THE ARTERIES OF THE BRAIN OF THE ORANG-UTAN

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INTRODUCTION

THE arteries of the brain of the Orang-utan have substantially the same
distribution and variation as those of the human brain. Apart however from
the general interest of the description of the vessels themselves, their method
of distribution and variation leads to a clearer understanding of the principles
which govern the arrangement and development of arteries generally. The
clinical importance of the enunciation of such principles is obvious.

I have to acknowledge that the description of the vessels in the Orang
would lack finality if it were not for the work of Stopford (1) on the vessels of
the hindbrain in man; for the method of injection used in my specimen was
unsuitable for the determination of their internal distribution. Any discussion
and presumption, therefore, concerning the internal distribution of the vessels
in the Orang are the result of his work in the case of the vessels of the hind-
brain, and of the work of Beevor (2) in the case of the forebrain.

The hypothesis which is advanced to explain the principles underlying the
distribution of arteries is the outcome of the writings of John Hilton (3), and
the result of an association with Professor Elliot Smith who suggested to me
the determination of the blood supply of the claustrum. He (4), himself,
appreciated the phylogenetic constancy of arteries as a factor in the inter-
pretation of morphological problems when he wrote: "One of the most re-
markable items of evidence in corroboration of the reality of homologies
expressed in these diagrams is the constancy of the position of relations of the
lateral striate artery.... In any mammalian or reptilian brain this arrangement
will be found."

The constancy of the position of the anterior spinal artery in any embryo,
pointed out by Dart and myself (5), the diagrammatic picture of the hypo-
glossal nucleus supplied by the same artery, as described by Stopford, and
finally the distribution of the internal maxillary artery in the supply of the
whole of the masticatory apparatus, including the incudo-malleolar joint—
the morphological lower jaw—drew my attention, four years ago, to the hypo-
thesis that arteries are laid down with precision, that they are ontogenetically
and phylogenetically stable, and that their constancy is due in all probability
to their nerve supply, which is distributed in such a manner as to adopt
functional areas.

The hypothesis is applied to all stages in the life of the animal; it is in the
embryo that the phylogenetic constancy of the vessels has always proved a

stumbling block to those who would attribute the arrangement of the vessels to mechanical causes. The hypothesis was first stated by me in reference to the artery of the claustrum. The reality of the homologies in this region was confirmed by the vascular distribution. Since then the late John I. Hunter has given remarkable confirmation to those observations in the unravelling of the striatal complex in the forebrain of *Apteryx australis*(6).

The postulates of Thoma were unsatisfying as an adequate explanation of the anatomical facts, and yet, at that time, the multiple functional supply of such an artery as the vertebral appeared to favour, in some measure, a more mechanical explanation. The evidence which can now be advanced explains the development and distribution of these arteries, although difficulties still arise in explaining the multiple blood supply of such a single cell as the motor cell of the Rolandic area and its axon. I am convinced, however, that the hypothesis, that the sympathetic nerve cells arise in common with the arteries as part of a functional mechanism, explains the fact in a more adequate manner than heretofore.

It is generally held that the arteries of the body are not laid down with that precision which marks the distribution of the nerves. Distribution of the vessels is commonly dealt with as though the vessels had little relationship with functional demands. The variations in origin of arteries (not of their final distribution) has been regarded as evidence of this very lack of precision, whereas it will be shown that it is in the variations of arteries that the principles of their distribution are most clearly seen.

The history of this question is both illuminating and interesting. John Hunter(7) put forward the views which are in great part still held to-day. He contrasted the distribution of the nerves with that of the arteries, and came to the conclusion that:

If their (the nerves) physiology was sufficiently known, we should find the distribution and complication of nerves so immediately connected with their particular uses, as readily to explain many of those peculiarities for which it is now so difficult to account. What naturally leads to this opinion is, the origin and number of nerves being constantly the same, and particular nerves being invariably destined for particular parts, of which the fourth and sixth pair of nerves are remarkable instances. We may therefore reasonably conclude, that to every part is allotted its particular branch, and that however complicated the distribution may be, the complication is always regular.... We observe no such uniformity in vessels carrying fluids,....The course of the arteries is such as will convey the blood most conveniently, and therefore not necessarily uniform....Whoever therefore, discovers a new artery, vein or lymphatic adds little to the stock of physiological knowledge.

His writings on the distribution of vessels are concerned with mechanical, rather than with functional, principles. He observed very closely their methods of branching, of anastomosing and of terminating. He discovered end arteries —a discovery usually attributed to Cohnheim. John Hunter went further than this, however, for he made the one observation which clearly proved that

the origin and primitive distribution of blood vessels has nothing whatever to do with the mechanical forces due to the heart's action.

The vessels are probably the very first active parts in the system, for we find them in action before they have formed themselves into a heart, and in such a state of parts we find them the only part that has any strength, while the other parts are only preparing for action; this is so remarkable, that we can dissect the vessels of a chicken in the egg without injection, the other parts easily giving way (p. 195).

Hunter, therefore, left us three important observations which are not open to dispute: (1) The nerves are constant; (2) Certain vessels are end arteries; and, (3) The vessels are laid down before the heart functions. It is unfortunate that Hunter did not know that the fibres of the sympathetic nervous system are distributed to the walls of the blood vessels, for the method of distribution of the nerves must be related to the method of distribution of the structure supplied. Whoever, therefore, discovers a new artery learns something of the distribution of nerves; and it is reasonable to suppose that the distribution and origin of the vessels depend on factors which also determine the distribution and, perhaps, the origin of the sympathetic nervous system.

Majendie[8] appreciated the relationship between the nervous system and the blood vessels when he wrote:

A general law of economy is that no organ continues to act without receiving arterial blood; from this results, that all the other functions are dependent on the circulation; but the circulation, in its turn, cannot continue without the respiration by which the arterial blood is formed, and without the action of the nervous system, which has a great influence upon the rapidity of the flowing of the blood, and upon its distribution in the organs.... Probably the distribution of the filaments of the great sympathetic on the sides of the arteries has some important use; but this is entirely unknown; we have received no light on this point by experiment.

John Hilton, many years later, drew attention to the distribution of the vessels in their relation to the function of the part supplied. He could see a clear relationship between the distribution of the internal maxillary artery and the function of mastication; and between the distribution of various arteries and such functions as respiration, deglutition and gastric secretion. He felt that, "the disposition on the part of anatomists to think and to teach that nerves are distributed with designed accuracy, but that there is very little design in the distribution of the arteries" was wrong.

The work of Beevor on the blood supply of the forebrain and that of Stopford on the blood supply of the hindbrain lend strong support to Hilton's views. The variations in point of origin of the vessels in the hindbrain at first sight appear to negative the functional interpretation; but the clear cut delineation of the hypoglossal nucleus on the injection of the anterior spinal artery demands some more logical explanation than the mechanical forces due to the heart beat; more especially so, when we know that in all probability this vessel was laid down and distributed before the advent of the circulation.

In the Orang it will be seen that the gross distribution of the cortical vessels, as far as could be determined without seriously injuring the specimen, almost as accurately surveys the functional regions of the cerebrum as the methods of Elliot Smith and Brodmann.

The subject will be dealt with under two heads:

I. The gross anatomy of the blood vessels of the brain of the Orang-utan.

II. The interpretation of variations and the relationship between blood vascular distribution and functional systems.

The material used in the investigation consisted of one Orang brain in which the arteries were well injected, and of the hindbrains of seven other Orangs in which the vessels were not injected, but in which many important features could be determined.

PART I

THE GROSS ANATOMY OF THE VESSELS OF THE BRAIN OF THE ORANG-UTAN

The Vertebral Artery

Pl. I, fig. 1 shows the level at which the vertebral arteries were severed; below this level no information is obtainable in any of the specimens. The artery is placed ventral to the rootlets of the hypoglossal nerve and ends at the level of the lower border of the olivary eminence by joining with its fellow to form the basilar artery. In all the specimens this level of origin of the basilar artery is found, whereas in the large number of human brains examined by Stopford such a low level or origin was found in only one case, although in five others it was situated at the mid-olivary level.

There is the same tendency to inequality in size as one finds in man. Of the eight specimens, in five cases the left artery was larger than the right; in one the right was larger than the left, and in the remaining two the vessels were equal in size.

The Branches of the Vertebral Artery

The branches of the vertebral artery are subject to a considerable degree of variation: and yet, the terminal branches of distribution are constant. The explanation of this apparent contradiction will be given in Part II; for the moment it will suffice to say that the branches are of two types, (1) perforating, or bulbar, branches which have a direct origin from the parent artery, and (2) longitudinal branches which give off branches of the first type to the brain stem. The branches of the second type form connecting channels between perforating or segmental vessels of the same value.

Perforating branches, whether arising directly or indirectly, are constant in their final distribution. The longitudinal channels have a variability depending on the level at which the perforating or segmental branches are used

as the stems of origin for the branches of the second order. The perforating arteries are the remains of the original segmental arteries of the body. The longitudinal arteries are intersegmental links developed to enhance the circulation of the perforating arteries.

The number and position of the perforating arteries bear a constant relation to the number and position of the longitudinal vessels.

The Perforating Branches of the Vertebral Artery

Stopford classifies these branches into upper, intermediate and lower. I have not had the opportunity of examining other than the upper set in the orang.

The upper set can be subdivided transversely into ventral, lateral and dorsal branches.

The ventral set enter the substance of the bulb medial to the rootlets of the hypoglossal nerve and are dependent for their existence upon the level of origin of the basilar and anterior spinal arteries. When the anterior spinal artery arises at "an unusually low level" Stopford finds that they are most numerous. In the orang the sites of origin of the two arteries are practically constant and in all the specimens fine perforating branches enter the antero-median fissure and the surface of the bulb as far laterally as the antero-lateral fissure. These are the perforating anterior spinal arteries which have failed to become linked up with the longitudinal anterior spinal artery. Their internal distribution will be considered with the longitudinal anterior spinal artery.

The lateral and dorsal sets of perforating branches are related to the posterior inferior cerebellar and posterior spinal arteries in the same way as the anterior set is related to the anterior spinal artery. They will be dealt with when their parent arteries are considered.

