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The organization of neocortical projections from the ventroposterior thalamic complex in the marsupial brush-tailed possum, *Trichosurus vulpecula*: a horseradish peroxidase study

J. R. HAIGHT AND L. NEYLON*

Department of Anatomy, University of Tasmania, Box 252C, GPO, Hobart, Tasmania 7001, Australia

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INTRODUCTION

The reports by Lende (1963*a*, *b*) of a total congruence of the motor and somatic sensory neocortical regions in the American marsupial, *Didelphis marsupialis* (= *Didelphis virginiana*), have led to the assumption that such congruence obtains with all marsupial mammals. This concept was firmly established after Lende's (1963*c*) comparison of the somatic sensory and motor regions of cortex in both *Didelphis* and a wallaby, *Macropus* (= *Thylogale*) *eugenii*, in which he used cortical surface recording and stimulating techniques to demonstrate the universality of the sensory–motor cortical amalgam within the marsupials. Further support was given to this concept by the anatomical degeneration study of Killackey & Ebner (1973) which showed that the ventroposterior (VP) and ventrolateral (VL) thalamic nuclei as well as the thalamic intralaminar nuclei have a convergent projection on to neocortex in *Didelphis*. Other investigators, using techniques similar to Lende's, have examined the sensory–motor cortex of the brush-tailed possum or phalanger, *Trichosurus vulpecula*; their results indicate that in this animal also the motor (Rees & Hore, 1970) and somatic sensory (Adey & Kerr, 1954) cortices occupy much the same area.

Recently, we and others have used a more precise microelectrode technique to map sensory projections from the body surface to neocortex in a number of diprotodontid marsupials including the common wombat, *Vombatus ursinus* (Johnson, Haight & Megirian, 1973; Megirian, Johnson & Haight, 1972), the Tasmanian pademelon, *Thylogale billardieri* (Weller, Haight, Neylon & Johnson, 1977) and the brush-tailed possum, *Trichosurus vulpecula* (Haight & Weller, 1973; Weller & Haight, 1973). In these animals an area of cortex along the rostral margin of the parietofrontal field (Figs. 1, 3B) was found to be free of mechanoceptive sensory projections, although an anatomical degeneration study (Ward & Watson, 1973) showed that VL projected heavily to this region in *Trichosurus*. Electrical stimulation of this same region had previously been reported to produce discrete body movements in *Trichosurus* and other marsupial mammals (Abbie, 1940; Goldby, 1939; Rees & Hore, 1970). This finding led us to suspect that, within the diprotodontid marsupials, the motor and somatic sensory cortices might not be fully congruent (Haight & Neylon, 1977*b*).

* Present address: Department of Therapy, Western Australian Institute of Technology, Selby Street, Shenton Park, Western Australia 6008.

We decided to ally our mapping studies with an anatomical analysis of the thalamic projections to the motor and somatic sensory cortical areas in *Trichosurus*. This, the first paper in a series, considers the cortical projection of the ventroposterior thalamic complex which relays somatic sensory information to neocortex. The recently developed horseradish peroxidase (HRP) technique for tracing neuronal connexions in the retrograde direction (Kristennson & Olsson, 1971; LaVail & LaVail, 1972; LaVail, Winston & Tish, 1973) suggested itself as an obvious method to employ. Hence, this paper is also concerned with some aspects of the general applicability and precision of the HRP technique as well as with the analysis of the cortical projection patterns of the VP complex.

In *Trichosurus* VP can be divided into three cytoarchitecturally distinct regions, a ventrolateral part or VPL, a dorsomedial part or VPM and a posteromedial part or VPP (Haight & Neylon, 1978*a*). VPL and VPM correspond to the similarly named subdivisions within the ventroposterior complex of many other mammals (Rockel, Heath & Jones, 1972). VPP may be unique to the diprotodontid marsupials and, in *Trichosurus*, exhibits considerable inter-animal cytoarchitectural variability, and occasionally cannot be identified (Haight & Neylon, 1977*a*, 1978*a*, *b*). As will be shown, each of these regions projects discretely and in a well organized manner to specific regions of the parietofrontal neocortex.

MATERIALS AND METHODS

A total of 37 adult brush-tailed possums of both sexes was used in this study. All were caught in the vicinity of Hobart, Tasmania.

Preparation and HRP injection procedure

Induction and maintenance of anaesthesia was by intraperitoneal injection of sodium pentobarbital (40 mg/kg, initial dose). The animals' heads were fixed in a cat stereotaxic frame and the desired area of neocortex exposed under aseptic conditions.

In each animal single injections of 0·3–1·0 μl of HRP solution (0·5 mg/μl Sigma Type VI HRP in 0·9 % saline) were made into one or both hemispheres using a 1·0 μl syringe with a 26 gauge coring needle which had been electrolytically tapered at the tip to a diameter of 0·25–0·30 mm. The syringe was rigidly mounted on the stereotaxic frame and a micro-drive apparatus used to depress its plunger. Injections were carried out over a 15–30 minutes interval and a similar time was allowed to lapse before the needle was removed at completion of the injection. The needle was driven approximately 2 mm into the hemisphere and then withdrawn 1 mm in order to lessen the depression 'dimple' on the brain surface caused by the needle tip. This procedure, in all but two cases, produced HRP injections which were restricted to the neocortex and did not intrude appreciably into the underlying white matter and other subcortical areas. Initially, injections were made using only one hemisphere per animal. Examination of these early experiments showed that the thalamic projections to neocortex were strictly ipsilateral. Consequently, later experiments used both hemispheres.

Tissue procedures

The following procedure was found to demonstrate the best labelling in the thalamus.

Following 24 hours' survival the animals were perfused, *per cardium*, with 0·9 %

saline solution followed by a solution of 0·5 % paraformaldehyde and 2·5 % glutaraldehyde in 0·1 M phosphate buffer (pH 7·6). The brains were removed at once and placed in the perfusant solution for 1–3 days, during which time they were photographed at various orientations and the penetration site(s) marked on the photographs. Prior to sectioning, the brains were soaked for 24 hours in the perfusant solution to which 20 % by volume of sucrose had been added.

The hemispheres were then separated from the brain stem and a block containing the thalamus was frozen and sectioned at 40–60 μm. Three thalami were cut in the sagittal plane, the remainder in the coronal plane. Three parallel series of sections were collected in 0·1 M phosphate buffer (pH 7·6), the first of which were mounted on gelatinized slides, stained with aqueous thionin and covered. This set served as a normal series for the identification of thalamic nuclei. The second and third series were transferred to a solution of 0·05 % 3-3′-diaminobenzidine tetrahydrochloride (Sigma) in 0·05 M Tris-HCl buffer (pH 7·6) to which 0·01 % hydrogen peroxide was added. After incubation for 15–20 minutes at room temperature the sections were returned to the phosphate buffer solution. The second series was mounted, otherwise unstained, on gelatinized slides and covered. The third series was counterstained with thionin before covering.

The cortices were dealt with separately. Where the penetrations were in the parietofrontal region (excepting along the supramarginal ridge of the sagittal fissure), this was circumscribed and removed, together with the underlying white matter, as shown in Figure 2. The resulting cortical slab was gently flattened, frozen and sectioned tangentially at 50–75 μm. The slices were gathered in two series, the first of which was stained with thionin and the second developed for the peroxidase reaction and then counterstained with thionin. The remaining cortices were sectioned coronally rather than tangentially. Otherwise their treatment was the same.

Analysis

Sections incubated for the peroxidase reaction were scanned using both bright and dark field to locate the sites to which HRP had been transported (Fig. 2D, E). The location of HRP labelled cells was determined by direct comparison with an immediately neighbouring section from the normal thionin series or, in the case of the counterstained sections, by direct placement of labelled cells in their respective thalamic nuclei. The location and extent of the HRP label was then indicated on an outline drawing of the thalamus taken from the normal series and, in all cases, referred to the right side.

In a number of cases the proportion of the VP cell population demonstrating HRP uptake was determined. Selecting the most prominent region of HRP label, the number of cells present in an area of VP was determined and the ratio of HRP labelled cells to total number of neurons was calculated. This procedure was repeated between three and five times at each of at least three selected levels in the thalamus.

The possum neocortex

Once the retrograde transport of HRP from axonal terminals in the cortex to cell bodies of origin in the thalamus has been demonstrated, it becomes necessary to establish criteria for comparing individual experiments. Though each cortical penetration site can be accurately placed in a given experiment, the positional relationships of the individual penetrations with respect to one another must also be known as accurately as possible. Fortunately, certain features of *Trichosurus*'

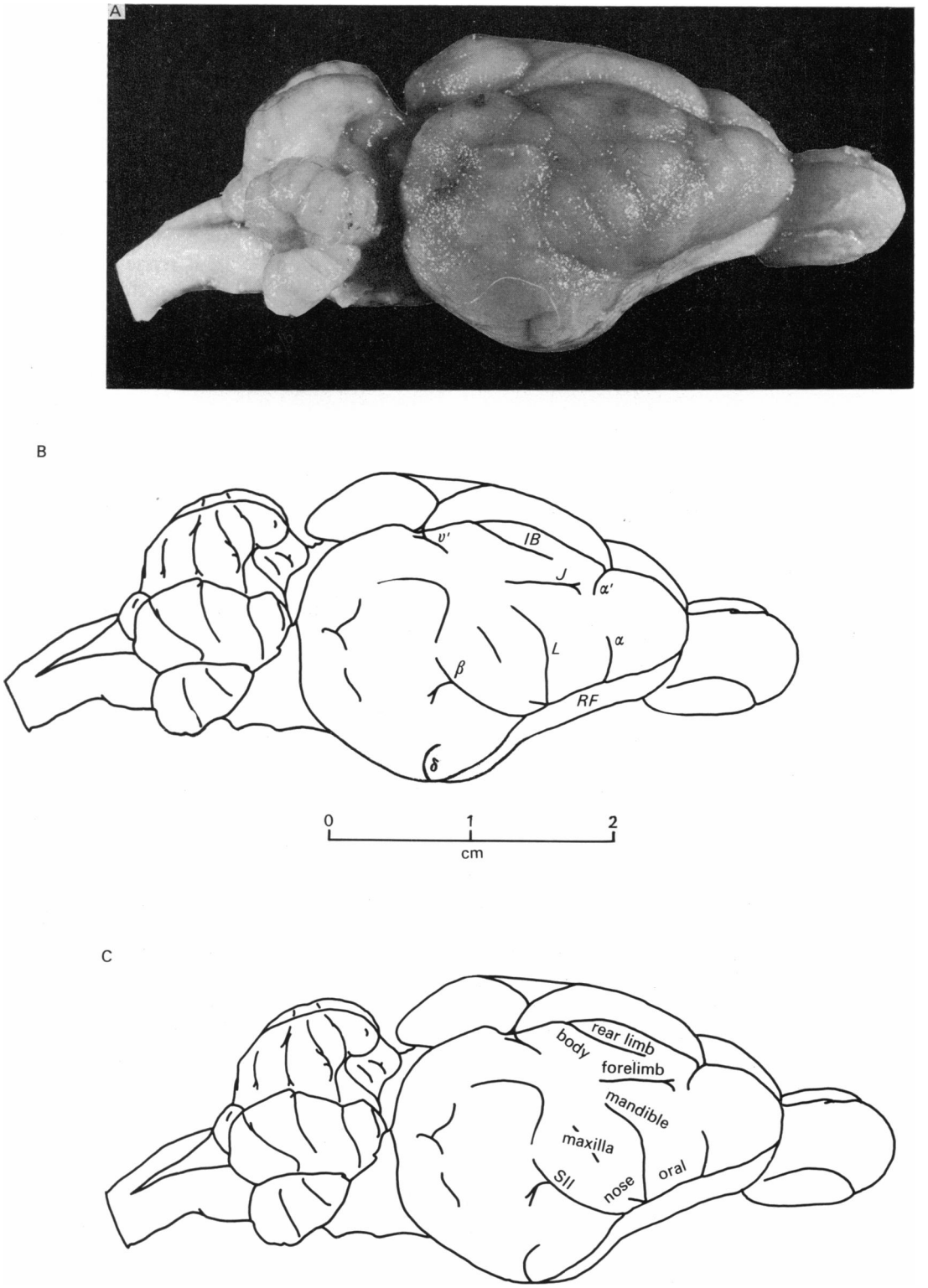
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Fig. 1

cortical mantle make this task feasible and permit a high degree of confidence in constructions such as Figure 3A, which shows all the successful HRP injection sites projected on to the cortex of a single, typical right hemisphere.

