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The Somatotopic Organization of the Ventroposterior Thalamus of the Squirrel Monkey, *Saimiri sciureus*

J.H. KAAS, R.J. NELSON, M. SUR, R.W. DYKES AND M.M.MERZENICH
Departments of Psychology (J.H.K., M.S.) and Anatomy (J.H.K., R.J.N.)
Vanderbilt University, Nashville, Tennessee 37240
Departments of Neurology and Neurosurgery and Surgery (R.W.D.)
McGill University, Montreal, Quebec, H3A, 1A1 and
Coleman Laboratory (M.M.M.), Departments of Physiology and Otolaryngology
University of California at San Francisco, California 94143

ABSTRACT

Multiunit microelectrode mapping techniques were used to investigate the organization of the somatosensory thalamus in squirrel monkeys. Receptive fields and response characteristics were determined for closely spaced recording sites along arrays of electrode penetrations that passed through the ventral thalamus dorsoventrally, rostrocaudally, or lateromedially. The results were related to thalamic architecture and led to the following conclusions: (1) A large, single, systematic representation of the body surface occupied most or all of the ventroposterior nucleus, VP. The nucleus was further defined by a distinct cytoarchitectonic appearance, produced by densely packed, deeply stained neurons. (2) Recording sequences in VP were characterized by (a) abrupt shifts in receptive field locations over short recording distances indicating that the electrode had crossed discontinuities or folds in the representation, (b) long sequences of overlapping receptive fields indicating regions of continuous representation and the maintenance of adjacency in the map, and (c) similar receptive field locations for sites along the trajectory of a penetration indicating regions of isorepresentation. Major somatotopic discontinuities were associated with crossing narrow cell-poor laminae that partially divided VP into subnuclei related to the hand, foot, trunk, and tail in lateral VP and the face in medial VP. Somatotopic discontinuities occurred for electrode penetrations in all three planes, but discontinuities were greater and more frequent for lateromedial electrode penetrations. Lines of isorepresentation and gradual change were most extensive in the rostrocaudal and dorsoventral planes. We hypothesize that the disruptions, regions of isorepresentation, and regions of gradual change result from the thickening, splitting, and folding of a two-dimensional representation of the skin surface to occupy a three-dimensional volume. (3) The magnifications of various skin surfaces in VP were variable so that some skin surfaces, especially the tips of the digits, occupied relatively large portions of the nucleus, while other skin surfaces such as the trunk activated little tissue. It appeared that regions of isorepresentation varied in extent according to magnification factor and position in the map. (4) Within VP, neurons could be classified as slowly adapting or rapidly adapting to maintained skin indentation. Each type of neuron formed small groups or clusters in the nucleus so that several successive recording sites typically encoun-

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Dr. R.J. Nelson's present address is Laboratory of Neuropsychology, National Institute of Mental Health, Bethesda, MD 20205.

Dr. M. Sur's present address is Section of Neuroanatomy, Yale University School of Medicine, New Haven, CT 06510.

tered one type before a sequence of the other type was observed. (5) Neurons ventrocaudal to VP formed a second representation of the body in the ventroposterior inferior nucleus (VPI). Recordings and cytoarchitecture suggest that VPI extends further caudal than generally recognized, to include a part of the region caudal to VP that is sometimes described as part of the posterior group (Po) of thalamic nuclei. Body parts represented in VP were represented again in VPI in a roughly parallel sequence so that in both nuclei the caudal body was lateral and the rostral body was medial. Neurons in VPI were activated by inputs from pacinianlike receptors. Such activation was not observed in VP. (6) A 1.0–1.5 mm thick band of tissue along the dorsal and rostrodorsal borders of VP was responsive to manipulation of deep body tissues including muscles and joints. The mapping evidence was compatible with the existence of one or more representations of deep receptors roughly parallel to the cutaneous representation in VP. Patterns of thalamocortical connections suggest subdividing the thalamic zone of activation by deep receptors into a ventroposterior oral nucleus, VPO, relaying muscle spindle information to cortical area 3a, and a ventroposterior superior nucleus, VPS, relaying deep receptor inputs to area 2.

Key words: microelectrode mapping, cutaneous representation, ventroposterior inferior nucleus

