DENDRITIC ORGANIZATION IN THE NEURONS OF THE VISUAL AND MOTOR CORTEXES OF THE CAT

By D. A. SHOLL

Department of Anatomy, University College, London

INTRODUCTION

The manner of transmission of the nerve impulse from one neuron to another in the cerebral cortex is unknown. Few terminal buttons are to be seen on the cell bodies of cortical neurons, and the nature of the synapse is obscure. It is possible to approach the problem of cortical organization in another way. In addition to studying the detailed appearance of particular synaptic junctions, one may attempt to assess the general principles of neuronal interaction from a consideration of the geometrical relationships subsisting between the neurons and between the neurons and the incoming axons. This could be done by measuring: (1) the density of packing of the cells; (2) the pattern of branching of the dendrites as shown by their diameter, number and length, and direction; (3) the pattern of branching of the axons. The present paper describes the results of studies on the dendritic branching pattern in the visual and motor cortices of the cat and the density of packing of the cells in the visual cortex. The axonal branching pattern will be discussed in a subsequent paper.

The dendritic organization of the cerebral cortex has been little studied in recent years. Ramón y Cajal [1894, reproduced 1911] pointed out changes occurring during ontogeny and compared them with differences found in the phylogenetic series. The investigations of Lorente de Nó [1922, 1923, 1934] and of O'Leary [1914] on cortical histology are of outstanding importance, but, apart from a short paper by Bok [1926], no other recent detailed studies of dendrites seem to have been made.

METHODS

It has been found possible consistently to stain cortical neurons with the Golgi-Cox method in the following way:

1. Cats are anaesthetized with nembutal (either leads to excessive bleeding) and pieces of cortex not more than 4 mm. thick are removed from the living animal.

2. These are rapidly rinsed in warm saline and put into about 50 ml. of the staining solution in a small stoppered bottle, the tissue resting on a piece of cotton-wool.

Staining solution—be freshly prepared

\[
\begin{align*}
5\% \text{ aqueous potassium dichromate} & \quad 20 \text{ ml.} \\
5\% \text{ aqueous mercuric chloride} & \quad 20 \text{ ml.} \\
\text{Distilled water} & \quad 40 \text{ ml.}
\end{align*}
\]

Mix together and then, with continuous stirring, add

5\% aqueous potassium chromate 8 ml.

(1) The bottles are left undisturbed in the dark at room temperature for 6 weeks (a shorter time for kittens and rabbits).

SCOTTISH AND MCGREGOR—VASCULARIZATION OF DERMATOMES AND DERMATOMES OF RABBIT SKIN
D. A. Sholl

The material, without previous washing, is first rinsed in a mixture of equal parts acetone and absolute alcohol, and then dehydrated in this mixture in a stoppered bottle for 24 hr. at 25°C.

(4) The material is transferred to a mixture of equal parts ether and absolute alcohol for 4 hr., and then,

(5) Placed in 2% colloid for 24 hr. and then in 12% colloid for 12 hr.

(6) Mounted on a fibre block in 12% colloid and hardened in chloroform vapour.

(7) Sections 100-200μ are cut in 70% alcohol on a sliding microtome.

(8) The sections are transferred to distilled water to which two to three drops of a wetting agent have been added.

(9) Reduction is made in a fairly large volume of 5% aqueous potassium sulphite to which a few drops of 5% aqueous oxalic acid have been added. (The addition of oxalic acid clears the background, leaving it colourless. I owe this suggestion to Mr. G. Hyde.)

(10) The sections are rinsed in distilled water for 10 min., transferred to a mixture of equal parts absolute alcohol and chloroform, and then put on the slide, flattened with filter-paper and coated with 1% colodium.

(11) The slide is transferred to a mixture of equal parts absolute alcohol and chloroform.

(12) The preparation is cleared in xylene, mounted in dammar xylol and transferred to the incubator to dry. It may be necessary to add more balsam during the drying process. No satisfactory plastic mountant has been found, and all suggested methods for applying cover-slips have led to rapid fading.