Though usually considered lissencephalic, the cerebral mantle of *Trichosurus* possesses considerable surface detail (Fig. 1). The neocortex is liberally supplied with furrows and grooves which, while highly variable in depth and extent, are nonetheless present in a reproducible pattern from animal to animal (Haight & Weller, 1973). As this and later papers in this series will show, and as electrophysiological recording studies have previously shown, many of these incipient sulci have a functional significance. They delimit the cortical projection fields of certain thalamic nuclei and separate sensory projections from particular body regions (Fig. 1C) within the primary somaesthetic region or SI (Haight & Weller, 1973; Johnson *et al.* 1973; Lende, 1963*c*; Megirian *et al.* 1972; Weller *et al.* 1977). These consistent sulcal patterns aid in comparing penetration sites from experiment to experiment, hence a few remarks on their naming and exact physiological significance are in order.

Because the naming of sulci in Australian marsupials by Ziehen (1897) has attained some currency, we decided to retain some of his more familiar non-functional terms and to combine these with some of the functional terms introduced by Johnson *et al.* (1973). This unfortunately, but necessarily, results in a hybrid nomenclature which uses both Greek and Roman symbols to denote sulci (Fig. 1B). We have not named gyri.

A 45° lateral view of a typical *Trichosurus* brain is seen in Figure 1A. The rhinal fissure (RF) is the only deep sulcus present, the remaining sulci being much shallower. The two notches along the midline, α' and ν', denote the anteromedial and posteromedial boundaries of the region of interest in this study, a region we call the parietofrontal cortex. Laterally, the anterior and posterior boundaries are marked by sulci α and β, respectively. Within this region three consistent shallow grooves are seen. Nearest the midline and running almost parallel with it is the interbrachial sulcus (IB). Lateral to IB is the jugular sulcus (J) while the labial (L) sulcus is seen extending medially from the rhinal fissure. As is shown in Figure 1C, these last named sulci serve to delimit projections to cortex from various body regions.

Another aid to precise localization of cortical penetrations is the presence in the parietofrontal cortex of the barrel field, an histological elaboration of cortical layer IV found in SI, and first described in *Trichosurus* by Weller (1972). This cortical feature has been found to be reproducible in shape, cytoarchitecture and position from animal to animal (Weller & Haight, 1973) and can be used to assess penetration placement among experimental subjects. When the parietofrontal cortex is removed, as shown in Figure 2, cut tangentially and stained, portions of the barrel field (Fig. 2B) are readily seen. Its use as a positional indicator in conjunction with associated sulci is easily appreciated.

In consequence of these considerations the cortical injection sites, especially within the parietofrontal region, can be placed with considerable accuracy on a

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Fig. 1. Descriptive and organizational features of possum neocortex. (A) 45° view of possum brain, showing major surface details. (B) Outline drawing of (A) with constant sulci named. Greek symbols are taken from Ziehen (1897). *IB*, interbrachial sulcus; *J*, jugular sulcus; *L*, labial sulcus; *RF*, rhinal fissure. (C) Synopsis of the distribution of mechanoceptive projections to possum neocortex. Note the relationship of sulci to projections from particular body regions (see text).

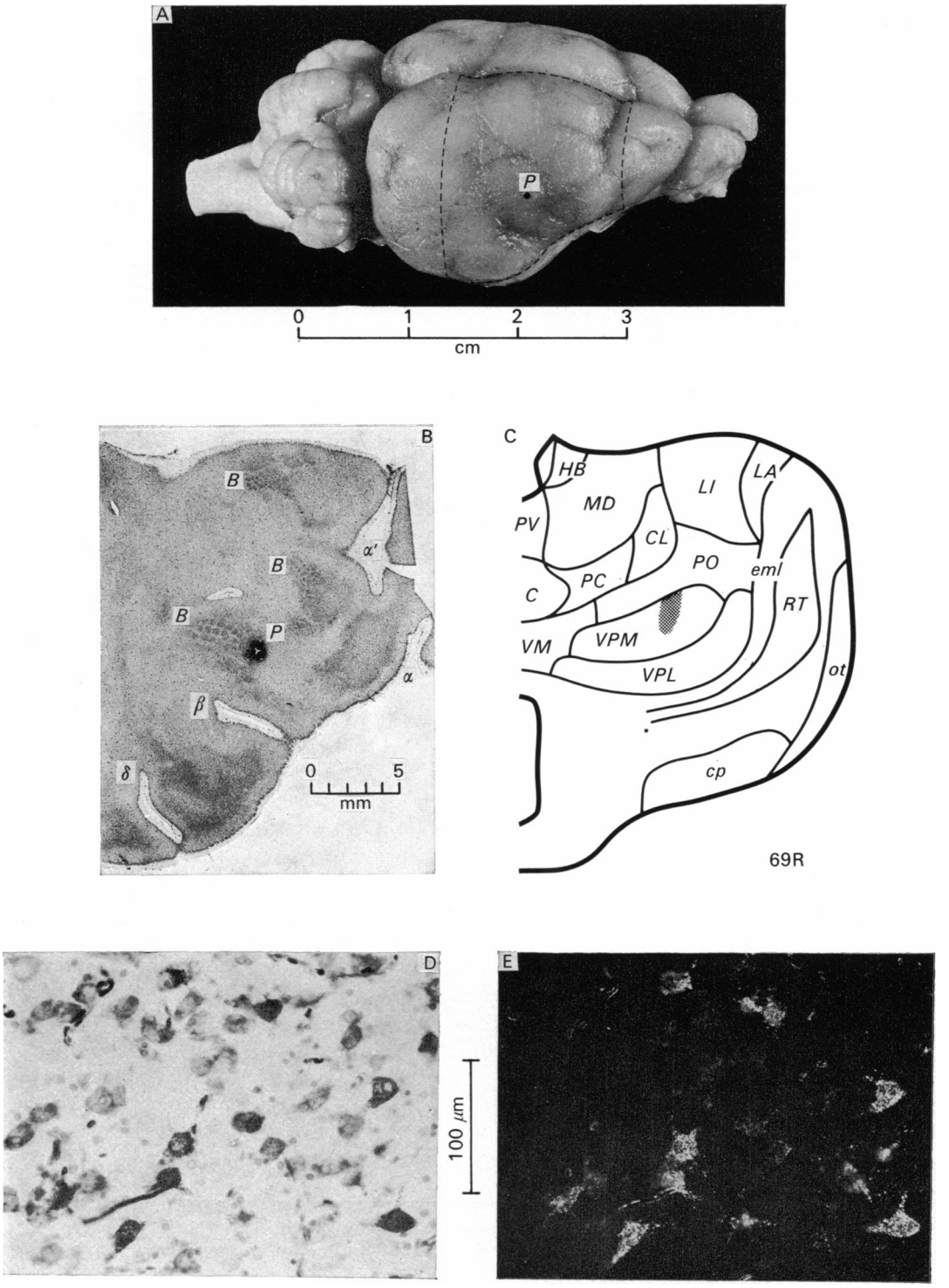
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Fig. 2

standard representation of the possum neocortex. Thus, all penetration sites and thalamocortical projection fields will be referred to a standard diagram of the brain as pictured in Figure 1.

RESULTS

The neocortical projection field of VP

Retrograde transport of HRP from neocortex to thalamus was successfully demonstrated in 57 separate hemispheres from the 37 possums. Of these 57 penetrations, 38 produced HRP label in VP neurons (Fig. 3A). As shown in Figure 3B, VP's cortical projection field is contained entirely within the parietofrontal region and, as determined by planimetric measurements, occupies nearly 35 % of the total neocortical area.

Within the parietofrontal region, three small areas apparently fail to receive VP projections. The first of these is a medially located patch of cortex just posterior to sulcus α'. Four closely spaced injections into this area consistently failed to produce label anywhere in VP. Another region just anterior to sulcus ν' also appears not to receive a VP projection. Both of these regions do, however, receive projections from other thalamic nuclei. The third VP projection-free area lies along the superior bank of the rhinal fissure and extends a short way along the superior bank of sulcus β (Fig. 3B). Repeated injections into this area failed to demonstrate any thalamic uptake, suggesting that it may be free of thalamic input.

The cytoarchitectural subdivisions of VP each project to discrete parts of the parietofrontal field (Fig. 4). Projections from VPL, except those to SII, are restricted to the region medial to the jugular sulcus. Lateral to the jugular sulcus are found projections from VPM and VPP.

VP neurons and HRP uptake

Those VP neurons displaying HRP label usually did so quite prominently. That is to say, in a given cell the HRP granules were numerous and, given optimal tissue processing, stained heavily. The most significant labelling variable encountered was the proportion of neurons displaying HRP uptake to the total number of neurons in a particular area of VP. Injections into most areas of the VP cortical field produced *dense* labelling of cells in VP. This we define as the case where 65 % or more of the neurons in the area of maximum label prominence display HRP granules. This figure ranged as high as 95 % in certain areas of VPL. Other cortical injections produced *sparse* labelling which involved 30 % or fewer of the neurons in a particular area of VP. Though considerable variability was noted within our classifications of *dense* and *sparse* thalamic label, the percentage gap between dense and sparse labelling was never filled. Either more than 65 % or fewer than 30 % of the neurons in a given area of VP were labelled after a cortical injection of HRP. These figures were verified in several experiments using the counting procedures outlined earlier.

Fig. 2. Outline of experimental procedures, taken from experiment 69R. (A) Right hemisphere. Dotted area outlines the area of cortex pictured in (B) below. *P* indicates the injection site. (B) A tangential section through neocortex corresponding to the outlined area in (A) above. Greek symbols denote sulci, see Fig. 1. *B* indicates portions of the barrel field in layer IV (see text) and *P* the penetration site. Note positional relationship of the penetration site with the sulci and barrel field. (C) Position of label in VP complex after injection of HRP at position *P* in (B) above. (D) Bright field microphotograph of thionin counterstained HRP labelled cells in the VP complex. (E) Same field as (D) above, dark field.