A number of recent observations suggest that longstanding views on thalamocortical organization in the somatosensory system of primates should be reconsidered. Until recently it was possible to argue for a single "ventroposterior" nucleus with a mixture of submodalities relaying to a single "primary" or "S-I" cortical representation. In a series of papers on the organization of somatosensory cortex in monkeys (Merzenich et al., '78, Kaas et al., '79; Nelson et al., '80a,b; Sur et al., '82; Felleman et al., '83; Pons et al., '83a,b; also see Paul et al., '72), we have presented evidence that the traditional "S-I" actually consists of four separate representations of the body, one for each of the architectonic fields 3a, 3b, 1, and 2 (for a recent alternative point of view, see McKenna et al., '82). Separate representations of the body surface were found in areas 3b and 1, while areas 3a and 2 were largely related to noncutaneous body receptors. Investigations of neuron response properties in monkeys indicated that area 3b is occupied by neurons that respond in either a slowly adapting (SA) or a rapidly adapting (RA) manner to maintained cutaneous stimuli (Paul et al., '72; Sur, '80; Sur et al., '81), area 1 is somewhat more dominated by rapidly adapting neurons and includes a small population of neurons apparently related to pacinian receptors (Paul et al., '72; Merzenich et al., '78; Sur, '80), area 3a is largely related to muscle spindle afferents (Phillips et al., '71; Lucier et al., '75; Hore et al., '76; Tanji and Wise, '81; Maendly et al., '81), and area 2 receives inputs from deep receptors including joints, and from cutaneous receptors (Powell and Mountcastle, '59; Burchfield and Duffy, '72; Merzenich et al., '78; Hyvärinen and Poranen, '78; Iwamura and Tanaka, '78; Pons et al., '83b). These observations, resulting in a reappraisal of cortical organization and the concept of "S-I," lead to a reconsideration of the relay nucleus for "S-I," the ventroposterior "nucleus." The present study used microelectrode mapping procedures to determine if multiple representations of the body exist in the somatosensory thalamus of monkeys, and to determine the detailed organization of the representation of cutaneous inputs in the thalamus.

From the first investigations of thalamocortical connections, there have been reasons to question the concept of a single relay nucleus for "S-I." In an early retrograde degeneration study, Le Gros Clark and Powell ('53) found little evidence of degeneration in the ventroposterior nucleus after lesions of area 2 and hypothesized that this division of cortex is subserved only by collaterals of axons projecting to areas 3b and 1. Later Jones and Powell ('70) recognized that after lesions in the ventroposterior nucleus, the resulting anterograde degeneration was most dense in area 3b. In addition, Mountcastle and Henneman ('52), and subsequently, Poggio and Mountcastle ('60), Pubols ('68), Loe et al. ('77), Pollin and Albe-Fessard ('79), and Jones and Friedman ('82) found that neurons in the thalamus activated by deep body receptors were largely dorsal to those activated by cutaneous receptors. While the concept of a single relay nucleus was not directly challenged in these early investigations, the results indicated that the ventroposterior thalamus was not uniform in function or connections.

Recently, the anatomical evidence for subdividing the ventral thalamus has become more compelling. We argued from horseradish peroxidase and ^{3}H-proline studies that a single somatotopic representation in a ventroposterior nucleus projects to two separate and parallel somatotopic representations in areas 3b and 1, and that a separate thalamic region projects to area 2 (Lin et al., '79; Nelson and Kaas, '81). There is now extensive evidence that one region of the ventroposterior thalamus projects to both areas 3b and 1, and another to area 2, although this difference typically has been described in terms of subdivisions ("core and shell") of a single nucleus rather than separate nuclei (Friedman and Jones, '80; Jones et al., '82). Further, there is evidence that a distinct rostrodorsal region of the ventroposterior thalamus projects to area 3a (Kalil, '78; Maendly et al., '81; Jones and Friedman, '82). These observations forcefully argue for separate body maps in the ventroposterior thalamus, and recently, after exploring the ventroposterior region with microelectrodes, Jones et al. ('82) have suggested that there are separate maps of deep and cutaneous receptors. A major goal of the present studies, therefore, was to determine if inputs from different receptor types mapped separately in the ventroposterior thalamus.

A second major goal was to determine the organization of the cutaneous input to the ventroposterior thalamus in detail. While the major features of the cutaneous represen-

tation are now well known (Mountcastle and Henneman, '52; Pubols, '68; Loe et al., '77; Pollin and Albe-Fessard, '79; Jones et al., '82), an understanding of the detailed structure of sensory maps can be very useful in the formulation of principles of organization, and in the interpretation of results from other types of experiments.

The present results support a concept of four distinct relay nuclei in the ventroposterior thalamus, each dominated by a different submodal input. The organization of the principal cutaneous nucleus, with mixed SA and RA cell groups, is summarized, and a theory of map thickening, splitting, and folding is presented to account for the transformation of a cutaneous two-dimensional receptor sheet onto a three-dimensional nucleus. Preliminary reports of some of these data have appeared elsewhere (Dykes et al., '81; Nelson et al., '82).

METHODS

Microelectrode mapping procedures were used to investigate the somatotopic organization of the ventroposterior nucleus and adjoining thalamus of eight adult squirrel monkeys, *Saimiri sciureus*. Recordings were limited to the thalamus on one side of the brain in six cases, while data were collected from both sides of the brain in two cases.

