

## THE VASCULARITY OF THE CEREBRAL CORTEX OF THE ALBINO RAT

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FIVE FIGURES

The work upon which the present paper is based is an extension of that previously reported by the writer ('20). In the former publication an account was given of the relative vascularity of various parts of the spinal cord, brain stem, and cerebellum of the albino rat, and this account is extended in the present communication to include the cerebral cortex of the same animal. In such a connection, there comes up for consideration not only the richness of the capillary supply of the cerebral cortex as compared with that of the parts previously studied, but also the relative vascularity of the various regions into which the cortex has been divided by physiologists and histologists. Also, little, if at all, behind these problems in interest comes the question of the conditions in the various layers which characterize the cortex.

The more important accounts of the cortical localization in rodents, in so far as they are based upon histological studies, are reviewed by Sugita in his paper ('17) on the growth in thickness of the cortex. He also correlates the various regions in which his measurements were made with the detailed description by Fortuyn ('14) of the conditions in the Norway rat and with the anatomico-physiological terms of Brodmann ('09)

Sugita found the cortex of the albino rat, as Fortuyn had found that of the Norway rat, to be divisible, in typical localities, into five laminae. His description of these laminae is as follows:

The cerebral cortex of the albino rat has five cell layers if a typical locality be taken. The most external layer is the lamina zonalis (I), which has a few scattered glia-cells. Under this, there is the lamina

pyramidalis (III) consisting of typical, deeply-staining, pyramidal cells lying closely together, which corresponds to the third layer of Brodmann ('09). In the rodent brain, the lamina granularis externa (II), or second layer of Brodmann, is always indistinct, and it is almost impossible to distinguish it from the lamina pyramidalis (III). Beneath the lamina pyramidalis, the lamina granularis interna (IV) is situated, composed of crowded, deeply-staining, small granules, somewhat resembling glia-cells. Below this layer, there is the lamina ganglionaris (V), which has dispersed, large-sized, deeply-staining pyramids. Next to the lamina ganglionaris, there is the lamina multiformis (VI) with polymorphous cells.

#### MATERIAL AND METHODS

The material consisted of eight of the ten brains used in the previous study ('20), to which reference is made above. These were numbered 16, 23, 24, 26, 31, 55, 56, 58, for the last four of which the writer is indebted to The Wistar Institute. The forebrains of the remaining two specimens used in the earlier work were, unfortunately, not in good enough condition for study. A full account of the animals from which these brains were obtained, as well as of the technic employed in preparing them and of the method of measuring the capillaries, is given in the former paper. It will be sufficient to repeat here that nos. 23, 24, 31, and 58 were male albino rats, nos. 16, 26, 55, and 56 females. Numbers 16, 23, 24, and 26 were obtained in Toronto, while the remaining four, as mentioned above, were secured at The Wistar Institute. The microscope, lenses (Leitz no. 7 objective and no. 3 ocular), and square-ruled micrometer employed in making the measurements were the same ones as were used before, but owing to the thinness of the cortical laminae, it was found much more convenient to measure the capillaries enclosed in only one half of the large square on the micrometer. Hence the measurements made were the total length of the capillaries enclosed in an area of  $\frac{1}{2} \times 189^2$  sq.  $\mu$  in each section, the length of one edge of the micrometer square being  $189\mu$ . As before, such measurements were made in the same region of each of ten successive sections, and as these sections were  $20\mu$  in thickness, the sum of the (10) readings gave the total length of the capillaries in a block of tissue of the volume  $\frac{1}{2} \times 189^2 \times 200$  c.  $\mu$ . These results are shown in the accompanying table (table 1).

The cortical localities selected for study are those general regions in which Sugita's measurements were made. The following is a list of these localities, using Brodmann's terminology, with the number of Sugita's region to which the position of the present measurements in each corresponds approximately, and the designations of the areas used in figure 1.

BRODMANN'S TERM	SUGITA'S NUMBER	DESIGNATIONS OF AREAS IN FIGURE 1
Regio praecentralis.....	II	A
Regio occipitalis.....	IV	D
Regio parietalis.....	VII	B
Regio insularis.....	VIII	E
Regio temporalis.....	XI	C

