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Interhemispheric pathways in the absence of a corpus callosum

An experimental study of commissural connexions in the marsupial phalanger

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INTRODUCTION

Although earlier workers such as Huxley (1906) recognized that the corpus callosum represents 'the greatest leap anywhere made by Nature in her brain work', until the late 1950s our understanding of the functions of this structure could be summed up in the words of Stensen (1669): 'certes, le corps calleux nous est si inconnu, que pour peu qu'on ayt d'esprit, on en peut dire tout ce qu'on veut'. Stensen's contemporary, William Harvey, considered that 'corpus callosum superior pars ventriculorum sustinet cerebrum' (Whitteridge, 1964) and identical sentiments were being expressed as late as 1951 by Lashley (Sperry, 1964). In the last 10–12 years, as a consequence of the work of Myers (1962*a*, *b*) and Sperry (1961) and their collaborators, the functional significance of the commissural fibres linking the two hemispheres has slowly been elucidated. It is now obvious that fibres joining the two hemispheres, particularly by way of the corpus callosum, but also *via* the anterior commissure and possibly by other routes as well, play a major role in the interhemispheric transfer of learning based upon sensory cues.

It is apparent, however, that the manner of connexion between the two cerebral cortices is by no means a simple point-to-point one. Some cortical areas may send fibres merely to their fellows of the opposite side, others may send fibres to (or receive fibres from) two quite divergent fields, while still others may be devoid of commissural connexions altogether (Myers, 1962*a*; Ebner & Myers, 1965; Garey, Jones & Powell, 1968; Diamond, Jones & Powell, 1968; Pandya & Vignolo, 1969; Jones & Powell, 1968, 1969). Considerable interest attaches to the last pattern of connexions because in the primary somatic (Pandya & Vignolo, 1969; Jones & Powell, 1968, 1969) and visual (Choudhury, Whitteridge & Wilson, 1965; Berlucchi, Gazzaniga & Rizzolati, 1967; Hubel & Wiesel, 1967; Garey *et al.* 1968; Hughes & Wilson, 1969) sensory areas of the cortex, parts representing the distal, freer parts of the limbs and the periphery of the visual field are not commissurally connected. On the other hand, those parts representing portions of the body in and adjacent to the midline and the midline portion of the visual field are heavily connected. These connexions presumably ensure the fusion and overlap of sensory messages emanating from midline portions of a bilaterally symmetrical receptor apparatus. The reason for the lack of connexions between the representations of the hands and feet and of the periphery of the visual field is obscure. Perhaps it plays a role in ensuring that confusion does not rise between sensory messages arriving from symmetrical but, in a sense, independent parts of the receptor apparatus.

The corpus callosum is a unique feature of the Eutherian brain, for it is not found in the monotremes, marsupials or other vertebrates. Despite this, it is obvious that the two cerebral hemispheres of the Prototherian and Metatherian brains are joined by commissural fibres passing by way of the anterior commissure (Abbie, 1939; Ebner, 1969). In the Polyprotodont marsupial, the opossum, the connexions joining the two cerebral cortices seem to conform to a more generalized pattern than that in the Eutheria. That is, there are no parts of the cortex devoid of commissural connexions (Ebner, 1967). There seems to be a case for investigating these connexions in a more advanced Diprotodont marsupial such as the phalanger (*Trichosurus vulpecula*), for a number of reasons: first, although this animal presents the primitive feature of an absent corpus callosum, certain parts of its nervous system, particularly the central connexions of the visual apparatus (Goldby, 1941; Hayhow, 1967), appear to conform to a more highly developed pattern – even approximating to that of the higher primates (Hayhow, 1967); second, as a Diprotodont, it has developed an additional neocortical commissure – the fasciculus aberrans – which is confined to this suborder of mammals (Elliot Smith, 1902; Abbie, 1939). The fasciculus aberrans bypasses the anterior commissure and apparently represents an interhemispheric pathway which is an alternative to the corpus callosum of the Eutheria.

