Cortico-cortical connections of the motor cortex in the brushtailed possum (*Trichosurus vulpecula*)

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INTRODUCTION

The motor cortex in the Australian marsupial brushtailed possum has been defined both physiologically by electrical stimulation of the brain (Goldby, 1939; Abbie, 1940; Rees & Hore, 1970) and anatomically by horseradish peroxidase mapping of the cortical projection field of the ventrolateral (VL) thalamic nucleus (Haight & Neylon, 1979). These studies have described a single motor area in parietofrontal cortex which partly overlaps the somatosensory cortex (Haight & Neylon, 1978, 1979), and as a consequence contains both a fifth cell layer with large pyramidal cells, and a definite fourth layer (Goldby, 1939; Abbie, 1940). In addition to its thalamic input from VL and the ventroposterior nucleus (VP), the motor cortex in the brushtailed possum receives input from a number of other thalamic nuclei (Neylon & Haight, 1983). Lesion studies have also described some of the efferent connections of the motor cortex in *Trichosurus*: these include terminations in the thalamus, mesencephalon, pons and medulla (Martin, Megirian & Roebuck, 1971; Martin & Megirian, 1972; Martin, Bresnahan, Henkel & Megirian, 1975).

We present here an examination of some of the cortico-cortical connections of motor cortex, mapped with horseradish peroxidase histochemistry. This study permits a comparison of the cortico-cortical connections of different cortical areas in the brushtailed possum; previous studies have examined cortical connectivity of auditory cortex (Aitkin & Gates, 1983) and visual cortex (Crewther, Crewther & Sanderson, 1984) as well as interhemispheric connections of the whole neocortex (Heath & Jones, 1971).

MATERIALS AND METHODS

Experiments were carried out on 7 adult possums of either sex, caught in Adelaide, South Australia. Possums were anaesthetised with fluothane, their heads were fixed in a stereotaxic frame and a restricted craniotomy was made over the desired cortical area. Horseradish peroxidase (HRP) was injected by pressure over a few minutes, using a glass micropipette, lowered to a depth of 2 mm below the cortical surface and then retracted 1 mm. A volume of 2–5 μl HRP (0·5 mg/μl, Boehringer Mannheim, in 0·9 % saline) was used. Spread of HRP at the injection sites was variable; in five cases HRP spread was small (Possums 4, 6, 7, 10 and 11 in Figure 1; Figures 2, 3 and 5 show HRP spread at small injection sites) and in two cases it was large (Possums 8 and 9 in Figure 1; Figure 7 shows the injection site in Possum 8).

Following 2 days survival possums were deeply anaesthetised with pentobarbitone sodium, and perfused via the heart with warm (37 °C) 2 % $NaNO_2$, followed by a
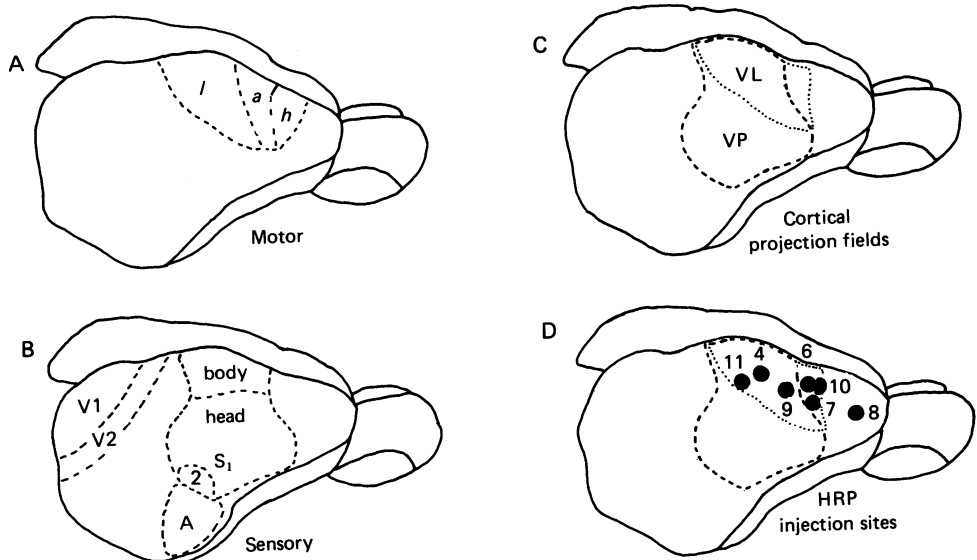
Fig. 1 (A–D). Line drawings of the possum neocortex, showing the locations of HRP injection sites of the present study in relation to the anatomically determined projection fields of VP and VL and physiologically determined motor and sensory areas of the cortex. The motor map (Fig. 1 A) is derived from cortex-surface stimulation (Goldby, 1939; Abbie, 1940; Rees & Hore, 1970) and shows the location of leg (*l*), arm (*a*) and head (*h*) areas. The sensory map (Fig. 1 B) shows the single auditory area (A – Gates & Aitkin, 1982) and primary and secondary somato-sensory cortex (S1, 2 – Haight & Neylon, 1979) which have been mapped physiologically. Primary and secondary visual cortex (VI, 2) have been only partly mapped physiologically (Crewther *et al.* 1984; Allman & Kaas – unpublished studies). The projection fields for VP (Haight & Neylon, 1978) and VL (Haight & Neylon, 1979) are shown respectively by dashed and dotted lines in Figure 1 C. Note the coincidence between the VP projection field in Figure 1 C and somatosensory cortex (S1, 2) in Figure 1 B. Figure 1 D shows the HRP injection sites of the present study – note that one is in prefrontal cortex (Possum 8), three are in agranular motor cortex (Possums 6, 7, 10) and three are in the area of sensory-motor overlap (Possums 4, 9, 11).