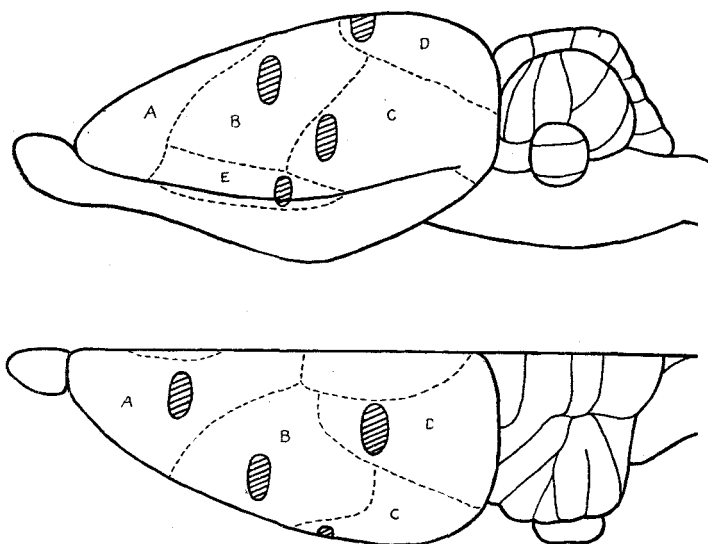


Fig. 1 Lateral and dorsal views of the left half of the brain to show the regions in which the measurements of vascularity were made. The exact location and relations of each of the areas represented is based on a comparison of figures by Fortuyn and Sugita, the names being applied in accordance with Sugita's correlation of Brodmann's terminology with these figures. Comparison with Brodmann's own figures and description seems to indicate that the anterior portion of area B is equivalent to the regio postcentralis. A, regio praecentralis; B, regio parietalis; C, regio temporalis; D, regio occipitalis; E, regio insularis.

TABLE I  
*Linear measurements obtained in  $\mu$  per  $\frac{1}{4} \times 189^2 \times 200$  c.  $\mu$*

Area	CEREBRAL CORTEX		F. R. 16, TO- R. ONTO	M. R. 23, TO- R. ONTO	M. R. 24, TO- R. ONTO	F. R. 26, TO- R. ONTO	M. R. 31, W. I.	F. R. 55, W. I.	F. R. 56, W. I.	M. R. 58, W. I.	HORIZONTAL AVERAGES	PROBABLE ERROR OF HORIZONTAL AVERAGES <i>per cent</i>
	Layer											
Insular.....	Lam. zonalis, I.....		2856	2203	2327	1914	2554	2620	2358	2743	2447	3.00
	Lam. pyram., III.....		3536	2654	2496	2527	2634	2886	2304	2904	2743	3.28
	Lam. gran. int., IV.....		3811	3086	2853	3016	3296	3135	2496	3497	3149	3.03
	Lam. gran. int., V.....		3853	2346	2604	2747	2642	2496	1898	3176	2720	4.90
	Lam. multif., VI.....		2897	2541	2598	2922	2186	2510	1983	2855	2562	3.16
Praecentral.....	Average.....		3391	2566	2576	2625	2662	2729	2208	3035		
	Lam. zonalis, I.....		2560	2254	3387	2720	3654	3982	3723	4649	3366	5.71
	Lam. pyram., III.....		2955	3000	4421	3910	3927	4060	3700	5073	3881	4.29
	Lam. gran. int., IV.....		3424	4013	5082	4447	3932	4571	3813	5237	4315	3.42
	Lam. gran. int., V.....		3172	3394	4071	4105	3493	4154	2879	4134	3675	3.27
Occipital.....	Lam. multif., VI.....		2803	2585	3159	3234	3010	2764	1995	3001	2819	3.34
	Average.....		2983	3049	4024	3683	3603	3906	3222	4419		
	Lam. zonalis, I.....		2581	3034	3424	2808	3797	4557	3531	3972	3463	4.48
	Lam. pyram., III.....		3253	3131	3864	3893	4431	4148	3312	4719	3844	3.59
	Lam. gran. int., IV.....		3919	3444	4485	4218	4542	4846	3708	5438	4325	3.56
Occipital.....	Lam. gran. int., V.....		3625	3284	4062	3892	4621	4474	3135	4496	3949	3.51
	Lam. multif., VI.....		3364	2531	3275	2834	3972	3103	2638	3956	3209	4.17
	Average.....		3348	3085	3822	3529	4273	4226	3265	4516		

Temporal.....	Lam. zonalis, I.....	2951	2780	3582	2548	2945	4489	2986	4340	3328	5.25
	Lam. pyram., III.....	3581	3689	4290	3416	3875	5184	3525	4835	4049	3.87
	Lam. gran. int., IV.....	4332	3769	5261	4711	4528	4966	3827	4832	4528	2.79
	Lam. gangl., V.....	3217	3514	3904	3880	3525	4327	2959	3888	3652	2.85
	Lam. multif., VI.....	3135	2819	3831	3329	2805	3417	2807	3731	3234	3.05
	Average.....	3443	3314	4174	3577	3536	4477	3221	4325		
	Lam. zonalis, I.....	3056	3150	3587	3464	3468	3860	4293	4942	3728	4.01
	Lam. pyram., III.....	4288	3705	4458	4158	4959	4756	4235	5539	4512	2.98
	Lam. gran. int., IV.....	4471	4404	5156	5047	5343	5083	4931	6726	5145	3.32
	Lam. gangl., V.....	3863	3461	4115	4452	3793	3905	3214	4820	3953	3.11
Parietal.....	Lam. multif., VI.....	3854	2601	3602	3663	3359	3125	2547	3698	3306	3.64
	Average.....	3906	3464	4184	4157	4184	4146	3844	5145		

The accompanying illustrations (fig. 1) show these areas with the points where the measurements of vascularity were made indicated approximately by the hatched spaces. The outlines of the cortical regions are based upon a comparison of Sugita's reproduction of Fortuyn's figures with the former author's own illustrations of sections, and his correlation of both these with Brodmann's terminology. The outline of the brain was taken in the first place from two injected specimens which had been carried only as far as the 70 per cent alcohol stage in preparation.