Measurements

The measurements were made using a binocular microscope and a 4 mm. objective with graticules in the eyepieces. The graticules were calibrated against a stage micrometer. Since it is impossible to use an all-immersion objective with thick sections, distances less than 2μ are difficult to estimate; consequently there may be a rather large error in the measurements made on small diameters. Two corrections to the measured lengths are necessary when the dendrites do not run parallel to the plane of section since, first, the observed length is the projection of the true length on the plane of section and, secondly, all measured widths are of apparent depths due to the refractive index of the mountant.

In order to catalogue the dendrites quickly and in such a way that the relations of any particular branch could be found easily, the conventional system of numbers was adopted. Branches arising directly from the perikaryon were numbered 1, 9, 8, 7, etc. The next branches have numbers 101, 102, 201, 902 where 911 and 912 are the two branches formed from 01. Very occasionally, when a branch gave rise to three new branches, there would be a branch having a number of the form 013.

Subsequently, measurements of length and diameter were plotted on diagrams of the kind shown in Text-fig. 1, each cell being allotted a separate sheet. In these diagrams the directions of the branches are ignored but the lengths are plotted to scale. The lengths of the short vertical lines have no meaning, for these lines merely indicate the position of branch points. Long vertical lines are drawn across the

Dendritic organization in cortical neurons

The figure alongside any branch is the mean value of its diameter, where branches are long and have a high taper, two such diameters are noted. Short thick perpendicular lines at the end of a branch show that the branch has been cut at this point. From diagrams of this kind it is easy to find the numbers of dendritic branches and terminations at different distances from the perikaryon.

Text-fig. 1. An example of the method of graphical representation of the lengths of dendritic branches for a single neuron.

Sampling

The sampling of the cells to be measured is difficult. The cells suitable for measurement in any section have already been partly selected in an uncontrollable manner. The staining method itself is selective and even with the greatest care it is impossible to ensure perfect orientation of the knife. Moreover, even under the best conditions, there will be an excess of complete small cells in any section. However, since all the types described by other workers have been seen, there are grounds for believing that cells of all shapes and sizes have been stained; consequently there is no reason to suppose that bias has been introduced. The number of complete large cells in any one section is small and the rule was adopted that, having measured a number of small cells at various cortical depths, all the complete cells in any section were measured. Cells have been classified into two broad categories, stellate and pyramidal; the former are those with a spherical or ellipsoidal perikaryon and with dendrites symmetrically disposed around the perikaryon, whilst the latter have a pyramidal perikaryon with a definite apical dendrite. Photographs of these two types are shown in Pl. 1 and Text-figs. 2 and 3 show diagrams of the same types. Only six of the cells could not be classified on this basis and three of these were of the inverted pyramidal type. These non-classified cells have not been further considered in this paper.
Table 1. General data relating to neurons from the visual and motor cortices of the cat

<table>
<thead>
<tr>
<th>Cell no.</th>
<th>Type</th>
<th>Depth (mm)</th>
<th>Thickness of cortex (μm)</th>
<th>Volume of perikaryon (μm$^3$)</th>
<th>Surface of perikaryon (μm$^2$)</th>
<th>Total length of dendrites (μm)</th>
<th>No. of dendritic branches (Fig. 9)</th>
<th>Tangential extent of dendrites (μm)</th>
<th>No. of promontary branches (10)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>P</td>
<td>0.80</td>
<td>1,850</td>
<td>1,400</td>
<td>1,200</td>
<td>954</td>
<td>40</td>
<td>885</td>
<td>10</td>
</tr>
<tr>
<td>9</td>
<td>P</td>
<td>1.00</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>10</td>
<td>P</td>
<td>1.20</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>12</td>
<td>P</td>
<td>1.40</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>15</td>
<td>P</td>
<td>1.60</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>20</td>
<td>P</td>
<td>1.80</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>21</td>
<td>P</td>
<td>2.00</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>22</td>
<td>N</td>
<td>2.20</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
<tr>
<td>23</td>
<td>N</td>
<td>2.40</td>
<td>1,700</td>
<td>1,600</td>
<td>1,900</td>
<td>950</td>
<td>71</td>
<td>170</td>
<td>100</td>
</tr>
</tbody>
</table>

