THE ORGANIZATION OF THE VISUAL CORTEX IN THE CAT

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In a previous paper (Sholl, 1953) the nature of the organization of the dendritic fields of cortical neurons was examined. The present study applies quantitative methods to the examination of the axonal distributions of cortical neurons and to the afferent supply to the visual cortex of the cat. The cortex is an aggregate of neurons infiltrated by afferent axons arising from different parts of the nervous system. This aggregate may be divided into subaggregates or groups wherein membership of a particular subaggregate is determined by the distribution of the processes of the neurons. The organization of the cortex is discussed in terms of certain subaggregates and their relationships to the incoming afferent fibres.

Neurons have been classified in accordance with the joint distributions of their axons and dendrites, as revealed in histological preparations made by the Golgi rapid method. These results have been compared with the neuronal density distributions found in Nissl preparations, and both relative and absolute estimates of the densities of the different types of neuron computed. The resulting neuronal organization has been further examined with reference to the afferent supply to the cortex.

These results lead only to a partial understanding of cortical activity but they supply knowledge about the number of afferent fibres, the number of efferent fibres and the quantitative relationships subsisting between these fibre groups and the cortical neurons; this knowledge is essential for progress in cortical physiology.

METHODS

This study was made on some 500 sections of the visual cortex of 21-day-old kittens stained by the Golgi rapid (osmic-dichromate) method and cut at 100–160 μ.

Each section was examined for 'completely' stained neurons; this criterion was considered to be satisfied if (*a*) the dendrites of a neuron appeared to be complete and uncut by the knife, and (*b*) if the axon could either be traced into the white matter or, tapering, appeared to end in the cortex. No other neurons were catalogued.

The neurons were classified into seven groups in accordance with the joint distribution of their axons and dendrites; neurons that did not satisfy the criteria of any of the groups were noted separately. This scheme of classification is shown in Fig. 1. Less than 2·5 % of the neurons studied failed to satisfy any of the criteria; if the 'inverted pyramid' type of neuron were classified as a deformed stellate cell (S_3), then even fewer neurons would be excluded.

Since the thickness of the cortex is highly variable and changes in curvature produce changes in thickness of cortical laminae which do not vary directly with the depth of the laminae, measurements of the absolute and relative depths of cells

are misleading (Bok, 1929). Consequently, the positions of the neurons were described in terms of zones that are easily recognizable in both Nissl and Golgi preparations. These zones are as follows:

Zone 1 The outermost, almost neuron free, layer.
Zone 2
Zone 3 The region of Gennari's line.
Zone 4
Zone 5 The region of the deep layer pyramids.
Zone 6

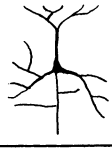
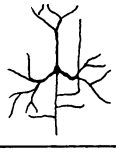
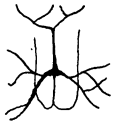
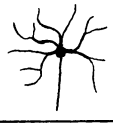
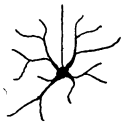
	Type	Description
	P_1	Pyramidal cell with unbranched axon to white matter
	P_2	Pyramidal cell with branched axon to white matter
	P_3	Pyramidal cell with branched axon to white matter and recurrent collaterals
	P_4	Pyramidal cell with axon forming recurrent collaterals and branches only
	S_1	Stellate cell with axon distributed within the dendritic field of the cell
	S_2	Stellate cell with axon to white matter
	S_2	Stellate cell with axon to outermost cortical zone

Fig. 1. Diagrams and description of the principal types of neuron found in the cerebral cortex.

Zones, 1, 3 and 5 are clearly recognizable, zones 2 and 4 are merely intercalated between these primary zones, while zone 6 is that part of the cortex between the primary zone 5 and the white matter. In the actual records zones 2 and 6 were subdivided into upper and lower portions but, since these subdivisions appeared to serve no useful purpose, the positions of the various neurons were finally only referred to the six zones described. There is no sharp division between any two zones, with the possible exception of zones 1 and 2.

The distributions of the terminations of the incoming axons were studied on the same preparations.

The sections used for the Nissl preparations were fixed by the perfusion of formol saline, embedded in paraffin and stained by buffered thionine. The total shrinkage factor is of the order 25%.

RESULTS

The organization of cortical neurons

The results of this survey are shown in Table 1. Altogether 553 complete neurons were available and thirteen (2·5%) did not fall within the present classification.

Since the method of staining is selective, it is desirable to have some indication that the types and numbers of cells studied form an adequate representation of the cell populations of the different zones. Complete certainty is unattainable but it is possible to show that the sampling is reasonably representative.