37 °C solution of 0·5 % paraformaldehyde and 2·5 % glutaraldehyde in 0·2 M phosphate buffer, pH 7·4. After 30 minutes fixation, the aldehyde mixture was followed by a 30 % solution of sucrose in phosphate buffer. Brains were then removed and stored in the sucrose-phosphate solution at 4 °C for up to 2 days. The brains were photographed and the injection sites marked on the photographs. Frozen 40 μm sections were cut in the frontal plane and 2 of every 5 sections through the cerebral cortex were processed for HRP activity, using the tetramethyl benzidine (TMB) blue reaction (Mesulam, 1978). Some TMB-processed sections were later counterstained with thionin (Adams, 1980). Labelled neurons and terminal fields were identified with brightfield and darkfield microscopy and then plotted onto outline drawings of the brain.

For presentation and analysis of results we identified within the cortex the approximate extent of the motor area from the thick fifth layer, and the body (SSB) and head (SSH) divisions of somatosensory cortex, from the thickness of the fourth layer, and the clumping of cells in the fourth layer in SSH (Neylon & Haight, 1983 – Fig. 2). In this study we have used the name 'agranular motor cortex' (AG) to describe the anterior motor cortex, which does not receive a mechanoreceptive input from VP,
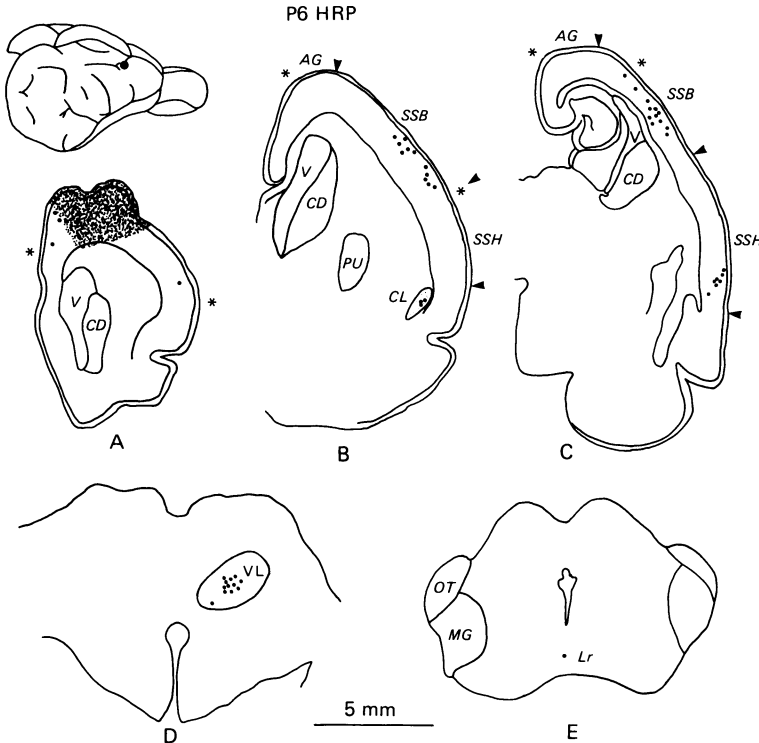
P6 HRP