THE LONGITUDINAL BRANCHES OF THE VERTEBRAL ARTERY

The Anterior Spinal Artery

The level of origin of this artery is fairly constant (fig. 2). In four cases, the contribution from each vertebral artery is given off symmetrically, and, after a series of transverse anastomoses, the median artery is formed. In the injected specimen the left contribution does not appear to join the median trunk. In one case the left branch is undoubtedly absent, and in the remainder the condition could not be determined with certainty. From an examination of this artery in man and in the orang, it is evident that it is a longitudinal anastomosis between ventral perforating branches. The stem of origin from the vertebral artery has the same value as the so-called reinforcing branches given to it at a lower level. Any variability is due to the choice of stem connecting it with the vertebral artery. It will be shown that the same explanation accounts for any variability which may occur in any of the arteries supplying the somatic functions of the body.

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From the similarity of the arrangement of this artery in the orang and in man, it can be assumed that the internal distribution would be the same. The perforating anterior spinal arteries, therefore, supply median somatic and certain suprasegmental structures in the medulla oblongata, whether the branches rise from the basilar, vertebral or longitudinal anterior spinal artery. There is no anastomotic invasion of the territories supplied by the lateral and dorsal systems. The longitudinal anterior spinal artery is thus a channel connecting segmental perforating vessels of the same function.
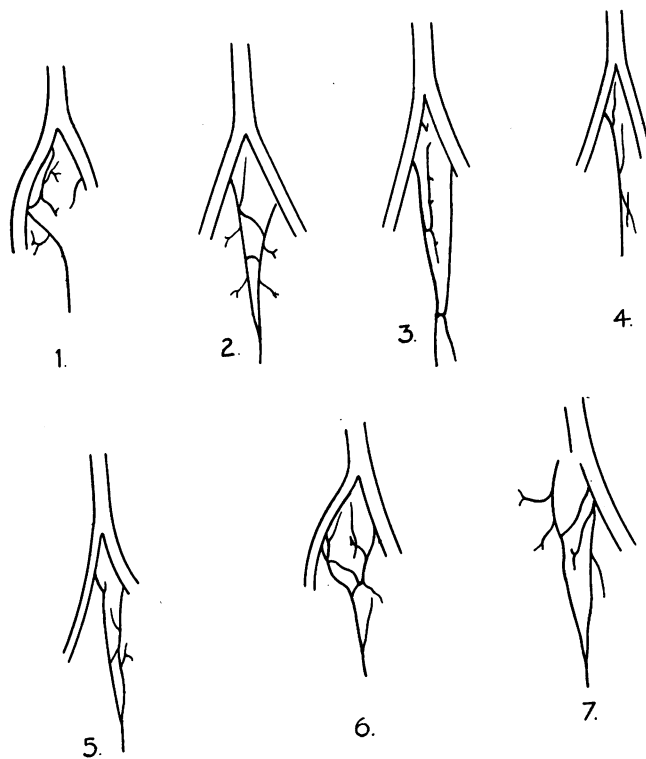

Fig. 2. The origin of the anterior spinal artery.

The Posterior Inferior Cerebellar Artery

This vessel is absent in the injected specimen. Its cerebellar supply is taken over by the anterior inferior cerebellar artery. In specimen, No 2 (Pl. I, fig. 3), the posterior inferior cerebellar artery arises from the vertebral on both sides and runs a course which is described as normal in the human brain by Stopford. It turns round the lower border of the pyramid and passes superiorly and laterally through the rootlets of the hypoglossal nerve to reach a point a few millimetres below the lower margin of the pons Varolii. In this part of its course it lies anterior to the rootlets of the vagus and glossopharyngeal nerves. It now turns back on its course, forming a well-marked curve, and descends

posterior to the vagus and glossopharyngeal rootlets, inclining at the same time towards the restiform body, to reach the region of the calamus scriptorius. It here gives off a branch which I take to be the posterior spinal artery and then proceeds to its cerebellar distribution.

For descriptive purposes the artery may be regarded as being composed of three portions:

1. A portion from its origin to the lower border of the·pons Varolii. This portion passes through the hypoglossal rootlets and lies anterior to the vagus and glossopharyngeal.

2. A portion from the lower border of the pons Varolii to the point at which the posterior spinal artery is given off.

3. A portion distributed to the cerebellum.

In those cases in which the artery is said to be absent, a branch of the vertebral can always be found arising from the same site as that from which the normal posterior inferior cerebellar artery arises. This branch passes through the rootlets of the hypoglossal nerve. It gives off lateral perforating branches to the medulla, and terminates in dorsal perforating branches entering the substance of the medulla dorsal to the vagus and glossopharyngeal rootlets. It occasionally gives origin to the posterior spinal artery. It fails, however, to form the well-marked loop, and as a rule gives no branches to the cerebellum. In such cases the third part of the posterior inferior cerebellar artery is replaced by the anterior inferior cerebellar artery. Such is the condition in the injected specimen.

The lateral perforating arteries are branches of the vertebral in those cases in which the posterior inferior cerebellar artery is absent. They supply the region of the bulb between the antero-lateral and postero-lateral sulci. I propose to name this system the lateral or radicular set of perforating arteries to distinguish them from the dorsal set which supply the structures arising from the rhombic lip in the embryo. As far as I can ascertain, both the lateral and dorsal sets arise from common stems. The functional value of the three portions of the posterior inferior cerebellar artery and of the branches therefrom will be discussed in Part II.

Speaking generally, the posterior inferior cerebellar artery is subject to the same variations in distribution and origin as Stopford found in man.

The Posterior Spinal Artery

The distribution of this artery could not be determined from the specimens.

The Basilar Artery

The basilar artery (Pl. I, fig. 1) commences at the level of the lower border of the olivary eminence. This level of origin is lower than that found in man, and is the same in all the specimens examined. In every case the artery terminates at the level of the upper border of the pons Varolii. It therefore appears to be longer than it is in man.

Branches

The branches are perforating, or pontine, anterior inferior cerebellar, internal auditory, superior cerebellar and posterior cerebral.

The perforating or pontine branches are ventral, lateral and dorsal, and have corresponding areas of supply to the same systems of the vertebral artery.

The Ventral Pontine, or Anterior Spinal Perforating Branches

These vessels are clearly seen in the injected specimen. They arise from the basilar artery throughout its extent; and, as Stopford describes in man, they are more numerous cranially and caudally. From his injections it is clear that their area of distribution is continuous with the area injected by the longitudinal anterior spinal and ventral perforating branches of the vertebral artery; in other words, these branches are serially homologous with the anterior spinal perforating arteries in the medulla and spinal cord.

The Lateral and Dorsal Perforating Branches

These two systems are dealt with together for they arise by common stem branches from the basilar artery. We have seen that the anterior spinal artery is a longitudinal vessel within the area of the ventral perforating branches, and I have indicated that similar longitudinal channels occur within the other somatic systems. The posterior spinal artery is such a channel within the area of the rhombic or dorsal system, as also is the free anastomosis between the cerebellar arteries on the cerebellum. The anterior branch of the posterior spinal artery, lying ventral to the postero-lateral sulcus in the spinal cord, is such a channel in the area of the radicular or lateral set of perforating branches. These longitudinal anastomoses connect with the vertebral and basilar arteries through stem branches common to both systems: so that, whereas the ventral system is distinct, there is free communication between the radicular and rhombic systems.

I have traced the transverse, or stem, branches of the basilar artery and find that the usual description of three cerebellar arteries is too schematic. Any of the branches may supply the cerebellum, but certain branches predominate, and these are named in accordance with the level at which the stem branch is selected. A glance at Pl. I, fig. 1, makes it clear that transverse branches have been so selected. The level of origin of the anterior inferior cerebellar artery is not the same on the two sides, but in both cases the artery lies ventral to the abducent nerve. Stopford insists on the importance of the relation of this nerve to the cerebellar arteries. He records cases in which the artery lies dorsal to the nerve. It seems evident that, in those cases in which the artery is dorsally situated, the internal auditory, or some higher stem branch, has been selected. In fact Stopford shows that the internal auditory artery arises more frequently from the anterior inferior cerebellar artery than from the basilar.

The transverse stem branches of the basilar artery pass outwards on the surface of the pons Varolii, and, after giving branches to the substance of the pons, end in the supply of the cerebellum. They do not communicate with the ventral system. Such is the description which applies equally well to any of the transverse branches of the basilar artery or of the vertebral artery. It can be said that where the stem branch is enlarged to join the cerebellar, or rhombic, anastomotic area, it is dignified by a special name. If it arises low down it takes the name of posterior inferior cerebellar; if somewhat higher, anterior inferior cerebellar, and if higher still, the internal auditory artery is said to arise from the anterior inferior cerebellar artery. The final distribution is the same; in other words, the variability is not haphazard, but follows a definite method which will be more fully described in Part II.

Stopford's work makes a more detailed description of these vessels unnecessary.

The superior cerebellar arteries arose from the posterior cerebral artery in every case examined.

The Circle of Willis

The circle of Willis is arranged in the usual manner. The vessels which enter into its composition are equal in size and symmetrically arranged on both sides. I do not propose to describe it fully.

The Posterior Cerebral Artery

The posterior cerebral artery, formed by the division of the basilar artery, passes slightly forwards and outwards, curving sharply round the third nerve; it then passes backwards curving round the cerebral peduncle and terminates within the sulcus calcarinus (Pl. I, fig. 1, and Pl. II, fig. 4). Immediately anterior to the point where it curves anterior to the third nerve, it is joined by the posterior communicating artery.

This artery is usually described in human anatomy as ending within the calcarine fissure by dividing into parieto-occipital and calcarine branches. In this specimen there is no parieto-occipital branch; its area of distribution is taken by the anterior cerebral artery.

Branches of the Posterior Cerebral Artery

The branches are cerebellar, perforating and cortical.

The *superior cerebellar arteries* are from two to three in number on each side and pass to the surface of the cerebellum. I have not been able to determine their distribution with any accuracy.

The *perforating arteries* can be seen entering the posterior perforated spot and are arranged in medial and lateral sets. I have frequently injected these arteries in man and found their distribution so precisely arranged, that I wrote in 1920 [11]:

The posterior cerebral and posterior communicating arteries are so precisely distributed in my specimens that the description given by Beevor of the

arterial supply of the optic thalmus could well have been made from my specimens.

Their internal distribution could not be determined in the orang.