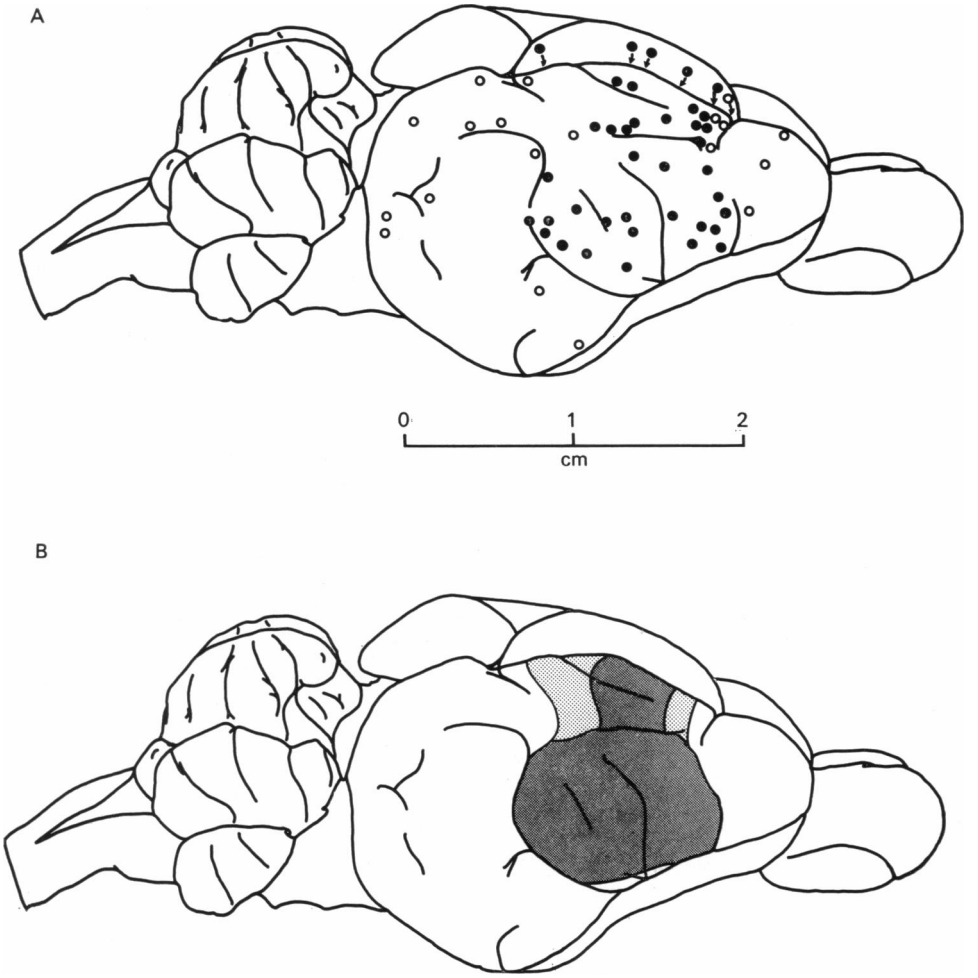

Fig. 3. Penetration sites and the cortical projection field of VP. (A) HRP injection sites which produced thalamic label. Open circles, experiments which produced label in thalamic nuclei other than in VP. Closed circles, experiments which produced label in VP. Arrows indicate a series of penetrations along the supramarginal ridge of the sagittal fissure and extending on to the medial bank of that fissure. (B) Area of cortex receiving VP projections as determined from the data in (A) above. Dark stipple corresponds to cortical area receiving *dense* projections from VP. The lightly stippled area receives *sparse* VP projections (see text for explanation of terms).

Eventually, we found that an accurate distinction between dense and sparse VP uptake could be made by visual inspection and the formal counting was discontinued except for occasional spot checks.

Injections lateral to the jugular sulcus almost invariably produced dense uptake in VP (dark stipple, Fig. 3B). The label in VP remained dense even after penetrations near the edge of the projection field. That is, a cortical penetration near the edge of the field would either produce no label at all in VP or it would result in dense labelling. Medial to the jugular sulcus dense labelling in VP only occurred from the six penetrations occupying the approximate middle third of the projection field. Six injections into the anterior, and five into the posterior, thirds resulted in a sparse uptake in VP (light stipple, Fig. 3B). The transition between the dense and sparse

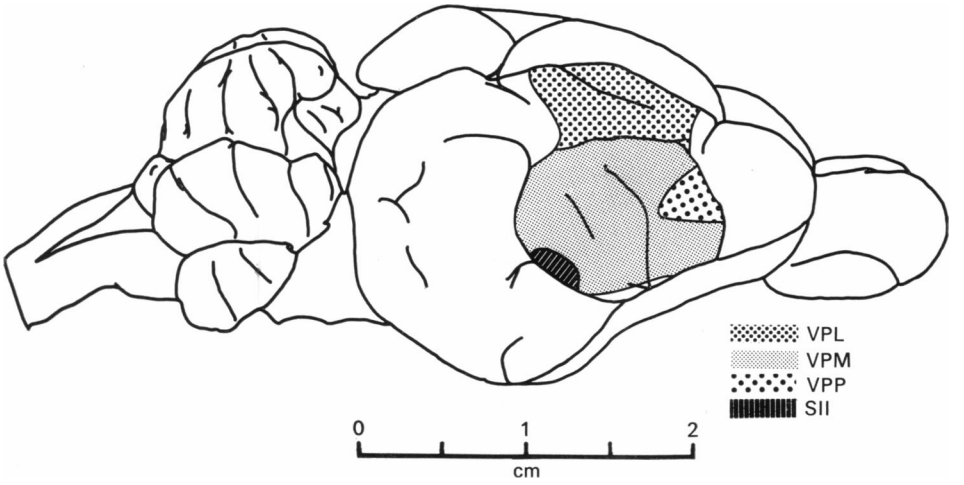

Fig. 4. The cortical projection fields of the VP subnuclei. The position of SII is also indicated.

uptake regions of the medial VP field was fairly sharp, occurring over very short distances of the order 1–2 mm (cf. penetrations 47R and 43L in Fig. 8). With penetrations placed near the anterior and posterior borders of the medial VP field the already sparse label produced in VP would gradually become even sparser, eventually fading out altogether. The label in the cells which did transport HRP, however, remained heavy.

Each HRP injection typically produced a solid band of label in VP which ran the full anteroposterior extent of the complex. This band tended to maintain its position within the complex. If, for example, the label was present in the ventromedial portion of the anterior part of VP, it would occupy the same position in the posterior part of VP as well.

Spread of HRP at the injection site and its effect upon VP uptake

Known volumes of HRP solution, ranging from 0·3 to 1·0 μl, were injected into the 57 hemispheres. The extent of radial spread of label from the injection site (Fig. 2B) seemed to bear no obvious relation to the amount injected. After incubation, the diameter of the stained area around the penetration site was usually between 1·5 and 3·0 mm, ranging from 0·7 to 9·0 mm. Spreads of less than 1·0 mm seldom produced any thalamic labelling. Spreads greater than 6·0 mm were noted in five cases. Later examination showed that the larger spreads were related to pial and cortical surface damage at the penetration site (three cases) or to injections which had penetrated deep into the white matter (two cases). The thalamic labelling in these cases did not appear to give anomalous results in VP, though the deep penetrations produced label in thalamic and other nuclei that did not take up label following more shallow injections into the same general cortical region.

We wished to know whether the measured, visible spread of label around the penetration site bore any relation to a measurable area of cortex from which HRP was transported back to the thalamus. Knowledge of this, even in a highly qualitative sense, could be useful in at least two ways. First, one could gain an idea of the number and regional distribution of the thalamic neurons projecting to a local cortical area of known size. Second, such information could provide an indication of

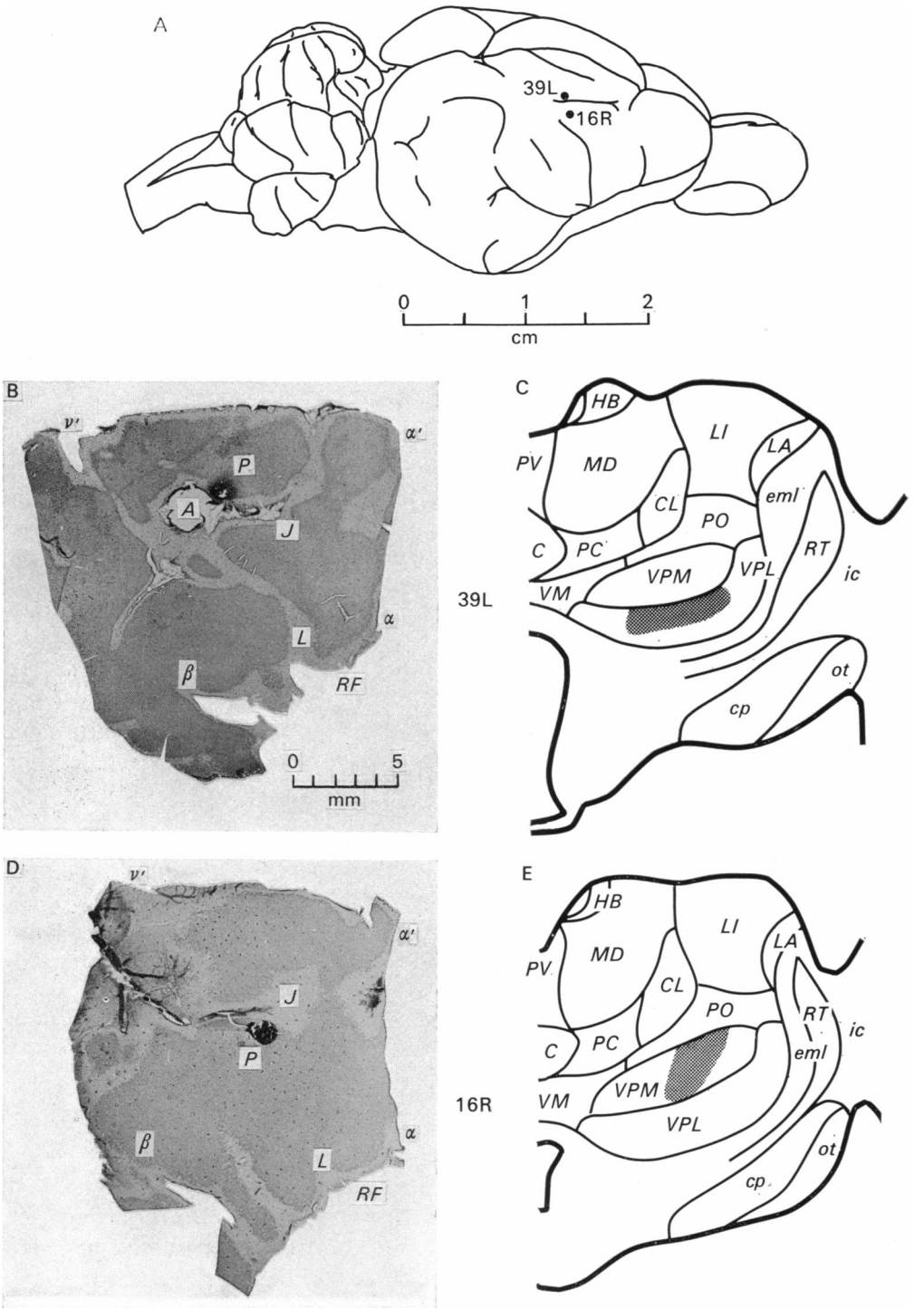
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Fig. 5

experimental precision. The topographical features of the possum cortex, plus the particular projectional relationships that the subdivisions of VP have with their cortical projection fields, suggested a way of approaching these questions.

