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The origin, course and termination of the corticospinal tracts of the Tasmanian potoroo (*Potorous apicalis*)

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INTRODUCTION

The corticospinal tracts of many placental mammals have been studied in detail by employing modern selective silver techniques (see Martin, Megirian & Roebuck, 1970 for a partial list of the forms studied). Such studies show that corticospinal fibres vary as to their origin, position and caudal extent within the spinal cord and their precise area of termination. In contrast, similar studies on the wide variety of available marsupials are relatively scarce.

Previous studies on the polyprotodont North American opossum, *Didelphis marsupialis virginiana*, (Martin & Fisher, 1968) and the diprotodont brush-tailed possum (phalanger), *Trichosurus vulpecula*, (Martin *et al.* 1970) indicate that the corticospinal tracts of these two marsupials vary in size, caudal extent and termination. The present study was designed to evaluate further the question of variation in marsupial corticospinal tracts by studying them in another diprotodont family and in a species with an entirely different habitat and method of ambulation from that of the brush-tailed possum. The Tasmanian potoroo (*Potorous apicalis*) (Fig. 1) was chosen for comparison because, unlike the brush-tailed possum, which is adapted well for arboreal life, it is capable of moving rapidly on the ground by hopping. In addition the potoroo is small, easily handled, and readily available in Tasmania.

MATERIALS AND METHODS

Lesions were placed by gentle suction in 17 adult animals (15 of them are illustrated in Fig. 6). Unilateral removal of essentially the whole neocortex was accomplished in three animals (one example illustrated in Fig. 6A). In the remainder, smaller lesions were made which were restricted to the cortex rostral to the small orbital sulcus (Fig. 6B–E), the cortex caudal to the same sulcus (Fig. 6F–I), the cortex rostral to the sulcus indicated by the large closed block arrow in Figs. 4 and 5 (Fig. 6J–L), the

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cortex immediately caudal to the same sulcus (Fig. 6M, N) and the insular-temporal region (Fig. 6O). The animals were maintained for 1–2 weeks before being sacrificed by an overdose of pentobarbital and perfused. Portions of selected spinal cord segments were cut in the transverse, the sagittal or the horizontal plane and the sections processed by either the Nauta–Gygax (1954) technique or the Fink–Heimer method (1967). In order to plot the position of degenerating fibres in terms of Rexed's (1952) laminae, selected sections from each segment studied were stained, utilizing the thionin method. The images of the impregnated spinal cord sections were enlarged by use of a Bausch and Lomb trisimplex projector and drawn on Bristol board. The location of degenerating fibres within each section was plotted and subsequently transposed to the drawing. In order to study the cytoarchitecture of the neocortex, several hemispheres on the side opposite the lesion were cut in the transverse, horizontal or sagittal plane and stained for Nissl substance.

Although short survival times are reported to be optimal for demonstrating boutonal degeneration with the Fink–Heimer method, this apparently is not the case for cortical efferent pathways in marsupials (see also Martin *et al.* 1970; Rees & Hore, 1970; Watson, 1971). Material from animals that survived for less than 10 days impregnated very poorly. In every case the area of the lesion was processed either by one of the silver methods or by the thionin technique in order to observe the full extent of the ablation.

RESULTS

To our knowledge the brain of potoroo has not been described previously in detail. For this reason the first part of the results deals with a few of its gross features and certain details of cortical cytoarchitecture which are pertinent to the origin of corticospinal fibres. This is followed by the experimental results related to the corticospinal tracts.

General description of the potoroo brain

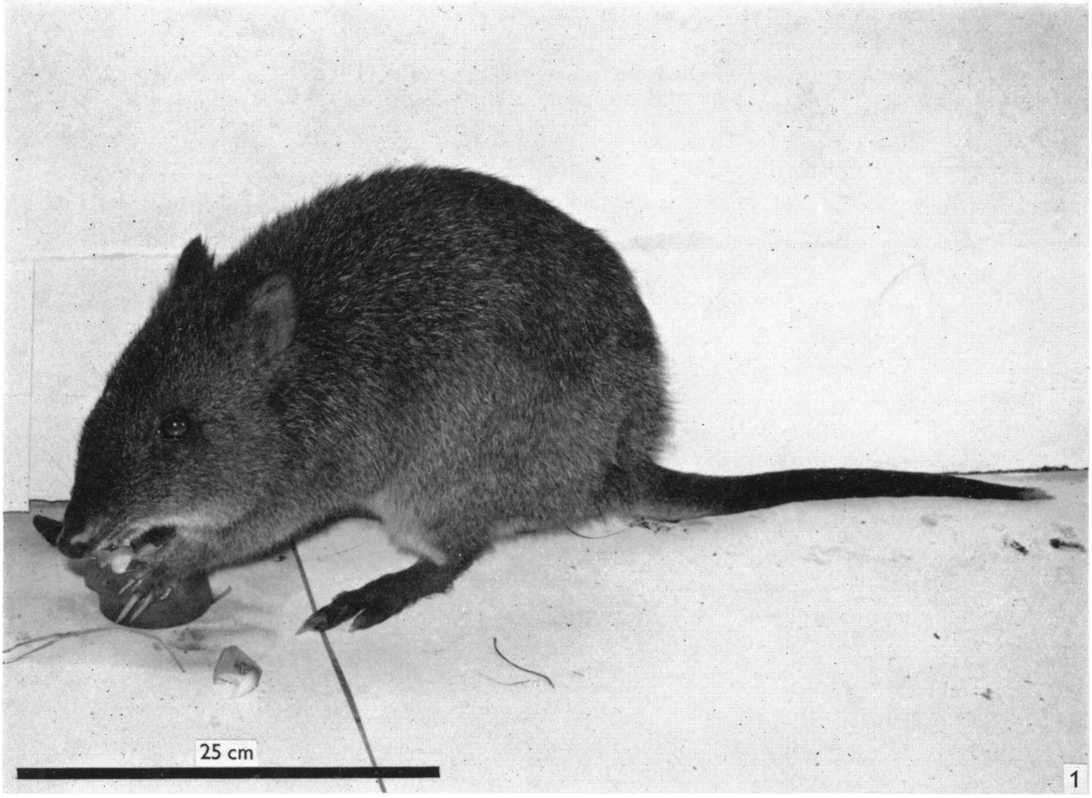
The brain of potoroo is somewhat shorter than that of the brush-tailed possum, but proportionately wider through the frontal and temporal poles (compare Figs. 2 and 3). The brain stem of potoroo is compact so that the interpeduncular fossa is not readily visible in a ventral view. Most of the basilar pontine grey is pretrigeminal; but, as in the brush-tailed possum, there is a small portion of the brachium pontis that circles the caudal aspect of the trigeminal nerve (small arrows, Figs. 2, 3). The pyramids are well developed, but are not as apparent on gross examination as those of the brush-tailed possum (large solid block arrows in Figs. 2, 3).

A small, indistinct orbital sulcus is present in most of the brains studied (open

Fig. 1. The Tasmanian potoroo. Note the claws on the forelimbs which are used for digging and the white tipped tail which is characteristic of this particular species.

Fig. 2. A ventral view of the potoroo brain. The large, solid block arrow points to a medullary pyramid; the smaller arrow indicates a bundle of pontocerebellar fibres which encircles the caudal aspect of the trigeminal nerve.

