Organization of Neurons in the Visual Cortex, Area 17, of the Monkey (*Macaca mulatta*) [1]

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ABSTRACT A study of neuron morphology in Golgi Rapid and Kopsch preparations of area 17 of the monkey has shown three basic cell groups — pyramidal neurons, stellate neurons with spinous dendrites and stellate neurons with spine-free or sparsely spined dendrites. These three neuron groups show different distributions in depth from pia to white matter and differ in their relationship to zones of concentrated termination of geniculo-cortical axons. The neuron type most closely related to the laminae receiving a heavy geniculo-cortical projection is the spinous stellate cell. This cell type is restricted to lamina IV. Included in this zone is the broadest band of geniculo-cortical axon projection (lamina IVC), the horizontal fiber band (lamina IVB) comprising the major portion of the stria of Gennari (receiving little or no thalamic projection) and the narrow band of thalamo-cortical fiber termination which occurs superficial to the stria of Gennari (lamina IVA). Pyramidal neuron cell bodies are almost totally excluded from lamina IVC and the apical dendrites of lower pyramidal neurons bear many fewer spines in lamina IVC than in laminae V and VI. The basal dendrites of upper pyramidal cells spread superficial and deep to lamina IVA rather than within it. Spine-free stellate neurons occur at all cortical levels and sparsely-spined varieties have not been impregnated in lamina IV, but occur in the other laminae.

Three groups of presumed thalamo-cortical axons have been identified, two of which resemble each other in morphology (having long collaterals which appear to terminate by means of spine-like projections of the axonal surface) but not in distribution. One group of these axons bearing spine-like projections distributes in laminae IVC (principally in the deeper half, IVCβ) and IVA; the other is restricted in distribution to the upper half of lamina IVC (IVCα). The third group of thalamo-cortical axons distributes to lamina I and appears to lack the spine-like projections shown by the other two axon groups.

Physiological studies of neuronal activity in the visual cortical areas of the monkey have yielded considerable information as to the functional organization of these areas (Hubel and Wiesel, '68, '70). The physiological study of area 17 (Hubel and Wiesel, '68) shows at least two systems of neurons occur, arranged in a series of columns extending from pia to white matter, one system having common receptive field properties within each column, the other system aggregated according to eye dominance. A horizontal organization is also evident corresponding to cortical layering separating simple monocular responses in lamina IV from complex or hypercomplex binocular responses in laminae II, III, V and VI. The morphological substrate of this physiological organization is poorly understood even though detailed light microscopic studies have been made of neuronal morphology in these areas of the cortex (Cajal, 1899, '11; Lorente de Nó, '49; Poljak, '57). The complexity of the mammalian neocortex in terms of the wealth of different neuron types present and the elaborate intrinsic neuron inter-

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connections presents severe technical difficulties in determining morphological correlates to the physiological activity of the region.

The present study of Golgi stained material from monkey (*Macaca mulatta*) visual cortex, area 17, has attempted to determine if there is some means of presenting a simpler basic plan of neuron organization in the visual cortex which might correlate with, or be testable by, physiological studies. Further, the study has looked for details of neuron morphology that might be identifiable in electron microscopic material and so serve as a means of linking specific neuron types with specific synaptic features. The monkey has been used because the primate primary visual cortex (area 17) is more sharply divided into a series of clearly limited laminae than is cat or rat, and these divisions provide a useful set of morphological landmarks. The Golgi method has been the principal tool in the investigation, as this shows the morphology of entire neurons, including the extent of their axons and dendrites.

As this paper neared completion, two reports appeared of Golgi studies on the same cortical area (Valverde, '71; Garey, '71).

MATERIALS AND METHODS

Tissue blocks were taken from normal primary visual cortex (area 17) of 15 monkeys (*Macaca mulatta*). These animals were either unoperated or had lesions of the contralateral lateral geniculate nucleus or the contralateral area 17 with survival times of 6–28 days for the purposes of another experiment. There is no reason to believe that these lesions affected the neuronal structure of those parts of the contralateral area 17 used in the present study. The animals in most cases were perfused with 4% paraformaldehyde in Millonig's phosphate buffer (Vaughn and Peters, '66). A few animals were perfused with 10% formalin in saline. After allowing the brain to harden in the fixative for at least 24 hours, several tissue blocks were cut from area 17, away from its junction with area 18, from the exposed occipital operculum and from the calcarine sulcus. The tissue was then processed by Golgi Rapid and Golgi Kopsch techniques. The Golgi Cox method (Sholl, '53) was tried but the samples prepared seemed poorly impregnated in the finer neuronal processes, a finding in accord with previous studies (Colonnier, '64). For the Golgi Rapid technique the tissue was placed in a solution consisting of 80 ml of 2.5% potassium dichromate, 16 ml of distilled water and 4 ml of 5% osmium tetroxide, for one week, then washed in distilled water, transferred through dilute silver nitrate solutions to 1.0% silver nitrate and left in 1.0% silver nitrate for a further week. For the Golgi Kopsch technique, the tissue was submerged in 3.5% potassium dichromate for one week then washed and transferred through dilute silver nitrate solutions and left in 1.0% silver nitrate for one week. The tissue blocks from both methods of impregnation were then dehydrated in equal parts of absolute alcohol and acetone for two hours, several brief changes of absolute alcohol, then of absolute alcohol and ether mixture, then embedded in parloidin (6%–1–2 days, 12%–1–2 days). Sections were cut 90 μ thick, chiefly perpendicular to the pial surface but in a few cases, series were cut horizontal to the pia. Some of the Golgi Kopsch material was counter-stained for cell bodies with alcoholic thionine on the loose sections. The Golgi stained sections were dehydrated through a butanol, cedarwood oil, toluene sequence and mounted under thin coverslips in "Permount" synthetic resin. An estimate of the degree of shrinkage of the cortical gray matter during the Golgi impregnation and mounting was obtained by measuring the distance from pial surface to white matter in sample blocks cut from the freshly fixed brain before any further treatment and comparing it with the same measurement in mounted sections from the same block faces after Golgi Kopsch or Golgi Rapid treatment. Additionally, a tissue block face immediately adjacent to each of these sample block surfaces was cut as frozen sections in the fixative used for perfusion, the sections mounted on gelatinized slides and stained with cresyl violet. The distance from pial surface to white matter in the untreated fixed blocks was closely comparable to that in the frozen sections stained for

Nissl substance. For the Golgi Rapid material the shrinkage was on average 4.5% (Valverde, '70, found approximately the same degree of shrinkage) and for the Kopsch material the shrinkage was on average 20%. It was found that the Golgi Rapid preparations were considerably more satisfactory than the Golgi Kopsch, showing more cell types, the cells being apparently less malformed by shrinkage, and the axons both extrinsic and intrinsic being much more frequently stained. Drawings were prepared of specific neuron types using the drawing tube attachment of the Wild microscope. In general, the drawings were made using × 100 oil immersion.

Determination of the position and limits of horizontal laminae in the visual cortex was made by comparing the concentrations of cell bodies shown in Nissl stained sections of area 17, the position of fiber bands seen in fresh tissue and particularly well in the Golgi Rapid material, and the concentrations of different neuron types at different levels shown by both Golgi methods. The Golgi Kopsch material counterstained with alcoholic thionine, provided a useful link between Nissl stained material and neuron types shown by the Golgi stain. Material from one monkey with a large but incomplete stereotaxic lesion of the lateral geniculate nucleus and seven days survival was stained with the Fink-Heimer technique, Method I, (Fink and Heimer, '67) to show the distribution of the degenerating thalamo-cortical pathway.

A preliminary report of some of the results of this Golgi study has been given elsewhere (Lund, '69).

RESULTS

Lamination

Study of the Nissl stained material, of the degeneration resulting from lesions in the lateral geniculate nucleus, and of the patterns of fiber bands and neurons seen in the Golgi material resulted in the adoption of the lamination numbering shown in plate 1. Brodmann's ('05) nomenclature for the divisions of lamina IV has been used since lamina IVA has more in common with laminae IVB and IVC — in the types of neurons included in it and in receiving a thalamic projection — than it does with lamina III. In the Nissl stained material the position of the central region of lamina IVA is sometimes seen as a prominent band of neurons (fig. 1). however the exact width of the lamina is not well defined in Nissl stained material of *Macaca mulatta* and its limits can only be seen clearly in Golgi Rapid preparations. Lamina IVC has been divided into two halves and numbered IVCα and IVCβ (Polyak, '57), IVCβ being the deeper cell rich zone and IVCα being the more superficial part less densely populated with neurons.

In Golgi Rapid preparations, when the axon plexuses have impregnated, two prominent bands of horizontally orientated axons are often evident. The deeper band, lamina V, has sharply defined upper and lower limits. The more superficial band coincides with the broad white band observable in fresh tissue — the line of Gennari or upper band of Baillarger — and includes lamina IVB and the upper half of lamina IVCα. This fiber band has a sharp upper boundary coincident with the upper limit of lamina IVB and grades off with a less sharply defined lower border about the middle of lamina IVCα. Classically, this band has been said to represent thalamo-cortical fiber termination (Polyak, '57). In comparison with degeneration of thalamo-cortical fibers described below, the line of Gennari bears little relationship to the area of termination of thalamic afferents and most probably represents myelinated intrinsic axons. This conclusion was also reached by Clark and Sunderland ('39) even before the Nauta techniques were available to define accurately the laminar termination of the thalamic pathway. For a comparison of the different laminar numbering systems used by earlier investigators of the primate visual cortex see Solnitzsky and Harman ('46).

Thalamo-cortical projection

Degeneration resulting from the geniculate lesion as stained by the Fink-Heimer ('67) technique appears concentrated in laminae IVCβ, IVCα, IVA (plate 2, fig. 5) and in part of lamina I (plate 3, fig. 10). This pattern of degeneration resembles that described by other workers (Hubel and Wiesel, '69; Garey and Powell, '71) and is

here repeated to allow comparison with the Golgi material. Laminae VI and V contain degenerating coarse fibers running in all directions with scattered granules between them. Lamina IVCβ is filled with granular degeneration. In IVCα the degeneration occurs more sparsely than in lamina IVCβ. Lamina IVB contains only a very few scattered granules and fine vertically orientated degenerating fibers. Lamina IVA contains a concentration of granular degeneration and degenerating horizontal or obliquely running fibers. Laminae III and II contain a very sparse scatter of granules and through these laminae rise fine vertically orientated degenerating axons. These axons run into lamina I to turn horizontally forming a degenerating fiber plexus in a narrow band located in the lower region of the upper half of layer 1.

In the Golgi stained material, particularly in Golgi Rapid preparations, a group of axons are seen which do not resemble any of those belonging to intrinsic neurons. These axons have their terminal ramification in those laminae which show the densest granular degeneration after lesions of the lateral geniculate nucleus and the orientation of their main trunks and their collaterals is the same as the orientation of fiber degeneration, suggesting that such axons are of geniculate origin. These axons have long collateral branches with complex arrays of spine-like projections along their length. These axonal spines resemble dendritic spines in having a narrow stalk and enlarged tip but may be more complex than dendritic spines in having several terminal enlargements at the end of a single stalk. One variety of these axons (plate 2, fig. 4A, B) typically starts to impregnate as a large trunk at the base of lamina IVCβ. Long oblique or horizontally orientated collaterals are given off from the main trunk, each covered with complex spine-like projections (plate 4, fig. 14Y, Z). From a single trunk profuse collaterals are given off in IVCβ, a few in IVCα and in lamina IVA the axon shaft becomes profusely spinous and may turn and run horizontally for a considerable distance within this narrow lamina. While individual axons have been seen to distribute only in IVCβ, the nature of the Golgi stain makes it impossible to say that the distribution of these large axons can be limited in some cases to lamina IVCβ since some processes may simply have failed to impregnate. However, it can be said with some certainty that a single axon can project to IVCβ, α and IVA. These same axons do not, however, seem to project to layer I.

In addition to these large axons, another group of presumed extrinsic axons are found which start to impregnate as short vertically orientated trunks in lamina IVCα (plate 2, fig. 3). These trunks give off long horizontally running collaterals which bear spine-like projections but which are somewhat finer than the larger axons previously described. The terminal field of these axons appears restricted to lamina IVCα with perhaps some encroachment on the upper part of IVCβ.

Axons bearing numerous spine-like processes like those just described for lamina IV have not been impregnated in layer I. Very occasionally axons have been impregnated in layer I which may be the thalamic projection to this layer (plate 3, fig. 11) since they have never been seen to arise from intrinsic neurons. These axons have stained as a stout trunk rising vertically through layers III and II to divide only on reaching layer I. Here they form a relatively sparsely branching system of coarse, rough surfaced collaterals, with a few spine-like projections running great distances horizontally in the middle to upper region of layer I.

Neurons stained by the Golgi Rapid and Kopsch techniques

The cell types present in the Golgi preparations of the present study can be divided into two broad classes on the basis of whether or not their dendrites bear a major population of spines (a spine is here defined as an appendage having a narrow neck and expanded tip).

I. *Cells with markedly spinous dendrites*

This division includes the classical pyramidal cell and also some stellate forms. In this study a cell with spinous dendrites has been called pyramidal if one dendrite — usually originating from the upper (pial) side of the cell — is markedly longer than the rest, giving an asymmetry to the

cell's dendritic field in the vertical plane. Typically, the axon originates from the base of the cell (from soma or from the initial portion of a basal dendrite) even if its major distribution is superficial to the cell itself. Included in this group are some cells that achieve the above characteristics by modified means, for example — a lateral dendrite may turn toward the pial surface and take the place of the apical dendrite and other cells which appear to be inverted or horizontally lying pyramidal cells. Similar abnormal orientations have been described by Van der Loos ('65) in the rabbit.

The stellate cell type with markedly spinous dendrites has no specialized apical dendrite, and while the dendrites do not necessarily form a field equal in extent on all sides of the cell body, each dendrite has roughly the same length and branching pattern as the rest.

