Intracortical Arborizations and Receptive Fields of Identified Ventrobasal Thalamocortical Afferents to the Primary Somatic Sensory Cortex in the Cat

PIERRE LANDRY AND MARTIN DESCHÊNES
Laboratoire de Neurophysiologie, Département de Physiologie, Faculté de Médecine, Université Laval, Québec, Canada GIK 7P4

ABSTRACT
The intracortical arborizations of neurons from the ventropostero-lateral thalamic nucleus (VPL) in the cat were studied by intraxonal injections of horseradish peroxidase (HRP) following identification of their receptive fields. In the primary somatic sensory cortex (SI) VPL cells terminated in different cytoarchitectonic areas according to their receptive field modality. Fibers excited by deep tissues or joint rotation arborized preferentially in area 3a. Those responding tonically to cutaneous stimuli were located in the anterior part of area 3b; hair-driven cells terminated in area 3b and in the rostral pole of area 1. All fibers had a similar laminar distribution within SI. Axons terminated mostly in layers VI, IV, and the lower part of layer III. None terminated in layers I and II. Most terminal arbors were oriented along the mediolateral axis of the brain. The main arborization of a single VPL cell formed a bush of about 500 μm in diameter. Some fibers generated two such bushes with an uninvaded region of about 300 μm between them. It is proposed that this patchy organization underlies in part the columnar organization of area SI. Many VPL cells had secondary projection sites in SI. These were issued from smaller-sized collaterals and were located in a different cytoarchitectonic area than that of the main terminal plexuses. A significant number of these collaterals projected to area 4. Insufficient filling of the collaterals by HRP prevented a more complete characterization of the secondary arbors.

The cortical column is a concept that has proved useful in understanding the cerebral cortex. The existence of columns was first suggested by Mountcastle (’57). He showed that cells recorded along a perpendicular tract in the primary somatic sensory (SI) cortex had overlapping receptive fields and that they all responded to the same modality of stimulation. Later, Hubel and Weisel (’62, ’69) demonstrated the existence of orientation and ocular dominance columns in the primary visual area. The radial arrangement of nerve cells in many cortical regions often suggests columnar arrangements. Lorente de Nó (’38) pointed out that the cortical unit is a narrow cylinder of cells stretching from layer II to layer VI and having roughly columnar shape. Colonnier (’66) stressed the preferential vertical orientation of axons of many cortical cells and suggested that they are for processing inputs into vertical chains of neurons. He also emphasized that if the cortical circuitry has the necessary wiring for supporting the existence of cortical columns “the anatomical columns are not distinct separate morphological entities.” This implicitly suggested that the territorial limits of the functional columns were determined by the connectivity of thalamocortical afferents and by the tangential spread of inhibition within the cortex. In the primary visual area, ocular dominance columns have their morphological basis in the alternating patches of terminal ramifications of geniculocortical afferents (Huber and Weisel, ’69; Ferster and LeVay, ’78; Gilbert and Weisel ’79). More recently, the patchy nature of the cortical projection from the ventroposterolateral (VPL) nucleus of the thalamus has also been demonstrated by autoradiography (Friedman and Jones, ’80). Since the topographic characteristics of cortical columns appear to be determined by thalamocortical input, we injected single VPL afferents below SI after identification of their receptive fields. The aim of this
study was to determine the areal distribution, laminar ramification, and topographic characteristics of single thalamocortical fibers having different receptive field modalities.

MATERIALS AND METHODS

Animal preparation

Adult cats weighing 2.5–5 kg were anesthetized with sodium pentobarbital (30 mg/kg) and paralyzed with gallamine triethiodide. Additional doses of barbiturate were given intravenously every 2–3 hours. End-expiratory CO₂ was monitored and maintained at 3.8%. Rectal temperature was maintained at 38°C by a heating pad. To reduce cortical pulsations bilateral pneumothorax, hip suspension, and cisternal drainage were routinely performed.

