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THE DEVELOPMENT OF THE POSTERIOR CEREBRAL ARTERY*

By D. B. MOFFAT

Department of Anatomy, University College, Cardiff

There have been surprisingly few detailed accounts of the development of the arteries of the brain, and, in particular, the development of the posterior cerebral artery has never been the subject of a complete investigation, probably because this vessel develops comparatively late, at a stage when the foetus is too large to be studied by serial sections and reconstruction. The most comprehensive account is given by Padget (1948) who described and illustrated the cranial arteries in twenty-two human embryos, but even in this paper the development of the posterior cerebral artery is not dealt with adequately. The present investigation forms part of a complete survey of the embryology of the arteries of the brain and is based chiefly upon dissections of injected rat embryos, since by using this technique a relatively large number of specimens may be investigated without spending an excessive amount of time in making reconstructions.

MATERIAL AND METHODS

The course and distribution of the posterior cerebral artery in the adult blackhooded rat was investigated by the dissection of twenty animals which had been prepared by the injection of Neoprene latex 572 into the aorta followed by fixation in acidified 10% formalin. This part of the work was necessary because I have been unable to find elsewhere an adequate description of the cerebral arteries in the rat, although a general account has been given by Greene (1935).

The technique for the injection of rat embryos has been given in detail in previous papers (Moffat, 1957, 1959) and will not therefore be described here. The injected embryos were fixed in acidified formalin and were then dissected under a binocular dissecting microscope, using watchmaker's forceps and fine glass needles. In all, 196 embryos were studied, varying in size from a c.R. length of 1.3 mm. up to full-term foetuses. In addition, five human specimens of c.R. lengths 77, 102, 131, 134 and 145 mm. were injected with Neoprene latex 572 via an umbilical artery, and were dissected after fixation in acidified formalin.

RESULTS

The posterior cerebral artery and the related vessels in the adult rat

As in man, two large vessels supply the brain on each side, namely the internal carotid and the vertebral arteries. Each internal carotid reaches the base of the brain by passing to the lateral side of the hypophysis, and after sending some small

* This work formed part of a thesis which has been approved for the award of the degree of M.D. in the University of London.

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branches to the structures at the base of the brain, it gives off the posterior communicating artery, the anterior choroidal artery, a branch to the optic nerve, and the middle and anterior cerebral arteries. The posterior communicating artery runs caudally to join the posterior cerebral artery, which is a terminal branch of the basilar, thus completing the circle of Willis. Often, however, the posterior communicating artery is larger than the first part of the posterior cerebral artery, so that the latter may then be regarded as a branch of the internal carotid.

The anterior choroidal artery runs dorsally around the cerebral peduncle which it supplies, gives small branches to the region of the hippocampus and the diencephalon and ends by supplying the postero-inferior part of the choroid plexus of the lateral ventricle, anastomosing with the lateral posterior choroidal artery. The choroid plexus of the lateral ventricle consists of two parts. The main portion resembles that of man, but in the postero-inferior part of the ventricle there is an additional small rectangular tongue of tela choroidea with its own subsidiary choroid plexus which is supplied by the anterior choroidal artery. In one case, the anterior choroidal artery supplied, in addition to its usual branches, four large vessels which passed over the medial surface of the hemisphere lateral to the posterior cerebral artery, and replaced some of the branches of the latter vessel.