(a) *Pyramidal cells.* A detailed study of all the pyramidal cell variants has not been made. However, certain particular features can be outlined. Pyramidal cell bodies occur in all laminae except IVC and I. In the considerable amount of material examined only one cell considered to be pyramidal has been found impregnated in lamina IVC and it has, therefore, been regarded as being aberrant in position. The apical dendrites of pyramidal cells lying in laminae V and VI show a marked reduction in the number of spines and often a reduction in diameter in the portion of the shaft lying in lamina IVC, particularly IVCβ, as compared to the densely spiny portion of the same shafts in laminae V and VI (plate 3, figs. 7, 8). The number of spines on the apical dendrites in general increases again in laminae above IVCβ but not to the level shown on the portion of the shaft and its branches in laminae VI and V. Those spines on the apical dendritic shafts in lamina IVC tend to be longer and finer than those at lower levels and sometimes appear to be in contact with fine rising axons which, in some cases, originate from the same cells. This marked reduction in spines on the apical dendritic shaft as it passes through lamina IVCβ is true of the great majority of the pyramidal cells of laminae VI and V including the giant pyramidal cells of Meynert (1871) whose cell bodies lie in the upper part of lamina VI and whose basal dendrites show an asymmetry as described by Clark ('42). Depending upon the size or variety of pyramidal cell, the shafts of the apical dendrites can give off side branches in laminae VI, V, IVCα and above, but very rarely do any give rise to side branches in lamina IVCβ. The apical dendrites of pyramidal cells of laminae V and VI appear to terminate at various levels between laminae IVCα and III. The largest pyramidal neuron of lamina V is the only variety in the deeper cortical laminae whose apical dendrite has been seen to make a consistent and marked contribution to lamina I neuropil. The apical dendrites of pyramidal cells lying in laminae IVB to II also show varying levels of termination but many reach and arborise in lamina I.

Two varieties of pyramidal cell whose cell bodies lie in lamina V have apical dendritic shafts particularly modified as they pass through lamina IVC. One large form, with a wide basal field of dendrites confined to the limits of lamina V, has a stout apical dendrite which eventually reaches lamina I. This apical dendrite remains spine-free from cell body to the upper limit of layer IVCβ and then becomes densely spiny and remains so along the rest of its length (plate 3, fig. 6). The initial spine-free region of the apical dendrite is therefore much longer than the normal spine-free region close to the soma seen in other pyramidal cells even relative to the size of the cell. The second particularly modified pyramidal cell in layer V is small to medium in size with a well-developed basal dendritic field and an apical dendrite that gives off prominent spinous side branches into layer V before the shaft leaves the lamina. As the shaft enters layer IVCβ it decreases markedly in diameter, is usually spine-free and as a fine process (thinner than the recurrent axon of the same cell) it continues vertically through lamina IVC and in this material its impregnation stops as it nears or enters lamina IVB (plate 3, fig. 9). The existence of this extremely fine apical dendrite suggests that these cells should be classed as pyramidal rather than stellate. The axon of this type of cell emerges from

the base of the soma, runs deep for a short distance giving off fine collaterals, then becomes recurrent as one or more stout branches which run vertically towards the pia but have not been impregnated to their termination. Other small to medium sized pyramidal cells of laminae V and VI show many thin recurrent axon collaterals with fine spine-like processes along their length traveling upward through the same laminae as their apical dendritic shafts. Other fine axon collaterals from these cells enter the horizontal axon plexus of lamina V and others pass downward toward the white matter.

The pyramidal cells of laminae IVB, IVA, III and II have axons that usually can be found to contribute heavily to the horizontal fiber bands of laminae IVB and V and usually a very fine axon process from each can be traced down into laminae VI before it ceases to impregnate. Obliquely running collaterals also run for long distances in laminae I, II and III. The main axon shaft running downward through layers II and III often bears spines, in morphology like those on the dendrites. The axon collaterals of these pyramidal cells are fine processes with small irregular dilations, and frequently with spine-like projections or small projections without a dilated tip (plate 4, fig. 14×). The basal dendrites of the pyramidal cells in IVB rarely enter laminae IVC or IVA. Although pyramidal cell bodies occur in lamina IVA and their dendrites pass through IVA without change in spininess, the pyramidal cell basal dendrites and side branches of the apical dendrites lie horizontally above or below lamina IVA rather than within it (plate 5, fig. 19). Pyramidal cells whose somata lie within lamina IVA have basal dendrites that turn sharply downward from the cell body until they enter lamina IVB where they spread horizontally (plate 5, fig. 19). These features of pyramidal cell dendritic orientation are one of several elements that define the upper and lower limits of IVA.

(b) *Spinous stellate cells.* In the material prepared for this study stellate cells with prominently spinous dendrites characterize lamina IV and occur in all its subdivisions. With the Golgi Rapid method, these cells stain most readily in laminae IVC and IVB and are certainly a major component of these layers. Prominently spinous stellate cells have not been impregnated in laminae other than the divisions of IV with the possible exception of lamina V. However, the vast majority of spinous cells in lamina V are clearly pyramidal cells. The very few neurons in lamina V which do not appear to have a clear apical dendrite have nevertheless been tentatively classed as pyramidal since they resemble in other respects the large population of pyramidal neurons in the lamina with very fine apical dendrites.

In lamina IVCβ there are at least two varieties of spinous stellate cells. One form has slender dendrites with very long fine stalked spines (plate 4, figs. 12, 13; plate 6, fig. 21). The other variety has coarser dendrites with shorter stalked, larger knobbed spines as well as small projections without dilated tips (plate 6, fig. 20). The dendritic field of both form of spinous stellate neurons in IVCβ is either roughly circular or may be elongated in the vertical plane. The spinous stellate cells of lamina IVCα seem more uniform in appearance and their dendritic fields are often elongated horizontally (plate 7, fig. 23, cells Y and Z). There is no abrupt boundary between the two divisions of IVC and the dendritic fields of some of these spinous cells, while lying predominantly in one or other lamina can extend above or below into the neighboring part of lamina IVC. Dendrites from spinous stellates in lamina IVB and IVCα may also intermingle in the transition zone between the two laminae. The dendritic fields of the spinous stellate cells of lamina IVB rarely cross into lamina IVA, tending to lie horizontally orientated in the fiber plexus if small to medium in size while the larger forms (plate 7, fig. 23, cell X), show a more radially orientated dendritic field. The spinous stellate neurons of IVA are rarely but consistently stained by both the Golgi Rapid and Kopsch techniques. In general, their cell bodies lie close to the border with IVB and their dendrites turn superficially to form a small dense field in lamina IVA (plate 5, fig. 18).

One of the characteristics justifying the division of lamina IVC into α and β parts is a difference in axonal projection of the spinous stellates lying in one or other part

to laminae superficial to IVC. The axons of spinous stellate cells of lamina IVCβ have prominent recurrent collateral axon trunks that project to lamina III and which do not appear to terminate in laminae IVB or IVA. The axons of spinous stellate neurons of lamina IVCα do not project to lamina III but ramify in laminae IVB and IVA. The axons of the spinous stellate neurons of lamina IVCβ generally emerge from the base of the cell body or initial part of a basal dendrite. The axons run initially toward the white matter but become recurrent before leaving the lamina. Fine collaterals are given off terminating in lamina IVC (plate 4, fig. 13; plate 6, fig. 20); some pass down through lamina V, sometimes contributing sparsely to it, to lamina VI with apparently a sparse terminal field in this lamina (plate 4, fig. 13). The recurrent axon runs vertically towards the pia as one or two stout trunks without side branches to layer III where it divides into a fan of collateral branches (plate 4, fig. 12; plate 5, figs. 15, 16). The fine spined stellates of IVCβ have small diameter axon collaterals that run long distances, maintain a fairly even diameter with occasional beading and occasional spine-like projections or irregular protrusions (plate 4, figs. 12, 13). The coarser dendritic form of spinous stellate neuron in IVCβ has an axon which shows very abrupt changes in diameter from main axon to collateral branches (plate 6, fig. 20), the collaterals having occasional beading. Its distribution appears to resemble that of the axon of the more slender variety of spinous stellate neuron.

The spinous stellate cells of laminae IVCα and IVB have axons that again arise in most cases from the base of the soma or a primary dendrite. They are fine, without prominent beading. Collaterals are given off which, in cells of IVCα, may rise to terminate in the zone of lamina IVB overlying the cell. Other collaterals run horizontally or obliquely upward for long distances in IVCα, in IVB and very occasionally also into IVA (plate 7, fig. 23, cells Y, Z). The axons of these spinous cells of IVCα and IVB have not been found to contribute to layer III or above, and while this may be due to failure to impregnate or trace such a projection, there is clearly a marked difference in axon projection of these spinous stellate cells compared to those of lamina IVCβ. The spinous stellate cells of lamina IVCα and IVB have in addition to the laminae IVB and IVCα projection, a fine axon process that extends downwards as far as lamina VI. The axons of the largest spinous stellates of IVB have not been impregnated beyond their initial segment but there is indication of some recurrent branches before the silver impregnation stops. The axons of the spinous stellates of IVA have been poorly impregnated in most cases. However, from those portions present, they can be seen to emerge basally with locally distributing collaterals, a strong recurrent branch contributes to layer III (plate 5, fig. 18) and long collaterals appear to descend obliquely through lamina IVB and upper IVCα.

II. *Neurons with spine-free or sparsely spined dendrites*

In all laminae of the striate cortex neurons have been impregnated that are clearly not pyramidal and which do not resemble the spinous stellate cells restricted to the divisions of lamina IV. These cells are generally much less frequently stained than the spinous cells in either Golgi Rapid or Kopsch material; however, on occasion, evidence is found of a large population of these cells, e.g., at the edges of Golgi Rapid blocks smooth dendritic forms sometimes outnumber pyramidal cells in lamina II and III and the characteristic axons of such cells can be a very prominent component of the general neuropil stained in Golgi Rapid material. It must, however, be emphasized in relation to these and all other varieties of neurons that it is impossible to say from Golgi impregnated material how frequently any one cell type occurs in the total neuron population. A wide variety of these cells exist and, while an attempt has been made to group them according to common features, it is felt that in some cases (particularly the sparsely spinous forms) too few examples have been found to allow a thorough analysis.

(a) *Neurons with spine-free dendrites.* These neurons occur in all laminae and their dendrites may be entirely smooth surfaced, regularly beaded along their length, or have an initial smooth region with bead-

ing in their more distal portions. It is difficult to determine if the dendritic beading seen is the normal morphological state of the dendrite or represents a shrinkage of certain portions of the dendrite due to the histological procedures. The beading seems more pronounced in Golgi Kopsch material where greater tissue shrinkage occurs which suggests that it may at least be enhanced by shrinkage factors. However, even in Golgi Kopsch material, cells with smooth dendrites are observed which suggests that there may be differences in character of dendrite in different varieties of these spineless cells (compare plate 6, fig. 22; plate 9, figs. 28, 29). The "beads" or wider portions along those dendrites that show them could represent regions of accumulation of internal structures, e.g., mitochondria, or could be regions of synaptic contact where shrinkage may occur less readily. Neurons with such smooth or beaded dendrites most frequently have axons with a smooth initial segment, which divides into a series of regularly beaded collaterals (in either Golgi Kopsch or Rapid material) with a major distribution within or close to the cell's dendritic field (e.g., plate 8, figs. 24, 25, 26; plate 9, fig. 28).

Layer IVCβ has a population of neurons with spine-free dendrites which have a rather restricted field. The axon rises from the upper part of the soma as an initial smooth shaft which gives off a swirling mass of beaded collaterals in IVC (plate 8, figs. 24, 26, 27). Axon collaterals also pass downward through V and VI. Other larger, smooth dendritic forms occur in lamina IVC with smooth unbeaded axons (plate 9, fig. 29). Layer IVCα has a population of smooth or beaded dendritic neurons (plate 6, fig. 22) with the dendritic field being horizontally oriented and the dendrites often rising into IVB. Their axons are beaded (sometimes the beads are of very large diameter, plate 4, fig. 14W) distributing mainly locally in IVC. Similar cells have been seen in laminae III (plate 10, fig. 30, cell Z), IVA (plate 5, fig. 17), IVB, V, and VI (plate 9, fig. 28).

In layer III neurons with smooth or beaded dendrites tend to have narrow vertically orientated dendritic fields sometimes with dendrites extending both above and below the cell body in double bush fashion (plate 10, fig. 30, cell X; plate 11, fig. 31, cells X, Z; plate 13, fig. 37) while in layers II and I their fields may become wider in horizontal extent (plate 10, fig. 30, cell Y; plate 12, figs. 32, 33). The axons of nonpyramidal cells of layers I, II and III usually have a locally distributing axon, but generally one or two collaterals from the axons of these stellate neurons pass down into lamina IVB axon plexus (plate 10, fig. 30, cell Y; plate 11, fig. 31, cells X, Z). Certain neurons of lamina II with wide dendritic fields orientated in a single vertical plane (plate 12, figs. 32, 33) may be exceptional in possessing axons that have their terminal field some distance from the cell body, but their axons have not impregnated beyond the initial segment in this material. Some stellate neurons of laminae II–III (plate 10, fig. 30, cell X) have axons that project to and arborise within I — so-called Martinotti cells (Martinotti, 1890; Cajal, '11). Neurons with smooth or distally beaded dendrites of laminae V and VI can be very large (plate 12, figs. 34, 35) and their dendrites may reach as far as lamina IVB. The axons of these larger, deeper cells have not been impregnated beyond the initial segment.

