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# The vascularity of the central nervous system in certain vertebrates

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BOSTON UNIVERSITY

GRADUATE SCHOOL

Thesis

THE VASCULARITY OF THE CENTRAL NERVOUS SYSTEM

IN CERTAIN VERTEBRATES

by

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## INTRODUCTION AND REVIEW OF THE LITERATURE

In the last thirty years capillaries have been rediscovered as a subject worthy of study and experimental research. Interest in them was undertaken independently and almost simultaneously in different countries, and has been developed by a great number of workers. It is therefore possible and desirable to review the results obtained on the capillary circulation of the various organs of animals, and to coordinate them into a sort of system. This paper, however, will be limited to a study of the capillaries in the central nervous system of different animals.

Krogh (1929) measured the capillaries in muscles and made a plea for more quantitative studies of this type, saying, " I believe that when taken up in earnest by competent anatomists, the field of quantitative anatomy will prove to be a rich and fruitful one. Many determinations of vascular and glandular surfaces are needed as a basis for quantitative physiological work." Professor Krogh went on to say, " I cannot but think that quantitative anatomy will prove a very attractive subject, especially when conducted as a comparative science."

The blood supply of the brain and the rest of the central nervous system has been the object of study on the part of many anatomists from the time of Galen to the present day and the relations of the principal vessels have long been known. The difference in vascularity between the gray and white matter in the brain and spinal cord has also been discussed by several authors.

Ekker (1853) made some general comparisons of capillary richness in various parts of the brain in the human, but although he recorded some measurements of the diameter of vessels, nothing of importance was noted. According to him, the portion of the brain which is most richly supplied is the corpus striatum. The earlier work on this subject appears to be unimportant. Guyot, in 1829, succeeded in isolating the vessels of the cerebral hemispheres with forceps and a stream of water, and because of the poorness in vascularity reached the conclusion that the white matter has not active function. Various writers following Ekker, including Luschka, Henle, and Frey reproduced his account, but added nothing, according to Duret (1873). Gerlach in 1858 made some similar observations, but without extending the knowledge of the subject.

The vessels on the surface of the brain, and the main branches which enter its substance were well described by Haller (1896, 1898, 1900), Willis (1878), Vicq d'Azyr (1805, 1813), and others, and their observations were extended and made more exact by many later workers.

Heubner was according to Beevor (1909) "the first to investigate methodically the distribution of the different branches of the cerebral arteries." He divided the arterial supply of the hemispheres into basal and cortical, the vessels of the former group being all 'end arteries', without anastomotic communications, while those of the latter group anastomose freely in the pia mater. Cohnheim (1872) concluded that



there were a few anastomoses between the arteries near the circle of Willis, but that the arteries to the brain were practically 'end arteries', and that the anastomoses within the brain substance were insignificant when present at all.

About the same time, Duret (1873, 1874) published an extensive study of the vascular supply to the brain. He found the cells of the bulbar nuclei to be surrounded by a very fine network of capillaries, while the mesh in the white tracts was large. In the cerebral cortex the outer tenth millimeter contained large quadrangular meshes parallel to the surface, forming fine anastomoses between the arteries which penetrate the convolution. The next two millimeters have a fine polygonal capillary meshwork, formed chiefly by collateral and terminal branches of the cortical arteries. The inner one millimeter had a transitional network, with larger meshes, but much less elongate than those of the white matter, into which they passed. In the white matter the length of the meshes was three or four times the diameter of those in the gray matter, and they ran parallel to the principle bundles which they surrounded.

Pfeifer (1928) gave an admirable account of the historical development of this subject. He also described the general arrangement of the capillaries of the pia, brain stem, and cerebrum, and illustrated his text with beautiful plates. Craigie (1928) believed that the richness of the capillary supply is directly related to functional activity, and his work on the albino rat showed that the nuclei of the brain stem are exceedingly vascular organs, more so than the white

matter; moreover certain nuclei are more vascular than others. He also made careful observations on the cerebral cortex and his quantitative studies show that the different cortical layers vary somewhat in richness of their capillary supply, the fourth layer (lamina granularis interna) being always the most vascular. The work carried out by Craigie will be studied later in this thesis.

Lorente de No (1927) describes and pictures the capillary network of the area striata, area peristriata, and Ammon's horn. In the occipital cortex, the fourth layer is the most vascular and, in Ammon's horn, the pyramidal layer, but capillary measurements were not given.

Krause (1876) found that the capillary network in the human spinal cord in addition to being wider meshed in the white matter than in the gray, was widest in the posterior funiculi.

The excess of the capillary supply of the gray matter over that of the white matter was noted by all succeeding authors who referred to the capillaries at all, (Rudanowsky 1876, Adamkiewicz 1881, Kadyi 1889, Hoche 1899, Sterzi 1904, Cajal 1909, etc.). Rudanowsky (1876) described the capillary network in the gray matter as being so fine as to encircle a single cell in the mesh. Adamkiewicz (1881) disagreed with him on this point, but found evidence of a delicate secondary net within the primary capillary meshes, which did not surround single cells as Rudanowsky described. The vessels of the spinal cord were subject to careful investigation by Ross (1880), Adamkiewicz (1881a), Kadyi (1889), Hoche (1899), Sterzi (1904), Hoskins (1914) and others who have described their development, arrangement, and distribution.

Adamkiewicz (1881a) found the capillaries in the gray matter of the human cord to be large, the net being the densest and the capillaries the largest in the cell groups. The net was poorer in the dorsal horns than anywhere else in the gray matter.

Kadyi (1889) observed that the density of the capillary net was not the same in all parts of the spinal cord gray matter. He spoke of 'true capillaries', -those vessels which are interpolated between the final arterial branches and the first tributaries, and the 'precapillaries' (Vorcapillaren), arterial and venous, -those vessels which divide into twigs of a lower order, but resemble the capillaries in the diameter of their lumen. Hoche (1899) also made this same distinction as Kadyi (1889). Kadyi's nomenclature for the vessels on the surface of the brain has been adopted by succeeding workers.

The most extensive comparative and embryological investigation of the blood supply of the spinal cord was that of Sterzi (1904), who described it in all groups of vertebrates, from the cyclostomes up, and showed how the vascularization improves as one passes up the series.

There is a good description of the vessels in the medulla oblongata by Adamkiewicz (1890), while those of the midbrain have been studied by D'Astros (1892) and Shimamura (1894).

Hoffmann (1900) dealt with the arteries on the surface of the brain from a comparative point of view. The comparative anatomy of the circle of Willis and its main branches in the mammalia has been worked over by Tandler (1899,1902), to whose observations some interesting additions were made by Beddard (1904).

The distribution of the vessels within the brain substance has also been described by Beevor (1909), and Stopford (1916). The former made a thorough and exact study of the source of blood supply of each part of the forebrain in the human, while the latter made a similar investigation of the pons and medulla oblongata. The paper of Aby (1899) was of particular interest since this investigator made a careful study of the arrangement and connections of the vessels in the cerebellum of the cat. He found the granular layer of the cerebral cortex to be the most highly vascular, and observed that the layer of Purkinje cells resembled the granular layer in its vascularization. Aby (1899) drew conclusions regarding the varying metabolic rates of activity in the different layers based upon the assumption that, "at a given age, in a given organ, the relative amount of blood capillaries in two regions is a certain index of the relative intensity of metabolic changes in those regions." This assumption may be compared with the observations of various writers that, "the richer a region is in nerve cells, the closer is the capillary network which supplies it, " (Obersteiner, 1890).

VASCULARITY OF THE CENTRAL NERVOUS SYSTEM IN THE PACIFIC DOGFISH

The blood vessels of the central nervous system in various selachians, have been described by Sterzi (1909), Parker (1887), and Hofmann (1900). Sterzi (1909) described in great detail not only the superficial vessels, but also the internal ones.

In the spinal cord, Sterzi (1909) observed that, while arterial branches penetrate the organ all round the periphery, they are more numerous opposite the dorsal and ventral gray columns. These arterial rami have walls "little thicker than those of the capillaries." They give off a few branches in the white matter and then enter into the capillary network of the gray matter. The meshes of the gray matter are irregular. Those of the ventral column are less numerous and larger than those of the dorsal column. From the network of the gray matter separate off transverse efferent branches, with capillary structure and are interconnected by anastomoses, which cross the white matter and empty into the superficial venous network.

Craigie (1928) found that in the brain of the Pacific dogfish, the terminal arterial vessels which penetrate the brain matter all over its periphery, do not exceed twenty-two microns in diameter and have the structure of capillaries. The cerebellar lamina has a very close network. The network in the cerebellar gray matter has a similar density to that in the medulla oblongata. In the optic lobes the inner third is less richly vascularized than are the other two-thirds, the former containing the fibers of the internal medullary layer. The network stops a short way

below the outer surface due to the presence of the external medullary layer, which entirely lack capillaries. The meshes of this net are less close together than those of the cerebellar columns.

The diencephalic walls are richly vascular, while the post-optic lamina is poorly supplied. The hypophyseal area contains numerous vessels, which form a net with very small meshes. In the telencephalon the preoptic lamina has a few capillaries while the corpus striatum has a fine network like that of the lateral walls of the diencephalon. In the cerebral hemispheres the capillaries form a similar network. The olfactory peduncles are supplied by a capillary network with large meshes, and the bulbs have a network which is well developed in the cellular layers.

The measurements of vascularity in the spinal cord were made in most cases in the fourth segment by Craigie (1928). It was found that the white matter is very poorly supplied with vessels, particularly in the ventral funiculus. The deep parts near the gray matter, appear to contain more capillaries than the superficial parts. In the rat, which will be discussed later, the medial longitudinal bundle is more richly vascular than any of the white matter of the cord.

The ventral gray column is the richest efferent center in the rat but in the dogfish it is the poorest of these regions. The deep part of the dorsal gray column is the only part of the gray matter which is still poorer. The latter is the region where the narrow bases of the dorsal columns unite, some distance from the central canal.

The substance of Rolando is well supplied with capillaries and is eleventh in order in Table 1.

The spino-occipital nucleus in the medulla oblongata was measured by Craigie (1928) close to the calamus scriptorius. The lobi vagi corresponds with the nucleus of the fasciculus solitarius which occurs in the rat. The inferior olivary nucleus is of considerable size in the dogfish.

According to Kappers (1920), the dorsal part of the acusticolateral lobe close to the cerebellar crest, receives the endings of the fibers from the incipient lagena of the internal ear.

The vascularity of the parts considered is shown graphically in Figure 1, in which data for the ratfish are also plotted.

Herrick (1926) attributed the greater vascularity of the sensory centers to the fact that in these, "there is considerable amount of correlation, a physiologically expensive 'legislative' function, while the motor centers are concerned with the physiologically simple, administrative processes".

The granular cells in the cerebellar cortex are collected in two large longitudinal ridges, the cerebellar columns, at either side of the median plane, and the areas in which measurements have been made are representative of the ventral section of the left column.

Johnston (1911, 1923) and Holmgren (1922) have furnished the knowledge of the elasmobranch forebrain, and a review of this is useful as a background for the study of the vascularity in the forebrain of the dogfish. Johnston (1911, 1923) showed that, besides

a very distinct tuberculum olfactorium, there are definite medial and lateral olfactory areas, and a dorsal pallial area which he designated primordium hippocampi. Holmgren brought out the fact that these regions and certain pallial subdivisions which were described by Sterzi (1912) are very distinct during development and while these become obscured by the diffuse arrangement of the cells in the adult they may still be recognised. The pallial divisions Holmgren (1922) called hippocampal pallium (medial), general pallium (dorsal) and pyriform pallium (lateral). Johnston (1923) confirmed Holmgren's observations, but maintained that the pyriform lobe is represented in the dorsal part of the lateral olfactory nucleus and that Holmgren's area is part of the hippocampus extending round the rostral pole and back to the olfactory peduncle. Backstrom (1924) pointed out that Holmgren's pyriform lobe has not only a precrural part as implied by Johnston (1923), but a supra- and post-crural part and is distinguishable from the hippocampal area structurally as well as topographically. Holmgren's (1922, 1926) pyriform area is pallial, the lateral olfactory nucleus sub-pallial, but Herrick (1922, 1926) did not attach meaning to the pallial subdivisions in the elasmobranch, but preferred to call the whole dorsal region olfactoria dorsalis.

The lengths of the capillaries in the forebrain are found in Table 2 and the averages are plotted in Figure 1. The richest among the forebrain regions is the lateral olfactory nucleus, which ranks vascularly between the motor V and dorsal motor X nuclei. It surpasses the spinal V nucleus, the lobus vagi, and the lagenar area, but is



poorer than the outer sensory and correlation centers. Next to it in the forebrain comes the pyriform lobe, and then the hippocampal pallium. The difference in vascularity between the three parts of the pallium seems to support the view that they differ physiologically.

Table 1.

Total length in microns of capillaries in  $\frac{1}{10}$  (189<sup>2</sup> X 200) c. of fresh tissue of the Central Nervous System of the Dogfish

Region	Number on Fig. 1	SS 16 ♂	SS 17 ♀	SS 18 ♀	SS 19 ♀	SS 31 ♂	SS 33 ♀	SS 34 ♂	SS 35 ♀	SS 40 ♂	SS 41 ♀	Per Cent Probable Error	Average
Dorsal funic.: cord....	3	183	141	140	261	169	126	110	103	203	203	6.4	164
Ventral funic.: cord...	1	70	140	56	78	96	132	124	246	83	134	10.0	116
Lateral funic.: cord...	4	258	248	225	212	326	190	172	145	81	199	6.9	206
Fasc. long. medialis...	2	210	291	148	185	120	133	158	136	90	108	7.9	158
Dorsal mot. X nucleus..	14	318	303	320	497	407	477	402	442	397	433	3.5	400
Motor VII nucleus.....	12	458	294	275	290	375	533	327	329	315	425	5.0	362
Spino-occip. nucleus...	8	208	240	330	293	169	291	431	367	290	242	5.7	286
Motor V nucleus.....	13	435	247	458	355	189	471	373	511	374	342	5.7	376
Ventral horn: cord.....	6	253	191	282	173	247	263	186	188	175	181	4.2	214
Lobus vagi.....	9	335	274	244	347	264	353	267	388	167	364	4.0	300
Spinal V nucleus.....	7	324	230	157	303	294	219	334	208	210	360	5.4	264
Deiters' nucleus.....	17	504	490	435	418	463	531	626	361	340	468	3.8	464
Molecular layer: cer- ebellum.....	16	421	598	434	324	509	386	462	580	235	408	5.4	436
Dorsal horn(deep):cord.	5	193	237	165	151	229	164	211	264	204	211	3.7	203
Dorsal horn(nuc. Rolan) cord.....	11	408	378	306	390	382	367	318	278	263	386	3.2	348
Inferior olive.....	15	393	405	420	454	475	410	306	564	428	344	3.6	420
Chief sens. V nucleus..	18	523	419	562	322	353	644	654	759	367	466	6.2	507
Granule layer: cerebel.	19	610	419	351	440	547	469	418	559	446	814	5.6	507
Nuc. lateralis cerebel.	20	542	664	586	486	449	502	704	497	622	783	4.0	584
Desc. VIII nucleus.....	21	497	491	549	507	616	624	661	870	559	468	4.4	584
'Lagenar nucleus'.....	10	262	288	190	316	391	427	461	405	289	438	5.5	347
Lob. lin. lat. ant.....	22	626	709	673	746	916	640	655	638	770	803	2.7	718

Craigie, 1928.

Table 2.

Length in microns of the capillaries in  $\frac{1}{2}$  ( 189<sup>2</sup> X 200)c.v. of tissue in the forebrain of the Dogfish.

Region	SS 16	SS 17	SS 18	SS 19	SS 31	SS 33	SS 34	SS 35	SS 40	SS 41	Average	Per Cent Probable Error of Average
Nuc. medialis septi...	218	174	208	194	229	344	300	340	196	281	248	5.4
Tuberc. olfact.....	136	205	177	260	171	259	187	226	72	248	194	7.7
Nuc. olfact. lat.....	260	401	435	323	500	441	332	417	398	321	383	4.0
Nuc. ventr. striatici.	170	98	190	161	275	338	194	213	215	184	204	6.8
Area somatica.....	176	359	143	210	182	305	285	284	198	184	233	6.4
Hippocampal pallium...	207	252	266	352	306	409	224	168	335	345	286	5.7
General pallium.....	160	143	124	203	94	165	182	194	238	165	167	8.4
Pyriiform pallium.....	393	363	315	288	292	303	389	437	206	313	330	4.3

Craigie, 1928.

Table 3.

Total length in microns of capillaries in 100 c.m. fresh tissue in the brain of the dogfish.

Region		Region	
Dorsal funiculus; cord	46	Chief sens. V nuc.	142
Ventral funiculus; cord	32	Granule layer; cerebel.	142
Lateral funiculus; cord	58	Nuc. lateralis cerebel.	164
Fas. long. med.	44	Deiters' nucleus	130
Dorsal motor X nuc.	112	Desc. VIII nuc.	164
Mot. VII nuc.	101	'Lagenar nuc.'	97
Mot. V. nuc.	105	Lob. lin. lat. ant.	201
Spino occipit. nuc.	80	Nuc. med. septi	69
Ventral horn; cord	60	Tuberc. olfact.	54
Lobus vagi	84	Nuc. olfact. lat.	107
Spinal V nuc.	74	Nuc. ventralis striati	57
Molec. layer; cerebel.	122	Area somatica	65
Dorsal horn; (nuc. Rolandi)	97	Hippocampal pal.	80
Dorsal horn; cord(deep)	57	General pallium	47
Inferior olive	118	Pyriiform pallium	92

Craigie, 1928.