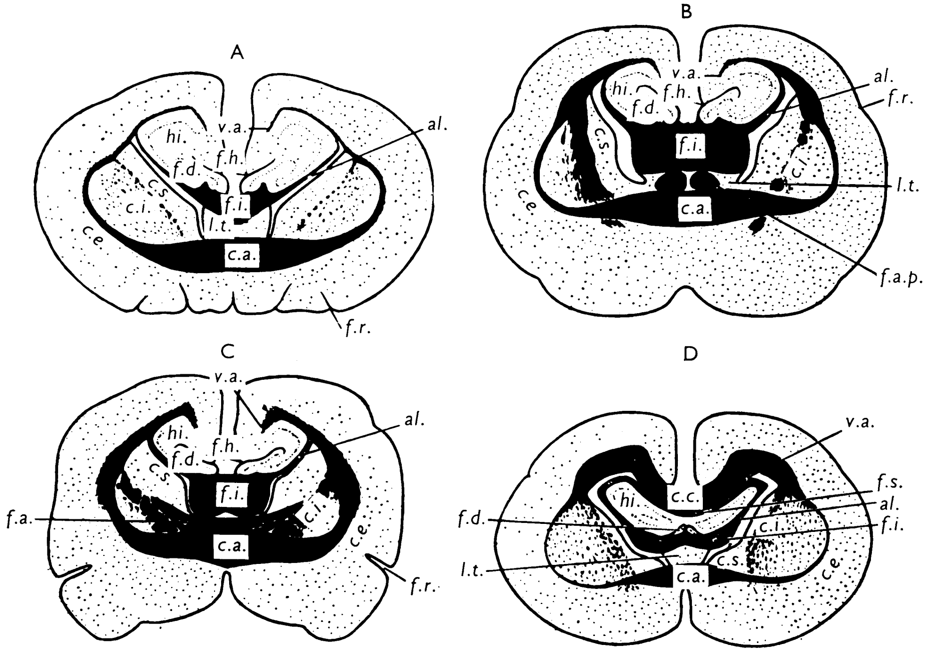
MATERIALS AND METHODS

This study is based upon experiments carried out in thirteen adult specimens of *T. vulpecula*. As the animals are extremely resistant to barbiturate anaesthesia, they were anaesthetized with ethyl chloride and maintained on an ether–oxygen mixture administered *via* an endotracheal tube. In five animals, the hippocampal and anterior commissures and the fasciculus aberrans were divided by means of a fine suction-aspirator; in order to visualize the commissures it was necessary to retract one hemisphere quite strongly, and the commissures were cut as close as possible to this hemisphere. The opposite hemisphere (used for the investigation) was not exposed. In two animals, the anterior commissure was not completely divided, and in one, only the fasciculus aberrans and the hippocampal commissure were cut. In two others, a hemidecortication was done, and in the remaining four, small lesions were placed in various localized areas of the cerebral cortex, particularly in the striate (Packer, 1941) and sensory-motor (Adey & Kerr, 1954) areas. The animals were killed 4–8 days postoperatively by perfusion with saline and formalin and the brains were cut on a freezing microtome at 25 μm. Alternate series of sections were stained by the Nauta & Gygax (1954) and Fink & Heimer (1967) techniques. In most cases, a further series was stained with thionin to show the main architectonic fields of the cerebral cortex. The distribution of degeneration was plotted on projection drawings of the sections and reconstructed on standard drawings of a brain prepared from photographs.

RESULTS

The forebrain commissures of the phalanger

Three main commissural pathways are visible in the forebrain of this animal (Fig. 1). In the dorsal aspect of the septum, the two fimbriae of the hippocampal formations come together and decussate as the hippocampal commissure. In the more ventral aspect of the septum lies the anterior commissure, the fibres of which are mainly continuous with those in the external capsule. Immediately applied to the



ABBREVIATIONS

Ac, c.a.	anterior commissure	*Py*	pyriform cortex
Am	amygdala	*Rs*	rhinal sulcus
C	cingulate cortex	*S*	striate cortex
D	dentate gyrus	*SI*	first somatic sensory area
E	entorhinal cortex	*SII*	second somatic sensory area
Fa, f.a.	fasciculus aberrans	*St*	striatum
H	hippocampus	*T*	temporal cortex
Ps	peristriate cortex	*Tr*	transitional cortex

Fig. 1. The various forms of forebrain commissures found in the mammalia. Reproduced with permission from Abbie (1939). A: a monotreme showing the small hippocampal (*f.i.*) and anterior commissures (*c.a.*) and the relatively small internal capsule (*c.i.*). B: a Polyprotodont marsupial in which the appearances are the same as in A, but in which the internal capsule is proportionately much larger. C: a Diprotodont marsupial showing the additional commissure, the fasciculus aberrans (*f.a.*), passing from the internal capsule through the dorsal part of the anterior commissure. D: a Eutherian mammal showing the corpus callosum (*c.c.*) passing dorsal to the hippocampal formation (*hi*). The anterior commissure and the external capsule (*c.e.*), with which it is continuous, are much reduced in size. According to Abbie, the corpus callosum is formed by fibres from the ventricular angle (*v.a.*) breaking through the opposed subicular cortex, dorsal to the hippocampal fissure (*f.h.*).

dorsal aspect of the anterior commissure proper is the fasciculus aberrans, whose contributing fibres appear to be mainly continuous with the internal capsule; it thus forms a shorter route for fibres passing between the more dorsal aspects of the hemispheres.