Fig. 3. A ventral view of the brush-tailed possum brain for comparison with the brain of the potoroo. The pyramidal bundles are indicated by the large, solid block arrow; the smaller arrow points to the pontocerebellar fibres which circumscribe the trigeminal nerve.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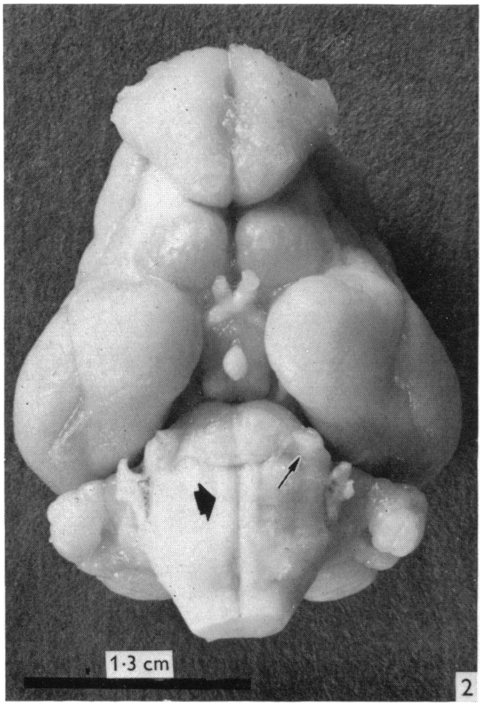
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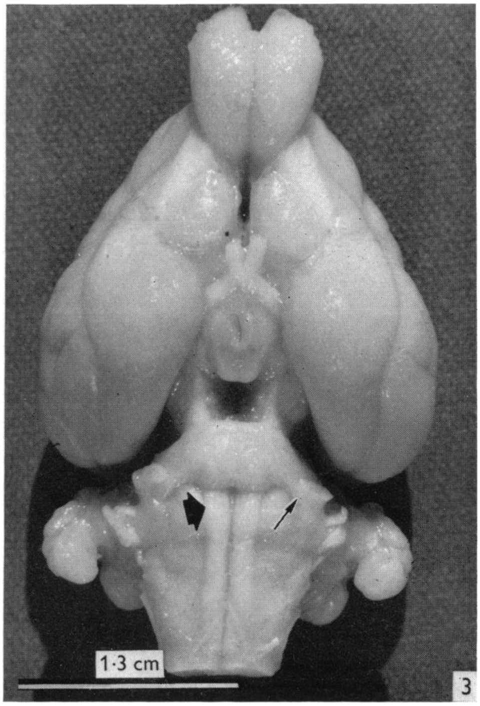
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block arrow in Fig. 4). Although the cerebral cortex of potoroo has not been studied by physiological techniques, the region caudal to the orbital sulcus has been shown to contain forelimb motor and sensory representation in the North American opossum (Lende, 1963*a*, *b*) and the brush-tailed possum (compare Abbie, 1940, with Adey & Kerr, 1954). In potoroo this cortical region is characterized by the presence of a well-developed internal pyramidal layer (approximately 375 μm thick) which is densely populated by dark-staining pyramidal neurons. This cortex is similar to that from the same region in the brush-tailed possum (see Martin & Megirian, 1972; Fig. 11). Most of the pyramidal neurons vary between 22 and 33 μm at their widest dimension (not including the stained portion of the apical dendrite). An internal granular layer is present, but poorly developed. In many sections it is difficult to locate the boundary between the internal granular layer and the external pyramidal layer. The internal granular layer becomes thicker and more compact caudally and ventrolaterally (parietal cortex, small solid block arrows in Fig. 5) and in some sections it measures up to 500 μm in thickness. An internal pyramidal layer is present in the parietal region although it is not as obvious as in the cortex caudal to the orbital sulcus.

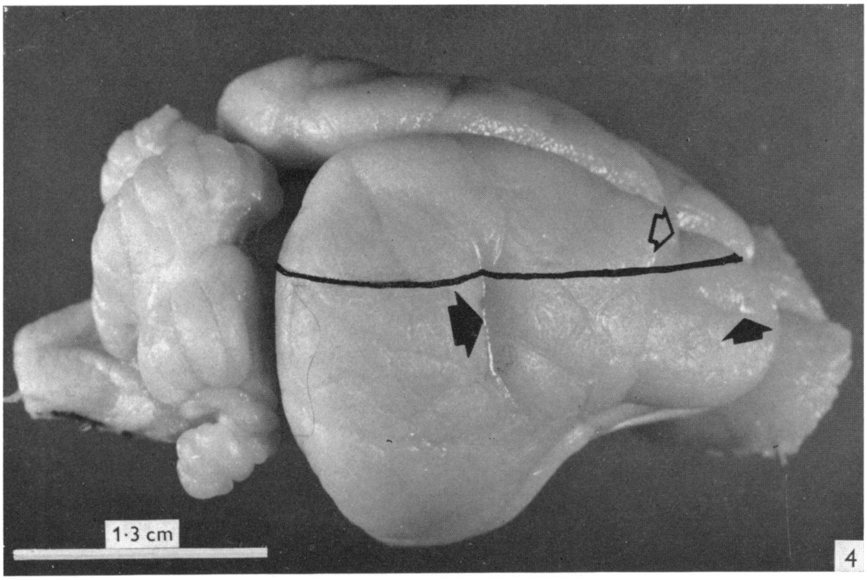
The cortex rostral to the orbital sulcus contains a well-developed internal pyramidal layer, which in most sections is not as thick and densely packed as that caudal to the sulcus. An internal granular layer is present in the preorbital area; but, as is the case in the rostral postorbital cortex, it is not well developed. Although the preorbital cortex has been studied physiologically in the North American opossum (Lende, 1963*a*, *b*) and the brush-tailed possum (Abbie, 1940), the function of this region in potoroo is not known. In most specimens there is a small sulcus which begins near the ventral extreme of the orbital sulcus and runs rostrally for a short distance (small solid block arrow in Fig. 4). A comparable cortical depression has been labelled sulcus η in the rat-kangaroo of New South Wales (*Aepyprymnus rufescens*) by Ziehen (1897). Nissl-stained transverse sections through this region do not reveal any striking differences between the cortex dorsal to the sulcus (preorbital cortex) and that ventral to it.

In all the specimens examined there is a more caudally placed sulcus which runs in a dorsal to ventral direction (large solid block arrow in Figs. 4, 5). This sulcus was referred to as sulcus ϵ in Ziehen's (1897) description of the brain of the rat-kangaroo of New South Wales and is not present in the brush-tailed possum brains studied. Horizontal sections through the sulcus reveal that it separates parietal cortex, rostrally, from a strip of cortex just rostral to the striate area (peristriate cortex). The internal granular layer of the peristriate region is thinner and more loosely packed than that of either the parietal or the striate area. The striate cortex is characterized by an obvious, densely packed internal granular layer, which in most sections is not as thick as that of the parietal area (open block arrow in Fig. 5).