Stimulation and recording

Fibers were identified by stimulating the medial lemniscus at the bulbar level and in the VPL nucleus of the thalamus with pairs of monopolar electrodes. Intraxonal penetrations were made with thin-wall pipettes filled with 5% solution of HRP (Sigma type VI or Boehringer Grad 1) dissolved in 0.5 M KCl and 0.05 M TRIS solution (pH 7.6). Tips of pipettes were broken to a diameter of 1–2 μm and bevelled to give a dc resistance of 12–25 MΩ. A 4% agar solution was poured over the cortex before each penetration. Fibers were stable even during extensive manipulations of the cat. Axons were impaled in the main trunk or in a large secondary branch at a depth of 1.5 to 3.5 mm below the surface of the cortex. HRP was injected by continuous dc currents of 5–15 nA while continuously monitoring the fiber response to lemniscal stimulation. In most experiments, a standard amplifier having a 15 V compliance voltage has been used for current injections. In later experiments an amplifier with 150 V was used. This greatly increased the number of successful injections. All successful penetrations were separated by at least 1.5 mm.

Experimental procedures

The medial lemniscus was stimulated continuously (2/second) while searching for fibers. The criteria used to differentiate fibers from cells were the absence of spontaneous or evoked postsynaptic potentials and the abrupt rise of the initial portion of spontaneous spikes. If a fiber was excited directly by VPL stimulation and transsynaptically by stimulation of the lemniscus, its peripheral receptive field was determined with natural stimuli. Modalities of receptive fields were classified into four categories: (1) hair (fibers activated by lightly blowing on hairs), (2) cutaneous (fibers activated by touching, or lightly pressing on the skin), (3) joint (fibers activated by flexion, extension, or rotation of a body segment), and (4) deep (fibers activated by firmly pressing on subcutaneous tissue, muscles or tendons). When possible, receptive fields were studied extracellularly and then briefly confirmed after impalement of the fiber. Most often, however, receptive fields had to be studied when the pipette was lodged in the axon. All signals were recorded on a four-channel FM tape recorder for later analysis.

Histology and fiber reconstruction

No more than 8 hours elapsed between a fiber injection and the perfusion of an animal. Perfusion was carried out as described by Rosene and Mesulam ('78). Parasagittal sections were cut 80 μm thick on a freezing microtome and reacted with benzidine di-HCl (BDHC). Sections were mounted without counterstaining to permit a better visualization of the fibers. Drawings were made with a camera lucida at a magnification of 600. Because the number of terminal boutons was enormous and because they could not be reproduced adequately on small-sized photographs they were not drawn. However, their location in cortical layers was noted. After reconstruction of the terminal arbors, coverslips were removed in toluene and sections were stained with thionin. The cytoarchitectonic areas were then identified by two independent observers according to the criteria of Hassler and Muhs-Clement ('64).

Axon diameters were measured with a 100 × oil immersion objective. The mediolateral extent of the main arborizations was measured by the number of sections on which the fiber was seen. The anteroposterior extent was measured directly from the final drawings.

Technical comments

The dorsal part of SI between the cruciate and ansate sulci where the contralateral forelimb projects was explored most often in this study. All penetrations were in areas 3a, 3b, and 1; none were in the more caudal area 2.

Because the receptive fields of most axons had to be determined with the pipette lodged within the fiber, we did not usually have enough time to characterize field submodalities extensively, such as the differentiation between slowly and rapidly adapting units. Moreover, some low-threshold phasic cutane-
TABLE 1. Morphological and functional characteristics of thalamocortical fibers from VPL injected with HRP after determination of their receptive fields