### VASCULARITY OF THE BRAIN IN THE RATFISH

The brain of the ratfish was studied by Craigie in 1927 in the same way as the dogfish brain was studied, the total length of the capillaries enclosed by a square-ruled eyepiece micrometer in ten sections. The material used consisted of brains of specimens which were selected from many preparations. The animals were killed by illuminating gas and injected with carmine gelatin. The brains were then fixed and cut in sections of twenty microns in thickness. The material was stained with picric acid. In studying the sections, a square-ruled disc micrometer was used, the total length of the pieces of capillaries enclosed by the square ruling (an area of  $189^2$  microns under Leitz objective number seven) in each of the sections was determined for each part studied in every brain. The final value recorded for each region studied was the total length of capillaries in a block of tissue measuring  $\frac{1}{2} (189^2 \times 200)$  cubic microns. These measurements were corrected for shrinkage so as to give a corresponding value for fresh tissue, the correction coefficient used being  $\frac{(W,H,L)^2}{(WHL)}$  where W,H,L is the product of the width, height, and length of the prepared mass of tissue, WHL being the product of the corresponding dimensions of the fresh brain. The figures obtained are recorded in Table 4, along with their average, and average reduced to the basis of a cube of tissue of one hundred microns in length.

The measurements in the spinal cord were all made in the sixth segment. The nucleus Rolandi, or superficial part of the dorsal horn,

corresponds in position with the nucleus Rolandi in the rat. The spino-occipital nucleus along the level of the calamus scriptorius was taken to correspond with the hypoglossal nucleus, the lobus vagi as representing the nucleus fasciculae solitariae. The medial longitudinal bundle and the spinal V nucleus were examined in the same sections as the spino-occipital nucleus. In the acusticolateral lobe, a selected group of cells representing Deiter's nucleus and the dorsal part of the lobe where Kappers (1906) states that the lagenar fibers of selachians are were selected by Craigie (1927) as was also the gray matter associated with the descending VIII root.

The measurements show the vascularity to be rather low. The medial longitudinal bundle is the poorest part of the white matter and the dorsal motor X nucleus is no richer than the ventral funiculus of the spinal cord. The nucleus lateralis cerebelli and both layers of the cerebellar cortex are richer while the descending VIII nucleus, the inferior olive, and the lobus lateralis anterior are richer still, being best supplied with capillaries.

The lateral line lobe, the descending VIII nucleus, the cerebellum and the nucleus lateralis and the inferior olive are rich in capillaries. The figures in Table 1 represent the lengths of the capillaries in the forebrain and they are low. Figure 1 represents graphically the vascularity in the brain of the ratfish.

Table 4.

Total length, in microns, of capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200) cubic microns of fresh tissue of the central nervous system of the ratfish.

Region	Number on graph	Specimen 1			Average in (100) <sup>3</sup> of tissue
		HC 10	HC 12	Average	
Dorsal funiculus; cord.....	2	386	317	351	98
Ventral funiculus.....	3	617	430	523	146
Lateral funiculus.....	4	606	595	600	168
Fasc. long. med.....	1	123	130	126	35
Dorsal motor X nuc.....	5	492	542	517	145
Nuc. mot. VII.....	9	677	599	638	178
Nuc. mot. V.....	8	654	609	630	176
Ventral horn; cord.....	12	860	568	714	200
Nuc. spino-occipital.....	13	797	680	738	206
Lobus vagi.....	6	648	572	610	171
Spinal V nucleus.....	7	631	605	618	173
Nuc. of Deiters.....	16	890	900	895	250
Molec. layers; cereb.....	17	1112	973	1042	292
Dorsal horn; cord.....	11	725	678	701	196
Dorsal horn; cord (nuc. Rolandi).....	14	787	698	742	208
Inferior olive.....	21	1522	1379	1450	406
Chief sensory V. nucleus.....	15	764	813	788	221
Granule layer; cerebellum.....	19	1370	1401	1385	388
Nuc. lateralis cerebelli.....	18	976	1213	1094	306
Desc. VIII. nuc.....	20	1374	1467	1420	397
'Lagenar nucleus'.....	10	637	656	647	181
Lobus lin. lat. anat.....	22	1760	1940	1850	518
Nuc. med. septi.....		545	330	437	122
Tuberc. olfact.....		508	383	445	125
Nuc. olfact. lat.....		762	585	673	188
Striatum.....		334	229	281	79
Pallium-medial.....		579	410	494	138
Pallium-lateral.....		412	463	437	122

Craigie, 1927.

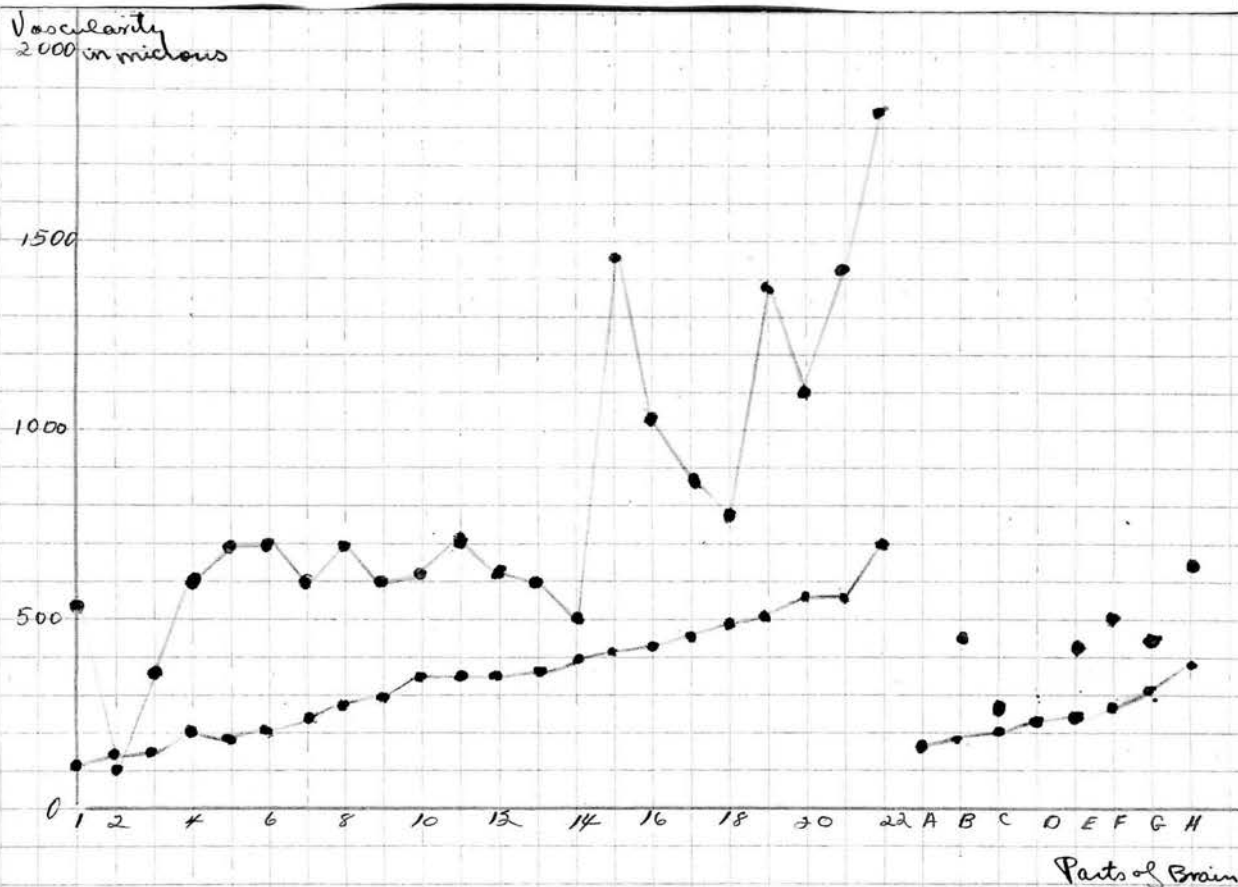


Figure 1. Graphic representation of the relative vascularity in the parts of the brain in the dogfish and ratfish.

Dogfish •

1. Ventral funiculus; spinal cord
2. Medial longitudinal bundle
3. Dorsal funiculus; cord
4. Lateral funiculus; cord
5. Dorsal cornu (deep); cord
6. Ventral cornu; cord
7. Spinal V nucleus
8. Spino-occipital nucleus
9. Lobus vagi
10. 'lagenar nucleus'
11. Dorsal cornu (nuc. Rolandi); cord
12. Motor VII nucleus
13. Motor V nucleus
14. Dorsal motor X nucleus
15. Inferior olivary nucleus
16. Molecular layer; cerebellum

• Ratfish

17. Nucleus of Deiters
18. Chief sensory V nucleus
19. Granular layer; cerebellum
20. Lateral cerebellar nucleus
21. Descending VIII nucleus
22. Anterior lateral line lobe
- A, General pallium
- B, Tuberculum olfactorium
- C, Nucleus ventralis striatici
- D, Somatic area
- E, Medial septal nucleus
- F, Hippocampal pallium
- G, Pyriform pallium
- H, Lateral olfactory nucleus



## THE VASCULARITY OF THE BRAIN IN THE MUDPUPPY

The total length of the capillaries in a unit volume of tissue of the mudpuppy was measured by Craigie (1940). The results are presented in Table 5 and are shown graphically in Figure 2 in comparison with the values obtained from studies in the salamander and the frog.

If the averages are compared with those for the salamander, it appears that the vascular supply is poorer in the salamander, being in most cases roughly about half as great or even only a third. The neuropil of the primordium piriforme approaches nearest to being equally vascularized in the two animals.

The neuropil of the primordium piriforme in the *Necturus* is as richly supplied with capillaries as the nucleus of nerve VIII, which in most of the animals studied is the richest region. The neuropil of the corpus striatum is not so rich in proportion to the other parts, being about equal with the primordium hippocampi and only about three quarters as rich as the neuropil of the primordium piriforme. The granular layer of the cerebellum is one of the least vascular parts found in the brain.

The palaeostriatum, is more or less poorly vascularized throughout the phylogenetic series, Campbell (1939) found it to be one of the poorest parts among those which he studied in the cat and a comparable condition was found by Craigie (1928) in the dogfish.

All of the parts of the hypothalamus are poorly supplied with

capillaries. In the cat Finley (1939) found that the hypothalamus contained centers of extremely wide difference in vascularity, the paraventricular and supraoptic nuclei, were very much richer than any other part of the brain, while the mamillary nuclei ranked with the richest parts elsewhere and the dorsomedial and ventromedial nuclei were among the poorest areas of gray matter. These conditions contrast with the conditions in the mudpuppy the vascularization of which is uniformly poor. The length of the capillaries in a unit volume of these nuclei is two hundred times as great in the rat as in the mudpuppy.

Table 5.  
Total length, in microns, of capillaries in  $\frac{1}{2}(189^2 \times 200)$  of tissue in the brain of the mudpuppy. (c.μ.)

(Not corrected for shrinkage except those in the last column)

	Mudpuppy											Aver- age	% P.E. of Aver- age	Length in 100 <sup>3</sup> c. of Fr.Tis.
	1	2	4	5	7	9	10	11	12	15	16			
Faso. long. medial.....	144	248	236	113	116	32	70	274	205	143	54	149	11.2	26
Nuc. motor. dors. X....	449	360	410	472	194	260	231	373	294	482	217	340	6.3	59
Nucleus XII.....	294	332	161	258	205	321	17	25	138	335	399	226	11.3	39
Nuc. motor. VII.....	416	280	242	410	315	188	396	311	315	259	83	292	7.0	51
Nuc. motor. V.....	230	79	270	132	103	0	62	353	320	193	251	181	12.6	31
Nuc. fasc. solitarii...	160	260	149	88	138	129	0	0	27	230	17	108	17.1	19
Nuc. spinalis V.....	50	283	247	119	40	95	246	32	211	71	0	127	16.2	22
Cerebel; molec. layer..	210	322	110	218	382	147	303	201	108	311	244	232	7.9	40
Nuc. sens. princip. V..	387	391	334	394	208	448	391	224	292	505	94	333	7.3	58
Cerebel; gran. layer...	29	35	83	0	17	0	114	0	0	5	35	29	24.9	5
Eminen. cerebel. ventr.	35	174	258	42	91	173	0	67	31	175	262	118	16.1	20
Nucleus VIII.....	439	383	457	644	574	415	409	605	553	702	529	519	4.2	90
Prim. hippocampi.....	474	493	430	333	305	233	416	310	418	215	241	352	5.7	61
Prim. pallii dorsalis..	182	145	111	175	227	195	0	0	45	152	21	114	14.9	20
Prim. piriforme.....	135	168	83	0	0	105	49	0	15	6	45	55	22.0	10
Neurop. of p. pirif....	672	648	495	456	307	276	417	512	505	628	581	500	5.3	87
Nuc. medialis septi....	340	385	251	298	239	200	175	231	94	205	213	239	6.8	41
Corp. striatum;pars.v..	91	151	25	5	37	0	0	87	0	56	35	44	22.4	8
Neuropil of corp. str.; pars ventr.....	595	503	440	311	389	228	317	333	316	495	328	387	5.7	67
Nuc. dorsolat. amygdal.	134	330	206	0	0	27	70	87	215	8	0	98	23.0	17
Nuc. preopticus magno- cellularis.....	95	39	142	38	79	0	0	0	78	26	115	56	17.9	10
Pars dors. hypothal; lobus ventralis.....	0		172	0	0	90	25	27	0	22	127	46	28.6	8
Pars vent. hypo;lob.ant.	100		0	0	67	148	0	18	23	0	0	36	30.9	6

Craigie, 1927.

## THE VASCULARITY OF THE BRAIN IN THE SALAMANDER

The total length of the capillaries in a unit volume of tissue in the brain of the salamander was measured by Craigie (1939). The results are presented in Tables 6 and 7.

The averages show the vascularization to be considerably poorer than in the mudpuppy and the leopard frog, in all except three regions, namely, the nucleus of the eighth nerve and the two areas of neuropil in the cerebral hemisphere. The nucleus VIII is richer than in the vestibular nucleus of the frog but much poorer than the cochlear nucleus of the same animal. Like the dorsal nucleus in other animals which have been studied, it is the richest center examined.

The difference in vascular richness of the forebrain neuropil is very noticeable. In the frog the two areas of this formation are the poorest parts of the gray matter and do not differ from the medial longitudinal bundle statistically, to a great extent. In the salamander however, the two neuropil areas are richer than any other part of the cerebral hemisphere and rank up among the gray regions of the hindbrain.

Apart from the neuropil, the cerebral hemisphere is poorly vascularized, the richest areas being the primordium hippocampi and the nucleus medialis septi which rank with the poorer regions in the hindbrain, while the other two pallial primordia, the corpus striatum, and the nucleus dorsolateralis amygdalae are poorer than the medial longitudinal bundle. The order of richness in the forebrain centers

is essentially the same as in the frog. As in the frog, the granular layer of the cerebellum is a poorly vascularized region. In both the frog and the salamander the molecular layer of the cerebellum is richer than the granular, particularly in the salamander. Figure 2 shows graphically the vascularity of the brain in the frog, salamander, and the mudpuppy.

Table 6.

Total length in microns of the capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200) c.m. of tissue in the Brain Stem and Cerebellum of the Tiger Salamander ( Not corrected for shrinkage )

	Salamander										Average	% P.E. of Average Tissue	Corrected Average Length in 100 c. of Fresh Tissue
	5 ♀	6 ♂	13 ♂	14 ♀	15 ♂	16 ♂	17 ♂	19 ♂	20 ♂	21 ♀			
Fasc. long. medialis..	243	307	336	320	288	295	221	205	201	297	271	3.9	61
Nuc. motorius dors. X.	479	597	408	383	497	562	429	357	572	442	473	3.8	106
Nucleus XII.....	618	308	315	569	313	404	512	432	436	572	448	5.5	100
Nuc. motorius VII.....	415	623	489	391	518	590	564	354	425	584	495	4.1	111
Nuc. motorius V.....	769	443	462	452	604	559	619	450	482	543	538	4.1	121
Nuc. fasc. solitarii..	409	267	168	401	207	241	216	196	321	423	285	7.2	64
Nuc. spinalis V.....	377	456	375	333	406	467	345	475	469	379	408	2.8	91
Cerebellum; molecular layer.....	684	721	-	564	-	-	525	360	330	767	565	7.8	127
Nuc. sens. principal V	594	820	650	768	792	546	772	526	752	804	702	3.4	157
Cerebellum; granular layer.....	541	481	423	350	194	-	205	338	205	269	334	8.6	75
Eminentia cerebelli ventr.....	536	571	485	303	303	-	340	359	321	308	392	6.2	88
Nucleus VIII.....	774	978	752	676	724	986	952	766	781	1019	841	3.2	188

Craigie, 1939.

Table 7.

Total length in microns of the capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200) p. of tissue in the Forebrain of the Tiger Salamander  
( Not corrected for shrinkage )

	Salamander										% P.E. of Average	Average Tissue	Corrected Average Length in 100% of Fresh Tissue
	5	6	13	14	15	16	17	19	20	21			
Primordium hippocampi.	559	356	595	331	412	349	551	354	549	404	5.0	446	100
Primordium pallii dorsalis.....	297	268	260	249	155	250	270	170	208	168	4.7	230	52
Primordium piriforme..	179	180	171	148	194	161	124	122	138	189	3.5	161	36
Neuropil of p. piriforme.....	567	401	403	475	559	688	563	615	477	590	3.7	534	120
Nucleus medialis septi	537	236	426	397	290	372	428	420	457	459	4.6	402	90
Corpus striatum: pars ventralis.....	175	70	96	147	213	98	182	188	221	112	7.6	150	34
Neuropil of corpus striatum: pars ventr.	732	867	600	531	662	774	685	544	608	453	3.4	628	141
Nuc. dorsolateralis amygdalae.....	277	288	111	235	210	255	127	163	205	145	6.6	202	45

Craigie, 1939.