EXPERIMENTAL RESULTS

Results of unilateral decortication

In cases of almost complete unilateral decortication (Fig. 6A) axonal degeneration is present throughout the internal capsule, the cerebral peduncle and the pyramidal bundle. With so large a lesion, degenerating fibres are obviously distributed to



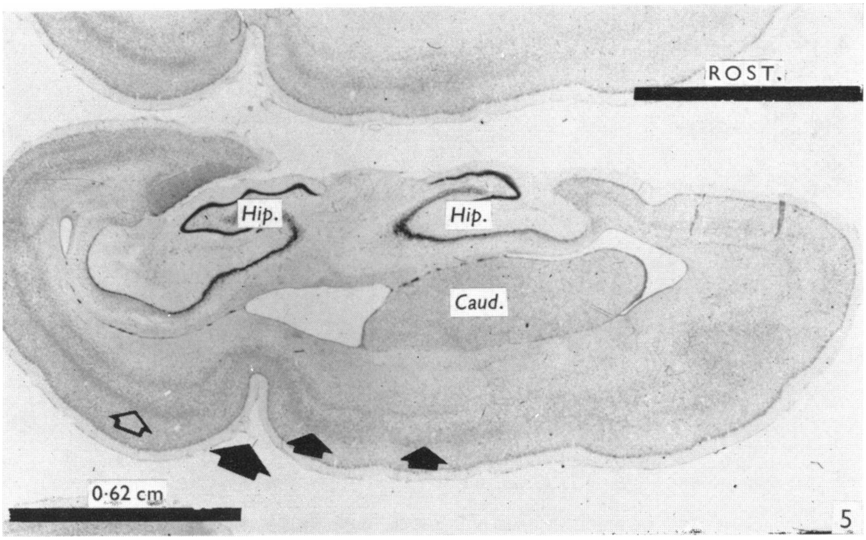


Fig. 4. A dorsolateral view of the brain of potoroo. The black line indicates the level of the horizontal section shown in Fig. 5. The small open block arrow points to the poorly developed orbital sulcus, whereas the small solid block arrow indicates a horizontal sulcus (sulcus η of Ziehen, 1897) which in some specimens joins the orbital sulcus caudally. The large solid block arrows points to the sulcus ϵ (Ziehen, 1897) delineated by the same sized arrow in Fig. 5.

Fig. 5. A thionin-stained, horizontal section through the brain of potoroo at the level indicated in Fig. 4. The hippocampus (*Hip.*) and the caudate nucleus (*Caud.*) are labelled for reference. The small open block arrow points to the internal granular layer of the striate cortex, whereas the two small solid block arrows indicate the wide internal granular layer of the parietal region. The large, solid block arrow points to the sulcus ϵ of Ziehen (1897).

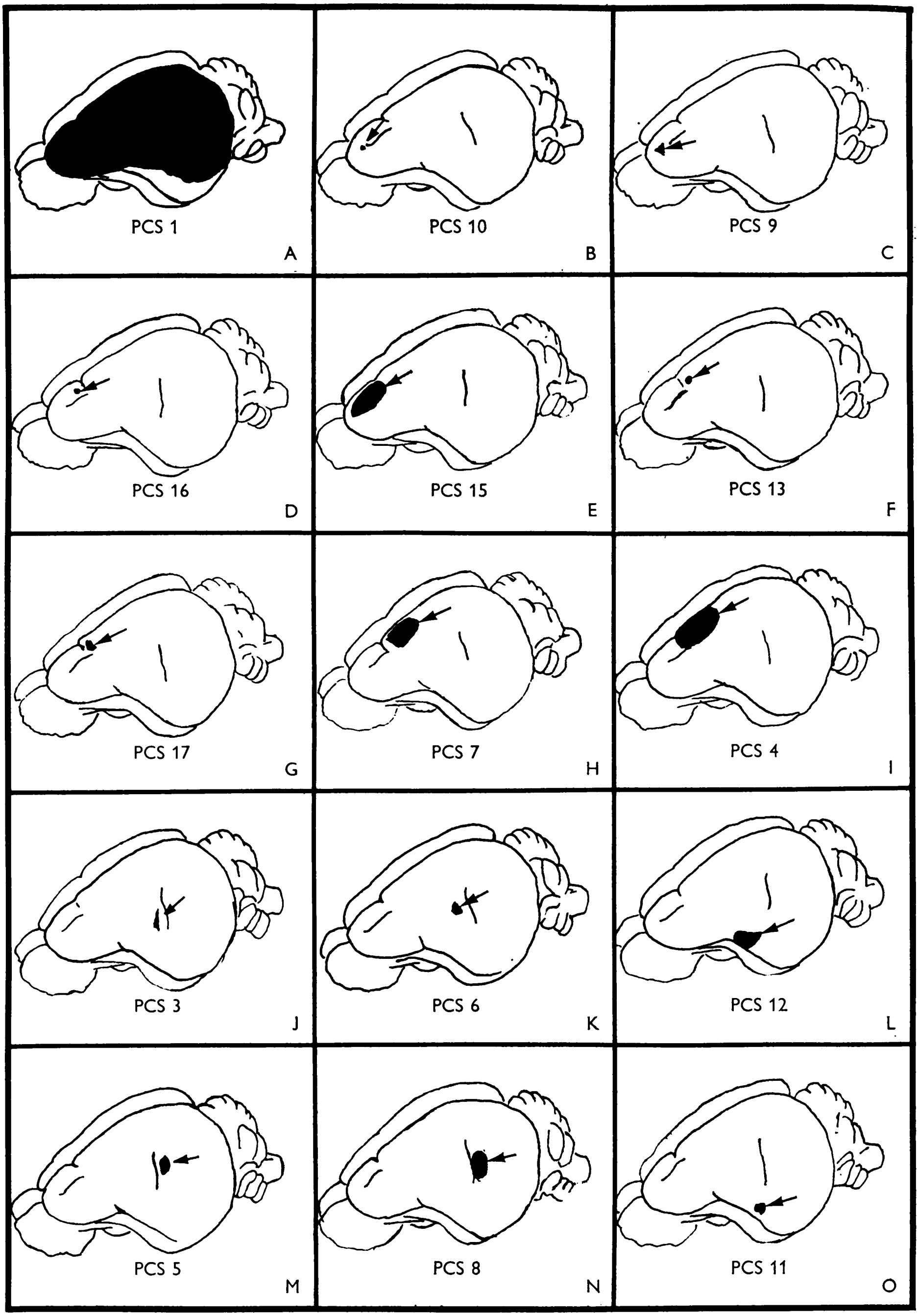


Fig. 6. A series of drawings (A–O) of 15 of the 17 specimens used in the present study. The laboratory number of each animal is listed. In each specimen the lesion is indicated by a small black arrow.

many regions of the brain stem which are beyond the scope of the present report; however, one region will be mentioned. At caudal medullary levels, degenerating fibres terminate within the subnucleus caudalis of the spinal trigeminal tract, the nucleus cuneatus (particularly at its 'hilum') and the lateral part of the nucleus gracilis. Degenerating fibres are not apparent within the medial area of the nucleus gracilis.

Most of the degenerating corticospinal fibres cross in the pyramidal decussation and are present as two tracts within the spinal cord. The largest numbers of degenerating fibres are located within the ventral portion of the contralateral dorsal funiculus, but a smaller group is present within the medial part of the lateral funiculus (Fig. 7). Many of the latter fibres are positioned within the fascicles which break up the lateral portion of laminae IV and V. In frontal sections corticospinal degeneration can be traced as far caudally as T. 12 in the dorsal tract and T. 8 in the lateral pathway. Horizontal sections of the lumbar intumescence reveal, in the base of the dorsal funiculus, a few impregnated fibres which might be interpreted as degenerating. However, no such fibres were observed in the grey matter at the same level in either frontal or horizontal sections.

Our material indicates that the greatest number of degenerating corticospinal fibres distribute to the cervical spinal cord. Throughout the cervical region numerous degenerating fibres end within laminae III to VI inclusive (Figs. 7, 10–16). Although fibre degeneration is present in lamina VII, it is relatively sparse. It should be emphasized that most of the terminal degeneration within laminae III to VI inclusive is located medially, close to the dorsal tract (Figs. 7, 10–15). Horizontal sections through laminae III and IV reveal numerous rows of agyrophilic axonal fragments (Fig. 16). In transverse sections these axonal fragments appear as isolated impregnated particles (Fig. 11). Such results strongly suggest that many fibres in these laminae course longitudinally for some distance before ending. Although most degenerating fibres arborize in the transverse and horizontal planes in laminae V and VI (Figs. 12, 14, 15), longitudinally coursing fibres are present also.