Table 2 shows the results of a comparison between the present sample and Nissl sample. The first two columns show the zones and their approximate thicknesses; column 3 states the cell densities at different depths (Sholl, 1953). Column 4 gives the mean zonal densities and column 5 the total numbers of neurons in the zone, k being a constant depending on the size of the piece of cortex. Zone 4 is the most sparsely populated zone, and comparison of the totals for the different zones with that of zone 4 will give a measure of the relative numbers of cells in these zones. These relative numbers are shown in column 6. Column 7 shows the total numbers of complete cells for each zone stained by the Golgi method (from Table 1). Again zone 4 has the smallest representation, and comparison with the other zones gives the results shown in the last column.

Comparison of column 6 with the last column shows that, in general, this survey of neurons stained by the Golgi method has produced a proportional representation of the neurons with the possible exception of the lowermost zone. This discrepancy may be due to the difficulty of defining the grey-white boundary in the Nissl preparations and to the possible inclusion of a certain number of neuroglial cells, which are often difficult to distinguish from small neurons in the Nissl picture.

Certain facts are immediately obvious.

(1) The majority of cortical neurons have axons leaving the grey matter and apical dendrites ramifying in the outermost zone of the cortex. These neurons are present at all depths in the cortex with the exception of the outermost layer.

(2) Neurons with their axonal ramifications locally distributed within their own dendritic field are mainly found among the terminations of the afferent fibres arising from the thalamus. There is a smaller concentration of these neurons among the terminations of a second group of afferent fibres.

Table 1. *The numbers, positions and types of all neurons studied in the visual cortex of the cat*

(Figures in brackets are the estimated numbers of cells of the different types found in a cortical volume of $10^6 \mu^3$.)

		Pyramidal cells														Stellate cells				
		Axon unbranched to white matter (P_1) Dendrites to zone				Axon branched to white matter (P_2) Dendrites to zone				Axon branched to white matter with recurrent collaterals (P_3) Dendrites to zone				Axon with recurrent collaterals only (P_4) Dendrites to zone				Axon within own dendritic field (S_1)	Axon to white matter (S_2)	Axon to zone 1 (S_3)		
Zone	Approx. depth (μ)	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4				Total	Unclassified cells included in the total
I	0–150	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1 horizontal cell
II	–550	53 (23)	—	—	—	60 (26)	—	—	—	36 (16)	—	—	—	4 (2)	—	—	—	16 (7)	6 (3)	9 (4)	189	1 pyramid with axons to zone 4 + recurrent collaterals 3 pyramids with axon to zone 4 1 inverted pyramid with axon to zone 1
III	–850	11 (7)	1	—	—	17 (10)	—	—	—	5 (3)	—	—	—	8 (5)	1	—	—	53 (30)	13 (7)	—	111	2 pyramids with branched axons to zone 5
IV	–950	13 (20)	—	—	—	3 (5)	2 (3)	1 (2)	—	9 (14)	4 (6)	—	—	10 (15)	—	1 (2)	—	—	1 (2)	—	44	—
V	–1150	50 (32)	—	—	—	37 (24)	—	1 (1)	—	2 (1)	—	—	—	—	—	—	—	3 (3)	—	1 (1)	95	1 inverted pyramid with axon to zone 2
VI	–1550	33 (23)	—	2 (1)	9 (6)	22 (15)	—	1 (1)	3 (2)	13 (9)	—	5 (3)	7 (5)	2 (1)	—	—	1 (1)	7 (5)	6 (4)	—	113	2 invert. pyramids with axons to zone 3–4
Totals		160	1	2	9	139	2	3	3	65	4	5	7	24	1	1	1	79	26	10	553	11

Table 2. *Comparison between the neuronal populations of the different cortical zones as shown by Nissl and Golgi methods*

		Nissl stain				Golgi stain	
Zone	Depth (μ)	Density of cells/$10^6 \mu^3$	Mean zone density	No. of cells in zone	Ratios of zonal cell numbers	No. of cells	Zonal ratios
II	151–250	104	82	$82 \times 4k$	4·9	189	4·3
	–350	84					
	–450	76					
	–550	64					
III	–650	57	62	$62 \times 3k$	2·8	111	2·5
	–750	60					
	–850	69					
IV	–950	67	67	$67 \times k$	1	44	1
V	–1050	56	61	$61 \times 2k$	1·8	95	2·2
	–1150	66					
VI	–1250	76	77	$77 \times 4k$	4·6	113	2·6
	–1350	82					
	–1450	79					
	–1550	70					

(3) Neurons whose axons have recurrent collaterals are especially prominent in the lower part of the cortex.

(4) A number of deep-lying pyramidal cells have the terminal ramifications of their apical dendrites in the zone of distribution of the terminations of fibres from the thalamus.

For some purposes it is convenient to express the results of the counts in terms of the actual numbers of cells per unit volume of cortex rather than merely in terms of the sample numbers. This is done by first expressing the numbers of each type of cell as a fraction of the total number in the zone and then transforming this ratio to the number of cells/$10^6\mu^3$ of cortex by means of the known cell densities found from Nissl preparations. For example, the number of pyramidal cells with unbranched axons to the white matter (P_1) in zone 2 found in the sample is 53 and the total number of cells sampled in the zone is 189 (Table 1). The Nissl density is $82/10^6\mu^3$ and the estimated number of cells of this type in each $10^6\mu^3$ of zone 2 is $(53 \times 82)/189 = 23$.