## VASCULARITY OF THE BRAIN IN THE FROG

Sterzi (1904 ) showed that the capillary bed of the spinal cord is peculiar in the frog in conducting blood only in a centrifugal direction. According to him the spinal cord in *Rana esculenta* and *Rana fusca* are supplied with blood through central arteries which reach the gray matter and bifurcate to form two longitudinal channels, one on each side, a little ventral to the central channel. In the white matter, the meshes and the capillaries composing them both increase in size towards the periphery, where the capillaries empty into superficial veins. The anterior spinal artery gives off only rare and small lateral branches and these do not send any vessel into the substance of the cord. Venous tributaries, however, leave the cord all over its surface. Thus the flow of blood through the substance of the spinal cord is entirely centrifugal, passing from the central arteries to the superficial veins. Craigie (1938 ) found that the same condition exists in the medulla oblongata of this animal, where the basilar artery gives off a series of central arteries which run vertically into the brain close to the median plane and branch in the deeper part of the tissue. Each artery branches to one side of the brain only, though capillary anastomoses occur freely across the median plane. The branches and capillaries stream out towards the surface and enter the veins all over the latter, so that the strict centrifugal course of the blood appears to be preserved in the medulla oblongata. In the rest of the brain, however, while



the flow is preponderantly centrifugal, the artery supply through the basal vessels, corresponding with the central arteries of the medulla, is supplemented by peripheral arteries which vary in importance in different regions.

Sterzi (1904) also observed that the capillaries composing the network in the matter of the central nervous system are relatively straight in the frog and become increasingly contorted as the vertebrate scale is ascended.

The total length of the capillaries in a unit volume of tissue in each of twenty-two parts of the brain in ten frogs is shown in Tables 8 and 9.

Table 8 shows that the medial longitudinal bundle, which is the only piece of white matter represented, is poorer than any gray region in the hindbrain. Table 9 which represents the lengths of the capillaries in the forebrain shows the dorso-lateral amygdaloid nucleus is less than 1.2 times as rich as the medial longitudinal bundle. The cochlear nucleus is seen to be the richest part of the brain in which measurements have been made.

In the forebrain it is evident that the values listed in Table 9 are in general low as compared with those in the hindbrain. The richest parts are the primordium hippocampi and the nucleus medialis septi, which are equally supplied, while the difference from those of the primordium of the dorsal pallium is not significant. The capillary supply of these is comparable with that in the dorsal motor nucleus of the vagus, the nucleus of the solitary bundle, and the molecular

layer of the cerebellum. The primordium piriforme and the corpus striatum are distinctly poorer, and do not differ significantly from each other or from the nucleus dorsolateralis amygdalae. They are comparable with the hypoglossal nucleus and are poorer than any sensory area in the hindbrain.

The two poorest regions, except the medial longitudinal bundle, are the two areas of neuropil, though that of the primordium piriforme does not differ to a mathematically significant degree from the dorso-lateral amygdaloid nucleus nor from the primordium piriforme itself. However, the difference of neither area of the neuropil from the medial longitudinal bundle is statistically significant, while the differences of all the cellular areas from that bundle are significant.

The corrected values have been plotted in Figure 2 and in the same graph the corresponding values for the mudpuppy and salamander are also present.

Figure 3 shows graphically the vascularity of the frog and the dogfish. In this graph the regions of the brain are arranged in order of increasing capillary richness in the dogfish, and it is clear that this order does not correspond with that in the frog. The richest region in the dogfish brain was the lateral line lobe, which is absent in the frog, while the possible forerunner of the cochlear nucleus, the 'lagenar nucleus' ( No. 5 on the graph ) is quite poor in the fish. The chief sensory V nucleus (No. 12 on Figure 3 ) is rather rich in both, but the cerebellar ( Nos. 10, 13, 14 on Figure 3 ) and

vestibular ( No. 11 on Figure 3 ) regions are among the richest in the fish. The differences between the various parts in the frog brain are in general greater than those in the dogfish brain. In the ratfish the differences are greater than in the dogfish and the values are higher, surpassing those for the frog in many cases. Thus the poorness of the cerebral capillary supply of the dogfish in comparison with that of the frog is not characteristic of all fishes or even of all elasmobranchs.

The forebrain is poorly vascularized in both fish and frog, but in the fish its poorest part is the primordium of dorsal pallium, while in the frog this area is one of the three richest parts of the hemisphere. The primordium piriforme, which is the richest division of the pallium in the dogfish, is behind the other two divisions in the frog. Comparing the gray matter of the hemisphere with the white matter of the medial longitudinal bundle, in the frog the richest part is not quite twice as rich as the latter fasciculus. In the dogfish the corresponding ratio is about as in the frog.

Herrick (1921,1927,1934a,1934b) has shown that the amphibian brain contains a large amount of neuropil and that some tissue of this type is concentrated in certain specialized areas in the deeper parts of the white matter of the cerebral hemispheres. The neuropil of the primordium piriforme and the ventral part of the corpus striatum are the poorest parts in respect of capillary supply with the exception of the medial longitudinal bundle, and do not differ significantly from the latter. The differences of the pyriform neuropil from the cellular pyriform primordium, corpus striatum, and the dorso-lateral amygdaloid

nucleus are not statistically significant.

These relations are meaningful on account of the work of Dunning and Wolf (1936,1937) in which strong evidence is shown in favor of the view that neuropil is more richly vascular than cellular nervous tissue.

Table 8.

Total length in microns of the capillaries in  $\frac{1}{2}$  ( 189<sup>2</sup> X 200)c.m. of tissue in the Brain Stem and Cerebellum of the Leopard Frog ( Not corrected for shrinkage )

Frog	Location on Fig. 2 and 3	105	106	107	109	110	124	131	136	141	145	Average	% Prob. Error of Average	Length in 100% c. . . 1 Fr. Tissue
Fasc. long. medialis...	1	339	431	434	319	384	436	385	435	366	352	388	2.4	87
Nuc. motorius dorsalis X	8	725	879	773	585	876	626	594	784	561	578	698	3.8	156
Nucleus XII.....	3	537	436	489	437	432	605	612	637	507	423	512	3.4	115
Nuc. motorius VII.....	6	968	1123	967	839	1072	984	886	779	786	849	925	3.1	207
Nuc. motorius V.....	7	708	1039	788	734	1083	880	1059	849	873	759	877	3.3	196
Nuc. fasc. solitarii...	4	876	725	647	703	597	611	613	842	643	658	692	3.0	155
Nucleus spinalis V.....	2	793	746	729	627	632	691	753	790	681	671	711	1.8	159
Cerebellum; molecular layer.....	10	660	888	614	529	560	704	718	546	752	577	655	3.7	147
Superior olive.....	9	1360	1682	1279	1223	1445	1678	1623	1285	1444	1444	1446	2.5	324
Nucleus sens. princip..	12	1144	1258	1145	1054	1097	1014	1006	1086	1100	1109	1101	1.4	247
Cerebellum; granular layer.....	13	633	709	596	505	454	577	607	553	491	619	574	2.8	129
Eminentia cerebelli ventralis.....	14	855	856	752	704	707	625	823	828	676	616	744	2.6	167
Nucleus ventralis VIII (vestibularis).....	11	684	597	776	639	871	836	781	889	866	625	756	3.1	169
Nucleus dorsalis VIII (cochlearis).....	5	1744	2055	1970	1655	1961	1697	2022	1900	1815	1654	1847	1.8	416

Craigie, 1938d.

1  
Corrected Average  
Length in 100% c. .  
Fresh Tissue

Table 9.

Total length in microns of the capillaries in  $\frac{1}{8}$ " (189<sup>2</sup> X 200)c. of tissue in the Forebrain of the Leopard Frog  
( Not corrected for shrinkage )

Frog	Location on Fig. 2 and 3	105	106	107	108	109	110	124	131	136	137	Average	Average of Prob. Err. <sup>1</sup>	Length in 100 <sup>3</sup> c. Fr. tissue <sup>1</sup>
Primordium hippocampi	E	672	829	687	525	619	675	627	806	683	634	676	2.8	151
Primordium pallii dorsalis.....	A	565	771	603	575	579	495	689	701	650	652	628	2.8	141
Primordium piriforme	F	517	602	490	423	475	582	448	557	436	445	498	2.8	112
Neuropil of primordium piriforme.....	G	320	499	503	398	279	509	580	544	354	542	453	5.0	101
Nucleus medialis septi.	D	755	725	650	606	605	753	640	734	693	648	681	1.9	153
Corpus striatum; pars ventralis.....	B	552	524	589	386	393	480	435	521	377	575	483	3.6	108
Neuropil of corpus striatum, pars ventralis	C	356	485	379	390	402	239	442	447	428	425	399	3.6	89
Nucleus dorsolateralis amygdalae.....	H	428	501	268	427	395	480	511	522	505	546	458	3.9	103

Craigie, 1938d.

<sup>1</sup>  
Corrected Average  
Length in 100<sup>3</sup>c. .  
Fresh Tissue

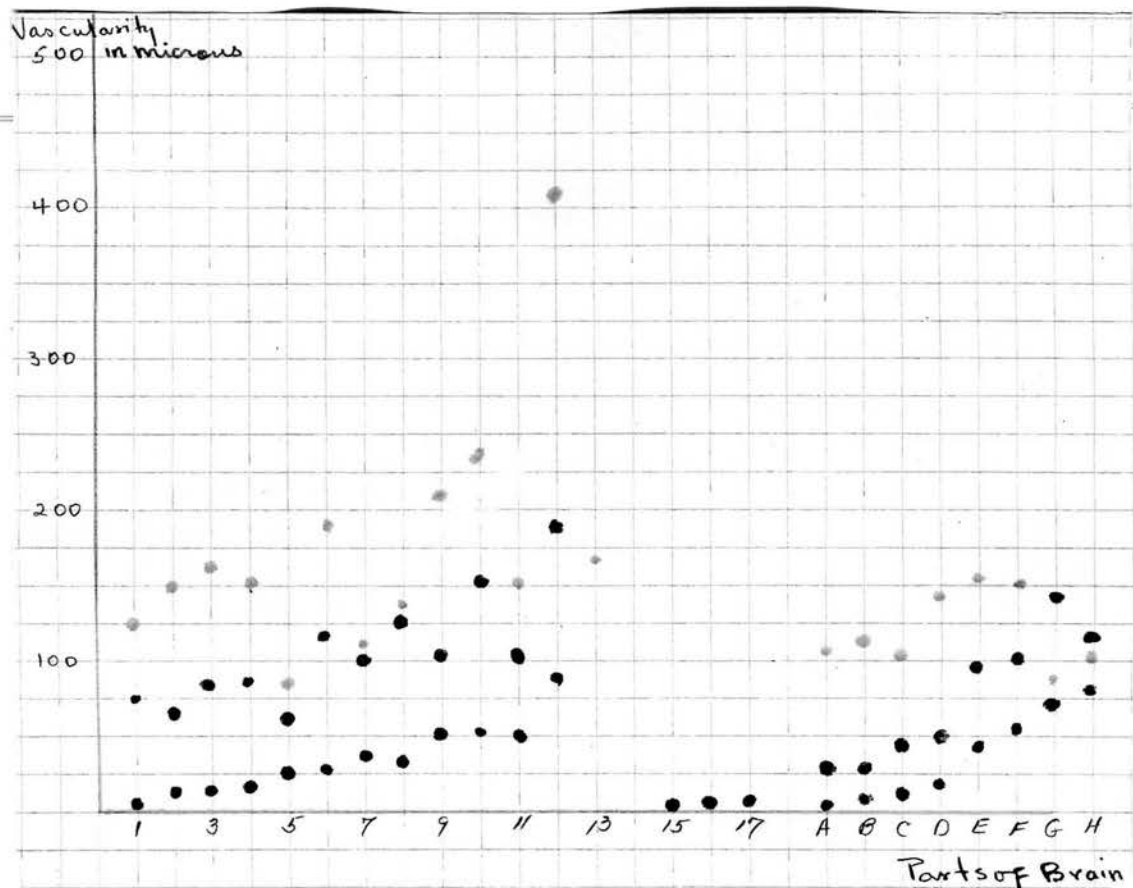


Figure 2. The length, in microns, of capillaries in  $100^3$  cubic microns of fresh tissue in various parts of the brains of amphibians.

• Mudpuppy

• Salamander

• Frog

1. Cerebellum; granular layer
2. Nucleus fasciculae solitarii
3. Eminentia cerebelli ventralis
4. Nucleus spinalis V
5. Fasc. longit. medialis
6. Nucleus motorius V
7. Nucleus XII
8. Cerebellum; molec. layer
9. Nucleus motorius VII
10. Nucleus sensorius princip. V
11. Nucleus motorius dors. X
12. Nucleus VIII
13. Vestibular nucleus

15. Pars ventralis hypothalami
16. Pars dorsalis hypothalami
17. Nucleus preopticus magnocellularis
- A. Corpus striatum; pars ventralis
- B. Primordium piriforme
- C. Nucleus dorsolateralis amygdalae
- D. Primordium pallii dorsalis
- E. Nucleus medialis septi
- F. Primordium hippocampi
- G. Neuropil of corpus striatum
- H. Neuropil of primordium piriforme

Craigie, 1938, 1939, 1940b.

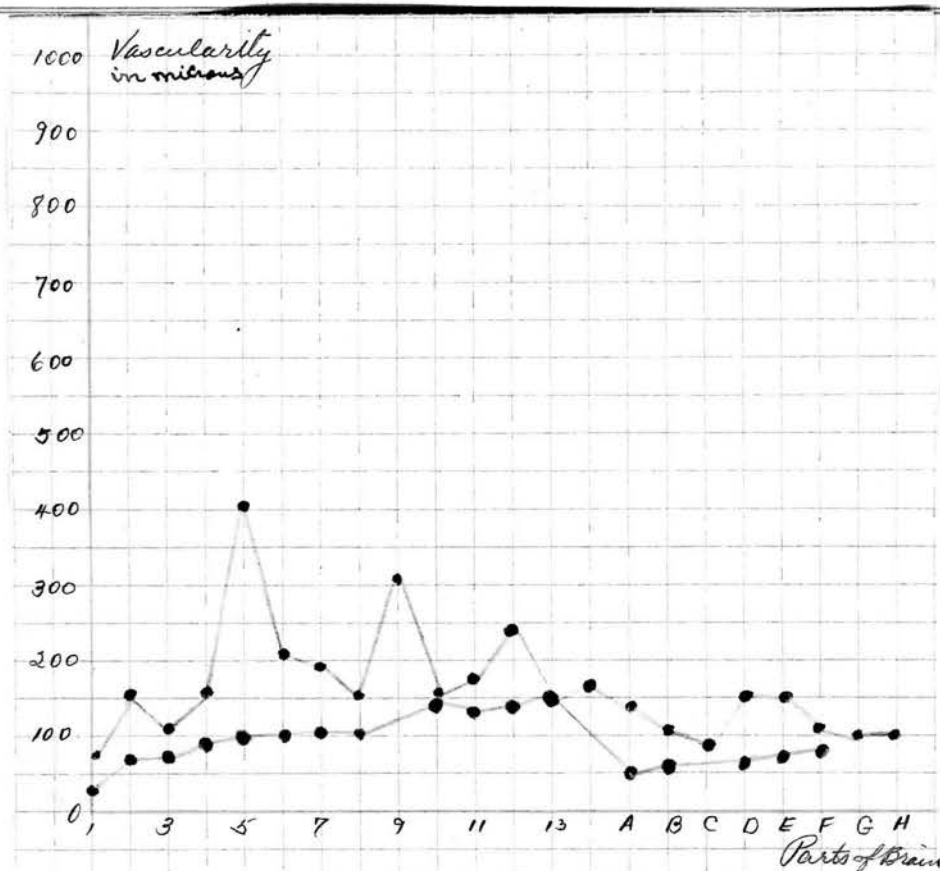


Figure 3. Graph showing the relative vascularity of the parts in the brain of the frog and of corresponding parts in the dogfish.

Frog •

1. Fasciculus longitudinalis medialis
2. Nucleus spinalis V
3. Nucleus XII
4. Nucleus fasciculus solitarii
5. Nucleus dorsalis VIII  
( 'lagenar' nucleus of dogfish )
6. Nucleus motorius VII
7. Nucleus motorius V
8. Nucleus motorius dorsalis X
9. Nucleus olivaris superior
10. Cerebellum; molecular layer
11. Nucleus ventralis VIII

• Dogfish

12. Nucleus principis sensorius V
13. Cerebellum; granular layer
14. Nucleus of ventral cerebellar eminence
- A, Primordium pallii dorsalis
- B, Corpus striatum ventralis
- C, Corpus striatum neuropil
- D, Nucleus medialis septi
- E, Primordium hippocampi
- F, Primordium piriforme
- G, Primordium piriforme neuropil
- H, Nucleus dorso-lateralis amygdalae

Craigie, 1928, 1938d.



## VASCULARITY OF THE BRAIN IN THE PAINTED TURTLE

Benedict (1932) showed that in turtles the rate of metabolism per unit surface area is higher than in other cold blooded animals, a fact which he believed to be due, at least partly, to richer blood circulation in the tissues, though the total amount passing through the system is relatively small. The metabolic rate of the tortoise is intermediate between those of snakes, lizards, and alligators, on one hand, and of warm blooded animals on the other.

The surface vessels of the brains of certain chelonians have been described by Hofmann (1900,1901), Beddard (1905), Kappers (1933), and in detail by Schepers (1939).

The nature of the capillary bed is of interest since Schobl (1878) and Sterzi (1904) have shown that in reptiles as in amphibians there exist two distinct types of capillary mechanisms. Many lizards have in their central nervous systems slender, non anastomosing capillary loops which differ from those of the salamander brains only in being much branched, while chameleons and other reptiles have a spongy capillary network such as occurs in other tissues and in the brains of most vertebrates.

Sterzi (1904) found that in the spinal cord of *Emys*, *Testudo*, and *Thalassochelys*, there are both central and radial arteries and veins, the arteries penetrating to the gray matter, where they break into a capillary net with curved and irregular meshes. This curving of the

meshes in chelonians and crocadians is intermediate between the rather straight sides of the meshes in fishes and salientians and the more complex twisting in birds and mammals. The meshes in the gray matter of the cord of *Emys* measured about twenty-four hundredths of a millimeter to twelve tenths of a millimeter, mostly being elongated in the direction of the spinal axis, while in the white matter the meshes were larger and mostly elongated transversely. These meshes were somewhat smaller than in lizards which have nets, or in snakes, indicating a more active exchange of materials.