<table>
<thead>
<tr>
<th>Fiber no.</th>
<th>Modality</th>
<th>Receptive field location</th>
<th>Areas of main arborization</th>
<th>Areas of secondary arborization</th>
<th>Extent of main arborization within the cortex (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F₁</td>
<td>J</td>
<td>Elbow</td>
<td>3a</td>
<td>—</td>
<td>960</td>
</tr>
<tr>
<td>F₂</td>
<td>J</td>
<td>Shoulder</td>
<td>3a</td>
<td>3b</td>
<td>1,360</td>
</tr>
<tr>
<td>F₃</td>
<td>J</td>
<td>Wrist</td>
<td>3a</td>
<td>—</td>
<td>1,280</td>
</tr>
<tr>
<td>F₄</td>
<td>D</td>
<td>Forearm</td>
<td>3a</td>
<td>—</td>
<td>1,280</td>
</tr>
<tr>
<td>F₅</td>
<td>J</td>
<td>Wrist</td>
<td>3b</td>
<td>3a and 4</td>
<td>960</td>
</tr>
<tr>
<td>F₆</td>
<td>J?</td>
<td>Elbow</td>
<td>3b</td>
<td>4</td>
<td>1,280</td>
</tr>
<tr>
<td>F₇</td>
<td>C</td>
<td>4th digit</td>
<td>3b</td>
<td>—</td>
<td>1,360</td>
</tr>
<tr>
<td>F₈</td>
<td>C</td>
<td>4th digit</td>
<td>3b</td>
<td>—</td>
<td>1,760</td>
</tr>
<tr>
<td>F₉</td>
<td>C</td>
<td>5th digit</td>
<td>3b</td>
<td>—</td>
<td>2,850</td>
</tr>
<tr>
<td>F₁₀</td>
<td>C</td>
<td>Around carpal pad</td>
<td>3b</td>
<td>3a or 4</td>
<td>850</td>
</tr>
<tr>
<td>F₁₁</td>
<td>H</td>
<td>Shoulder</td>
<td>3b</td>
<td>3a or 4</td>
<td>720</td>
</tr>
<tr>
<td>F₁₂</td>
<td>H</td>
<td>Forearm</td>
<td>3b</td>
<td>1</td>
<td>1,920</td>
</tr>
<tr>
<td>F₁₃</td>
<td>H</td>
<td>Elbow</td>
<td>3b</td>
<td>3a and 4</td>
<td>960</td>
</tr>
<tr>
<td>F₁₄</td>
<td>H</td>
<td>5th digit</td>
<td>3b</td>
<td>—</td>
<td>1,680</td>
</tr>
<tr>
<td>F₁₅</td>
<td>H</td>
<td>5th digit</td>
<td>3b</td>
<td>1</td>
<td>2,080</td>
</tr>
<tr>
<td>F₁₆</td>
<td>H</td>
<td>Hindpaw</td>
<td>3b or 1</td>
<td>2</td>
<td>960</td>
</tr>
<tr>
<td>F₁₇</td>
<td>H</td>
<td>Forearm</td>
<td>1</td>
<td>1 or 2</td>
<td>960</td>
</tr>
</tbody>
</table>

1: J: joint; D: deep; C: cutaneous; H: hairs. When no number appears the above characteristic was not present or the cell was not filled enough to allow a full reconstruction of its morphology. Asterisks (*) indicate incomplete filling of the fiber; M-L: mediolateral; A-P: anteroposterior. The total extent of main arborizations includes the total area covered by all branches belonging to a single fiber with the interlaying gap. It includes also some poorly branched side collaterals that ran out of the main plexus. The size of main terminal patches is better estimated from the drawing in Figures 1–8.

ous afferents might have been classified as hair afferent units, since blowing on hairs may induce a deformation of the underlying skin. Nevertheless, this rather simple determination of receptive field modalities did not appear to interfere with the validity of the present findings.

RESULTS

Seventeen fibers activated from the VPL nucleus and the medial lemniscus were injected with HRP (Table 1). Four of these (F₃, F₄, F₁₀, and F₁₆) were partially filled and their main terminal arborizations were not entirely stained. A peripheral receptive field was found for all fibers. Five fibers responded to joint movement (F₁, F₂, F₃, F₅, F₆), one to deep pressure (F₄), four to cutaneous stimuli (F₇–F₁₀), and the remaining seven were driven by hair movement (F₁₁–F₁₇).

Axonal path and branch size

In white matter, main axons had diameters of 0.4–0.6 msec to VPL stimulation (Fig. 1a). On the basis of a distance of 15 mm between the stimulating and recording sites, this yields conduction velocities of 25 to 37 meters/second. The latencies of transsynaptic activation following medial lemniscus stimulation ranged between 2 and 2.5 msec (Fig. 1b).