The terminal branches of the basilar artery are the anterior cerebellar and the posterior cerebral arteries. The anterior cerebellar artery is a large vessel which passes dorsally around the brainstem before dividing into anterior and posterior branches. The posterior cerebral artery passes dorsally into the cleft between the cerebral hemisphere and the brainstem. After a short course, it gives off from its caudal aspect, branches to the dorsal part of the mid-brain and a medial posterior choroidal artery which may be as large as the main continuation of the posterior cerebral artery. The medial posterior choroidal artery runs cranially, medial to and alongside the main posterior cerebral trunk, and gives numerous branches to the diencephalon including the pineal body. It then gives a branch which passes laterally to supply the medial side of the cerebral hemisphere where it reinforces the cranial end of the posterior cerebral artery, and finally it travels ventrally to supply the anterior part of the choroid plexuses of the third and lateral ventricles. anastomosing with the anterior cerebral artery. The next branch of the posterior cerebral artery is the lateral posterior choroidal artery which passes forwards and laterally to supply a large part of the choroid plexus of the lateral ventricle. Finally, the posterior cerebral artery continues its course on the medial side of the cerebral hemisphere, giving branches to the neighbouring regions of the cortex and eventually anastomosing with the branch of the medial posterior choroidal artery mentioned above.

Embryological findings

In embryos having a c.r. length below 4 mm. the arteries of the brain are still in a very primitive state and the brain is covered by a dense capillary plexus, except for wide midline non-vascular strips on its dorsal and ventral surfaces. Embryos, having a c.r. length between 4 and 6 mm., show several of the vessels which will later be of importance in the formation of the posterior cerebral artery, and these may be seen in Pl. 1, fig. 1, which depicts a 5.0 mm. embryos. The internal carotid artery passes to the lateral side of the developing hypophysis, and after giving off

some small branches it divides into large cranial and caudal rami. The cranial ramus passes dorsal to the optic stalk and gives off a number of branches, only one of which is of interest in the present account. This is the anterior choroidal artery, which at this stage is a small vessel running dorsally in the shallow groove between the diencephalon and the telencephalic vesicle, supplying branches to both these parts of the brain. Occasionally, the anterior choroidal artery takes origin from the proximal part of the caudal ramus. The caudal ramus passes towards the midbrain flexure, where it gives off a large vessel which very soon divides into diencephalic and mesencephalic arteries. The former passes cranially and divides into several branches, while the latter sweeps caudally over the lateral surface of the midbrain. The caudal ramus of the internal carotid artery then passes towards the midline where it joins the corresponding vessel of the other side. The combined trunk almost immediately divides again to form the right and left anterior cerebellar arteries, which correspond to the superior cerebellar arteries of man. At this stage, therefore, the anterior cerebellar arteries are supplied by the carotid system rather than by the basilar artery, which at this stage is still unformed (Moffat, 1957).

In embryos having a c.r. length of between 6 and 9 mm. various changes in the vascular pattern have taken place, and these can be seen in Pl. 1, figs. 2 and 3. The internal carotid still divides into caudal and cranial rami and each of these still follows a course similar to that seen in the previous stage. The anterior choroidal artery still passes into the groove between the telencephalic vesicle and the diencephalon, but the former has grown caudally to cover the artery so that only the most proximal part of this vessel is visible in Pl. 1, fig. 2. In Pl. 1, fig. 3, however, the right telencephalic vesicle has been removed, together with the distal part of the anterior choroidal artery, and the whole can be viewed from the medial side. The choroid plexus of the lateral ventricle, at this early stage of its development, is represented by two shallow invaginations of the medial wall of the telencephalic vesicle-a ventral smaller and a dorsal larger invagination. These are unfortunately not visible in Pl. 1, fig. 3, but the position of the ridge which separates the two ingrowths is marked by the position of the anterior choroidal artery which runs along it, giving small branches to the adjacent surfaces of the diencephalon and the telencephalon. The cranial end of the anterior choroidal artery breaks up into branches which anastomose with the end of the developing anterior cerebral artery.

The caudal ramus of the internal carotid artery gives off the common stem of origin of the mesencephalic and diencephalic arteries, but two new vessels have now appeared in this region. One of these, the posterior choroidal artery, arises from the common stem just proximal to the diencephalic artery, although occasionally it has a separate origin from the caudal ramus. In Pl. 1, fig. 2, it can be seen to disappear behind the expanding telencephalon. Pl. 1, fig. 3, however, shows how this vessel breaks up into branches on the lateral wall of the diencephalon, anastomosing with branches of the anterior choroidal artery. Occasionally, the posterior choroidal artery may take origin separately from the caudal ramus of the internal carotid artery. Arising from the common stem or from the mesencephalic artery itself is a small, but remarkably constant, vessel which will be referred to as the accessory mesencephalic artery. The diencephalic and mesencephalic arteries remain prominent, and Pl. 1, fig. 3, shows particularly well the manner in which these two vessels curve cranially and caudally respectively.