The total length of the capillaries in a unit volume of tissue in twenty-four parts of the brain, thirteen in the hindbrain, three in the hypothalamus, and eight in the cerebral hemisphere, appears in Table 10. The averages are plotted together with the averages for the frog in Figure 4.

The range of difference in vascular richness in the various parts is considerable and the great majority of the differences are statistically significant. The differences between the motor VII and V nuclei of the two layers of the cerebellar cortex is not significant, but that of the two layers of the primordium neopallii is.

No part of the gray matter is so poorly supplied with capillaries as is the medial longitudinal bundle. This condition contrasts with the situations in amphibians, where some gray matter is as poor or poorer than the white medial longitudinal bundle.

The spinal V nucleus is one of the poorest parts of the hindbrain

in amphibians and in the Painted turtle is the poorest gray region in that subdivision. The hypoglossal is the poorest motor nucleus as in the frog and salamander, but as will be seen, in contrast to relations in the rat where the dorsal motor X nucleus occupies this rank.

While the chief sensory V and ventrolateral vestibular nuclei are considerably richer than the motor centers, the cerebellar cortex is not, a relation like that in amphibians but unlike that in mammals. The lateral nucleus of the cerebellum is relatively richly vascularized, in contrast to the ventral cerebellar eminence of the salamander and mudpuppy. The frog is intermediate between the salamanders and the turtle in this respect.

The cochlear nucleus is the most richly vascular part in the brain, the only exception to this being in the case of certain nuclei of the mammalian hypothalamus. The hypothalamus of mammals contains both some of the most poorly vascularized gray matter of the brain and its richest centers, the paraventricular and supra-optic nuclei being more vascular than even the dorsal cochlear nucleus and being the only parts found to surpass the latter (Finley, 1939, 1940). In the *Necturus* the hypothalamus is uniformly poor in capillary supply, poorer even than the medial longitudinal bundle. The hypothalamus of the turtle is also poor, though less uniformly or extremely than that of the mudpuppy. It is noticeable that the primordium of the supra-optic nucleus is the poorest of the hypothalamic regions though the corresponding nucleus is the richest of all in the rat. The lateral mamillary nucleus has a vascular supply equal to that of the motor

centers, while in the rat it is considerably richer than these, being on a level with the dorsal cochlear nucleus. In both the turtle and the rat it is much better supplied than the ventro-medial hypothalamic nucleus.

The forebrain in the dogfish and amphibians has a relatively sparse capillary distribution and the same is true for the turtle. The primordium neopallii is the richest of the pallial parts, but the cell layer of this is poorer than any gray matter except the spinal V and XII nuclei. The molecular layer of the primordium neopallii is more vascular than the cell layer. Like the dorso-lateralis amygdalae of the amphibians, the basal amygdalar nucleus is not well vascularized.

The palaeostriatum which is very poor in capillaries in both dogfish and amphibians is well supplied in the turtle, ranking between the motor and chief sensory V nuclei of the hindbrain.

The neostriatum is the richest part of the hemisphere and the second richest part in the whole brain.

In general it can be said that the brain of the Painted turtle is only a little better vascularized than that of the frog.

Table 10.

Total length in microns of capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200) c.<sub>100</sub> of tissue in the Brain of the Painted Turtle  
(Not corrected for shrinkage)

	Turtle										Aver- age	% P. E. of Average	Corrected Average Length in 100 <sup>0</sup> c. . of Fr. Tiss.
	32 ♀	33 ♀	40 ♀	45 ♀	47 ♀	48 ♀	49 ♀	50 ♂	51 ♀	54 ♂			
Fasc. long. medialis..	577	568	485	389	515	322	302	345	302	297	410	6.0	82
Nuc. motorius dors. X.	923	1146	1139	913	827	841	934	904	835	832	929	2.7	190
Nucleus XII.....	836	781	888	754	747	698	769	848	811	845	798	1.5	159
Nuc. motorius VII.....	1056	975	1028	972	1146	1093	1147	1045	997	1034	1049	1.3	209
Nuc. motorius V.....	991	1096	1042	1069	1068	1007	961	1023	1028	1016	1030	0.8	205
Nuc. fasc. solitarii..	1007	1024	961	951	1017	1165	1254	1166	1058	1234	1084	2.2	216
Nuc. spinalis V.....	880	668	800	731	824	631	700	676	656	767	733	2.4	146
Cerebellum; molecular layer.....	1121	1057	734	952	1164	916	816	752	768	1034	931	3.6	185
Nuc. sens. principal.V	1305	1134	1132	1269	1069	1316	1215	1213	1223	1255	1213	1.4	241
Cerebellum; granular layer.....	1092	1077	1023	1025	981	959	947	986	954	985	1003	1.1	200
Cerebellum; lateral nucleus.....	1359	1211	1580	1597	1505	1142	1233	1437	1489	1477	1403	2.2	279
Nuc. vestib. ventrolat.	1350	1202	1128	1176	1159	1325	1259	1398	1331	1435	1276	1.8	259
Nuc. coch. magnocel...	1859	1866	1726	1742	1658	1754	1788	1894	1624	1836	1775	1.1	353
Primord. nuc. supra- opticus.....	561	476	596	698	650	652	574	516	643	665	603	1.9	120

Craigie, 1941a.

Table 10.  
(continued)

	Turtle										Aver- age	% P.E. of Average	Corrected Average Length in 100 c. . Fr. Tiss.
	32 ♀	33 ♀	40 ♀	45 ♀	47 ♀	48 ♀	49 ♀	50 ♂	51 ♀	54 ♂			
Nuc. mamil. lat.....	1029	854	966	999	991	1020	1080	1122	1037	1186	1028	1.9	205
Nuc. hypothal. ventro- medial.....	967	857	987	794	834	664	762	657	562	567	765	4.2	152
Hippocampus.....	881	651	840	655	806	653	622	607	620	866	631	3.3	143
Parahippocampal cortex	662	770	595	632	658	568	581	591	656	599	808	1.2	126
Prim. neopallii: cell. layer.....	779	866	837	795	781	756	861	724	884	795	956	1.4	161
Prim. neopallii: molec. layer.....	843	934	872	827	1090	1037	1031	1061	879	981	1144	2.2	190
Palaeostriatum: nuc. lentiformis.....	1269	1248	1222	1063	1157	1271	1058	983	979	1192	1339	2.1	228
Neostriatum: core nuc.	1291	1449	1594	1252	1465	1232	1260	1228	1390	1229	1339	2.0	266
Lobus piriforme.....	518	517	428	450	576	418	465	475	397	392	464	2.7	92
Archistriatum: nuc. bas. amygdalae.....	716	691	536	687	727	673	523	526	565	575	622	2.9	124

Craigie, 1941a.

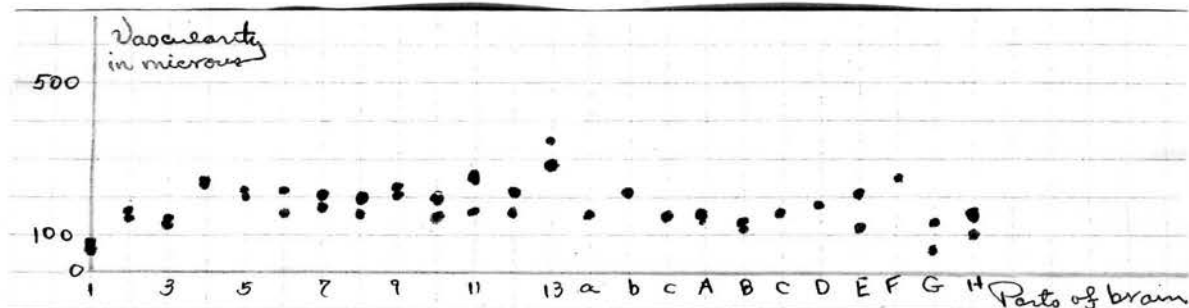


Figure 4. Graph showing the relative vascularity, in microns per  $100^3$  cubic microns of tissue, of the parts studied in the brains of the frog and turtle.

• Frog

- 1, Fasc. long. medial.
- 2, Nucleus mot. dors. X.
- 3, Nucleus XII
- 4, Nucleus motorius VII
- 5, Nucleus motorius V
- 6, Nucleus fasc. solitarii
- 7, Nucleus spinalis V
- 8, Cerebellum; molec. layer
- 9, Nucleus sensorius prin. V
- 10, Cerebellum; gran. layer
- 11, Cerebellum; lateral nucleus
- 12, Nuc-vestib. ventro-lateralis

• Turtle

- 13, Nuc. coch. magnocellularis
- a, Prim. nuc. supraoptic
- b, Nuc. mamillaris lateralis
- c, Nuc. hypothal. ventro-medial.
- A, Hippocampus (cell layer)
- B, Para-hippocampal cortex (cell layer)
- C, Prim. neopallii (cell layer)
- D, Prim. neopallii (molec. layer)
- E, Paleostriatum; nuc. lentiform.
- F, Neostriatum; core nucleus
- G, Pyriform lobe cortex
- H, Archistriatum; nuc. basal. amygdalae

Craigie, 1938d.  
Craigie, 1941 .

## VASCULARITY OF THE BRAIN IN THE NEW ZEALAND LIZARD

The results of the study made by Craigie (1941) on the richness of the capillary supply in the cerebrum appear in Table 11.

In the neostriatum and the archistriatum, the measurements were made in the cellular layer. All of the regions were chosen to correspond as closely as possible with those selected for study in the Painted turtle.

The values are, in general, rather low, much lower than in the turtle. The nucleus fasciculi solitarii is about the same as in the turtle. All of the forebrain areas except the hippocampal cortex and some of the hindbrain centers are richer than in the Tiger salamander, but all are considerably lower than in the frog. The trigeminal centers and both layers of the cerebellar cortex are notably poor, while as in other animals, the cochlear nucleus is the richest part found.

The low general level of the vascular supply suggests a low metabolic rate, which would be in keeping with the sluggish habits of the New Zealand lizard.

For identification of the parts, the accounts of Cairney (1926), Durward (1930), Christensen (1927), and Kappers, Huber and Crosby (1936) were used by Craigie (1941).



Table 11.

Total length in microns of the capillaries contained in 100 c.c.<sup>u</sup> of tissue in various parts of the brain of the New Zealand lizard.

Nucleus motorius X.....	125	Vestibular nucleus.....	126
Nucleus XII.....	121	Hippocampal cortex.....	79
Nucleus motorius V.....	69	Parahippocampal cortex....	64
Nuc. fasciculi solitarii.....	213	Pyriform lobe cortex.....	75
Nuc. spinalis V.....	58	Palaeostriatum.....	60
Cerebellum: molecular layer ..	86	Neostriatum (hypopallium	
Cerebellum: granular layer....	71	anterius).....	140
Nuc. sens. principalis V.....	94	Hypopallium posterius.....	54
Nucleus supraopticus.....	75	Nucleus medialis amyg-	
Cochlear nucleus.....	241	dalae.....	63

Craigie, 1941b.

## VASCULARITY OF THE CEREBRAL CORTEX IN THE APTERYX

It was found that the most distinctly laminated regions of the cerebral cortex and the non-laminating thickening of the pallium, the cortex medio-dorsalis, have had studies made on their capillary supply. However, the direct measurements are not comparable with those which have been made in other specimens because of the difference in the thickness of the sections studied. In all of the other cases, the sections were twenty microns in thickness but in the Apteryx the sections examined were thirty microns in thickness. Consequently, the original figures have been reduced to represent the total length of the vessels in  $\frac{1}{2}$  (  $189^2 \times 200$  ) c.μ. of tissue and also to a basis of 100 c.μ. of tissue. The vascularity is markedly higher than in the dogfish, and also over the ratfish. As in the fishes, the vascularity of the forebrain tends to be rather low as compared with that in the brain stem. The true laminated cortex, moreover, both archi- and neo-cortex, is definitely poorer than the non-laminated pallial thickening, the hyperstriatum superius (see Table 12). It is poorer than the neostriatum and the mesostriatum, and its richer layers are about equal with the archistriatum.

The relation of the different layers of the neocortex are represented graphically in Figure 5.

The poorness in capillaries in the laminae as compared with other parts of the brain may be connected with the small functional importance which they have in the only bird where they are known to occur at all.

Table 12.

Vascularity of the pallium in the brain of Aptyryx.  
(Not corrected for shrinkage)

	Average diameter in microns of fifty capillaries	Total length in microns of cap- illaries in $\frac{1}{2}$ X 189 <sup>2</sup> X 200c. of tissue.	Total length in microns of capillaries in 100 c. . of tissue.
Hyperstriatum superius		1595	447
Neocortex (ventro-lat.)			
L. zonalis I.....	4.0	1167	327
L. pyramidalis II and III.....		1240	347
L. gran. int. IV...		1295	362
L. ganglionaris V..	4.5	956	261
L. multiformis VI..		860	241
Archicortex- Ammon's formation.			
L. zonalis.....		977	274
Pyramids.....		1365	382
Archicortex- fascia dentata.			
L. zonalis.....		864	242
cell layer.....	4.0	1121	314

Craigie, 1929.

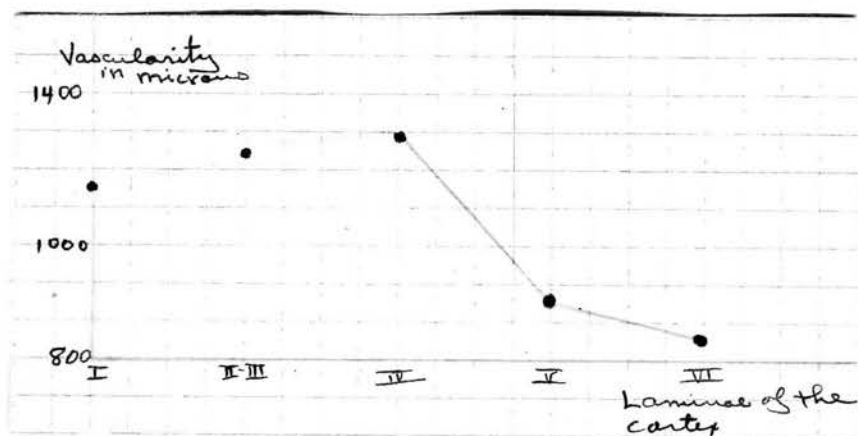


Figure 5. Graphic representation of the capillary richness of the various laminae in the ventro-lateral part of the neocortex of *Apteryx*. The Arabic numerals represent the length in microns of the capillaries in  $\frac{1}{2} \times 189^2 \times 200$  cubic microns of tissue. The Roman numerals represent the laminae of the cortex.

Craigie, 1929.

## VASCULARITY OF THE ARCHICORTEX IN THE RABBIT

Cobb (1929) gave a great deal of information concerning the cerebral circulation in the rabbit, by giving quantitative data concerning the capillary blood supply of certain laminae of the rhinencephalon. Capillary counts were made in three laminae of the hippocampus. A complete study of the rhinencephalon was produced by Rose in 1926.

The relationships of the various layers were confused by the convoluted form of Ammon's horn, but taking the dentate fascia as the outer surface of the structure, there are: first, the lamina molecularis; beneath this, the not well defined lamina lacunaris; and between this and the lamina pyramidalis, a wide layer of dendrites from the pyramidal cells. In the hippocampus, 1500 capillary counts were made by Cobb (1929), ten animals were used, and in each animal areas for counting were chosen at random in each of three localities, the lamina pyramidalis, the stratum radiatum, and the granular layer of the gyrus dentatus. Five capillary counts were made in each of these localities in each of ten slides from each of the ten animals. The average of all the observations fell at about four hundred and fifty millimeters of capillary per cubic millimeter of brain substance; this may be taken as a general rough estimate for the vascularity of the region of Ammon's horn.

The lamina pyramidalis was found by Cobb to be more vascular than

the granule layer of the fascia dentata, and much more vascular than the stratum radiatum. The average length per cubic millimeter in the lamina pyramidalis was approximately 680 mm.. The measurements for the granule cell layer of the dentate gyrus averaged 400 mm. per cubic millimeter. Lastly, the stratum radiatum, averaged only about 300 mm. of capillary per cubic millimeter.

Pfeifer, however pointed out that the injections might not be complete and one animal might have more capillaries filled than another.

Craigie (1920) emphasized the importance of reckoning the amount of shrinkage.

In comparing these figures with other measurements on other areas made by Cobb and Talbott (1927), it is seen that the motor cortex of the cerebral hemisphere in the rabbit is more vascular than the Ammon's horn, the former having 515 mm. of capillary per cubic millimeter, and the latter having 450 mm. per cubic millimeter. The visual cortex is more vascular, with a capillary length of about 555 mm. per cubic millimeter.

Pfeifer (1928), in his calculations of the capillary content of the brain substance, found for the rhinencephalon, at a point near the tractus olfactorius at the base of the brain, a capillary length of 805.5 mm. contained in one cubic millimeter of tissue. In the gyrus lateralis of the cerebral cortex he calculated 1018.7 mm. per cubic millimeter. His figure for Ammon's horn was not very different from Cobb's figure for the lamina pyramidalis but it is higher; the figure for the gyrus lateralis was considerably higher than Pfeifer's.