At thoracic levels, the degenerating corticospinal tracts rapidly diminish in size, and the dorsal tract becomes restricted to that portion of the dorsal funiculus directly adjacent to the dorsal horn. The area of termination of corticospinal fibres also becomes progressively smaller. Although fibre degeneration is located within laminae III to V inclusive between T. 2 and T. 5 (lamina VI is not present caudal to T. 2), it becomes limited mainly to the medial portion of lamina V at more caudal levels.

After decortication some fibre degeneration is present in the ipsilateral dorsal and lateral corticospinal tracts. These fibres are so few in number that it is difficult to plot their distribution within the grey matter. However, those present are located within the medial part of laminae V and VI. Because of their sparsity it is difficult to delimit their caudal extent.

It should be mentioned that even after decortication, ambulatory deficits are not obvious in potoroo. However, such observations must be interpreted with extreme care since controlled measurements of 'motor' deficits were not performed.

Results from lesions caudal to the orbital sulcus

Large lesions caudal to the orbital sulcus (the area of abundant pyramidal cells plus some dorsal parietal cortex, Fig. 6H, I) produce terminal degeneration within

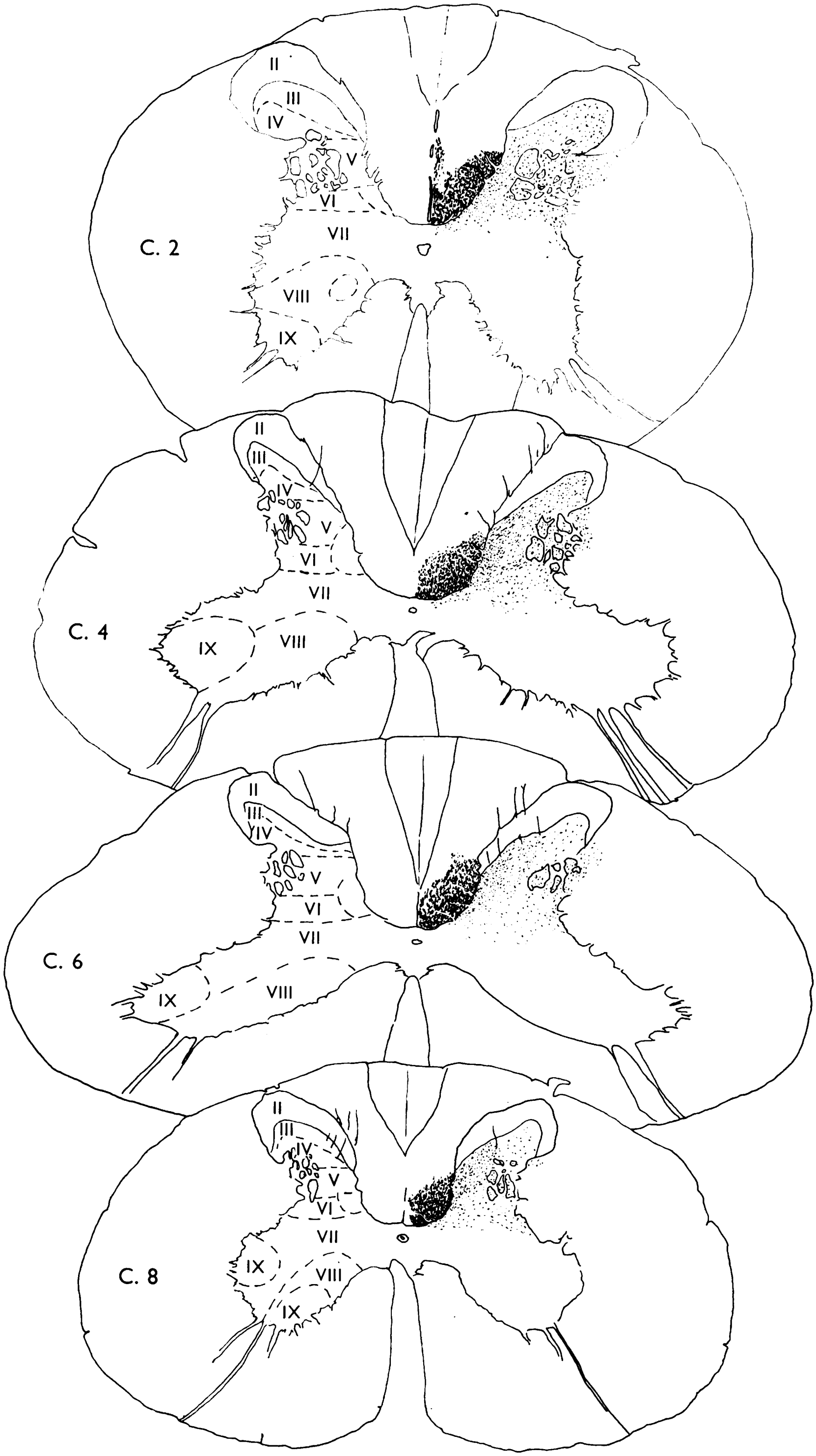


Fig. 7. A series of stacked drawings of frontally sectioned spinal cord segments from a decorticate specimen (Fig. 6A). Rexed's laminae are drawn and labelled on the reader's left; the degenerating fibres present on the side opposite the lesion are plotted on the right.

the contralateral nucleus cuneatus and lateral nucleus gracilis, but little within the caudal nucleus of the spinal trigeminal tract. Involvement of white matter in some of the cases produced no change in the distribution of fibre degeneration. Axonal degeneration is present also in the contralateral corticospinal tracts, which can be traced to approximately the same levels as in the decorticate animals. The fibre degeneration is scattered throughout the dorsal corticospinal tract as well as within the lateral pathway. At rostral cervical levels (C. 1 to C. 4 inclusive), terminal degeneration is abundant in the medial portion of laminae IV–VI on the side opposite the lesion (Fig. 8). Degenerating fibres also end in the lateral parts of the same laminae as well as in lamina VII. However, at the cervical enlargement, degenerating axons distribute to the medial part of lamina III as well as to the regions described above (C. 6, Fig. 8). In thoracic sections the terminal degeneration becomes restricted to the medial part of lamina V. Although some degenerating fibres are present on the side of the lesion, their sparseness makes it difficult to plot accurately either their caudal extent or their termination.

Small lesions restricted to the cortex caudal to the orbital sulcus (Fig. 6F, G) produce only minimal degeneration within the corticospinal tracts. Some terminal degeneration is present in the medial portions of laminae IV to VI inclusive, as in the larger ablations; but none is obvious in lamina III at any level.

Results from midcortical (parietal) lesions

All the lesions ventral and lateral to the 'postorbital area', but rostral to the sulcus labelled ϵ by Ziehen (1897) (Fig. 6J, K), involved some underlying white matter. In such cases fibre degeneration was present in the nucleus cuneatus and in the caudal spinal trigeminal nucleus (particularly the dorsomedial area). Most of the degenerating fibres within the nucleus cuneatus appeared to pass through it to reach the base of the fasiculus cuneatus, whereas those within the caudal spinal trigeminal nucleus appeared to be terminal. The same lesions also produced axonal degeneration within both the dorsal and lateral corticospinal tracts, particularly contralaterally (Fig. 9). However, there was noticeably less degeneration in the ventromedial part of the dorsal tract than was present after more dorsal lesions (Fig. 9, C. 2, C. 4). In one specimen (Fig. 6J), the fibre degeneration could be traced to T. 8, and it may have been present in more caudal sections. The brain illustrated in Fig. 6L also contained some corticospinal degeneration, but the lesion undercut a considerable amount of white matter.