Visual area

Motor area
RESULTS

Table 1 shows the dendrite lengths of thirty cells. In the second column, the letters P and S denote pyramidal and stellate cells respectively. The depths of the cells were measured from the pial surface to the lowest point of the perikaryon. The total cortical thickness is the distance from the pial surface to the grey-white boundary; this boundary is not sharp. The volumes and surfaces of the perikaryons were estimated from measurements of heights and diameters by treating the perikaryons as solids of revolution. The total lengths of the dendritic branches are the sums of the lengths of the individual branches; the figures have not been rounded off. The tangential extent of the dendrites of each neuron was measured under a low power and is the length of a straight line drawn between the extreme ramifications of the non-spinal dendrites in a direction parallel to the pial surface. An examination of the figures in column 4 shows a considerable variation in cortical thickness within any one area; this variation does not necessarily depend on any apparent change in curvature of the pial surface. It must be remembered also that any change in cortical thickness does not lead to a uniform displacement of cells at different depths (Böök, 1925); consequently, the recorded depths of the cells in column 5 must be regarded as a general guide to their positions.

The relationship between dendritic branches, depth of cell and volume of perikaryon

The correlation diagrams, Text-figs. 4-6, show that there is no simple relationship between the total number of branches or the total length of the dendrites and the depth or volume of the perikaryon. The most that can be said is that very deep and very large cells do not have few branches or very short dendrites. The only well correlated variables are total dendritic length and number of branches (Text-fig. 7).

Mean values

Mean values taken over such a heterogeneous set of data may be misleading and difficult to interpret, but it may be noted that the mean dendritic length in the visual area does not differ significantly from that found in the motor area (column 7), whereas the mean number of branches found in the visual area is somewhat higher than for the motor area.

Tangential extent of dendrites

Column 9 shows that the extent of dendrites is large; usually more than 0·25 mm. and in several cases reaching 0·5 mm. The number of proximal branches is never less than four and seldom greater than seven, but there are examples both of stellate cells and pyramidal cells having more of these branches.

The manner of dendritic branching

In order to study the way in which the number of branches varies with the distance from the perikaryon, it is convenient to use a series of concentric spherical shells as co-ordinates of reference. In the case of the stellate cells and for the basal dendrites of pyramidal cells, these shells have their common centre in the perikaryon. Pyramidal cells have an apical ramification superimposed upon this basal distribu-
Dendritic organization in cortical neurons

The main pattern difference between the more superficial and the deeper lying pyramids lies in the length of the main, unbranched part of the apical dendrite; it is as if a terminal ramification were joined to the perikaryon by a 'stalk' of varying length. It is convenient, therefore, to refer the numbers of branches of this apical ramification to distances from the main bifurcation of the apical dendrite (Text-figs. 2 and 8).

Text-fig. 6. Correlation diagram for the relationship between the number of dendritic branches and the volume of the perikaryon.

Text-fig. 7. Correlation diagram for the relationship between the total length of dendrites and the number of dendritic branches.

Text-fig. 8. Histograms showing the distributions of numbers of dendritic branches with the distance from the perikaryon.

Tables 2 and 8 show the numbers of dendritic branches, together with their mean diameters, for the stellate cells and for the basal ramifications of the pyramids. These figures were compiled from graphs of the kind shown in Text-fig. 1. Four histograms have been drawn from the data of Tables 2 and 8, the stellate and pyramidal cells for the visual and motor areas being treated separately. The results are shown in Text-fig. 8; certain similarities and differences may be indicated.