The Cortical Branches (Pl. I, fig. 4, and fig. 5)

The main cortical branches were traced to their final distribution and the areas demarcated by conventional signs (fig. 5). These branches are so arranged that they mark out the functional areas already determined by Elliot Smith[9] and Brodmann[10]. There are four main branches; the first two are generally named the anterior temporal branches, the third is the posterior temporal and the fourth the calcarine.

The first anterior temporal artery is small and supplies the area No. 20, or area temporalis inferior of Brodmann. The second anterior temporal branch supplies the area No. 37, or area occipito-temporalis of Brodmann. The posterior temporal artery supplies the area No. 19, or area prae-occipitalis of Brodmann, as far superiorly as the sulcus praelunatus. The final branches mark out almost exactly the striate cortex on the medial and lateral aspects of the hemisphere. It is to be remarked, however, that the extreme edge of the striate cortex bordering the sulcus lunatus is supplied by the anterior and middle cerebral arteries (Pl. II, fig. 6).

The close correspondence between the distribution of the calcarine branches and the striate cortex has previously been noted in the human brain. The fact that the sulci, not only of the occipital region, but also of the parietal region, are so diagrammatic in the brain of the Chinese, makes the examination of the blood supply of the brain of this race of peculiar interest. I have been able to confirm the fact that the cortical supply is arranged in accordance with functional areas, and am making this the subject of another communication. The area temporalis polaris of Elliot Smith, being supplied by a distinct branch of the middle
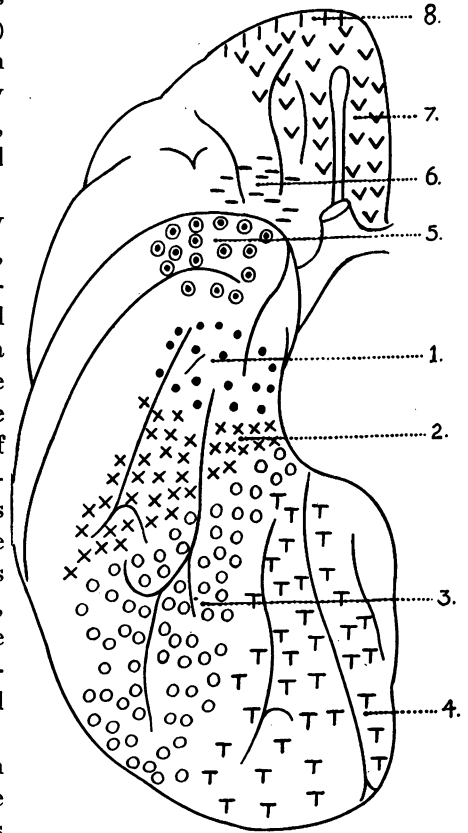

Fig. 5. Areas of distribution of cortical arteries. 1. and 2. Anterior temporal. 3. Posterior temporal. 4. Calcarine branches of the posterior cerebral artery. 5. Arteria temporalis polaris. 6. Arteria orbitalis of middle cerebral. 7. Arteria praefrontalis. 8. Arteria frontalis polaris of anterior cerebral artery.

cerebral artery in both the orang and man, accentuates the fixity of the distribution of the posterior cerebral artery.

The posterior cerebral artery is, therefore, predominantly visual. It supplies the pulvinar, the lateral geniculate body, the superior corpus quadrigeminum and the cortex concerned with the reception of visual impulses. It also supplies the anterior nucleus of the thalamus and the inferior temporal convolution.

The Anterior Cerebral Artery

It is convenient to divide this artery into two parts for the purposes of description. The first part extends from its origin from the internal carotid artery to the point at which the anterior communicating artery is formed; the second part constitutes the remainder of the artery.
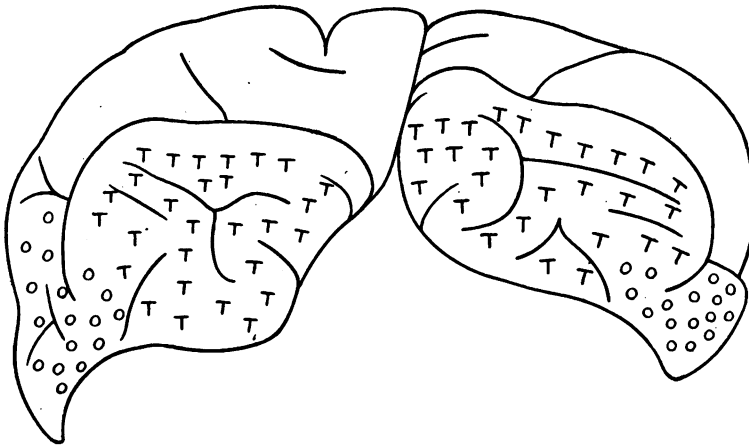

Fig. 7. The distribution of the posterior cerebral artery in the area of the striate cortex.

The distribution of the first part (fig. 7) is very closely associated with the sense of smell; it supplies that portion of the corpus striatum which lies anterior to the anterior commissure, the anterior commissure itself, the olfactory tract, the medial and lateral olfactory striae, the tuberculum olfactorium, the corpus paraterminale and the proximal part of the gyrus cinguli. I have not been able to determine the supply of the olfactory bulb.

In the specimen under consideration, the first part of the artery shows a remarkable anomaly on the left side. There is a well-marked perforation where the artery lies ventral to the medial olfactory stria: the artery divides and joins up again. Stopford records instances of perforations in the vertebral and basilar arteries, through which, in some cases, rootlets of nerves may pass. I know of no other instance of a similar condition in the anterior cerebral artery (fig. 7).

Branches of the First Part of the Anterior Cerebral Artery

It will be convenient to describe the branches of the middle cerebral artery which enter the anterior perforated spot with those of the first part of the anterior cerebral artery, since they are so closely related with each other in the supply of those areas of the brain which Elliot Smith has named the palaeostriatal and hypopallial areas. On the left side of the brain of the orang (fig. 7), there is a direct inosculation between the recurrent branch of the anterior cerebral artery and the branch of the middle cerebral artery which gives off the striate arteries to the site of the erased endorhinal fissure. The usual condition is seen on the right side where the striatal branches of the two arteries are separate from one another. Since these arteries are of such clinical and morphological importance, and since the condition in the orang is so similar to that in man, I hope I may be allowed a short digression to discuss their disposition in man. Fig. 7 will then suffice to describe the specimen.

As far as their internal distribution is concerned the work of Beevor is so complete that, with the exception of the blood supply of the claustrum, there is nothing to add to his original paper. I have confirmed all his observations.

Duret's account of the gross anatomy of these vessels has been the basis for most subsequent description, and continued repetition has detracted from the accuracy of his own description. Charcot, forming his conclusions on cerebral haemorrhage on Duret's work, laid the foundation for the accepted belief that, "the arteries of the central system, at their origin, are directed perpendicularly to the main trunk." John Hunter's observations, however, referring to the angles at which the vessels arise, are more accurate:

I have already observed that the angles at which the branches of an artery arise may either retard or allow a freer motion of the blood; but nature appears to have taken still more care in retarding the blood's motion when velocity might do mischief. She seems also to have taken more care about the blood's motion in some parts than in others; as for example, in the brain, a part which cannot bear the same irregularity, in quantity or velocity of the blood, as many parts of the body.

The arteries which pass through the anterior perforated space belong to two groups:

1. Those which enter along the site of the erased endorhinal fissure; and
2. Those which enter posterior to the fissure.

There are three different sets of arteries belonging to the first group. Two of these arise from the middle cerebral artery, or from one of its branches, and one from the recurrent branch of the anterior cerebral artery. The first set which arise from the middle cerebral artery are arranged in linear order along the site of the endorhinal fissure; the anterior cerebral group lies anterior to and parallel with them. The third set arises from the middle cerebral or one of its branches, well lateral to the anterior perforated space; these vessels then return to be concentrated at the angle of the space in a well-marked bunch.

In the orang, figured, the first two sets of branches to the site of the endorhinal fissure, appear to arise in common from the recurrent branch of the anterior cerebral artery which has inosculated with the branch of the middle cerebral artery.

The anterior cerebral artery supplies the remaining branches which enter the anterior perforated space. These are:

1. Small branches which supply the trigonum olfactorium;

2. One large branch which enters immediately laterally to the optic tract and probably supplies the caudate nucleus.

I described these arteries in 1920, and at that time did not know that H. F. Aitken had published in 1909, "A Report on the Circulation of the lobar ganglia," in which the arteries which are named above were fully described. This report is one of the most important contributions on the subject.

The claustral arteries are given off in series with the lateral striate arteries; they are separate and distinct end arteries which perforate the lower part of the insula and pass to the claustrum.

In fig. 6 of Beevor's paper, the internal distribution of the arteries just enumerated shows a constant relation to the anterior commissure. The nucleus caudatus, anterior to the commissure, is supplied by the perforating branches of the anterior cerebral artery. The area situated lateral and postero-lateral to the commissure is supplied by the middle cerebral artery, outside which lies the claustrum supplied by its own vessels. Finally, the area posterior to the commissure, consisting of a portion of the lenticular nucleus, the internal capsule and the thalamus, is supplied by three vessels—the anterior choroidal, the posterior communicating and the posterior cerebral arteries.

From the work of Elliot Smith on this difficult region we are enabled to gain an insight into the cause of this multiplicity and yet constancy of its blood supply. In comparison with the primitive mammalia, the cortex and basal nuclei in man have increased enormously, whilst the areas related to the primitive sense of smell have become relatively reduced; and yet, the primitive vessels to these areas still retain their individuality.

The Second Part of the Anterior Cerebral Artery

The second part of the anterior cerebral artery (fig. 8, Pl. III, figs. 9 and 10) is entirely confined to the supply of the cortex. From the point at which it is joined by the anterior communicating artery it passes into the great longitudinal fissure; turning round the genu of the corpus callosum it lies closely applied to that structure as far as the splenium and then turns abruptly upwards for a short distance to pass into the parieto-occipital fissure. The second part of the anterior cerebral artery is of great interest for the areas supplied by its individual branches approximate very closely to the areas which have been defined by other methods.

The first branch is the medial orbital branch of human anatomy. Its exact area of supply is the area praefrontalis of Elliot Smith. The artery arises

immediately anterior to the recurrent branch which supplies the gyrus sub-callosus; it passes to the orbital region of the frontal lobe by passing dorsal to the olfactory tract. It gives branches to the medial surface of the hemisphere as far as the sulcus subrostralis. On the orbital surface its supply is limited by the sulcus orbitalis. Its area of distribution exactly corresponds with area No. 11 of Brodmann.