At cervical levels, a few degenerating fibres are present in lamina V, but most are located within lamina IV and (to a lesser extent) lamina III (Fig. 9). Terminal degeneration is restricted mainly to the medial part of laminae III and IV at rostral cervical levels, but tends to spread out in these laminae more caudally (Fig. 9). Close attention to the orientation of degenerating fibres suggests that many of those which enter the medial part of lamina V do not end there, but continue into laminae IV and III. It appears that the fibres which leave the dorsal tract tend to end medially in laminae III and IV, whereas those that emanate from the lateral bundles distribute to lateral areas of the same laminae.

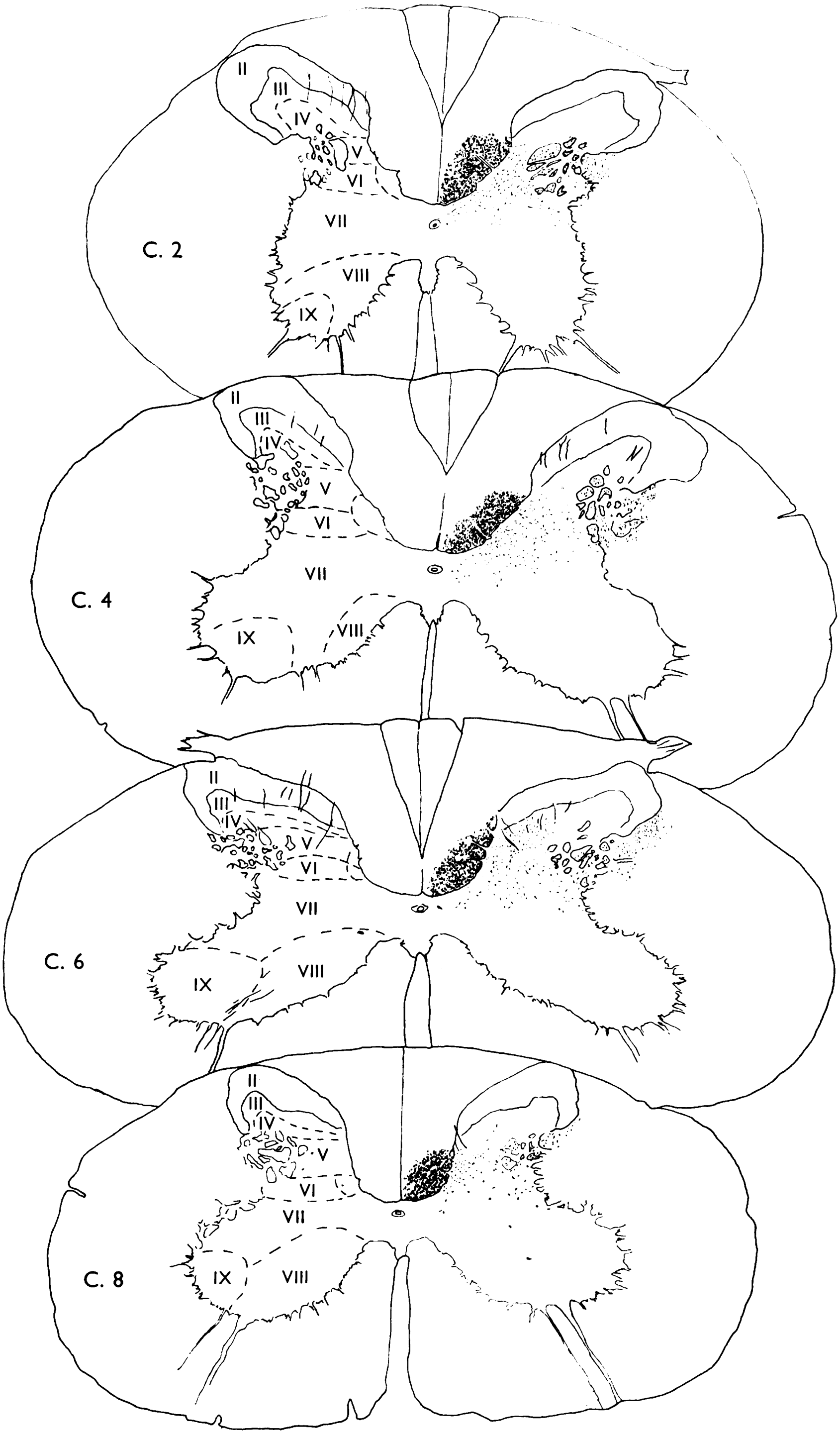


Fig. 8. A series of stacked drawings of frontally sectioned spinal cord segments from an animal with a large lesion caudal to the orbital sulcus (Fig. 6I). Rexed's laminae are drawn and labelled on the reader's left; the degenerating fibres are plotted on the right.