Fig. 2(A–E). Possum 6 – HRP injection into agranular (*AG*) motor cortex. Injection site is shown in Section A, and is indicated on the outline drawing of the brain by a black dot. Many retrogradely labelled neurons (heavy dots) are located in sensorimotor cortex, mainly in the superficial layers. The borders of motor cortex, as defined by the prominent pyramidal cells in Layer 5, are marked with stars. The borders of the body (*SSB*) and head (*SSH*) regions of somatosensory cortex are marked by arrowheads. Note the overlap of somatosensory and motor cortex, excluding agranular motor cortex. Retrogradely labelled neurons are located also in *VL* (section D), linearis raphe (*Lr* – section E) and the claustrum (*CL* – section B). Anterograde label (fine dots) is present also in the claustrum. *CD*, caudate; *MG*, medial geniculate; *OT*, optic tract; *PU*, putamen; *V*, ventricle.

and does not have the granular layer 4 which is seen in adjacent somatosensory cortex.

RESULTS

Figure 1 shows the location of the HRP injection sites in the possum neocortex, together with maps of physiologically defined motor and sensory areas, and the cortical projection fields of the thalamic nuclei VP and VL. For purposes of clarity the cortical projection fields of VP and VL (Haight & Neylon, 1978, 1979) are shown once by themselves (Fig. 1C) and again on a map which has superimposed on it the HRP injection sites of the present study (Fig. 1D). Note that the HRP injection site for Possum 8 is in prefrontal cortex. The other six injection sites are within motor cortex. Those for Possums 6, 7 and 10 are within agranular motor cortex, which receives thalamic input only from VL. HRP injection sites for Possums 4, 9 and 11 are within the area which has sensory-motor overlap and receives thalamic input from both VP and VL. All seven HRP injections labelled neurons in the cortex and
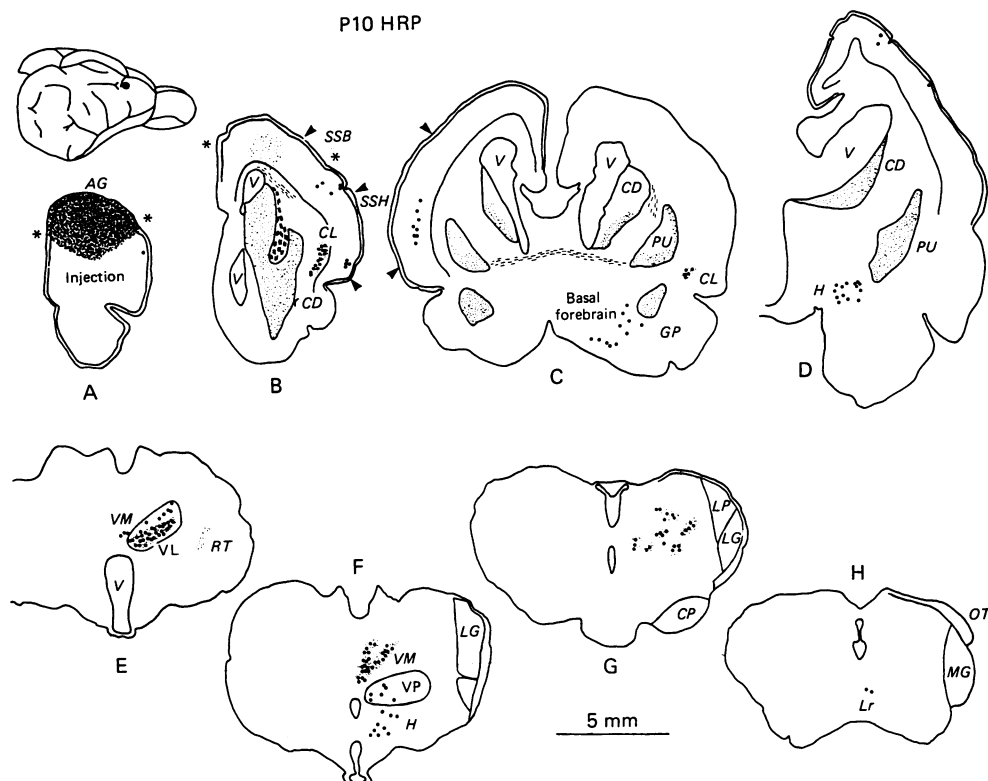
P10 HRP