The laminae of the cortex were by no means easily distinguished in many cases, the simple picric-acid stain which was employed not being well adapted for such a purpose. By careful comparison, however, with a series of sections stained with toluidine blue and erythrosin and with the specimens in which the layers were more distinct, they were located fairly accurately, it is believed, even in the more difficult cases.

Figure 2 shows the cell lamination and the vascular supply in the occipital cortex of one rat.

#### OBSERVATIONS

The measurements obtained are presented in table 1. The results for the eight brains have been averaged and the probable error of the averages calculated, these figures being given at the right-hand side of the table. The probability of error tends, of course, to be a little higher than was the case in the previous study on account of the use of only eight brains instead of ten. The ratios of the averages to the readings for the ventral white funiculus and the ventral gray cornu of the spinal cord in the same individuals<sup>1</sup> are given in the last columns of table 3. The sex of each rat has been indicated in table 1 by placing M. or F. in front of its identification number, while its locality is shown by adding 'Toronto' or 'W. I.' (The Wistar Institute).

In the preparation of the tables the mean values for the five laminae in each area, as shown in table 1, were averaged, and the areas were arranged in order of increasing vascularity, as thus determined. These averages are recorded in table 2. The

<sup>1</sup> See Craigie ('20).

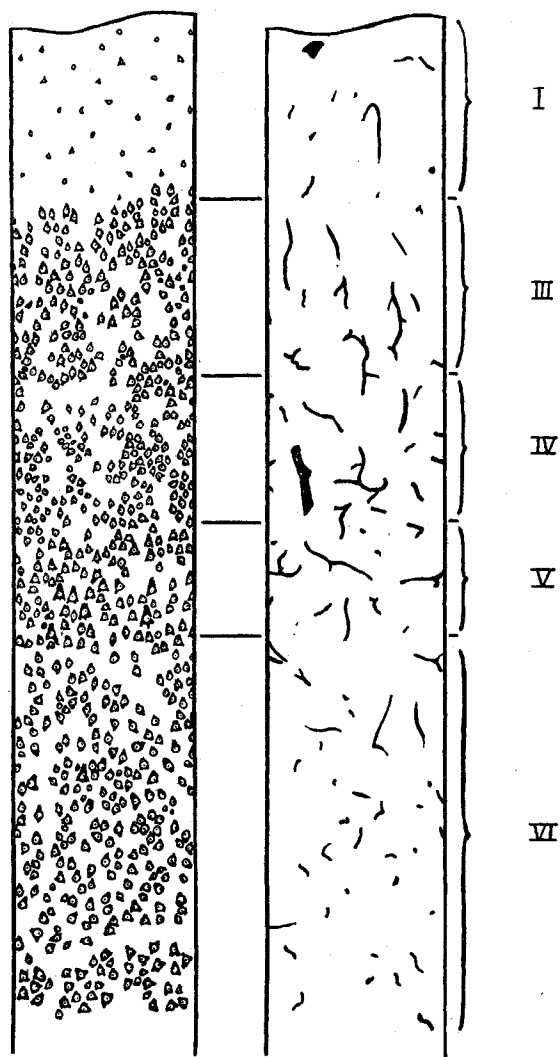


Fig. 2 On the right, a drawing of the blood vessels in a small part of the occipital cortex of R 26. On the left, a diagram of the cell lamination in the same piece of cortex.  $\times 112$ . *I*, lamina zonalis; *III*, lamina pyramidalis; *IV*, lamina granularis interna; *V*, lamina ganglionaris; *VI*, lamina multiformis.

average vascularity of the five layers is the same in the occipital and temporal regions, and it is very little less in the praecentral region. The parietal region is distinctly the richest, while the insular is much the poorest.

With regard to individual variation, it is noticeable that the same individuals tend to give rather high or rather low results in all the cortical areas, but the values obtained in the lower, subcortical centers of these individuals were not always similarly high or low. These differences are reflected in the ratios of the cortical values to those for the ventral white column and the ventral gray cornu of the cord, which have been set down in a detailed table, not published, from which table 1 has been con-

TABLE 2

*Average vascularity of five areas of the cerebral cortex. (The averages of the values shown for the five laminae of each area in the second last column of table 1)*

CORTICAL AREA	$\mu\text{PER } \frac{1}{2} \times 189^{\circ} \times 200 \text{ c. } \mu$
Insular.....	2724
Praecentral.....	3611
Occipital.....	3758
Temporal.....	3758
Parietal.....	4128

densed, and which show considerable fluctuation. The individual ratios referred to have all been averaged, and the results are found to correspond so satisfactorily with the ratios of the average readings, shown in table 3, that it is considered sufficient to publish the latter.