The next stage which is of interest in the present study occurs in embryos of a c.R. length between 9 and 12 mm. and is marked by the development of one or more large branches of the anterior choroidal artery which supply the medial wall of the posterior part of the telencephalic vesicle. Pl. 1, fig. 4, shows the vessels lying in relation to the medial wall of the right telencephalic vesicle and is taken from an 11.7 mm. embryo, while Pl. 2, fig. 5, represents both telencephalic vesicles of a 12.0 mm. embryo. The diencephalic and posterior choroidal arteries both still end by ramifying on the side wall of the diencephalon and are therefore not seen in these specimens. The anterior choroidal artery is prominent and it gives a large branch which passes dorsally, dips into the shallow choroidal fissure, and then breaks up on the wall of the telencephalic vesicle. This branch may become larger than the continuation of its parent vessel (Pl. 1, fig. 4). Often, two or more branches are present in this situation. The branches of the anterior choroidal artery form a rather dense plexus which is beginning to show signs of a longitudinal arrangement, and it is in this plexus that the distal part of the posterior cerebral artery will develop. As well as the main choroidal fissure there is still a much shorter, more ventral fissure which will give rise to the accessory choroid plexus in the adult. The main stem of the anterior choroidal artery still runs along the ridge between the two fissures and gives branches to each. Its terminal branches communicate with the terminal branches of the anterior cerebral artery, which supply the cranial extremity of the choroidal fissure. Numerous branches are also given off to the region of the diencephalic-telencephalic junction.

In embryos having a c.r. length of over 12 mm., the anterior choroidal artery loses its large telencephalic branch or branches, the longitudinal plexus on the medial wall of the telencephalon acquiring a new vessel of supply derived from the posterior choroidal artery and another, shortly afterwards, from the diencephalic artery. Pl. 2, fig. 6, shows the medial wall of the right telencephalic vesicle in a 14 mm. embryo, in which the posterior choroidal artery has been stripped from the side of the diencephalon and left attached to the telencephalon. The anterior choroidal artery still gives a few very small branches to the longitudinal plexus on the medial wall, but the main vessel of supply to this plexus is now a new laterally directed branch of the posterior choroidal artery which crosses the narrow space between the diencephalon and the telencephalon. The distal part of the posterior choroidal artery still gives some small diencephalic branches but ends by anastomosing with the cranial end of the anterior choroidal and with the descending terminal branch of the anterior cerebral artery and gives a number of small, laterally directed branches into the choroidal fissure. Part of the plexus on the medial side of the telencephalon now has a short segment of a single vessel running through it, and this will form the terminal portion of the posterior cerebral artery. Between this vessel and the anterior cerebral artery the plexus shows a particularly dense area, and this marks the point where a small branch of the diencephalic artery runs laterally to join the plexus. The choroidal fissure cannot be seen in the photograph since at this stage it is no longer a wide groove into which dip the large vessels of the telencephalon, but is now reduced to a narrow slit through which only very small vessels can pass.

These vessels are derived from the anterior cerebral, the posterior choroidal and the anterior choroidal arteries. The terminal branches of the anterior choroidal artery now supply only the posterior part of the choroidal fissure and they no longer anastomose directly with the anterior cerebral artery.