In Figure 5 the thalamo-cortical relationships of two neighbouring penetrations are presented in some detail. The two penetrations are approximately 1 mm on either side of the jugular sulcus (j) and, if both penetrations had been placed in the same hemisphere, would be approximately 2·0–2·5 mm apart. The measurable spread of HRP around both penetration sites has a diameter of the order 1·5 mm near the surface of the cortex (Fig. 5B, D) and extends to slightly more than 2·0 mm at its widest point, approximately a millimetre beneath the surface (not illustrated). In neither case was any HRP reaction product seen in the bank of the jugular sulcus opposite that in which the injection had been placed. As stated above, the jugular sulcus separates cortical projections from VPL and VPM (Fig. 4). If the effective spread of HRP in the cortex had been much greater than the diameter of the visibly stained regions shown in Figure 5B and D, a certain amount of label overflow from VPL into VPM would have been expected from experiment 39L. This did not happen (Fig. 5C). The converse argument would have applied to experiment 16R (Fig. 5E) but, as with experiment 39L, the label is strictly confined in VP to the subdivision appropriate to the injection site. These results suggest that the area of effective uptake in cortex cannot be appreciably greater than the visible area of HRP spread surrounding the injection site.

A question might remain as to whether a shallow sulcus such as the jugular could form a barrier to the spread of HRP in cortex and, thus, account for the results shown in Figure 5. Figure 6, which compares a relatively large area of cortical spread with a smallish one, shows that a shallow sulcus is not a barrier to the spread of HRP. In experiment 53L the diameter of observed spread around the penetration site was nearly 6 mm and was centred in the area just posterior to sulcus α' which receives no VP projections (Figs. 3, 4). In this experiment the HRP spread forward and across sulcus α', a sulcus much deeper in most animals than the jugular. Posteriorly, the label extended well into the area which receives VPL projections (cf. Figs. 4, 6A). By way of comparison, penetration 39R was centred on the anterior fringe of the VPL projection field lateral to, slightly posterior to, and displayed considerably less spread of HRP around the penetration site than did 53L. If these two injections had been made into the same hemisphere, the spread of label in experiment 53L would have wholly contained that from experiment 39R (Fig. 6A). However, experiment 53L, in spite of its extensive cortical spread of HRP, produced no label at all in VP, although label appeared in other thalamic nuclei, including VL. Experiment 39R produced label in both VP and VL (Fig. 6). These results show that the area of effective HRP uptake can be considerably less than the extent of visible spread around the injection site and, in fact, that the uptake region may be confined to the immediate vicinity of the needle. The results shown in Figure

Fig. 5. Relationship of jugular sulcus to projections from VPL and VPM (see text). (A) Outline drawing of cortex showing HRP injection sites on either side of jugular sulcus. (B, D) Tangential sections of cortex showing position of penetrations with respect to jugular sulcus and indicating the extent of radial spread of HRP around the injection site. These sections were taken from near the cortical surface in order to emphasize the positional relationships of the penetrations and cortical surface features. For sulcus names, see Fig. 1; *A*, artifact, *P*, penetration site. Scale in (B) and (D) is the same. (C, E) Outline drawings of thalamic sections showing position of HRP label. Note that experiment 39L did not produce label in VPM and that 16R failed to produce label in VPL. For thalamic abbreviations see list on p. 485.

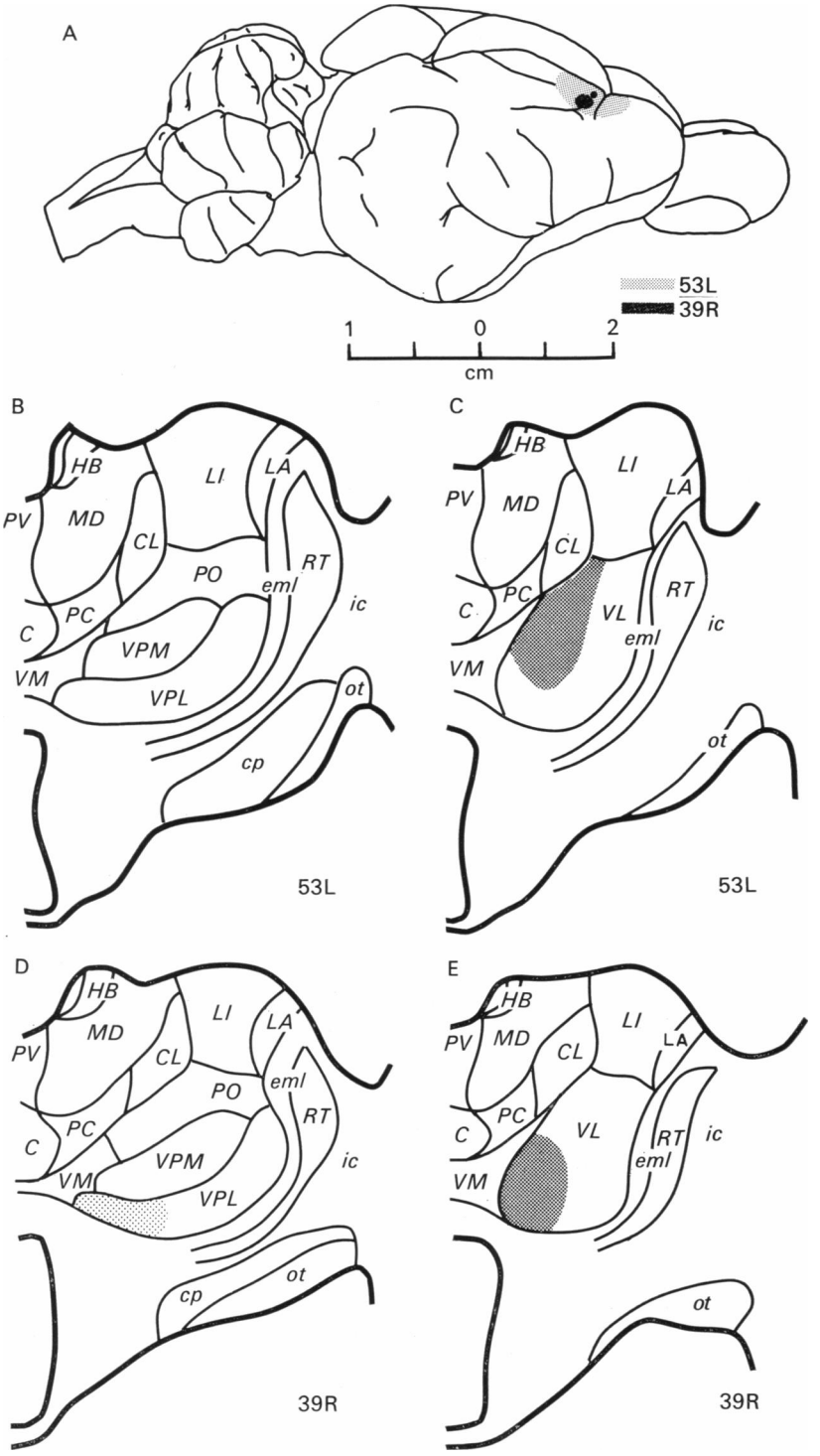
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Fig. 6

6 would suggest that the effective uptake region does not exceed 2 mm in diameter and is very likely less, otherwise experiment 53L would definitely have produced label in VP. These results also indicate that the spread of HRP around the injection site is not a reliable means of establishing the effective cortical uptake area. The results portrayed in Figures 5 and 6 do suggest that, provided an accurate means of comparing inter-experimental penetration loci exists, the HRP technique affords a high degree of experimental precision, the degree of which will become apparent in the following sections.

Organization of VPL projections to neocortex

With the exception of a small projection to the upper bank of sulcus β, which corresponds to the location of the secondary somaesthetic region or SII, the ventrolateral subdivision of VP or VPL projects to the portion of the parietofrontal cortex medial to the jugular sulcus and extending on to the bank of the sagittal fissure. Projections from VPL do not extend anteriorly as far as sulcus α' or posteriorly as far as sulcus ν' (Fig. 4). As mentioned earlier, each cortical injection produced a bank of label which spanned the anteroposterior extent of VPL while otherwise remaining in a constant position within the subnucleus. This finding permits the label field in a single thalamic section to be representative of the entire band of label in VPL. Hence, the results of each cortical injection into the VPL field are presented on thalamic drawings corresponding approximately to *Level A* in Figure 7, which is a drawing of a horizontal section through the ventroposterior complex.

Precise homotypic relationships (Welker, 1973) were apparent between the regions of label produced in VPL and the cortical penetration sites. Injections into the posterior regions of the VPL field produced label in the lateral part of VPL. More anterior penetrations produced a medial shift of label within VPL. Additionally, penetrations located in the medial portion of the VPL field (Fig. 8) labelled the ventral aspect of VPL, while more laterally placed penetrations (Fig. 9) resulted in a dorsal progression of label in VPL.

Considerable variation in the density of VPL label was noted as a function of the injection site. Injections into the anterior and posterior thirds of the VPL field produced sparse labelling in VPL (Fig. 3B). Results from these penetrations are indicated in Figures 8 and 9 by light stipple in the thalamic outlines. Injections into the middle third (approximately) produced dense label in VPL (dark stipple in Figs. 8, 9). This resulted in the lateral and medial portions of VPL displaying sparse label while the intermediate part of the subnucleus usually demonstrated dense label. While a given penetration in cortex resulted in either a wholly dense or a wholly

Fig. 6. The extent of HRP spread around the cortical penetration site and its effect upon thalamic labelling (see text). (A) Outline drawing of cortex showing injection sites (dark circles) with radial spread of HRP indicated by stippling. Note that experiment 53L was centred upon the parietofrontal region which does not receive VP projections (Fig. 3). The slightly more laterally and posteriorly placed experiment 39R is located on the most anterior fringe of the VP field. (B, C) Label in parts of the ventral thalamus produced by experiment 53L. Note that in spite of the extensive spread of label from the injection site over the rostral portion of the VP field, no label was detected in VP, though VL labelled heavily. (D, E) Label in parts of the ventral thalamus produced by experiment 39R. This penetration, located on the border of the VP projection field, displays label in both VP and VL, even though the radial spread of HRP from the injection site is very much less than that seen in experiment 53L. For thalamic abbreviations see list on p. 485.

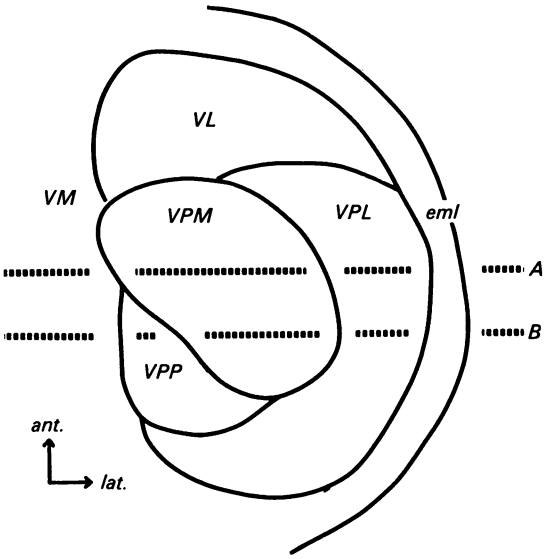

Fig. 7. Drawing of a horizontal section through the VP complex showing the approximate representational level of thalamic sections in the following figures. For abbreviations see list on p. 485.

sparse band of label in VPL, the homotypic relationships between thalamus and cortex were not affected by variations in labelling density.