The distribution of the types of neuron at different cortical levels and the manner in which the distribution of a given type varies with depth could be shown by means of a set of histograms. These different distributions are more easily visualized by means of the contour diagram shown in Fig. 2.

In this diagram the different types of neuron are shown along the top and the cortical zones, with their relative thicknesses, on the left-hand side. Vertical lines show that the neurons have been classified discretely and the absence of horizontal lines emphasizes the lack of sharp boundaries between the various zones. The numbers denote the estimated number of neurons of a given type contained in a cortical volume of $10^6\mu^3$ to be found within the appropriate zone. The contour lines are drawn at 5-neuron intervals in the same way as contours for changes in height on a map. The different varieties of distribution may be found by drawing either horizontal or vertical lines across the diagram. Horizontal lines will give the distribution of the different neuronal types at a given depth, whereas vertical lines will give the distribution of a given neuronal type with changing depth.

The dendritic distributions of cortical neurons have been studied previously (Sholl, 1953). As a result of further measurements it may be said that the extent of the basal dendrites appears to be normally distributed about a mean radius of 160μ with a standard deviation of 45μ: the standard deviation of the mean is approximately 10μ.

The afferent fibres to the visual cortex

There appear to be three groups of fibres bringing impulses to the visual cortex:

(1) Those whose terminations are concentrated around the region of Gennari's line (zone 3).

(2) Those with terminations mainly between Gennari's line and the outermost layer of the cortex (zone 2).

(3) The tangentially running fibres in the outermost zone (zone 1).

The first group, whose extensive terminal branches were noted by Cajal and very well illustrated by O'Leary (1941), enter the cortex as comparatively coarse fibres and appear to arise mainly from the lateral geniculate body. The present

study confirms the distributions of the terminations of the fibres described in this previous work and measurements have been made on the extent to which the terminations of any one geniculate fibre may ramify. From measurements on a small sample the mean distance between the tips of the most widely spread branches was found to be 650 μ and it must be emphasized that a single thalamic fibre may have a termination in the lower part of zone 3 and another in the upper part of this zone, the tips being also widely separated in a direction parallel to the pial surface.