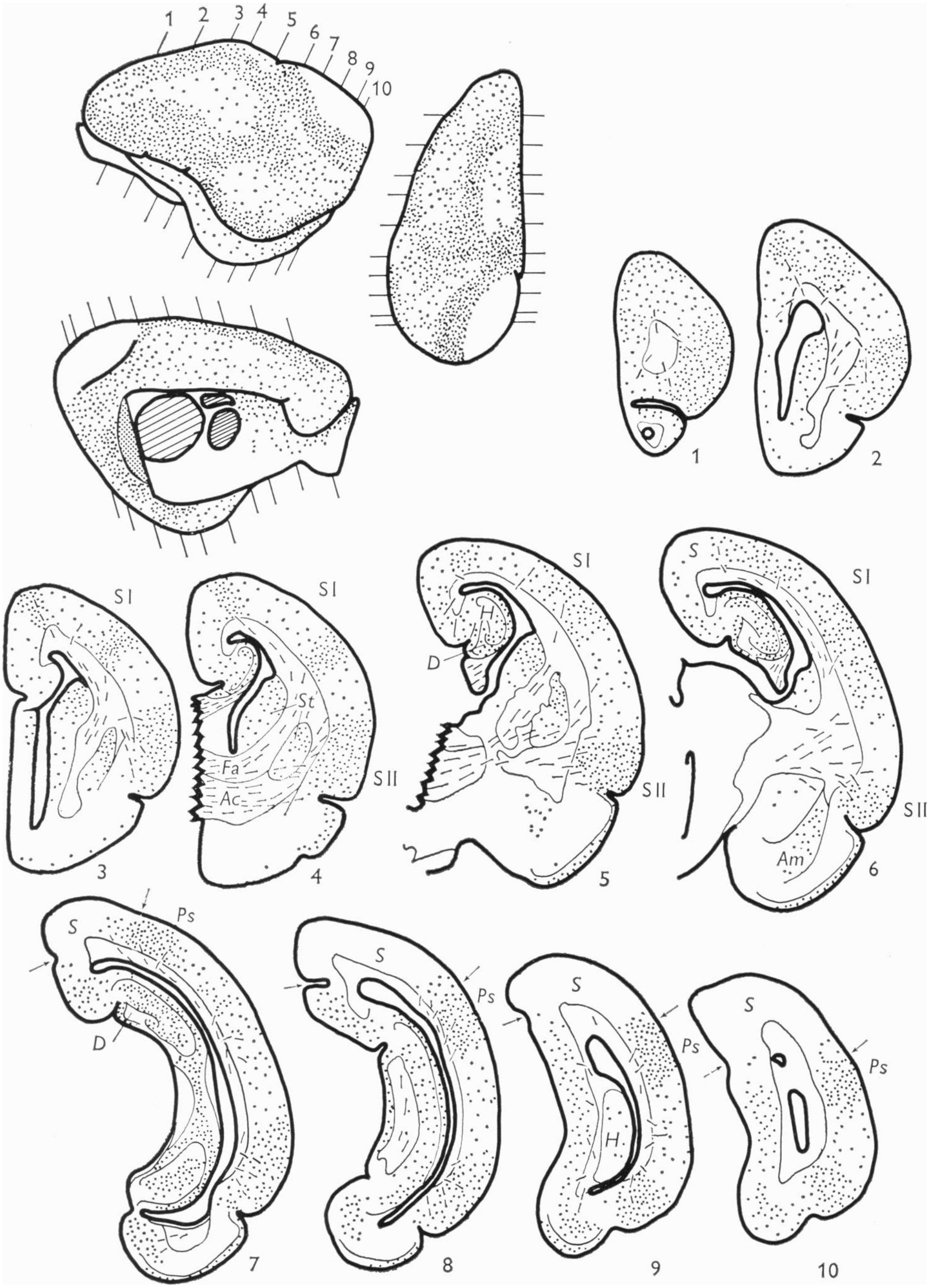


Fig. 2

The total commissural projection

This may be described by reference to Expt. 6 (Fig. 2) in which the pattern of degeneration is representative of the five experiments in which all the commissures were divided. The pattern of degeneration in the neocortex is identical in the two brains with virtually complete hemidecortications. Degenerating fibres pass laterally from the fasciculus aberrans and anterior commissure through the internal and external capsules respectively, and enter the deep layers of the cerebral cortex with varying degrees of obliquity. Terminal degeneration is found in all cortical layers but is particularly dense in layers I and II and in the adjoining parts of layers III and IV (Fig. 5).

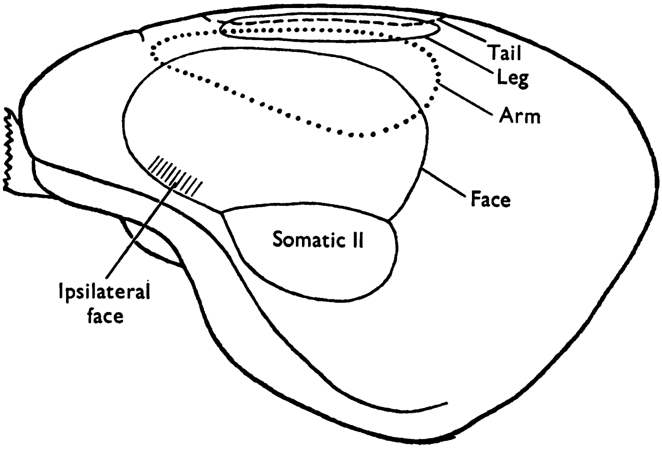


Fig. 3. The evoked potential map of Adey & Kerr (1954) showing the extent of the first and second somatic sensory areas of the phalanger. Note the extensive overlap in the representation of the body form in SI. This area is probably co-extensive with the motor cortex. Reproduced with permission of the publishers.

With the exception of most of the striate area, all areas of the cerebral cortex receive degenerating commissural fibres. The striate area has a distinctive cytoarchitecture (Fig. 7) with a particularly prominent internal granular layer which may be recognized even in Nauta-stained sections. The narrow peristriate area which bounds it rostrally, laterally and caudally lacks the prominent internal granular layer, and consists of less densely packed cells; the deeper layers show a very clear-cut hori-

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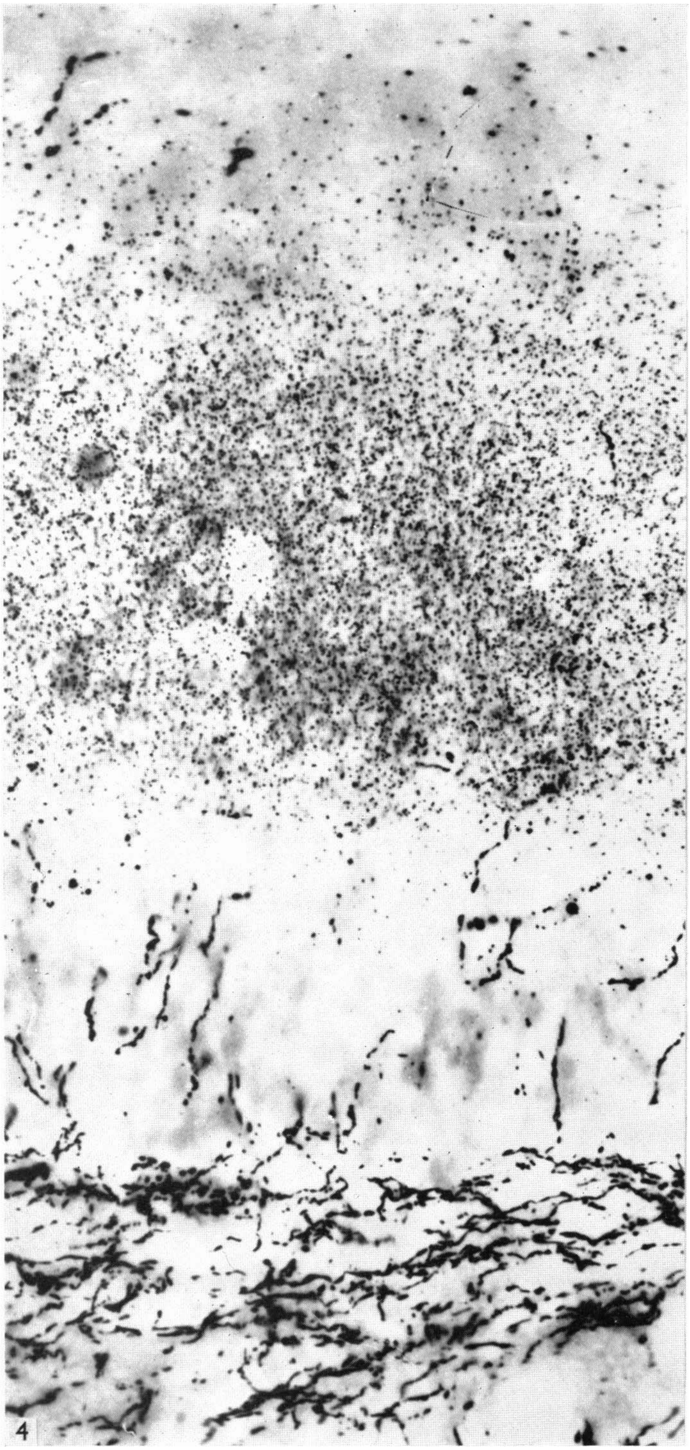
Fig. 2. The distribution of degenerating commissural fibres in Expt. 6 in which the forebrain commissures were completely divided. At top left, the extent of the degeneration in the cerebral cortex has been reconstructed on lateral, medial and dorsal views of the hemisphere. Note the absence of degeneration in the greater part of the striate cortex (S) at the caudal aspect of the hemisphere and the relatively bare areas in the forelimb and hindlimb areas of the first (SI) and second (SII) somatic sensory areas (cf. Fig. 3). The sections are taken from the levels indicated and, as well as showing the distribution and relative intensity of degeneration in the various parts of the cortex, also show the commissural degeneration in the hippocampus (H) and dentate gyrus (*D*), in the striatum (*St*) and in the amygdala (*Am*). The lesion is indicated by the irregular line in sections 4 and 5. In this and subsequent diagrams, terminal degeneration is represented by dots and degenerating fibres by short lines.