One to three millimeters before reaching their main target area, some fibers were seen to ramify into thinner branches (1–3 µm in diameter) that ran toward secondary projection sites (Fig. 10C). The diameter of the parent axon did not decrease at such branch points. As the main target area was approached, axons bifurcated and here again the axonal diameters of the first main branches were often as large as that of the originating axon (Fig. 10F). Other than in these subcortical cases, the diameter of daughter branches generally decreased with subsequent branching. The use of BDHC as a substrate for HRP histochemistry enables visualization of the myelin sheath (Deschénes et al., '79). Axonal branches remained myelinated very far into the terminal arbor. They became unmyelinated only a few hundred micrometers before giving rise to terminals.

The most common types of branching pattern were bifurcations and trifurcations. Quite often, in the very dense plexuses of hair affer-
ents multiple branches (up to five) were seen to stem from the same node. In fact, one of the characteristic features of cutaneous and hair afferents was their dense plexuses in areas 3b and 1. Joint and deep afferents in area 3a had more loosely organized terminal arbors. Hair afferent fibers \( F_{11} \) and \( F_{17} \), that were located in the posterior part of area 3b and in area 1 respectively had the smallest and densest terminal arbors (Figs. 5, 8).

**Distribution of afferent fibers in SI**

**Areal distribution of main arbors.** Fiber modality was clearly related to cytoarchitectonic area of termination (see Table 1). Joint and deep afferents terminated primarily in area 3a. Tonic cutaneous afferents (driven by skin pressure) distributed in area 3b, particularly in the rostral pole. Hair-driven fibers terminated in areas 3b and 1. Fiber \( F_{11} \), was interesting in this respect (Fig. 5); it was running toward the rostral pole of area 3b, but on arrival in the lower part of layer VI, it gave rise to secondary branches that turned at a 90° angle and ran tangentially for 700 \( \mu \)m before arborizing in the posterior part of area 3b. It was as if the path of this fiber had been corrected during early development in order for it to reach the right target area. This observation reinforces the idea that there is a precise segregation of modalities within the cytoarchitectonic areas of SI.

**Laminar distribution of terminals.** All VPL afferents to SI had a similar laminar distribution. Terminals were present in layers VI, IV, and in the lower part of layer III (see Figs. 1–8, 10a,b,d,e). Very few were found in layer V or in the upper part of layer III. None were found in layers I and II. This result could not have been due to incomplete filling of the fibers since an afferent fiber of unknown origin was injected and found to terminate in layers III and I (Fig. 9). We failed to identify the fiber in Figure 9 by stimulating VPL at even high intensities, although it was driven at a latency of 2.0 msec by lemniscal stimulation; thus the laminar distribution of VPL afferents to SI appears likely to be restricted to lamina VI, IV, and the lower part of lamina III.

**Size and tangential extent of main arbors.** The best measure of width and orientation of terminal arbors would require computer reconstruction. However a reasonable estimate can be made from camera lucida drawings. Table 1 gives the tangential spread of the main arbors as measured at the level of upper layer IV. The extent of the main arborization was clearly oriented along the mediolateral plane for most fibers. This asymmetry was most notable in the case of hair-driven cells. Fibers located in the rostral pole of SI tended to have a wider anteroposterior domain than those located in the caudal pole (compare the A-P extent of \( F_{11} \) and \( F_{13} \) in area 3a to that of \( F_{11} \) and \( F_{17} \) located in the caudal part of 3b and in area 1).

The data in Table 1 give a reasonable estimate of the terminal arbor orientation, but fail to show the patchy nature of the thalamic projection (see footnote to Table 1). The arborization of a fiber could contain one bush or even two bushes separated by an uninvaded gap (see fibers \( F_{11} \), \( F_{13} \), and \( F_{13} \) in Figs. 3, 6, and 7). The size of these bushes was of the order of 500 \( \mu \)m; the uninvaded territories were somewhat smaller (\( \approx \)300 \( \mu \)m). The bushes of fibers \( F_{11} \), \( F_{13} \), and \( F_{17} \) were aligned along the mediolateral axis of the cortex so that they were not revealed in sagittal representations. It is also worth mentioning that in our sample of injected fibers those driven phasically by blowing on hairs arborized frequently in two separate patches.