A slightly later stage is seen in Pl. 2, fig. 7, which shows the medial side of the right telencephalic vesicle in a 21.8 mm. embryo. The telencephalic branch of the posterior choroidal artery is now large and forms part of the posterior cerebral artery, which continues on the medial wall of the telencephalon. Eventually, this telencephalic branch will become larger than the continuation of the posterior choroidal artery so that the latter vessel, in adult terminology, will become a branch of the posterior cerebral artery, and will, in fact, form the lateral posterior choroidal artery. The diencephalic artery is large, and after giving branches to the



Text-fig. 1. Diagram of the medial surface of the right cerebral hemisphere to show the components of the posterior cerebral artery. A segment of the diencephalic artery has been removed. Horizontal hatching: common trunk of origin of brainstem arteries; oblique hatching: posterior choroidal artery; heavy stipple: diencephalic artery; light stipple: lateral branch of posterior choroidal artery; small crosses: new vessel from plexus on medial wall of telencephalic vesicle; solid black: mesencephalic artery. AC, anterior choroidal artery; PC, main stem of posterior cerebral artery; MPC, adult medial posterior choroidal artery; LPC, adult lateral posterior choroidal artery.

diencephalon, it gives off its telencephalic branch and then passes ventrally to anastomose with one of the terminal branches of the anterior cerebral artery. In Pl. 2, fig. 7, the diencephalic artery has been divided so that only its telencephalic branch (which reinforces the cranial end of the posterior cerebral artery) and its terminal descending portion are visible and the latter, in this photograph, appears to be a continuation of the posterior cerebral. The diencephalic artery persists into adult life as the medial posterior choroidal artery which supplies the choroid plexus

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of the third and lateral ventricles, and sends a laterally directed branch to reinforce the posterior cerebral artery. At this stage, therefore, the choroid plexus is supplied by the anterior cerebral, the diencephalic, the posterior choroidal and the anterior choroidal arteries, from before backwards, and this arrangement persists into adult life.

To sum up, the definitive posterior cerebral artery (Text-fig. 1) is formed proximally from part of the caudal ramus of the internal carotid artery followed by the elongated common trunk of the mesencephalic, diencephalic and posterior choroidal arteries. The intermediate portion is formed by the proximal portion of the original posterior choroidal artery, the distal portion of this vessel becoming the adult lateral posterior choroidal artery. The distal portion is formed by the lateral branch of the original posterior choroidal artery, together with a vessel which develops from the plexus on the medial wall of the telencephalic vesicle. The diencephalic artery forms the medial posterior choroidal branch of the posterior cerebral artery while the mesencephalic and accessory mesencephalic arteries form its midbrain branches.

The five human specimens showed many resemblances to the rat embryos, and in three of these, namely those of 77, 102 and 134 mm., the arrangement of vessels was very similar to that shown in Pl. 2, fig. 7. The vessel which was recognizable as the posterior cerebral artery gave off mesencephalic branches, a large diencephalic branch, a choroidal branch (the lateral posterior choroidal artery) and finally ended by supplying the medial aspect of the posterior pole of the brain. The diencephalic branch supplied the brain stem and ended by bridging the gap between diencephalon and telencephalon and supplying the medial wall of the latter. It also supplied a choroidal branch in the 72 and 102 mm. embryos but this could not be traced in the 134 mm. specimen, possibly because the injection was incomplete. At 131 and 145 mm., the diencephalic artery no longer supplied the telencephalon but ended as a choroidal branch. The loss of the telencephalic branch appears to be due to the enormous growth in a caudal direction of this part of the brain.

DISCUSSION

The adult human posterior cerebral artery bears a fairly close resemblance to the corresponding artery in the rat, although there are a few points of difference. In the human, in the 'normal' circle of Willis, the posterior cerebral artery arises from the basilar artery and is twice the size of the posterior communicating artery (Padget, 1945), whereas in the rat the vessel usually receives its blood from the carotid and basilar arteries in approximately equal proportions. In the rat, the medial posterior choroidal artery (i.e. the vessel derived from the diencephalic artery) supplies a branch to the medial wall of the cerebral artery. A rather similar state of affairs occurs in the rabbit, in which the posterior cerebral artery gives off a large branch which supplies mesencephalic and diencephalic derivatives and which ends by giving a few branches to the medial side of the cerebral hemisphere (Nilges, 1944).