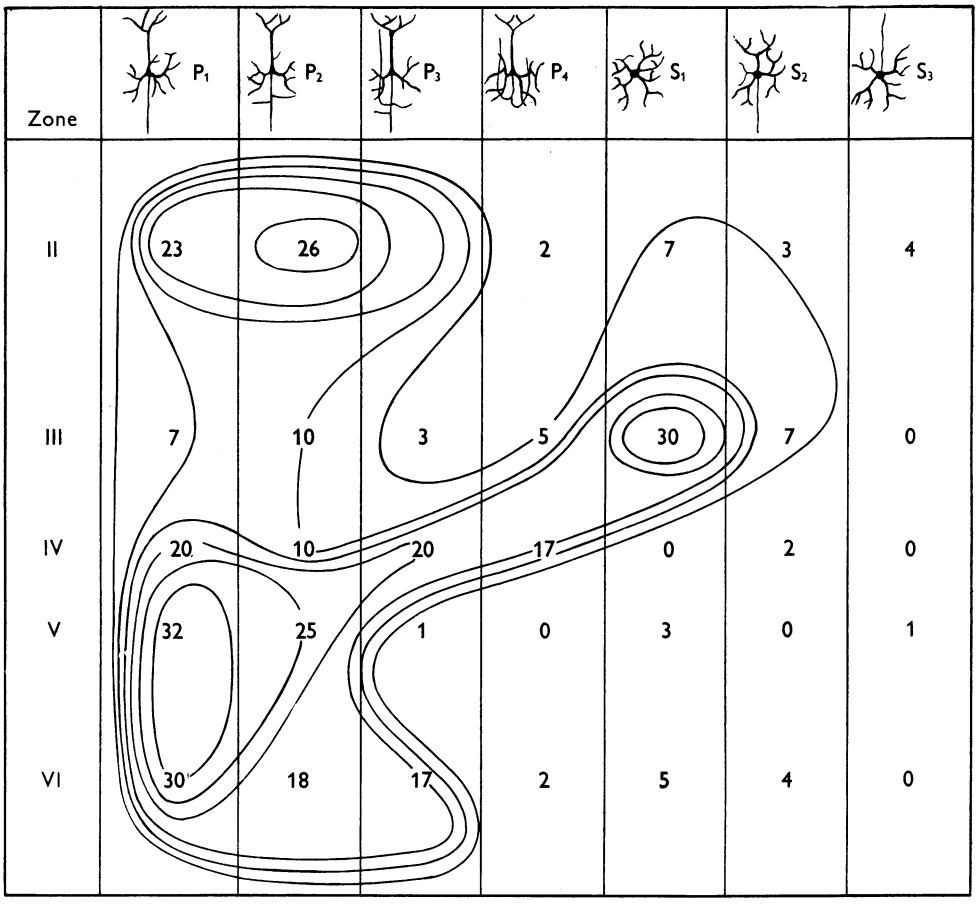


Fig. 2. Contour diagram showing the numbers of cells of different types contained in a cortical volume of $10^6\mu^3$ in the different cortical zones. Contour lines are drawn for densities of 5, 10, 15, 20, 25 and 30 neurons per $10^6\mu^3$ of cortex.

The axons of the second set of incoming fibres are much thinner and again these branch before terminating. They are said to be commissural and association fibres (Lorente de Nó, 1949; Chang, 1953; Nauta, 1954), but their origin is still uncertain.

The set of very fine axons running in the outermost layer of the cortex is the most difficult of all to study. Staining is difficult with all the techniques that have been tried, but good silver impregnations (Bielschowsky and Holmes) show that these

fibres are present in large numbers. The only positive evidence of their origin found in the present work is that a number of deeper lying cortical neurons have axons running to this layer and then turning to run tangentially.

An estimate of the density of afferent fibres leaving the white matter was made by making a number of counts of the total number of fibres as stained in silver preparations cutting a unit area of the grey-white boundary in silver preparations of sections of measured thickness cut perpendicularly to the pial surface. This

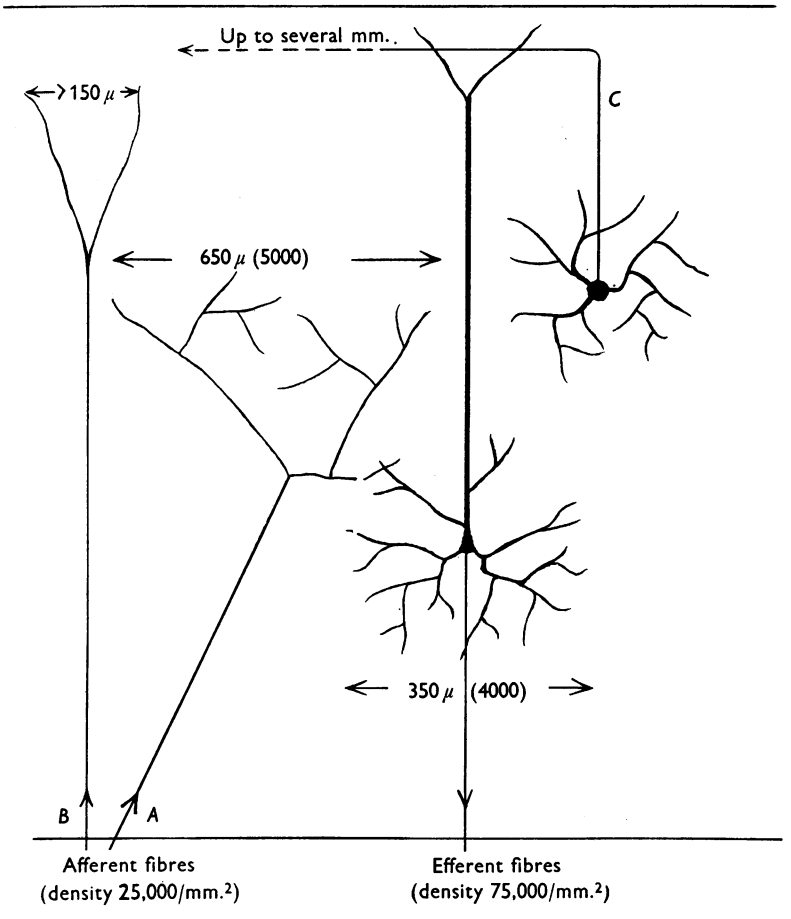


Fig. 3. Diagram to illustrate certain quantitative features in the visual cortex of the cat. Numbers in brackets denote the approximate numbers of neurons under the immediate influence of two of these systems.

was found to be of the order 10^5 fibres per mm.^{2}. Since 70% of all the cortical neurons have axons running into the white matter, the number of fibres leaving the cortex can be estimated from the neuronal densities found in Nissl preparations. The estimated density of such axons is of the order 75×10^3 axons per mm.^{2}.

Some of the quantitative relationships subsisting between the afferent fibres are shown diagrammatically in Fig. 3.