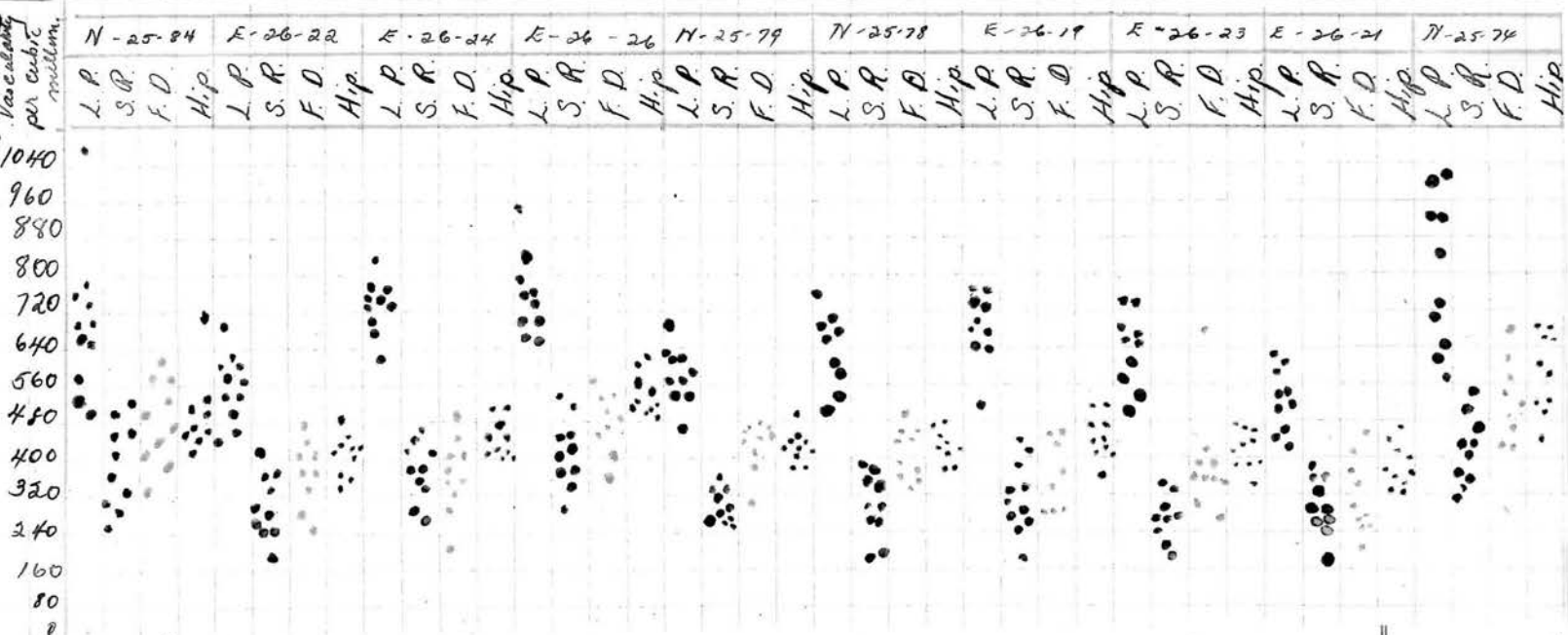


Figure 6. The measurements of capillary lengths in millimeters per cubic millimeter of brain substance are plotted for each of the three laminae measured in Ammon's horn of ten rabbits. Lamina pyramidalis is indicated by \*; stratum radiatum by ●; the granule cell layer of the fascia dentata, by ○; and the average of all these three, called hippocampus, by ●; These are the uncorrected measurements as made from microscopic slides.

Cobb, 1929.

VASCULARITY OF THE CENTRAL NERVOUS SYSTEM IN THE RAT  
i. THE SPINAL CORD, MEDULLA OBLONGATA, AND CEREBELLUM OF  
THE ALBINO RAT

Measurements of the capillary richness in twenty-one regions in the spinal cord, medulla oblongata, and cerebellum were made by Craigie (1920). The results obtained from these measurements are presented in Table 13 and Figure 7.

Among the motor centers, the poorest is the motor nucleus of the facial nerve, the richest is the ventral cornu of the spinal cord. The richest of the sensory centers is the dorsal cochlear nucleus, while after it come respectively the chief vestibular nucleus, and the granular layer of the cerebellar cortex. It was observed that even the molecular layer of the cerebellar cortex, though poorer than the granular layer is more richly supplied with capillaries than the motor, and even some of the sensory centers. Krause (1876) in his studies on human anatomy remarked that the inferior olive and the dentate nucleus are conspicuous in their regions because of their richness in capillaries.

The data recorded by Craigie (1920) corresponds fairly well with Hoche's (1899) regarding the relative vascularity of the gray and white matter in the cord, however Craigie (1920) does not agree with Hoche's (1899) finding that part of the dorsal funiculus is the richest part of the white matter in the dog, nor with Krause's (1876) conclusions on the relative richness of the white columns in the human spinal cord. In the albino rat, the pyramidal tract and the lateral



Table 13.

Total length in microns of the capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200)c. of tissue in the Central Nervous System of the Albino Rat.

Albino Rat	Locality	R. 26		R. 31			R. 55		Average 189 <sup>2</sup> X 200 cubic microns	Probable Error of Average %		
		per 189 <sup>2</sup> X 200 c.	Ratio white Vent.	Ratio gray Vent.	per 189 <sup>2</sup> X 200 c.	Ratio white Vent.	Ratio gray Vent.	per 189 <sup>2</sup> X 200 c.			Ratio white Vent.	Ratio gray Vent.
Fasc. cuneatus.....	1	1234	0.93		1727	1.27		1698	1.08	1318	3.2	
Ventral column.....	2	1331	1.00		1365	1.00		1569	1.00	1413	2.1	
Lateral column.....	3	1399	1.05		1413	1.04		1880	1.20	1593	2.6	
Pyramidal tract.....	4	2699	2.03		2323	1.70		2947	1.83	2501	2.5	
Fasc. long. dors.....	5	2326	1.75		2882	2.11		3518	2.23	3401	3.2	
Sub.gelat. Rolandi....	6	4008	3.07	0.82	4261	3.12	0.79	5598	3.56	0.78	4159	5.4
Nuc. mot. VII.....	7	3974	2.99	0.79	4285	3.14	0.80	5779	3.68	0.81	5230	3.2
Nuc. XII.....	8	4848	3.64	0.97	4861	3.56	0.90	6839	4.36	0.96	5732	3.5
Nuc. mot. V.....	9	5120	3.85	1.02	4726	3.46	0.88	5957	3.80	0.84	5837	2.9
Ventral horn; cord....	10	5005	3.76	1.00	5374	3.94	1.00	7132	4.54	1.00	6430	2.7
Spinalis V nucleus....	11	4711	3.54	0.94	6016	4.41	1.12	6790	4.33	0.95	6592	3.8
Deiters' nucleus.....	12	5811	4.37	1.16	6279	4.60	1.17	7854	5.02	1.10	6677	2.9
Molec. layer; cerebel.	13	6253	4.70	1.25	5514	4.04	1.03	7267	4.63	1.02	7116	2.9
Dorsal horn; cord....	14	6214	4.60	1.22	6171	4.52	1.15	7698	4.91	1.08	7203	2.6
Inferior olive.....	15	5334	4.01	1.07	6625	4.85	1.23	9342	5.95	1.31	7693	3.6
Superior olive.....	16	5743	4.32	1.15	6707	4.92	1.25	10457	6.60	1.45	8008	4.0
Chief sens. V nucleus.	17	7365	5.53	1.47	6748	4.94	1.26	8148	5.19	1.14	8072	2.3
Granule layer; cerebel.	18	8542	6.42	1.71	6688	4.90	1.24	8668	5.52	1.22	8762	2.3
Nuc. dentatus.....	19	9596	6.46	1.72	8097	5.93	1.51	9988	6.37	1.40	9089	2.7
Chief vestib. nucleus.	20	11131	8.36	2.22	7682	5.63	1.43	10288	6.55	1.44	9742	2.8
Dorsal cochlear nuc...	21	9056	6.80	1.81	8416	6.16	1.57	11886	6.91	1.67	10523	3.0

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Craigie, 1920.

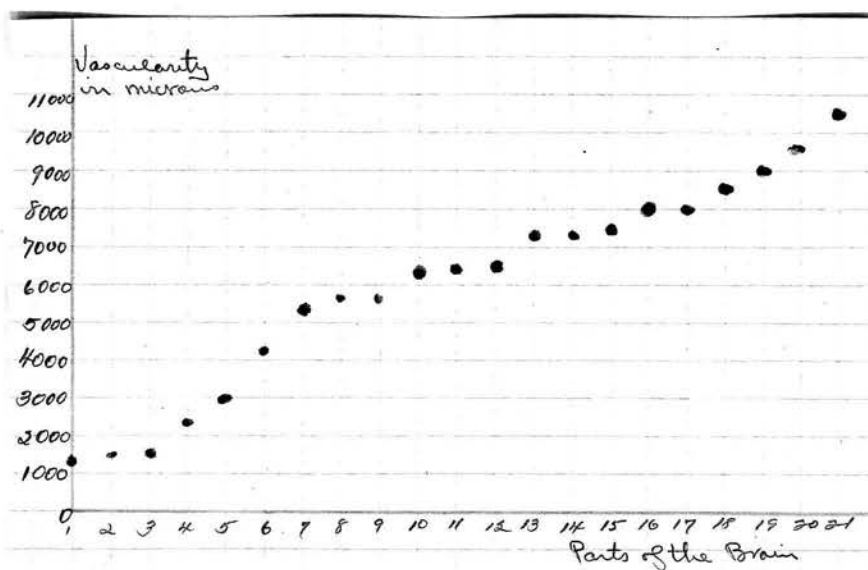


Figure 7. Graph showing the relative average vascularity of the regions studied in the albino rat.

- |                                       |                                       |
|---------------------------------------|---------------------------------------|
| 1. Fasciculus cuneatus                | 11. Spinal V nucleus                  |
| 2. Ventral column                     | 12. Nucleus of Deiters                |
| 3. Lateral column                     | 13. Molecular layer of cerebel. cort. |
| 4. Pyramidal tract                    | 14. Dorsal horn; spinal cord          |
| 5. Fasciculus longitudinalis dorsalis | 15. Inferior olive                    |
| 6. Substantia gelatinosa Rolandi      | 16. Superior olive                    |
| 7. Nucleus motorius VII               | 17. Chief sensory V nucleus           |
| 8. Nucleus XII                        | 18. Granule layer of cerebel. cortex  |
| 9. Nucleus motorius V                 | 19. Nucleus dentatus                  |
| 10. Ventral horn; spinal cord         | 20. Chief vestibular nucleus          |
|                                       | 21. Dorsal cochlear nucleus           |

Craigie, 1920.

funiculus are richer than the ventral funiculus and the fasciculus cuneatus, which are about alike.

#### ii. THE CEREBRAL CORTEX OF THE ALBINO RAT

In a discussion of the relative vascularity of the cerebral cortex in the rat, there comes up for consideration not only the richness of the capillary supply of the cerebral cortex as compared with that of the parts of the central nervous system previously studied, but also the relative vascularity of the various regions into which the cortex has been divided by physiologists and histologists. Also behind these problems 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 (1917) 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 (1914) of the conditions in the Norway rat and with the anatomico-physiological terms of Brodmann (1909).

Sugita (1917) found the cortex of the albino rat, as Fortuyn (1914) 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, which has a few scattered glia-cells. Under this, there is the lamina pyramidalis consisting of typical, deeply staining, pyramidal cells lying closely together, which corresponds to the third layer of Brodmann (1909). In the rodent brain, the lamina granularis externa, or second layer of Brodmann (1909), is always indistinct, and it is almost impossible to distinguish it from the lamina pyramidalis. Beneath the lamina pyramidalis, the lamina granularis interna is situated, composed of crowded, deeply staining, small granules, somewhat resembling glia cells. Below this layer is the lamina ganglionaris, which has dispersed, large-sized, deeply-staining pyramids. Next to the lamina ganglionaris, there is the lamina multiformis with polymorphous cells."

The lengths of the capillaries are presented in Table 14. The results for the eight brains studied by Craigie (1921) were averaged and the probable error of the averages calculated, these figures being given at the right-hand side of the table.

In the preparation of the Table (14) the mean values for the five laminae in each area averaged by Craigie (1921) and the areas were arranged in order of increasing vascularity. The average vascularity of the five layers is the same in the occipital and temporal regions, and it is a very little less in the precentral region. The parietal region is distinctly the richest, while the insular is the poorest.

The averages for the various layers of each area, as recorded in next to the last column of Table 14, are represented graphically in Figure 8, which illustrates the relation between the different

regions as well as that between the five laminae in each.

It is observed that the relative vascularity of the five laminae in the various regions studied is fairly constant, not only as regards the averages, but even so to a smaller extent, in the different individuals, as shown in Table 14. The greatest irregularity which appears is in the case of H. 56, in which the lamina zonalis tends to be richer than is the case in the rest of the brains.

In all five areas, the lamina granularis interna is decidedly the richest, the lamina pyramidalis coming next, with the lamina ganglionaris very little behind it. The fourth in order of richness is the lamina zonalis, while the lamina multiformis is the poorest in every region except the insular.

These observations may be compared with the description of Duret in 1874. He found that the outer tenth millimeter of the human cerebral cortex contained large quadrangular meshes parallel to the surface, the next two millimeters are filled with rather fine polygonal capillary meshes, while the inner one millimeter has a transitional network with larger meshes, which, however, are much less elongate than those of the white matter into which they pass.

The vascular supply of the cortex, on the whole, 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. It is 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

Table 14.  
Total length in microns of the capillaries in  $\frac{1}{2}$  (189 $\times$ 200) % of tissue in the Cerebral Cortex  
of the Albino Rat.

Cerebral cortex		R.16	R.23	R.24	R.26	R.31	R.55	R.56	R.58	Horizon- tal Averages	% P.E. of Hor. Aver.
Area	Layer										
Insular.....	Lam. zonalis.....	2856	2203	2327	1914	2554	2620	2358	2743	2447	3.00
	Lam. pyram.....	3536	2654	2496	2527	2634	2886	2304	2904	2743	3.28
	Lam. gran. int.....	3811	3086	2853	3016	3296	3135	2496	3497	3149	3.03
	Lam. gang.....	3853	2346	2604	2747	2642	2496	1898	3176	2720	4.90
	Lam. multif.....	2897	2541	2598	2922	2186	2510	1983	2855	2562	3.16
	Average.....	<u>3391</u>	<u>2566</u>	<u>2576</u>	<u>2625</u>	<u>2662</u>	<u>2729</u>	<u>2208</u>	<u>3035</u>		
Praecentral....	Lam. zonalis.....	2560	2254	3387	2720	3654	3982	3723	4649	3366	5.71
	Lam. pyram.....	2955	3000	4421	3910	3927	4060	3700	5073	3881	4.29
	Lam. gran. int.....	3424	4013	5082	4447	3932	4571	3813	5237	4315	3.42
	Lam. gang.....	3172	3394	4071	4105	3493	4154	2879	4134	3675	3.27
	Lam. multif.....	2803	2585	3159	3234	3010	2764	1995	3001	2819	3.34
	Average.....	<u>2983</u>	<u>3049</u>	<u>4024</u>	<u>3683</u>	<u>3603</u>	<u>3906</u>	<u>3222</u>	<u>4419</u>		
Occipital.....	Lam. zonalis.....	2581	3034	3424	2808	3797	4557	3531	3972	3463	4.48
	Lam. pyram.....	3253	3131	3864	3893	4431	4148	3312	4719	3844	3.59
	Lam. gran. int.....	3919	3444	4485	4218	4542	4846	3708	5438	4325	3.56
	Lam. gang.....	3625	3284	4062	3892	4621	4474	3135	4496	3949	3.51
	Lam. multif.....	3364	2531	3275	2834	3972	3103	2638	3956	3209	4.17
	Average.....	<u>3348</u>	<u>3085</u>	<u>3822</u>	<u>3529</u>	<u>4273</u>	<u>4226</u>	<u>3265</u>	<u>4516</u>		
Temporal.....	Lam. zonalis.....	2951	2780	3582	2548	2945	4489	2986	4340	3328	5.25
	Lam. pyram.....	3581	3689	4290	3416	3875	5174	3525	4835	4049	3.87
	Lam. gran. int.....	4332	3769	5261	4711	4528	4966	3827	4832	4528	2.79
	Lam. gang.....	3217	3514	3904	3880	3525	4327	2959	3888	3652	2.85
	Lam. multif.....	3135	2819	3831	3329	2805	3417	2807	3731	3234	3.05
	Average.....	<u>3443</u>	<u>3314</u>	<u>4174</u>	<u>3577</u>	<u>3536</u>	<u>4477</u>	<u>3221</u>	<u>4325</u>		
Parietal..... Craigie, 1925.	Lam. zonalis.....	3056	3150	3587	3464	3468	3860	4293	4942	3728	4.01
	Lam. pyram.....	4288	3705	4458	4158	4959	4756	4235	5539	4512	2.98
	Lam. gran. int.....	4471	3461	4115	4452	3793	3905	3214	6726	5145	3.32
	Lam. gang.....	3863	3461	4115	4452	3793	3905	3214	4820	3953	3.11
	Lam. multif.....	3854	2601	3602	3663	3359	3125	2547	3698	3306	3.64
	Average.....	<u>3906</u>	<u>3464</u>	<u>4184</u>	<u>4157</u>	<u>4184</u>	<u>4146</u>	<u>3844</u>	<u>5145</u>		

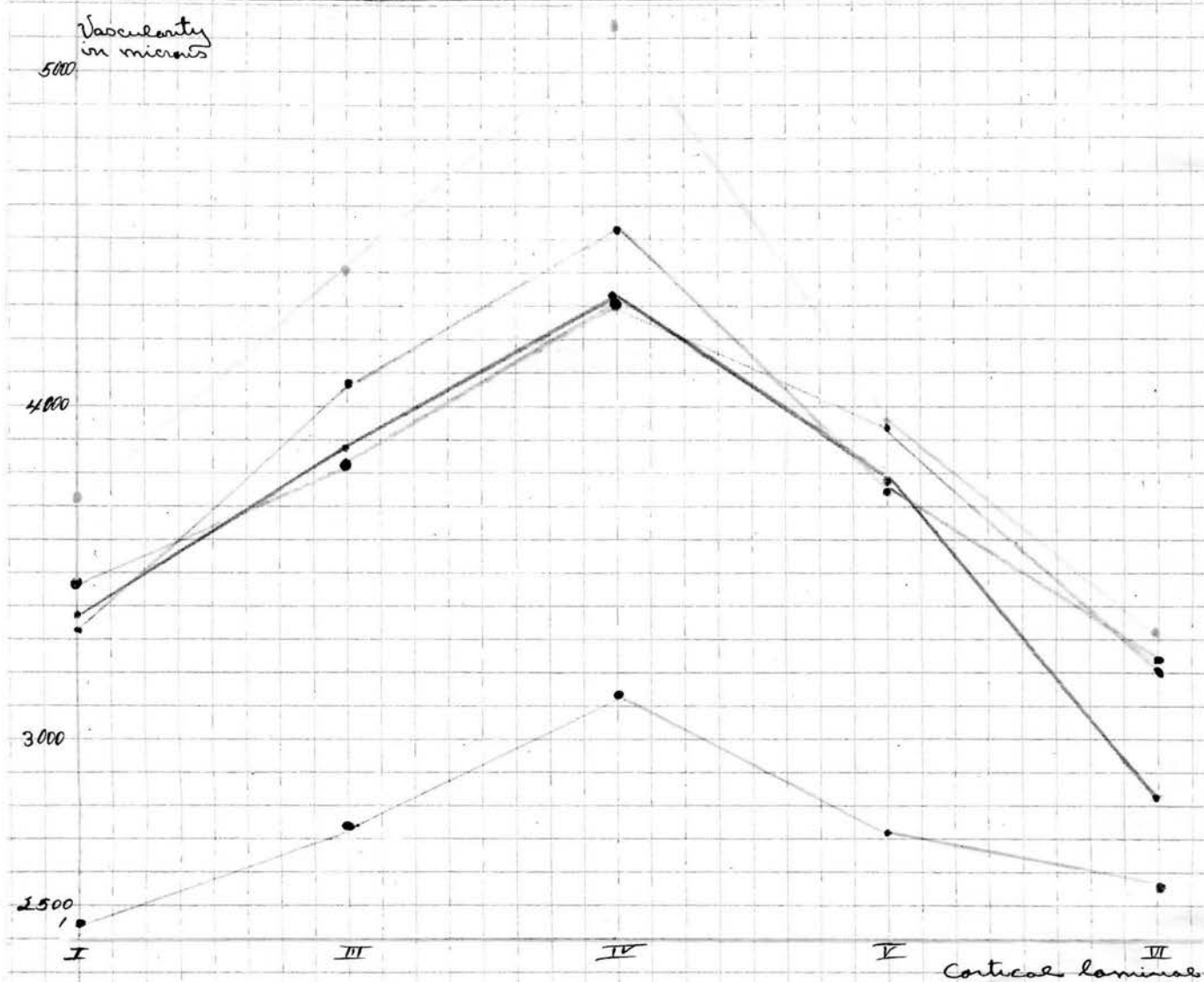


Figure 8. Graphic representation of the relative vascularity of the five cortical areas and of the five laminae of each.

