while the proportion of alkali-feldspar to total feldspar (Vsp) varies only between 0.87 (Erzgebirge) and 0.93 (rapakivi). *The tin-granites are evidently more or less end-stages of differentiation of acid magmas, which in the proportions of main constituents do not differ essentially from non-stanniferous common biotite-granites. There are however indications that a higher content of rarer elements, which tend to be concentrated in granite-pegmatites, distinguish them from common granites:* e.g. the unusual content of rare earths in Malayan granites; small quantities of Sn in dark mica, quartz and feldspars from Banka-granites [22]); traces of Li, Sn, Bi, Cu, Co and U in lithionite-mica from Saxonian tin-granites [34]), and of Ga, Sn and W in biotite from granite in the East Pool-Mine near Redruth, Cornwall [33]). It should be remarked in this connection that the stanniferous Eibenstock-granite (Saxony) is a lithionite-albite-granite, whereas the neighbouring and presumably somewhat older Kirchberg biotite-granite is non-stanniferous [34]). The question of minor constituents deserves further consideration for tin-granites all over the world.

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[33]) J. CH. BROWN, Lagerstätten und erzmikroskopische Untersuchung der Zinnerzgänge der East Pool-Mine bei Redruth in Cornwall. Neues Jahrb. für Miner., Geol., und Paläont. **68**, Beil. — Bd. A, p. 331—332 (1934).

[34]) K. DALMER, l.c.

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Histology. — *The branching of the dendrites in the cerebral cortex.* By Prof. Dr. S. T. BOK. (Communicated by Prof. M. W. WOERDEMAN).

(Communicated at the meeting of November 28, 1936).

The theory of the neurone pattern, published in my paper "A quantitative analysis of the structure of the cerebral cortex" [1]), included two provisional conclusions about the way in which the dendrites of the cortical ganglion cells split up into branches: in neurones of different sizes the radius of the dendrite field was assumed to be proportional to the volume of the nucleus, and, secondly, the total length of the dendrites and its branches was assumed to be proportional to the square of that radius. These two proportionalities had to remain hypothetical untill the dendrites themselves were measured, the theory being based upon the measurements of the nuclei and cell bodies only and upon some peculiarities of the dendrites suggested by drawings made by CAJAL.

After this theory was published, measurements of the dendrites and their

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[1]) Verhandelingen Koninklijke Akademie v. Wetenschappen te Amsterdam, Afdeeling Natuurkunde, 2e Sectie, deel XXXV, No. 2, 1936.

branches were executed. They confirmed both conclusions and showed what leads to them.

The research was made in eight nerve cells, lying pretty close to each other in the 2d and 3d layer of the cerebral cortex in a section of a cat's brain, coloured after the Cox modification of the GOLGI method. The distances were measured between the point where a dendrite originates from the cell body and all the points where it bifurcates or ends.

In order to measure these distances the body and the dendrites of each neurone were drawn with the aid of a drawing prism placed on the microscope. The linear enlargement of the drawings (300 ×) was controled by drawing an object micrometer (glass with a scale, divided into intervals of 0,01 mm) under the same conditions.

The distance between two points in the drawing divided by 300 is not the real distance between the corresponding points in the section, but its projection on a plane, perpendicular to the optic axis of the microscope. The real distance can be calculated if the difference in the height of the two points is known (the difference of their coordinates parallel to the optic axis). Therefore at each point of origin, bifurcation or ending of a dendrite the figure is noted, indicated on the scale of the micrometer screw of the microscope when this point was focussed. The figures, indicated when the lower and the upper surface of the section were focussed differing 45 unites and the section being 150 μ thick, a difference of n units of two figures in the drawings means a difference of $n \times 150/45 = n \times 3^1/_3\ \mu$ in the height of the corresponding points of the section. (The micrometer screw of the microscope used causes an elevation of the tube proportional to the angle of its turning and consequently proportional to the figures indicated on its scale).

The real distance is the hypotenusa of a rightangular triangle, the other sides being as long as these two perpendicular coordinates. As unit of measuring a length of $3^1/_3\ \mu$ was chosen, corresponding with 1 mm in the drawing and with 1 unit of the scale on the micrometer screw.