The averages for the various layers of each area, as recorded in next to the last column of the first table, are represented graphically in figure 3, which illustrates the relation between the different regions as well as that between the five laminae in each.

It will be observed that the relative vascularity of the five laminae in the various areas studied is fairly constant, not only as regards the averages, but even, though to a smaller extent, in the different individuals, as shown in table 1. The greatest irregularity which appears is in the case of R.56, in which the



*Table showing the average vascularity of each of the parts of the central nervous system studied, expressed in terms of the length in  $\mu$  of the capillaries in a cube of tissue of 100  $\mu$  edge*

REGION	$\mu$ PER 100 <sup>3</sup> C. $\mu$	RATIO		CEREBRAL CORTEX		$\mu$ PER 100 <sup>3</sup> C. $\mu$		RATIO	
		Ventral white	Ventral gray	Area	Lamina			Ventral white	Ventral gray
Fasc. cuneatus.....	184	0.93		Insular.....	Lam. zonalis, I.....	685		3.46	0.76
Ventral column.....	198 <sup>1</sup>	1.00			Lam. pyram., III..	768		3.88	0.85
Lateral column.....	223	1.13			Lam. gran. int., IV	881		4.46	0.98
Pyramidal tract.....	350	1.77			Lam. gangl., V.....	761		3.85	0.85
Fasc. long. dors.....	426	2.15			Lam. multif., VI..	701		3.63	0.80
Subst. gelat. Rolandi.....	582	2.94	0.65	Praecentral..	Lam. zonalis, I.....	942		4.76	1.05
Nuc. mot., VII.....	732	3.70	0.81		Lam. pyram., III..	1086		5.49	1.21
Nuc., XII.....	802	4.06	0.89		Lam. gran. int., IV	1208		6.11	1.34
Nuc. mot., V.....	817	4.13	0.91		Lam. gangl., V.....	1029		5.20	1.14
Ventral horn; cord.....	900 <sup>2</sup>	4.55	1.00		Lam. multif., VI..	789		3.99	0.88
Spinal V. nucleus.....	923	4.67	1.03	Occipital.....	Lam. zonalis, I.....	969		4.90	1.08
Deiters' nucleus.....	935	4.73	1.04		Lam. pyram., III..	1076		5.44	1.20
Molec. layer; cerebellum.....	996	5.04	1.11		Lam. gran. int., IV	1211		6.12	1.35
Dorsal horn; cord.....	1008	5.10	1.12		Lam. gangl., V.....	1105		5.59	1.23
Inferior olive.....	1076	5.45	1.20		Lam. multif., VI..	898		4.54	1.00
Superior olive.....	1120	5.67	1.25	Temporal....	Lam. zonalis, I.....	931		4.71	1.04
Chief sens. V. nucleus.....	1130	5.71	1.26		Lam. pyram., III..	1133		5.73	1.26
Granule layer; cerebellum.....	1227	6.20	1.36		Lam. gran. int., IV	1268		6.41	1.41
Nuc. dentatus.....	1272	6.43	1.41		Lam. gangl., V.....	1022		5.17	1.14
Chief vestib. nucleus.....	1363	6.90	1.52		Lam. multif., VI..	905		4.58	1.01
Dors. cochlear nucleus.....	1472	7.45	1.64	Parietal.....	Lam. zonalis, I.....	1043		5.28	1.15
					Lam. pyram., III..	1263		6.39	1.40
					Lam. gran. int., IV	1440		7.28	1.60
					Lam. gangl., V.....	1106		5.60	1.23
					Lam. multif., VI..	923		4.67	1.03

<sup>1</sup> The original average from which this figure was calculated was used as the standard for the ventral white matter.

<sup>2</sup> The original average from which this figure was calculated was used as the standard for the ventral gray matter.

lamina zonalis tends to be richer as compared with the other layers than is the case in the rest of the brains studied. This is believed to be due to an unexplained vacuolate appearance

