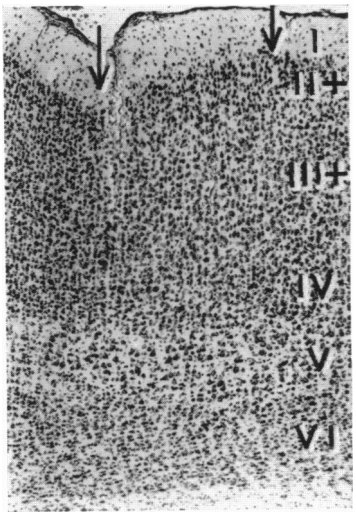

Fig. 9

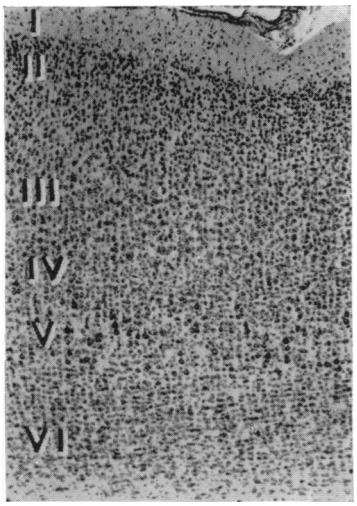

Fig. 10

Fig. 9. Nissl preparation showing areas 3 and 1. Note the pale band in layer V and fusion of layers II, III and IV in area 3 (left of groove). In area I (between arrows) the individual layers are more recognizable. + indicates fusion of layers. × 50.

Fig. 10. Nissl preparation of area 2. Note dark-staining pyramids in layers II and IV. × 50.

layer. It consists of pyramidal cells interspersed with granule cells. The inner granular layer, which starts as an indefinite band within the posterior extent of area 4, broadens out to invade the superficial layers and the fusion of layers is thus prominent within the entire extent of area 3, although the blurring is more pronounced in the posterior half of the area (Fig. 4). Posterior to area 3 the granular invasion gradually subsides as one passes into area 1. The ganglionic layer V is represented by a broad pale band which in coronal and horizontal sections is clearly visible even to the naked eye. Along this band are found scattered medium-sized pyramidal cells and occasional larger ones.

Area 1 is distinguished from area 3 by the reduction in the blurring of the supra-ganglionic layers whereby the inner granular and outer pyramidal layers become more distinct (Figs. 4, 9). Moreover, there is an increase in the number and

size of the ganglion cells within layer V. In addition, dark-stained pyramids appear within layer III and present a striking contrast to layer III of area 3, where these cells are masked by the granular invasion. Area 2 is the most ill-defined portion (Figs. 4, 10), in which the inner granular lamina becomes thicker while the ganglion cells show further increase in number when compared with area 1. Furthermore, dark-stained pyramidal cells are seen in both layers II and III, but the presence of dark-staining small pyramids in layer II is by no means constant since it was observed only in the coronal and horizontal series but not in the sagittal sections. Area 2 is bounded posteriorly by the parietal region, which forms the thickest portion

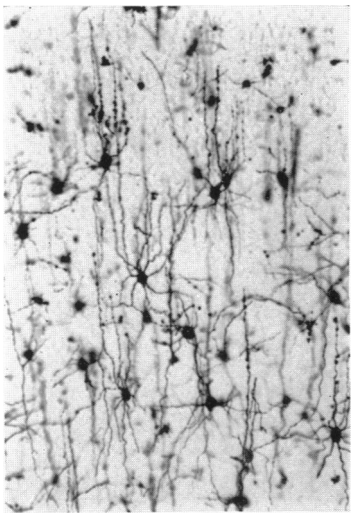

Fig. 11

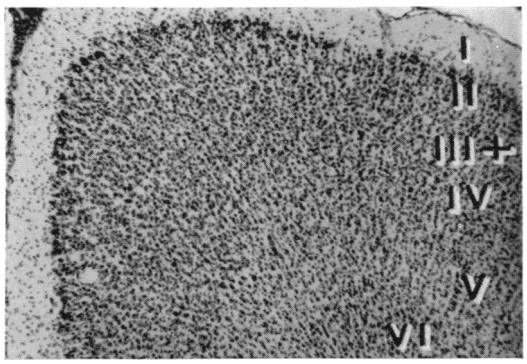

Fig. 12

Fig. 11. Some stellate neurons from the stellate (inner granular) layer of area 3. × 100.