Fig. 1 shows these distances measured in a middle sized cell [1]. In the graph to the right each point indicating a bifurcation or an ending is placed

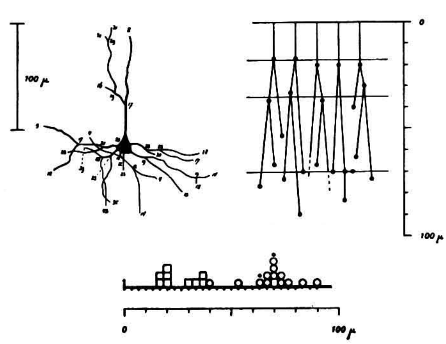

Fig. 1.

in such a distance from the upper horizontal line, that the vertical scale gives its distance from the cell body. The lines that combine these points

[1] The main dendrite, going upwards towards the pia mater, is not discussed in this paper. By dendrites the local (or basal) dendrites are meant.

indicate the dendrite branches to which they belong. In the lower diagram each bifurcation is registered by a small quadrate, each dendrite ending by a small circle placed on a horizontal scale, giving its distance from the cell.

The first bifurcations of each of the 5 dendrites lie at a distance from the pericaryon of 5, 5, 6, 6 and 6 length units of $3^1/_3\ \mu$ resp., the second bifurcations and one ending at distances of resp. 9, 10, 11, 11 and 12 units, the other endings (and one bifurcation) at 16, 19, 20, 20, 21, 21, 21, 21, 22, 22, 23, 25 and 27 units of $3^1/_3\ \mu$. It is clear that they form three well defined groups, the first group at an average distance of $5{,}6 \times 3^1/_3 = 18^2/_3\ \mu$, the second group at an average distance of $10{,}6 \times 3^1/_3 = 35^1/_3\ \mu$, and the third at an average distance of $21{,}4 \times 3^1/_3 = 71^1/_3\ \mu$.

If these average distances — measured as $18\ ^2/_3$, $35^1/_3$ and $71^1/_3\ \mu$ — were found to be 18, 36 and 72, they would exactly have shown the proportion 1 : 2 : 4. From that exact proportion they differ less than 1 μ each. The unit of measuring used being $3^1/_3\ \mu$, we may state that these groups show the proportion 1 : 2 : 4 within the unit of the measurements.

In other words the bifurcations and endings of the dendrites of this neurone lie in the neighbourhood of the surfaces of spheres round the body each with a radius twice as large as the former. Or, formulated in yet another way, *the 5 dendrites of this neurone first bifurcate at an equal distance from the cell body, their branches tend to bifurcate or end at points, each two times farther from the cell than the former bifurcations.*

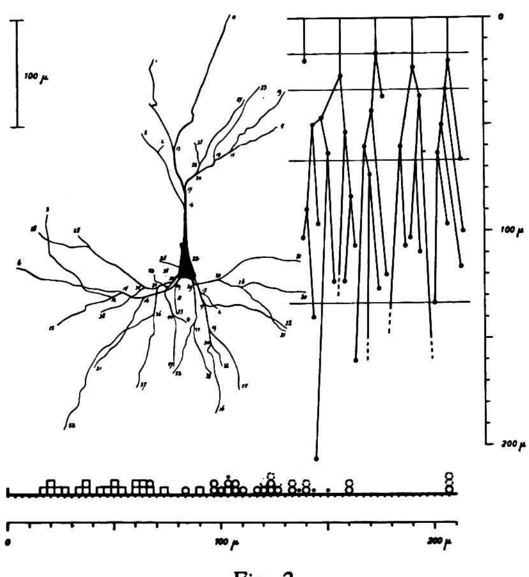

Fig. 2.

Not all the cells measured show this relation as clearly. In the largest neurones it is even impossible to distinguish groups of related distances. If this were due to a larger inexactitude in following up the same rule, the number of bifurcations and endings would not vary with the distance. That is to say between 20 and 40 μ from the cell about the same number of bifurcations and endings would be found as for instance between 80 and 100 μ or between 120 and 140 μ distance.