I, Lamina zonalis

III, Lamina pyramidalis

IV, Lamina granularis interna

V, Lamina ganglionaris

VI, Lamina multiformis

● Insular area

● Occipital area

● Parietal area

● Praecentral area

● Temporal area

Craigie, 1921.

sensory and correlation centers in the lower part of the brain, though the richest part of the cortex is slightly poorer than the richest lower down, the dorsal cochlear nucleus.

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.

### iii. THE ARCHICORTEX OF THE ALBINO RAT

Cobb (1929) made a study of the capillaries in the hippocampus of the rabbit. Cobb (1929) reported data for only two laminae of the hippocampus proper, or Ammon's formation, and one lamina of the dentate fascia.

Craigie (1930) studied the vascularity in the strata molecularis, radiatum, pyramidalis, and oriens in the hippocampus of the adult albino rat. He omitted a study of the stratum lacunaris because of its narrowness, and made measurements of the capillaries in the molecular, granular, and polymorphic layers of the fascia dentata. The measurements obtained by Craigie (1930) are recorded in Table 15 and are plotted, together with the averages of the neocortex, in Figure 9.

It is observed that the molecular layer in the two hippocampal regions have about the same blood supply, quantitatively, and the same is true of the stratum oriens of the Ammon's formation and the polymorphic layer of the dentate fascia.

The molecular layer in each case is the most richly vascular



Table 15.

Total length, in microns, of the capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200)c.<sub>m</sub> of tissue in each layer of the Archicortex of the Albino Rat.

	R 16	R 23	R 24	R 26	R 31	R 55	R 56	R 58	Aver- age	% Prob. Error of Aver.	Aver- age corr. for shrin.	Corr. Aver. Length in 100 <sup>o</sup> c. Tiss.
<b>Left hippocampus:</b>												
stratum molec.....	3849	3537	4299	3682	4026	4050	3507	4167	3890	1.80	3112	871
stratum radiat.....	1763	2274	1649	1912	1785	2529	1575	2005	1937	4.86	1549	434
stratum pyramid.....	2689	2562	2676	3024	2488	3210	2355	3467	2809	3.27	2247	629
stratum oriens.....	2111	2188	2550	2502	2227	2997	2373	3394	2405	2.80	1924	537
<b>Left fascia dentata:</b>												
stratum molec.....	3789	4232	3705	4069	3009	4201	3138	4126	3784	3.00	3027	847
stratum granul.....	2680	2235	1792	2523	1568	1888	1564	2095	2043	4.87	1635	458
stratum multif.....	2267	2296	2319	2705	2496	2742	2071	3068	2496	3.24	1996	559

Craigie, 1930.

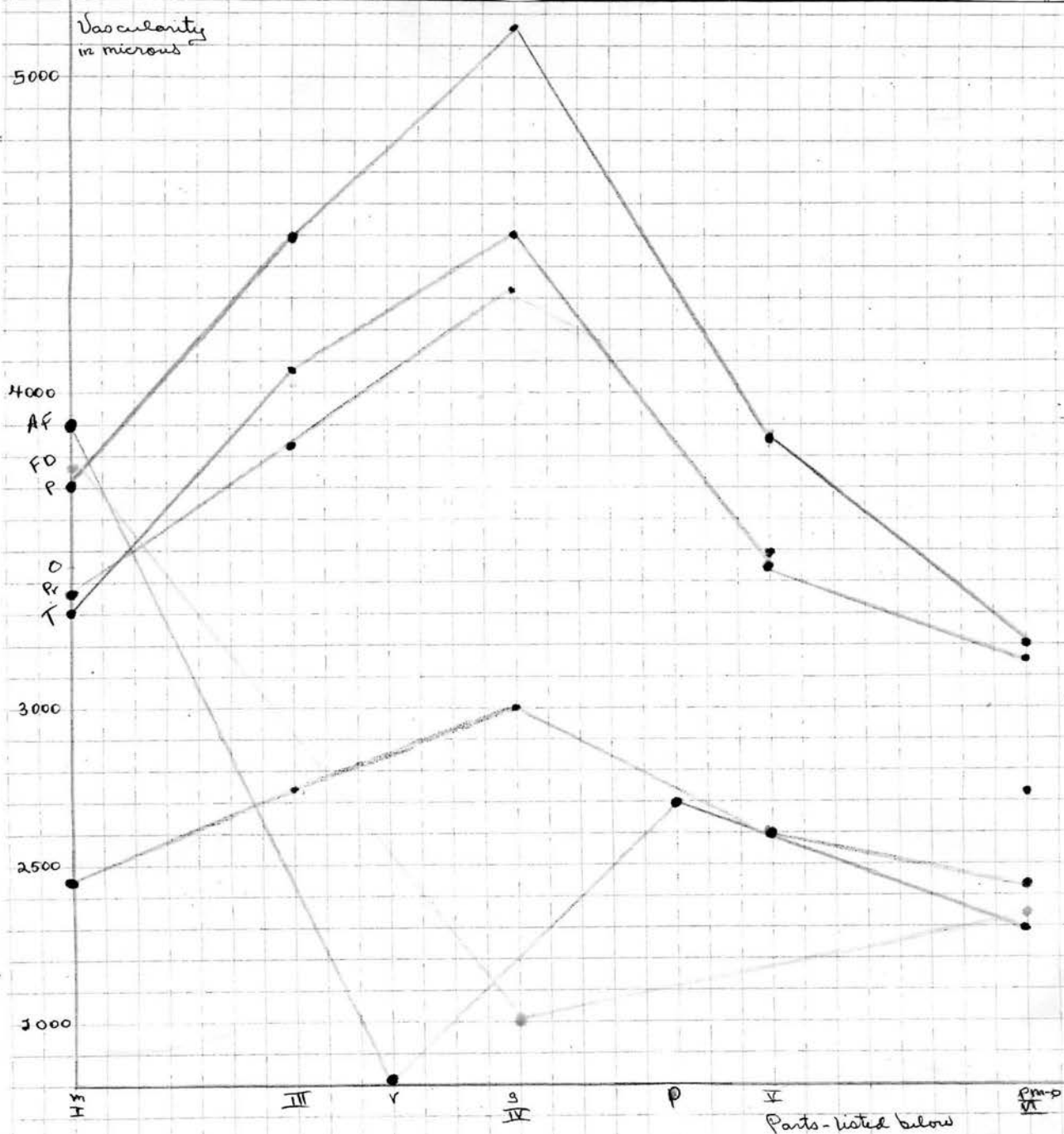


Figure 9. Graphic representation of the capillary richness of the archicortex and of certain parts of the neocortex in adult albino rats. The values have not been corrected for shrinkage since all measurements were made in the same specimens. The Roman numerals indicate the laminae of the neocortex; the letters along the base line those of the archicortex.

g, stratum granulare  
m, stratum moleculare  
o, stratum oriens  
p, stratum pyramidale  
pm, stratum multiforme  
r, stratum radiatum

AF, hippocampus proper  
FD, dentate fascia  
I, insular area  
O, occipital area  
P, parietal area  
Pr, precentral area

T, temporal area

Craigie, 1930.

stratum. In the hippocampus proper the layers of pyramidal cells comes next, and is followed by the polymorphic layer, the stratum radiatum being the poorest. In the fascia dentata, the granular layer is the poorest, the average being slightly higher than that of the stratum radiatum of the Ammon's formation.

#### iv. ARCHICORTEX OF THE ALBINO RAT AT BIRTH

According to Craigie (1924, 1925), the vascularity of the brain of the albino rat is much lower at birth than in the adult and increases with the establishment of normal functional activity.

The vascularity in all parts of the hippocampal formation is much lower at birth than in the adult rat. The differences between the various laminae are less pronounced according to Table 16 and Figure 10, and do not correspond exactly with those in the adult animal. In the hippocampus proper, the difference between the stratum radiatum and the stratum oriens is not mathematically significant, but the differences between the other layers are, and so are those between the lamina of the fascia dentata. The stratum radiatum, which is the poorest layer in the adult, is here not so poor as either the pyramidal or the granular layer.

As in the adult, the capillary supply in the hippocampal formation is less rich than in the neocortex except in the molecular layer. The molecular layer of the fascia dentata diverges in being poorer than that in any part of the neocortex studied except the insular layer,

Table 16.

Total length, in microns, of capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200)c. of tissue in the Archicortex of the Albino Rat at birth.

	R 63	R 64	R 66	R 76	R 77	Aver- age	% Prob. Error of Aver-	Aver- Corr. in for shri. coeff.100 <sup>3</sup>	Corr. Aver-
Hippocampus:									
stratum molec....	2080	1983	1789	1810	2171	1967	2.62	1455	407
stratum radiat...	1456	1409	1220	1235	925	1249	5.04	924	259
stratum pyramid..	630	918	873	940	836	836	4.48	609	170
stratum oriens...	1178	1718	1027	1413	1382	1344	5.88	994	278
Fascia dentata:									
stratum molec....	887	912	935	1308	1031	1031	5.23	763	214
stratum granul...	589	630	618	557	542	589	7.20	401	112
stratum multif...	1068	1563	1164	1374	1299	1092	4.46	961	269

Craigie, 1931.

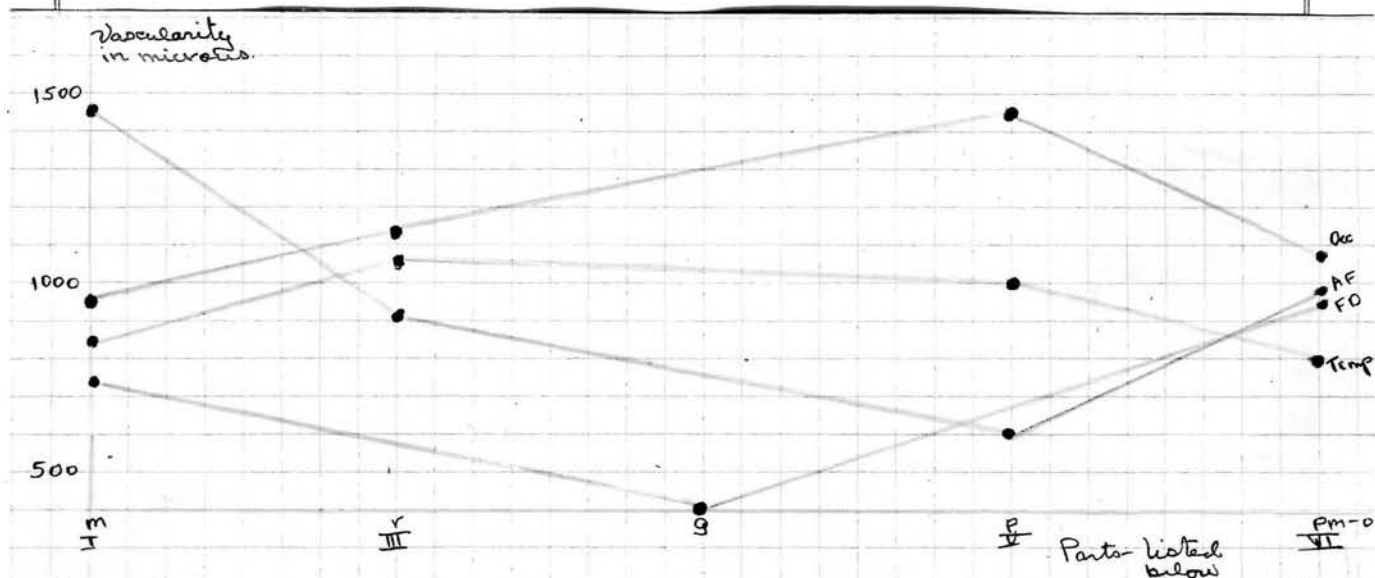


Figure 10. Graphic representation of the relative vascularity in the archicortex and in the temporal and occipital areas of the neocortex in newborn albino rats. The Roman numerals indicate the laminae of the neocortex; the letters along the base line, those of the archicortex.

AF, hippocampus proper  
 FD, dentate fascia  
 g, stratum granulare  
 m, stratum moleculare  
 o, stratum oriens

Occ, occipital area  
 p, stratum pyramidale  
 pm, stratum multiforme  
 r, stratum radiatum  
 Temp, temporal area

Craigie, 1931.

while the lamina multiformis of the temporal cortex is poorer than the corresponding hippocampal layers.

#### v. THE ARCHICORTEX OF THE WILD GRAY RAT

The length of the capillaries in a unit volume of tissue was measured by Craigie (1931) in the same parts where such measurements were made in the brains of the albino rats.

Table 17 shows the total length of the capillaries in  $\frac{1}{8}$  (  $189^2 \times 200$  ) cubic microns of tissue in each of the three layers of the fascia dentata and in each of the four layers of the hippocampus proper in the various specimens, with the average for each stratum. The data were all corrected for shrinkage and the averages for the corrected measurements are recorded in Table 18. The uncorrected averages are in all cases notably lower than the corresponding figures for the albino rat, and the correction for shrinkage increases these differences. The variability, as indicated by the per cent probable error, is greatest in the granular layer of the fascia dentata in both albino and wild rats, especially in the latter. The pyramidal layer comes next in the wild rats, but not in the albinos, where the stratum radiatum varies almost as much as the stratum granulare.

Figure 11 is a graphic representation of the capillary richness of the archicortex in wild Norway rats and in domesticated albinos.

Table 17.

Total length in microns of the capillaries in  $\frac{1}{2}$  (189<sup>2</sup> X 200)c.A. of tissue in the Archicortex of the Wild Gray Rat.

	NR 10	NR 50	NR 51	NR 55	NR 57	NR 58	NR 59	NR 60	Average
Left hippocampus:									
stratum molecul..	3050	3184	3497	3074	3289	2939	3082	3101	3152
stratum radiatum.	1640	1803	1579	1413	1714	1496	1637	1660	1618
stratum pyramid..	1741	2743	2339	2351	2102	1819	1969	1791	2108
stratum oriens...	2123	2349	1808	2215	2065	1585	1706	1828	1960
Left fascia dentate									
stratum molecul..	3605	3010	3119	3360	3087	3169	2922	3081	3169
stratum granulare	1272	2029	1471	1823	1124	1237	1107	1156	1402
stratum multiforme	2395	2003	2017	2233	1660	2090	1669	1685	1969

Craigie, 1931a.

Table 18.

Total length in microns of the capillaries in fresh tissue of the Archicortex of the Wild Gray Rat.  
(obtained by correcting and averaging the individual measurements in Table 17)

	Average length in $\frac{1}{2}$ X189 <sup>2</sup> X200 c. . tissue	% Probable Error of Average	Average length in 100 <sup>3</sup> c. . tissue
Left hippocampus:			
stratum moleculare.....	2320	1.96	649
stratum radiatum.....	1190	2.06	333
stratum pyramidale.....	1556	4.68	436
stratum oriens.....	1447	4.17	415
Left fascia dentata:			
stratum moleculare.....	2345	2.90	656
stratum granulare.....	1041	6.89	291
stratum multiform.....	1460	4.72	409

Craigie, 1931a.