Cunningham's text book describes this branch as supplying the medial orbital gyrus, the gyrus rectus and the olfactory bulb. In the Orang-utan the bulb is missing, but I am inclined to the opinion that the olfactory bulb is supplied by the recurrent branch of the anterior cerebral artery. These branches have, however, been torn in the specimen with the olfactory tract.
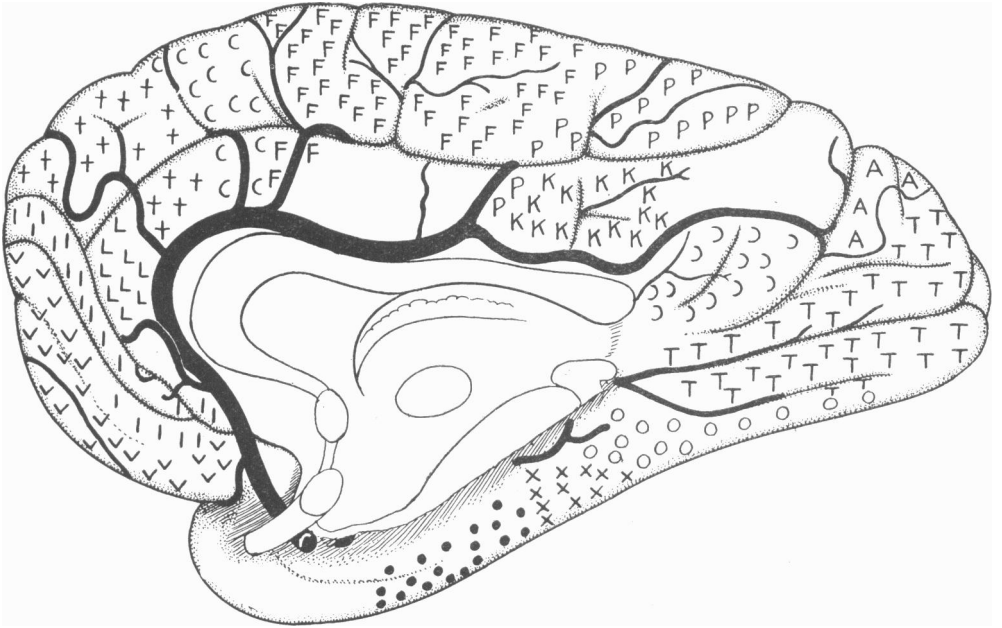

Fig. 8. The distribution of the right anterior cerebral artery in the orang.

If fig. 585 in Cunningham's text book is referred to, this artery will be found to supply the area marked with green dots. The area orbitalis is limited by a distinct branch of the middle cerebral artery.

The second branch is the anterior medial frontal artery. The area of dis-tribution is the area fronto-polaris of Elliot Smith. This area lies between the sulcus subrostralis and the sulcus rostralis. The sulcus rostralis is a deep operculated sulcus in the brain of the orang and extends to the lower part of the superior frontal gyrus on the lateral surface of the hemisphere. The distri-bution of the artery extends on to the lateral surface and coincides with the area fronto-polaris. I will, therefore, name this the arteria fronto-polaris.

The third branch is included with the second in most text books as anterior

medial frontal. On both sides in the specimen the third branch is distinct, and supplies the anterior frontal area of Elliot Smith.

The intermediate and posterior medial frontal branches supply the superior frontal and paracentral gyri respectively, but it is not possible to dogmatise too closely in the specimen. Besides these named branches, there are separate branches supplying the posterior part of the gyrus cinguli and the area para-splenialis. The more exact determination of the areas of supply of the different vessels must be investigated on a larger series of brains; and I now engaged in that investigation on the blood supply of the Chinese brain.

A full description of the distribution of the middle cerebral artery is not possible without causing considerable damage to the specimen. For this reason, the opinion that the cortical supply is related to functional areas, can only be regarded as a working hypothesis until more extended observations have been made.

Pl. IV, fig. 11, shows the cortical distribution of this artery.

PART II

THE INTERPRETATION OF VARIATION IN ARTERIAL DISTRIBUTION

The variations which occur in the vessels of the brain of man can only be adequately explained by a critical examination of the development and subsequent distribution of the arteries of the body.

The development takes place in two stages; firstly, a segmental stage in which the segmental character of the body is most clearly seen; and, secondly, an intersegmental stage in which the transformation of the body into an intersegmental and suprasegmental organism leaves its impress on the vascular system as clearly as it does on the nervous and muscular systems.

The First or Segmental Stage in Arterial Development

The final distribution of the arteries of the body is governed by the pattern which is laid down before the establishment of the circulation. The origin of the primitive blood vessels from angioblastic cells, derived from the mesenchyme, has been established by Miss Sabin[13]. She has demonstrated that the first vessels to arise in the embryo appear before the circulation of the blood is established. This had been suspected since the time of John Hunter who says:

The vessels are probably the very first active parts in the system, for we find them in action before they have formed themselves into a heart, and in such a state of parts we find them the only part that has any strength, while the other parts are only preparing for action.

She has further demonstrated that the heart beats for a considerable time before the circulation begins.

Stockard[14], Knower[15], Chapman[16] and others have attempted to

determine the effect of the removal of the heart on the developing circulation. Stockard found in Fundulus embryos, chemically treated, that although there had never been a heart beat, the aorta developed into a vessel of considerable size. He, furthermore, established the law that an arrest in development at a particular time, from whatever cause, had the effect of causing malformations of definite type depending on the time of arrest. From this it is apparent that any experiment, in which the heart is removed, must be examined, not only from the point of view of the immediate mechanical effect on the animal, but also from the point of view of arrests in development produced by the mutilation itself.

Even assuming, however, that no other effect is produced than that consequent upon the loss of the mechanical forces produced by the heart's action, these experiments abundantly prove that the development of the segmental vessels has no relation to the mechanical forces due to the heart's action. Knower found that, "even after extensive operation, involving much of the neighbouring tissues, before the heart is clearly differentiated, the aorta, the large veins and the segmental vessels are laid down." Chapman used the experiment to prove that the circulation is laid down in accordance with the postulates of Thoma. It is difficult to follow his line of reasoning which led him to the conclusion that whilst certain vessels are developed by "hereditary factors," the remainder are dependent on the mechanical forces derived from the heart's action. He admits, however, that by the time the circulation begins, the embryo has a primitive but complete system of blood vessels, and that, "if the time of circulation is delayed the further development of the vascular systen is not inhibited."

There is no question of any other mechanical factors concerned in the development of the circulation than those produced by the heart beat. This is in general agreement with the view of those who would attribute the further development of the circulation to mechanical factors. Any theory which is put forward to explain the vascular distribution should stand the test of explaining the whole circulation. If the mechanical force of the heart beat is eliminated, those who look to the postulates of Thoma for their explanation must fall back on such vague terms as "hereditary factors" to account for it.

We are, however, not dealing with the circulation of embryos which have been multiplied, but with normal living embryos whose blood vessels are distributed for the purpose of supplying organic structures. Neither are we dealing with arteries merely as arteries separated from organs, but with the development of arteries which can be traced to the organs which they supply— in other words, with distribution.

The arteries will, therefore, be considered in the order of their appearance and in relation to the order of appearance of the organs supplied by them.

The hypothesis which it is my purpose to prove is:

That the segmental arteries of the body are developed *in situ* in relationship with the organ which they are to supply; that these arteries are phylo-

genetically and ontogenetically stable; that having been developed to supply an organ, they supply that organ throughout life; and, finally, that when a primitive functional area develops greater function, the vessels supplying the greater functioning area are derived from those supplying the primitive area.

It is apparent that the proof of this hypothesis must lead to the abandonment of the vicious doctrine that muscles, nerves and arteries develop independently of one another by a process of "self-differentiation."

The first arteries to appear in the body, apart from the extra-embryonic vessels, are segmental in character and are distributed in accordance with the functional needs of the body as a segmental structure. If gill clefts were present in each segment, there would be no need for either a heart or an aorta. The segmental arteries are sufficient for the needs of a segmental organism. The functions of the body are, however, threefold: segmental, intersegmental and suprasegmental. There is the suprasegmental heart, the intersegmental vessels, of which the most striking is the aorta, and the segmental vessels. In the nervous system there is the segmental reflex arc, governed by intersegmental and suprasegmental mechanisms. The muscles are arranged, first segmentally, then intersegmentally, and finally suprasegmentally. The musculature of the arm is designed to respond to suprasegmental cerebral stimuli—the vertebral and subclavian arteries arise from the same segment.

The segmental pattern of the vessels of the embryo is fairly well established: it is represented diagramatically in Cunningham's *Text Book of Anatomy*, in Keibel and Mall's *Manual of Human Embryology* (17) and in other works. The vessels are arranged in three groups: somatic, genito-urinary and visceral. The visceral group is included for descriptive purpose only, since there is no evidence that the gut is segmentally arranged. The arteries of these three groups belong to three main functional systems, in which the main artery to each system is an artery of functional value and an end artery—that is, there is no arterial anastomosis between the groups.

The end artery with which this paper is particularly concerned is the segmental somatic artery. Its area of supply is the area of the segmental reflex arc. As a whole it supplies the skin, or receptors, the sensory ganglion, the segmental intercalated region of the neural tube, the motor ganglion cells, or effectors, and finally the muscles, or expressors.

But whilst the whole is a functional system, distinct from the genito-urinary and visceral systems, so also each component of it is a functional system and the artery to each component is an end artery.

THE FUNCTIONAL UNITS OF THE SEGMENTAL SOMATIC ARTERY
The Effector, or Perforating Anterior Spinal Artery

Professor R. A. Dart and I (5) called attention to this artery in 1922. Its position and relations are the same in all embryos. It is depicted by Hensen, His and most writers on the origin of the peripheral nervous system. It is situated immediately internal to the motor ganglion cells of the anterior

horn. If sections of the medullary tube, impregnated by Cajal's method, are examined at this stage, the line which is taken by this artery will be found to be the line taken by the fibres of the anterior commissure which is developing at the same time (Hertwig, "Embryology of Vertebrates," Vol. IV, figs. 153 and 154)(18). Obviously the stage of development is later than the pure segmented stage of the embryo, for already intercalated or intersegmental fibres have developed sufficiently to become impregnated. It must, therefore, be determined how this vessel came into this position which is retained throughout life. Obviously it did not arise within the medullary tube; and, therefore, the angioblastic cord must have migrated in from the outside by an active process, or it must have become circumvested by the encroaching external layer of the medullary tube by a passive process of intrusion.