Theoretically this can be easily understood by comparing the two theoretical frequency curves of fig. 3. The first diagram gives the distances that would be found if all the bifurcations and endings followed the rule in an ideal degree (if they all lay precisely at the surface of the spheres mentioned above). In the second diagram they are drawn supposing the inexactitude in following this rule should be so large that the summits of the frequency curves were flattened out. In this second diagram the frequency appears to be the same all over the length of the scale. That it does not increase or decrease from the left to the right is caused by the fact, that if the rule indicated was exactly obeyed (first diagram), each distance between two groups would be twice as large as the former distance and that each group would contain a number twice as large as the former group (each bifurcation of the former group giving two branches bifurcating in the following group).

If the dendrite branching obeyed another rule, another distribution of the frequencies of bifurcation and ending distances would be found.

As a matter of fact the larger cells show a constant frequency, independent of the distance from the cell. Fig. 2 gives the distances measured in the largest cell; between 20 and 40 μ, between 40 and 60 μ etc. up to 140 μ distance [1]) we find 7, 5, 7, 4, 7 and 8 bifurcations or endings.

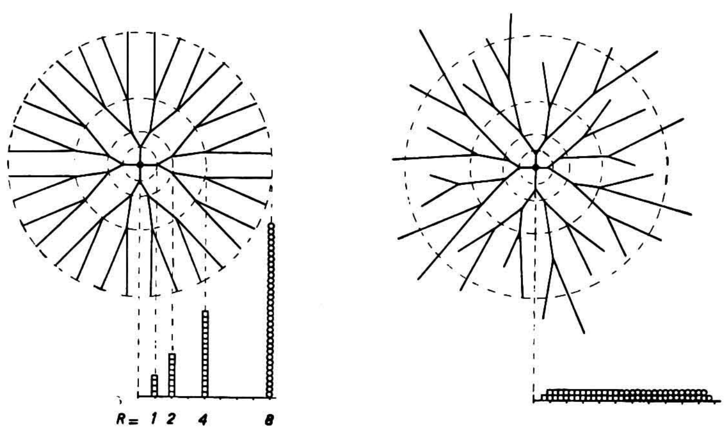

Fig. 3.

Some of the small circles in this diagram are dotted. The section being only 150μ thick, the whole dendrite complex of the cell is not present in it, some dendrite endings falling higher or lower than its surfaces. This is demonstrated by the fact that some of the drawn dendrite branches end in a surface of the section: they are cut by the microtome. In the graph to the right they are registered by elongating the line at the

[1]) More exactly: between 19 and 39μ, 39 and 59μ, etc.

point of cutting by dots, in the lower diagram they are indicated by a point. In order to calculate the probable distances and number of the real endings, absent in the studied section, a sphere was imagined through each ending present in the section, the centre of which lay in the cell. If only $^{1}/p$ part of the surface of that sphere fell inside the section, it is probable that in the whole surface p endings would occur, because the dendrite fields, seen from the pia (in a section parallel to the pia) appear to be almost round and equally built in the different radial directions. By this calculation a small number of probable ending distances are added to the distances measured and these are registered by dotted circles.

In the upper part of fig. 4 all the distances measured in each of the 8 cells are shown. In the smaller cells the general rule is demonstrated by groups and summits at distances proportional to 1 : 2 : 4, in the larger cells