It is clear that the distributions for both types of cells, whether stellate or pyramidal, from any one of the cortical regions are similar, while there is a difference between the distributions for the two different areas. The histograms for the visual...
cortex show fairly sharp modal values, while those for the motor region tend to be more flattened with no clearly defined mode. Secondly, the mean numbers of branches are almost always uniformly less in the motor cortex than in the visual.

This branching problem can be approached in another way. Examination of a number of cells shows an apparently uniform distribution of dendrites around the perikaryon, the spacial randomization being excluded for the present. There is no obvious asymmetry of dendrites, and although the precise manner of the distribution may vary, a general uniformity is maintained. If we assume this general uniformity of distribution, then the number of intersections per unit area can be found from the known number of branches at any distance from the perikaryon by dividing this branch number by the area of the appropriate spherical shell (Text-figs. 2 and 3).

The results of this method applied to a single cell for increasing distances from the perikaryon are shown on the left-hand side of Text-fig. 9. This graph suggests that the mean number of intersections/unit area falls off exponentially with the distance. This is easily tested by plotting the logarithms of these numbers against the distance (Text-fig. 9, right-hand side) and the result is clearly linear. Complete linearity is evidently impossible since the number of intersections becomes zero, whereas the negative exponential function only approaches this value asymptotically.

Text-fig. 10 shows the result of plotting the logarithms of the numbers of intersections/unit area for all the stellate cells of the visual region. The general linearity is maintained, with the scatter increasing as more and more branches terminate. Similar results for the stellate cells of the motor region are shown in Text-fig. 11.

The graphs for the basal dendrites of pyramidal cells are shown on the left-hand sides of Text-figs. 12 and 18. In the latter figure, only the mean values are plotted in order to show the general trend; the line fitted to the points has, of course, been computed from all the observations and not from the mean values.
Dendritic organization in cortical neurons

In all these cases, lines have been fitted to the logarithmic form of $y = ae^{bx}$, where $a$ is a parameter of position and $b$ of slope. The values for the parameter estimates are shown in Table 4. These results show significant differences between the slopes of the line for the visual stellates and the slopes for the lines for the other cells. The numbers of dendritic branches of stellate cells from the visual cortex fall off more rapidly than the branches from other cells or, in other words, the numbers of dendritic intersections/unit area from pyramidal and stellate cells of the motor area and of pyramidal cells from the visual area fall off exponentially with distance from the perikaryon at the same rate, and this is lower than the rate for stellate cells of the visual cortex.

<table>
<thead>
<tr>
<th>Type of</th>
<th>Cortical</th>
<th>Type of</th>
<th>Estimate of</th>
<th>Estimate of b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dendrite</td>
<td>area</td>
<td>cell</td>
<td>(estimated s.e.)</td>
<td>(estimated s.e.)</td>
</tr>
<tr>
<td>Non-apical Visual</td>
<td>Stellate</td>
<td>$-3.98$</td>
<td>$0.017$</td>
<td></td>
</tr>
<tr>
<td>Non-apical Motor</td>
<td>Stellate</td>
<td>$-6.45$</td>
<td>$0.043$</td>
<td></td>
</tr>
<tr>
<td>Non-apical Visual</td>
<td>Pyramid</td>
<td>$-6.25$</td>
<td>$0.043$</td>
<td></td>
</tr>
<tr>
<td>Non-apical Motor</td>
<td>Pyramid</td>
<td>$-6.27$</td>
<td>$0.029$</td>
<td></td>
</tr>
<tr>
<td>Apical Visual</td>
<td>Pyramid</td>
<td>$-7.32$</td>
<td>$0.09$</td>
<td></td>
</tr>
<tr>
<td>Apical Motor</td>
<td>Pyramid</td>
<td>$-7.33$</td>
<td>$0.06$</td>
<td></td>
</tr>
</tbody>
</table>

In the case of the non-apical dendrites the lines have been fitted to the logarithmic form of $y = ae^{bx}(\log p - \log a - \log b)$, while the logarithmic form of $y = ae^{-bx}(\log p - \log a - \log b)$ has been used for the apical dendrites.
Dendritic organization in cortical neurons