The anterior choroidal artery in both the rat and the human embryo appears at an early stage and in both species it gives branches to the diencephalon before passing to the choroidal fissure. It is described, or illustrated, by His (1904), Mall (1904), de Vriese (1905), Evans (1912), Thyng (1914) and Padget (1948, 1956). There are, however, no previous references to its importance in providing the main blood supply to the caudal pole of the telencephalic vesicle in the early stages of development, although His notes that the choroidal fissure is at first very wide and that the vessels of the choroid plexus are at first only a part of the general network on the medial wall of the telencephalic vesicle.

Previous accounts of the development of the posterior cerebral artery have been vague and inconclusive. Mall states that it is formed from 'all of the branches together arising from the circle of Willis between the third and fourth nerves behind and the origin of the middle cerebral in front...'. Thyng, in his plate 2, shows a loop passing from the caudal ramus of the internal carotid from which arise four branches to the midbrain and diencephalon, and this is labelled the posterior cerebral artery. Bremer (1943) discusses Thyng's embryo and suggests that these multiple branches become the posterior cerebral artery by the absorption of all but one of the capillary roots by which they arise. Padget (1948) notes that the posterior cerebral artery could not be definitely identified in her series of human embryos (from 3 mm. up to 43 mm.), but states that its distal part emerges 'by means of an elaboration of one of the large diencephalic or mesencephalic branches of the posterior communicating artery...'. In a later paper, however (Padget, 1956), she states that 'the prominent (dorsal) diencephalic artery of the embryo, from which the posterior cerebral artery arises, is represented by at least one adult posterior choroid artery'.

The findings in the five human specimens described above suggest that the development of the posterior cerebral artery is similar in both rat and man, and if this be accepted, many of the anomalies of the vessel in the human adult can be explained. The persistence of the embryonic condition in which the posterior cerebral artery is fed mainly by the caudal ramus of the internal carotid artery is of course well known. The posterior cerebral may occasionally be replaced by a branch of the anterior choroidal artery (Adachi, 1928; von Mitterwallner, 1955). Since the anterior choroidal forms the main blood supply to the occipital pole of the brain at one stage of development, it is easy to see how it may form the stem of the posterior cerebral artery if the telencephalic branch of the embryonic posterior choroidal artery does not take over the supply of the hemisphere. A double posterior cerebral artery is met with infrequently (Windle, 1888; Longo, 1905; Gordon-Shaw, 1910; von Mitterwallner, 1955; Alpers, Berry & Paddison, 1959). This is surprising, since the condition is presumably due to one of the brainstem vessels arising independently instead of from the common trunk and this is often seen in rat embryos, and in the human embryos illustrated in Padget's paper. The close association between the anterior and posterior choroidal arteries in the embryo explains the important anastomoses which link these two vessels in the adult which have been described by numerous authors.

The development of the posterior cerebral artery in the rat is an interesting example of the Law of Recapitulation. The present investigation has shown that the blood supply of the caudal part of the telencephalon is derived first from a branch of the cranial ramus of the internal carotid, then from the posterior choroidal artery. The latter is later reinforced by the diencephalic artery and finally, a branch of the

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basilar artery may form the stem of origin of the posterior cerebral artery. In this way, it can be seen that as the telencephalon grows caudally, it receives its blood supply from vessels which take their origin from progressively more caudal sources. Abbie (1934) has shown that a similar caudal migration of the origin of the posterior cerebral artery has occurred during the phylogenetic history of this vessel in response to the backward growth of the telencephalon. In reptiles, the posterior cerebral artery takes its origin from the cranial ramus of the internal carotid, and as the evolutionary scale is ascended, the artery utilizes other, more posterior parts of the primitive network to form its stem of origin until, in the primates, it has consolidated its most posterior stem of origin in the 'anterior midbrain channels'. A similar caudal displacement of the origin of the posterior cerebral artery was noted by Hoffmann (1900), who, in fact, gave four possible positions for the origin of the vessel in different species.