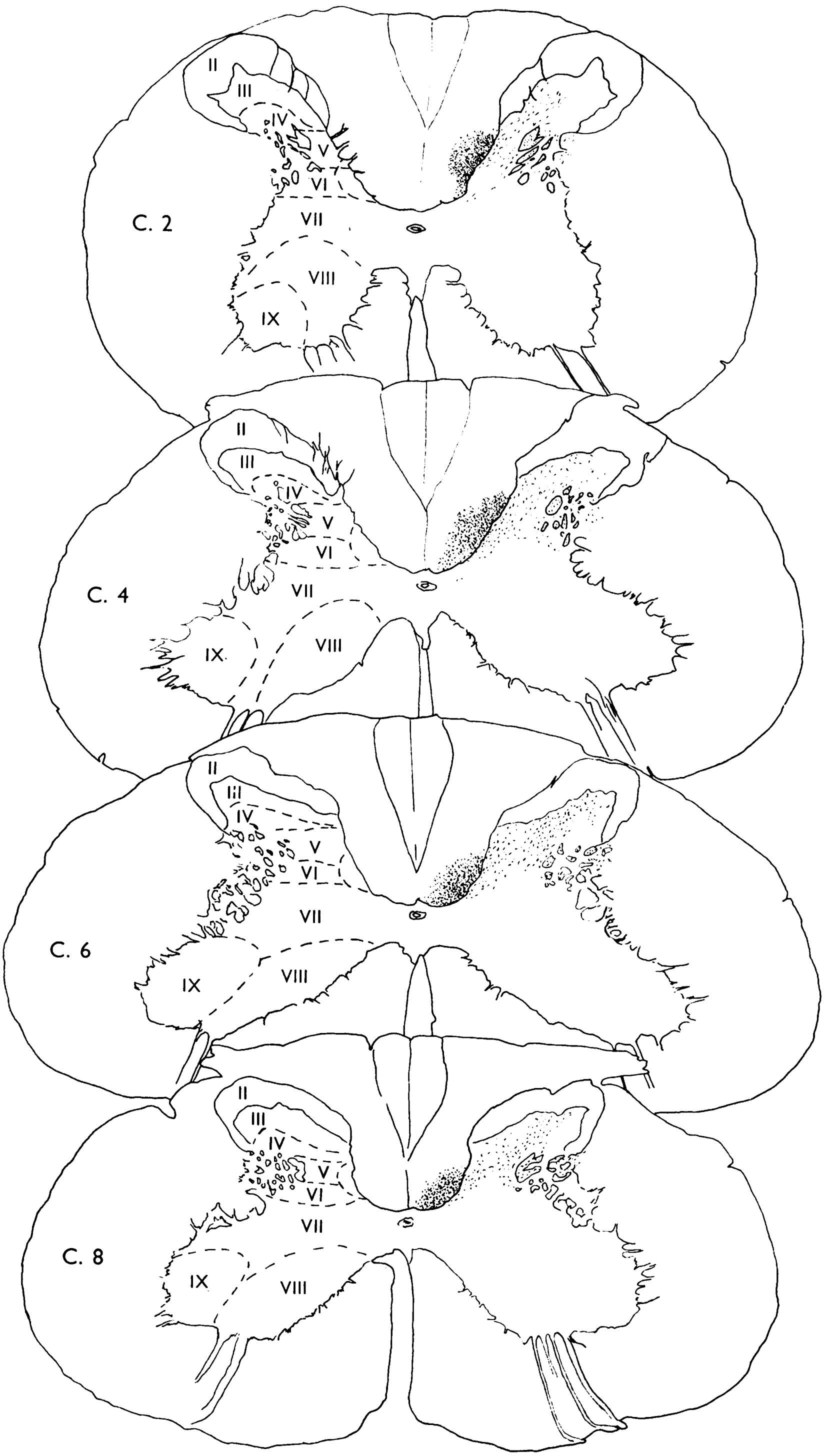


Fig. 9. A series of stacked drawings of frontally sectioned spinal cord segments from an animal with a lesion in the lateral parietal cortex (Fig. 6J). Rexed's laminae are illustrated on the reader's left; the degenerating fibres are indicated on the right.

Results from additional cortical lesions

The corticospinal tracts contain no degenerating fibres in the two specimens with lesions caudal to the sulcus ϵ of Ziehen (1897) (Fig. 6M, N) even though there was considerable involvement of white matter in the case illustrated in Fig. 6N. In both specimens degenerating fibres are located in regions of the thalamus and brain stem, which attest to the visual nature of the injured cortex (geniculate nuclei, superficial layers of the superior colliculus, etc.). Specimens with lesions located either in the temporal area of the neocortex (Fig. 6O) or in the cortex rostral to the orbital sulcus (Fig. 6B–E) contain no recognizable fibre degeneration within the spinal cord even though some of them show involvement of white matter. However, in each case degenerating fibres are present elsewhere in the neuraxis, indicating that the negative findings in the spinal cord are not due to technical difficulties.

DISCUSSION

The same area of neocortex which gives rise to corticospinal fibres in potoroo also projects to the dorsal column nuclei (particularly the nucleus cuneatus) and the spinal trigeminal complex. However, our results suggest that the majority of corticospinal fibres arise from that cortex caudal to the orbital sulcus which relays mainly to the dorsal column nuclei. Similar findings have been reported for the brush-tailed possum (Martin, Megirian & Roebuck, 1970, 1971) and the North American opossum (Martin & West, 1967; Martin & Fisher, 1968).

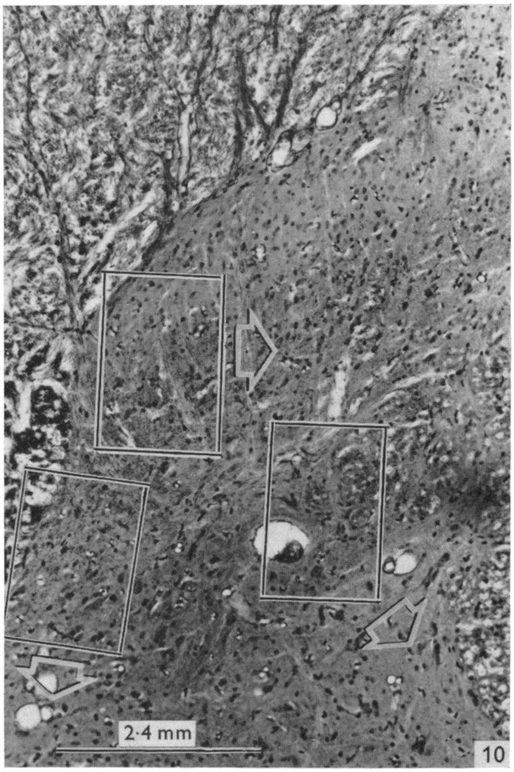
In potoroo fibre degeneration was not present within the lumbosacral spinal cord even after destruction of all possible hindlimb cortex by decortication. The limited caudal extent of the corticospinal tracts in potoroo (present study) as well as in the North American opossum (Bautista & Matzke, 1965; Martin & Fisher, 1968), the brush-tailed possum (Martin *et al.* 1970; Rees & Hore, 1970) and the quokka wallaby (Watson, 1971) suggests that cortical control over the lumbosacral spinal cord in these marsupials is strongly dependent upon subcortical relays in the brain stem and/or spinal cord. A recent study (Hore & Porter, 1971) provides physiological

Fig. 10 A frontal section of the dorsal horn (C. 6) from an animal subjected to decortication on the opposite side (Fig. 6A). The upper rectangle delineates the area of laminae II and III shown at a higher power in Fig. 11. The lower left rectangle outlines the area of laminae V and VI shown in Fig. 12; the lower right rectangle surrounds the region of the same laminae shown in Fig. 13. Fink–Heimer technique.

Fig. 11. A high power photomicrograph of the region outlined in the upper rectangle in Fig. 10. The substantia gelatinosa (lamina II) is indicated (S.G.) and the arrow points to a fascicle of dorsal root fibres. Degenerating impregnated fibres are cut mainly in cross-section within lamina III. Fink–Heimer technique.

Fig. 12. A high power photomicrograph of the region of laminae V and VI delineated by the lower left rectangle in Fig. 10. Compare the amount of fibre degeneration with that present in Fig. 13. Fink–Heimer technique.

Fig. 13. A high power photomicrograph of the lateral part of laminae V and VI outlined by the lower right rectangle in Fig. 10. Compare the amount of fibre degeneration with that present in Fig. 12. Fink–Heimer technique.



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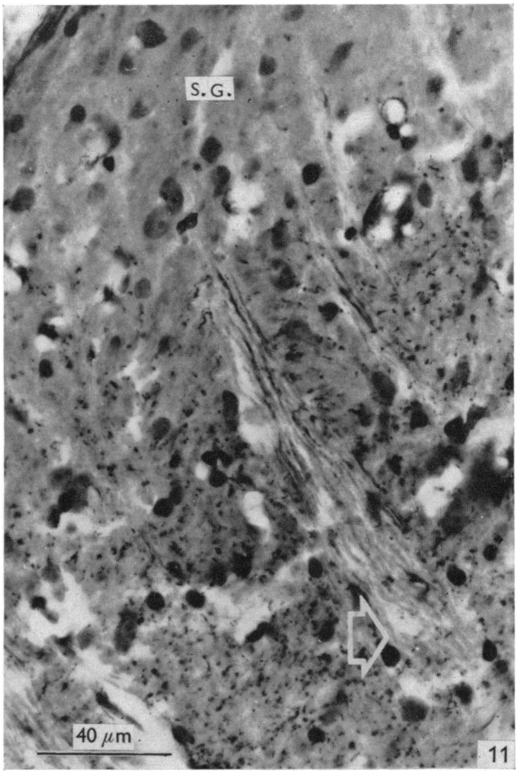