## Vascularity

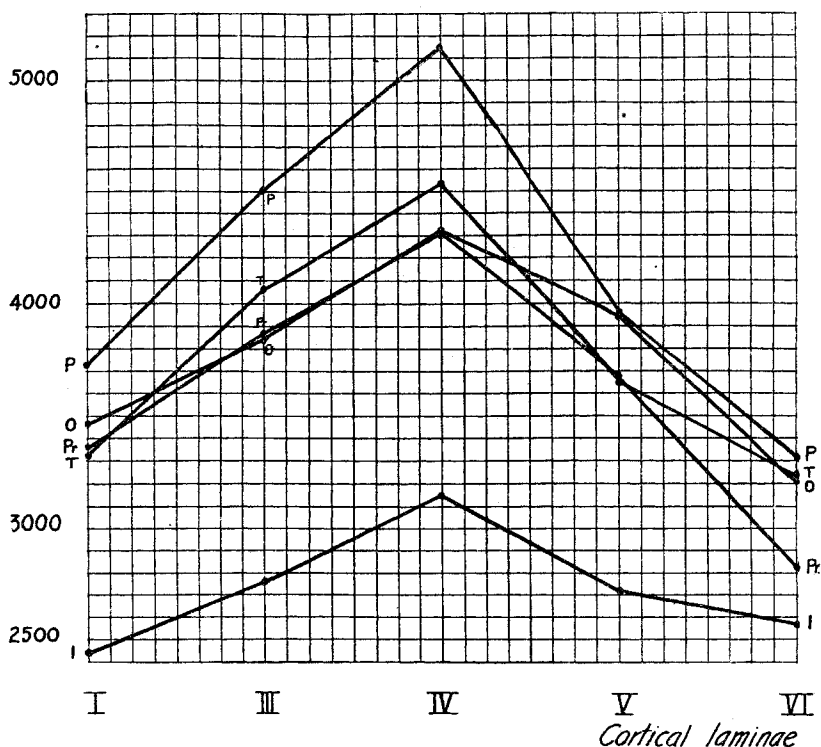


Fig. 3 Chart showing the relative vascularity of the five cortical areas studied and of the five laminae in each.

I, lamina zonalis  
 III, lamina pyramidalis  
 IV, lamina granularis interna  
 V, lamina ganglionaris  
 VI, lamina multiiformis

I, insular area  
 O, occipital area  
 P, parietal area  
 Pr, praecentral area  
 T, temporal area

in this specimen of all the layers except the lamina zonalis. It seems probable that this condition of the tissue has resulted in the measurements for all the inner layers in R.56 being a little lower than they should have been. As these results fell

within the range of variation of the other individuals, however, it was decided not to discard them.

In all the five areas studied, the lamina granularis interna (IV) is decidedly the richest, the lamina pyramidalis (III) coming next, with the lamina ganglionaris (V) very little behind it. The fourth in order of richness is the lamina zonalis (I), while the lamina multiformis (VI) is the poorest in every region except the insular. It may be remarked that the lamina granularis interna, which is absent from the praecentral region of many mammals, is distinct, though thin, in that portion of the cortex of the rat, and it is interesting to note that it is not relatively poorer in its capillary supply there than in the other areas.

These observations may be compared with the description of Duret ('74) fifty years ago. He found that the outer 0.1 mm. of the human cerebral cortex contained large quadrangular meshes parallel to the surface, the next 2 mm. is filled with rather fine polygonal capillary meshes, while the inner 1 mm. has a transitional network with larger meshes, which, however, are much less elongate than those of the white matter into which they pass.

There is little certainty at the present time regarding the functions of the different layers of the cerebral cortex. Bolton ('00) noticed twenty years ago that, while the deeper layers did not vary appreciably in thickness as a result of age or chronic insanity, "there is an almost exact correspondence between the thickness of the conjoined first and second layers<sup>2</sup> of the cortex and the degree of amentia or dementia existing in the patient." Nine years later, Kappers ('09) concluded upon the basis of comparative evidence that "the granular layer in the cortex is primary in character, and has originally receptive functions," that the subgranular layers (V, VI) have chiefly the functions of projection and intraregional association, while the supragranular layers (II, III), which are the last to appear phylogenetically, are concerned chiefly with association of a higher order (inter-regional), including intellectual processes.

<sup>2</sup> The 'second layer' of Bolton appears to be equivalent to Brodmann's laminae II and III, i.e., the supragranular layers.

Brodmann (*loc. cit.*) considers Kappers' theory groundless, describing it as a wild hypothesis which is quite untenable and erroneous. Van Valkenburg ('13, '13 a [?]), however, has brought forward certain evidence which seems to support Kappers' view; as have also Nissl, Nieuwenhuijse, and Bielschowsky, whose contributions are summarized by Van't Hoog ('20). The last-mentioned author also adduces further evidence in favor of the theory of Kappers, and stresses particularly the rôle of the cells in the lamina granularis interna. These he considers, emphasizing a point concerning which Kappers had been less positive, to be 'matrix cells,' i.e., cells which have retained much of their primitive character and potentialities, which are still capable of a wide range of differentiation, and from which the other layers have probably been derived phylogenetically. It may be pointed out that, in the ontogeny of the cerebral cortex of the rat, this layer is the last one to become distinguishable according to Sugita ('17), but, on the other hand, it is said by Tandler and Kantor ('07) to be the first to appear in the embryological development of the reptilian cortex. Thus practically all the available evidence, whether it be conclusive or not, seems to point in the direction outlined by Kappers.