The animals were prepared for recording after being anesthetized with ketamine hydrochloride (33.3 mg/kg; I.M.; White et al, '82). Smaller additional doses were given during surgery and recording as needed to maintain the anesthetic state. Body temperature was maintained at 37°C. Each monkey was placed in a stereotaxic head holder and part of the brain surface was exposed by a craniotomy so that electrodes could penetrate into the thalamus along one of the axes of the Horsley-Clark coordinate system. Since electrode penetrations into the ventroposterior nucleus were made in one of three different orthogonal directions in individual experiments, the portions of the brain exposed varied. For vertical dorsoventral electrode penetrations, the bone over parietal cortex was removed, and for horizontal lateromedial electrode penetrations the temporal bone was removed. Horizontal rostrocaudal electrode penetrations were accomplished by removing the ipsilateral eye and underlying bone. For frontal and temporal approaches, the animal's head was rotated so that the electrode penetrations would be vertical with respect to the stereotaxic frame. In all experiments, the dura was reflected, and an acrylic dam was constructed around the craniotomy to hold a pool of warm silicone to protect the exposed brain. After the skull was fixed to a bar with acrylic, the exposed cortical surface was photographed, and vascular landmarks in the photo graph were assigned stereotaxic coordinates. The stereotaxic frame was then removed to allow greater access to the body surface. Animals were maintained in stereotaxic alignment relative to the electrode carrier by the attached bar, which was held in a vise.

In each experiment, the ventroposterior thalamus was approached and studied in a series of parallel electrode penetrations which started at the surface of the brain and terminated after somatosensory responses ceased or the expected distance across the ventroposterior regions was exceeded (Fig. 1). The recording electrode was typically advanced while stimulating and moving various parts of the body until a response was obtained. Then, receptive field locations and response properties were studied in a series of stepwise electrode advances. Since preliminary recordings indicated that electrode advances of 50 μm or more were usually needed to reveal significant shifts in receptive field locations for successive recording sites, observations were made routinely at every 50 μm within the responsive zone. Recording locations were always noted relative to a stereotaxic reference, and most of the electrode penetrations were marked with electrolytic lesions (Fig. 2), usually at the start or end of the responsive zone, or both, by passing a DC current (10μA, 5 seconds) through the recording electrode. Electrode penetrations were placed in rows in a stereotaxic plane and several rows of penetrations were introduced for a typical experiment. Because the electrode penetrations damaged the ventroposterior thalamus, individual penetrations were usually separated by distances of 200 μm or more. Consequently, the somatosensory thalamus was sampled with a 50 μm resolution only along the length of the electrode tracts.

Recordings were made with glass-coated, platinum-iridium microelectrodes with impedances between 1–2.5 MΩ(at 1 KHz). Most recordings were from small clusters of neurons. Electrodes were advanced with a manually controlled micropositioner for the initial 8–11 mm of a penetration and thereafter by a hydraulic microdrive controlled by a stepping motor. Signals were conventionally amplified and monitored. Neurons were first activated by manipulating, tapping, or touching the body until a region capable of driving the recorded neurons was found. Then, a systematic effort was made to define the precise location of the receptive fields and the submodality of the effective stimulation. Neurons were classified as cutaneous if they responded to light stimulation of the skin surface, and noncutaneous or deep if they responded only to manipulation of joints and muscles. If the neurons clearly responded to the rotation and movement of specific joints, this was noted. Otherwise responses to noncutaneous stimuli were simply classified as arising from deep receptors.

As in our previous experiments on somatosensory cortex (Merzenich et al., '78; Nelson et al., '80a,b) minimum receptive fields were determined for neurons responsive to cuta-

Abbreviations

CE	Central medial nucleus
CL	Central lateral nucleus
CM	Center median nucleus
D_{1-5}	Digits from thumb to little finger or from great to little toe
GP	Globus pallidus
Hb	Habenular nuclei
IP	Inferior pulvinar complex
LD	Lateral dorsal nucleus
LGN	Lateral geniculate nucleus
LP	Lateral posterior nucleus
MD	Medial dorsal nucleus
MG	Medial geniculate nucleus
P_{1-4}	Pads of hand and foot
P_h	Hypothenar pad
P_{th}	Thenar pad
Pac	Pacinian-type response
Pf	Parafascicular nucleus
PG	Pregeniculate nucleus
Po	Posterior complex
Pul	Pulvinar complex
Put	Putamen
RT	Reticular nucleus
VA	Ventral anterior nucleus
VL	Ventral lateral nucleus
VM	Ventral medial nucleus
VP	Ventroposterior nucleus
VPI	Ventroposterior inferior nucleus
VPL	Lateral division of VP
VPM	Medial division of VP