(b) *Neurons with sparsely spinous dendrites.* Stellate cells with very occasional dendritic spines and other dendritic appendages occur in layers outside lamina IV but have not been found in the divisions of lamina IV (plate 13, figs. 36, 37). They do not have the population of regularly occurring spines found on the spinous stellate neurons in lamina IV. These cells have impregnated infrequently in the present material. Their axons are fine without prominent beading and generally distribute locally in a field rather greater in extent than the cell's dendritic field. These cells include those resembling the double bush cells of Cajal ('11) in having their dendrites distributing in two bunches, above and below the cell body and in having their axon forming a vertically orientated cascade. However, in the present material the major part of such axon cascades does not seem to pass the boundary between lamina III and lamina IV, although one or two fine axon collaterals may travel through its junction.

Stellate neurons with axons giving rise to pericellular baskets as described for visual cortex (Cajal, 1899, '11), motor cortex (Marin-Padilla, '69) and somatosensory cortex of cat (Szentágothai, '69) have not been observed.

SUMMARY OF LAMINAR CHARACTERISTICS

Lamina I

This is a narrow lamina adjacent to the pia appearing sparsely populated with cells in Nissl stained material. It receives a thalamic projection which appears to form a horizontally orientated axon plexus in the lower part of the upper half of the lamina. The lamina also receives a projection from pyramidal cell axon collaterals and it is the principal target of the axons of some stellate neurons of laminae II and III. It contains neurons with sparsely spined or smooth dendrites whose cell bodies often lie close to the junction with lamina II. The axons of these neurons may either be confined to the lamina or project downwards into laminae II and III, sometimes with collaterals reaching the axon plexus of lamina IVB (plate 10, fig. 30, cell Y; plate 11, fig. 31, cell Y). The terminal branches of apical dendrites of pyramidal cells of deeper laminae (the largest pyramidal cells of lamina V and many pyramidal cells of laminae IVB, IVA, III and II) contribute heavily to the laminar neuropil.

Laminae II and III

These laminae are not in direct contact with a concentrated termination of thalamic axons. The upper border of lamina II is abrupt and marked by the sudden decrease in the number of neurons in Nissl stained sections and the absence of pyramidal cell somata typifying lamina I. There is sometimes in Nissl stained material a prominent band one to two cell bodies deep at the junction of laminae I and II. Laminae II and III merge gradually into one another and the only justification for distinguishing the two laminae is the apparent increase in number and varieties of stellate neurons in lamina II compared to lamina III and the projection of neurons of lower laminae principally into lamina III rather than lamina II. The lower border of lamina III is a well-defined boundary. Its limit is marked by the start of the arborisation of axon trunks rising from neurons in the lower cortical layers (plate 5, fig. 16) a major component of which being the axons of spinous stellate neurons of lamina IVCβ.

The laminae contain pyramidal neurons and an abundance of different stellate neurons of both smooth (or beaded) dendritic forms and sparsely spined forms (plate 10, fig. 30, cells X, Z; plate 11, fig. 31, cells X, Z; plate 13, fig. 37). Prominently spinous stellate cells do not occur. The axons of pyramidal cells of these layers distribute to all laminae except laminae IVA and IVC. Pyramidal neurons whose cell bodies lie at the lower border of the lamina have basal dendrites principally orientated horizontally above lamina IVA but their basal dendrites do occasionally pass through lamina IVA.

Lamina IVA

This narrow lamina receives a direct thalamic projection composed of densely spinous collaterals of axons that also supply lamina IVC. These axons, on entering lamina IVA, turn and run horizontally within the lamina. The lamina contains stellate neurons with densely spinous dendrites confined to the lamina; the axons of these cells appear to project to laminae III, IVB and IVCα as well as within IVA. Smooth or beaded dendritic stellate neurons are also present. The lamina contains pyramidal cell somata, the basal dendrites of which turn down into lamina IVB and the apical dendrites do not bear side branches until they enter lamina III (plate 5, fig. 19). The lower border of the lamina is sharply defined by the start of the axon plexus of lamina IVB.

Lamina IVB

A dense horizontally orientated axon plexus identifies this lamina. The lamina does not receive a terminal arborisation of thalamic axons. Pyramidal cells, spinous stellate neurons (including the largest spinous stellate form present in area 17 which characterizes the lamina, see plate 7, fig. 23, cell X) and smooth (or beaded) dendritic stellate neurons are present. The axon plexus in the lamina is derived from axon collaterals of pyramidal and stellate

neurons lying within the lamina, from neurons in the more superficial laminae and from the spinous stellate neurons of lamina IVCα. Lamina IVB is distinguished from lamina IVCα by the absence of pyramidal cell bodies in lamina IVCα and by the presence of a thalamic projection to lamina IVC. The axon plexus which is dense in lamina IVB is gradually thinned in the upper half of lamina IVCα where its chief composition is horizontal axon collaterals from spiny stellate neurons lying in laminae IVCα and IVB.

Lamina IVCα

This lamina receives projections from two types of presumed thalamic axon. One of these types also sends collaterals to laminae IVCβ and IVA while the other variety appears to be confined in distribution to IVCα. The lamina contains stellate cells with spinous dendrites and also stellate forms with smooth or beaded dendrites. No pyramidal cell bodies are found, but the apical dendrites arising from pyramidal cell bodies in laminae V and VI may start to bear side branches in this lamina. The apical dendrites of the largest pyramidal cells of lamina V become profusely spinous for the first time as they enter and pass through this lamina. The axons of spinous stellate cells of this lamina have been traced to laminae IVA, IVB, IVCβ, V and VI as well as ramifying within lamina IVCα itself.

Lamina IVCβ

This lamina receives a dense presumed thalamic projection from large axons that also project less profusely to laminae IVCα and also to lamina IVA. No pyramidal cells occur in this lamina and the apical dendrites of lower pyramidal cells undergo a marked reduction in the number of spines on their surface and often a reduction in diameter of the dendritic shaft on entering the lamina. The large population of spinous stellate cells in the lamina project heavily to lamina III, within IVC, and also to laminae V and VI. Stellate cells with smooth (or beaded) dendrites are also present in the lamina and their beaded axons form a prominent component of the general neuropil of the lamina.

Lamina V

A dense plexus of horizontally orientated axons forms the substance of the lamina. The axons are collaterals derived from pyramidal cells of all laminae and axons of stellate neurons at least of lamina IV, V and VI. The lamina contains pyramidal cells of many sizes often with recurrent vertically rising axon collaterals. Some of the smallest pyramidal cells have extremely fine, spine-free, apical dendrites and axons that seem principally recurrent. Neurons with smooth, beaded and sparsely spined dendrites are present (some with very large dendritic fields extending into laminae VI and as far as IVB) but the spinous stellate forms found in the divisions of lamina IV probably do not occur in lamina V. The lamina does not appear to receive a marked thalamic projection.

Lamina VI

This lamina is a zone of pyramidal neurons, neurons with smooth or beaded dendrites, and stellate neurons with sparsely spined dendrites lying between the white matter and the horizontal axon plexus of lamina V. Some of the stellate neurons with smooth dendrites are of very large size with dendrites extending as far as IVB. The lamina does not receive a marked thalamic projection.

DISCUSSION

It has been customary to divide cortical neurons into two major groups — pyramidal neurons and stellate neurons (for example, Sholl, '56; and class I and II of Globus and Scheibel, '67a). In the present study the neurons occurring in area 17 of the monkey seem rather to fall into three main categories on the basis of dendritic morphology — pyramidal neurons, spinous stellate neurons and stellate neurons with dendrites bearing few or no spines. These three groups are not only morphologically distinct but they have different distributions in relation to zones of thalamic axon termination. The neuron type most closely related to the heaviest terminal distribution of the geniculo-cortical projection is the spinous stellate cell. However, such neurons do not occur in lamina I which receives a thalamic projection and they are present in lamina IVB which does not ap-

pear to receive a direct thalamic projection.

It is difficult to classify the neurons of area 17 on the basis of whether their axons distribute locally (short axon or Golgi type II) or more distant to the cell body. Spatz, Tigges and Tigges ('70) have shown in Nauta stained material of squirrel monkey (*Saimiri*) visual cortex that neuronal components in the upper cortical laminae, down to and including the equivalent of IVB of the present study, project heavily to layer V and contribute also a projection to area 18. In the present study the pyramidal cells of lamina IVB upwards as well as often having collaterals projecting into the same lamina as their cell body seem to contribute to the fiber bands of both laminae IVB and V and there is usually a fine continuing axon process with occasional spines into layer VI. It is unclear in the present material whether this fine process becomes myelinated and leaves the cortex or terminates in layer VI. Many of the small to medium sized pyramidal neurons of laminae V and VI have axons that have a major recurrent system of axon collaterals and only a very fine process continues downward deep into lamina VI. The largest pyramidal cells of laminae V and VI and the largest spinous stellate cells of lamina IVB have stout initial axon segments that cease to impregnate not far from the cell body, presumably as myelination begins and it may be that these cells are the principal sources of extrinsic projections from the visual cortex. Cajal ('11) and Clark and Sunderland ('39) gave some evidence that the large spinous stellate neurons of lamina IVB (plate 7, fig. 23, cell X) give rise to axons leaving the visual cortex.

While some of the stellate neurons not having a marked population of dendritic spines have axons that distribute close to their own dendritic field, others have axons that have been traced into neighboring laminae outside the laminar extent of their dendrites. Since many of the stellate neurons with smooth, beaded or sparsely spined dendrites of laminae II and III as well as having a local axon distribution also contribute axon collaterals to the horizontal fiber plexus of lamina IVB, they cannot be considered as "short" axon cells having only a very local axon distribution close to their own dendritic field. Their axon distribution does, however, differ from that of pyramidal neurons most of whose axon collaterals generally travel considerable distances from the cell of origin even if terminating in the same lamina. In contrast to the stellate neurons with few or no spines, the axon distribution of the spinous stellate neurons of lamina IV seems to resemble the more widespread distribution of the axon collaterals of pyramidal cells rather than forming a close-knit local field.

Spine bearing dendrites of pyramidal cells are largely absent from laminae IVC (particularly IVCβ) and IVA. In lamina IVC there are no pyramidal cell bodies and an absence of pyramidal cell basal dendritic fields. In lamina IVCβ there is a reduction in the number of spines and absence of side branches on the apical dendrites rising from pyramidal cells in laminae V and VI. The basal dendrites of pyramidal cells with somata lying in lamina IVA turn basally out of the lamina to spread in lamina IVB. Side branches from the apical dendrites of these same cells are only given off as the dendrite enters lamina III. Lamina I differs from the other zones receiving a thalamic projection in also having within its boundaries a profuse spinous arborisation of pyramidal cell dendrites. While the spine bearing dendritic surface of pyramidal cells seems reduced in laminae IVC and IVA which might suggest they are not the primary target for geniculo-cortical axons, it is possible that thalamic contacts could be concentrated on the surface of the apical dendritic shafts in lamina IVC and on the pyramidal cell bodies in lamina IVA. However, in the case of the pyramidal cell somata electron microscopic studies of cortical synapses have so far suggested that thalamo-cortical axon terminals have a different morphology from those contacting pyramidal cell somata (Colonnier, '68; Lund and Lund, '70; Jones and Powell, '70; Garey and Powell, '71), and studies by Szentágothai ('65) suggest an intrinsic origin for axons contacting pyramidal cell bodies. The decrease in the number of spines on pyramidal cell apical dendrites as they pass through lamina IVCβ in the normal monkey has apparently no corre-

late in other animals where the apical dendrites remain densely spiny through lamina IV unless the animal is reared under conditions of visual deprivation (Globus and Scheibel, '67b; Valverde, '68; Valverde and Ruiz-Marcos, '69).

Each division of lamina IV is unique in its relationship to pyramidal cell dendritic surface and in the axon projections of its population of spinous stellate cells. This suggests that each subdivision of lamina IV has a different functional role even though laminae IVA, IVCα and IVCβ can receive at least some of their input from the same thalamic axon. In considering the different laminar projections of the axons of each group of spinous stellate neurons and assuming that they may influence directly or indirectly pyramidal cells (particularly the basal dendritic fields) in their zone of axon termination, it is suggested that pyramidal cells of lamina III will be influenced by the stellate neurons of lamina IVCβ and the pyramidal neurons of laminae IVB and IVA will be influenced by the projection from lamina IVCα. Both groups of pyramidal cells may, however, share a projection from the spinous stellate neurons of lamina IVA.

The thalamic projection to lamina I appears limited to a band just above the midpoint of the lamina. No correlation has been seen between this level of projection and any other morphological feature localized at this same level. Since the thalamo-cortical axons projecting to lamina IV have not been traced to lamina I and there are apparently no axons in lamina I of similar morphology to those projecting to lamina IV, it is probable that the projection to lamina I is from a different thalamic axon population from those terminating in the divisions of lamina IV.

The distribution of spinous non-pyramidal neurons correlates with the distribution of simple and monocular responses of cells, and pyramidal neuron distribution correlates with complex, binocular responses as found physiologically by Hubel and Wiesel ('68). Although no evidence for differences in physiological function has yet been described for the subdivisions of lamina IV or for lamina I, Hubel and Wiesel ('69 and personal communication) have anatomical evidence that the magnocellular laminae of the lateral geniculate nucleus project to lamina IVCα and that the parvocellular laminae of the lateral geniculate project to laminae IVCβ and IVA. These findings suggest that the large axons, described as sending many collaterals to IVCβ, fewer to IVCα and projecting also to IVA, could arise from neurons of the parvocellular dorsal geniculate laminae. However, the sparse collateralisation in IVCα of these axons observed in the Golgi material may present a problem to such interpretation since terminal degeneration from lesions in the parvocellular geniculate laminae appears limited to precisely the boundaries of IVCβ and to IVA. The finer axons distributing chiefly in IVCα may arise from neurons in the ventral magnocellular laminae.

In this study four subdivisions have been included in lamina IV. This lamina is characterized by the presence of stellate neurons with heavily spined dendrites. Hassler ('66) has suggested that in the monkey the broad division of III should be extended to include all the upper zone containing pyramidal cells. By this criterion, only IVC of the present study would be considered lamina IV; IVB and IVA would then be designated divisions of lamina III. It would seem advisable to wait until physiological studies have produced more information concerning the functional similarities and dissimilarities between the various laminae before attempting to defend either of these or other numbering systems.