It would be an interesting observation if it was really the more recent and more highly specialized portions of the cortex which were the less richly vascular, and we have possibly a somewhat similar case among the lower centers studied. Reference to table 3 will show that the chief vestibular nucleus is more highly vascular than the cerebellar cortex, the dentate nucleus, or Deiters' nucleus. Now the cerebellar gray matter is a highly specialized derivative of the primitive acoustico-lateral area, from which, of course, both the other nuclei are also developed. Moreover, the chief vestibular nucleus is composed of small, granule-like cells, most of the axones of which are said to take up a longitudinal direction in the substantia reticularis, so that it seems not unreasonable to suppose that it may be less highly differentiated than either the nucleus of Deiters or the cerebellum. This, however, is pure speculation without definite authority or conclusive basis.

Kappers (*loc. cit.*) offers a suggestion, in another connection altogether, which seems to provide a very plausible explanation, at least in part, for the special vascular richness of the lamina granularis, and perhaps also of the sensory nuclei. In discussing the importance of the granule cells in relation to his principle of neurobiotaxis, he points out that, "while in projection cells the nervous current is directly realized and led away, on the contrary, in the granular cells with short axis cylinders forming an intricate network the stimulation is kept within a certain region." He goes on to point out that the long ascending and descending tracts very often end in relation with such cells, citing among other examples the case of the sensory root fibers ending in the medulla oblongata "and (less general) in the cord." Such a region of concentrated or localized activity might reasonably be expected to have a relatively rich blood supply, and no doubt this is one at any rate of the factors giving rise to the observed differences.

To facilitate comparison of the vascularity of the cerebral cortex with that of the lower centers previously studied, table 3 has been prepared. In this table all the values have been reduced to the basis of a cube of tissue of 100  $\mu$  edge, so that the figures given represent the total length of the capillaries in a block of tissue of volume 1,000,000 c.  $\mu$ , or 0.001 c. mm. This not only makes easy the direct comparison of the figures in the table, but also provides a unit with which comparisons may readily be made in future studies. It may be remarked that the ratios in the table were calculated from the original readings, not from the reduced figures which are tabulated beside them. These ratios show that, on the whole, the vascular supply of the cortex is not much greater than that of the ventral cornu of the gray matter in the spinal cord, but exceeds that of the ventral funiculus of the white matter from three and a half to over seven times.

It will be observed that the vascularity of the insular cortex corresponds roughly with the values obtained for the motor centers, while the various laminae in the other areas cover about the same range as the sensory and correlation centers in the lower

part of the brain, though the richest part of the cortex studied is slightly poorer than the richest center lower down—the dorsal cochlear nucleus. May it be that, great and intense as the activity of the cortex probably is, that activity is nevertheless more intermittent in any one area than is the activity of the lower sensory nuclei? The latter, as was pointed out in the previous paper, are in more or less constant receipt of stimuli, but only a small proportion of these give rise to any reflex, and only a still smaller proportion, when any, reach the cerebral cortex. Many impulses are, no doubt, generated within the cortex itself, and such generation may possibly involve a greater expenditure of energy than the mere passage of an impulse caused by a stimulus somewhere else, so that the cortex may reasonably be expected to be relatively rich in most areas; but the activity in any one portion of the cortex is probably less constant than that in a sensory nucleus, so that greater vascularity is not required.

It might perhaps be mentioned here that what appears to be a clear example of a direct relation between vascularity and functional activity has been described recently in Cajal's laboratory by De Castro ('20), who found such a relation distinctly shown in comparing the vessels belonging to the olfactory glomeruli in man with those in macrosmatic animals.

It may be remarked that, while the 'motor cortex' (*regio praecentralis*) ranks low among the five areas studied, it is very little poorer than the occipital and temporal areas, and is considerably richer than the *regio insularis*.

Finally, we note that the values obtained for the vascularity of the lamina zonalis in the four richer areas are very similar to the figure representing the condition in the molecular layer of the cerebellar cortex.

As in the previous study, the results for the two sexes have been separated and averaged, and the comparison of these is made in the charts in figure 4. The difference between the sexes is much more definite than it was found to be in the lower centers, the vascularity in the males being greater in every lamina of the parietal, temporal, occipital, and praecentral

areas, though the females surpass the males in three of the laminae of the insular cortex. In the subcortical regions the tendency was for the females to be richer than the males. It is perhaps hardly justifiable to base any conclusion upon the averages of so few individuals, especially when the difference is