Organization of VPM projections to neocortex

The cortical projection field of VPM occupies most of the lateral parietofrontal field (Fig. 4). Injections within the VPM field invariably produced dense labelling within VPM, in distinct contrast to the situation found in VPL. Except for three experiments in which the penetrations were located along the extreme anterior margin of the VPM field, label arising from a given penetration appeared throughout the anteroposterior extent of VPM.

Injections into the posteromedial corner of the VPM field produced label in the lateral part of VPM, as indicated by the symbol *l* in Figure 10. Taking this corner of the VPM field as a focal centre, injections within the field at increasing distance produced VPM label in progressively more medial parts of the subnucleus, as shown by the symbols *i* (intermediate) and *m* (medial) in Figure 10. Thus, a row of penetrations directed radially outward from the *l* region across the VPM field would produce a lateromedial shift of label in VPM. Figure 11 shows such a progression of label in VPM resulting from a row of penetrations posterior to and parallel with the labial sulcus. Figure 12 shows a similar progression resulting from a row of penetrations directed anteriorly and approximately parallel to the jugular sulcus.

Though a given injection would produce a band of label in VPM whose position was fixed throughout the anteroposterior extent of the subnucleus, there did not appear to be precise homotypy in the dorsoventral direction. For example, penetrations within the intermediate region of the VPM field (Fig. 10) would always produce label in the intermediate zone of VPM, but the position of label could and did end up anywhere dorsally or ventrally within the zone. Comparison of experiments 69R (Fig. 2), 31R (Fig. 11), 81L (Fig. 12) and 79L (Fig. 15) illustrates this point. In all

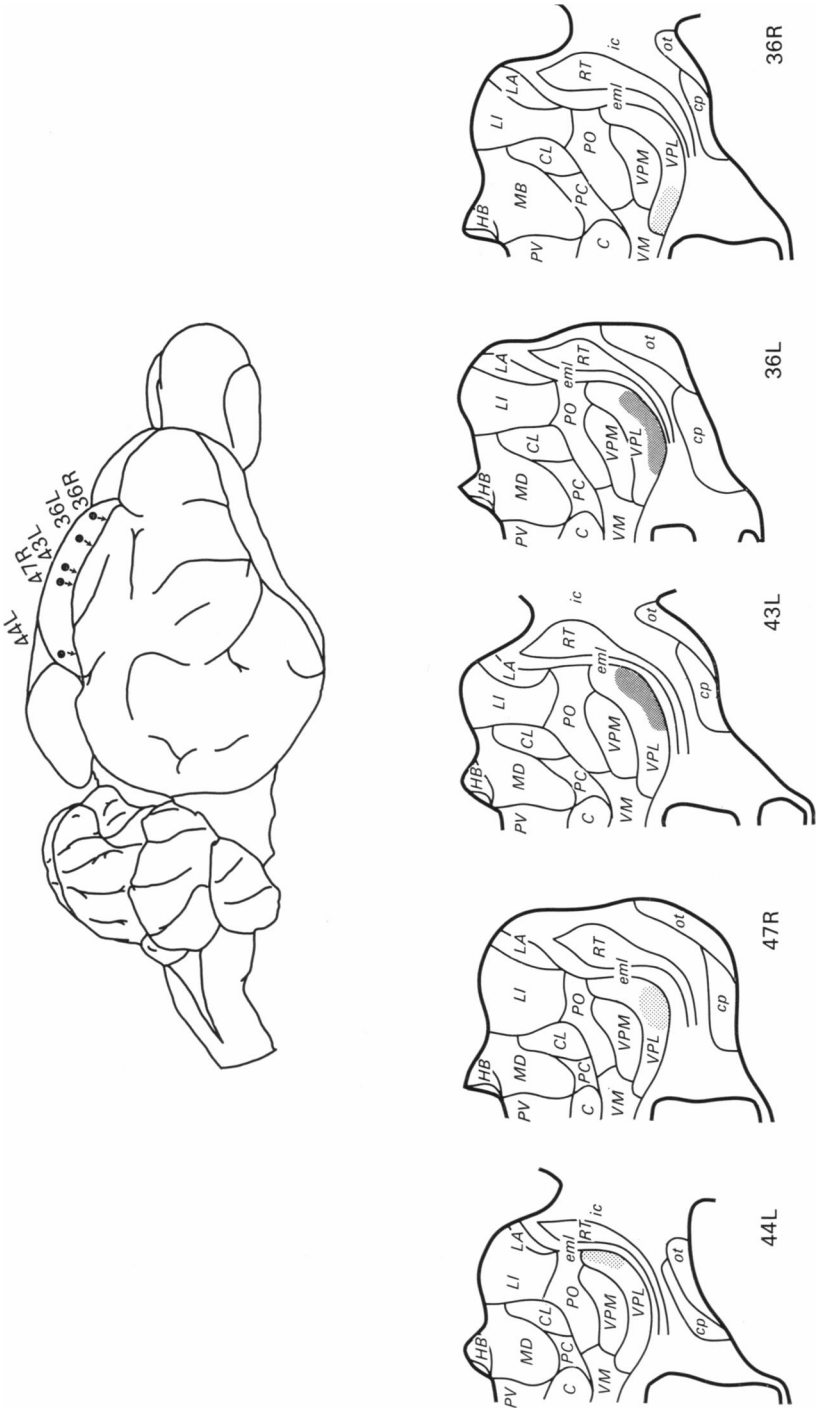

Fig. 8. Thalamic label resulting from a row of HRP injections along the medial part of the VPL projection field. Thalamic sections correspond to *Level A* in Fig. 7. Note the homotypic relationship between cortex and thalamus. Posterior cortical injections produced label in lateral VPL with more anterior injections in cortex causing a medial shift of label in VPL. Note also that label from this row of injections is confined to the ventral aspect of VPL. Dark stipple represents dense labelling in thalamus; light stipple, sparse labelling (see text). Arrows indicate that the penetrations were made on the medial aspect of the supramarginal ridge. For abbreviations see list on p. 485.

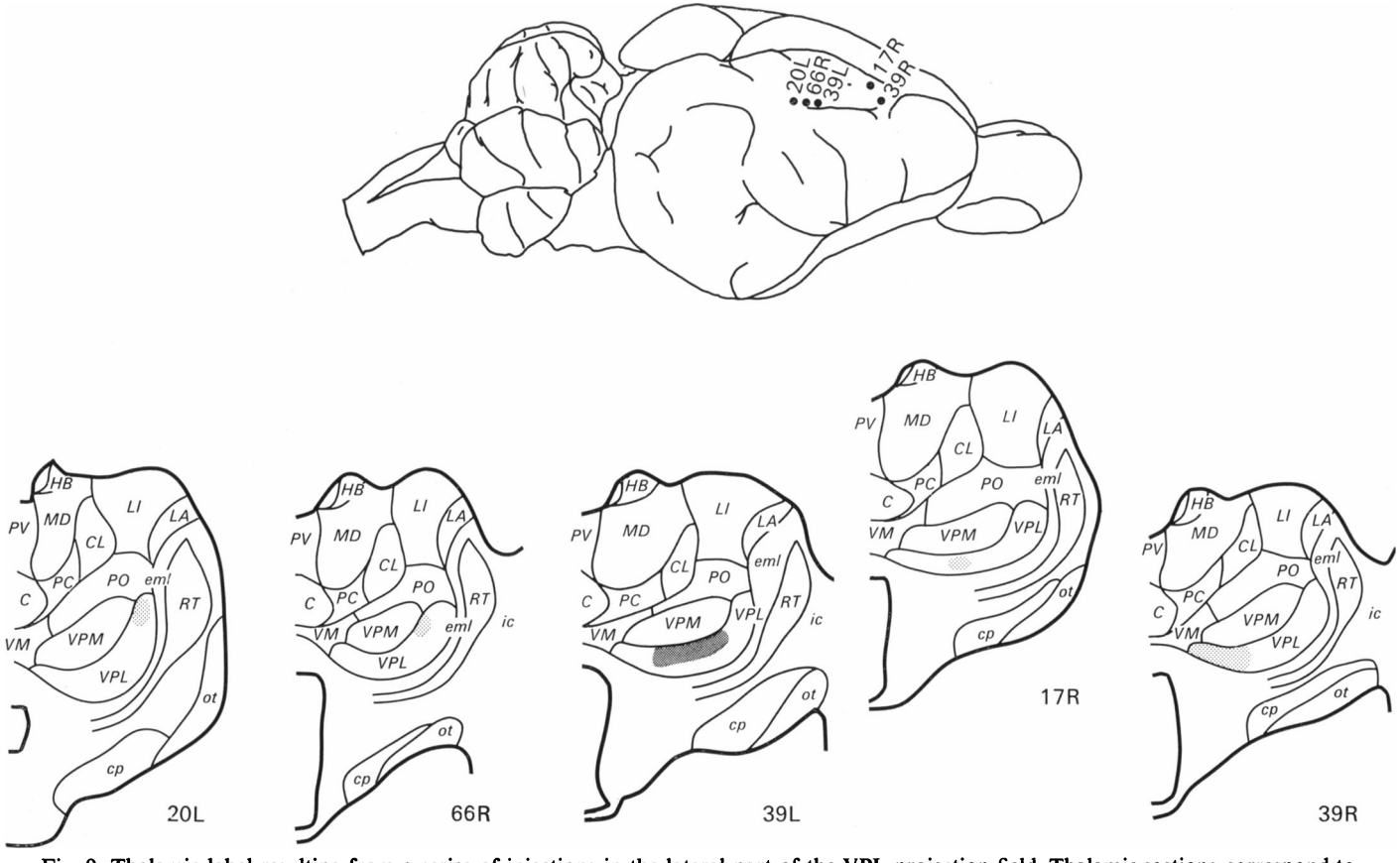

Fig. 9. Thalamic label resulting from a series of injections in the lateral part of the VPL projection field. Thalamic sections correspond to *Level A* in Fig. 7. A posterior to anterior sequence of cortical penetrations produced a lateral to medial shift of label in VPL. Note that the label from these injections was confined primarily to the dorsal aspect of VPL adjacent to the VPM border. Experiment 17R occupies an intermediate position in this respect. Dark and light stipple represent dense and sparse labelling in thalamus, respectively (see text). For abbreviations see list on p. 485.