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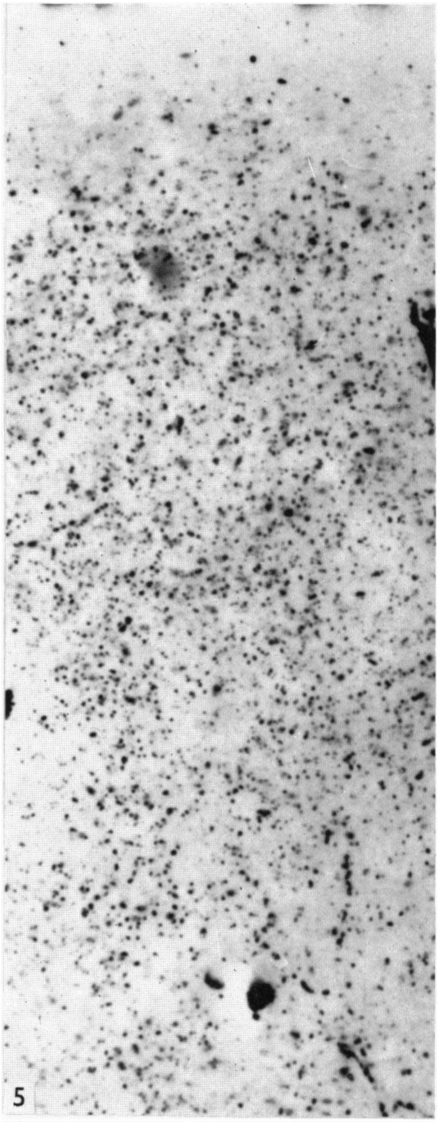

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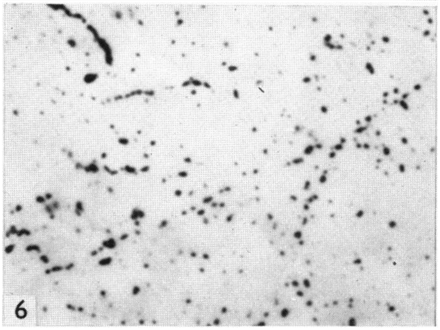

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zontal lamination. The boundary between the two areas is sharp and easily recognized. Most of the striate area is free of degeneration. However, along the clearly defined boundary between the striate and the peristriate areas there is a band of dense degeneration, which chiefly occupies the peristriate area and almost encircles the striate area, being found on the lateral and caudal but not the medial aspects of the hemisphere. However, from a comparison with Nissl-stained sections, and even from the Nauta sections themselves, it is clear that the degeneration extends for 1–2 mm into the peripheral part of the striate area itself, but only on the dorsolateral surface of the brain. On the medial surface, the degeneration in the adjoining cingulate cortex stops abruptly at its boundary with the striate area. In the peristriate area, the degeneration is heaviest in the part adjacent to the striate area and it becomes less dense on moving laterally and into the 'temporal' cortex. However, on the lateral aspect of the brain at the extreme lower edge of the temporal cortex there is a small focus of intense degeneration just above the caudal part of the rhinal sulcus. Further reference will be made to this focus later.

Degeneration fills the cortex outside the striate area but there are three small areas on the dorsolateral and lateral aspects of the hemisphere in which it is much less intense than elsewhere. A comparison with Nissl sections indicates that two of these areas are within the granular cortex typical of the first somatic sensory area (SI) and the third is in the cortex more typical of the second somatic sensory area (SII). These areas are shown (Fig. 3) in the evoked potential map of Adey & Kerr (1954), and further comparison with this map suggests that these areas of less dense degeneration are in the forelimb and hindlimb regions of SI and in the common limb region of SII. Degeneration is moderately heavy in all other parts of the somatic cortex, especially in the relatively large tail area of SI along the dorsal margin of the hemisphere and in the face areas of SI and SII occupying most of the middle one-third of the lateral surface of the hemisphere. Elsewhere, degeneration extends forwards to the rostral pole of the hemisphere; caudally it fills the temporal cortex situated below and behind SII and separating SII from the peristriate area, and medially it fills the cingulate cortex lying in front of the striate area and medial to the tail area of SI.

Fine degenerating fibres and terminal degeneration are found throughout most of the caudate nucleus and putamen (Fig. 6). Although the terminal degeneration is maximal in the dorsolateral aspects of the head of the caudate nucleus and of the putamen, no part of the striatum is completely free of degeneration. Degenerating fibres are seen passing through the globus pallidus and claustrum but there is no obvious terminal degeneration in these structures.

Sharply demarcated bands of dense terminal degeneration are seen throughout the extent of the hippocampus and dentate gyrus (Fig. 4). The pattern closely resembles that described in the rat by Raisman, Cowan & Powell (1965). Degenerating fibres

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Fig. 4. Degenerating commissural fibres (below) passing upwards through the granular layer of the dentate gyrus to distribute heavy terminal degeneration (above) to the deep part of the molecular layer. Fink–Heimer stain. × 300.

Fig. 5. Intense terminal degeneration in the deep part of layer I and in layer II of the neocortex. The surface of the brain is towards the top. Fink–Heimer stain. × 500.

Fig. 6. Terminal degeneration in the caudate nucleus of the undamaged hemisphere following section of the commissures. Fink–Heimer stain. × 500.