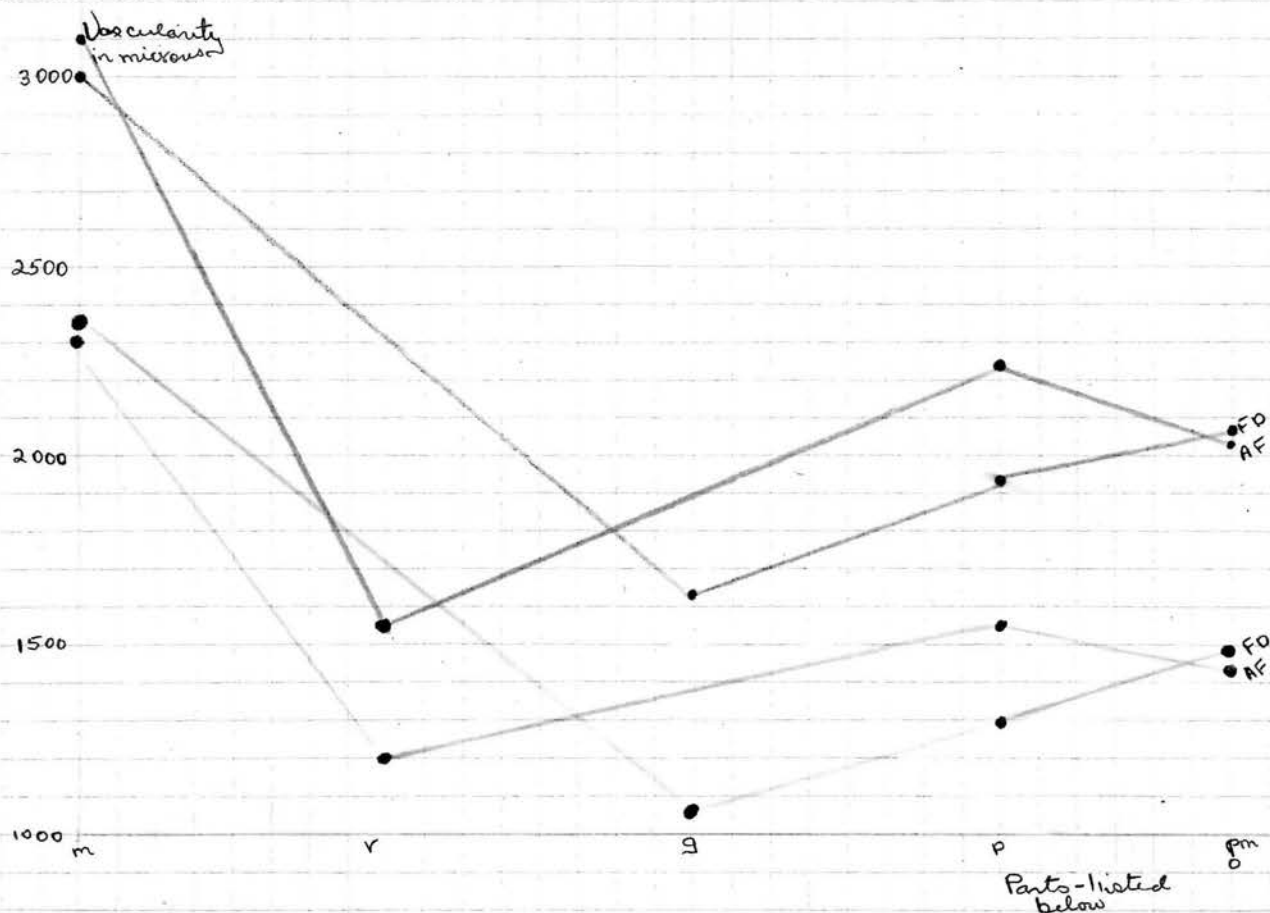


Figure 11. Graphic representation of the capillary richness of the archicortex in Wild Norway Rats (●) and in domesticated albinos of the same species (○). The values have been corrected for shrinkage in both cases.

AF, hippocampus proper  
FD, fascia dentata  
g, stratum granulare  
m, stratum moleculare

o, stratum oriens  
p, stratum pyramidale  
pm, stratum multiforme  
r, stratum radiatum

Craigie, 1931a.

vi. THE SPINAL CORD, BRAIN STEM, AND CEREBELLUM OF THE WILD NORWAY RAT

The total length of the capillaries in a unit volume of tissue was measured by Craigie (1931b) in fourteen of the twenty-four parts in the spinal cord, brain stem, and cerebellum. The results of these measurements are directly comparable with those recorded for the same regions in the albino rat (Craigie, 1920,1921) except that the unit volume of tissue considered is only half as large as that used in the measurements in the albino. All the measurements were corrected for shrinkage. For comparison the averages of the same parts in the adult albino rats were also corrected for shrinkage. The results are presented in the fourth column of Table 19. The corrected values for both wild and albino rats are shown graphically in Figure 12.

Of the fourteen regions, only six present differences between the wild and albino forms which are mathematically significant, namely, the pyramidal tract, the medial longitudinal bundle, the facial nucleus, the two layers of the cerebellar cortex and the dorsal cochlear nucleus. In four of these, the albino is the richer, so that the differences tend in the same direction of the archicortex which is definitely richer in capillaries in the albino than in the wild rat. Only the medial longitudinal bundle and the motor facial nucleus are richer in the wild form.

The parts are tabulated in order of increasing richness in the albino rat, except in the case of the nucleus of the solitary bundle, the poorest sensory center, and it is seen that the relation is

essentially the same in the wild gray animal. The motor facial nucleus diverges in surpassing the hypoglossal nucleus but the differences between these is not mathematically significant. The same is true of the relations between the spinal V and Deiters' nuclei, which are essentially equal, and between the chief vestibular and dorsal cochlear nuclei. The molecular layer of the cerebellar cortex is poorer, as is also the situation in the granular layer.

Table 19.

Total length, in microns, of capillaries in fresh tissue. The values for the wild rats were obtained by correcting the individual measurements which were made and by averaging the results. Those for the albino rats were obtained by correcting the averages in Table 13.

	No. on Graph	Wild Norway Rats			Domesticated Albino Rats	
		Average length in $\frac{1}{2}$ X189 <sup>2</sup> X200 c. of tissue	Per Cent Prob- able Error of Average	Average length in 100 c. . . of Tissue	Average length in $\frac{1}{2}$ X189 <sup>2</sup> X200 c. of tissue	Average length in 100 c. . . of Tissue
Fasc. cuneatus.....	1	535	4.43	150	527	148
Tr. pyramidalis.....	4	909	2.96	255	1000	280
Fasc, long. medialis.....	5	1392	2.64	390	1216	340
Nuc. motorius dorsalis X	A	1842	1.93	516	1847	517
Nuc. motorius VII.....	7	2537	4.24	710	2092	586
Nuc. motorius XII.....	8	2433	2.73	681	2293	642
Nuc. sensorius (fasc. solitarii).....	B	2144	2.96	600	2250	630
Ventral horn; spinal cord	10	2567	1.67	719	2572	720
Nuc. spinalis V.....	11	2740	2.30	767	2637	738
Nuc. deitersi.....	12	2700	2.80	756	2637	748
Cerebellum; molec. layer.	13	2431	2.17	681	2846	797
Cerebellum; gran. layer..	18	2908	1.15	814	3505	981
Nuc. vestibuli princip...	20	3757	3.12	1052	3897	1091
Nuc. cochlearis dorsalis.	21	3534	3.00	989	4209	1178

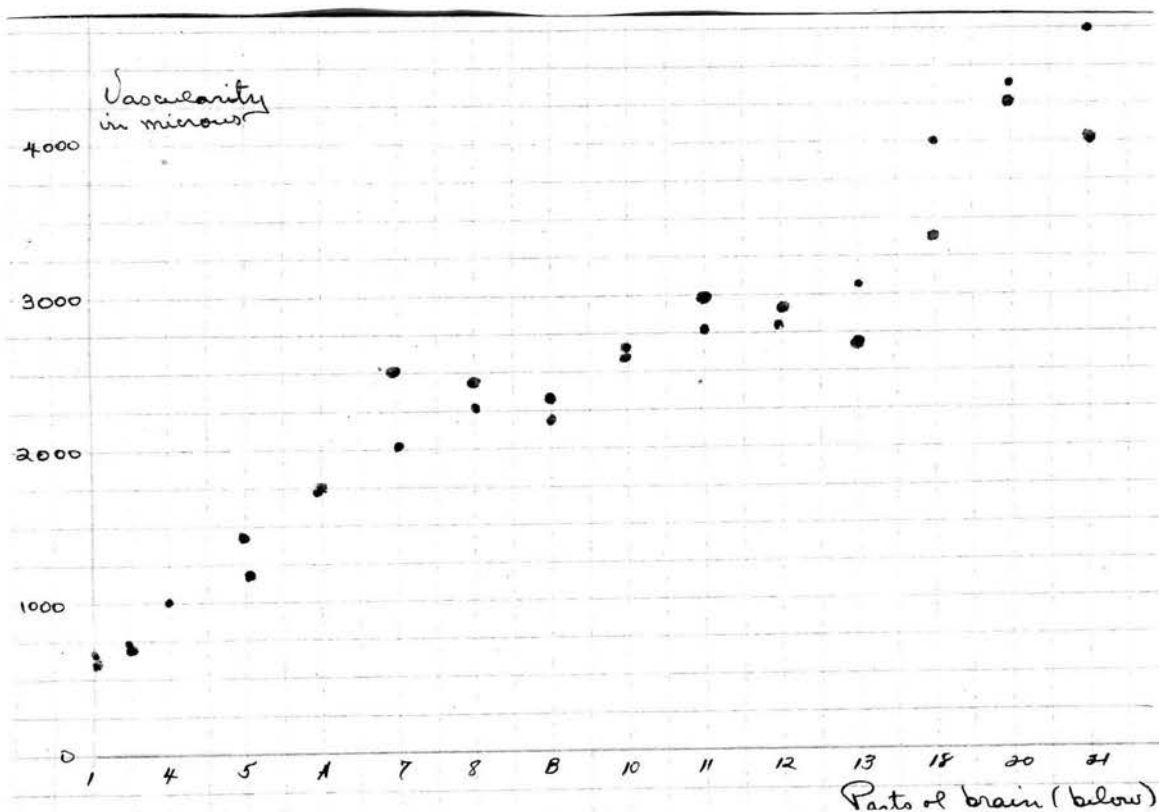


Figure 12. Graphic representation of the relative vascularity of the parts of the central nervous system studied in the wild gray Norway rat and in the domesticated albino. The red lines represent records for the wild animals. The blue lines represent the records for the albino. The first and fourth columns of Table 19 show that the values plotted are the corrected averages.

- |                             |                                 |
|-----------------------------|---------------------------------|
| 1, Fasc. cuneatus           | 10, Ventral horn; spinal cord   |
| 4, Tr. pyramidalis          | 11, Nuc. spinalis V             |
| 5, Fasc. long. medialis     | 12, Nuc. deitersi               |
| A, Nuc. motorius dorsalis X | 13, Cerebellum; molecular layer |
| 7, Nuc. motorius VII        | 18, Cerebellum; granular layer  |
| 8, Nuc. motorius XII        | 20, Nuc. vestibuli principalis  |
| B, Nuc. fasc. solitarii     | 21, Nuc. cochlearis dorsalis    |

Craigie, 1931b.

## SUMMARY

The total length of the capillaries in a unit volume of tissue in the Pacific dogfish is considerably less than in the corresponding regions in the ratfish and albino rat. The differences between different parts are also less than in the other cases. The sensory centers are not uniformly richer in capillaries than the motor ones. The vestibulo-latero-cerebellar groups of centers, as in the ratfish, are the most richly vascular, though they do not surpass the other parts nearly so markedly as in the latter fish. The anterior lateral-line lobe is the richest area. It seems probable that the relatively rich capillary supply of these parts is correlated with particularly great functional activity. The forebrain ranks relatively low in vascularity. The general pallium is the poorest region, and both it and the tuberculum olfactorium are less well supplied with capillaries than is the white matter in the lateral funiculus of the spinal cord. The richest among the forebrain regions studied by Craigie (1928), the lateral olfactory nucleus, is poorer than the dorsal motor nucleus of the vagus. This low vascularity in the forebrain may correspond with low metabolic activity in an animal where it has not yet become the dominant part of the brain. The three parts of the pallium distinguished by Holmgren (1922) differ in vascular richness. While the general pallium of his account is the least well-supplied part studied in the forebrain, the posterural portion of the pyriform lobe is best provided, except the lateral olfactory nucleus.

In the ratfish, twelve parts of the gray matter of the spinal cord and medulla oblongata are a little more richly supplied with capillaries than is the white matter, and differ little among themselves. Six centers belonging to the vestibulolatero-cerebellar are richer than the others, by far the richest is the anterior lateral-line lobe. The forebrain is poorly provided with capillaries.

The length of the capillaries in a unit volume of tissue in the mudpuppy is the least found in any animal, being only about one-third to one-half as great as in the Tiger salamander. The neuropil of the primordium piriforme and that of the corpus striatum are rich, the former being one of the richest parts found in the brain and being comparable with nucleus VIII. The molecular layer of the cerebellum is also much richer than the granular layer. The cellular part of the corpus striatum and the granular layer of the cerebellum are almost completely lacking in capillaries. The hypothalamus is poorly vascularized throughout and the magnocellular preoptic nucleus shows no sign of the capillary richness of its mammalian derivatives.

Vascularization in the Tiger salamander is poorer than in the frog in most regions. The nucleus VIII is richer than the vestibular and poorer than the cochlear nucleus of the Leopard frog, and is the richest center found in the Tiger salamander. The forebrain neuropil is richer than in the frog, where it is very poor. It is richer also than the corresponding cellular area and than any other part in the cerebral hemisphere, which in general is poorly vascularized. The molecular layer of the cerebellum also is richer than the granular layer.

The average total length of capillaries in a unit volume of tissue in the Leopard frog is intermediate between those of the dogfish and the newborn rat, about as in the ratfish, and differences between parts are greater than in the dogfish. The richest regions are the cochlear and superior olivary nuclei. The vestibulo-cerebellar centers are poorer than some motor areas and the forebrain is also relatively poor. The primordial dorsal pallium is poorer than the primordium hippocampi. The two poorest regions, other than the medial longitudinal bundle, are the neuropil areas of the primordium piriforme and corpus striatum, neither of which differs significantly in vascularity from the white tract mentioned. Amphibians and elasmobranchs, as classes, do not differ widely in general cerebral vascularity.

In general, the brain of the Painted turtle is only a little better vascularized than that of the Leopard frog. As in mammals, in contrast with amphibians, no part of the gray matter is as poorly vascularized as the white medial longitudinal bundle. As in amphibians but not in mammals, the cerebellar cortex is no better supplied with capillaries than are motor centers. The lateral nucleus of the cerebellum, however, is richly vascular, resembling in this respect the dentate nucleus of the rat and contrasting with the ventral cerebellar eminence of salamanders. The cochlear (magnocellular) nucleus is the richest part found in the brain. The hypothalamus is poorly supplied with vessels and, of the three parts, the poorest is the primordial supraoptic nucleus. The forebrain has a relatively diffuse capillary



network and the appearance of true cerebral cortex is not accompanied by a quantitative increase in vascularization, except perhaps in the primordium neopallii. The lentiform nucleus is relatively richer in vessels than is the amphibian palaeostriatum and the core nucleus of the neostriatum is the second richest part in the whole brain.

The vascularization of the brain of the New Zealand lizard is relatively poor from a quantitative standpoint, poorer than in the Painted turtle or in the Leopard frog. The relative vascularity of different parts agrees fairly well with that in other animals though trigeminal centers and cerebellum are poor. The various observations showing a poor vascular supply agree in suggesting a low metabolic rate in the New Zealand lizard.

In the brain of the Apteryx the vascularity is, in general, much less than in the adult albino rat, though greater than the dogfish. The vascularity in the forebrain is relatively low and that of the cerebral cortex is lower than in most parts of the corpus striatum. The layers of the neocortex have essentially the same relation in point of vascularity as those of the neocortex in the rat, the zone representing the internal granular layer being the richest and the supragranular being richer than the subgranular laminae.

In the archicortex of the rabbit, the lamina pyramidalis is more vascular than the granule layer of the fascia dentata, and much more vascular than the stratum radiatum. The values found by Cobb (1929) are lower than those which Craigie (1930) found in the albino rat.

In the albino rat, it is seen that in the twenty-one regions of the spinal cord, medulla oblongata, and cerebellum the gray matter is much richer in capillaries than is the white matter, the poorest part of the gray being nearly half as rich as the richest part of the white. All parts of the white matter are not equally vascular, the pyramidal tract, the richest part of the spinal cord, being about twice as rich as the fasciculus cuneatus, while the fasciculus longitudinalis dorsalis in the medulla is still richer. The gray centers can be sharply divided into two groups, the motor nuclei and the sensory and the correlation centers, of which the latter are richer than the former. Though the richest motor region (ventral cornu) is but little poorer than the poorest sensory one (spinal V nucleus), the two groups do not overlap in those regions, except in a few individuals. The substantia gelatinosa Rolandi of the spinal cord is the only part which does not conform with this statement. The richest of the centers is the dorsal cochlear nucleus, which is more than half as rich as the ventral cornu, about two and a half times as rich as the substantia gelatinosa Rolandi ( the poorest gray region ), and eight times as rich as the fasciculus cuneatus.

In the cerebral cortex of the albino rat, the relative vascularity of the five laminae in a single region is similar in all the cortical areas, the lamina granularis interna being the richest in every case. The supragranular layers show a tendency to be a little richer than the infragranular ones, the poorest layer being the lamina multiformis in every case except the insular, where the lamina zonalis is very slightly

poorer. The average vascularity of the five layers is the same in the occipital and temporal regions, and is only slightly less in the praecentral region. The parietal area is richer than the others, while the insular cortex is much the poorest. The vascularity of the other areas corresponds approximately to that of the sensory and correlation nuclei. The vascularity of the cerebellar cortex is of about the same order of magnitude as that of the cerebral cortex taken as a whole.

In the fascia dentata and hippocampus proper of the archicortex of the albino rat, the molecular layer is richest in vascularity, surpassing also the corresponding layer in all parts of the neocortex. The other laminae are poor as compared with the neocortex. The strata pyramidale, oriens, and radiatum rank in that order in the case of Ammon's formation, while the stratum granulare of the fascia dentata is particularly poor.

The capillary richness in the hippocampal formation in the newborn albino rats is considerably less than in the adult, and the differences in vascularity between the different laminae are less marked. The capillary supply tends to be poorer than in the neocortex, though this difference is less marked than in older animals.