The non-recurrent collaterals usually leave the main axon within the basal dendritic field of their parent neuron, i.e. within 200 μ of the cell body, and many of them do not extend outside the zone of the basal dendrites. However, it is not unusual to find branches stretching for more than 1 mm. The recurrent collaterals of neurons in the upper part of the cortex usually have their terminations within the basal dendritic field of their cell of origin but in the deeper parts of the cortex

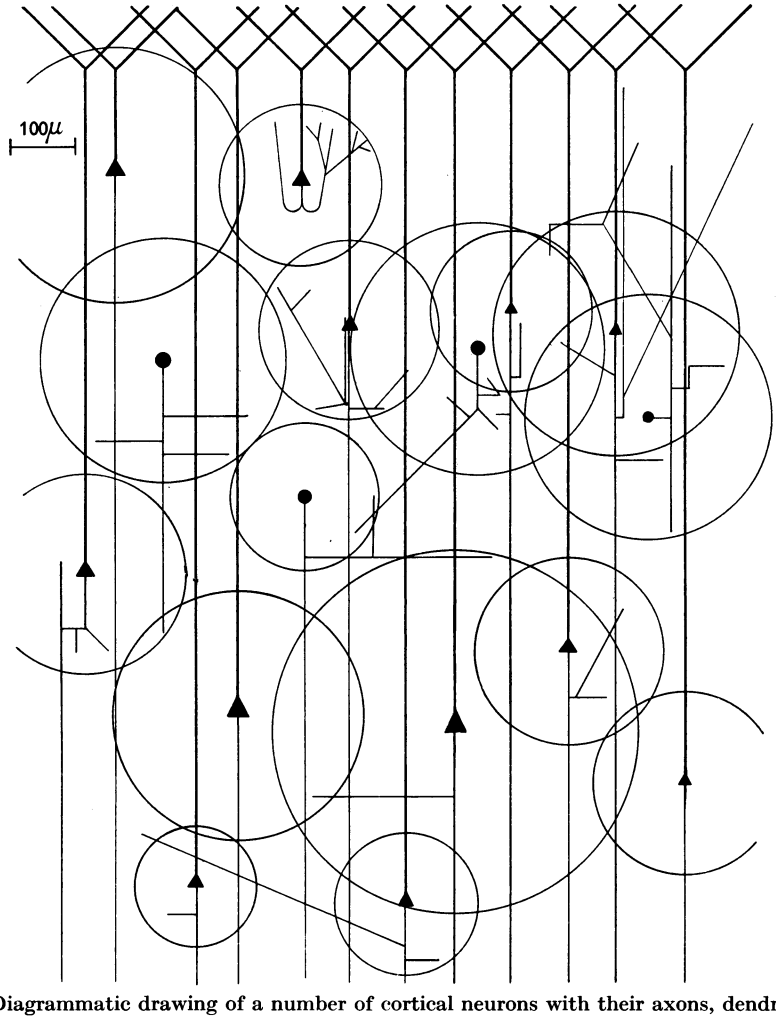


Fig. 4. Diagrammatic drawing of a number of cortical neurons with their axons, dendritic fields and axonal branches drawn to scale.

the recurrent collaterals extend much further but none has been found with terminations above the Gennari region. Some of these facts are illustrated in Fig. 4.

Many of the implications of these quantitative results are most easily seen from a diagram constructed in the following way. The Nissl studies (Table 2) show that, excluding the almost neuron-free outermost zone, the ratios of the numbers of cells in the different zones are approximately 5 : 3 : 1 : 2 : 4, and the Golgi studies show

that in the zone with the fewest cells (zone 4), four types of neuron must be represented even if types that form less than 5 % of the total are ignored. Consequently, in order to preserve the proportional relationships in their simplest form we must consider a column of cells with four neurons in zone 4 and hence twenty cells in zone 2, twelve in zone 3, eight in zone 5 and sixteen in zone 6. Furthermore, the total number of neurons represented in each zone must be subdivided in proportion