In attempting to correlate ultrastructural studies of cortical synaptology with particular cell types, it becomes difficult to be certain whether dendritic spines observed using the electron microscope in the divisions of lamina IV belong to pyramidal or stellate neurons. Outside lamina IV spines belong in the great majority of cases to pyramidal cells. In laminae IVCα and β spines are more likely to belong to stellate cell dendrites than to pyramidal cells. In laminae IVB and IVA spines could belong to either pyramidal or stellate cells. Smooth or beaded dendrites seen by electron microscopy in any layer are likely to belong to stellate neurons having these characteristics by the light microscope. However, the spines on the spiny stellate

neurons of lamina IV can be quite widely spaced on the dendrites which might lead to misinterpretation of apparently spine-free segments as belonging to smooth dendritic forms. Moreover, some of the largest pyramidal cells of laminae V and VI can bear relatively few spines on their basal dendrites and segments of their dendrites seen under the electron microscope could potentially be confused with the large spine-free stellate neurons occurring in these layers. Strongly beaded axons are almost certainly those of spine-free stellate neurons except in lamina IVC where there is the possibility that some also belong to spinous stellate cells.

Many of the morphological observations of Valverde's ('71) study of laminae III–V are shared by the current work. However, several differences are evident that are of particular interest. One of the basic differences between the two studies is the positioning of the limits of the various laminae. The way in which the cortex is divided into horizontal laminae can be considered largely a matter of choice by the investigator. However, the boundaries established in the present study have been used to indicate anatomical differences and, therefore, perhaps functional differences between succeeding levels. Each lamina of the present study is internally homogeneous in its neuronal composition and these boundaries, established on the basis of the distribution of intrinsic neuronal populations, are found also to relate to the zones of thalamic axon termination. The laminar boundaries described in Valverde's study neither define zones of specific neuron composition nor zones of thalamic axon termination. The lower border of his lamina III lies below the narrow band of thalamic axon termination included in lamina IVA of the present study (he did not apparently impregnate the spinous stellate cells within lamina IVA). The junction of his laminae IVA and IVB apparently occurs in the middle of the present study's lamina IVB, i.e., his lamina IVA includes part of the upper horizontal fiber plexus cutting across the sharp upper border of this fiber band. Valverde's lamina IVB has an upper part containing pyramidal cell bodies and no thalamic axon projection and a lower half (which includes lamina IVCα of the present study) containing no pyramidal cell bodies and receiving a thalamic projection.

A clear distinction has been made in the present study between pyramidal cells and spinous stellate neurons. Valverde ('71) does not make such a distinction but describes large stellate neurons of his lamina IVB as often having a well developed apical dendrite. In the present study it is felt that an apical dendrite is such a distinct specialization of a neuron's dendritic field that such cells should be considered separately from neurons having no such specialized dendrite. Justification for this distinction is found in the different distribution of these two forms of spinous neuron at different depths in the cortex.

A further difference in the conclusions of the present study from that of Valverde ('71) relates to the neuronal composition of the lower area of thalamic axon projection, called in the present study laminae IVCα and β. Valverde describes glomerular arrangements of neurons in his lamina IVC, including both spinous and beaded dendritic ("clewed") stellate neurons. The author of the present study sees similar such clumps of neurons impregnated in the Golgi Rapid material but here they seem to be due more to the vagaries of Golgi staining than to be distinct anatomical entities. The same neuron types occur within the clumps as are stained separately without a surrounding mass of axonal and dendritic processes.

In the present study a division has been made of lamina IVC into α and β parts on the basis of the difference in axon projection of the spinous stellate neurons predominating in the upper part compared to the lower part. The spinous neurons of IVCβ do not appear to project to laminae IVB or IVA but arborise profusely in lamina III. In contrast, axons of spinous stellate neurons in lamina IVCα have not been traced above lamina IVA. Valverde ('71) has, however, traced axon trunks from spinous cells in his lamina IVB (corresponding in level to this study's IVCα) as far as lamina I before they collateralise. The author feels this additional projection does not invalidate the separation of IVC into two divisions as described in the

present study since such a projection still does not resemble that shown by the spinous neurons of the lower half of the lamina.

The Golgi Kopsch technique used by Garey ('71) in his study of monkey and cat visual cortical areas was found in the present study to produce considerable malformation by shrinkage of the impregnated neurons as compared to the Golgi Rapid material. Comparison of the Golgi Kopsch and Rapid material of the present study suggests that in the Kopsch dendritic beading is more pronounced, the dendritic fields often appear reduced and, if no counterstain is used, the laminar boundaries are difficult to determine since the axon plexuses are rarely stained. In the present study the stellate neurons with spinous dendrites of the divisions of lamina IV showed little or no dendritic beading in the Golgi Rapid material; the sparsely spined neurons observed in the present study were of medium size compared to the other forms of stellate cells, not small as were those described by Garey; the largest stellate neurons with smooth dendrites were found in the present study to have cell bodies lying in laminae V and VI, whereas the largest spinous stellate neuron variety occurs in layer IVB. The number of any particular cell type present is extremely difficult to assess in Golgi material and while in agreement with Garey ('71) that the spinous stellate neurons seem to form a large population in the middle region of the cortex of area 17 (in the divisions of IV as defined in the present study) other forms of stellate neuron were impregnated in roughly equal numbers throughout the cortex.

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PLATE 1

EXPLANATION OF FIGURES

1 Nissl stained section of area 17 of *Macaca mulatta* from the perimacula area of the occipital operculum. Average depth in this area from pia to white matter in frozen sections is 1,700 μ; average depth for lamina I = 100 μ, lamina II and III = 650 μ, lamina IVA = 70 μ, lamina IVB = 150 μ, lamina IVCα = 140 μ, lamina IVCβ = 140 μ, lamina V = 210 μ, lamina VI = 240 μ.

2 Golgi Rapid preparation of perimacula area 17. The position of the stria of Gennari is indicated by the line G. Large pyramidal cells of Meynert can be seen in lamina VI.

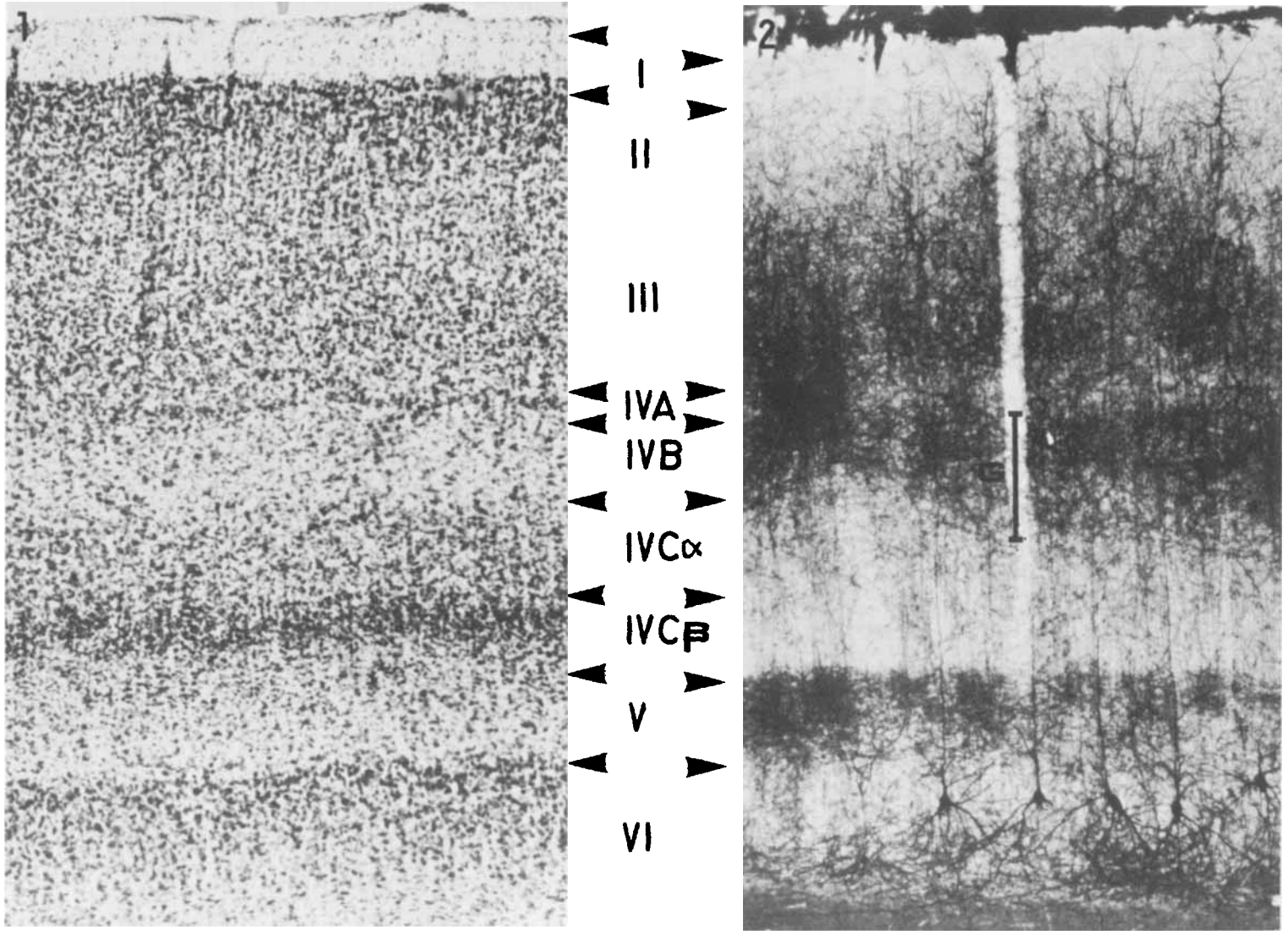

1
I
II
III
IVA
IVB
IVCα
IVCβ
V
VI
2

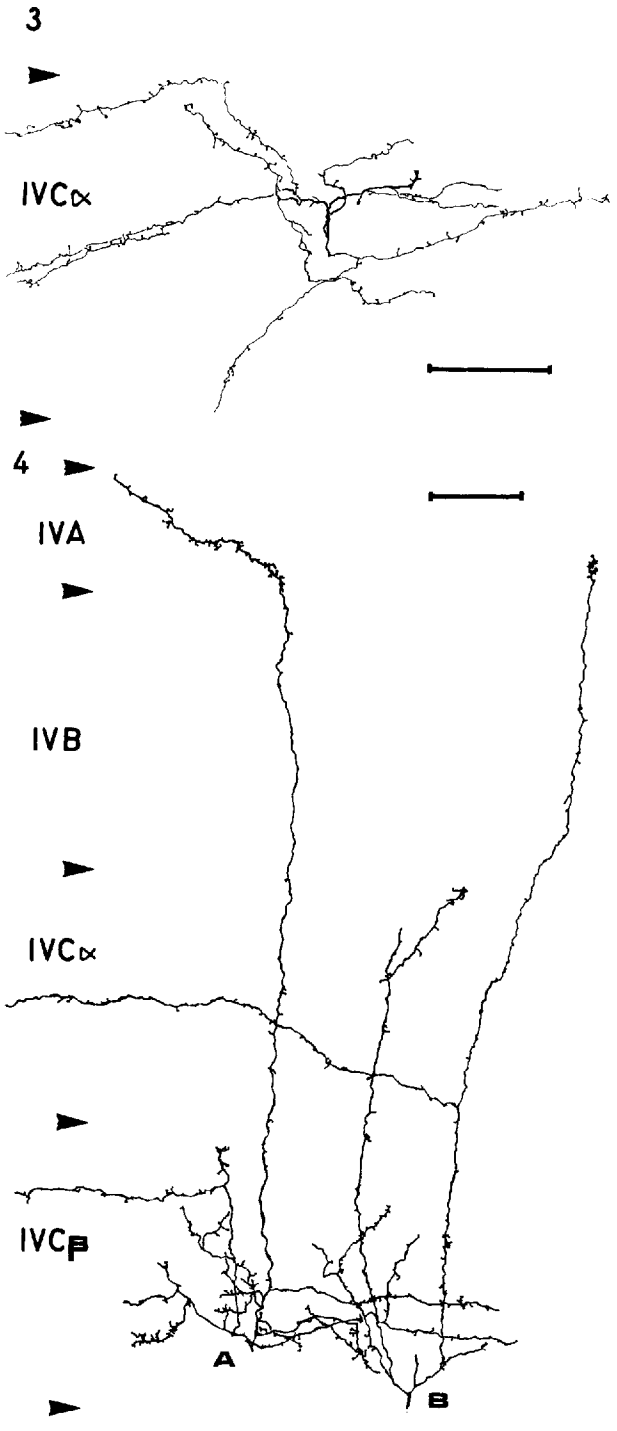
PLATE 2

EXPLANATION OF FIGURES

3 Typical axon of extrinsic origin (believed to arise from neurons in the lateral geniculate nucleus) with distribution confined to lamina IVCα. Golgi Rapid, scale, 50 μ.

4 Two axons (A and B) of extrinsic origin (believed to arise in the lateral geniculate nucleus) with distribution of collaterals in IVCβ, IVCα and IVA. Golgi Rapid, scale, 50 μ.

5 Degenerating geniculo-cortical axons in laminae III–V, stained by the Fink and Heimer (Method I) technique. Scale, 50 μ.