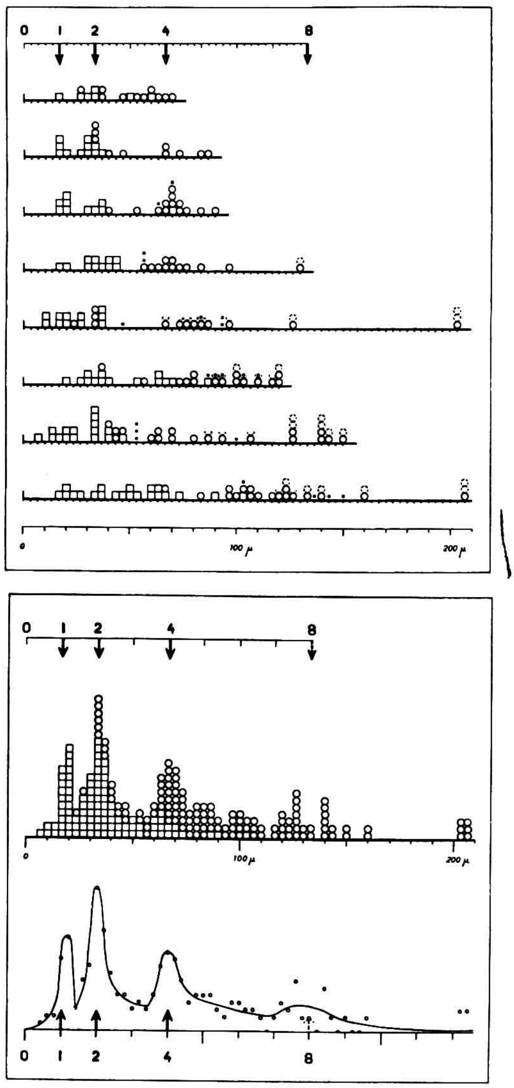

Fig. 4.

by the fact that the frequency does not perceptably increase or decrease from the left to the right.

The lower part of this fig. 4 shows the addition of the 8 graphs of the upper part. High and sharp summits are present at distances proportional to 1 : 2 : 4. At the distance 8 the summit is not yet clearly formed. Perhaps this would have been the fact if still larger cells had been measured. They were not present in this section.

The addition giving such sharp summits, it is evident that the different cells have exactly the same "basal distance", to which the other distances are proportional according to the general rule 1 : 2 : 4 : 8. Within each cell this rule may be obeyed with more or less exactitude, the basal unit of distance, to which the distances tend to have these proportions, must be exactly the same in these 8 cells. If that basal distance had been different in the different cells, the relatively vague summits, occurring in each cell, would have vanished in the addition of the graphs. In the studied section this basal unit of distance can be calculated as 17 μ (in the living cat it will be larger, the section being shrunk by the fixation and impregnation).

In consequence of the type of branching discussed, the total length of the dendrites (with all their branches) in each neurone is proportional to the square of the radius of its dendrite field.

Dendrites of larger and smaller neurones, exactly obeying the rule stated, would answer to a smaller or a larger part of the first scheme in fig. 3. It is easy to count that a dendrite (and its branches), reaching a sphere with a radius 1, 2, 4, 8 or 16 times the basal length, will have a total length of about 1, 3, 11, 43 or 171 basal lengths. These values are nearly proportional to the square of the radius: multiplying these total lengths with $1\frac{1}{2}$ gives the values $1\frac{1}{2}$, $4\frac{1}{2}$, $16\frac{1}{2}$, $64\frac{1}{2}$, $256\frac{1}{2}$, differing from the squares of the radii (1, 4, 16, 64, 256) by the constant value $\frac{1}{2}$ only, which is a relatively small difference in the larger neurones. According to this scheme the total dendrite length practically would be proportional to the square of the radius of the dendrite field.

This relation is simply due to the fact, that each time a dendrite grows out towards a following sphere of twice the radius, the branches added are twice as many and twice as long as the former time. Each time the radius is doubled, the addition to the total length is four times the former addition. The small difference equal to $\frac{1}{2}\,b^2$ (b = basal length) is caused by the fact, that the dendrite does not bifurcate during the first outgrowth from the cell body till the basal length is reached.

The relation $L \sim R^2$, theoretically deduced for the case of the dendrite branching exactly following the rule stated, is found to be present in the measured cells.

It would have been a too laborious task to measure exactly the total length of the dendrites themselves, they being smoothly curved over nearly their whole extension. In stead of the length of these curved lines the distance is measured between each point of bifurcation and the following bifurcation of ending : in stead of measuring the length of each undivided part of a dendrite itself, the length is measured of a straight line running between its endpoints [1]).

With "radius of the dendrite field" the distance between the dendrite endings and the perikaryon is meant. The dendrite branches of each neurone not ending at equal distances from the cell body, the distances of the endings in each neurone were averaged and in fig. 5 the total dendrite length was compared with the square of this average ending distance (average length of the dendrites).

In accordance with the theoretical inferencies of the rule the diagram demonstrates a fairly exact proportionality between the total length of the dendrites of a neurone and the square of its average ending distance.