Fig. 3(A–H). Possum 10 – HRP injection into agranular cortex. This injection must have encroached slightly on somatosensory cortex, since labelled thalamic neurons are present in *VP* (section F) as well as *VL* (section E). Other labelled thalamic areas include *VM* (sections E, F), some posterior thalamic nuclei (section G) and the reticular nucleus (*RT*, with antero-grade label only – section E). Note also label in the hypothalamus (*H* – sections D, F), linearis raphe (*Lr* – section H), basal forebrain (section C) and claustrum (*CL* – sections B, C). Within the cortex labelled neurons are located in *SSB* and *SSH* (section B), in *SSH* of the opposite hemisphere (section C), and in parietal cortex (section D). *CP*, cerebral peduncle; *GP*, globus pallidus; *LG*, lateral geniculate; *LP*, lateral posterior.

in subcortical areas. In addition, in each case there was anterograde labelling of terminal fields.

HRP injections in agranular motor cortex

Figures 2 and 3 show the distribution of HRP-labelled neurons from two of the three injections in agranular motor cortex. In the ipsilateral cortex there were labelled neurons adjacent to the injection site (Figs. 2A, 3A), and in the body (SSB – Figs. 2B, C, 3B) and head (SSH – Figs. 2C, 3B) areas of sensorimotor cortex. Most labelled neurons were located in Layers 2 and 3 with a few also in Layers 4, 5 and 6. In Possum 10 there was also anterograde label in the patches of retrogradely filled neurons in SSH, indicating the existence of reciprocal cortico-cortical connections between areas AG and SSH. Figure 4 is a photomicrograph showing labelled neurons within SSH in Possum 6. In the contralateral cortex labelled neurons were located in SSB in Layers 2 and 3 in one animal (Possum 7 – not illustrated) and in SSH in Layer 5 in another case (Possum 10 – Fig. 3C).

As well as the cortico-cortical connections, the HRP injections in agranular motor
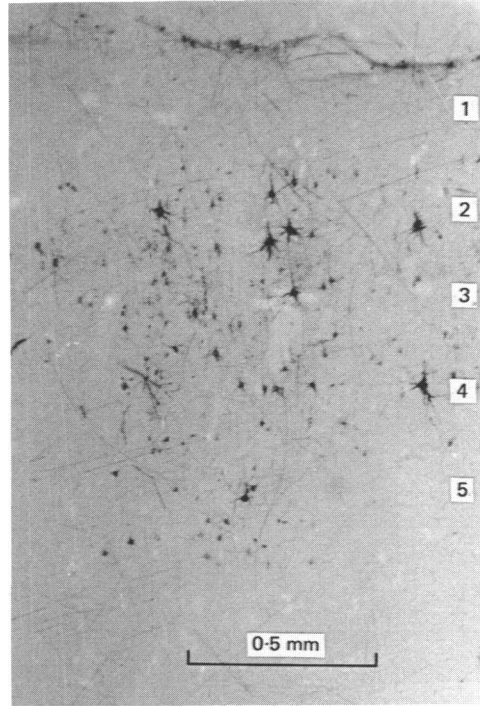
Fig. 4. Photomicrograph showing HRP-filled neurons in Area SSH, following an injection of agranular motor cortex in Possum 6. The photograph was taken from a section nearly adjacent to the one depicted in Figure 2C. Note that most retrogradely filled neurons are in the upper cortical layers. Cortical layers 1–5 are numbered.

cortex revealed reciprocal connections between motor cortex and several thalamic nuclei, including VL (Haight & Neylon, 1978, 1979). Two injections must have encroached slightly on sensorimotor cortex, since within the thalamus there was label in VP as well as VL (Possums 7, 10 – Fig. 3E, F); the third injection (Possum 6 – Fig. 2D) labelled cells in the thalamus only in VL. Other reciprocal thalamic connections of motor cortex are with the ventromedial thalamus (VM – Fig. 3E, F) and the posterior nucleus (PO – Neylon & Haight, 1983). HRP injections in the rostral motor cortex of the marsupial native cat also label neurons in VM (Haight & Neylon, 1981).