Fig. 12. Nissl preparation of area 41. Note fusion of layers II, III and IV and general smallness of cells. Compare with Fig. 9 (area 3) where blurring is more pronounced. + indicates fusion of layers. × 50.

of the cortex. The parietal cortex shows a marked columnar arrangement of cells while the pale band present within the ganglionic layer of area 3 disappears. In the parietal area the inner granular lamina also becomes broader, while the ganglionic layer is several cells thick (Fig. 4).

In Golgi–Cox preparations, areas 3, 1 and 2 in comparison with areas 4 and 6 are divisible into five layers, the additional layer being the stellate zone which corresponds to the inner granular lamina. It is in this layer that the greatest concentration of stellate cells is found (Fig. 11). The pyramidal zone corresponding to layers II and III of Brodmann has a large number of stellate cells rather evenly distributed amongst the pyramids, while the infragranular layers have only an occasional stellate cell, although at the junctional zone between areas 4 and 3 quite a few stellate cells are observed in the infragranular layers. The inner and outer bands of Baillarger are distinct in Bodian preparations and form a contrast to area 4, where the bands are only faintly seen.

Area 41

This area resembles to a large degree the area 3 of the cortex. The fusion of layers III and IV and the presence of a pale band in layer V are the chief characteristics observed in both horizontal and coronal sections. However, the blurring of layers is less marked than in the posterior part of area 3 and the striate cortex. A columnar arrangement of cells prevails within the area.

The outer granular lamina in area 41 is distinctly darker staining than the outer pyramidal layer and shows a tendency to form clusters as in the striate cortex (Fig. 12). The outer pyramidal layer consists of small pyramids interspersed with small granule cells. The infiltration of granule cells is more pronounced towards the deeper part of layer III. The granular layer consists of small granule cells some of which also invade the ganglionic layer with the result that the pale band in layer V is not as distinct as it is in area 3 and striate area of the cortex. The ganglionic layer contains small- to medium-sized pyramids scattered within the layer and some of them, mostly the small dark-staining pyramids, appear within the inner granular lamina. The results from Golgi–Cox preparations are essentially similar to those of areas 3, 1 and 2, with a heavy concentration of stellate cells within the inner granular layer.

The cortical areas which occupy the upper and lower banks of the Sylvian fissure and which correspond to the somatic sensory area II and a portion of the auditory area are structurally intermediate between the cortex overlying the claustrum on the one hand and areas 3 and 41 on the other. Both these areas show a gradual reduction of size in the inner granular layer and in the number of ganglion cells in layer V when traced towards the claustrocortex. The auditory cortex, however, possesses, in general, smaller cells than that of somatic sensory area II.

Striate area (*area* 17)

This is one of the most well-defined of all neopallial areas. Undoubtedly the fusion of layers III and IV is quite remarkable. Equally noteworthy are the outer granular layer and the pale band which intervenes between the inner granular and fusiform layers.

The outer granular layer forms a distinct row of heavily stained cells arranged in clusters, a feature clearly brought out in our Nissl preparations (Fig. 13). This feature in itself serves as a guide in demarcating the extent of the striate area. The outer pyramidal layer is broad and is made up of granule cells interspersed with small pyramidal cells. Moreover, there are some darker-staining pyramids which are intermediate in size between the cells of Meynert and the small pyramids of layer III. The inner granular layer, which is not demarcated from the outer pyramidal lamina, is formed of deeply stained, densely packed small granule cells. It is divisible into a superficial part abutting against the outer pyramidal layer and a deeper portion composed of a band of dark-stained granule cells. The intervening zone between these two layers forming the band of Gennari is poorly defined in the 25 μ sections whereas the band is more evident in Golgi–Cox preparations which were counterstained with cresyl violet. The fifth lamina is represented by a broad pale band containing dark-stained large polygonal cells of Meynert and medium-sized