The capillary richness in the same parts of the hippocampal formation in the wild Norway rats as in the albino rats is lower in all cases. The relative vascularity of the seven layers are practically identical with that in the albinos. The only difference is that the stratum granulare of the fascia is poorer than the stratum radiatum of the hippocampus proper in the wild rat. The values obtained by Craigie

(1931) were lower not only than those for the albino rat, but also than those for the rabbit in the stratum pyramidale and stratum granulare of the three layers studied by Cobb (1929).

Fourteen of the twenty-five regions in the spinal cord, brain stem, and cerebellum of the albino rat were examined by Craigie (1931b) in the wild gray Norway rat. Eight of the fourteen regions show differences from the records for the domesticated albinos which are not mathematically significant. The medial longitudinal bundle and the motor facial nucleus are richer in the wild rat; the pyramidal tract, the dorsal cochlear nucleus, and the two layers of the cerebellar cortex are richer in the albino. The relation, in point of vascularity, between the parts examined by Craigie (1931b) is essentially the same in the wild rat as in the albino, though the poorness of the cerebellar cortex is notable.

1. The vascularity of the central nervous system in the Pacific dogfish is less than in the central nervous system of the ratfish and albino rat. The low vascularity of the forebrain in the Pacific dogfish may correspond with low metabolic activity in an animal where it has not yet become the dominant part of the brain.

2. The vascularity of the brain of the ratfish is intermediate between the brains of the Pacific dogfish and the newborn rat. The forebrain of the ratfish is poorly provided with capillaries.

3. The length of the capillaries in a unit volume of tissue in the brain of the mudpuppy is the least found in any animal, being only about one-third to one-half as great as in the Tiger salamander. The magno-

cellular preoptic nucleus shows no sign of the capillary richness of its mammalian derivatives.

4. Vascularization in the brain of the Tiger salamander is poorer than in the Leopard frog.

5. The total length of the capillaries in a unit volume of tissue in the brain of the Leopard frog is intermediate between those of the Pacific dogfish and the newborn rat, and about as in the ratfish.

6. Amphibians and elasmobranchs, as classes, do not differ widely in general cerebral vascularity.

7. The brain of the Painted turtle is a little better vascularized than that of the Leopard frog.

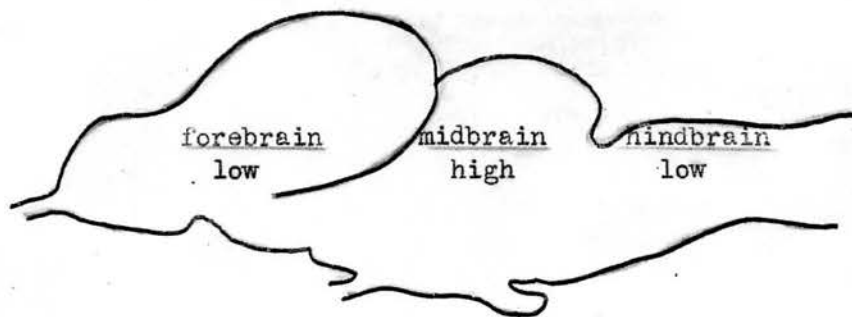
8. The vascularization of the brain of the New Zealand lizard is poor, poorer than in the Painted turtle or in the Leopard frog. The various observations showing a poor vascular supply agree in suggesting a low metabolic rate in the New Zealand lizard.

9. In the brain of Aptyryx the vascularity is, in general, much less than in the adult albino rat, though greater than the Pacific dogfish. The quantitative relations of the capillary supply provide evidence in favor of the view that the layers of the neocortex in the Aptyryx are probably homologous with those of the mammalian neocortex.

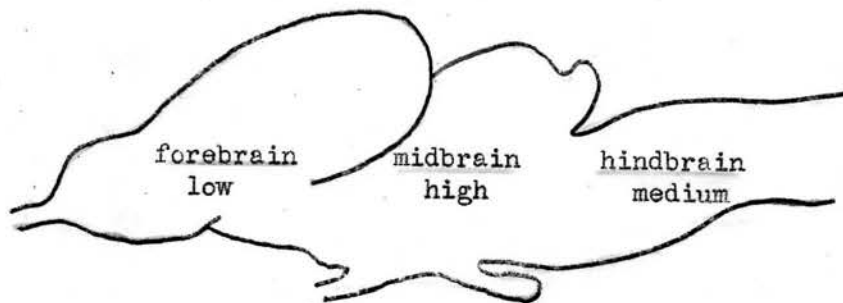
10. In the rat, the brain and other parts of the central nervous system are well vascularized pointing to a high metabolic rate.

11. In most cases the gray matter of the spinal cord, brain stem, and cerebellum is much richer in capillaries than is the white matter.

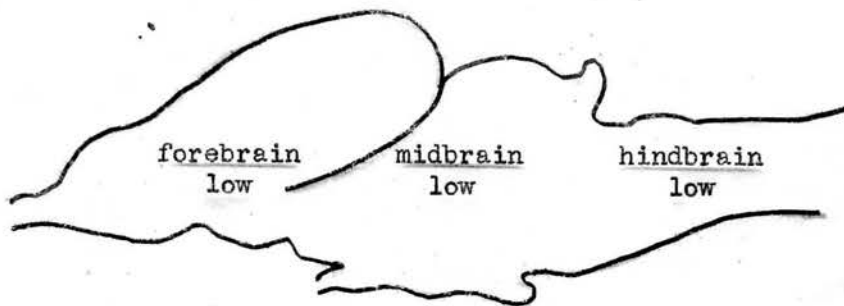
12. The vascularity of the central nervous system in the wild gray rat is essentially the same as in the albino rat.



Pacific Dogfish

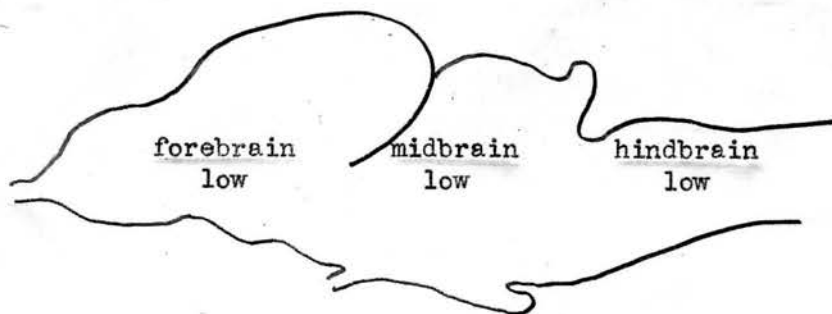


Ratfish

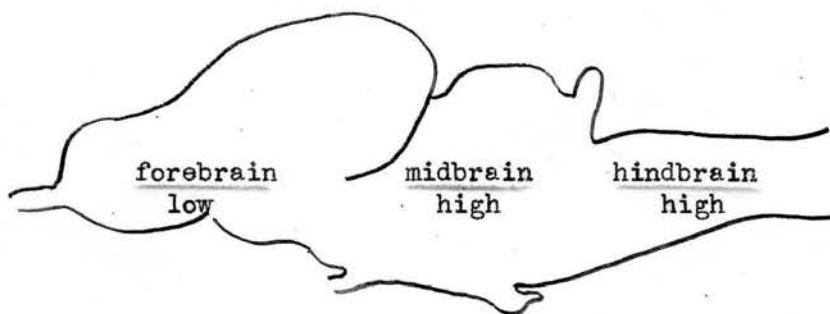


Mudpuppy

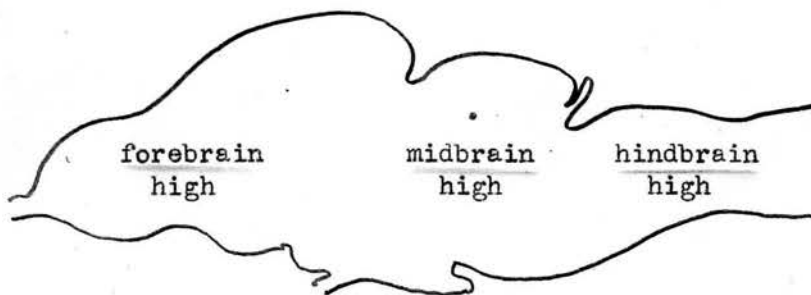
Figure 13. General representation of the vascularity of the brains in certain vertebrates. (continued on pages 81 and 82).



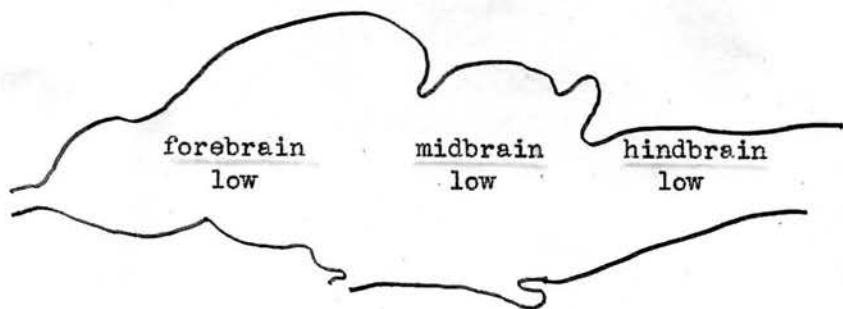
Tiger Salamander



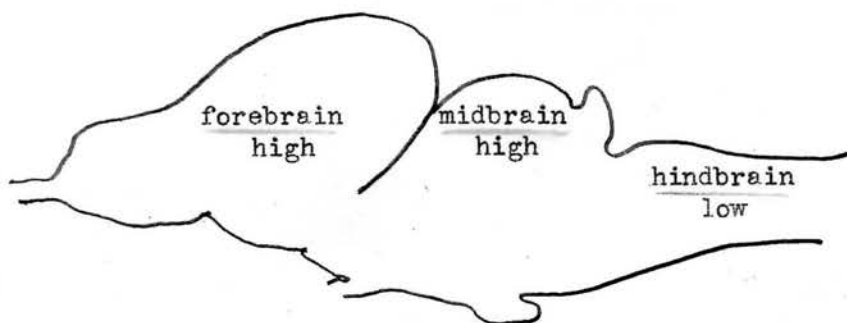
Leopard Frog



Painted Turtle



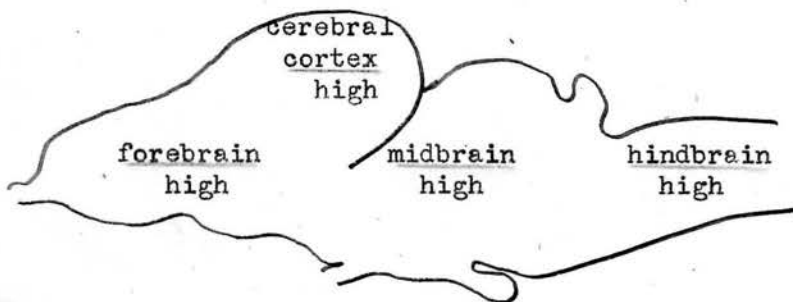
New Zealand Lizard



Apteryx



Rabbit



Rat



## ABSTRACT

The literature and various theories regarding the vascularity of the central nervous system are reviewed. Particular emphasis is placed on the theories of Craigie (bibliog.), Sterzi (bibliog.), Hofmann (1900, 1901), Beddard (1905), Kappers (bibliog.), Finley (bibliog.) Cobb (1929), Pfeifer (bibliog.), and Duret (bibliog.) .

The different parts of the central nervous system of most of the animals were studied essentially, in the same way by Craigie (bibliog.). The animals were killed by illuminating gas and injected with carmine gelatin. The brains and the other parts of the central nervous system were then fixed and cut in sections of twenty microns in thickness. The material was stained with picric acid. In studying the sections, a square-ruled disc micrometer was used; the total length of the pieces of capillaries enclosed by the square ruling ( an area of  $189^2$  microns under Leitz objective number seven) in each of the sections was determined for each part. The final value recorded for each region was the total length of capillaries in a block of tissue measuring  $\frac{1}{2}$  (  $189^2 \times 200$ )cubic microns. These measurements , in most cases,were corrected for shrinkage so as to give a corresponding value for fresh tissue.

The method used by Cobb (1929) in his study of the vascularity of the cerebral cortex of the rabbit differs slightly from Craigie's (bibliog.).

The thesis deals with the vascularity of parts of the central nervous system in the Pacific dogfish, ratfish, mudpuppy, Tiger salam-

ander, Leopard frog, New Zealand lizard, Apteryx, Rabbit, and, the albino and wild gray Norway rat.

The total length of the capillaries in a unit volume of tissue in the Pacific dogfish is less than in the corresponding regions in the ratfish and albino rat. The sensory centers are not uniformly richer in capillaries than the motor ones. The vestibulo-latero-cerebellar groups of centers, as in the ratfish, are the most richly vascular. The anterior lateral-line lobe is the richest area. The forebrain ranks relatively low in vascularity. The general pallium is the poorest region, and both it and the tuberculum olfactorium are less well supplied with capillaries than is the white matter in the lateral funiculus of the spinal cord. The lateral olfactory nucleus is poorer than the dorsal motor nucleus of the vagus.

In the ratfish, twelve parts of the gray matter of the spinal cord and medulla oblongata are more richly supplied with capillaries than is the white matter. Six centers belonging to the vestibulo-cerebellar apparatus are richer than the others. The forebrain is poorly provided with capillaries.

The length of the capillaries in a unit volume of tissue in the mudpuppy is the least found in any animal. The neuropil of the primordium piriforme and that of the corpus striatum are rich. The molecular layer of the cerebellum is almost completely lacking in capillaries. The hypothalamus is poorly vascularized and the magnocellular preoptic nucleus shows no sign of capillary richness.

Vascularization in the Tiger salamander is poorer than in the frog

in most regions. The nucleus VIII is the richest center found in the Tiger salamander, and is richer than the vestibular and poorer than the cochlear nucleus of the Leopard frog. The forebrain neuropil is richer than in the frog, where it is very poor. It is richer also than the corresponding cellular area and than any other part in the cerebral hemisphere. The molecular layer of the cerebellum also is richer than the granular layer.

The average length of the capillaries in a unit volume of tissue in the Leopard frog is about as in the ratfish, intermediate between the those of the dogfish and the newborn rat, and differences between parts are greater than in the dogfish. The richest regions are the cochlear and superior olivary nuclei. The vestibulo-cerebellar centers are poorer than some motor ones and the forebrain is also relatively poor. The primordial dorsal pallium is poorer than the primordium hippocampi. The two poorest regions, other than the medial longitudinal bundle, are the neuropil areas of the primordium piriforme and the corpus striatum. Amphibians and elasmobranchs, as classes, do not differ widely in general cerebral vascularity.

The brain of the Painted turtle is only a little better vascularized than that of the Leopard frog. No part of the gray matter is as poorly vascularized as the white medial longitudinal bundle. The cerebellar cortex is no better supplied with capillaries than are the motor centers. The lateral nucleus of the cerebellum is richly vascular. The cochlear nucleus is the richest part in the brain. The hypothalamus is poorly vascularized and, of the three parts, the poorest is the primordial

supraoptic nucleus. The forebrain has a diffuse capillary network. The lentiform nucleus is richer in vessels than is the amphibian palaeostriatum and the core nucleus of the neostriatum is the second richest part in the whole brain.

The vascularization of the brain of the New Zealand lizard is poorer than in the Painted turtle or in the Leopard frog. The vascularity of the different parts agrees fairly well with that in other animals though the trigeminal centers and cerebellum are poor.

In the brain of the Apteryx the vascularity is less than in the adult albino rat, though greater than the dogfish. The vascularity in the forebrain is low and that of the cerebral cortex is lower than in most parts of the corpus striatum. In the neocortex, the zone representing the internal granular layer is the richest and the supragranular is richer than the subgranular laminae.

In the archicortex of the rabbit, the lamina pyramidalis is richer than the granule layer of the fascia dentata, and much more vascular than the stratum radiatum.

In the albino rat, in twenty-one regions of the spinal cord, medulla oblongata, and cerebellum, the gray matter is richer in capillaries than is the white matter, the poorest part of the gray matter being half as rich as the richest part of the white. The pyramidal tract is about twice as rich as the fasciculus cuneatus, while the fasciculus longitudinalis dorsalis in the medulla is still richer. The sensory and the correlation centers are richer than the motor nuclei. The richest of the centers is the dorsal cochlear nucleus, which is more than half as

rich as the ventral cornu, which is the richest motor region of the gray centers.

In the cerebral cortex of the albino rat, the relative vascularity of the five laminae in a single region is similar in all the cortical areas, the lamina granularis interna being the richest in every case. The supragranular layers are richer than the infragranular ones. The poorest layer is the lamina multiformis in every case except the insular. The parietal area is richer than the others, while the insular cortex is the poorest.

In the fascia dentata and hippocampus proper of the archicortex of the albino rat, the molecular layer is richest in vascularity. The other laminae are poor as compared with the neocortex. The strata pyramidale, oriens, and radiatum rank in that order in the case of Ammon's formation, while the stratum granulare of the fascia dentata is particularly poor.

The capillary richness in the hippocampal formation in the newborn albino rats is less than in the adult, and the differences in vascularity between the different laminae are less marked. The capillary supply is poorer than in the neocortex.

The capillary richness in the same parts of the hippocampal formation in the wild Norway rats as in albino rats is lower in all cases. The relative vascularity of the seven layers are practically identical with that in the albinos. The only difference is that the stratum granulare of the fascia is poorer than the stratum radiatum of the hippocampus proper in the wild rat.

Fourteen of the twenty-five regions in the spinal cord, brain stem, and cerebellum of the albino rat were examined by Craigie (1931a) in the wild gray Norway rat. Eight of the fourteen regions show differences from the records for the albinos which are not mathematically significant. The medial longitudinal bundle and the motor facial nucleus are richer in the wild rat; the pyramidal tract, the dorsal cochlear nucleus, and the two layers of the cerebellar cortex are richer in the albino.

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