The presence of this exact proportionality in the measured values shows in the first place, that the rule stated above is actually obeyed by the dendrites. In the second place it shows that the inexactitudes in following this rule are of such a type, that the relation $L \sim R^2$ is undisturbed. In the third place it indicates, that the number of the dendrites is constant. If the

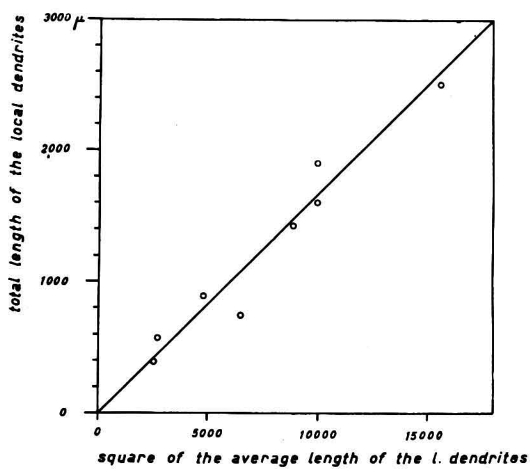

Fig. 5.

number of dendrites varied with the size of the cell, the total length of the dendrites would not be proportional to R^2.

Yet the number of dendrites originating from the cells is not the same in all the neurones of a cortex. Many of the larger cells have more dendrites than the smaller ones. This means that in larger cells the first part of a dendrite, the part between its origin and the point of its first prescripted

[1]) The few parts of the longest dendrite branches cut away by the microtome were calculated in the same way as the dendrite endings not present in the section studied.

bifurcation, might be divided into two separate roots: then one more dendrite would originate from the cell body, but the total fibre length would increase for a relatively small value only (equal to one basal length). In accordance with this subdivision of dendrite roots in these dendrites the bifurcation at the basal distance is absent.

It was assumed in my previous paper that the total length of the dendrites was proportional to the square of the radius of the dendrite field, that is with the square of the average ending distance. This proportionality now being confirmed without any doubt in the measurements of the dendrites, this assumption is proved to be correct.

Moreover the dendrite measurements have demonstrated that this relation is caused by the fact, that the bifurcations and endings tend to occur at distances from the cell body, equal to 1, 2, 4, 8 etc. times a constant basal length.

The other assumption in my previous paper, a proportionality between the radius of the dendrite field and the nucleus volume, was also confirmed.

The nucleus of the nerve cell is not visible in the sections, impregnated after the COX method, the cell bodies being coloured a deep black. Measurements in sections, coloured after the method of NISSL, however, have shown that the nucleus volume is exactly proportional to the surface of the cell body (see the figs. 29 and 30 and the corresponding texte l.c.). In the COX preparations the surface of the cell bodies could be measured in the same way as in the NISSL preparations (l.c. page 46). *Actually the measured surfaces of the 8 cells appear to be proportional to the radius of the dendrite fields,* as is shown by fig. 6, giving the relation between these

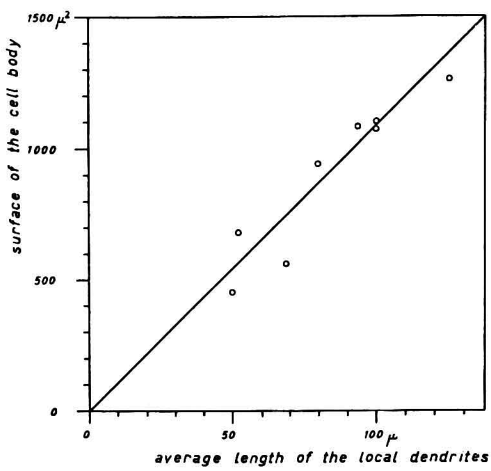

Fig. 6.

measured surfaces (ordinates) and the average dendrite lengths (abscissae).

The type of branching shown by these measurements causes yet another remarkable peculiarity. If the dendrites exactly followed the rule stated, the number of dendrite endings would be proportional to the length of the dendrites : each of the branches of a dendrite, growing out towards twice its length, would bifurcate once and thereby the number of its endings would be doubled. In the diagram of fig. 7 the number of dendrite endings