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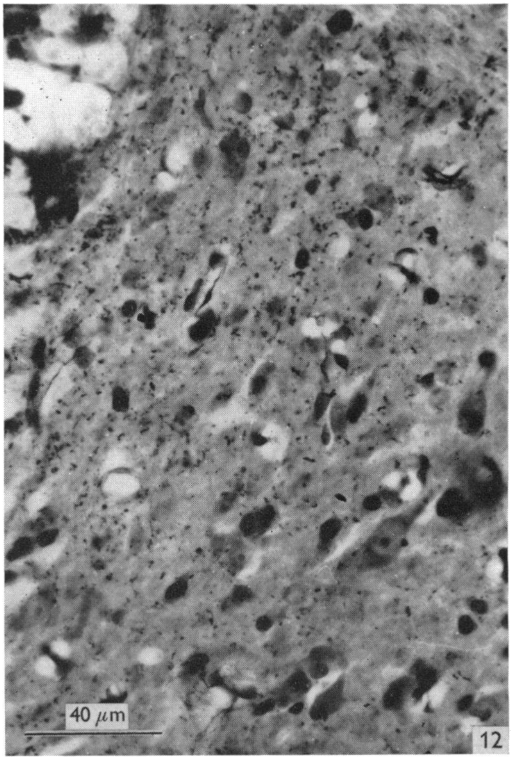

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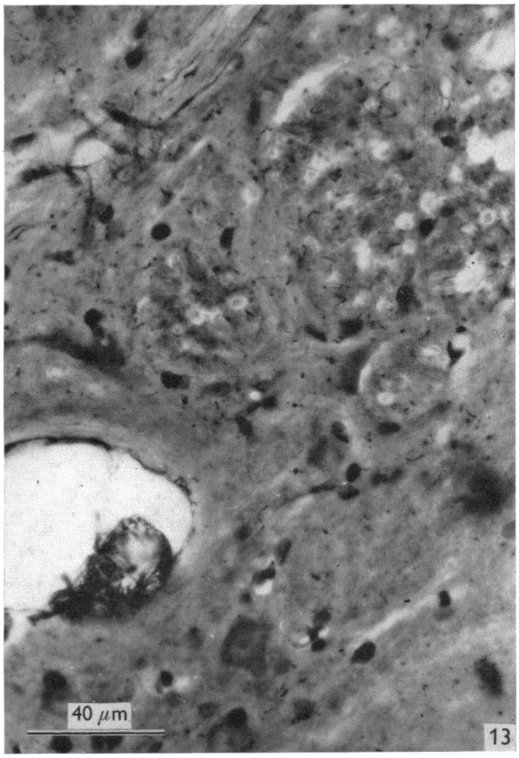

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evidence that the brain stem efferent pathways are particularly critical in the brush-tailed possum.

Corticospinal fibres in the marsupials studied to date (the North American opossum, Bautista & Matzke, 1965, Martin & Fisher, 1968; the brush-tailed possum, Martin *et al.* 1970, Rees & Hore, 1970; and the quokka wallaby, Watson, 1971) terminate mainly in the medial part of the dorsal horn (laminae III–VI). Similar observations have been reported for certain placental mammals [the tree shrew (Shriver & Noback, 1967; Jane, Campbell & Yashon, 1969), the armadillo (Dom *et al.* 1971), at least one representative of the order Chiroptera (Broere, 1971), various rodents (see Broere, 1971, for review), and *Provacia* (Verhaart, 1967; Verhaart & Voogd, 1968; Broere, 1971)]. However, in still other placental mammals [e.g. the cat (Nyberg-Hansen & Brodal, 1963), the dog and raccoon (Buxton & Goodman, 1967), the rhesus monkey (Liu & Chambers, 1964), and the squirrel monkey (Harting & Noback, 1970)] a large contingent of cortical fibres ends ventrally and laterally within the grey matter as well as within the medial portion of the dorsal horn. It has been shown that most of the corticospinal fibres which end in the medial part of the dorsal horn in the cat and monkey originate within the primary sensory cortex (SmI), whereas those from the primary motor area (MsI) end ventrally and laterally. The predominant distribution of cortical fibres to the medial part of the dorsal horn in the marsupials studied suggests that one of the major functions of their corticospinal tracts is to modulate incoming sensory information. Of course, such fibres (as well as those ending more laterally and ventrally) exert an indirect effect on ventral horn cells by influencing internuncial neurons of spinal reflex arcs. It should be mentioned that the cortex which gives rise to corticospinal fibres in the North American opossum [compare Lende (1963*a*, *b*) with Martin & Fisher (1968)] and the brush-tailed possum [compare Abbie (1940) and Adey & Kerr (1954) with Martin *et al.* (1970)] demonstrates considerable overlap of 'motor' and 'sensory' representation.

As is the case with the brush-tailed possum (Martin *et al.* 1970; Rees & Hore, 1970) some corticospinal fibres end laterally and ventrally within laminae V to VII inclusive. Golgi-impregnated material from the North American opossum (collection of Dr James S. King, The Ohio State University) shows that the dendrites of large ventral horn cells extend out of the confines of lamina IX, as has been reported for other forms. If this is true for potoroo and the brush-tailed possum, the existence of distal axodendritic connections of a small number of cortical fibres with ventral cells cannot be ruled out.

It is well known that corticospinal fibres arborize within the confines of lamina IX in certain primates [the slow loris (Campbell, Yashon & Jane, 1966), the rhesus

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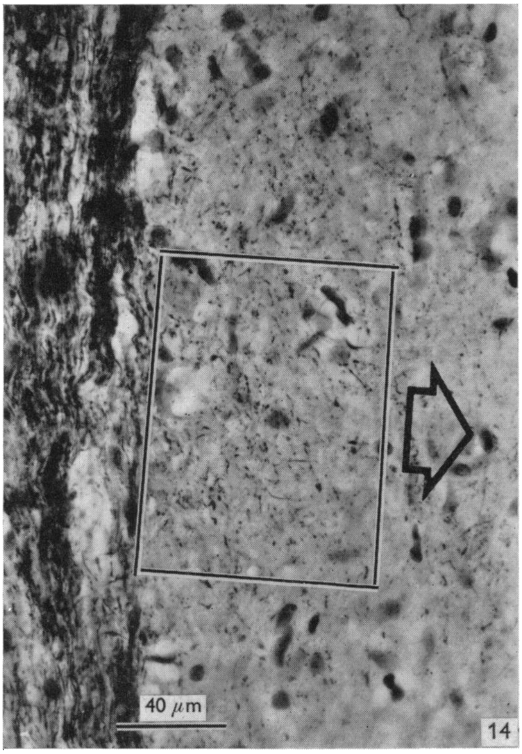
Fig. 14. Photomicrograph of a horizontal section (C. 6) through lamina V on the side opposite a decortication (Fig. 6A). The impregnated, degenerating corticospinal fibres at the base of the dorsal funiculus can be seen to the reader's left. The rectangle outlines the area seen at higher power in Fig. 15. Fink–Heimer technique.

Fig. 15. High power photomicrograph (oil) of the region of lamina V outlined in Fig. 14. Fink–Heimer technique.

Fig. 16. A horizontal section through lamina III on the side opposite a decortication. Longitudinally coursing degenerating fibres are indicated by the arrows. Fink–Heimer technique.