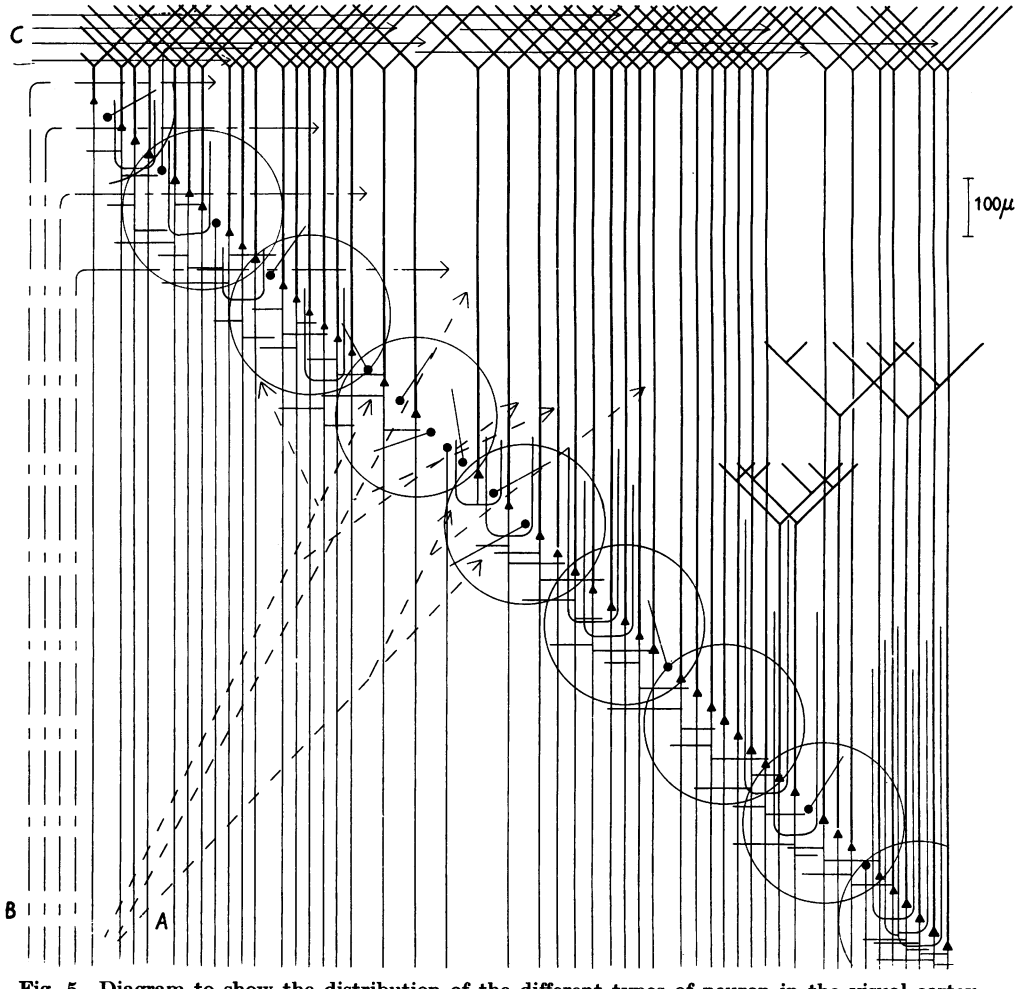


Fig. 5. Diagram to show the distribution of the different types of neuron in the visual cortex of the cat. The three sets of afferent fibres (*A*, *B*, *C*) and their terminations are also shown.

to the number of each type found in that zone. The diagram shown in Fig. 5 has been constructed on this principle. The representative column of cells has been staggered in order to make the separate axonal ramifications clear; it must be remembered that each neuron in the figure represents a group of cortical neurons. The destinations and directions of the axons and their branches are preserved but individual variations are not shown (see Fig. 4). The manner of termination of the

apical dendrites has been formalized, and the extent of the basal dendritic fields shown by circles each with a radius equal to that of the mean dendritic field. The general distributions of the three sets of afferent fibres (A, B and C) are shown formally. The diagram attempts to illustrate a statistical average of cortical organization.

DISCUSSION

The cerebral cortex is an organization of neurons and their processes such that streams of impulses arriving from various sources along afferent fibres interact with one another and with some engram derived from the past history of the animal. The impulses resulting from this activity lead to changes in behaviour and in the cortical engram. Any attempt to discuss the mode of activity of the cortex demands hypotheses relating to the properties of neurons and the manner in which impulses propagated along an axon may affect other neurons. The precise nature and method of operation of cortical synapses is unknown, but it seems reasonable to assume that activity associated with axons that are sufficiently near to the perikaryon and dendrites of a neuron will lead to a local depolarization of its surfaces. If this depolarization is sufficiently extensive as a result of spatial and temporal summation, an action potential will be propagated along the axon and its branches; moreover, the production of such an action potential leads to some shorter or longer change in the condition of the perikaryon and dendrites.

The present work is an attempt to make a quantitative study of some features of the cortex by considering the relative sizes and relationships of subaggregates or groups of neurons, membership of a group being determined by certain geometrical properties of the axons and dendrites. Size must be a parameter of first importance in determining the part played by each neuron. For example, the wider is the dendritic field of a cell, the greater the number and variety of influences falling upon it.

The cortical zones

The zones used in the present study were defined in order to describe the positions of the cell bodies in an objective way that avoids reference to the highly variable thickness of the cortex. They are equivalent to zones marked out in commencing an ecological survey of a district; once the map has been made these artificial boundaries are discarded and the terrain is examined as a whole. In another region of the cortex different zones would almost certainly be convenient, for Gennari's line would no longer serve as a landmark.

The relationship between these zones and the various schemes for cortical lamination will not be described since no importance, tectogenic or otherwise, is ascribed to the zones.