**Somatotopic projections of VPL cells in SI**

Afferents from VPL arborized in different regions of SI according to the location of their receptive fields. They conformed to the usual picture of the somatotopic representation in the cat SI area: Distal forelimb receptive fields were represented laterally, proximal forelimb receptive fields were represented medially, and the trunk and hindlimb representations were more medial. The tangential span of VPL fibers in SI was not correlated with the size or location of their receptive fields. The larger representation of distal forelimb regions as compared to other somatic regions in SI is thus due to a greater number of afferent fibers in SI and not to afferent span.

**Secondary projections of VPL cells in SI**

The main arbor of VPL fibers was always located in a single cytoarchitectonic area. Ten out of seventeen fibers had branches that gave rise to secondary arbors in other cytoarchitectonic regions. These secondary branches were thinner than the originating axon and were never filled completely (except for fiber \( F_{11} \)). We have the impression that they are much less dense than the main plexuses. It might be sig-
nificant that fibers with receptive fields on the digits did not generally show collateral projections (Table 1). Incomplete filling may, however, account for this apparent exception.

Single fibers often projected to several cytoarchitectonic areas; area 4 received a significant number of these secondary projections. In two cases, VPL fibers activated by joint stimulation were seen arborizing selectively in area 4 (unpublished observation). These fibers were rarely encountered in the present study because electrode penetrations were always caudal to area 4. Collaterals of fibers F<sub>3</sub>, F<sub>6</sub>, F<sub>10</sub>, and F<sub>12</sub> were located on the same anteroposterior plane as the main fiber arborization. On the other hand, fibers F<sub>3</sub> and F<sub>11</sub> had secondary projections localized on a different anteroposterior plane, while fiber F<sub>17</sub> sent a collateral branch that ran medially for more than 2 mm, suggesting a projection to a cortical region that represented a different body region.

DISCUSSION

This study has revealed four aspects of the organization of VPL input to area SI: (1) the selective areal distribution of fibers according to modality, (2) the patchy nature and orientation of terminal arbors, (3) the restricted laminar distribution of VPL afferents to lamina VI and IV and to the lower part of lamina III, and (4) the presence of secondary sites of projection for many fibers.

Areal distribution

Our results confirm the spatial distribution of modality input to SI as previously found by physiological experiments (Whitsel et al., '71; Paul et al., '72; Merzenich et al., '78; Kaas and al., '79; Dykes et al., '80). They also confirm a recent report showing that modality changes in cat correlate with cytoarchitectonic boundaries (Dykes et al., '80). Deep and joint afferents reach mostly area 3a. The apparent exception of fibers F<sub>3</sub> and F<sub>6</sub> might be due to misidentification of the cytoarchitectonic boundary between areas 3a and 3b or to an incorrect determination of the receptive field modality in the case of fiber F<sub>6</sub>. Other joint and deep afferent fibers that were recorded and partially injected in the course of this study had main axons that ran toward areas 3a or 4. However, the possibility that some deep and joint inputs reach area 3b cannot be completely excluded. It must be emphasized that “joint units,” as defined in our experiments, were not necessarily activated by joint receptors. They could represent a class of VPL neurons carrying muscle afferent information that were best driven by joint movements. The preferential termination of tonic cutaneous afferents in the rostral pole of area 3b confirms Dykes et al. ('80), while the preferential distribution of hair afferents to areas 3b and 1 is in agreement with a number of other studies (Powell and Mountcastle, '59; Whitsel et al., '71; Paul et al., '72; Dreyer et al., '75; Friedman and Jones, '80; Dykes et al., '80). The fact that no main terminal arbors were seen overlapping two cytoarchitectonic areas reinforces the hypothesis of modality segregation in SI. This observation also fits well with the notion that each cytoarchitectonic area contains a separate map of the body representation.