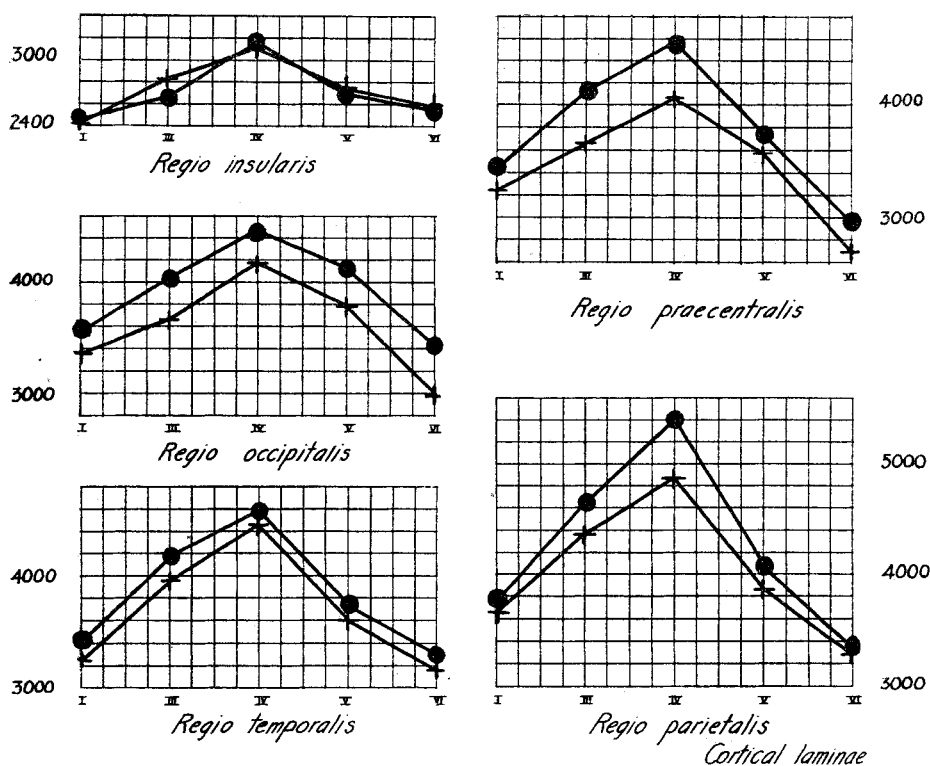


Fig. 4 Graphs showing the relative vascularity of the cerebral cortex of the two sexes in each lamina of the five areas studied. Male ●. Female +.

not very great, being less than the amount of individual variation, and when the poorer group includes the specimen (R. 56) for which the results are suspected of being rather low. Nevertheless, it seems distinctly suggestive that the sexual difference should be so uniform and so much more definite in the cortex cerebri than in the lower centers studied.

A comparison of the groups according to locality has also been made, the average of the results for the four Toronto animals being compared with that for the four specimens from the standard colony of The Wistar Institute. The differences

### Vascularity

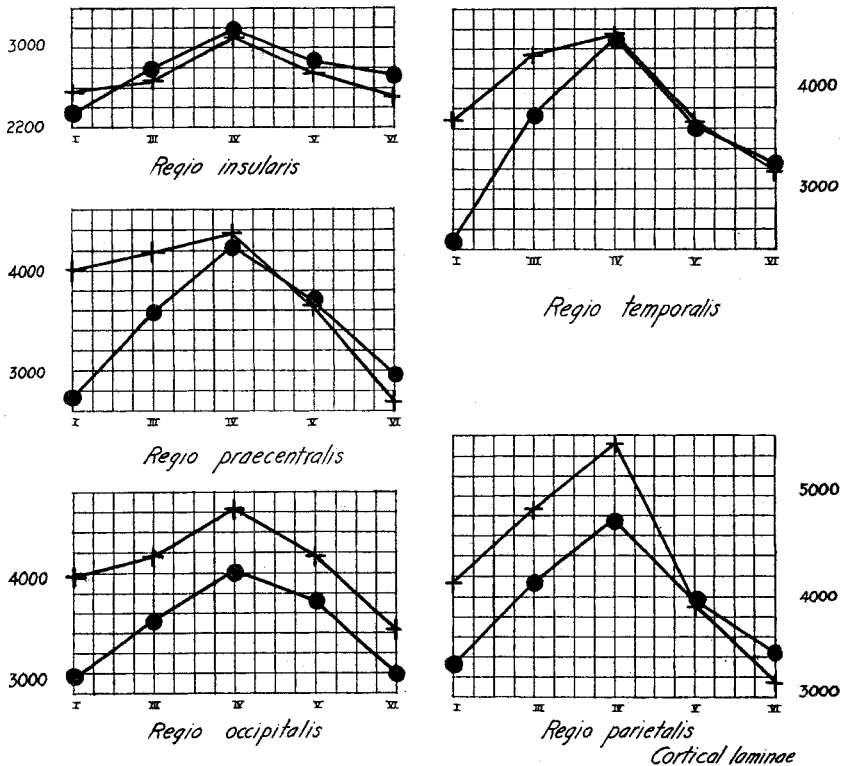


Fig. 5 Graphs showing in the same way as in figure 4 the relative vascularity of the cerebral cortex in rats from two different localities. Toronto ●. The Wistar Institute +.

between these groups are illustrated graphically in figure 5. Here again, the difference is a little more decided than in the lower parts, though less definite than that between the sexes. In this case, however, the suspected specimen (R. 56) belongs to the group which is richer in most layers (the group from The



Wistar Institute). It may be noticed that, in all cases where the Wistar average is less than the Toronto one, it is the deepest layers which are involved, the lamina multiformis being poorer in the Wistar group in four of the five areas, the lamina ganglionaris in three, the laminae granularis interna and pyramidalis in only one, and the lamina zonalis in none. It should be pointed out in this connection that each local group contains two specimens of each sex.