The difficulties of accepting the first supposition are that:

1. Similar active migrations are unknown in the body in the case of the blood vessels, or at least have not been proved:

2. The constancy of the position of the artery: and,

3. The absence of any evidence that the external limiting membrane is the same structure at different ages of development.

The second supposition is the more probable, but its acceptance demands a reconsideration of the current views on nerve development.

The somatic segmental artery arises before the circulation is established, at a time when the medullary tube is segmented and when its marginal layer is defined by the so-called external limiting membrane, when nerve fibres are not impregnatable, when the cells of the medullary tube are undifferentiated, and when the dorsal element of the somatic segmental artery is external to the medullary tube with evidence of commencing development of branches (Keibel and Mall, fig. 439). So that whichever supposition is correct the rudiments of the anterior spinal artery are outside the medullary tube. In the next stage (see Hertwig, fig. 154), a great change has taken place in all parts of the embryo. The development of an entirely new system of arteries has taken place and the heart has begun to function. The new system of arteries comprises the longitudinal intersegmental arteries—the aorta, the vertebral, the longitudinal anterior spinal artery and others. The advent of intersegmental function has been signalled by a re-arrangement of the myotomic and lateral muscle sheets, producing an intersegmental arrangement of the vessels of the trunk and limbs. The nervous system has responded by the development of impregnatable neurofibrillae arising from the mantle layer of the medullary tube. These fibres, both commissural and intersegmental, have become impregnated in the region which is recognised as the marginal layer of the earlier stage. It is here also that the anterior spinal artery is seen. The motor ganglion cells lie external to the artery and to the position of the external limiting membrane of the earlier stage as well as to the impregnated fibres belonging to the intercalated neurones. Clearly the artery has not penetrated the external limiting membrane of the segmented stage.

This interpretation infers that the external limiting membrane of the medullary tube is not a fixed structural entity, but that with each succeeding stage in development the so-called external limiting membrane occupies a more lateral position, being as it were re-formed, not expanded. This accounts for the fact that the impregnated cells of motor type are always external to the anterior spinal artery in the medullary tube. In the further growth of the embryo these relations are maintained. In support of the hypothesis that the motor cells and anterior spinal artery have become absorbed into the neural tube, as an expression of the advent of intersegmental function, we find that the radicular and rhombic arteries have likewise become absorbed into the dorsal region of the medullary tube, together with the dorsal columns of the cord, which are clearly of extra-neural origin. It is in the dorsal region that the limits and form of the earlier medullary tube can be most plainly seen. There can be no doubt that, if the sensory ganglia had become included in the medullary tube (as is perhaps the case with a portion of the fifth nerve), the medullary tube origin of all sensory nerve cells would have become the subject of a scientific dogma. The present teaching of nerve development denies to nerve elements that which must be granted to the vascular elements, that is, absorption from the outside.

A digression is here necessary, for if the anterior spinal artery is developed as a part of the reflex mechanism, and, if it does arise *in situ* with the anterior horn cells—as the evidence would tend to show—then the conclusions arrived at by Harrison[19] from an experimental study of the tissues of tadpoles must be abandoned. The present doctrines of development are founded on the conception that the tissues of the body develop by a process of "self-differentiation." A mental picture of disconnected units ultimately uniting to produce functional systems dominates the teachings of anatomy. But if it is accepted that the reflex mechanism develops as a whole, in which each of the component parts is intimately linked together from the beginning, then it cannot be accepted that the nerve and muscle develop independently without anatomical connection.

The brilliance of the operative procedure of Harrison is beyond question. A repetition of his experiments would in all probability lead to the same results; but the conclusions which have been deduced therefrom are open to other interpretations. His two classical experiments, which would at first sight appear to negative the idea of continuity of the structural elements involved in a functional mechanism are:

1. The experiment which proves that a nerve cell grown in a culture medium behaves in a specific manner: and,

2. The experiment which is designed to prove that, when a muscle is separated from its nerve, the muscle is capable of independent development.

Graham Kerr[20] has brought a considerable amount of evidence in disproof of the theory that the medullary tube and myotome are not in organic continuity. He has discussed the question fully in his textbook of embryology, and

having examined his specimens of Lepidosiren, there is no other conclusion to be arrived at than that there is structural continuity between the myotome and the muscle. But it is an interesting fact, which has been missed by the contestants in this discussion, that Harrison's experiment actually proves the opposite from that which he says it does. He has shown that there can be no amoeboid movement of a nerve cell unless there be a bridge for the protoplasm to use. His experiment is of great value, for it gives information of the behaviour of a nerve cell—or perhaps only a part of a nerve cell—in a fluid medium, and in a medium in which a supporting tissue is present. Unfortunately it fails to give the information required. What is the behaviour of a nerve cell in the body of a living normal embryo? What is the behaviour of a nerve cell which is the subject of changes consequent upon the transformation from segmental to intersegmental and suprasegmental function? Harrison's experiments fail to take into account the laws of neurobiotaxis set forth by Ariens Kappers.

In the second experiment, Harrison inserts a quill between the medullary tube and myotome at an early stage. In this experiment he severs the connection which is already in existence, although he denied this. The muscles separated show the reaction of degeneration as far as one can tell. Unfortunately we have no evidence of the appearance of a degenerating nerve in a tadpole, but Harrison says that the muscle develops normally and that *it does not respond to either mechanical or electrical stimulation.*

To resume. The somatic segmental artery responds to the myotomic differentiation by providing the perforating anterior spinal artery. Where this artery is injected by the method of Beevor the picture produced is diagrammatic. The anterior horn cells are invariably supplied. Similarly Stopford says, "Invariably the trigonum hypoglossi was accurately defined by the stain of the injection."

The Sensory Arteries of the Segment

There appears to be a distinct branch of supply to the sensory ganglia. In the medullary tube itself, two systems of perforating arteries can be distinguished in the embryo. One system is distributed to the region posterior to the entrance of the dorsal nerve roots, and one system anterior to them. The first system is the one I have referred to as the rhombic system of perforating arteries; the second system is the radicular system. There is no apparent anastomosis between the areas concerned. It is apparent that the classification here put forward might be somewhat schematic, and that Stopford is correct in issuing a warning against such a threefold classification. He says that:

The subject is somewhat controversial, and often rendered obscure by many writers in their endeavour to divide the cord into three districts—first the part supplied by the anterior system, secondly a part supplied by the posterior, and lastly the part supplied by both.

In justification of such a schematic rendering, however, I must refer to his own pictures (figs. 7, 8, 12 and 19). There can be no question of the definite entity of vessels which would so clearly define the hypoglossal and vagal triangles (both of which observations I have personally confirmed), and of vessels which should so separate the posterior columns and their nuclei. But with the lateral somatic motor nucleus supplied, apparently by the radicular system, it is clear that the establishment of the hypothesis put forward here requires even more discriminating work than that which has been done by Stopford.

The rhombic system of vessels supplies the structures derived from the rhombic lip in the embryo; and the radicular system supplies the intercalated nuclei, including the vagal nuclei, amongst other structures in the medullary tube.

The Muscular Branches of the Somatic Segmental Artery

Leaving out of account the arteries which supply the bones and supporting structures, the remaining branches of the segmental artery are muscular, supplying both dorsal and lateral musculature. The best example of the lateral somatic supply is seen in the vessels of the forelimb. This has been investigated by Woollard(21) and others. Whilst the pure segmental supply cannot be ascertained with certainty by the method of injection, the first stage described by Woollard is so early in the intersegmental stage that the assumption is justified that the segmental arteries of the limb are derived from the same segments as the nerves and muscles. Woollard lays stress on the fact that there is no variability at this stage.

It can, therefore, be said that the arteries of the animal in the segmental stage are constant in distribution. They are definitely distributed in relation to the function of the part supplied and are end arteries within that area. They develop synchronously with the structures which they supply, and arise *in sutu* from angioblastic cells. Furthermore, at this stage the distribution can in no way be attributed to mechanical forces.

Before proceeding to the description of the changes which take place on the advent of intersegmental function, it is necessary to make a clear distinction between two definite elements of each functional segmental artery; for it is clear that if each artery is an end artery within its own area, then no intersegmental circulation can be established. The two elements are the stem of origin and the terminal portion of distribution.

The Establishment of the Intersegmental Circulation

"The establishment of the intersegmental circulation is brought about by longitudinal anastomosis between stem arteries of equal functional value." The terminal portions remain distinct and supply the area to which they were originally allotted. Any accession of function produces arteries for its supply from the capillary network distributed within the area of the function from which the new function arose. The proof of this hypothesis disposes of the

postulates of Thoma, for the definitive circulation is prefigured in the distribution which is laid down before the heart begins to beat.

The attention of embryologists has been unduly attracted to the vessels which are prominent in the adult, with the result that the importance of the terminal vessels to the organs has been lost sight of. The fact that the developing longitudinal vessels arise from stem arteries of the same value, permits some stems to be done away with. The efficiency of the circulation to the terminal segmental portions can thereby be assured; and, moreover, the blood can be distributed in response to intersegmental rather than to segmental stimuli. This method of opening up new channels allows of a certain choice of route, but the final destination remains the same. Every variation in vascular distribution can be thus explained. The variation is, however, more apparent than real, since every longitudinal vessel must consist of a stem artery as its commencement and the longitudinal anastomosis within the function of that stem. The direction of the blood stream, or the distribution of the vessels, is governed by the direction of the functional development.

Longitudinal channels arising in terminal functional areas must be entirely confined to the area of that function. Herein lies the explanation of the longitudinal anterior spinal artery and of the longitudinal radicular and rhombic channels. They are the terminal anastomotic channels in the terminal areas of function of the somatic segmental reflex.

The injection of the longitudinal anterior spinal artery reveals the blood supply of the median somatic motor nuclei. The variability of its origin from the vertebral artery is purely a question of the segmental stem which forms its commencement.