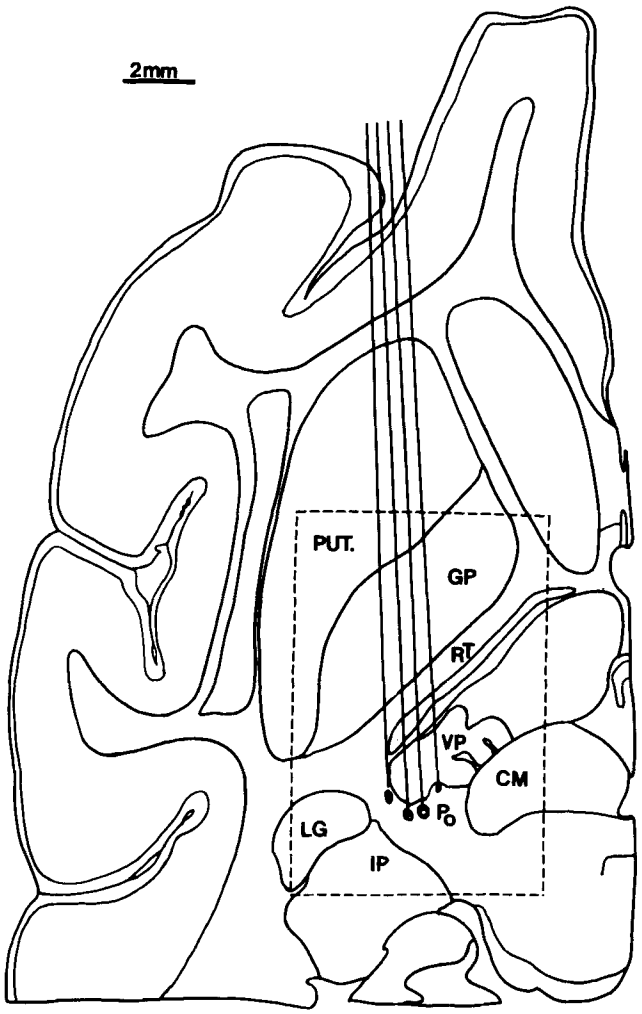

Fig. 1. Electrode tracks in a horizontal section from the left cerebral hemisphere of a brain of a squirrel monkey that was blocked caudal to the thalamus. The section was cut almost perfectly in the plane of the electrode tracks which extended from the surface of frontal cortex through the ventroposterior nucleus (VP) and terminated with small electrolytic lesions (circles.) The boxed area is shown in photomicrograph A of Figure 2. An adjacent section that was more appropriate for the terminal extent of the electrode tracks is shown with recording sites in Figure 12.

neous stimuli by using fine, blunted, hand-held glass probes to make just visible indentations of the skin and movement of hairs. Neuronal responses to steady skin indentations by a probe were often further classified as rapidly adapting (RA) when there was only a transient response, and slowly adapting (SA) when the response was sustained. Neurons judged to be activated by pacinianlike receptors (Pac) typically had very large and poorly delimited receptive fields, and high sensitivity to low-amplitude mechanical stimuli so that even light taps and vibrations on the recording table were effective stimuli (also, see Dykes et al., '81). While neurons with these characteristics were quite different from those in area 3a (Sur et al., '82), which received muscle spindle inputs (see Tanji and Wise,'81, for review), the possibility of muscle spindle activation is not completely ruled out by these tests.

In two experiments, subjective judgments of response classes were supported by quantitative measurements. A mechanical stimulator (Chubbuck, '66) capable of delivering precisely controlled sinusoidal and stepwise probe displacements of the skin were used to deliver stimuli to the receptive fields. Poststimulus time histograms were obtained for up to 25 presentations of a 1-second step indentation of the skin for each recording site tested. Responses to sinusoidal displacements over a range of frequencies and indentation depths were also analyzed. RA sites were classified as those that produced only transient onset and offset responses to the skin indentations, while SA sites were those that also produced a sustained discharge during the indentation. Sites where rapidly adapting neurons were activated by high-velocity (150–400 Hz) low-amplitude sinusoidal stimulation of the skin were judged to be related to pacinian receptors (see Talbot et al.,'69; Merzenich and Harrington, '69; Dykes et al., '81). Results based on quantitative measurements were consistent with those obtained by qualitative procedures.

At the end of each experiment, animals were deeply anesthetized and perfused intracardially with 0.9% saline followed by 10% formal-saline. The brains were blocked stereotaxically and cut on a freezing microtome at 50 μm in either the coronal, or the sagittal, or the horizontal plane. Alternate sections through the somatic thalamus were stained with cresylecht violet for Nissl substance, or with hematoxylin for fibers (Lin and Kaas, '77). These sections were examined and each electrode track was identified. The electrode tracks were reconstructed using the reference lesions and the stereotaxic recording distances to locate recording sites relative to the cytoarchitecture of the brain sections.

RESULTS

The results are presented in three parts. First, an overview of the cytoarchitecture of the ventroposterior nucleus and adjacent thalamus is given. Next the somatotopic organization of the ventroposterior nucleus is described. Finally, the response properties of neurons in the ventroposterior nucleus and parts of adjacent thalamus are discussed.