If we now turn to the apical ramification (Table 5), where the distances have been measured from the main bifurcation, the state of affairs is quite different and is shown by the graphs on the right-hand sides of Text-figs. 13 and 14. These graphs confirm the impression formed from qualitative observation, that the apical dendrites do not terminate as fast as other dendritic branches. Logarithmic plotting (Text-fig. 14) shows that one may consider the relationship to be of the form \( y = ax^b \) (i.e. \( y = \alpha x^{-1.08} \)), and in this case the exponential decay falls off with log \( x \) instead of with \( x \). This slower rate of decay is found in both the motor and the visual areas. It may be said that there is no difference between the branching patterns of the apical dendrites of cells from these two areas.

![Graph showing the double logarithmic plotting of data shown on the right of Text-figs. 13 and 14.]

The packing density of perikarya

The packing density or number of perikarya contained in a unit volume of cortex can be found from Nissl preparations by counting the number of cells at different cortical depths in known volumes of tissue: from these numbers the mean distances between cells at different depths can be estimated. This work has been carried out extensively for the human brain (van Albada, 1948). Complete figures for the cat are not yet available, but Table 6 gives the mean values for the number of cells contained in \( 10^2 \mu^2 \) (16-4 mm.\(^2\)) found in the cat visual cortex at different depths. These figures are based on counts with seven replications made by Miss C. Blockley. For the region in the neighbourhood of Gennari's line this mean number is 60.

Since the average volume of such perikarya is 4000\( \mu^3 \), it is clear that the perikarya occupy about 23% of the cortex by volume. Again, since sixty perikarya are contained in 10\( \mu^2 \) of cortex, the volume of cortex available to each perikaryon is
D. A. Sholl

10^9.60^2 = 16 × 10^9/m^3. The cube root of this number is approximately equal to 25 and we may imagine each perikaryon to be placed at the centre of a cube of side 25^2 with a distance of about 25 μ between the centres of neighbouring perikarya.

Consider now a stellar cell with 10 dendrites extending throughout a cortical sphere of radius 200 μ. The volume of this sphere will be 4π × (200)^3 μ^3, i.e. about 32 × 10^9 μ^3, and hence it will contain about 60 × 162 = 2600 cells; a cell with a dendritic field of 250 μ will have about 4000 cells within its dendritic field.

The packing density of the dendrites

The dendritic population of any region of the cortex will be formed from the contributions of a number of cells, the nearby cells making up the major part of the total. If the concentric shell method is used again, the number of intersections made by the dendrites at different distances is known and, with a knowledge of the numbers of cells between the pairs of concentric shells, the number of dendrites cutting a small area, say 100 μ^2, of cortex may be estimated. For example, in the Gennari region, and fixing a point, it is found that, within a radius of 20 μ there are an average of two perikarya, each of which will contribute 0.15 intersections per 100 μ^2; between the 20 μ shell and the 60 μ shell there are 12 perikarya contributing 0.06 intersections per 100 μ^2 and so on. As a result we find that such a thin sheet of cortex will have a mean number of 6 intersections. The mean dendritic diameter is 1-5 μ; and, consequently, the total area of dendritic sections will be 10 × 0.56 μ^2, i.e. about 18 μ^3 of the cortex. If we again consider a square sheet of cortex of side 10 μ with the dendrites uniformly spaced, it is clear that there will be a distance of the order 2-5 μ between their surfaces.

The connective zone of a neuron

Knowledge of the organization of cortical synapses is still fragmentary, and the conditions under which effective connexions are made unknown. It is, however, possible to arrive at some rather general conclusions about the region that will be called the connective zone of the neuron.