The same condition is found in the case of the lateral somatic muscular arteries of the forelimb. At the same moment as the longitudinal anastomoses are occurring elsewhere—that is, at the moment of the advent of intersegmental function—the segmental arteries of the forelimb are being connected together by a longitudinal anastomosis which passes cranially and caudally in the limb bud. This is the time when the anterior horn cells are being influenced in their position by the development of intercalated and commissural fibres.

Woollard, in describing this stage, says:

> This stage shows the dominance of the lateral branch of the seventh segmental artery so enlarged that it constitutes the main axial trunk of the forelimb bud....The contributions from the other segments are disappearing.

The accuracy of his observations and the clearness of his pictures permit of a complete understanding of the changes which have occurred. The method of injection fails, however, in one important particular. It fails to distinguish the stem portion of the artery from the terminal branches of distribution. The main axial trunk of the forelimb bears the same relation to the seventh segmental artery as the vertebral artery does. It would not be correct to say that the dorsal branch of the seventh segmental artery is so enlarged that it forms

the main trunk of the vertebral artery. The only portion of the vertebral artery which is constituted by the seventh segmental artery is the stem of origin; the same is the case with the main axial trunk of the forelimb. It is the proximal or stem portions of the fifth, sixth, eighth and ninth segmentals which disappear, not, as Woollard states, "the contributions from these segments," for the final vessels of distribution remain.

The axial trunk of the forelimb is, therefore, mainly a longitudinal vessel which is formed in a terminal functional area in the sense in which I have described. The limb artery may be said to be a functional artery for the supply of lateral somatic musculature which has been converted from segmental to intersegmental function. The forelimb is one of the important organs for the expression of willed movements determined in the cerebrum; and so it is not a matter for surprise that the same segment should be the one from which both the vertebral and subclavian arteries should arise, and that they should both develop at the same time. Congdon (22), losing sight of the development of the suprasegmental structures—particularly the cerebrum—says, "There would never be a vertebral artery did not the aorta shift caudally." Then one may ask, what would supply the higher nerve structures? It is as reasonable to say that there would never be a vertebral artery did not the head grow cranially.

. The rhombic and radicular longitudinal channels are similarly anastomoses in areas of terminal function. The rhombic system supplies the structures which are derived from the rhombic lip in the embryo. The second portion of the posterior inferior cerebellar artery is a part of this channel: and thus we have the explanation of the frequent origin of the posterior spinal artery from the posterior inferior cerebellar artery.

The radicular longitudinal channel is formed ventral to the posterior nerve roots. It supplies, among other structures, the intercalated elements of the reflex arc. The first portion of the posterior inferior cerebellar artery consists of this longitudinal anastomosis with the important addition of the stem branch which connects it with the vertebral artery. The stem branch of the anterior spinal artery is a stem branch of a single functional system; the stem branch to the radicular and rhombic systems supplies at least two functions developed on the sensory side.

If we turn for a moment to the development of the aorta and its main branches this will become clear. The aorta for the greater part of its extent is the main longitudinal channel connecting up the functional arteries of each segment. It is the great intersegmental artery. Any branch which it gives off must of necessity start as a stem branch of a single functional system of segmental value and then pass to a longitudinal vessel. Starting from the point at which the vertebral leaves the subclavian artery, the commencement is the stem of the dorsal segmental artery; it must then pass to all the elements concerned in the dorsal part of the segmental reflex arc. The course of the circulation is thus established; it always passes from an area of higher function to areas of subordinate function derived from the higher function. The longi-

tudinal anastomoses take place at each point of differentiation of function. The variability of the posterior inferior cerebellar, the anterior inferior cerebellar and internal auditory arteries and their interdependence on one another has here its explanation. The commencement of any one of them is a stem of equal value, and whichever stem is used the distribution remains the same, since the stem leads to the same longitudinal channels. The free anastomosis on the surface of the cerebellum is due to the tendency of longitudinal anastomoses to take place within areas of the same function.

To summarise, the distribution of the blood is governed by the segmental pattern laid down before the advent of the intersegmental functions; and since the segmental vessels are end arteries in the sense that they do not enter into arterial anastomosis with arteries of different function, the establishment of the intersegmental circulation can only take place by the opening up of anastomoses between arteries of the same function. The direction of the circulation is thus determined, passing as a general rule from a system of higher function to a system of lower function developed from it. All the arteries of the body are laid down, therefore, in response to the functional needs of the body.

The first law of arterial distribution in the segmented embryo is: "All segmental arteries are end arteries and are distributed to areas of functional value." This must be modified for the intersegmental animal as follows: "All arteries which retain their segmental value are distributed to one area of function and are end arteries within that area; all intersegmental links take place between areas of the same function."

It follows from this that, "all arterial anastomoses in the body connect areas of similar function." "Areas of dissimilar function are connected by capillaries."

The Establishment of Commissural Circulation

A change which is quite as important to the animal is the development of commissural function. It takes place at the same time as the development of intersegmental function and impresses itself on the vascular system at the same time as it does on the nervous system. The sites at which commissures are formed are the sites of transverse anastomoses between the two sides of the body. The transverse anastomoses follow the same law as the longitudinal anastomoses; they take place between arteries of equal function. The median longitudinal anterior spinal artery is therefore both longitudinal—or intersegmental, and commissural. It takes place at the same time as the anterior commissures are being formed in the medullary tube. The main sensory decussations do not take place until the hindbrain is reached: and here where both the pyramidal and sensory decussations occur we find the basilar artery.

The Cause of the Vascular Distribution

The clue to the underlying cause of the vascular distribution is to be found in the fact that the sympathetic nervous system arises *in situ* in relation to the

organs which it supplies. The ectodermal origin of the whole of the peripheral nervous system can no longer be upheld. I do not intend to discuss here the question of the development of the peripheral nervous system; suffice it to say that the first rudiments of the sympathetic nervous system are found away from the ectoderm. Elliot Smith(9) says, "The observations of Professor J. P. Hill upon embryos of Echidna seem to suggest that in mammals these gustatory neuroblasts are derived from the entoderm." Dr Dart and I have found that certain of the gustatory neuroblasts arise from entoderm in both the elasmobranchs and the amphibians. The fact that the sympathetic nerves arise in common with the tissues they supply, means continuity of functional mechanisms from the beginning. It is the distribution of the sympathetic nervous system which governs the distribution of the blood vessels. John Hilton said that, "there is a disposition on the part of anatomists to think and to teach that nerves are distributed with designed accuracy, but that there is very little design in the distribution of the arteries." This was written half a century ago, and the disposition is still existent, for during the interval the anatomical world has been dominated by the mechanistic mind of His. Students understand full well the three germ layers in the coloured diagrams of text-books, but fail to recognise them in the embryo itself. Miss Sabin has proved beyond question that vessels are laid down before any mechanical forces are operative:

It is thus clear that at the stage of 12 somites, when the head of the embryo contains a complete aorta and a neural system of vessels which consists of a plexus of large vessels on the forebrain and midbrain, and a single channel on the hindbrain, there is no circulation through these vessels due to the beat of the heart.

In spite of that work, the mechanical postulates of Thoma still obscure the vital living processes which are going on in the body.

One might well ask, which vessels in the body are laid down in accordance with these postulates? For the postulates of Thoma are as follows:

1. An acceleration of the current leads to an enlargement of the lumen of the vessel, and a slowing of the current leads to its narrowing and final disappearance.

2. An increase in the blood-pressure is the cause of new formation of capillaries.

3. The growth in thickness of the vessel wall depends on the tension of the wall, which in turn is dependent upon the blood-pressure and the diameter of the vessel.

The first and third postulates can have nothing whatever to do with the distribution of the vessels for they refer to vessels already laid down. That the vessel wall may, and probably does, respond to mechanical forces cannot be disputed; but if Miss Sabin is right, and there is little doubt that she is, the aorta not only forms, but also increases, in surface and thickness before the heart beats. In two-headed monsters the distribution of the vessels is in

accord with function. Are the mechanical forces the same as in normal embryos? Further, are the mechanical forces the same in elasmobranch fishes as they are in human embryos? Some other explanation must be found for blood vascular distribution. I know of no evidence for the second postulate.

Those who regard the vascular distribution as being governed by these laws have not specified the particular arteries to which they refer. This omission makes it imperative to specify the arteries of the body which are laid down in response to functional stimuli. It must also be shown that the sympathetic nerves are uniformly distributed in the same areas to prove that the distribution of the muscles, nerves and arteries are laid down in the form of operative mechanisms. The establishment of the common origin of these structures must overthrow the three germ layer theory in so far as the layers are regarded as being the originators of structures which are separated from one another in the beginning and later join together.

The cells of the myotome can be regarded as mother cells capable of specialising into neuromuscular cells of two types. The differentiation of the two types of cells leads to a further specialisation of neural and muscle cells. In the case of the neural cells supplying striped muscle there is an absorption into the medullary tube in response to intersegmental needs; in the case of the neural cells supplying the smooth muscle of the arteries, the intercalation takes place at the periphery.

Some Functional Arteries of the Body

The distribution of the arteries to the forelimb have already been discussed in referring to the work of Woollard. The limb arteries belong to the same segments as those from which the nerves and muscles arise. The exact distribution of the sympathetic nerves to the vessels has not been fully established; it is probable, however, that the main axial trunk carries only those derived from the seventh segment, whereas the remaining nerves are distributed for a variable distance in the nerve trunks before being given off to the vessels.

The functional differentiation of the axial musculature reveals a similar functional differentiation of the arterial supply. Thus we find segmentally arranged vessels supplying both the epiaxial and hypaxial musculature. The deep cervical artery is the longitudinal vessel of the musculature, reinforced by segmental branches of the vertebral artery—the artery of the segmental reflex arc. The hypaxial artery is the ascending cervical in the neck region, and below that the internal mammary artery. The arterial supply of the diaphragm reveals a definite functional distribution. The diaphragm is derived from various sources. The ventro-lateral portion is derived from the ventral longitudinal muscular sheets which also give rise to the rectus abdominis and the depressors of the hyoid bone. The artery of supply of this portion is the internal mammary artery. It is the longitudinal artery in the area of the ventral longitudinal musculature. It can be taken together with the ascending cervical

artery; in fact, the internal mammary artery frequently springs from a higher level than usual and then arises in common with the ascending cervical from the thyroid axis artery. The arterial supply of the diaphragm is closely associated with the supply of the phrenic nerve, as pointed out by Hilton. Not only is the phrenic nerve supplied by the arteria comes nervi phrenici of the internal mammary, but also by the ascending cervical artery in its upper part. The variations in the origin of the internal mammary in no way alter its distribution.