3
IVCα
4
IVA
IVB
IVCα
IVCβ
A
B

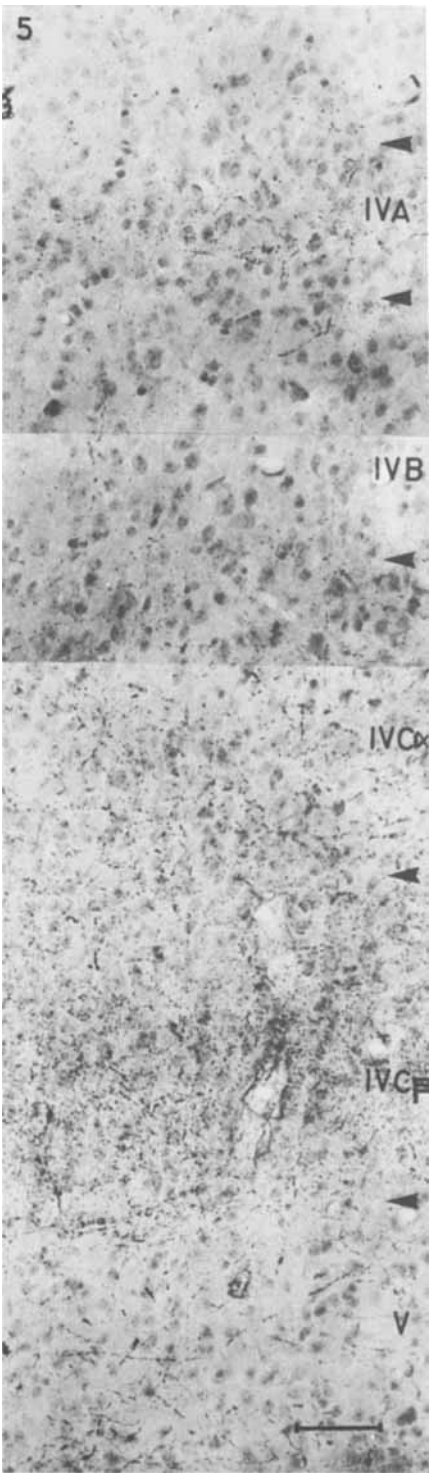

5
IVA
IVB
IVCα
IVCβ
V

PLATE 3

EXPLANATION OF FIGURES

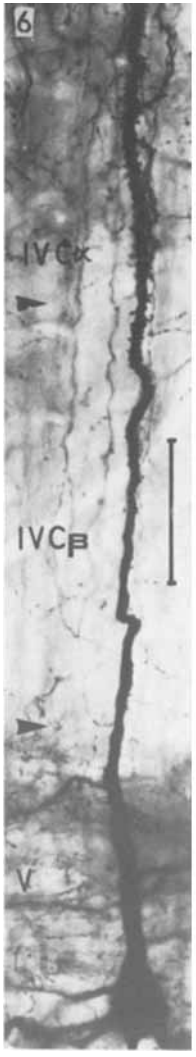
6 Apical dendrite of the largest form of pyramidal cell of lamina V as it passes through laminae V, IVCβ and IVCα. The shaft becomes profusely spinous only on reaching lamina IVCα. Golgi Rapid, scale, 50 μ.

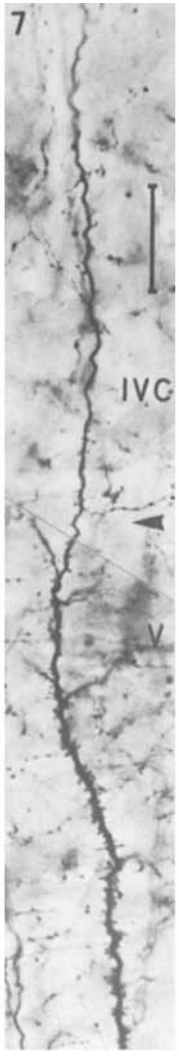
7–8 Apical dendrites of two medium size pyramidal cells of lamina VI, passing through laminae V and IVC. The shafts are profusely spinous in lamina V but on entering IVC become sparsely spined and are reduced in diameter. Golgi Rapid, scale, 50 μ.

9 Small pyramidal cell of lamina V with fine apical dendrite (ApD) and stout recurrent axon (Ax) passing through lamina IVC. Golgi Rapid, scale, 50 μ.

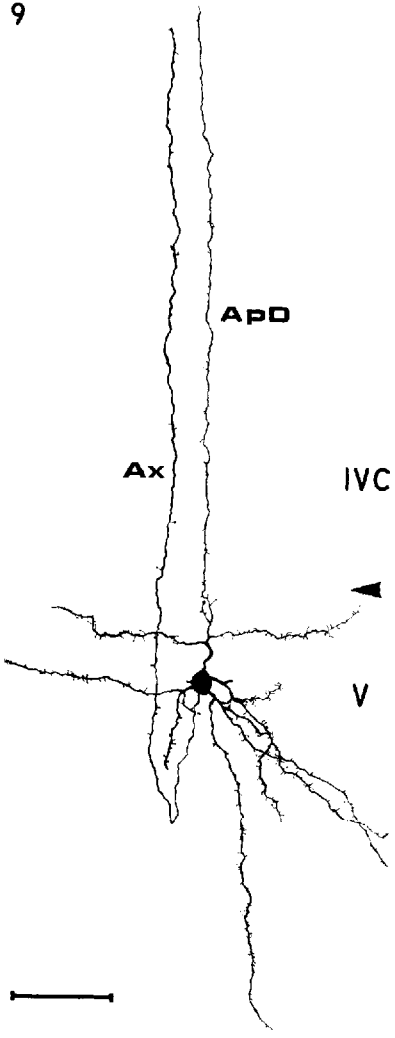
10 Degenerating geniculo-cortical axons, stained by the Fink and Heimer (Method I) technique, rising as fine fibers through layer II to arborise in a horizontal plexus in the middle region of lamina I. Scale, 50 μ.

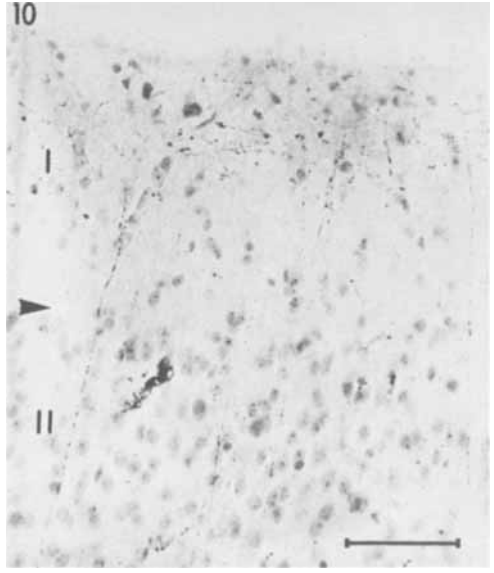
11 Axon type distributing in lamina I that may be of geniculate origin. Processes 1, 2 and 3 extend for several hundred micra in lamina I. Golgi Rapid, scale, 50 μ.


6
IVCα
IVCβ
V


7
IVC
V


8
IVC
V


9
ApD
Ax
IVC
V


10
I
II

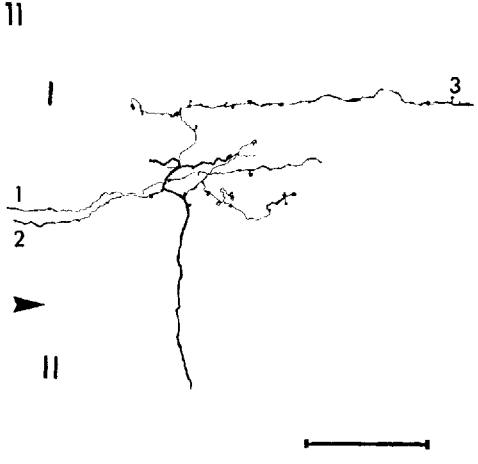

11
I
3
1
2
II

PLATE 4

EXPLANATION OF FIGURES

12 Stellate neuron with spinous dendrites in lamina IVCβ. Both recurrent axon trunks arborised in lamina III, one is shown (AC). Golgi Rapid, scale, 50 μ.

13 Stellate neuron of lamina IVCβ. A descending axon collateral reaches lamina VI. Golgi Rapid, scale as in figure 12.

14 Comparison of axon morphology. W, collaterals of the largest variety of beaded axon found in lamina IVC. X, initial axon region of a pyramidal cell of lamina II. Y and Z, collaterals of extrinsic axons, believed to be of geniculate origin, in lamina IVCβ. Golgi Rapid, scale, 50 μ.

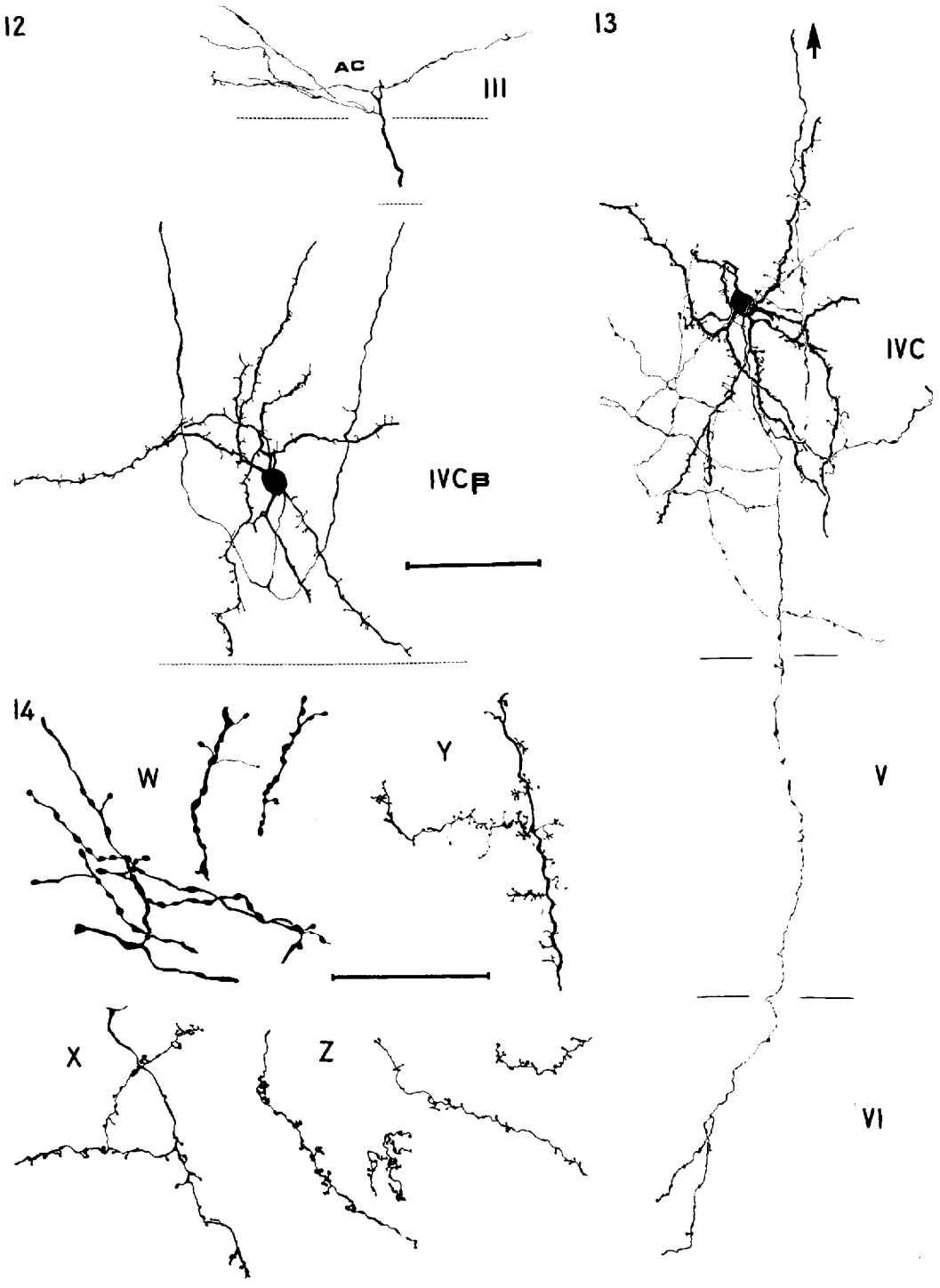

12
AC
III
IVCβ
13
IVC
V
VI
14
W
Y
X
Z

PLATE 5

EXPLANATION OF FIGURES

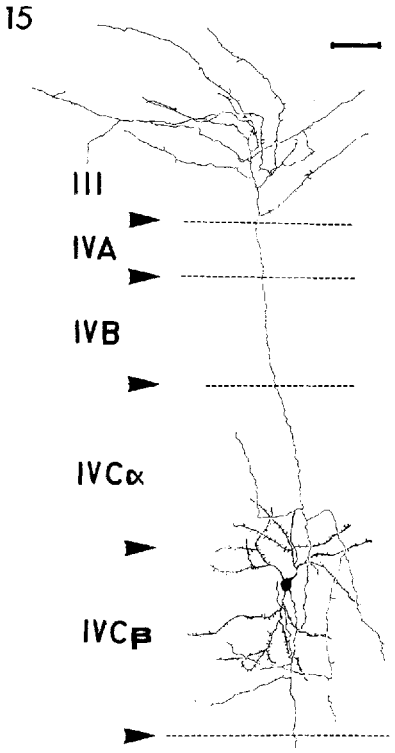
15 Stellate neuron with spinous dendrites lying in lamina IVCβ. One recurrent axon collateral arborises in lamina III. Golgi Rapid, scale, 50 μ.

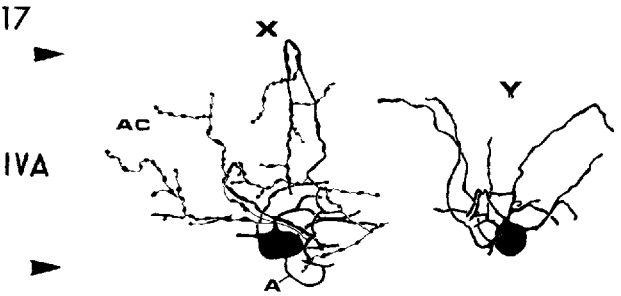
16 Axon bundles rising from neurons in lower cortical laminae (especially of the neuron type shown in fig. 15) arborising in lamina III. The start of their arborisation defines the upper limit of lamina IVA. Golgi Rapid, scale, 50 μ.