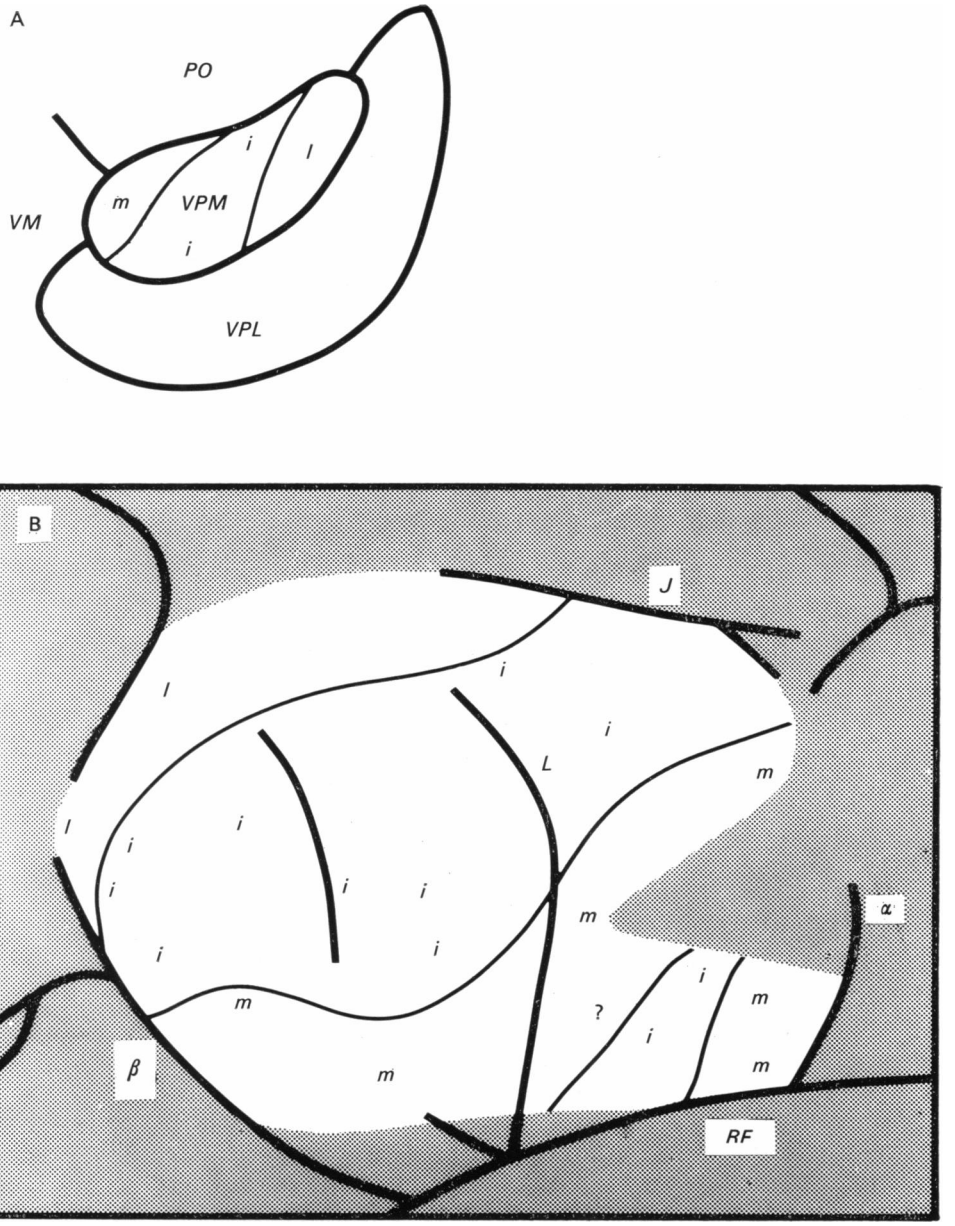

Fig. 10. Organization of VPM projections to cortex. (A) Diagram of ventroposterior complex with VPM divided into lateral (*l*), intermediate (*i*) and medial (*m*) zones. For abbreviations see list on p. 485. (B) Diagrammatic representation of the VPM cortical projection field. Each letter symbol represents a penetration site with medial (*m*), intermediate (*i*) and lateral (*l*) zones of VPM projecting to correspondingly labelled regions in the VPM field. Note that the intermediate and medial zones of VPM project independently to the anterolateral corner of the VPM field. The ? suggests that this region may receive projections from lateral VPM. Our data are not conclusive on this point (cf. Fig. 13). *J*, jugular sulcus; *L*, labial sulcus; *RF*, rhinal fissure; sulci α and β bound the VPM field anteriorly and posteriorly. SII is not indicated on this figure.

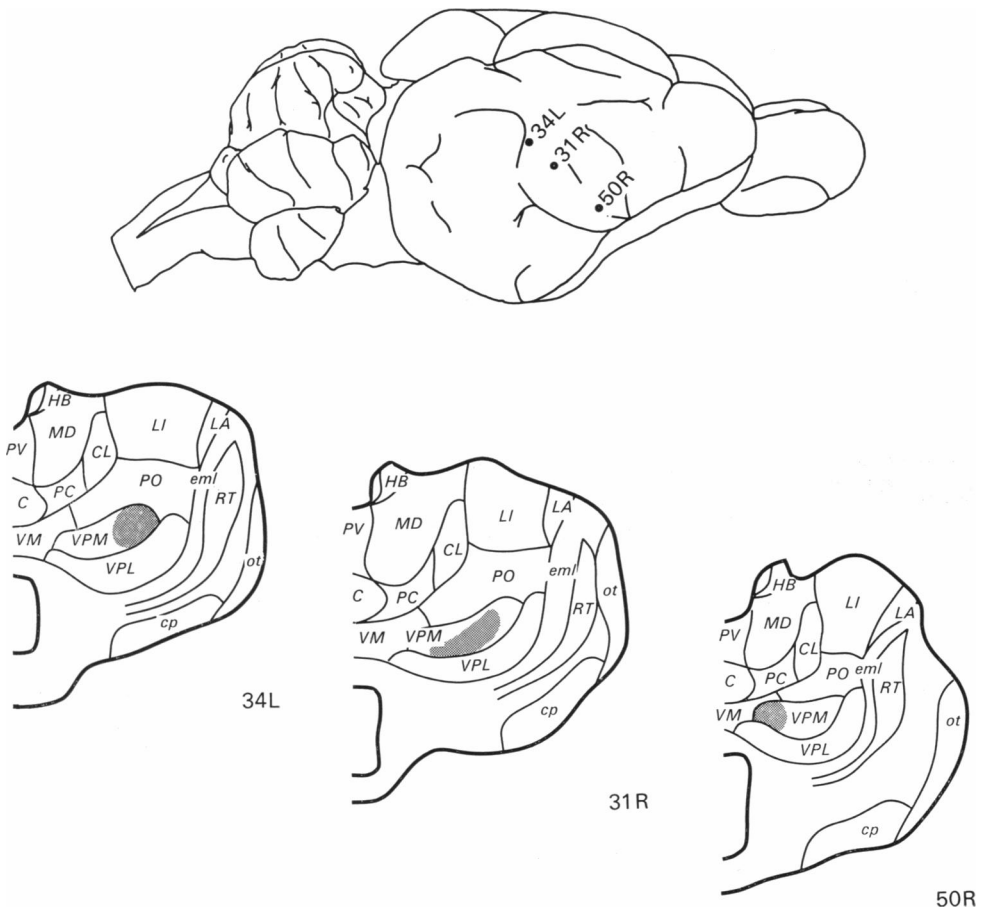

Fig. 11. Thalamic label resulting from HRP injections into the post-labial portion of the VPM field. Thalamic sections correspond to *Level A* in Fig. 7. Compare also the position of penetration and thalamic label in Figs. 2, 15. A mediolateral shift of label in VPM as a function of injection site is apparent, but the dorsoventral positions of label within VPM are not homotypically related to the penetration loci in a well-organized manner. For abbreviations see list on p. 485.

of these experiments the position of label within the intermediate zone of VPM appears to be randomly related to the position of the cortical penetration.

Injections into the extreme anterolateral corner of the VPM field (Fig. 10), along the rhinal fissure and posterior to sulcus α, produced a labelling pattern in VPM that appeared to be independent of the foregoing considerations. The four penetrations into this region (Fig. 13) produced label throughout most of VPM, suggesting that this area of cortex may form a separate functional subdivision within the VPM field. It will be noted that homotypy is revealed between thalamus and cortex with the most anterior cortical penetrations producing label in the medial aspect of VPM, while injections posterior to these labelled the intermediate zone of VPM. The '?' in Figure 10 asks whether the picture might be completed by having the lateral part of VPM project to this region. Our data suggest, but do not confirm absolutely, that this might be the case.

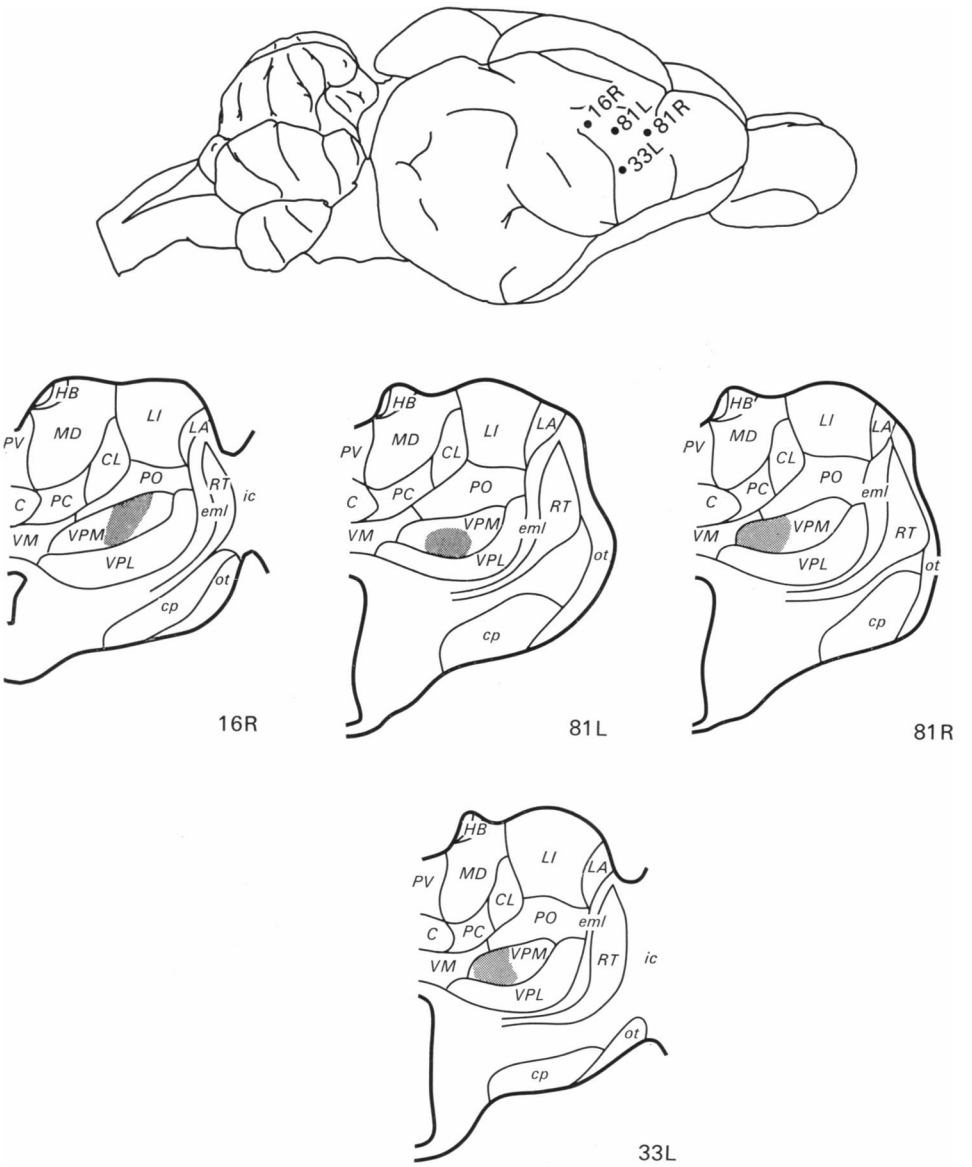

Fig. 12. Thalamic label resulting from HRP injections into the anterior or mandibular (see Fig. 1C) portion of the VPM cortical field. Thalamic sections correspond to *Level A* in Fig. 7. In this region of cortex a row of cortical penetrations directed roughly in the anteroposterior direction produces a mediolateral shift of label in VPM. For abbreviations see list on p. 485.