The homologies of the branchial musculature are not settled. It has been classified by some as visceral; this is a matter of little importance as far as the arterial supply is concerned, but I cannot see the logic of classifying striped musculature supplied by effector neurones of somatic type as visceral. This question has been discussed by Dart (23) and Herrick (24) and it will here suffice to say that I regard the nucleus ambiguus as being serially homologous with the lateral groups of nerve cells supplying limb musculature; in other words, I regard the limb musculature as branchial in origin. I hope to be able at a later date to differentiate the arterial supply of the nucleus ambiguus from the rest of the radicular area of supply; until this has been done, the opinion that the limb musculature is branchial in origin can only be regarded as a working hypothesis founded on the serial character of the nerve supply.

The arterial supply of the branchial musculature is precise in its distribution. It is phylogenetically and ontogenetically constant. The blood supply of the masticatory apparatus is confined to the internal maxillary artery. John Hilton speaks of this artery as the "true masticatory" artery.

The internal maxillary artery supplies the teeth, the bones from which all the masticatory muscles arise, the muscles and nerves concerned with this function. It supplies both the old and the new mandibular joints. Some branches would, at first sight, appear to have no relation with mastication, such as the middle meningeal; some of these have been dealt with by Hilton. He omitted, however, to mention the branches which it sends to the ear. The membrana tympani, developed in part from the first branchial cleft, receives its supply from it; more interesting, however, in the light of the work of D. M. S. Watson on the evolution of the ear, is the fact that the incudo-malleolar joint is supplied by the same artery. The law of phylogenetic constancy here receives remarkable confirmation.

The external maxillary artery supplies the structures derived from the second arch. It supplies the Eustachian tube, the tonsil and the muscles derived from that arch. It is surely obvious then that there is a force more potent than mere mechanical convenience which shows a distribution, so explainable on phylogenetic grounds.

Hilton says:

Look at the arterial distribution of the blood to the soft palate, derived from several different sources. The soft palate is functionally connected with respiration, deglutition and mastication, so we ought to discover that its arteries

are derived from the trunks of those arteries which supply the face and lips, those which supply the masticatory apparatus, and the walls of the pharynx. Curiously enough, this soft palate receives six arteries, three on each side: one from the facial, the ascending palatine which seems to take a wandering course up to the soft palate; one from the ascending pharyngeal, and one from the internal maxillary, the "true" masticatory artery:...Here then is a simple piece of anatomy which shows the precision and purpose of the distribution of arteries which seem to be associated with three different functions: one in relation to respiration, associated with the muscles of the mouth derived from the facial artery; another in relation to deglutition, receiving its supply from the ascending pharyngeal artery; and a third in relation to mastication, receiving its supply from the masticatory artery.

But whereas difficulties may occur in unravelling the somatic muscular areas of the body, owing to the complex nature of the re-arrangement of the myotomic masses, the distribution of the vessels in accordance with function is more clearly indicated in dealing with the visceral and genito-urinary systems.

In the visceral tract the coeliac axis artery—the secretory artery—is distributed within the area of the secretory organs. The hepatic artery supplies the liver: the splenic artery supplies the pancreas, the spleen and the stomach in part; the gastric arteries supply the remainder of the stomach. The anasto-moses between these arteries of similar function is very free, but their terminal branches of distribution appear to be end arteries. The whole of the area supplied, with the exception of the spleen, is concerned with secretion. This area terminates roughly at the duodenal papilla where the supply is taken on by the superior mesenteric artery—the artery of absorption. The excretory portion of the gut is supplied by the inferior mesenteric artery, with the ex-ception of the area developed in association with the cloacal musculature. This area is supplied by the internal pudic artery, the precise nature of which has been referred to by Hilton.

The Functional Distribution of the Arteries of the Brain

It is here that we must turn to the work of Stopford and Beevor, the greater part of which I have personally confirmed. I have cited the precise nature of the blood supply of the various organs of the body as an introduction to the condition in the brain. Whilst in some respects the hypothesis put forward by me would appear to be clearly proved, in other respects difficulties arise. For example, the same artery which supplies the hypoglossal nucleus appears to supply also the pyramidal and other tracts; the same artery which supplies the radicular intercalated neurones supplies the lateral somatic nucleus or nucleus ambiguus; in the cerebrum the Rolandic area is supplied by two arteries, the middle and anterior cerebral; moreover, the blood supply of the cell bodies is different from that of the axone. These difficulties must be over-come before the hypothesis put forward can be set on a firm basis as a law. I feel, however, that the distribution is so regular as to warrant the opinion

that when more is known of the development of the brain tracts, it will be found that their arterial supply follows the same law as that of the other arteries of the body.

In a previous communication, I have referred to the importance of the vessels to the corpus striatum and optic thalamus, and have dealt with the precise nature of the blood supply of the brain. That work, together with the clear evidence produced by Stopford and Beevor, leaves little more to be said. It is necessary, however, to refer once more to the remarkable precision of the supply to the cortical areas of the cerebrum. It was satisfying to find that, after I had demarcated the areas of supply of the anterior and posterior cerebral arteries, these areas should so closely agree with those worked out by the methods of Elliot Smith and Brodmann. The posterior cerebral artery might well be named the artery of central vision to distinguish it from its companion the retinal artery or artery of peripheral vision, both of which tell of the method of vascular distribution.

I must here refer to the work of Elliot Smith on the forebrain. We owe to him the knowledge of the homologies of the olfactory and of the way the neopallium has been gradually formed from the interpolated region between the hippocampal and pyriform areas. The anterior cerebral artery is the great artery of the olfactory sense, including the hippocampus. The middle and posterior cerebral arteries are the arteries of the pyriform and neopallial areas. Now, since new developments of function arising out of pre-existing areas take place towards the periphery of existing vascular supplies, the greater development of the neopallium has taken place at the junctional area of the three cerebral arteries. This explains the fact that the last areas to be developed in the human brain have their counterpart in just those areas where the distribution was difficult to determine in the Orang:—in other words, the areas of junction between the three arteries. Now, since the last areas to form are those particularly concerned with the higher and more complex cerebral functions, it is not surprising that one or other of these arteries should have been found to be abnormal in the brains of the insane. Neither is it surprising that the areas which are peripheral, as far as the arterial supply is concerned, should be the first to be affected in chronic vascular lesions associated with senility.

GENERAL SUMMARY

1. The arteries of the brain of the Orang-utan closely resemble those of the human brain in both their distribution and variations.

2. The arteries of the hindbrain are perforating or segmental and longitudinal or intersegmental. The perforating arteries belong to three groups:

    (i) Anterior spinal or motor arteries:

    (ii) Lateral, radicular or intercalated arteries:

    (iii) Posterior spinal or rhombic arteries supplying the structures derived from the rhombic lip in the embryo.

3. The arteries of the brain are developed first segmentally, then intersegmentally and suprasegmentally.

The segmental arteries are functional in their distribution, the main somatic segmental artery being the artery of the reflex arc. The intersegmental and suprasegmental arteries arise in response to intersegmental, suprasegmental and commissural demands.

4. The arteries are phylogenetically and ontogenetically stable. The intersegmental arteries are formed by anastomoses between segmental arterial stems of equal functional value; so that the direction of the circulation is in the direction of differentation of function.

5. Variations of arteries are all explainable by the choice of stem artery which is used to form the commencement of the intersegmental arteries. The intersegmental arteries are thus variable to that extent: the final distribution is constant.

6. Areas of equal functional value tend to be joined by arterial anastomoses: areas of different functional value are joined by capillary anastomoses.
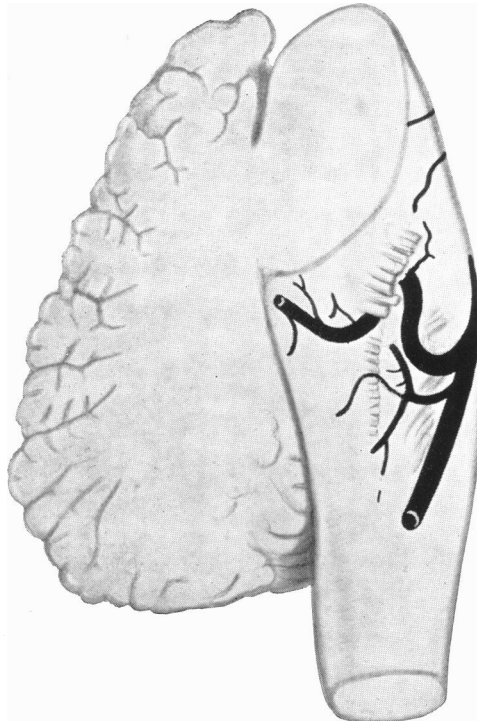
7. The arteries of the body are distributed to definite functional areas. The hypothesis is put forward that this is brought about by the fact that they arise in common with the sympathetic nerve elements which supply them, and that they are therefore distributed to respond more readily to nervous stimuli.
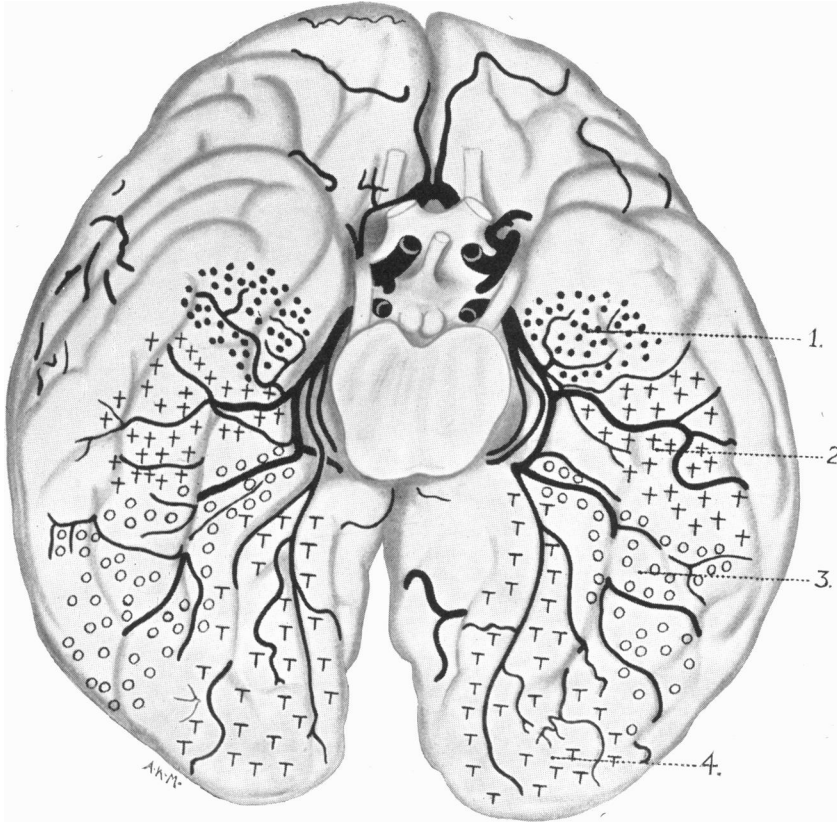
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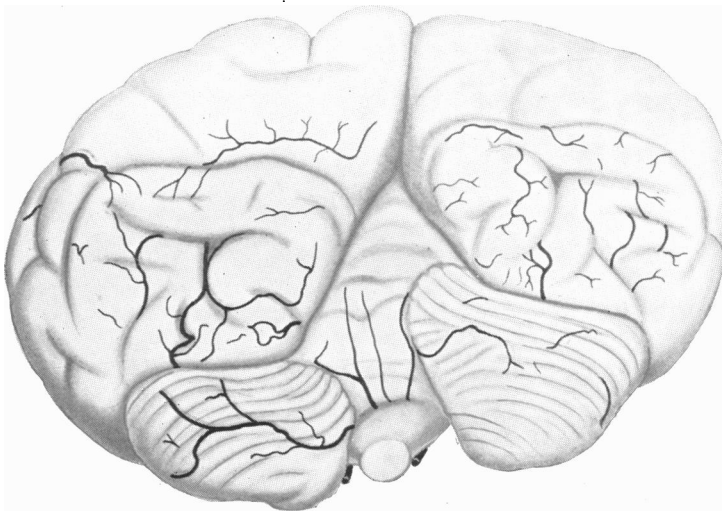
Fig. 1.