Size and orientation of terminal arbors

Terminal arbors of VPL neurons in SI are made of bushes of about 500 μm in diameter. In about half of the neurons injected (mostly hair-driven units) two such bushes were present, spaced by an uninved gap of about 300 μm. The whole extent of the arborization was aligned preferentially along the mediolateral axis of the cortex, especially in area 3b. It must be stressed that for a folded structure like the cortex the mediolateral axis of the brain might not be a significant axis. Rather, the terminal bushes might be oriented along the long curved axis of cytoarchitectonic areas. Only in the more dorsal or medial part would both axes coincide. The patchy VPL projection to SI is similar to that of the geniculate projection in the visual area (Hubel and Weisel, '69; Ferster and LeVay, '78; Gilbert and Weisel, '79). In this latter area, the tangential spread of thalamic afferents determine the width of ocular dominance columns and these columns create tangential wavy patterns in layer IV. In the somatosensory areas anatomical methods have also shown that commissural and association fibers terminated in alternating patches making stripes along the mediolateral axis of the cortex (Jones et al., '75; Jones and Wise, '75). Recently it was also demonstrated that in the monkey somatosensory areas the projections of a small group of thalamic cells form clusters of terminals of about 500 μm in diameter (Friedman and Jones, '80). These data suggest that some basic anatomical similarities exist in the organization of afferents in the visual and somatosensory areas. They also raise fundamental questions: Does the patchy VPL projection to SI also specify a columnar organization? To what extent can the columnar model of the visual cortex be extrapolated to other cortical
Fig. 1. Electrophysiological identification, receptive field and morphology of a joint afferent fiber from VPL projecting to SI recorded intraaxonally and injected with HRP (fiber F). A. Orthodromic responses to VPL stimulation (th). B. Monosynaptic activation following stimulation of the medial lemniscus (ml). C and D. Receptive field location and cellular responses to flexion (fl) and extension (ext) of the forelimb. Note the different patterns of discharges in response to these two antagonistic movements. The location of the terminal arbor is shown in F on the parasagittal plane that is indicated by the dashed line in E. CRU: cruciate sulcus; Pcd: postcruciate dimple; COR: coronal sulcus; PRE and POST refer to the anterior and posterior part of the cortex. G. Camera lucida drawing of fiber F, and distribution of its branches within cortical layers. For some drawings, layer boundaries represent an approximation of their real position since sections were not always cut normal to the cortical surface.
VENTROBASAL AFFERENTS TO SI IN THE CAT
Fig. 3. Receptive-field morphology of a joint afferent fiber from VPL projecting to SI fiber F. A: Area of stimulation and effect of secondary branches. B: Area of stimulation and effect of fibers already shown in A. C: Downward displacement of the shoulder; upward arrow, upward displacement of the shoulder. D: Camera lucida drawing of fiber F, and details will appear in following legends.
Figure 3
Fig. 3. Receptive field and morphology of a cutaneous afferent fiber from VPL projecting to SI (fiber F8). This fiber responded tonically to skin pressure (bars below recordings). Slight increments of pressure increased the rate of discharges (lower trace). This fiber was located at the edge of the coronal gyrus so that the right part of its arborization was cut parallel to the cortical surface. Note the presence of two separate bushes in D.
Figure 4
Fig. 4. Receptive field and morphology of a cutaneous afferent fiber from VPL projecting to SI (fiber F9). This fiber responded to skin pressure as in Figure 3.
Figure 5
Fig. 5. Receptive field and morphology of a hair afferent fiber from VPL projecting to SI (fiber $F_{11}$).
Fig. 6. Receptive field and morphology of a hair afferent fiber from VPL projecting to SI (fiber F12).
Fig. 7. Receptive field and morphology of a hair afferent fiber from VPL projecting to SI (fiber F15).
Figure 8
Fig. 8. Receptive field and morphology of a hair afferent fiber from VPL projecting to SI (fiber F<sub>17</sub>).
Fig. 9. Receptive field and morphology of a hair afferent fiber projecting to SI. The thalamic origin of this fiber could not be determined. It was driven by hair stimulation.
Fig. 10. Photomicrographs of fibers injected intraaxonally with HRP. A. Part of the arborization of a fiber in layers VI and V of area 3b. Many small branches are seen in layer VI (arrow) while a nonbifurcating fiber (curved arrow) is seen ascending through layer V. B. Part of the arborization of a fiber in layers V, IV, and III of area 3b. Again a nonbifurcating fiber ascends through layer V (curved arrow) and branches in layer IV and III (arrow). C. Small-sized collateral originating from the main axon in white matter. This collateral was traced into area 1 while the main axon gave its terminal arbor in area 3b. In A, B, and C: Nissl-stained material; calibration bars, 50 μm. D. Terminal boutons in layer VI and E grapelike terminals in layer IV taken from a hair-driven unit. F. Bifurcation of a main axon in white matter. Each branch generated separate terminal bushes. Note the HRP-positive material at the node of Ranvier (BDHC reaction). Calibration bars in D, E, and F: 10 μm.
regions? To answer these questions it might be useful to define what is meant by a cortical column. Quite often the terms columns, patches, slabs, bands, or stripes are used indiscriminately. Within the frame of reference of the visual cortex physiology these terms mean precise anatomical and physiological entities although as already discussed by Hubel and Weisel ('74), the term columns applied to ocular dominance patches is a convenient misnaming. These latter columns appear as patches or slabs of tissue depending upon the plane of sectioning. Because the visual pathway is half-crossed the thalamocortical projection maintains retinotopy by alternated juxtaposition in the cortex of inputs coming from both eyes. This creates discontinuities in the thalamocortical projection with respect to the left or right origin of the visual input. This discontinuous visual projection, which can be demonstrated by anatomical and electrophysiological methods, simply reflects the fine retinotopy existing in the visual system. On the other hand orientation columns are definable only by functional criteria. They are not reducible only to some kind of fine retinotopy. Their existence depends upon intracortical processing of incoming inputs, and inhibitory mechanisms appear to play a major role in sculpturing their functional properties (Berardi et al., '80; Hendriksen et al., '80). Orientation columns appear then as the only true "functional columns" while ocular dominance bands result from fine-grained retinotopy.