Organization of VPP projections to neocortex

The cortical projection field of VPP lies at the anterior margin of the VP field and is surrounded posteriorly by the VPM field (Fig. 4). Four injections produced label in VPP and are illustrated in Figure 14. As VPP is found only at the posteromedial edge of the VP complex (Fig. 7), the label is shown in thalamic sections posterior to

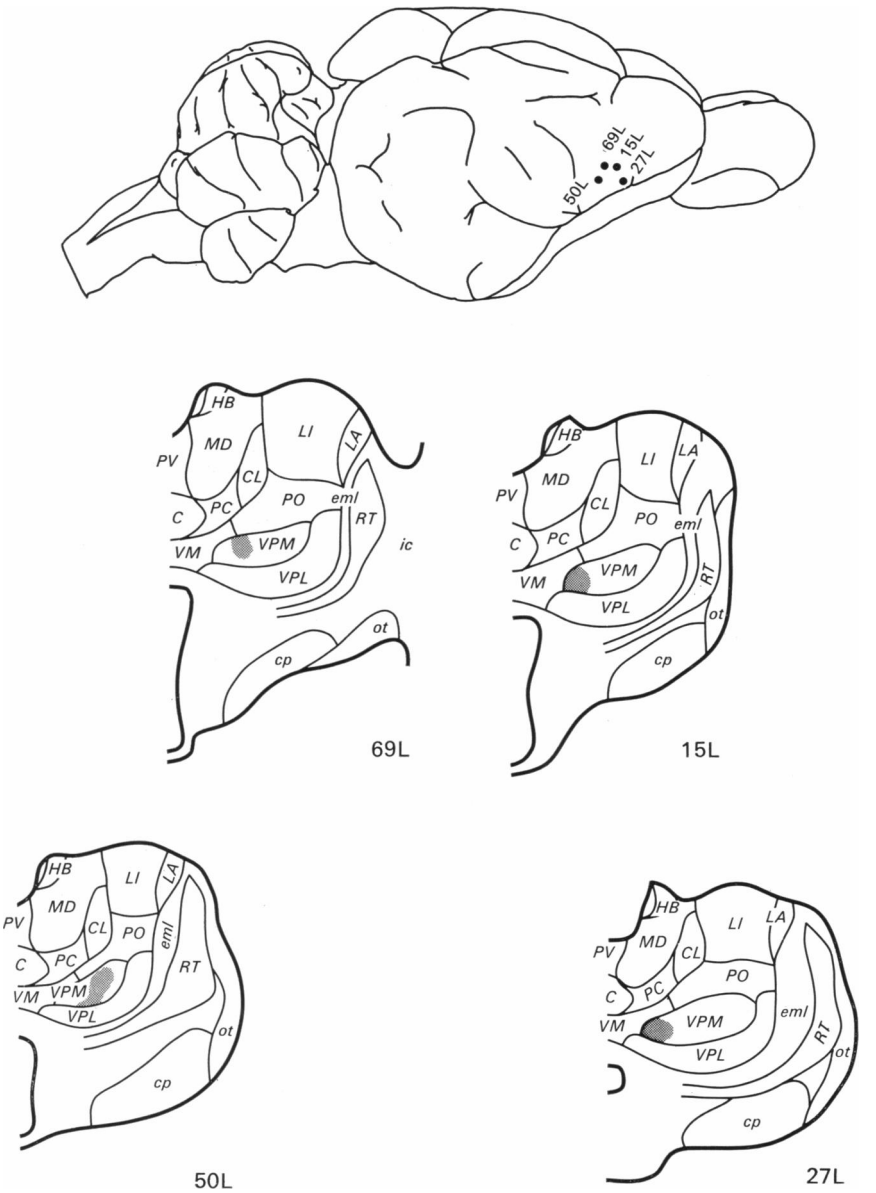

Fig. 13. Thalamic label resulting from HRP injections into the anterolateral or intraoral part of the VPM field (see Fig. 1C). Thalamic sections correspond to *Level A* in Fig. 7. This small cortical region receives projections from most of VPM, thus forming a separate homotypic projection within the VPM projection field. For abbreviations see list on p. 485.

those used in previous illustrations (Fig. 7, *Level B*). In two experiments, 52R and 79R, label was found in VPP and in no other part of the VP complex. The other two experiments, 33L and 81R, produced label in the medial part of VPM as well. The data suggest that a homotypic relationship between thalamus and cortex is also present in this system. The most posterior penetration (33L) placed label in the

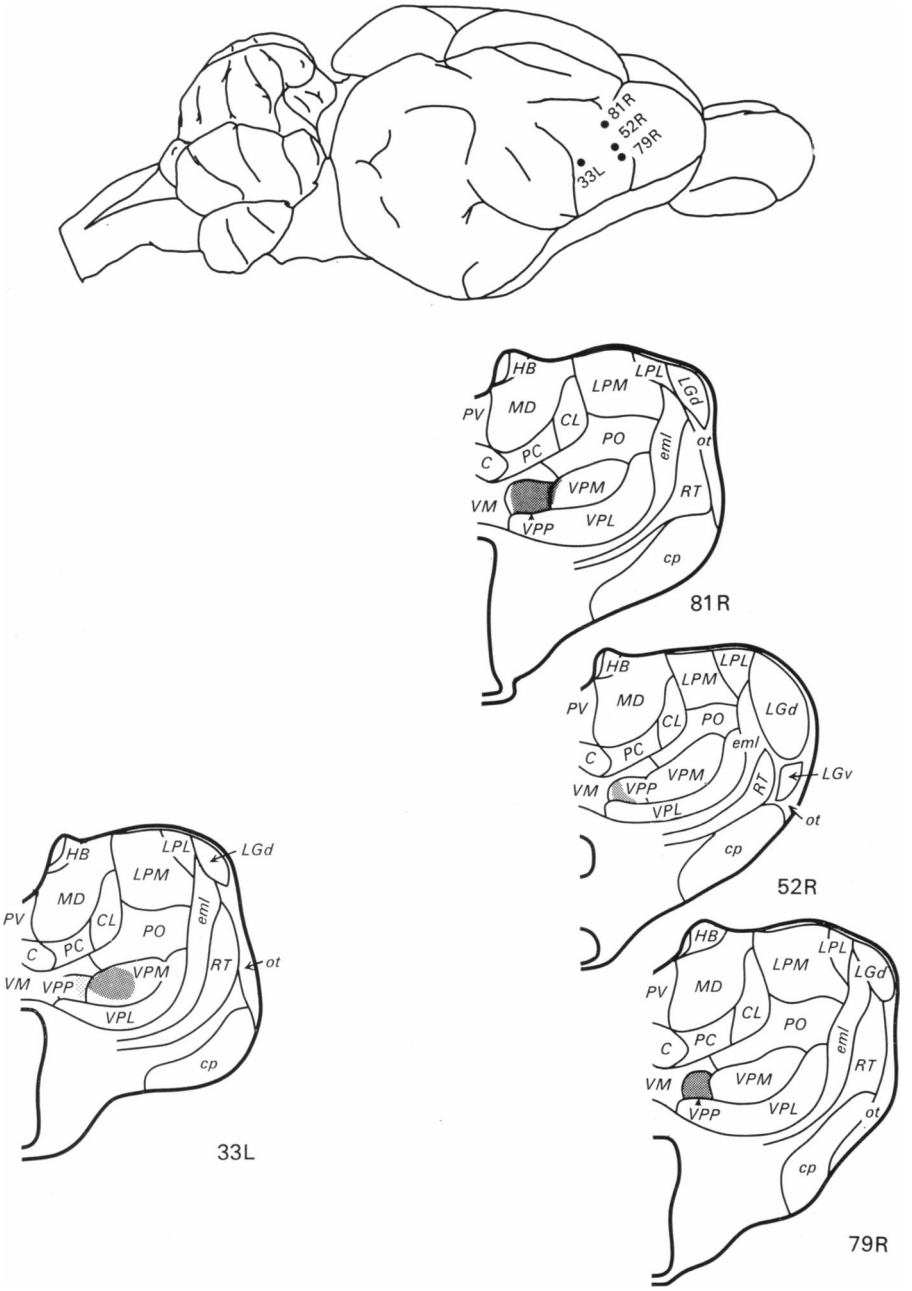

Fig. 14. Thalamic label resulting from HRP injections into the VPP projection field. Thalamic sections correspond to *Level B* in Fig. 7. Experiments 33L and 81R also produced label in VPM; experiments 52R and 79R labelled no other part of the VP complex. Dark stipple represents dense thalamic labelling; sparse labelling is represented by light stipple. For abbreviations see list on p. 485.

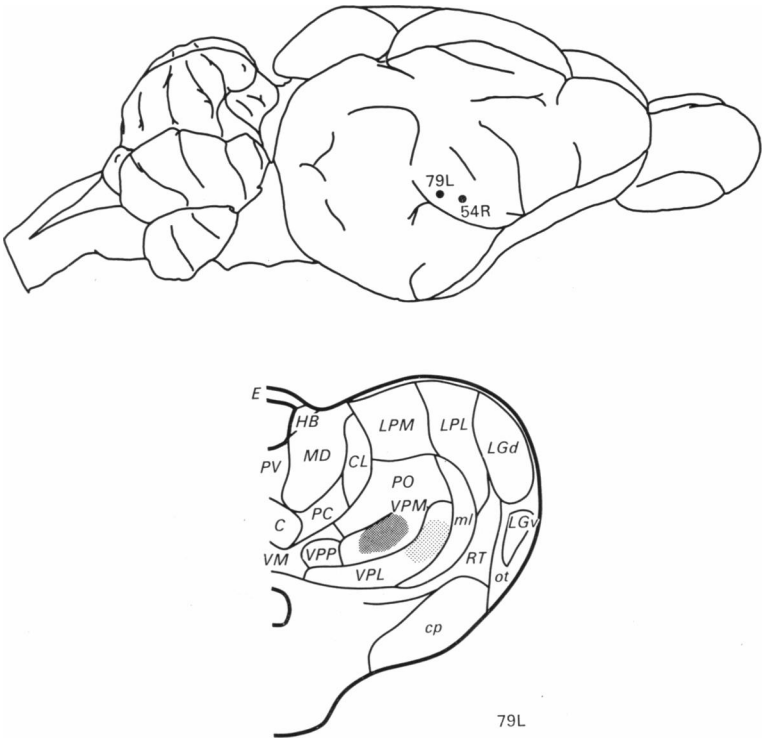

Fig. 15. Dual uptake of label into VPL and VPM after injections into the SII cortical area. Thalamic section corresponds roughly to *Level B* in Fig. 7. VPL label was sparse, weak and confined to the posterior third of VPL. VPM label was dense and extended throughout the anteroposterior extent of the subnucleus. The thalamus of 54R was cut in the sagittal plane and is not pictured. The results were analogous to those of experiment 79L (pictured). For abbreviations see list on p. 485.

lateral part of VPP, while one of the anterior penetrations (52R) labelled the medial part of the subnucleus. Finally, VPP displays both dense and sparse label and, in this regard, resembles VPL.