17 Stellate neurons with beaded axons (cell X) and smooth dendrites (cell Y) present in lamina IVA. Golgi Kopsch, scale as in figure 18.

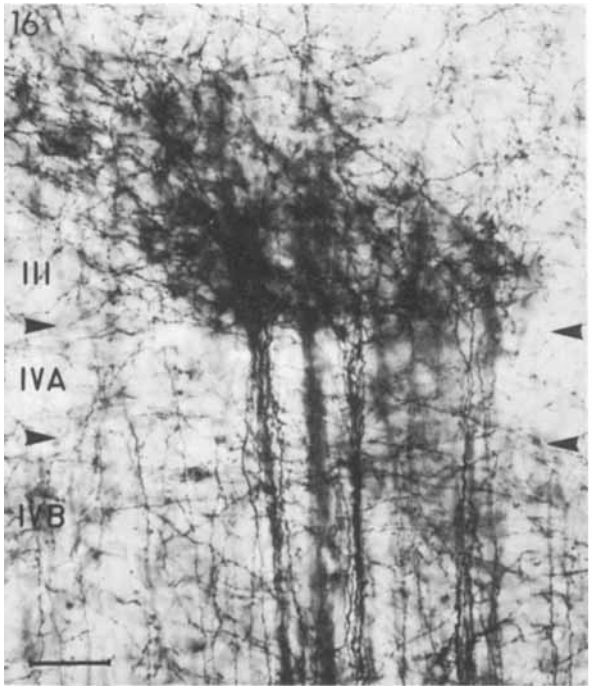
18 Stellate neurons with spinous dendrites and fine axons present in lamina IVA. A indicates initial axon segment. Golgi Rapid, scale, 50 μ.

19 Typical pyramidal cell dendritic orientation around lamina IVA. The basal dendrites of pyramidal cells in lamina IVA turn basally into lamina IVB where they spread horizontally. Side branches of the apical dendrite arise as it enters lamina III. The basal dendrites of pyramidal cells at the bottom of lamina III tend to lie horizontally above IVA but do occasionally pass vertically through the lamina. Golgi Rapid, scale, 50 μ.


15
III
IVA
IVB
IVCα
IVCβ


17
IVA
X
Y
AC
A


18
IVA
A
A


16
III
IVA
IVB

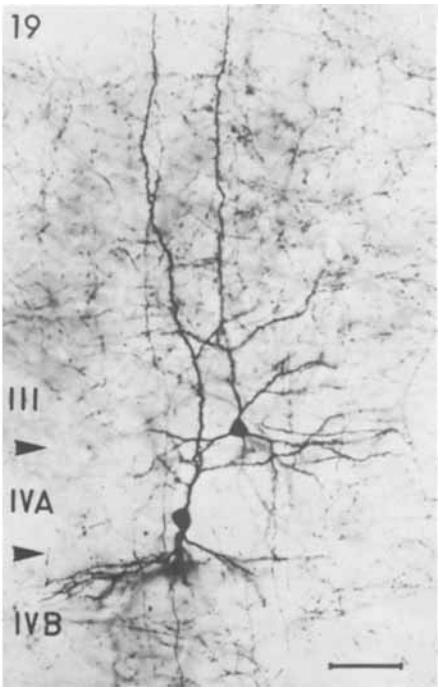

19
III
IVA
IVB

PLATE 6

EXPLANATION OF FIGURES

20 Stellate neuron of lamina IVCβ with coarser spines and stouter dendrites than the neuron type shown in figure 21. The axon of this type of spinous stellate neuron is beaded in the finer collaterals and shows abrupt changes in diameter along its length. Golgi Rapid, scale, 50 μ.

21 Stellate neuron, with fine spines on slender dendrites, found in lamina IVCβ. Golgi Rapid, scale, 50 μ.

22 Variety of stellate neurons found in lamina IVCα. X, shows the dendrites; the marked dendritic beading may have been enhanced by shrinkage which occurs in the Kopsch preparations. A indicates the initial axon segment. Y, shows the axon morphology of a similar cell. Golgi Kopsch, scale as in figure 20.

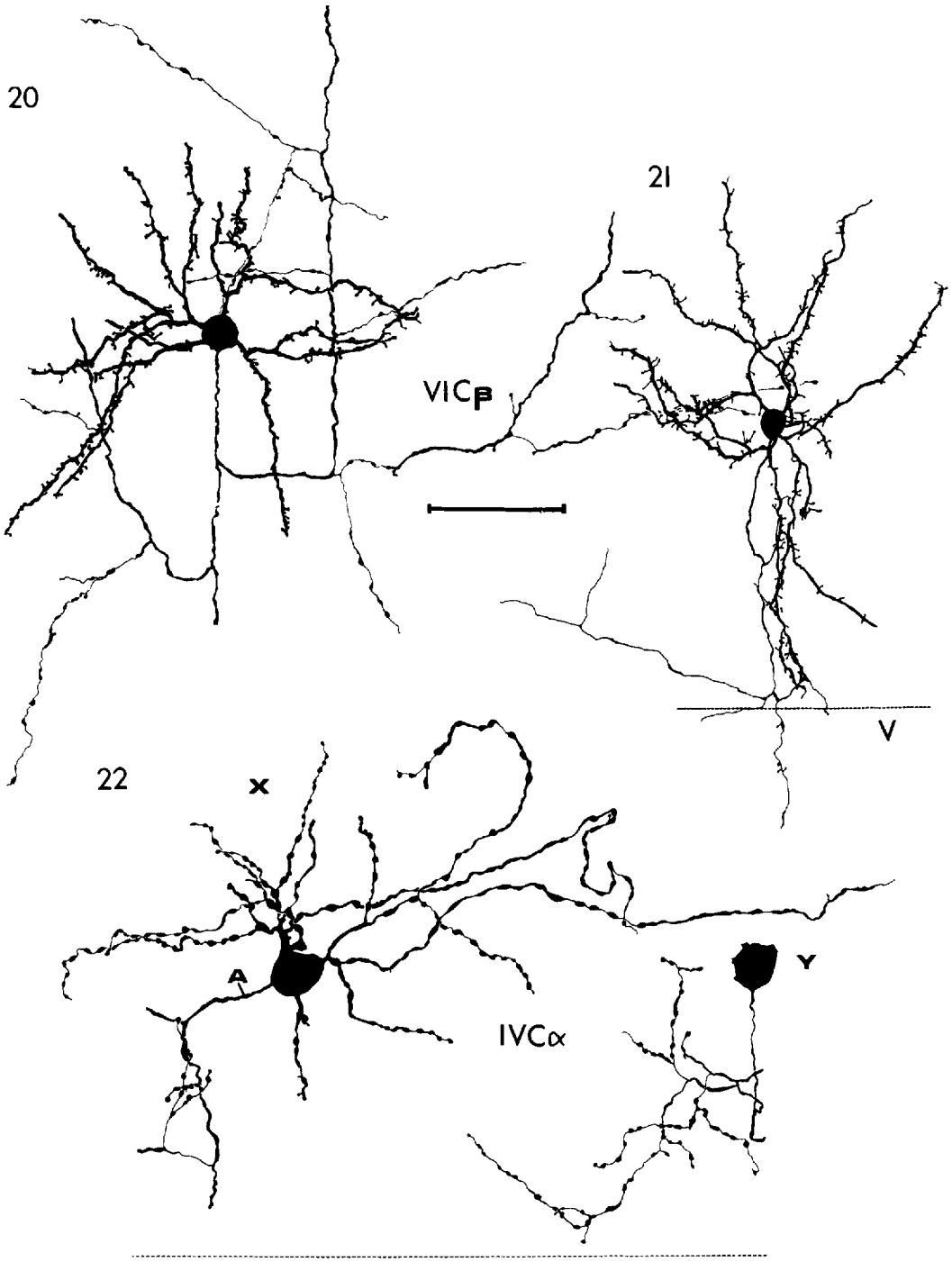

20
21
VICβ
V
22
X
A
IVCα
Y

PLATE 7

EXPLANATION OF FIGURE

23 Cell X, largest variety of stellate neuron with spinous dendrites, a unique feature of lamina IVB. Golgi Rapid, cells Y and Z, stellate neurons with spinous dendrites of lamina IVCα. ACY indicates an axon collateral of cell Y which enters lamina IVA. Golgi Rapid, scale, 50 μ.

23

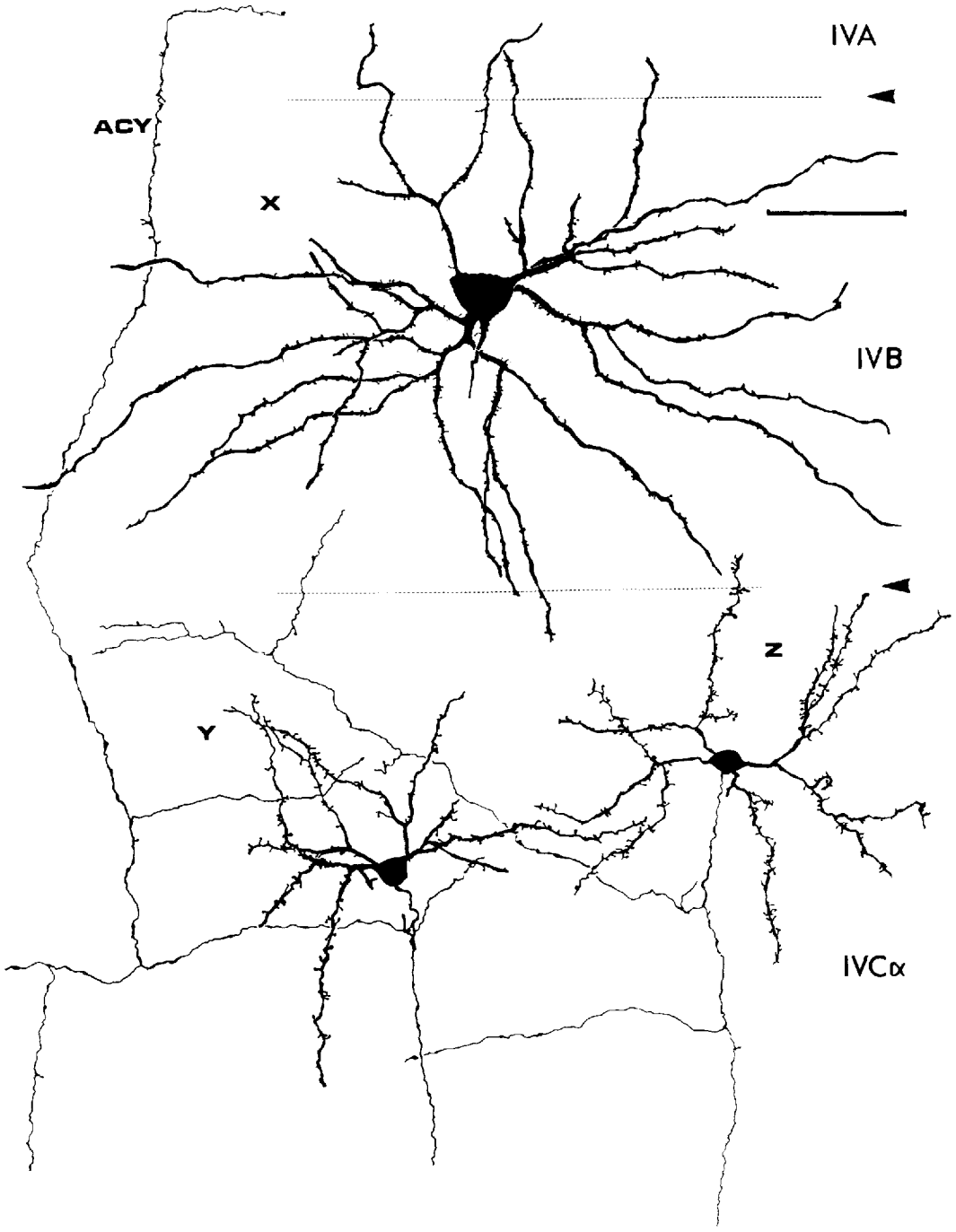


PLATE 8

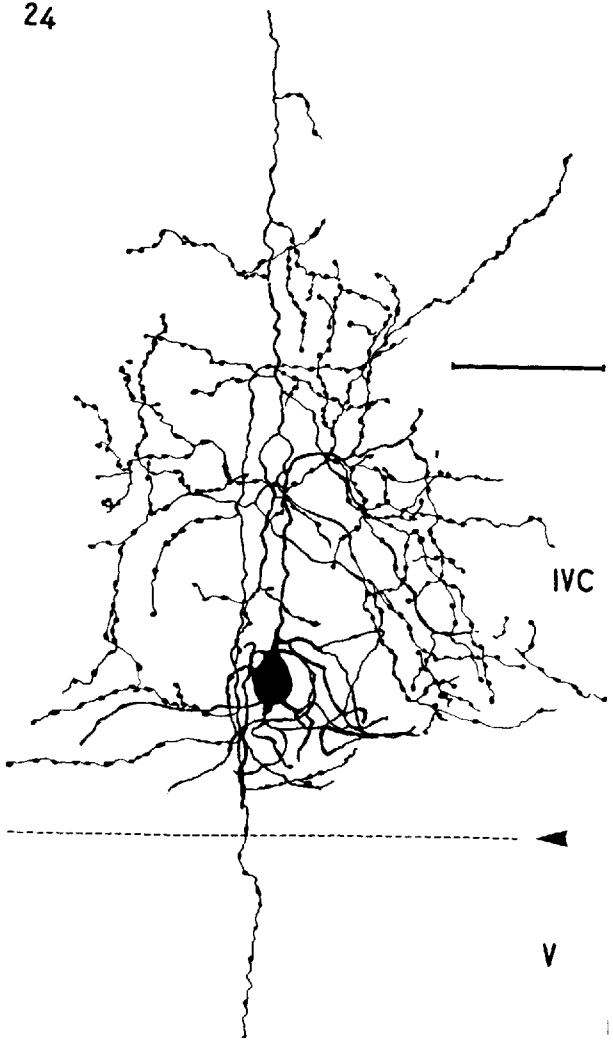
EXPLANATION OF FIGURES

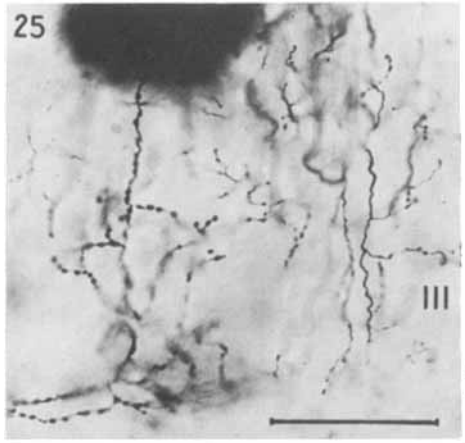
24 Stellate neuron with limited field of smooth dendrites and extensive beaded axon typical of lamina IVCβ. Golgi Kopsch, scale, 50 μ.