Table 7. Density of connective field of a neuron at increasing distances from the centre of its perikaryon

<table>
<thead>
<tr>
<th>Distance (μ)</th>
<th>Target volume (μ^3)</th>
<th>Total volume (μ^3)</th>
<th>Density of connective field (μ^-1)</th>
<th>Natural logon of density</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
<td>1605</td>
<td>26,110</td>
<td>0.095</td>
<td>1.59</td>
</tr>
<tr>
<td>40</td>
<td>1605</td>
<td>26,110</td>
<td>0.095</td>
<td>1.59</td>
</tr>
<tr>
<td>60</td>
<td>1605</td>
<td>26,110</td>
<td>0.095</td>
<td>1.59</td>
</tr>
<tr>
<td>80</td>
<td>1605</td>
<td>26,110</td>
<td>0.095</td>
<td>1.59</td>
</tr>
<tr>
<td>100</td>
<td>1605</td>
<td>26,110</td>
<td>0.095</td>
<td>1.59</td>
</tr>
</tbody>
</table>

Dendritic organization in cortical neurons

branch lying within this connective zone may be said to "make a contact" with the neuron. The region between any consecutive pair of the spherical shells that have been previously considered will have a total volume V and contain a connective zone of volume T; these quantities may be computed from the data, and the value of the ratio T/V will be called the density of the connective field for this region.

A set of values for this ratio T/V is given in Table 7 for a stellar cell from the Gennari region and corresponding graphs in Text-fig. 15. Such graphs show that the value of the density of the connective field falls off exponentially with the distance from the perikaryon; in the case illustrated, the slope of the fitted line is 0.05. This exponential relationship appears to hold well except for the region adjacent to the perikaryon, where the connective zone is enormously increased as a result of the presence of the perikaryon itself.

![Graph showing exponential decrease of connective field density](image-url)

DENDRITIC BRANCHING

In the early stages of study of dendrites in the cerebral cortex the observer is at first bewildered by the extent and complexity of the ramifications of these dendrites but, later, he becomes aware that there are certain common features among the dendritic patterns of the various neurons and certain differences as well. These similarities and diversities are difficult to specify qualitatively, and only quantitative methods serve to make them clear. Bok (1946) appreciated this situation, and made the only available previous quantitative study of dendritic branching. However, he measured only eight cells from the outer layers of an unspecified part of the cortex and was mainly concerned with a possible indirect relationship between the number of dendritic branches and the nuclear volume of the cell.
At first sight it would appear reasonable to assume that there would be simple relationships between the numbers of branches and the size of the perikaryon or the depth of the cell within the cortex. The correlation diagrams show that this is not the case; in general, the correlations are low and no simple relationships of these kinds appear. The only simple relationship is that which shows that the number of dendritic branches is proportional to the total dendritic length (Text-fig. 9), a fact which suggests that each branch, as it grows longer, has an increasing tendency either to form a new pair of branches or to terminate.

These facts become a little clearer when the histograms of Text-fig. 8 are examined. It has been noted earlier that the numbers of branches in the cells of the visual cortex appear to show sharper modes in the visual cortex than those of the motor area and, in addition, the numbers of branches in the neighbourhood of the perikaryon are also greater in the visual area. These histograms must also be considered together with another aspect of the branching illustrated in the graphs showing the intersections per unit area. The slopes of the fitted lines are a measure of the rate of decay of the numbers of branches with distance from the perikaryon; this rate is the same for all the cells considered, apart from the stellate cells, the visual area and in that case the rate is significantly higher. Altogether these results suggest that these latter cells have a relatively small field of interaction, and it must be remembered that they are associated with the terminations of the axons arriving from the lateral geniculate body and that many of them have short, many-branched axons.

The contrast between the basal and the apical branching patterns shows that, in the apical ramification, the tendency for a branch to bifurcate rather than to end is greater than amongst the basal dendrites; this is combined with a tendency for all branches to terminate within a comparatively small volume near the pial surface, whereas the basal dendrites branch within a more diffuse local field of axons, infiltrating a more extended spherical volume. A definition has been suggested for the connective zone of a neuron as a thin sleeve surrounding the perikaryon and dendrites. Furthermore, it has been shown that each neuron has a connective field associated with it in such a way that the density of this field falls off exponentially with the distance from its centre.