SII

Two penetrations in the posterolateral part of the VPM field produced a scattered, faint label in VPL as well as the usual dense label in VPM (Fig. 15). Label in VPL was restricted to the posterior third of that subnucleus. This region of cortex corresponds to that which has been identified as SII in *Trichosurus* using electrophysiological mapping techniques (Haight & Weller, 1973).

DISCUSSION

The technique

This study has shown that the HRP method can provide a relatively simple, rapid and accurate method of examining thalamocortical pathways. Used with proper attention to the placement of injections and to inter-experimental procedural consistency, the method is not only capable of demonstrating connectivity between

particular thalamic nuclei and their cortical fields, but also of disclosing some of the organizational details of these relationships.

It appears that the apparent spread of HRP around the cortical penetration is not a reliable indicator of the actual area of cortex involved in HRP uptake. Our results also suggest that the actual measured area of cortex from which terminals take up HRP is limited to a zone very near the needle hole, perhaps as little as 1·0–2·0 mm in diameter. It follows from this that results from penetrations spaced as closely as 2·0 mm could be resolved as differences in label location and pattern in the thalamus. This expectation was met numerous times in the present study as reference to Figures 8, 9, 11, 12, 13 and 14 will show. Our observations are also in agreement with those of Jones & Leavitt (1974) who found that multiple HRP injections into the same hemisphere, spaced a few millimetres apart, could be resolved in the thalamus even though their procedure resulted in a coalescence of label spread from the various penetrations.

Parietofrontal cortex

Our determination of VP's cortical projection field agrees in most particulars with that of Goldby (1943) who, observing retrograde degeneration in thalamus after cortical ablations, also mapped some thalamocortical fields in *Trichosurus*. Electrophysiological mapping of mechanoceptive projections from the body surface to SI, using both surface (Adey & Kerr, 1954) and microelectrode recording methods (Haight & Weller, 1973; Weller & Haight, 1973), indicates that SI and the VP projection field are identical. The present anatomical study shows that the area just posterior to sulcus α' does not receive VP projections. The physiological studies show that this region does not receive mechanoceptive input from the body surface. However, as noted earlier, this region does receive a VL input (Fig. 5, this paper; Ward & Watson, 1973) and electrical stimulation of this area does elicit peripheral motor activity (Abbie, 1940; Goldby, 1939; Rees & Hore, 1970). These studies showed that electrical stimulation over much of SI also elicits motor activity. These facts suggest that there is some overlap of motor and somatic sensory cortical function in *Trichosurus*, but that this overlap is by no means complete. In *Didelphis*, it will be recalled, the congruence is perfect. A future paper in this series will examine the cortical projection of VL in *Trichosurus* with the object of determining the extent of this functional and anatomical overlap.

VPL

Electrophysiological mapping has repeatedly shown that sensory information from different body regions is projected with an orderly somatotopy through the brain stem nuclei and thalamus to cortex (Fig. 1C). Anatomically, this relationship is probably reflected by the precise point-to-point relationship between the bands of label in VPL and the cortical penetration sites. This homotypic precision was not affected by changes in the proportion of VPL cells projecting to cortex. Medial and lateral parts of VPL labelled sparsely following injections into the anterior and posterior zones of the VPL field. The middle third of VPL, it will be recalled, labelled densely following injections into the central part of the VPL field. If dense labelling, as defined earlier, occurs when the majority of cells in a given region have their axon terminals in close proximity to the penetration site, and if, on the other hand, sparse labelling occurs when a minority of cells have their terminals so situated, then since VP cells which displayed label at all were usually labelled heavily, this would suggest that most VP cells have their primary terminal arborizations restricted to a limited cortical area. It is arguable that a cell which arborized

widely would not label as heavily, because a given injection would affect a relatively small proportion of its terminals. Within VPL cell density and distribution is uniform. Hence, the dense and sparse labelling of VPL neurons may reflect one or more of the following possibilities. First, the medial and lateral parts of VPL may contain a higher proportion of interneurons; second, a higher proportion of cells in medial and lateral VPL may project to cortical areas removed from the immediate vicinity of a given HRP injection; third, a higher proportion of cells in medial and lateral VPL may project to non-cortical centres.

A higher proportion of interneurons in certain areas of VPL would presumably result in cytoarchitectural inhomogeneity. Since the cytoarchitecture of VPL appears uniform throughout, the first alternative is unlikely, With respect to the second alternative, since we never observed VP projections to any area of cortex except to the parietofrontal region, any alternative cortical projection would have to be located within that region. One possibility could be that neurons in medial and lateral VPL project more diffusely, covering larger areas of the VPL field. This is unlikely because any appreciable projection of VPL neurons to areas of the VPL field outside their homotypically destined area would tend to obscure that very precision which marks the VPL cortical projection in the first place. However, at least some neurons in VPL do project to SII. In the cat the part of SII that receives a VP projection does so primarily by means of collaterals from axons directed to SI (i.e. to the VPL field). Of the VP neurons which project to cortex not more than 10 % project directly to SII (Manson, 1969; Rowe & Sessle, 1968). In *Trichosurus*, as in the cat, it might be expected that some VPL neurons do project solely to SII. The facts remain, however, that SII appears to receive projections only from the posterior portion of VPL whereas VPL exhibits sparse labelling throughout its anteroposterior extent; that the labelling density in VPL after SII injections is extremely sparse; and that the cells in VPL that do label after a SII injection are faint and difficult to see, which suggests that *Trichosurus*' SII, like the cat's, may be innervated primarily by collaterals. These observations suggest that the second alternative can account for only a small fraction of the unlabelled cells in the medial and lateral parts of VPL, and that a higher proportion of cells in these areas of VPL are projecting to non-cortical centres.

VPM

The organization of the cortical projection from VPM differs from that of VPL. First, label in VPM was always dense, with no significant variation in the proportion of labelled cells. This suggests that a more-or-less constant proportion of VPM cells project to cortex from all areas of the subnucleus. Second, although a homotypic relationship between VPM and cortex was apparent (Figs. 11, 12, 13), the organization differed from that observed in VPL, appearing to be more diffuse and lacking some of the exactness of the point-to-point relationships which characterized the VPL–cortex system. We interpret these observations as indicating a valid organizational difference between the cortical projections of VPM and VPL.

The above comments create certain interpretative problems. Mapping of sensory projections to cortex (Fig. 1 C) indicates an orderly somatotopy in *Trichosurus* from both the body (lemniscal–VPL) and head (trigeminal–VPM). Put simply, this implies that a given area in VP receives projections from a particular body area and projects to a particular area of cortex. A neighbouring region of VP would then receive projections from a body region contiguous with the first and, likewise,

project to a contiguous area of cortex. This is the homotypic principle of mapping. Our anatomical observations in VPL appear to confirm these principles (Figs. 8, 9). In VPM the picture is somewhat confused. The apparent absence of strict homotypy between VPM and cortex with respect to the dorsoventral orientation in VPM may simply be a reflexion of increased complexity and/or distortion of the projectional map. Further comment must await more data on the somatotopic organization of both neocortex and the ventroposterior complex in *Trichosurus*.

If *Trichosurus* is compared with the American opossum, the only other marsupial mammal for which data are available, a further difference appears. Mapping of the somatic sensory cortex in *Didelphis* has disclosed a dual representation in SI of certain regions of the head (Pubols *et al.* 1976). However, sensory mapping of VP in *Didelphis* has not disclosed a dual head representation at that level (Pubols & Pubols, 1966; Sousa, Oswaldo-Cruz & Gattass, 1971), the presumption being that the dual cortical representation of the head must arise as a consequence of the organization of the VPM cortical projection. In *Trichosurus* our data disclose that VPM projects to two distinct areas of SI (Fig. 10), but our mapping data in the cortex (Fig. 1C) suggest that *Trichosurus* and *Didelphis* are by no means similarly organized at cortical levels. Cortical mapping in *Trichosurus* does not disclose a dual head representation as reported for *Didelphis*. The small area of cortex which, on the basis of our HRP findings, receives an additional projection from VPM is an area devoted to projections from the oral region only (Fig. 1C). Thus, it appears that the trigeminal–VPM–cortex systems are organized differently in *Trichosurus* and *Didelphis* and that both animals present features which distinguish them from the placental mammals thus far examined (Welker, 1973 for discussion and review).

VPP

In most animals VPP was a cytoarchitecturally distinct region (Haight & Neylon, 1977*a*, 1978*a*, *b*). It projects discretely to the anterior part of the VP cortical field. Nothing is known of its input relationships. Our electrophysiological observations indicate that the VPP field is properly included within SI, which suggests that VPP is indeed part of the ventroposterior complex.

SUMMARY

Retrograde transport of horseradish peroxidase (HRP) was used to determine the extent and some of the organizational details of the cortical projection of the ventroposterior thalamic complex (VP) in the marsupial brush-tailed possum, *Trichosurus vulpecula*. The cortical projection field of VP is coincident with SI as determined by electrophysiological methods, and would appear not to overlap fully the primary motor cortex. Thus, in *Trichosurus* it appears that the motor and somatic sensory cortical regions are not fully congruent, unlike those of the American opossum, *Didelphis*, which are. Each division of VP projects discretely, in a non-overlapping manner, to various regions within SI. The ventrolateral subdivision or VPL projects medially and in a strict homotypic manner, though the proportion of VPL cells projecting to cortex is subject to a large amount of variation. The dorsomedial division of VP or VPM projects uniformly to cortex from all areas of that subnucleus, but the strict homotypy characteristic of VPL's projection was not as apparent. VPM also projects to two distinct regions within its cortical field. The posteromedial division of VP or VPP projects to an area of cortex that receives no other VP input but, on the basis of cortical mapping studies, appears to belong to SI.

Projections from VPL (and presumably from VPM) to a small area of cortex in the extreme posterolateral part of the VP field correspond to the position expected for, and electrophysiologically confirmed to be, SII.

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LIST OF ABBREVIATIONS

C	Central nucleus	*ml*	medial lemniscus
CL	Centrolateral nucleus	*ot*	optic tract
cp	cerebral peduncle	*PC*	Paracentral nucleus
E	Epiphysis	*PO*	Posterior nucleus
eml	external medullary lamina	*PV*	Paraventricular nucleus
HB	Habenular nuclei	*RT*	Reticular nucleus
ic	internal capsule	*SI*	Primary somatic sensory area
LA	Lateroanterior nucleus	*SII*	Secondary somatic sensory area
LGd	Dorsal lateral geniculate nucleus	*VL*	Ventrolateral nucleus
LGv	Ventral lateral geniculate nucleus	*VM*	Ventromedial nucleus
LI	Laterointermediate nucleus	*VP*	Ventroposterior nucleus
LPL	Lateral lateroposterior nucleus	*VPL*	Lateral ventroposterior nucleus
LPM	Medial lateroposterior nucleus	*VPM*	Medial ventroposterior nucleus
MD	Mediodorsal nucleus	*VPP*	Posteromedial ventroposterior nucleus