Fig. 7. Showing the architectonic fields of the cortex in the caudal part of the cerebral hemisphere. Note the extent of the striate (*S*) and peristriate (*Ps*) areas. This figure should be compared with Fig. 8, where it approximately corresponds to section 2. Thionin stain. × 9.

enter the hippocampus from the fimbria and alveus, and the stratum oriens is filled with terminal degeneration. Degenerating fibres pass through the stratum pyramidalis and stratum lucidum but these layers contain no terminal degeneration. Further dense terminal degeneration, however, is found in the next layer – the stratum radiatum. In the dentate gyrus, relatively coarse fibres are seen passing through the stratum polymorphe and stratum granulosum and there is a sharply defined band of intense terminal degeneration in the deep (juxtagranular) one-third of the stratum moleculare. This band is best defined rostrally and fades away caudally almost to nothing. Moderately heavy degeneration is present throughout the adjoining subiculum.

There is dense terminal degeneration in the deep layers of the whole entorhinal cortex and sparse degeneration in the molecular layer of the pyriform cortex. Definite, but sparse, degeneration is also present in the amygdala but is mainly confined to the baso-lateral nuclei. No degeneration was found in the amygdala in the experiments in which hemidecortications were done. Similarly, degeneration was seen in the molecular layer of the pyriform cortex only when the commissures were totally sectioned. None appeared in this area in the two experiments in which only the dorsal parts of the anterior commissure were damaged. One of the five brains with total sections of the commissures was cut horizontally. In this brain degenerating terminals were clearly visible in the internal granular layer of the olfactory bulb but very few encroached upon the more superficial layers.

Localized lesions

In order to investigate certain details of the commissural projection, in four animals small lesions were placed in various areas of the cerebral cortex. Two were in the visual areas and two involved the somatic sensory areas.

In Expt. 26 (Fig. 8) the lesion is confined to the striate area but spares its margins. On the ipsilateral side, heavy degeneration fills the striate and peristriate areas and a small focus of moderately heavy degeneration is present immediately dorsal to the rhinal sulcus. This is separated from the peristriate area by a region which is free of degeneration, and it appears to occupy the same position as the small focus seen here after section of the commissures. There is no degeneration in the contralateral cerebral cortex.

In Expt. 7 (Fig. 8) a similar lesion of the striate cortex extends rostrally and laterally to involve the margins of the striate area and the adjoining parts of the peristriate cortex. The pattern of degeneration in the ipsilateral hemisphere is no different from that seen in the preceding experiment. In the contralateral cortex, degenerating fibres and terminals fill a narrow peristriate band which occupies medial portions of the peristriate cortex lying on the dorsal and lateral aspects of the hemisphere and overlaps into the rostral and lateral margins of the striate area. There is also sparse commissural degeneration in the additional small focus lying just above the rhinal sulcus and described above. There is no degeneration in the contralateral striatum (caudate nucleus and putamen) in either of these experiments with lesions of the visual cortex.

In Expt. 4 (Fig. 9) a large lesion destroys much of SI and degenerating fragments are found throughout the contralateral SI. Terminal degeneration is particularly dense in the tail, trunk and face regions but relatively sparse in the limb regions. Some terminal degeneration is present in SII, being heaviest in the rostral part, where the face is represented.

In Expt. 12 (Fig. 9) the lesion is larger and occupies a wide band of cortex on the

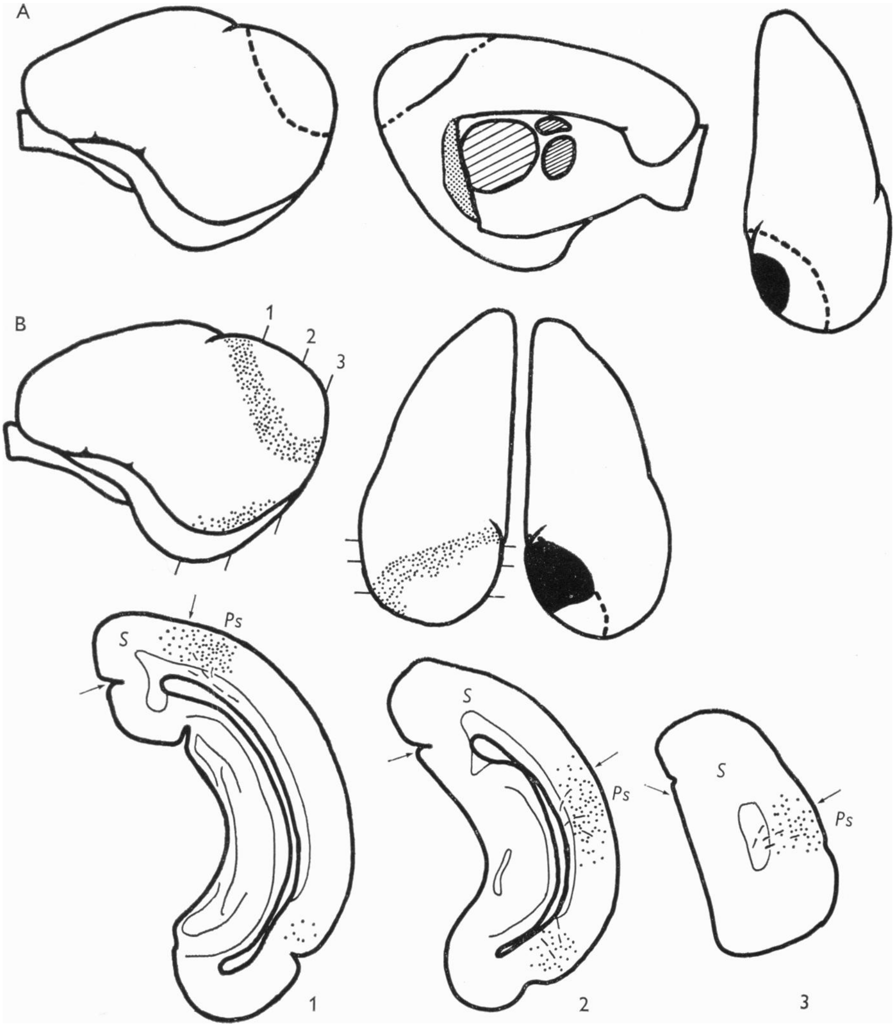

Fig. 8. A: the lateral margin (broken line) of the striate area reconstructed on lateral, medial and dorsal views of the hemisphere. The dorsal view is from the hemisphere opposite the other two and is to facilitate comparison with B. A lesion (black) confined to the middle of the striate area in this brain caused no degeneration in the contralateral cortex.