HRP injections in motor cortex also labelled neurons in the raphe nuclei of the midbrain (Figs. 2E, 3H) the basal forebrain (Fig. 3C) and the hypothalamus (Fig. 3D, F). Reciprocal connections were evident between motor cortex and the claustrum (Figs. 2B, 3B, C) and there was dense anterograde label in the caudate nucleus, putamen and globus pallidus (Fig. 3B–D.) These connections are well known in placental mammals (Donoghue & Parham, 1983).

HRP injections in sensorimotor (granular) cortex

Figure 5 shows the distribution of label resulting from one of the three HRP injections in this region. In the ipsilateral cortex the injections labelled cells adjacent to the injection site (Possums 9, 11 – not illustrated), in agranular motor cortex (Possum 4 – Fig. 5A), in SSH (Possum 4 – Fig. 5E) and in somatosensory Area 2 (S2) (Possum 9 – Fig. 6). Most labelled neurons were located in cortical Layers 2 and
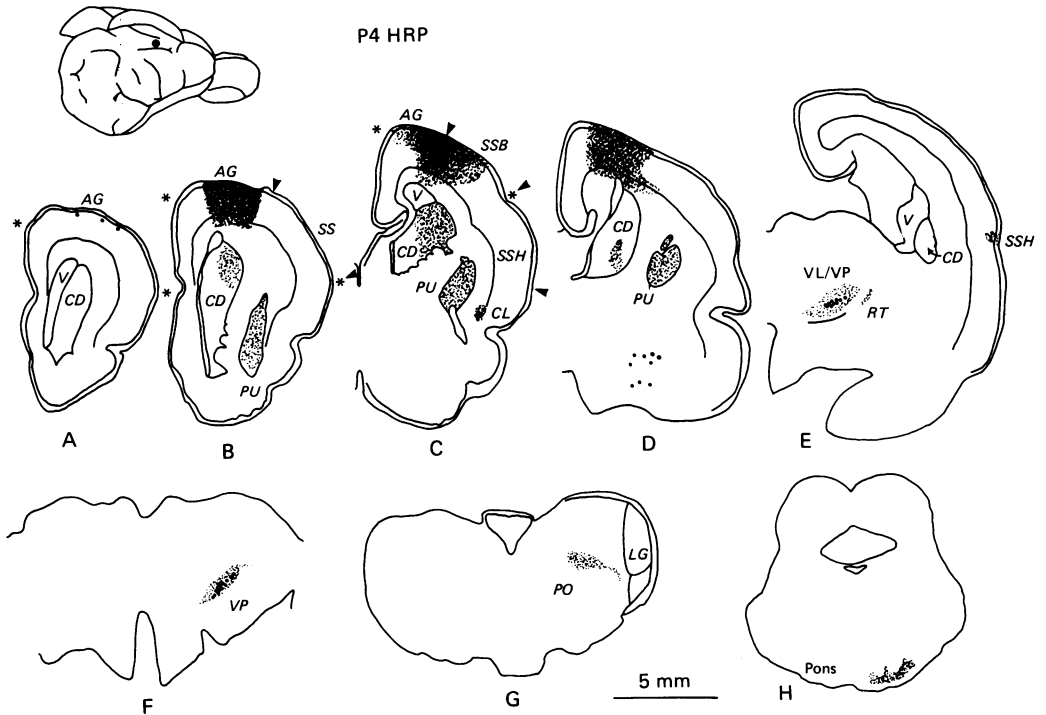
Fig. 5(A–H). Possum 4 – HRP injection in sensorimotor cortex, including agranular motor cortex (*AG* – sections B, C) and the body region of somatosensory cortex (*SSB* – section C). Note retrogradely labelled cells in the basal forebrain (dots – section D) and anterograde label in the posterior nucleus of the thalamus (*PO* – section G) and in the pons (section H). Labelled neurons in the cortex are located in *AG* (section A) and in *SSH* (section E – also contains anterograde label).