Cytoarchitecture of the ventroposterior thalamus

The major subdivisions of the thalamus of squirrel monkeys used in this study are based on delineations of Emmers and Akert ('63), although variations may occur since boundaries of nuclei are not indicated in their atlas. Most of our electrophysiological data relate to the ventroposterior nucleus (VP), which is distinguished by densely packed and deeply stained cells (Fig. 2). However, VP is not homogeneous. Rather, it consists of islands of densely packed cells partly isolated by cell-poor zones or laminae containing fibers. Both the sizes of the cell groups and the widths of the isolating fiber bands vary with location in the nucleus. Traditionally, two major subdivisions of VP have been recognized: ventroposterior medialis (VPM), which represents the head, and ventroposterior lateralis (VPL), which represents the body. These two divisions are similar in cellular composition, but are separated by a fiber band, the arcuate lamina, that is distinct in most preparations (Fig. 2A). Both VPM and VPL are further subdivided by additional laminae. These laminae partially separate VPL into four main subnuclei that elsewhere we have labeled as A, B, C, and D (Lin et al., '79; also see Fig. 12). Subnucleus A is immediately lateral to VPM and represents the hand. Subnucleus B is more lateral and represents the foot. These two subnuclei encompass a major portion of VPL and the

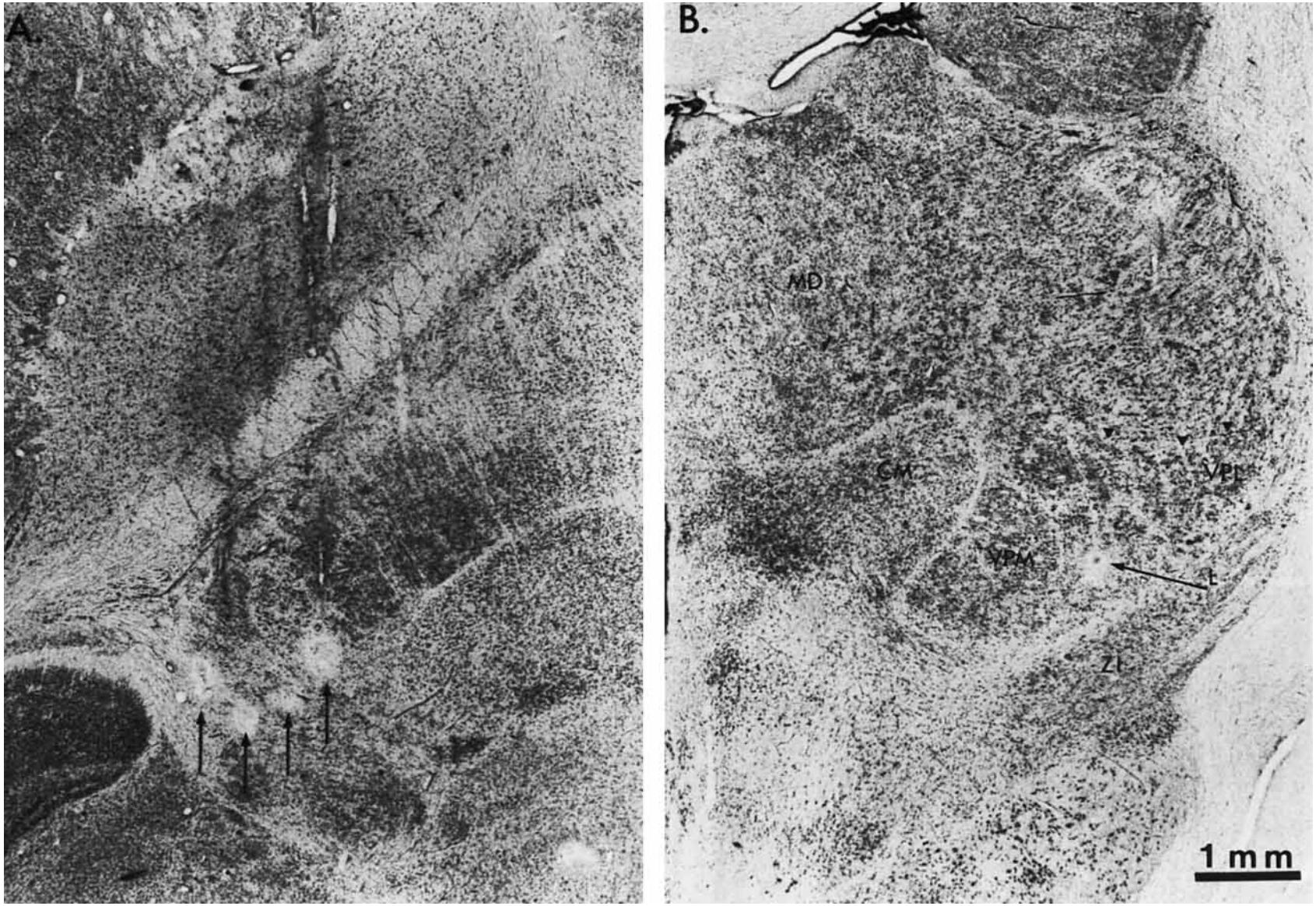

Fig. 2. Photomicrographs of the ventroposterior nucleus and adjacent thalamus. A. A horizontal section with four electrode tracks through VP ending in electrolytic lesions (arrows). The area shown corresponds to the enclosed box in Figure 1. VP is identified by darkly stained, densely packed cells. Medial, right; rostral, top. B. A coronal section with the VPM and VPL divisions of VP indicated. An arrow marks a lesion along an electrode track that corresponds to the junction of VP with VPI. The dorsal border of VP is indicated by the change from densely packed stained cells to more scattered cells and by three small triangles. Medial, left; ventral, below. Figure 3 is of a comparable thalamic section in another case.