B: the distribution of degeneration in the contralateral cortex following a lesion (black) which affected the lateral margins of the striate area and which encroached on the peristriate area. Note that commissural degeneration fills the peristriate area and encroaches upon the lateral aspect of the striate area. The boundaries of the latter are indicated by the arrows on the sections. There is an additional small focus of degeneration at the lower margin of the neocortex in what may be a further visual area.

lateral aspect of the hemisphere. It involves the lower part of SI, a part of SII and the cortex caudal to it, and encroaches upon the peristriate area. In the somatic sensory areas of the opposite side, the pattern of degeneration does not differ significantly from that of the preceding experiment. In addition, there is degeneration at the junction of the striate and peristriate areas and in the temporal cortex below and behind SII. In both of these experiments there is degeneration throughout the caudate nucleus and putamen in a pattern similar to that described in the experiments in which the commissures were sectioned.

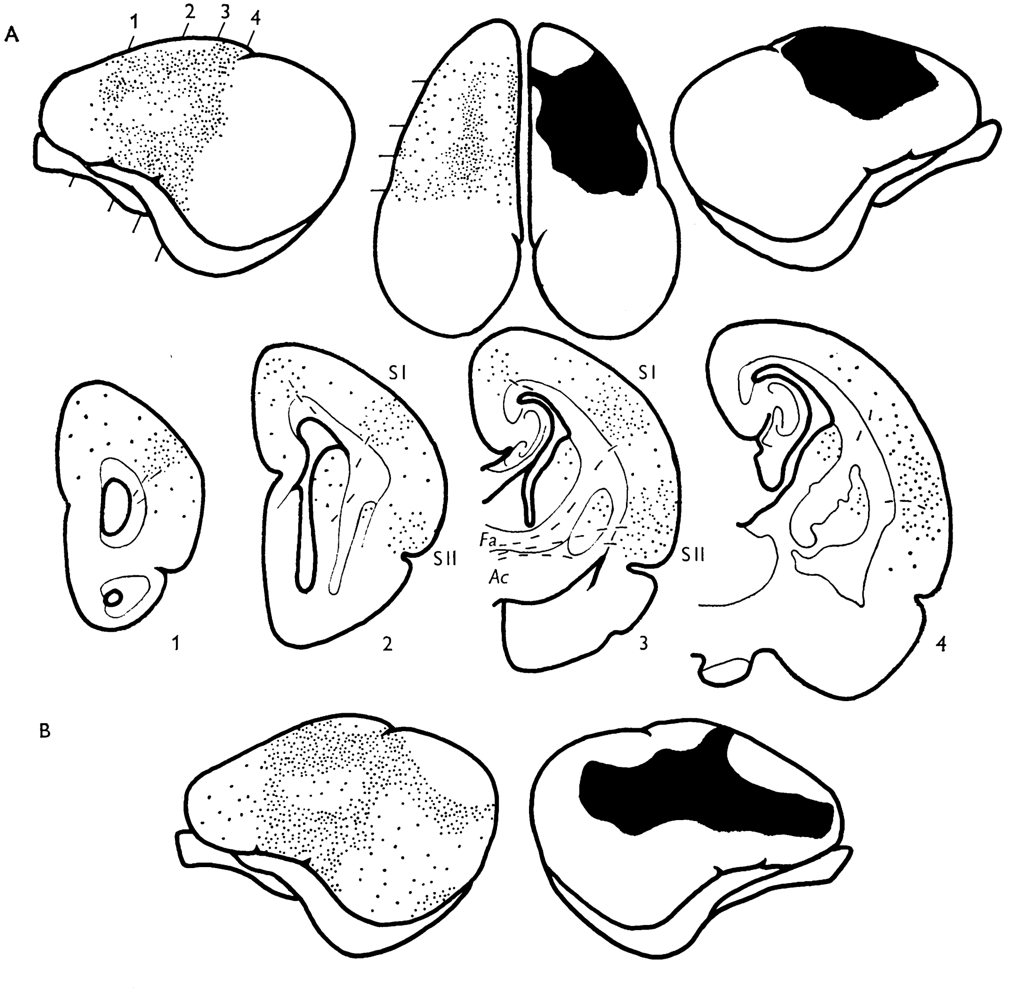

Fig. 9. The distribution of degenerating commissural fibres in two experiments with lesions of the cortex. In A, mainly SI is damaged. The degeneration in the contralateral cortex fills SI and SII but is concentrated in the face, trunk and tail areas. There is additional degeneration in the striatum.

In B, a larger lesion damages the somatic, frontal and visual areas and the distribution of the commissural degeneration corresponds to that seen in preceding experiments.

The fasciculus aberrans

Two experiments show the distribution of the fasciculus aberrans and suggest some topographic organization within the anterior commissure proper. The hippocampal commissure and the fasciculus aberrans were divided in Expt. 10 (Fig. 10). The degeneration in the subiculum, hippocampus and dentate gyrus is the same as that described in Expt. 6. In the neocortex, degeneration is confined to a broad band extending along the dorsal aspect of the hemisphere from the rostral to the caudal poles. The dorsal part of SI is involved and in it there is a small area of less dense degeneration corresponding to the representation of the hindlimb. There is further degeneration in the band at the periphery of the striate cortex but none is present in the face area of SI, in SII, nor in the cortex below and behind SII. There is additional degeneration in the striatum but none is found in the amygdala or pyriform cortex. A similar lesion in Expt. 31 (Fig. 10), but with added involvement of the dorsal half of the anterior commissure, gives a pattern of degeneration very similar to that seen after total section of the commissures, except that there is a small area devoid of degeneration in the rostral and ventral aspect of the neocortex. There is sparse terminal degeneration in the amygdala but not in the pyriform cortex.