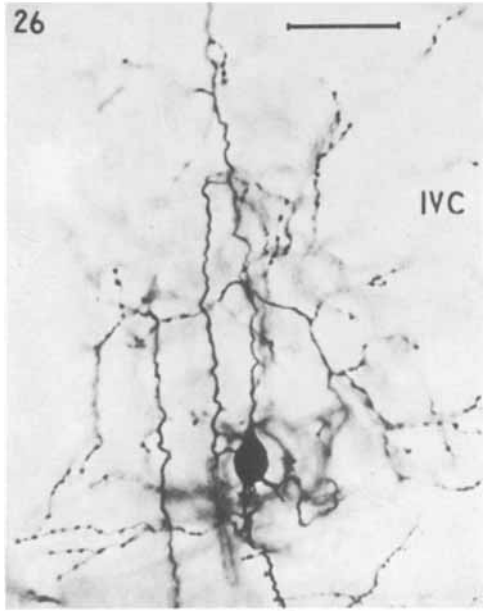
25 Two varieties of beaded axons found in lamina III arising from neurons with smooth or beaded dendrites. Golgi Kopsch, scale, 50 μ.

26 Photograph of the neuron shown in figure 24 for purposes of comparison of actual material with drawings. Golgi Kopsch, scale, 50 μ.

27 Similar stellate neuron to that shown in figure 24 with axon collaterals extending into laminae V and VI. Golgi Kopsch, scale, 50 μ.


24
IVC
V


25
III


26
IVC

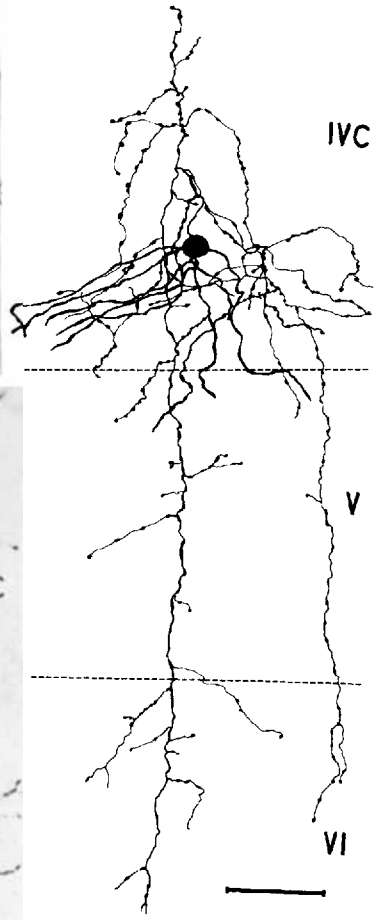

27
IVC
V
VI

PLATE 9

EXPLANATION OF FIGURES

28 Stellate neuron with beaded axon (a, initial axon segment) and smooth dendrites in laminae V and VI. Golgi Kopsch, scale as in figure 29.

29 Stellate neuron in laminae IVCα and β with smooth dendrites and fine axon (a, initial axon segment) without beading. Golgi Kopsch, scale, 50 μ.

28

29

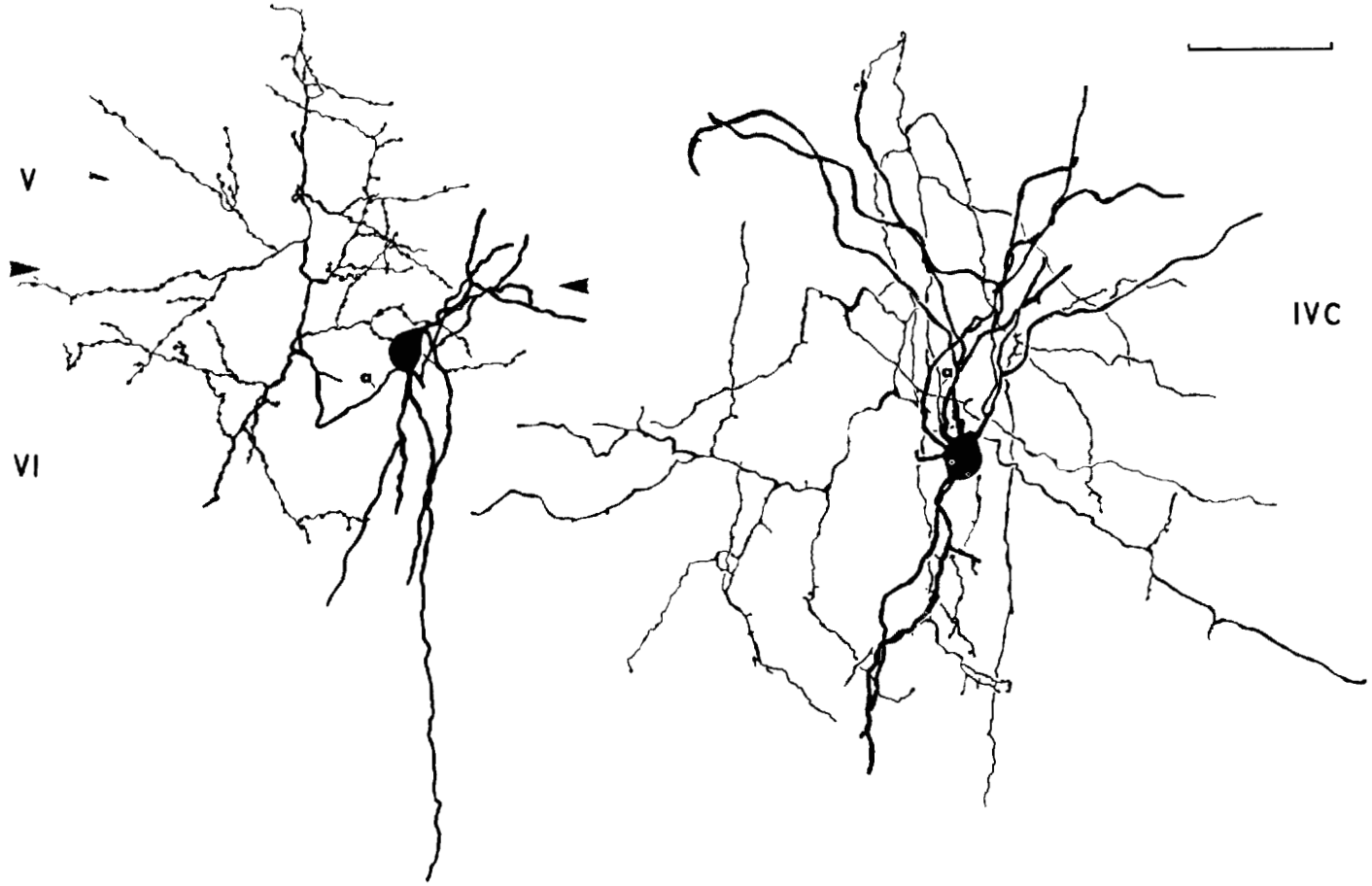


PLATE 10

EXPLANATION OF FIGURE

30 X, stellate neuron in lamina II with very sparsely spined dendrites and axon (A, initial segment) which arborises in lamina I (ACX). Golgi Rapid. Y, stellate neuron of lamina I with very sparsely spined dendrites and beaded axon spreading in laminae II and III. Axon process with arrow continued downward to lamina IVB axon plexus. Golgi Rapid. Z, stellate neuron of lamina III with smooth dendrites and axon with heavily beaded collaterals. Golgi Rapid, scale, 50 μ.

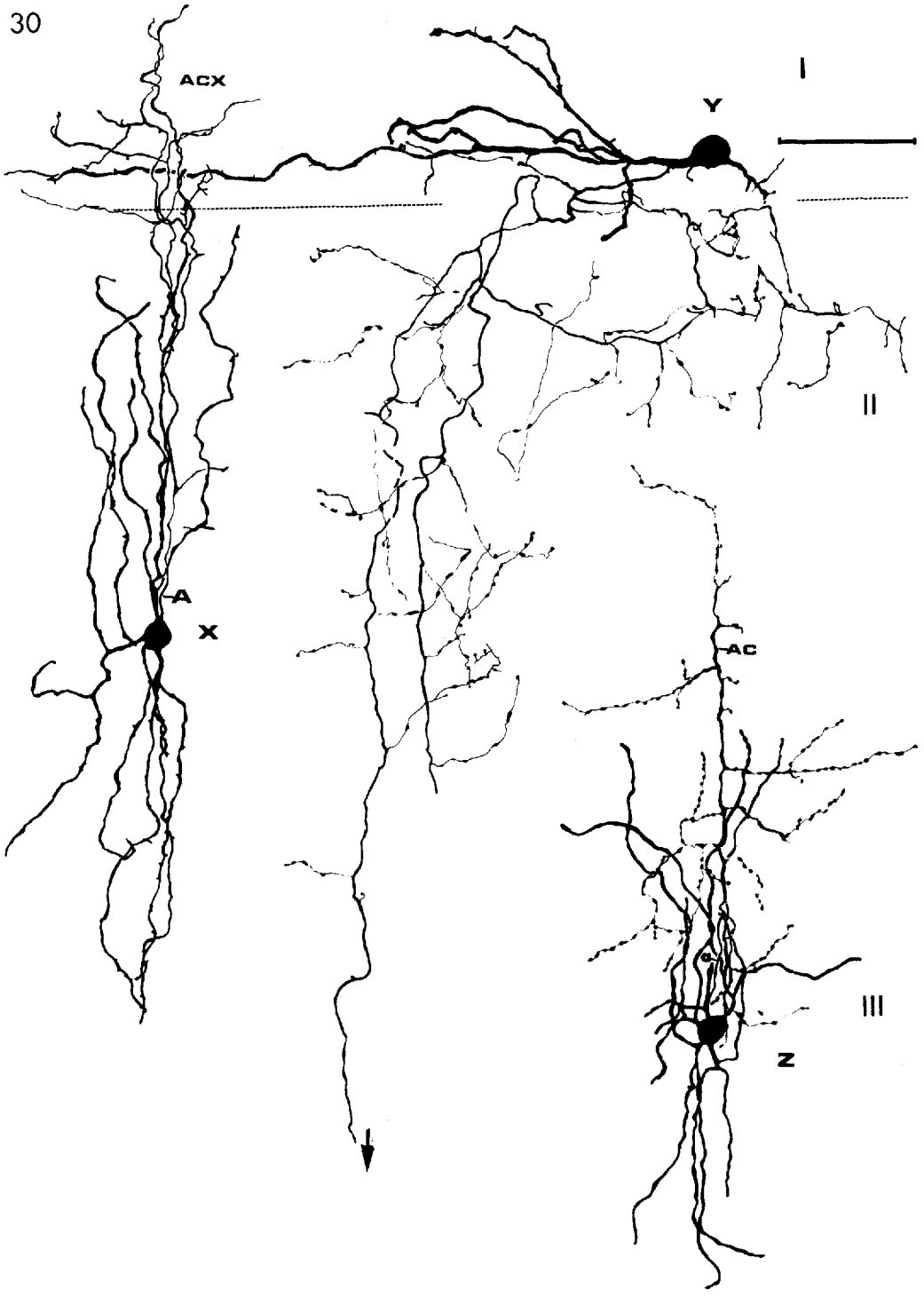

30
ACX
Y
I
II
A
X
AC
III
Z

PLATE 11

EXPLANATION OF FIGURE

31 X, stellate neuron of lamina II with smooth dendrites and axon with beaded collaterals. A indicates initial axon segment. The axon collateral with arrow continued downward to lamina IVB. Golgi Rapid. Y, stellate neuron of lamina I–II border region with smooth dendrites and fine axon. Golgi Rapid. Z, stellate neuron of lamina II with smooth and partially beaded dendrites and with a beaded axon with a stout collateral branch to lamina IVB. Golgi Kopsch. Scale, 50 μ.