fiber band separating them is usually quite distinct. From the middle to the caudal parts of VPL, immediately lateral to subnucleus B, a less-conspicuous fiber band separates a small group of cells, subnucleus D, which represents the tail. These subnuclei are bordered dorsally and caudally by a large mediolaterally extending group of cells, subnucleus C, which is devoted to the trunk and limbs. VPM also has obvious subdivisions. In particular, fiber bands partially separate lateral subnuclei representing the face from medial subnuclei representing the teeth and the oral mucosa (Fig. 13). It should be noted that these subnuclear groups are not completely isolated. Rather subnucleus C of VPL is connected to subnuclei A, B, and D, and to VPM, by bridges of cells. Within the subnuclei of VP, there are smaller groups of cells separated by cell-poor zones of varying widths and joining each other in varying places. The more obvious of these smaller cell-poor zones commonly appear to separate groups of cells representing disjunctive body parts (see below). The fiber bands separating major parts of the body representation in VP of monkeys and other mammals have been illustrated and discussed more fully elsewhere (e.g., Lin et al., '79; Johnson, '80; Nelson and Kaas, '81).

The ventroposterior inferior nucleus (VPI) is immediately ventral and caudal to VP (Figs. 2B, 3–5). VPI is identified by its rather pale appearance in Nissl-stained sections because it contains small, scattered, lightly stained cells which stand out in marked contrast to the deeply stained cells of VP. Our recordings suggest that VPI extends caudal to VP, but the exact boundaries of the nucleus are difficult to determine in this region because adjoining portions of the posterior complex (Po) or pulvinar complex (Pul) also consist of lightly stained scattered cells that fail to contrast with VPI.

A region rostral and dorsal to VP contains one or more separate nuclei related to deep receptors. We have not drawn borders for this region since our electrophysiological recordings from this vicinity are incomplete. The region extends for 2 mm or less rostrally and dorsally from VP and is composed of scattered larger cells so that it has a less compact appearance than either VP or the more dorsal and rostral thalamus usually designated ventral lateral (VL) or lateral posterior (LP).

Receptive field locations for recording sites in VP

The representation of the body surface in the ventroposterior nucleus was explored by locating receptive fields for neurons at closely spaced recording sites in microelectrode penetrations through the nucleus. Results from penetrations along each axis are presented below. To reduce crowding in the illustrations, receptive fields are shown for approximately every other recording site. The illustrated results were consistent with those not illustrated.

Dorsoventral penetrations. Observations from dorsal to ventral microelectrode penetrations were obtained from five monkeys and six cerebral hemispheres. Results from one of these cases are illustrated in Figures 3–5. Figure 3 shows receptive fields for recording sites for a lateral to medial row of electrode penetrations across the most rostral margin of VP. In each penetration, responses at the recording sites illustrated within VP were elicited by light cutaneous stimuli. Sites above VP (not shown) were activated by stronger stimuli, and appeared to be related to noncutaneous receptors. Sites in VPI were activated by pacinian-like receptors.

Receptive fields for recording sites in VP in penetration one indicated that digit tips of the foot are represented rostrally, that middle phalanges are dorsal to distal phalanges, and that the representations of the digits are arranged so that there is a tendency to move from medial to lateral and thus from digit 2 to digit 3 with increasing recording depths. The results from penetrations 2 and 3, both within the part of VP representing the hand, confirmed these features of organization and added further observations. First, there was clear evidence that proximal parts of the digits were represented dorsal to distal parts. This was most obvious from the progression of receptive fields for penetration 3, which started on the palmar pads and proceeded to the tip of digit 2. A progression from the middle phalanx of digit 4 to the tip of digit 5 was found for penetration 2. Second, ulnar digits were found lateral to radial digits in the nucleus. Third, the representations of the digits were not perfectly aligned in the vertical axis so that the receptive fields at deeper recording sites in ventral progressions were likely to shift from ulnar to radial digits. Recordings from penetrations 4 and 5 were from VPM, and all receptive fields were on the face. The recordings indicated that the representation of the upper lip was medial to that of the lower lip, and that the representation of the lateral jaw was dorsal to that of the midline of the lower lip.