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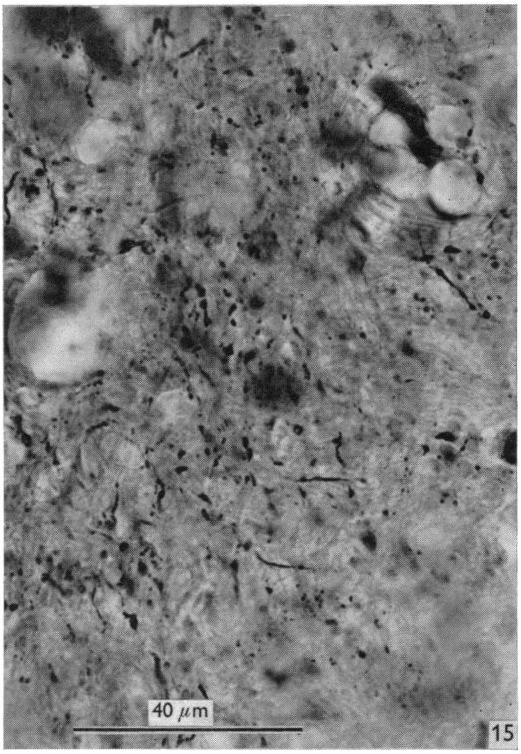

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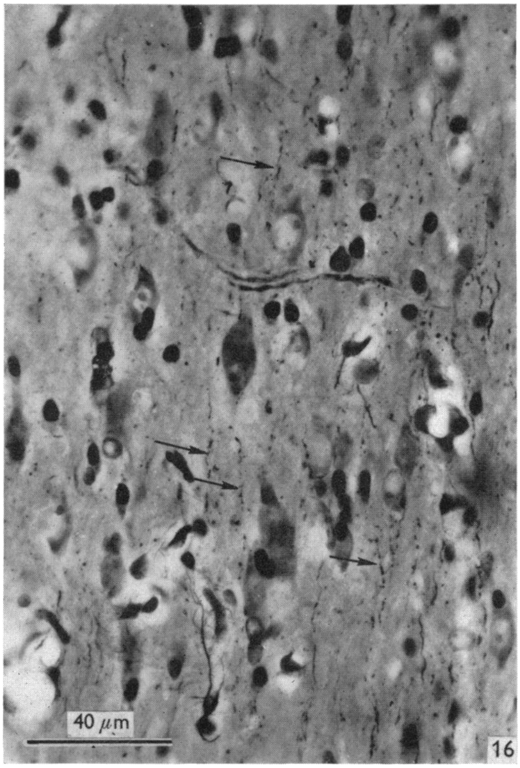

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monkey (Liu & Chambers, 1964), the capuchin, spider, woolly and vervet monkey (Petras 1968), the gibbon (Petras 1968), the chimpanzee (Petras, 1968)] and the raccoon (Buxton & Goodman, 1967; Petras & Lehman, 1966) and that direct cortical connexions with the lower motor neurons of lamina IX can be correlated with the ability to utilize individual digits for fine, rapid, co-ordinated movements. In spite of their motor dexterity, neither the potoroo (personal observations) nor the brush-tailed possum (personal observations; Rees & Hore, 1970) possess the ability to employ individual digits; thus, the lack of corticospinal fibres within lamina IX is not surprising.

The apparent differences in the terminal course of corticospinal fibres within the different laminae of the dorsal horn deserves mention. Horizontal sections of cervical cord segments from decorticate specimens reveal that most of the degenerating fibres within laminae III and IV have a longitudinal trajectory. In contrast, most of the degenerating axons which enter laminae V and VI ramify in the frontal and horizontal planes, although longitudinally coursing fibres are present. Although the organization of degenerating fibres must be interpreted with care because of the lack of continuity of individual axons, the pattern seen in our material correlates to some extent with the observations of Scheibel & Scheibel (1969) on Golgi-impregnated kitten spinal cords. They report that the dendrites in laminae II to IV inclusive spread in the longitudinal axis in the form of rectangles (lamina II) or cones (laminae III and IV). In contrast, the dendrites of neurons in lamina V and VI (as well as laminae VII–IX) are spread in the transverse plane (Scheibel & Scheibel, 1969). In addition, rapid Golgi material reveals that the input to laminae II and III forms densely arborized neuropil sheets (flame-shaped bushy arbors) that run for hundreds of micra along the longitudinal axis of the cord (Scheibel & Scheibel, 1969), whereas the fibres in lamina V and VI (as well as VII and VIII) terminate as a series of transversely orientated neuropil sheets. If a similar organization exists in potoroo, it is possible that the longitudinally coursing corticospinal fibres in laminae III and IV enter the longitudinal neuropil within those laminae, whereas those fibres in laminae V and VI which ramify in the frontal plane conform to the transversely orientated neuropil. It is of interest that the longitudinally coursing fibres in laminae III and IV (at least rostral to the cervical enlargement) appear to arise primarily from parietal cortex, whereas the fibres which arborize within laminae V and VI take origin predominantly from the cortex directly caudal to the orbital sulcus.

The corticospinal tracts of the diprotodonts studied to date [potoroo, (present study), the brush-tailed possum (Martin *et al.* 1970; Rees & Hore, 1970) and the quokka wallaby (Watson, 1971)] are larger and extend for a greater distance within the spinal cord than those of the polyprotodont North American opossum (Bautista & Matzke, 1965; Martin & Fisher, 1968). Such observations, together with the results of stimulation (Abbie, 1940) and the appearance of the diprotodont and polyprotodont brains available to us, make it tempting to assume that the diprotodont corticospinal tracts are better developed than those of the polyprotodonts. However, before such a broad generalization can be made, more sampling is necessary. It would be particularly interesting to study the corticospinal tract of a polyprotodont, such as the Tasmanian cat, which is extremely fast and mobile in contrast to the relatively slow moving North American opossum.

It was felt that if differences in motor performance among diprotodonts could be correlated with variations in the corticospinal tracts, it would become apparent by comparing and contrasting this tract in potoroo and the brush-tailed possum. Comparison of material from decorticate brains of both species suggests that there are more cortical fibres in laminae VII and VIII in the brush-tailed possum than in potoroo. These fibres in the brush-tailed possum may be responsible for the close physiological coupling between corticospinal fibres and cervical ventral horn neurons (Hore & Porter, 1971) which has been correlated with the ability of the animal to manipulate the forelimbs while climbing and grasping food (Martin *et al.* 1970; Hore & Porter, 1971). Although the forepaws of potoroo are used to grasp food they are not used with any dexterity for climbing and are often employed for digging.

However, in spite of the apparent difference in the number of fibres in laminae VII and VIII, the similarities in corticospinal fibres of the two forms outweigh the differences. They are similar in their origin, course, caudal extent, and area of termination. The most striking similarity is the dense projection to the medial part of the cervical dorsal horn (laminae III–VI), which is also characteristic of the quokka wallaby (Watson, 1971) and the North American opossum (Martin & Fisher, 1968). Only further sampling will tell whether or not this is a pattern common to all marsupials.

SUMMARY

Many corticospinal fibres in potoroo arise from the cortex directly caudal to the orbital sulcus, which is characterized by abundant pyramidal neurons in the internal pyramidal layer. Additional fibres arise from the more ventrally and laterally located parietal cortex, in which the internal granular layer is particularly well developed. The large dorsal corticospinal tract extends as far caudally as T. 12, whereas the smaller lateral tract can be traced only to T. 8. Both pathways are mainly crossed.

Corticospinal fibres distribute extensively to the medial portions of laminae III to VI inclusive and, although to a lesser extent, to the lateral portions of the same regions. A few fibres penetrate into lamina VII. Longitudinal sections of the cord reveal that many of the corticospinal fibres in the dorsal horn (laminae III and IV particularly) run longitudinally for some distance before ending. Although some fibres course longitudinally in laminae V and VI, others arborize in the frontal and horizontal planes. There is evidence to suggest that the fibres which end in the medial part of laminae V and VI arise mainly from the cortex caudal to the orbital sulcus, whereas many of those that enter lamina III and IV (especially rostral to the cervical enlargement) take origin from the lateral parietal area.

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