3 with a few also in Layers 4, 5 and 6. There was both anterograde and retrograde label in some cortical areas, implying reciprocal connections between the injection site and the labelled area; anterograde label to SSH in Possum 4 (Fig. 5E) and to S2 in Possum 9 (Fig. 6) was distributed through most cortical layers including Layer 1. The large HRP injection of sensorimotor cortex (Possum 9) labelled many neurons in Layer 5 of the contralateral cortex.

In addition to the label in cortical areas, there was both retrograde and anterograde label in three thalamic nuclei – VL, VP and PO (Fig. 5E–G). We also demonstrated reciprocal connections between sensorimotor cortex and the claustrum (Fig. 5C), projections from the basal forebrain (Fig. 5D), and projections to the caudate, putamen and pons (Fig. 5B – D, H).

HRP injection in prefrontal cortex

There was one large injection of HRP in prefrontal cortex, without involvement of motor cortex: the injection did not appear to invade motor cortex and there was no labelling of the specific brain sites which connect with motor cortex. Figure 7 shows sites labelled in the brain by the injection in prefrontal cortex. There is considerable anterograde and retrograde label in the medial-dorsal (MD) thalamic nucleus (Fig. 7D); connections between prefrontal cortex and MD are well known in other species (Brodal, 1981). In agreement with studies in placental mammals (Brodal, 1981) we
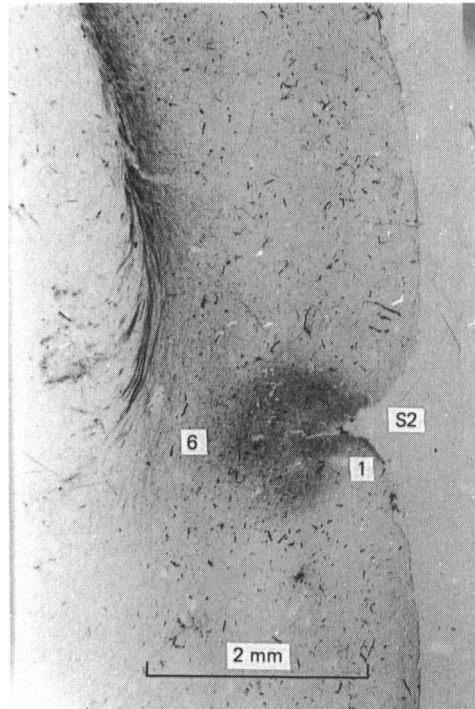
Fig. 6. Photomicrograph showing label in somatosensory area 2 following a large injection of HRP in sensorimotor cortex in Possum 9. The labelled patch in S2 contains both retrogradely labelled cells and anterograde label, which fills most cortical layers (numbers 1 and 6 indicate cortical layers); in the photomicrograph only anterograde label is readily visible. Note also the labelled fibres descending from the injection site.

also observed projections from cingulate cortex (Fig. 7B–D), raphe nuclei (Fig. 7E, F) and hippocampus (Fig. 7E). Projections from hypothalamus (H – Fig. 7C) and substantia nigra (SN – Fig. 7E) would need to be confirmed with smaller injections, to exclude the possibility that label shown in these areas in Figure 7 results from spread of the injected HRP into olfactory areas at the base of the brain. Finally Figure 7 shows projections from prefrontal cortex to the deeper layers of the superior colliculus (SC – Fig. 7F) and to the peri-aqueductal grey (PAG – Fig. 7F).

DISCUSSION

Cortico-cortical connections of motor cortex in Trichosurus

For the discussion we have combined the results of HRP injections in agranular and granular motor cortex, since differences between the connections of the two divisions of motor cortex were not large, and in addition the patterns of cortico-cortical connections demonstrated by the three injections into a single division of motor cortex were themselves slightly different.