Besides specific features of the organization of the most rostral portion of VP, the data in Figure 3 also illustrate some general findings that are substantiated further in following figures. First, the general progression of the representation from rostral to caudal on the body was demonstrated across the medial to lateral extent of the nucleus. Second, changes in representational distance across the skin were much smaller across the vertical dimension of the nucleus than those across the mediolateral dimension. Finally, the sequences of receptive fields within penetrations indicate that across the vertical dimension, there were (1) short regions with little change in somatotopy (recording sites A and A′ and B and B′ in penetration 3, for example), (2) regions of gradual change of receptive fields with continuously shifting overlaps (E–J, penetration 3), and (3) small jumps or somatotopic discontinuities in representation (A and B in penetrations 1 and 2 are examples where receptive fields for adjacent recording sites shifted to nonoverlapping locations on the skin). Similar recording sequences indicating regions of isorepresentation, somatotopic continuity, and somatotopic discontinuity are also apparent in Figures 4 and 5.

Figure 4 illustrates results from a second row of recording sites in the same animal taken from a plane 200 μm behind that shown in Figure 3. Receptive fields for penetration 6 show that the trunk was represented dorsally in VP. A major discontinuity occurred between recording sites C and D, since receptive field locations for adjacent recording sites shifted from the trunk to the glabrous sole of the foot. The most dorsal recording sites in the representation of the foot had receptive fields on the sole near the heel, followed by a progression of receptive fields toward digit 1 along the thenar pad with deeper recording sites. Digits 1 and 2 were represented ventrally, with the digit tips most ventral. A sudden change in the representation from digit 1 to digit 2 occurred along the electrode track. Finally, there was evidence from recording sites M and N for the representation of the dorsum of the digits most ventrally in VP.

Penetrations 8 and 9 provided more information about the representation of the hand in VP. Again, the more proximal parts of the palm and digits were represented dorsally in the nucleus while more distal parts were repre-