Evidently the difference between the regio insularis and the other four regions is either of some other nature or of a much greater degree than their differences from each other. It is this area which is so much more poorly vascularized than the others; it is this area in which the female average exceeds that of the males in three laminae; and it is this area in which the average for the Wistar animals is poorer in four laminae than that for the Toronto animals.

It should be remarked here that it is possible that some of the differences in the measurements of vascularity are possibly attributable to differences in brain weight. The situation in this respect is summed up by Donaldson<sup>3</sup> as follows:

If the vascular supply grows in proportion to the brain—within the limits of variation of brain size in full grown rats—then a sample of a fixed volume of tissue from one brain will be comparable with that from another.

If the increase in the volume of the entire brain is more rapid than that of the vascular supply, then the supply in a fixed volume of tissue will appear less in the larger brain—and vice-versa.

Which of these conditions obtains, the writer is not at present in a position to state definitely, but he is inclined to believe that the second supposition is the one which represents the facts. This would not account, however, for the differences in the relations seen in the different parts of the central nervous system. Unfortunately, the weights of the brains employed in the present study were not recorded, but the body weight and body length of the four rats from The Wistar Institute are known. From these data the probable brain weights may be determined from

<sup>3</sup> Personal communication.

the normal tables for the albino rat (Donaldson, '15, table 68), which give the following results:

RAT	SEX	BODY LENGTH	BODY WEIGHT	BRAIN WEIGHT CALCULATED FROM BODY LENGTH	BRAIN WEIGHT CALCULATED FROM BODY WEIGHT
		<i>mm.</i>	<i>grams</i>	<i>grams</i>	<i>grams</i>
31	♂	200	228.4	1.858	1.900
55	♀	185	159.2	1.782	1.773
56	♀	198	197.4	1.841	1.835
58	♂	210	234.8	1.903	1.907

It is thus evident that the female brains may be regarded as slightly smaller than those of the males. Since the vascularity of the cerebral cortex is poorer in the female brain, rather than richer, the sexual difference cannot be explained upon the basis of size in the manner suggested above.

Since measurements were not recorded for the Toronto animals, a similar scrutiny cannot be applied to the comparison of local groups. It seems not improbable that the difference in this case may be capable of explanation on the above basis, though this would not account for the greater difference found in the cortex as compared with the subcortical regions.

While one must hesitate to generalize upon only two comparisons with the limitations already pointed out, these data seem to suggest a greater susceptibility in the cortical vascularization than in that of the more ancient portions of the central nervous system to differences either within or without the body—sexual, hereditary, or environmental.

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#### SUMMARY

1. The vascularity of each of the five distinguishable layers in five different areas of the cerebral cortex has been measured in eight albino rat brains out of the ten which were used in the prosecution of a study, already reported (Craigie, '20), upon

the relative vascularity of various parts of the cerebellum, medulla oblongata, and spinal cord.

2. The relative vascularity of the five laminae in a single region is found to be similar in all the cortical areas examined, the lamina granularis interna (IV) being the richest in every case.

3. The supragranular layers show a tendency to be a little richer than the infragranular ones, the poorest layer being the lamina multiformis (VI) in every area except the insular, where the lamina zonalis (I) is very slightly poorer.

4. It seems probable that the granular and supragranular layers are receptive and associative in function, while the infragranular layers give rise to corticofugal fibers. This suggests a comparison with the lower centers, where the sensory and correlation nuclei were found to be more richly vascular than the motor nuclei. Moreover, it has been suggested that the lamina granularis interna is composed of relatively less highly differentiated cells than the other layers, which gives rise to speculation as to why it should be more vascular than the remaining laminae.

5. The average vascularity of the five layers is the same in the occipital and temporal areas, and is only slightly less in the praecentral region. The parietal area is distinctly richer than the others, while the insular cortex is much the poorest.

6. The vascularity of the five laminae in the insular cortex covers about the same range as that of the various motor centers studied in the brain stem and spinal cord (table 3), while the vascularity of the other areas corresponds approximately to that of the sensory and correlation nuclei.

7. The vascularity of the cerebellar cortex is of about the same order of magnitude as that of the cerebral cortex taken as a whole.

8. Sexual and racial differences appear to be more marked in the cortex cerebri than in the parts of the central nervous system previously studied, suggesting that the vascularization of the more recently evolved centers is more susceptible than that of more ancient regions to sexual, hereditary, or environmental influences.

9. The fact that the vascularity of the regio insularis not only is much poorer than that of the other four areas, but also differs from them in its sexual and racial characteristics, seems to indicate that this area differs from the rest more than they do from each other.

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