In the somatosensory cortex, it is known that modality-specific regions exist, and among these, area 3b receives almost exclusively cutaneous information. Within area 3b, it has been shown that slowly adapting (SA) and rapidly adapting (RA) units form two topographically distinct populations. If one looks at the mapping of cutaneous units made in the cat area 3b (see Fig. 2 of Dykes et al., '80) it is clear that starting at the rostral pole of area 3b there is first a zone of RA units followed by a region of SA units and more caudally by another zone of RA units. Such a RA-SA sequence has been confirmed in more recent experiments (R. Dykes, personal communication). In the shoulder area, the SA zone abuts directly on the caudal pole of area 3a, while in the leg region, the SA zone divides in two halves. These alternate regions of RA and SA units form irregular stripes elongated along the mediolateral extent of area 3b in the upper forelimb in the trunk and in the hindlimb regions. In the forearm and forepaw representations (where most of our results were obtained) the geometry of the bands becomes more irregular and there is a general tendency for the bands to turn rostrally and be aligned along the rostrocaudal axis of the brain. The width of the RA and SA bands is not yet exactly known. It may vary from 300 μm to almost 1 mm depending upon the somatic region represented. This estimate fits reasonably well with the size of the terminal arbors of VPL fibers in area 3b. Moreover some fibers (mostly hair-driven cells from the forepaw region) were seen to arborize in two bushes separated by an uninvaded gap. Tentatively it might be postulated that each bush would be located in two different bands representing the same submodality and that another submodality would lie in between. However, the present results do not allow any clear statement concerning the type of thalamic input that would arborize in these uninvaded gaps.

It appears then from the above-mentioned physiological and morphological results that the RA-SA banding in area 3b may represent the basic topographical layout of the somatosensory cortex. These bands would be equivalent to the ocular dominance stripes of the primary visual area. An even finer-grained arrangement (a possible equivalent of orientation columns in the visual cortex) might be present within these RA-SA bands. However, physiological criteria that would define these columns have still to be found.