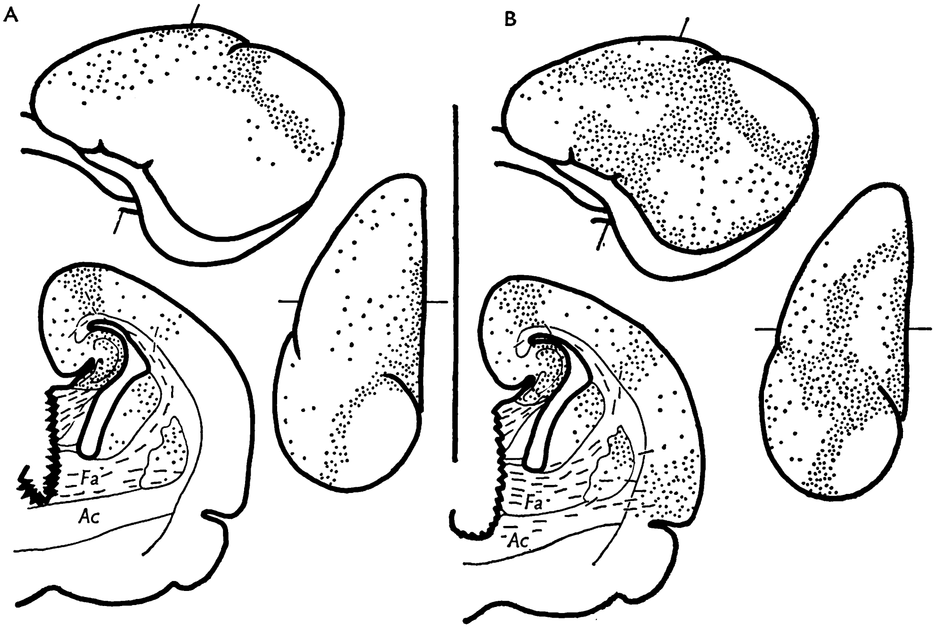

Fig. 10. A: the distribution of degeneration in the undamaged cortex of a brain in which only the fasciculus aberrans (*Fa*) was cut. Degeneration is mainly confined to the dorsal aspect of the cortex and to the striatum.

B: the distribution of commissural degeneration in an experiment in which the fasciculus aberrans and the dorsal aspect of the anterior commissure (*Ac*) were cut. Degeneration fills the neocortex with the exception of the frontal pole. There is no degeneration in the pyriform cortex.

Effect of survival time

The intensity of the terminal degeneration in the cortex, and particularly the density of the degenerating terminals in layers I and II, appears to be a function of the survival time. At seven days it is marked but at shorter and longer survival periods it is not so pronounced. No degeneration is present in layers I and II at four days, and even at five and six days it is patchy and inconstant. At seven days there is degeneration in all laminae but concentrated in layers I and II and in adjacent parts of layers III and IV. At eight days the degeneration in layers I and II is again patchy and sparse. The seven-day survival period is optimum for both the Nauta and Fink–Heimer techniques and in this animal there is no significant difference in the pattern or intensity of the terminal degeneration with either technique.

DISCUSSION

The results of this study demonstrate that even in the absence of a corpus callosum there is a comprehensive set of connexions joining the two hemispheres. Recent anatomical (Martin, 1967; Ebner, 1967, 1969) and electrophysiological (Nelson & Lende, 1965) work has shown the presence of interhemispheric neocortical connexions in the American opossum *Didelphis*, and the present results confirm this for a more specialized Australian marsupial. However, the inter-neocortical connexions appear to be less specialized in the opossum: although parts of the sensory-motor and visual areas display fewer connexions than the remainder of the cortex, no parts are devoid of commissural connexions (Ebner, 1967). By contrast, in *Trichosurus* one part of the system of commissural connexions – the visual – approximates very closely to the pattern seen in the more advanced Eutheria. Most of the striate area is devoid of commissural connexions but its rostral and lateral margins, together with adjoining parts of the peristriate area, are heavily interconnected. An identical pattern is seen in the rabbit (Hughes & Wilson, 1969), cat (Choudhury *et al.* 1965; Berlucchi *et al.* 1967; Hubel & Wiesel, 1967; Garey *et al.* 1968) and monkey (Zeki, 1970; Cragg, 1969), where the juxtastriate band contains the adjoining two representations of the vertical meridian of the visual field, in visual areas VI and VII (areas 17 and 18). By analogy, therefore, we may predict that there is probably a similarly organized dual representation of the visual field in the phalanger. A dual representation is present in the opossum (Lende, 1963*a*) but this matter has not been investigated in the phalanger. Also of note, and probably further indicative of an advanced pattern of organization in the phalanger visual system, is the small area close to the rhinal sulcus which receives fibres from the striate and peristriate cortex of both sides. This may represent the third visual area (VIII or area 19) of the cat brain (Hubel & Wiesel, 1965). Alternatively, and perhaps more likely, since it is separated by a zone relatively free of commissural degeneration, it may be the equivalent of the fourth or lateral suprasylvian visual area of the cat (Clare & Bishop, 1954; Hubel & Wiesel, 1969).

Goldby (1941) and Hayhow (1967) have already noted that the visual projection upon the thalamus in the phalanger resembles that of the primates. Thus, there is a substantial ipsilateral retino-geniculate projection, the lateral geniculate nucleus displays a clear-cut lamination, consisting of six layers, and ipsi- and contralateral retinal fibres end in alternate layers. The present results suggest that this similarity is carried to the cortical level as well. The Diprotodont marsupials are generally considered to have diverged considerably from the direct phylogenetic line leading to the Eutheria, so that this similarity may reflect convergence in relation to similar environmental demands. The phalanger may, in this respect, be even more highly advanced than those more generalized Eutherian mammals, such as the hedgehog, in which the commissural connexions of the visual cortex resemble those of the opossum (Ebner, 1969). Diamond & Hall (1969) have shown that, although the feline and primate visual systems display many similarities, certain differences point to their independent development also. It would be interesting to determine whether the organization of the cortical visual system in other Diprotodont marsupials, such as the kangaroo, is identical to or different from that of *Trichosurus*. As is well known, the Diprotodont marsupials display a range of adaptive variation almost as great as that found among the Eutheria. Conceivably, therefore, in regard to the connexions of the visual cortex, some may have retained the more primitive Polyprotodont condition while others, like the phalanger, may have developed connexions similar to those of the more advanced Eutheria. It is equally possible, of course, that all may have developed the higher Eutherian pattern, but the retention of the more generalized pattern in the hedgehog may be an argument against this.