pyramidal cells as well as some scattered granule cells. The fusiform layer is narrow and is sharply defined from the underlying white matter. The cells in the deeper portion of this layer lie parallel to the surface, an appearance which is particularly well marked in the depths of the retro-calcarine fissure. This description is applicable to both central and peripheral sectors (Solnitzky & Harman, 1946*a*) although the central sector is undoubtedly thicker than the peripheral sector.

The presence of a complete calcarine system consisting of the pre-, para- and retro-calcarine sulci, together with an insula-like portion of the cortex lying in the

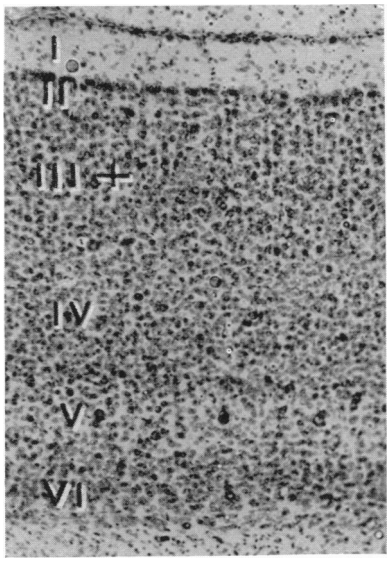

Fig. 13

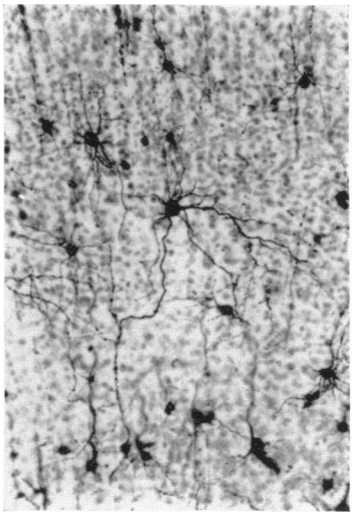

Fig. 14

Fig. 13. Nissl preparation of area 17. Band of Gennari is indistinct. × 100.

Fig. 14. Modified Golgi–Cox preparation counterstained with cresyl violet, showing giant stellate cell of Meynert within inner granular layer. × 100.

depths of the retro-calcarine sulcus and an absence of the posterior horn of the lateral ventricle which were previously reported by Kanagasuntheram & Mahran (1960), is confirmed by the present study. However, in the horizontal series a microscopic backward projection of the lateral ventricle to form an incipient posterior horn is discernible.

Golgi–Cox preparations reveal the presence of stellate cells in all layers of the striate cortex. The inner granular layer contains the heaviest concentration, followed by the pyramidal zone corresponding to layers II and III of Brodmann, while there is a sharp decline in the number of stellate cells in the ganglionic and fusiform layers. However, occasional concentration of stellate cells occurs in patches within the ganglionic and fusiform layers. Moreover, a heavy concentration of stellate cells is observed at the junction of striate and peristriate areas. At this junctional zone, the margo magnocellularis is clearly seen although it was not so clear in Nissl preparations. It is also a remarkable feature that a large number of cells of the

striate cortex show all ranges of variation in their shapes so that a classification of them into pyramidal or stellate group becomes difficult. Such cells are commonly observed in the pyramidal zone immediately beneath the molecular layer. The dendrites of these cells are all turned in a spray-like fashion into the molecular layer. Giant stellate cells of Meynert are frequently present in layer V and occasionally in layer IV (Fig. 14). In Bodian preparations, the outer band of Baillarger is seen to lie in the region of the band of Gennari while the inner band is situated within the ganglionic layer.