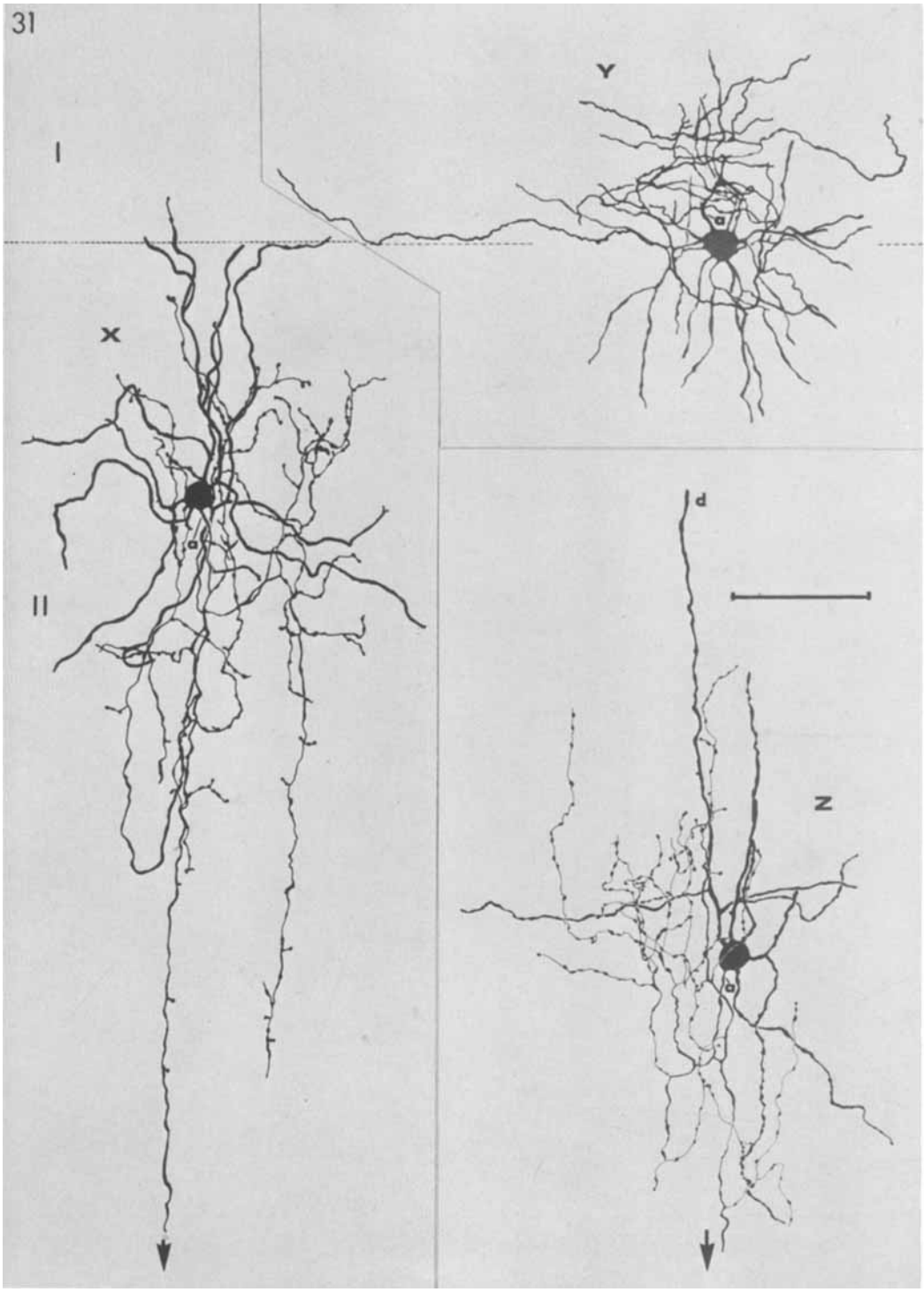

31
I
II
X
Y
Z
d

PLATE 12

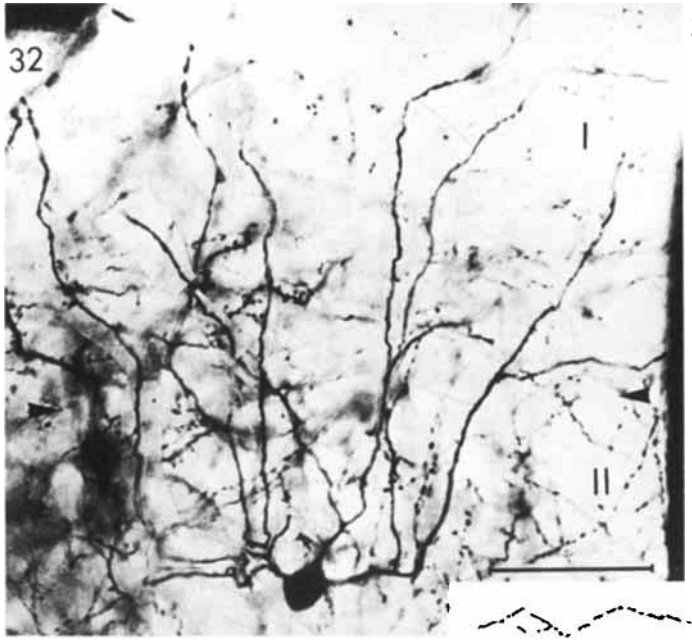
EXPLANATION OF FIGURES

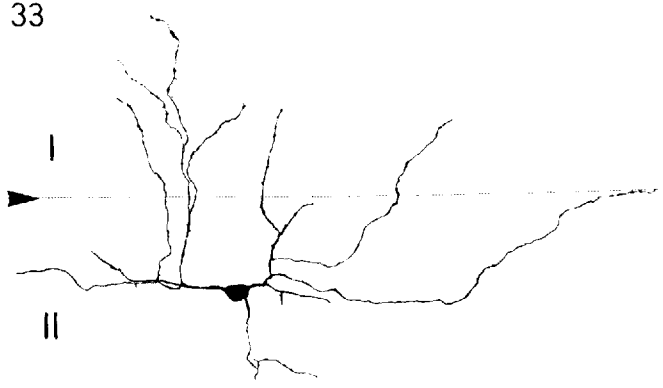
32 Photographic reconstruction of a stellate neuron of lamina II-I. The smooth dendrites spread and rise in a narrow vertical plane. Golgi Rapid. Scale, 50 μ.

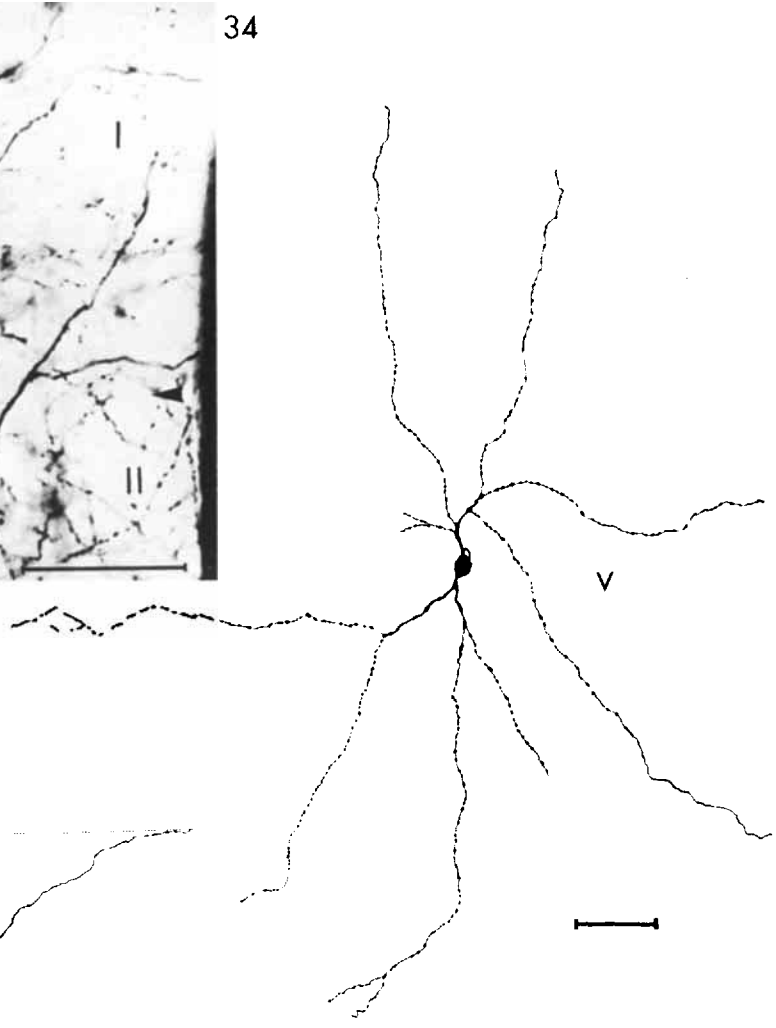
33 A similar stellate neuron to that shown in figure 32. The dendrites lie in a narrow vertical plane. Golgi Rapid, scale as in figure 34.

34 Stellate neuron with beaded dendrites (axon not impregnated) in lamina V; from a horizontal section 90 μ thick. Golgi Kopsch, scale, 50 μ.

35 Stellate neuron with smooth dendrites extending from lamina IVB to lamina VI. The axon was not impregnated. Golgi Rapid, scale as in figure 34.


32
I
II


33
I
II


34
V

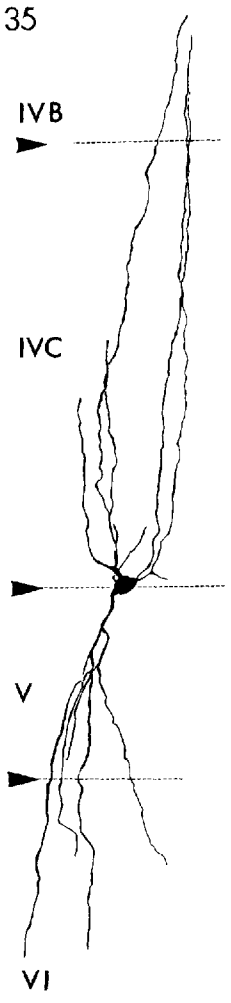
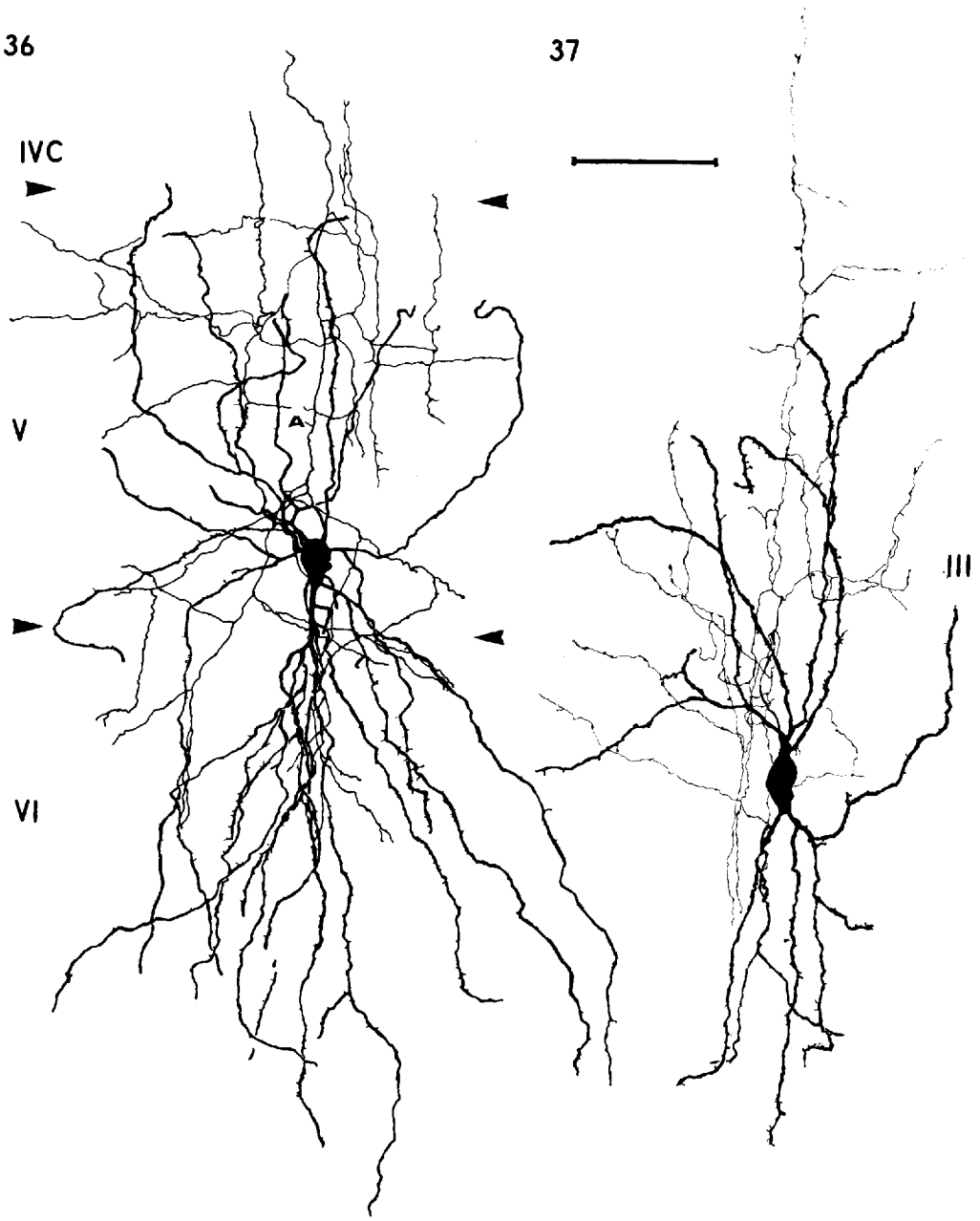

35
IVB
IVC
V
VI

PLATE 13

EXPLANATION OF FIGURES

36 Stellate neuron with sparsely spined dendrites extending from lamina IVC to lamina VI. The axon (A indicates initial segment) is fine without beading. Golgi Kopsch. Scale as in figure 37.

37 Stellate neuron of lamina III with sparsely spined dendrites. The axon is fine without prominent beading. Golgi Rapid, scale, 50 μ.


36
37
IVC
V
VI
III