Although the visual cortex of the phalanger appears to be highly advanced, the somatic sensory cortex clearly is not. In the first place, there is considerable overlap, perhaps even superimposition, of the first somatic sensory area and the excitable motor cortex (Goldby, 1939; Abbie, 1940; Adey & Kerr, 1954; Rees & Hore, 1970), just as in the opossum (Lende, 1963*a*, *b*). In the second, the commissural connexions of this sensory–motor area also resemble those of the opossum: although the forelimb and hindlimb areas receive fewer interhemispheric fibres than the parts representing the trunk, tail and face, no parts of the representation lack such connexions. Separate motor and sensory representations and a lack of commissural connexions between the distal fore- and hindlimb regions are features of the sensory–motor cortex of all but one of the Eutherian mammals which have been investigated (Ebner & Myers, 1965; Jones & Powell, 1968, 1969; Pandya & Vignolo, 1969). The exception is the hedgehog, which of all living mammals is probably the most generalized and closest to the basic mammalian stock. In this animal there is extensive overlap of somatic sensory, motor, visual and auditory representations (Lende, 1969) and commissural connexions join all areas (Ebner, 1969). In the less densely connected forelimb and hindlimb areas of the sensory–motor cortex of the phalanger it is possible that the cells related to the limbs may not be commissurally connected but the lack of such connexions may be obscured by the extensive overlap between all parts of the representation (Adey & Kerr, 1954). Alternatively, these cells may be connected but may have fewer connexions than their neighbours in the face, trunk and tail regions.

A point of similarity with the higher mammals is that SI sends commissural fibres to both the opposite SI and SII (Jones & Powell, 1968, 1969) suggesting that this pattern is fundamental to both the marsupials and Eutheria. A further point of difference, which may again be indicative of the relative lack of specialization in the sensory–motor cortex, is the quite extensive projection to the contralateral striatum.

In the present study most of the neocortex, with the exception of the visual areas, appears to contribute to this projection, and although the commissural fibres are distributed mainly to the dorsolateral aspects of the caudate nucleus and of the putamen, no part of the opposite striatum is devoid of such connexions. In higher mammals, by contrast, the contralateral cortico-striate projection arises only from rostral parts of the hemisphere – perhaps from the motor areas alone – and the fibres terminate in a very restricted part of the striatum (Carman, Cowan, Powell & Webster, 1965).

The high degree of development of the cortical visual areas in the phalanger and the relative lack of differentiation of the sensory–motor area may be compared with the different degrees of development of the somatic sensory and motor areas in the raccoon. In the raccoon, apparently in conjunction with certain characteristic behavioural attributes, the somatic sensory pathway is exceedingly well developed and, at the cortical level, individual small gyri are devoted to the representation of each of the digits and palmar pads of the forepaw (Welker & Seidenstein, 1959; Welker & Campos, 1963). The representation of the forepaw is strikingly devoid of commissural connexions (Ebner & Myers, 1965). However, the cortical motor area of the raccoon is not nearly so highly developed and the representation of some muscles is not well defined (Hardin, Arumugasamy & Jameson, 1968). These two examples indicate that in a single species the development of certain cortical areas, and possibly of whole systems, may be markedly out of step with that of others.

In possessing an additional commissure – the fasciculus aberrans – the Diprotodont brain is clearly unique. However, the possession of this pathway does not appear to confer any unique pattern of commissural connexions. The present results suggest that it merely represents a route whereby fibres emanating from the more dorsal aspects of the cortex may cross the midline. According to Elliot Smith (1902) and Abbie (1939), its development appears to have been coexistent with the expansion of the dorsal areas of the neopallium. However, there appears to be no reason for assuming that commissural fibres emanating from a more recently developed cortical area need necessarily follow the newest interhemispheric route. In the primate, for example, many commissural fibres joining the recently enlarged temporal neocortex appear to pass by way of the phylogenetically old anterior commissure (Pandya, Hallett & Mukherjee, 1969) rather than *via* the newer corpus callosum.

According to Elliot Smith (1902) 'the same determining cause which in the Eutheria calls the corpus callosum into being is probably functional in bringing into existence the aberrant bundle in the Diprotodontia'. The inability of the fasciculus aberrans to expand in its present position was seen by Elliot Smith as a limiting factor in preventing the further development of the marsupial brain. By contrast, the corpus callosum '...not only furnishes the shortest and most direct path of communication ...between the two hemispheres, but also permits of an unimpeded expansion (which is so freely exercised by the corpus callosum)'. Elliot Smith (1897) considered that the corpus callosum developed by commissural fibres breaking through the hippocampus, invading the alveus, and crossing in the dorsal part of the hippocampal commissure such as is seen in the marsupial brain. Further evidence in favour of this idea was later adduced by Goldby (1940). An opposing view is that of Abbie (1939), who considered that the corpus callosum is developed by fibres passing dorsal to the hippocampus and then crossing the midline by piercing the opposed subicula (Fig. 1). Perhaps (but not necessarily) in keeping with Abbie's view, we have not observed any degenerating fibres in the hippocampal commissure following neocortical lesions in the phalanger.

In the present study, the commissural connexions of the hippocampal formation, olfactory bulb and basal forebrain structures appear to be identical to those described in other mammals (see for example Blackstad, 1956; Raisman *et al.* 1965) and the details need not be discussed. Presumably, this similarity reflects the fundamental nature and importance of most of these structures to all classes of mammals and, indeed, to all vertebrates. Finally, in the brains with neocortical lesions, we observed degeneration in the thalamus of the ipsilateral but not of the contralateral side. In the opossum (Nelson & Lende, 1965), there occurs a delayed interhemispheric electrophysiological response which survives section of the forebrain commissures and of the rostral parts of the midbrain, and is thought to be mediated by fibres joining the two thalami (Bodian, 1940). In the absence of a crossed corticothalamic projection, it may be assumed that this is an indirect interhemispheric pathway.

SUMMARY

Commissural connexions have been examined in a marsupial, *Trichosurus vulpecula*, by means of the Nauta technique. Although this animal lacks a corpus callosum, an extensive set of connexions joins the two cerebral hemispheres *via* the anterior commissure and the fasciculus aberrans, an additional commissure which is peculiar to the Diprotodont marsupials.

The commissural connexions of certain parts of the neocortex, particularly the visual areas, resemble those found in the brains of the more advanced Eutheria but the connexions of other areas conform more to the generalized pattern of the simpler Polyprotodont marsupial *Didelphis*, a pattern which is also found in the hedgehog. There is evidence in *Trichosurus* and in other animals that the development of certain cortical areas, and even of whole systems, may be markedly in advance of that of other areas and systems.

Although the fasciculus aberrans is unique to the Diprotodont marsupials, it is not associated with any unique pattern of commissural connexions and it serves to join together the more dorsal aspects of the neocortex. The commissural connexions of the olfactory regions, the hippocampal formation and the basal forebrain areas are the same as in other mammals.

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