Our results show that motor cortex in *Trichosurus* receives projections from somatosensory Area 1 and somatosensory Area 2 on the same side of the brain, and also from the contralateral S1. In one animal cells in parietal cortex just caudal to S1 were also labelled. Most of the cortical cells which project to motor cortex from the same hemisphere are located in Layers 2–4, with a few in Layers 5 and 6. In
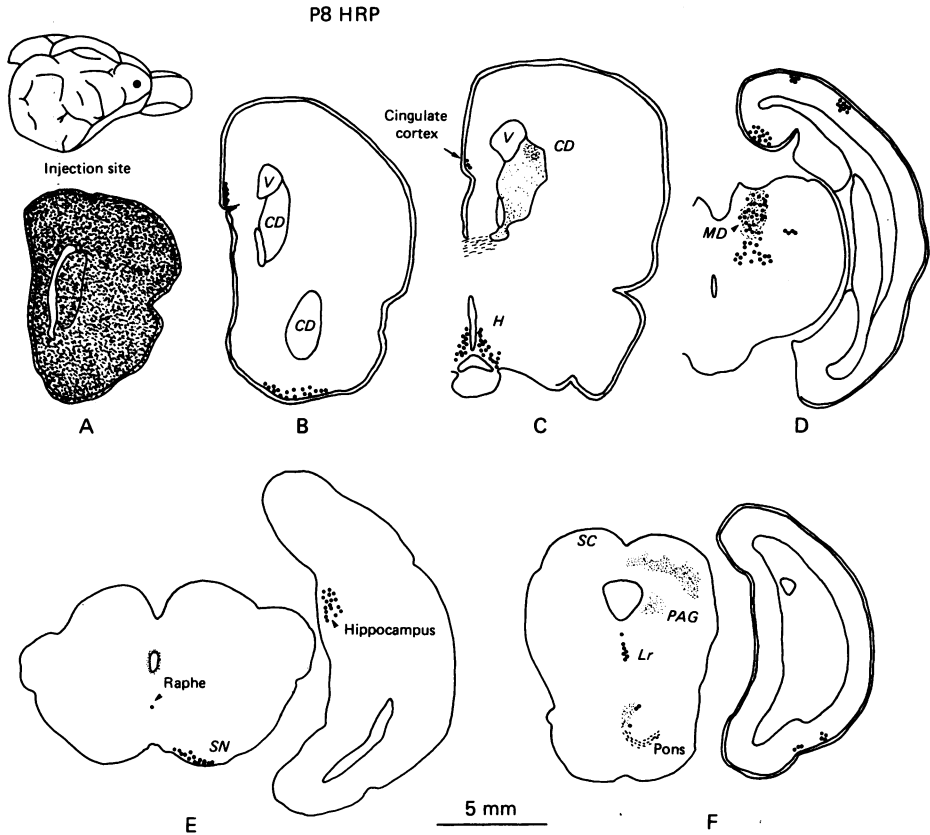
P8 HRP

Fig. 7(A–F). Possum 8 – a large HRP injection in prefrontal cortex. Note the dense antero-grade and retrograde label in the medial-dorsal thalamic nucleus (*MD* – section D; the area of *l*abel also includes other thalamic nuclei). Labelled cortical regions include the cingulate cortex (sections B–D), posterior parietal cortex (section D) and temporal cortex (section F). Note that the labelled areas in the brain are mostly different from those labelled by HRP injections in sensorimotor cortex. *PAG*, peri-aqueductal grey; *SC*, superior colliculus; *SN*, substantia nigra.

addition, in each experiment, there were labelled cells in the superficial layers of motor cortex, close to the injection site. In some experiments there was anterograde transport of HRP to the same areas which contained retrogradely labelled cells, indicating that at least some of the cortico-cortical connections of motor cortex with somatosensory cortex are reciprocal. The commissural inputs to motor cortex were quite prominent in two animals (Possums 9 and 10) with labelled cell bodies mostly in cortical Layer 5. The pattern of commissural labelling of cortical cells, while derived only in three animals, is comparable to the termination areas of commissural fibres described by Heath & Jones (1971): they described dense interhemispheric terminations in the face and trunk areas of S1, with smaller input to the limb areas of S1.

Our observations on cortico-cortical connections of motor cortex in *Trichosurus* complement the previous studies of cortico-cortical connections of the primary auditory and visual cortices. Primary auditory cortex receives input from cells in the deeper layers of contralateral auditory cortex; no projections from other areas in the same hemisphere have been described (Aitkin & Gates, 1983). Primary visual cortex

has connections with four other visual areas in the occipital lobe of the same hemi-sphere, and connections with peristriate cortex and lateral temporal cortex in the opposite hemisphere (Heath & Jones, 1971; Crewther, Crewther & Sanderson, 1984). Taken together these studies suggest that the primary sensory and motor areas in *Trichosurus* have cortico-cortical connections mainly with other areas of the same sensory modality. A technical point which has been noted in all of the HRP studies of *Trichosurus* is that cortico-cortical connections are more difficult to demonstrate than connections between cortex and subcortical regions; and further that large HRP injections of cortex retrogradely label many cortical cells which are not shown by the small injections – this is of course unfortunate, because the large HRP injections almost always invade more than one cortical area. A possible explanation for this phenomenon is that there might be considerable branching of the axons of cortical neurons (Bullier, 1986), and that neurons with branched axons would be most effectively labelled with HRP when the injection site included axon terminals from the different axon collaterals.