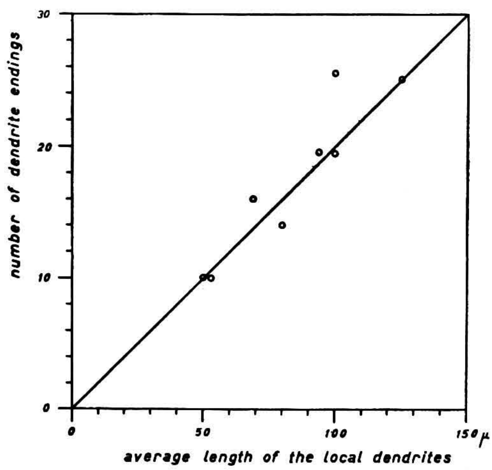

Fig. 7.

is compared with the average dendrite length : 7 of the 8 points lie in the neighbourhood of the straight line drawn, one point shows a difference of 27 %. *In the neurones studied the number of dendrite endings is practically proportional to the average dendrite length.*

And the average length of the dendrites being found to be proportional to the nucleus volume, the number of dendrite endings is proportional to that nucleus volume also.

A neurone may receive its stimuli in different ways.

One category of stimuli is received by the surface of the perikaryon, this surface being surrounded by numerous neurite branches, which in most parts of the nervous system even built footlets on it. The volume of the nucleus being exactly proportional to this surface, it is proportional to the number of stimuli, that may be received in this way (or better : the nucleus volume is exactly proportional to the capacity of the neurone in receiving this category of stimuli).

A second category of stimuli will enter the neurone where the dendrites end. The number of these endings being proportional to the nucleus volume also, this volume is proportional to the number of stimuli of this second category as well.

It is unknown, if the dendrites may receive stimuli from neurites, passing them sideways between their origin and their endings. If so, the dendrites through their whole length would be a third receiving organ of the neurone. The total dendrite length being proportional to the square of the nucleus volume and the density of the nerve fibres passing being constant, the number of stimuli, received in this third way, would be proportional to the square of the nucleus volume.

The third category of stimuli, consequently, would behave in different ways to the stimuli of the first and second category : the third category if present, would be proportional to the square of the nucleus volume, where as the first and second categories reaching the neurone at the surface of the cell body and at the end points of the dendrites both are proportional to the nucleus volume itself.

Summarising, it could be read from the different measurements, discussed in this and in my previous paper, that the nucleus volume is proportional to three morphological properties of its neurone, viz: the surface of its perikaryon, the number of its dendrite endings and the average distance of these endings from the perikaryon (called the radius of the dendrite field or the average length of the dendrites). Moreover the square value of this nucleus volume is proportional to three other properties : the volume of the perikaryon, the total length of its dendrites and the volume of its "territory" (l.c. page 26). The small inexactitude the values measured show in obeying these proportionalities, is as large as the inexactitude of the measurements can be reckoned to be. In my opinion the real properties of the cortical neurones obey these proportionalities to a high degree of exactitude.

In the manner, in which the dendrites split up into branches, a general rule could be observed : *the dendrites of the cortical neurones tend to bifurcate or end at distances from the cell body equal to 1, 2, 4, 8 etc. times a constant basal length* (constant within one individual!). This rule is *not* obeyed with a high exactitude. On the contrary large deviations occur, in consequence of which the different branches of the dendrites of one neurone end at points, lying at very unequal distances from the cell body. These individual variations of the bifurcations and endings are important to understand the simple scheme present in the neurone pattern of the cerebral cortex. They are not discussed in this paper; I confirmed myself to stating that they happen in such a way that two implications of the general rule — the total length of the dendrites being proportional to the square of the average ending distance and, secondly, the number of dendrite endings being proportional to the average ending distance itself — remain undisturbed.

Medicine. — *Eine wirksame kristallinische Substanz aus der Rinde der Nebenniere, Corticosteron.* Von T. REICHSTEIN, ERNST LAQUEUR, I. E. UYLDERT, P. DE FREMERY und R. W. SPANHOFF [1]). (Communicated by Prof. B. BROUWER).

(Communicated at the meeting of November 28, 1936).

Der eine von uns (R) hat in früheren Arbeiten an Hand der physiologischen Eichung (nach EVERSE und DE FREMERY ausgeführt durch SPANHOFF)

[1]) (Aus dem organischen Laboratorium der Eidgenössischen Technischen Hochschule Zürich, aus dem Pharmaco-therapeutischen Laboratorium der Universität Amsterdam und aus dem Research-Laboratorium der N.V. Organon Oss (Holland)).