Results of electro-physiological experiments

Figures 2 and 3 show the relative extents from which tactile sensory, motor and auditory responses were elicited. A summary of the results was given by Jameson *et al.* (1963). Broadly speaking, it may be stated that the best motor and sensory responses were obtained over areas 4 and 3 respectively and there was a tendency for the responses to fade off both rostral and caudal to the area concerned. While discrete movements were obtained on stimulation of the superolateral surface and the posterior portions of the medial surface of the motor area of the cortex, stimulation of the anterior part of the medial surface produced widespread bilateral movements. The lines in Fig. 2 indicate the zones of transition from predominantly face representation (farthest lateral) to fore limb (mid-portion of the fronto-parietal shaded region), to hind limb and tail (medially on the convexity and over on to the mesial surface of the hemisphere).

The best auditory responses were obtained over area 41 (Fig. 3), although almost equally good responses were elicited from the lower bank of the Sylvian fissure. The second sensory area was located on the upper bank of the Sylvian fissure while the supplementary motor area and motor area II were not explored.

DISCUSSION AND CONCLUSIONS

The present qualitative study of some neocortical areas in *Galago* is based chiefly, if not entirely, on Nissl preparations. This method of investigation has been severely criticized by Lashley & Clark (1946) and more recently by Sholl (1956). Despite some of its drawbacks, the value of cytoarchitectural studies has been clearly outlined by Le Gros Clark (1952) in his note on cortical cytoarchitectonics. Moreover, Bailey & Bonin (1951) have remarked on the unreliability of myeloarchitectural investigations as substitutes for cytoarchitectural ones. They have also noted that 'in the case of Golgi preparations so few cells are impregnated that again the architecture of a given area cannot be made out'. Furthermore, the criticisms of Lashley & Clarke (1946) and Sholl (1956) could not be applied to those areas of the cortex chosen for the present investigation since it has been established that the areas under review have indeed some underlying functional significance. The researches of Rose (1949) and Rose & Woolsey (1949) on the auditory cortex of the cat, the investigations of Powell & Mountcastle (1959*a*, *b*) on the sensory cortex of the monkey, and the contributions by Mott & Halliburton (1908) and Zuckerman & Fulton (1941) on the motor area of some lemurs and of *Perodicticus potto* and *Galago demidovii* have confirmed the view that these areas have a characteristic structural pattern of their own so that they could be identified with some certainty in serial sections. The

striate cortex, which is also included in the present study, has long been recognized as one of the most well-defined of all neopallial areas. Its functional contribution to vision is equally well accepted. However, it must be emphasized that in mapping out the various cortical areas it is essential to have serial celloidin sections cut in different planes, since paraffin sections alone or sections cut in one plane only may prove insufficient for a proper definition of the cortical areas.

One of the most remarkable features in the histology of areas 4 and 6 is their close similarity in structure, with only a few giant pyramidal cells within area 4, a feature which contrasts sharply with the observations of Bonin & Bailey (1947) and Bailey & Bonin (1951) in higher primates. Moreover, the presence of granule cells either scattered amongst the layers or forming an indefinite band is another characteristic observed within areas 4 and 6 of *Galago*. It is these histological findings which might perhaps account for some of the results obtained from electrophysiological studies in *Galago*.

It will be evident from Figs. 1 and 2 that the motor area on the lateral surface of the cortex is confined to areas 4 and 6. Thus the posterior limit of the excitable cortex corresponds closely to the posterior boundary of area 4. This is in conformity with the findings of Mott & Halliburton (1908) in *Lemur macaco* and *L. catta*, Zuckerman & Fulton (1941) in *Perodicticus potto* and *Galago demidovii* and Glees (1961) in the monkey. However, other workers in this field—for example Welker, Benjamin, Miles & Woolsey (1957), Woolsey, Chang & Bard (1947), Woolsey, Travis, Barnard & Ostenso (1953) and Woolsey (1958)—have recorded motor responses from the postcentral area in both New and Old World monkeys. In the light of these observations it is not easy to explain the absence of motor responses within areas 3, 1 and 2 in *Galago*. Perhaps the strength of the stimulus used by us was insufficient to produce responses from areas 3, 1 and 2, where the threshold is usually higher than in the classical motor area.