SUMMARY

1. The development of the posterior cerebral artery has been studied in 196 injected rat embryos.

2. The arterial supply to the medial aspect of the posterior part of the telencephalon is at first provided by one or more large branches of the anterior choroidal artery.

3. At a later stage the posterior choroidal artery gives off a large lateral branch which bridges the gap between the diencephalon and telencephalic vesicle and takes over the supply of the plexus on the medial wall of the vesicle from the anterior choroidal artery.

4. The distal portion of the posterior cerebral artery develops as a longitudinal vessel derived from this plexus and it is reinforced at its cranial end by a laterally directed branch of the diencephalic artery.

5. The adult posterior cerebral artery is thus derived from a part of the posterior communicating artery, the common stem of origin of the posterior choroidal, diencephalic and mesencephalic arteries, the proximal part of the posterior choroidal artery, its lateral branch, and a new vessel which develops in the plexus on the medial wall of the telencephalic vesicle.

6. The distal part of the embryonic posterior choroidal artery persists as the adult lateral posterior choroidal artery, while the diencephalic artery forms the medial posterior choroidal artery.

I should like to express my thanks to Mr A. Welch who is responsible for the photography, and to Miss Valerie Mahoney for technical assistance and for drawing the diagram.

I should also like to acknowledge here the help, advice and encouragement which I received during the course of this work from the late Prof. J. S. Baxter.

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EXPLANATION OF PLATES

PLATE 1

- Fig. 1. Right side of the cranial region of a 5 mm. embryo (\times 24). The cranial ramus of the internal carotid passes dorsal to the optic stalk, which has been divided. The caudal ramus passes ventral to the midbrain flexure where it gives off by a common trunk the diencephalic and mesencephalic arteries.
- Fig. 2. Left side of the cranial region of a 6.9 mm. embryo ($\times 17$). The plexiform middle cerebral artery is developing on the side of the telencephalic vesicle, which hides all but the most proximal portion of the anterior choroidal artery. At the midbrain flexure, the caudal ramus of the internal carotid artery gives off a common trunk which divides into posterior choroidal, diencephalic and mesencephalic arteries.
- Fig. 3. Right side of the mid- and fore-brain of a 7.0 mm. embryo ($\times 17$). The right telencephalic vesicle has been detached and turned over to display its medial surface with the anterior choroidal (arrowed) and anterior cerebral arteries.
- Fig. 4. Medial surface of the right telencephalic vesicle of an 11-7 mm. embryo ($\times 23$). The anterior choroidal artery arises from the cranial ramus of the internal carotid artery and gives off a large branch which supplies a longitudinal plexus on the medial wall of the hemisphere.

PLATE 2

Fig. 5. The medial surfaces of the right and left cerebral hemispheres of a 12.0 mm. embryo ($\times 32$). The caudal poles are towards the centre of the photograph. The anterior cerebral artery is a single midline vessel for most of its course, and has remained adherent to the left hemisphere. On both sides it gives a descending branch to the cranial end of the choroidal fissure. The anterior choroidal artery also supplies the fissure, but its largest branch on each side supplies the plexus on the medial wall of the hemisphere.

- Fig. 6. Medial surface of the right hemisphere of a 14.0 mm. embryo (×23). The posterior choroidal artery has been removed from the side of the diencephalon and remains adherent to the specimen. Its lateral branch (arrowed) has now taken over the supply of the plexus on the medial wall of the hemisphere in which part of the posterior cerebral artery can be seen.
- Fig. 7. Medial surface of the right cerebral hemisphere of a 21.8 mm. embryo (×18). The choroid plexus is supplied, from before backwards, by the anterior cerebral, diencephalic, posterior choroidal and anterior choroidal arteries. The lateral branch of the posterior choroidal artery (slightly out of focus) now forms part of the posterior cerebral artery which continues on the medial wall of the hemisphere and which is reinforced at its cranial end by a branch of the diencephalic artery.



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