The afferent fibres to the visual cortex

Many fibres can be traced from the white matter to their terminations. The origin of these fibres can only be rigorously determined by degeneration methods. The fibres that end in the region of Gennari's line (group A) have been studied extensively by Poliak (1927), who concluded that they had their origin in the lateral geniculate body. The nature of the branching of these fibres in the cat has been

described and illustrated by O'Leary (1941) who says that: 'The horizontal branches of the exogenous fibres within the stria are significantly longer than is generally believed, and may issue as many as twelve secondary branches each of which ramifies more extensively.' The present work confirms this statement; the final terminal twigs may be separated by distances of the order of 1 mm. It follows from the estimates of cell density (Sholl, 1953) that up to 5000 neurons and a volume of 0·1 mm.^{3} of cortex are within the immediate zone of influence of impulses transmitted by a single thalamic fibre. The more precise description of the mode of branching and of the extent of the terminal ramifications of these fibres requires further examination.

The second set of incoming fibres (B fibres) appears to have its main terminations superficial to the Gennari zone. These fibres are considerably thinner on emergence from the white matter than the group A fibres, and their source is still speculative. The third set (C fibres) which forms the fine tangentially running fibres of the outermost layer of the cortex and is immersed in the dense ramifications of apical dendrites also has an unknown origin. Undoubtedly a number of the fibres are the axons of deeper lying cortical neurons, but whether these axons form the major part of this set cannot be stated at present. Both the origin and extent of the ramification of these axons are under investigation. Nauta (1954), working with his degeneration method, has described intra-cortical and callosal fibres ending in all layers of the cortex. Details of this work are not yet available and further correlated studies of degeneration and Golgi preparations must be made.

The efferent fibres from the cortex

The present work emphasizes that axons running into the white matter originate from all levels of the cortex with the exception of the outermost layer and, in fact, the majority of the cortical neurons have axons of this kind. Little can be said about the destination of these axons; Dusser de Barenne (1934) and Le Gros Clark & Sunderland (1939) provide evidence that many of the axons arising from the deep lying neurons travel to subcortical structures. The destination of the axons from the upper layers of the cortex is uncertain.

The general organization of the visual cortex

The diagram shown in Fig. 5 represents not only the manner in which the cortical neurons are related to the different sets of afferent fibres but also indicates the relationship between the neurons themselves. For simplicity only a single column of cells has been shown, and even here a single neuron in the diagram represents a group of actual neurons. Furthermore, it must not be assumed that such a column of cells indicates the existence of some kind of cortical unit; the branches of each afferent fibre come into relationship with the neurons of a number of such columns and the axons of any column have branches ramifying to other columns. The variation in the extent of inter-neuronal interaction is shown more clearly in Fig. 6, where a number of neurons have been drawn to scale to show the varied manner of axonal branching and the overlap of dendritic fields.

Bearing in mind the hypotheses stated earlier we may consider the situation shown in Fig. 5 and in a more simplified and less exact form in Fig. 6. Here the main

principles of the more complicated figure are preserved but it is no longer possible to show the different types of neurons in their correct proportions when the total number of neurons depicted has been so radically reduced. Examination of Figs. 2 and 5 makes the manner of distribution of the principal subaggregates or groups clear. A large group of stellate cells is associated with the terminations of the A sets