**Laminar distribution**

The exact laminar distribution of VPL afferents in area SI has been the subject of controversy. Using anterograde degeneration tracing techniques, Jones and Powell ('69) found terminals mainly in layer IV, with a small overlap in layers III and V, and a small amount of degeneration in layer I in cat SI area. In the squirrel monkey, degeneration and anterograde transport studies (Jones '75a) have shown that the lower part of lamina III and lamina IV were the main targets of VPL afferents in areas 3b and 3a. A small constant projection was again reported to layer I. Wise and Jones ('78) have reported that in the rat, thalamocortical terminals in the somatosensory cortex are concentrated in layers I, IV, and VI. Fibers terminating in layers IV and VI were considered to arise from a different thalamic region than those terminating in layer I. In the rat also Herkenham ('80) reported terminals labeling in layers IV and VI following amino acid injections in VPL. All thalamocortical fi-
bers from VPL in the present study terminated in layers VI and IV and in the lower part of layer III. None were seen in superficial layers. This could not be due to incomplete filling since many fibers were very densely filled with HRP reaction product and some of their branches were seen running for millimeters from the site of injection. Moreover, one particular unidentified afferent fiber (presumed to originate in a structure other than VPL) was seen branching profusely in layer III, with some branches reaching layer I. This fiber could have originated from a thalamic nucleus other than VPL given its short latency activation (2.0 msec) after lemniscal stimulation. A thalamic projection to SI from the central lateral and the posterior group nuclei has been described in the cat (Rowe and Sessle ’68; Jones and Leavitt ’74; Jones and Burton ’74). The possibility still exists that this fiber represents a special kind of VPL afferent that we were unable to identify electrophysiologically. The last possibility would be that VPL afferents terminating in layer I have small diameters and could not be impaled and studied for the long periods of time required in this experiment. This must be kept in mind since the VPL thalamocortical input includes also fibers that are slower conducting than those studied in our experiments (Tsumoto, ’74).

As already noted by Jones (’75a), the density of terminal plexuses issuing from VPL fibers in the squirrel monkey is much greater in area 3b than in area 3a. The same was observed in cat. The density of thalamocortical plexuses increases as one moves from area 4 back to areas 3a and 3b. In area 4, ventrolateral afferents (and VPL afferents) generate the most loosely organized trees in layers VI and III (Deschenes and Hammond, ’80) while the density of the intracortical thalamic afferent plexuses in area 3b is the most intense. This may be related to the relative concentration in layer IV (or in layer III in area 4) of a special cell type on which thalamocortical afferents preferentially terminate (see Jones, ’75b).

All VPL afferents in SI give terminal branches in layer VI. Most corticothalamic neurons are located in this layer and this raises the possibility that the receptive field properties of VPL cells might be regulated by the cortex. Interestingly, in the rabbit, the receptive field properties of geniculocortical cells are markedly changed following acute lesion or functional disruption of the corticothalamic input from the primary visual areas (Molotchnikoff et al., ’80).

Secondary projections

As defined in the present report, secondary projections were those issued from small collateral branches of the main axon. They were running toward or arborizing in different cytarchitectonic areas from that of the main axon. We suspect that this is a common feature of all VPL afferents to SI. Data of Table 1 suggest that fibers carrying information from the digits do not have collateral projections but in the case of the most filled fiber (F1), which was also excited by digit stimulation, a secondary site of projection was also present. These secondary projections were generally located on the same sagittal plane as the main arborizations, thus suggesting that they project to similar somatotopic areas. Some may reach cortical regions where other body segments are represented. These latter projections may be responsible for the displacement of peripheral receptive fields observed in cortical cells during epidural block of some dorsal roots (Metzler and Marks, ’79).

A significant aspect about these secondary projections is the important collateral input from VPL cells in area 4. Even some joint afferent fibers from VPL were seen arborizing mainly in the motor area. These morphological observations fit well with the well-known somatic input that has been described in area 4 by physiological recordings (see the review of Jones and Porter, ’80). Thus it appears that the motor cortex receives its somatic information from three different sources: (1) a direct thalamic input from VPL cells (Asanuma et al., ’79); (2) a collateral projection from some VPL afferents impinging mainly in SI, and (3) a corticocortical input from layers II and III cells of the somatic sensory cortex (Zarcecki et al., ’78; Jones et al., ’75). These multiple sources of sensory information to area 4 may explain the complex polysensory nature of the receptive fields of motor cortical cells (Welt et al., ’67).

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