The extension of the motor area into area 6 in *Galago* is not surprising on the basis of its cortical histology. There are gradients in regard to the ganglionic and inner granular layers in the rostro-caudal and caudo-rostral directions commencing from the anterior portion of area 4, where the ganglionic layer is most pronounced while the granular zone is least distinct. Such gradients would account for the extension of the motor field anteriorly into area 6 and posteriorly into the posterior portions of area 4. Similar gradients have been recently described by Sanides (1964*a*, *b*) in the frontal cortex of man. Indeed, motor responses were elicited from area 6 in man by Foerster (1931, 1936) and extension of the motor cortex into area 6 also appears to be evident when comparison is made of the motor map of Woolsey (1958) in the monkey with the cytoarchitectonic charts by Brodmann (1909) and Bonin & Bailey (1947) in the same animal. However, Zuckerman & Fulton (1941) in *Perodicticus potto* and *Galago demidovii* and Glees (1961) in the monkey have found the motor cortex confined only to area 4.

The medial surface of the cortex in *Galago* shows that the histological differences between areas 4 and 6 are even less remarkable than on the lateral surface and there is an extension of the motor cortex from area 4 into area 6. However, from the most anterior part of the motor area, bilateral motor responses were obtained without any appreciable increase in the threshold of the stimulus. It is suggested that this

may be the supplementary motor area which has been described by Woolsey *et al.* (1951) in the macaque, by Penfield & Rasmussen (1952) in man and by Benjamin & Welker (1957) in the squirrel monkey. If the area in question (i.e. the most anterior part of the motor field on the medial surface of the hemisphere in *Galago*) does, in fact, turn out to be the supplementary motor area, then we have an instance in *Galago* where the differences in threshold which normally exist between the classical motor and supplementary motor areas are not evident. Similarly, the motor responses obtained from the cingulate gyrus in *Galago* may be explained, although here too the threshold ought to be higher than in the motor area (Showers, 1959; Hughes & Mazurowski, 1962).

In *Galago*, areas 3, 1 and 2 form a strip of cortex lying behind and parallel to area 4 and correspond to the postcentral area of higher primates in which a central sulcus is present. Areas 3 and 1 are histologically definable in *Galago* while the criteria for defining area 2 are vague. The position of areas 3, 1 and 2 in our specimens of *Galago* resembles that in *Lemur* (Brodmann, 1908) more closely than that of *Tupaia* (Le Gros Clark, 1959), *Microcebus* (Le Gros Clark, 1931), *Galago demidovii* (Bonin, 1945) or *Tarsius* (Woollard, 1925). It appears that the areas numbered 3, 43 and 44 in the brain of *G. demidovii* (Bonin, 1945) correspond to areas 3, 1 and 2 in our specimens of *Galago*.

It will be seen from Figs. 1 and 2 that the sensory cortex from which tactile stimuli produced evoked potentials extends far beyond areas 3, 1 and 2 and occupies a large part of the motor area as well. This is not altogether unexpected since the entire motor area in *Galago* contained granule cells either scattered or in the form of an indefinite inner granular layer. In fact, even the pyramidal layers III and V are not as pronounced as they are in higher primates. In view of the extension of the sensory area into the motor cortex, Dusser de Barenne (1935*a*, *b*) and Woolsey (1958) have proposed to call both these regions the sensorimotor cortex. Evoked potentials recorded from within the motor area, as seen in *Galago*, are also reported by Benjamin & Welker (1957) in the squirrel monkey and by Woolsey (1958) in some other mammals. Evoked potentials recorded within the motor area may be due to termination of collaterals from the thalamic radiation fibres on their way to areas 3, 1 and 2. However, Woolsey (1958) is of the opinion that there may be a separate sensory organization within the motor cortex as distinct from that seen within the normal receiving areas 3, 1 and 2.