Fig. 3.

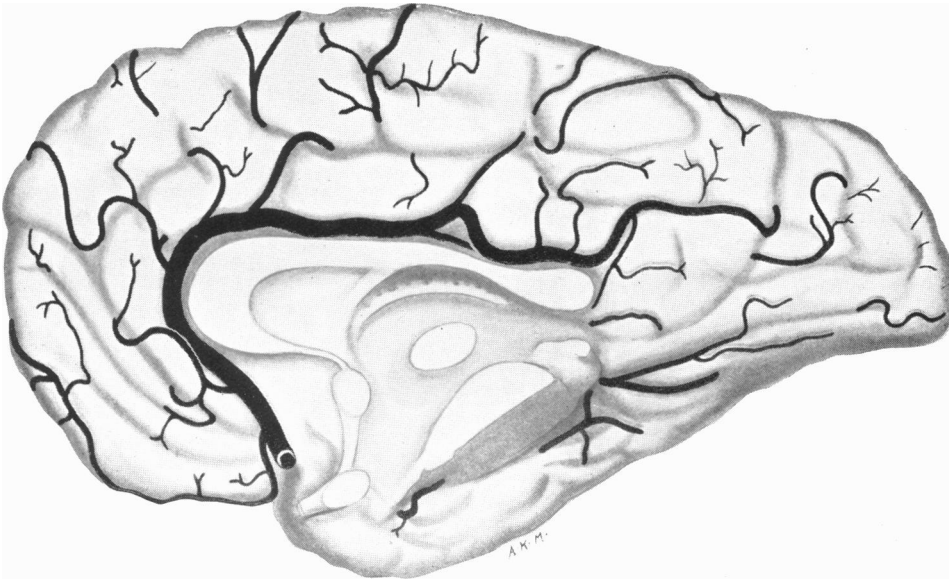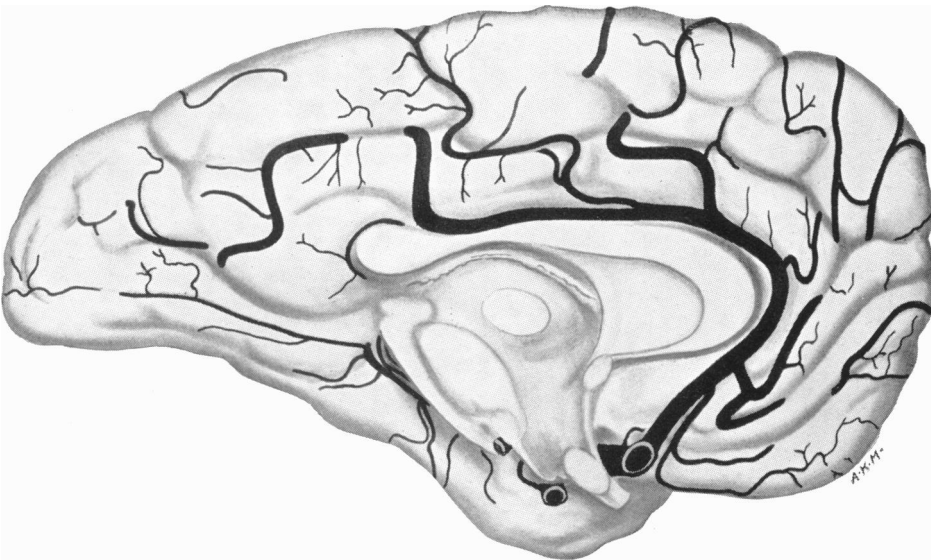SHELLSHEAR—THE ARTERIES OF THE BRAIN OF THE ORANG-UTAN

Fig. 4.

Fig. 6.

SHELLSHEAR—The Arteries of the Brain of the Orang-utan
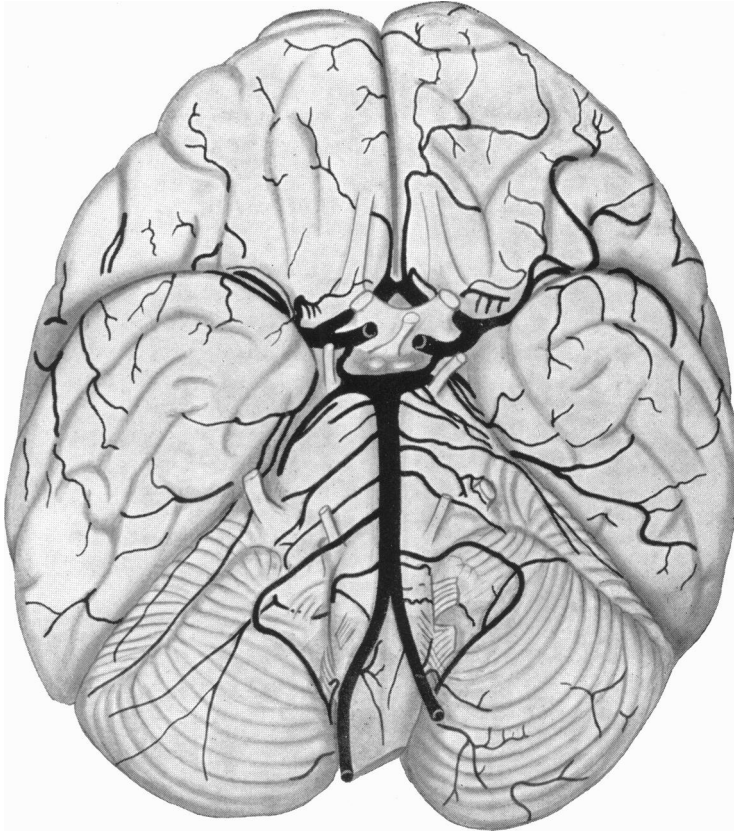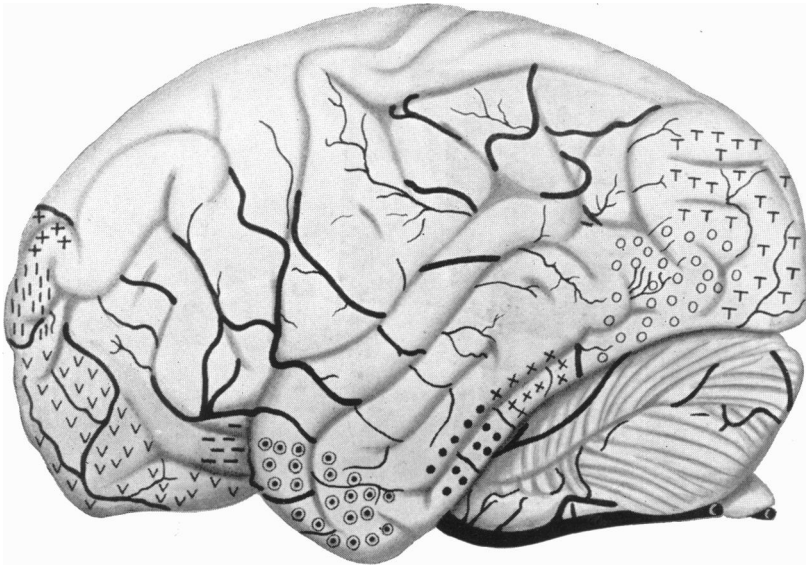
Fig. 9.

Fig. 10.

Fig. 11.

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DESCRIPTION OF FIGURES IN PLATES I–IV

Fig. 1. The arteries of the base of the brain in the Orang-utan.

Fig. 3. The course of the posterior inferior cerebellar artery in the Orang-utan.

Fig. 4. The distribution of the posterior cerebral artery in the Orang-utan. 1 and 2. Anterior temporal branches. 3. Posterior cerebral branches. 4. Calcarine branches to striate cortex.

Fig. 6. The distribution of the posterior cerebral artery in the area of the striate cortex.

Fig. 9. The areas of distribution of the right anterior and posterior cerebral arteries in the Orang.

Fig. 10. The distribution of the left anterior cerebral artery in the Orang.

Fig. 11. The distribution of the vessels on the surface of the left cerebral hemisphere in the Orang.