Comparisons with other mammals

The Virginia opossum

In the opossum there is complete overlap of somatic sensory and motor repre-sentations (Lende, 1963*a, b*). Connections of the forepaw region of sensorimotor cortex have been studied (Ebner, 1967; Foster & Ebner, 1977; Foster & Donoghue, 1979; Foster, Donoghue & Ebner, 1981): there are interhemispheric connections, and within the same hemisphere reciprocal connections with other sites in S1, with S2, and with two areas adjacent to S1. The cortico-cortical connections originate mainly in Layers 2 and 3 of parietal cortex, with some contribution from cells in deeper layers. This organisation is similar to that seen in our study on *Trichosurus*.

Rodents

In the rat, like the possum, there is a partial overlap of the primary somatosensory and motor areas (Welker, 1971; Hall & Lindholm, 1974; Donoghue & Wise, 1982; Sanderson, Welker & Shambes, 1984). Connections have been mapped both for the lateral agranular field (AG1) of motor cortex (Donoghue & Parham, 1983) and also for the granular and dysgranular zones of somatosensory cortex (Killackey, 1983). AG1 contains the motor head, trunk and part of the forelimb representations. Projections to AG1 arise from AG1 in the opposite hemisphere, and within the same hemisphere from S1, S2 and the medial agranular field which is adjacent to AG1. The cells of origin of these pathways are in Layers 2 and 3 and also 5 and 6. The medial agranular field of motor cortex, which contains the rat frontal eye fields (Hall & Lindholm, 1974) is reciprocally connected with visual cortex (Miller & Vogt, 1984; Sanderson, Dreher & Shameem, 1984). Connections similar to those described for AG1 in the rat have been observed for the vibrissal region of motor cortex in the mouse (Porter & White, 1983).

Monkeys

In monkeys there is complete separation of the primary somatosensory (S1) and motor (M1) representations in the cortex, and as a consequence it has been possible to study the separate connections of S1 and M1. Recent micromapping techniques have revealed multiple somatosensory representations in S1 (Kaas, Nelson, Sur &

Merzenich, 1979) and adjacent cortex (Robinson & Burton, 1980), and multiple motor representations within M1 (Strick & Preston, 1982) and adjacent cortex (Wise & Evarts, 1981). Primary motor cortex has connections within the same hemisphere with premotor cortex, supplementary motor cortex, posterior parietal cortex, S2 and part of S1 (Jones, Coulter & Hendry, 1978; Jurgens, 1984; Matelli, Camarda, Glickstein & Rizzolatti, 1984) and most connections are reciprocal. Callosal connections of motor cortex are mostly homotypic with the exception of the hand and foot areas in M1 (Jones & Wise, 1977; Jenny, 1979).

In summary cortico-cortical connections of motor cortex in species with complete, partial or no overlap of S1 and M1 are similar: within the same hemisphere motor cortex has reciprocal connections with S1, S2 and one or more supplementary or premotor areas, and there may also be connections with a parietal area just caudal to S1. There are usually intrinsic connections within motor cortex also. The interhemispheric connections are with M1, sometimes sparing the limb areas, and often with S1.

SUMMARY

Cortico-cortical connections of motor cortex in the marsupial brushtailed possum were traced by making injections of horseradish peroxidase (HRP) into two parts of motor cortex: the rostral agranular part which does not overlap somatosensory cortex, and the caudal part which does. Following injections in motor cortex, labelled neurons were observed on the same side of the brain within somatosensory areas 1 and 2 and in parietal cortex just caudal to S1, with most neurons in cortical Layers 2–4. Commissural connections were found in half of the experiments, with many labelled neurons in cortical Layer 5. We have compared the pattern of cortico-cortical connections in the possum with those seen in some other mammals, which appear generally similar.

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