Various analogies with known computing mechanisms and switching devices have been suggested in order to account for that pattern discrimination which is believed to be one of the activities of the cortex. None of these models has shown any very striking agreement with our limited knowledge of the organization of the cortex and no guidance for future research has resulted from their description. In collaboration with Dr A. M. Utley, an attempt has been made to consider the possibilities of a model that should have at least some features in common with this part of the cortex; the basic principles of such a machine have been discussed elsewhere, and it has been shown that it is possible to design and construct a model in accordance with these principles (Sholl & Utley, 1968). A machine designed to such a specification has certain features: (1) the connections between the inputs and the units can be random, i.e. only describable in terms of probabilities; (2) the machine can have limited storage; (3) all the units are identical. This machine is able to measure pattern differences by comparing a new presentation with a stored

**SUMMARY**

1. The sizes and arrangement of the dendrites of neurons in the visual and motor areas of the cerebral cortex of the adult cat have been studied quantitatively in Golgi-Cox preparations.

2. There is no simple relationship between the number of dendritic branches and the depth of the cell below the pial surface or with the volume of the perikaryon of the cell of origin.

3. The dendrites of stellate cells and the basal dendrites of pyramidal cells may extend to a distance of 0.25-0.5 mm around the perikaryon. The region infiltrated by the dendrites of one cell contains between 2000 and 4000 perikarya.

4. The distributions of the numbers of dendritic branches of neurons at increasing distances from the perikaryon in the visual cortex show a sharp modal value about 60-80μ from the perikaryon. Comparative histograms for the motor cortex are generally flatter, with no sharp mode.

5. At corresponding distances from the perikaryon, the numbers of dendritic branches in neurons from the visual cortex are generally greater than in the motor cortex.

6. The number of branches of stellate cells and of the basal dendrites of pyramidal cells crossing a unit area falls off exponentially with the distance from the perikaryon. This rate of decay is higher in the stellate cells of the visual cortex than in any other type of cell studied.

7. The number of branches in the apical ramification of pyramidal cells falls off more slowly, the logarithms of the branch numbers falling off with the logarithm of the distance.

8. Studies of Nissl preparations show that, in the visual area, 25-35% of the cortex is occupied by perikarya while, from the complementary examination of both Nissl and Golgi-Cox preparations, it was found that the dendrites in this region occupied 20-30% of the cortical volume.
9. In the region of Gennari's line, the mean spacing between the centres of perikarya is 25μ, while the mean distance between the surfaces of neighbouring dendrites is 3-5μ.

10. A connective zone and a connective field are defined for a neuron. It is shown that the density of the connective field falls off exponentially with distance from its centre.

11. An analogy between the visual cortex and a statistical machine with a random input is considered.

I should like to thank Prof. J. Z. Young, not only for his continued encouragement, but for the constructive criticism that has enabled work which tended to be diffuse to be brought to a focus. Dr R. Lorente de No has given me the benefit of his unrivalled knowledge of cortical histology while many conversations with Mr H. G. Crag and Dr A. M. Utley have been most helpful. I am grateful to Mr G. Hyde for his valuable assistance on the technical side. The plates are from some of the last photographs made by the late Mr F. J. Pittcock, F.R.P.S.

REFERENCES


EXPLANATION OF PLATE

Plate 1

Fig. 1. Pyramidal cell from visual cortex of adult cat. Preparation as in Fig. 2. Unstained photograph of animalised tissue.

Fig. 2. Stellate cell from visual cortex of adult cat. Golgi-Cox stain with alkaline cupric reduction and cut at 150μ. The axon runs towards the right-hand bottom corner of the photograph to the left of a large dendrite. Several axonal branches can be seen.

SHOLL—DESCRIPTIVE ORGANIZATION IN CORTEXAL NEURON