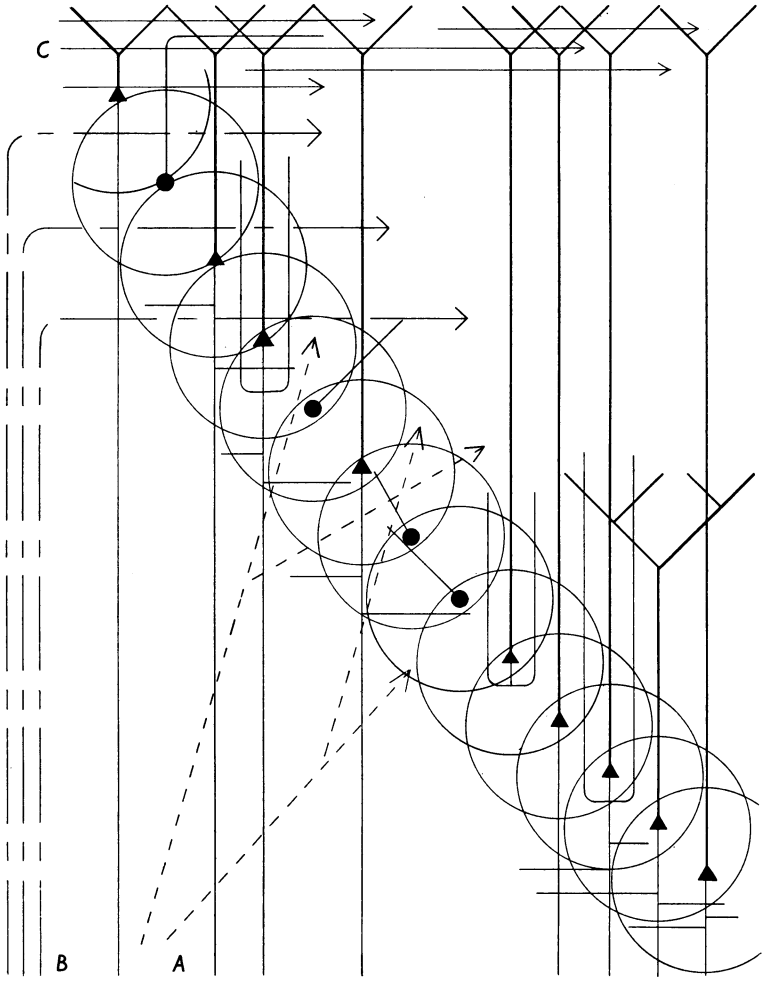


Fig. 6. A simplified diagram of the relationships between cortical neurons and the afferent fibres to the cortex. The main principles illustrated in Fig. 5 are preserved but the proportions of the different types of neuron are less accurate.

of afferent fibres and a smaller group with the B set. Large groups of pyramidal cells, showing branched and unbranched axons in approximately equal numbers, are found in the upper and lower layers of the cortex while neurons with recurrent collaterals are mainly concentrated below the Gennari zone. Neurons with axons running into the outermost zone occur mainly in the upper part of the cortex.

Other much smaller subaggregates occur but it is suggested that they play so small a part in the general cortical organization that they may be ignored.

If these diagrams are now examined more closely from a purely static point of view, and remembering that each neuron in the drawings represents a group of cortical neurons, it is immediately apparent that impulses arriving along a single thalamic fibre will be dispersed amongst the 5000 neurons distributed around its terminal branches. The precise number of neurons within this set influenced by the afferents is unkown, but it may be that as much as 0·1 mm.^{3} of cortex has its state modified. Activity may spread from the neurons nearest to the terminal branches and may lead not only to impulses leaving the cortex but to activity in further groups of neurons above and below this region. The presence of a large group of neurons with recurrent collaterals beneath the Gennari zone suggests that the effects of the downward flow of activity will lead to secondary influences at the higher level. This type of activity might be of the 'reverberating circuit' type suggested by Lorente de Nó (1933, 1934).

A similar examination of the afferent fibres of set B again shows that some of the neurons under the immediate influence of these fibres give rise to impulses leaving the cortex, while others also mediate impulses that travel back to the region of the distribution of the afferent terminations. In this case, however, a greater proportion of the neurons directly associated with the afferent terminations have axons that leave the cortex; in both cases, recurrent collaterals convey impulses back to the primary afferent region. Impulses travelling along the tangential axons of the outermost part of the cortex will influence some 70 % of all cortical neurons through the ramifications of the apical dendrites.

The cortex is a dynamic system and important as these purely spatial and static considerations may be, they would be most misleading if considered apart from the temporal relations existing between the activities of the neurons and the different sets of afferent fibres. The method adopted in this study gives no information about the connectivity of individual neurons with one another and with the afferent fibres and, consequently, discussion of the temporal factors involved would be purely speculative. Further important parameters may emerge from similar investigations on different areas of cortex and from phylogenetic and ontogenetic studies.

This work shows that some aspects of the problem of cortical organization may be approached from a statistical point of view in the sense that the parameters of groups of elements are considered. The value of this method has been clearly shown in the development of statistical physics in which the states of an aggregate composed of a large number of elements have been investigated. In the systems so far studied by statistical mechanics certain assumptions regarding the homogeneity of the elements are acceptable; no such homogeneity can be assumed for the neurons of the cerebral cortex. Adequate statistical methods for resolving these problems have still to be found.

SUMMARY

1. A quantitative analysis of the distribution of the neurons of the visual cortex of the cat has been carried out in accordance with the joint distributions of their axons and dendrites.

2. The study of Golgi and Nissl preparations enables both the relative and absolute densities of the different types of neuron to be estimated.

3. The majority of cortical neurons have axons leaving the grey matter and apical dendrites ramifying in the outermost zone of the cortex.

4. Neurons with their axonal ramifications locally distributed within their own dendritic field are mainly found among the terminations of two sets of afferent fibres.

5. Neurons whose axons have recurrent collaterals are especially numerous in the deeper part of the cortex.

6. A number of deep lying pyramidal cells have the terminal ramifications of their apical dendrites in the zone of distribution of the terminations of fibres from the thalamus.

7. Three sets of afferent fibres are described.

8. Fibres arising in the lateral geniculate body branch extensively within the cortex, the distance between the tips of their terminal branches being of the order of 0·5 mm. Each thalamic fibre may directly influence the state of about 0·1 mm.^{3} of cortex in which lie 5000 neurons.

9. The density of efferent fibres from the cat visual cortex at the grey-white boundary is about 75,000 fibres/mm.^{2}. Approximately 25,000 fibres/mm^2 enter the cortex from the white matter.

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