Le Gros Clark & Powell (1953) have shown that area 2 in the monkey has distinct thalamic connexions while Powell & Mountcastle (1959*b*) have observed that this area receives chiefly kinaesthetic impulses whereas area 3 receives mainly tactile afferents. The extension of evoked potentials into area 2 in our experiments on *Galago* may therefore be due to some tactile afferents ending in area 2 or due to the termination of collaterals from tactile fibres passing to area 3.

The presence of a horizontal groove along the entire length of areas 6, 4, 3, 1 and 2 (Fig. 1) in *Galago* deserves comment. When a comparison of the position of this groove is made with Fig. 2 it becomes evident that the groove corresponds to the physiological demarcations between fore-limb and hind-limb areas of the cortex. The appearance of grooves or sulci between physiological subdivisions of the cortex has been explicit from the observations of Welker & Seidenstein (1959) and Woolsey

(1960) in the racoon, in which each sulcus or dimple is seen to separate one physiological subdivision from the other such as the hand from the foot or the foot from the digits. The most recent observations of Krishnamurti & Welker (1965, personal communication) and Sanides & Krishnamurti (1965, personal communication) on the Slow Loris, in which sulcus 'c' separates foot from hand area and the sagittal portion of the sulcus 'e' separates hand and head areas, lead to similar conclusions that sulci, with certain exceptions, intervene between distinct physiological subdivisions.

The presence of small-celled elements and the fusion of supra-ganglionic layers within area 41 agrees well with the observations of Rose (1949) on the auditory area A 1 of the cat. It is also clear from Figs. 1 and 3 that area 41 and the area from which good auditory responses were obtained from the lateral surface of the temporal cortex in *Galago* are very similar. It is therefore predicted that area 41 would turn out to be A 1 in *Galago* while portions of the adjacent temporal cortex, the lower part of the somatic sensory area and the lower bank of the Sylvian fissure may correspond to other subdivisions of the auditory area described by Rose (1949), Rose & Woolsey (1949) and Woolsey (1962, personal communication). The extension of the auditory area beyond the limits of area 41 is well known in man and other mammals (Penfield & Rasmussen, 1952; Pribram, Rosner & Rosenblith, 1954; Neff & Diamond, 1958). There is also the suggestion by Rose & Woolsey (1958) that some portions of the auditory cortex other than A 1 may receive projections not only from the medial geniculate body but also from the posterior group of the thalamic nuclei.

The striate area of *Galago* as shown in Fig. 1 corresponds closely to the same area as demarcated by Solnitzky & Harman (1946*b*) in *Galago demidovii*. It is therefore difficult to understand why Bonin (1942, 1945) confined the striate cortex of *G. demidovii* only to the mesial surface of the hemisphere below the calcarine sulcus. The present findings that the band of Gennari is faintly represented in *Galago* is also supported by the observations of Bonin (1942, 1945) and Solnitzky & Harman (1946*b*). The presence of a large number of stellate cells within the striate cortex in comparison with other regions investigated by us is in agreement with similar observations made by Mitra (1955) and Sarkisov (1960), while the presence of giant stellate cells of Meynert observed by Le Gros Clark (1925) within the inner granular and ganglionic layers is also borne out by the present investigation.

SUMMARY

1. The structure of some cortical areas in *Galago* has been described. Both Nissl and modified Golgi–Cox preparations have been used for the present study.

2. Cortical areas defined by the cytoarchitectural method are compared with those obtained by electro-physiological studies. These results show that part of the auditory cortex, possibly the first auditory field, the entire motor area and at least portions of the sensory cortex can be defined in cytoarchitectonic terms.

3. Areas 3, 17 and 41 show structural similarities in that they exhibit varying degrees of fusion of layers II, III and IV, and the blurring of layers is most pronounced in area 17 and least marked in area 41, with area 3 occupying an intermediate position.

4. Areas 4 and 6 are characterized by partial or almost total absence of the inner granular layer but the pyramidal layers are not as prominent as they are in the motor area of higher primates.

5. Evoked potentials obtained within the motor area are explicable on the basis of gradients in laminar patterns.

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