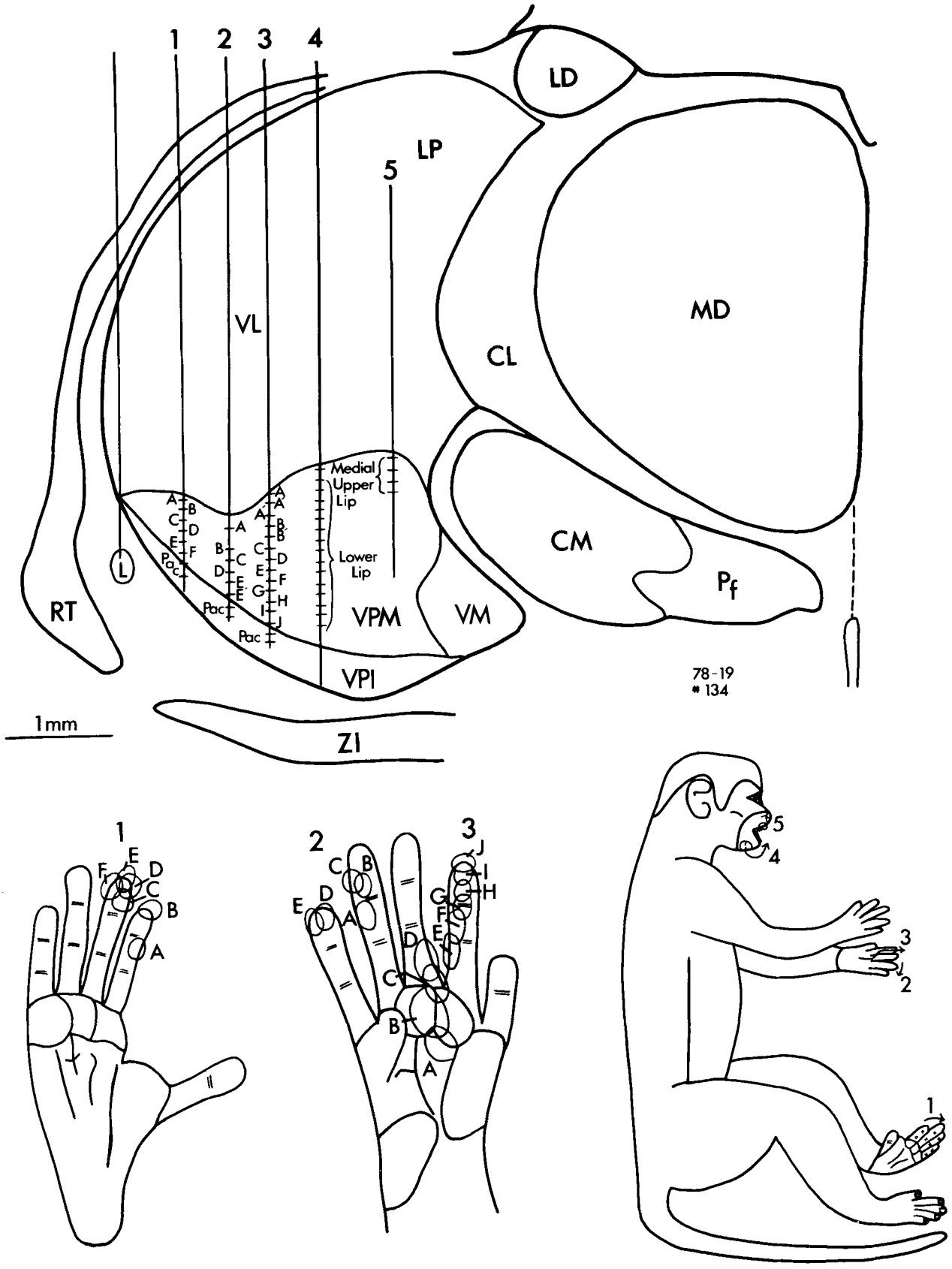

Fig. 3. Receptive fields for recording sites along electrode penetrations in a coronal section through the rostral portion of VP. The most lateral penetration is marked by a lesion (L). Receptive fields for recording sites in each penetration are shown on body parts below. Primed letters such as A' and B' in penetration 3 indicate recording sites where the receptive field location changed very little and is not shown. See text for details.

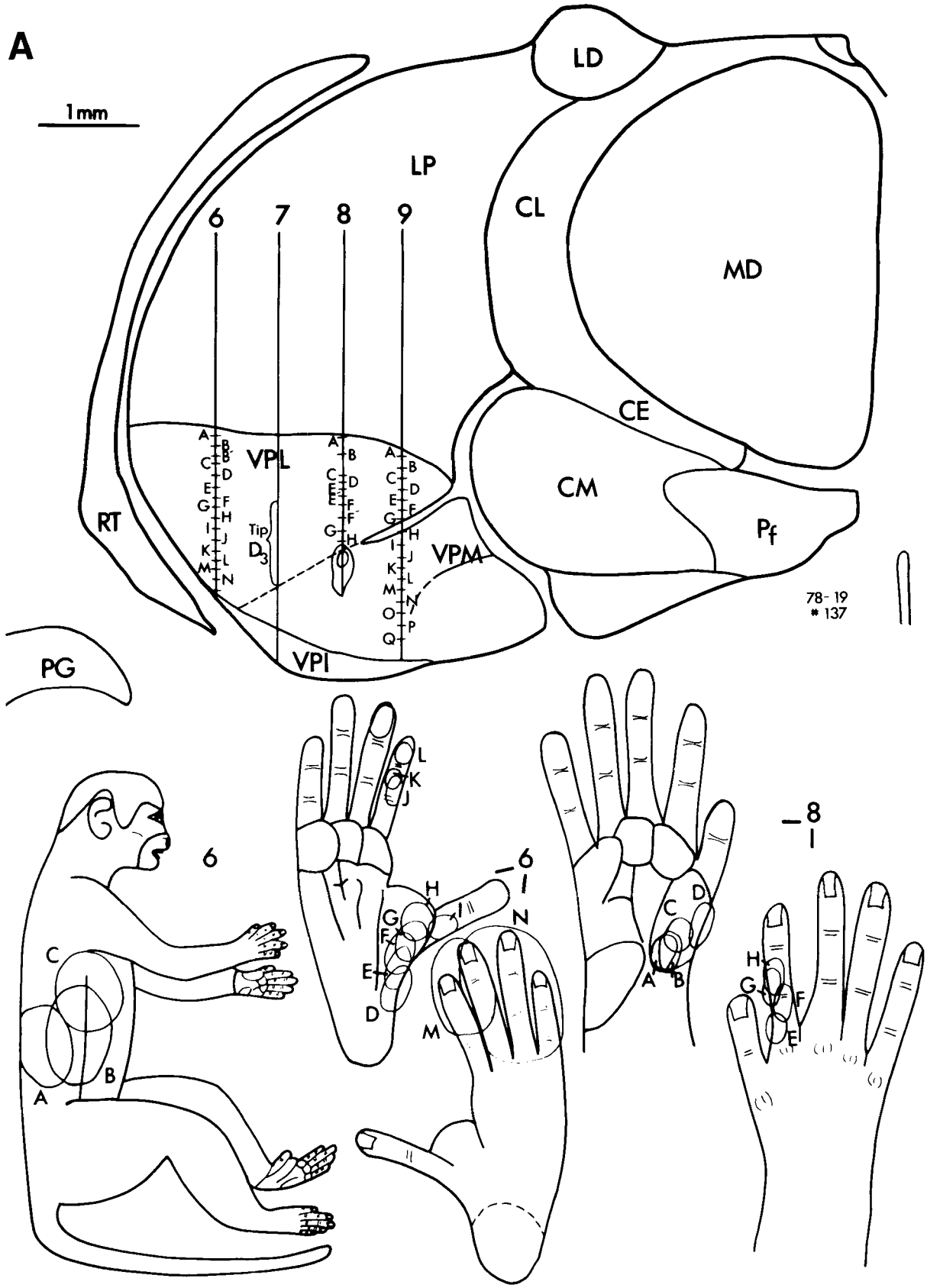

Fig. 4. Receptive fields for recording sites along electrode penetrations at a more caudal level of VP. Coronal section.

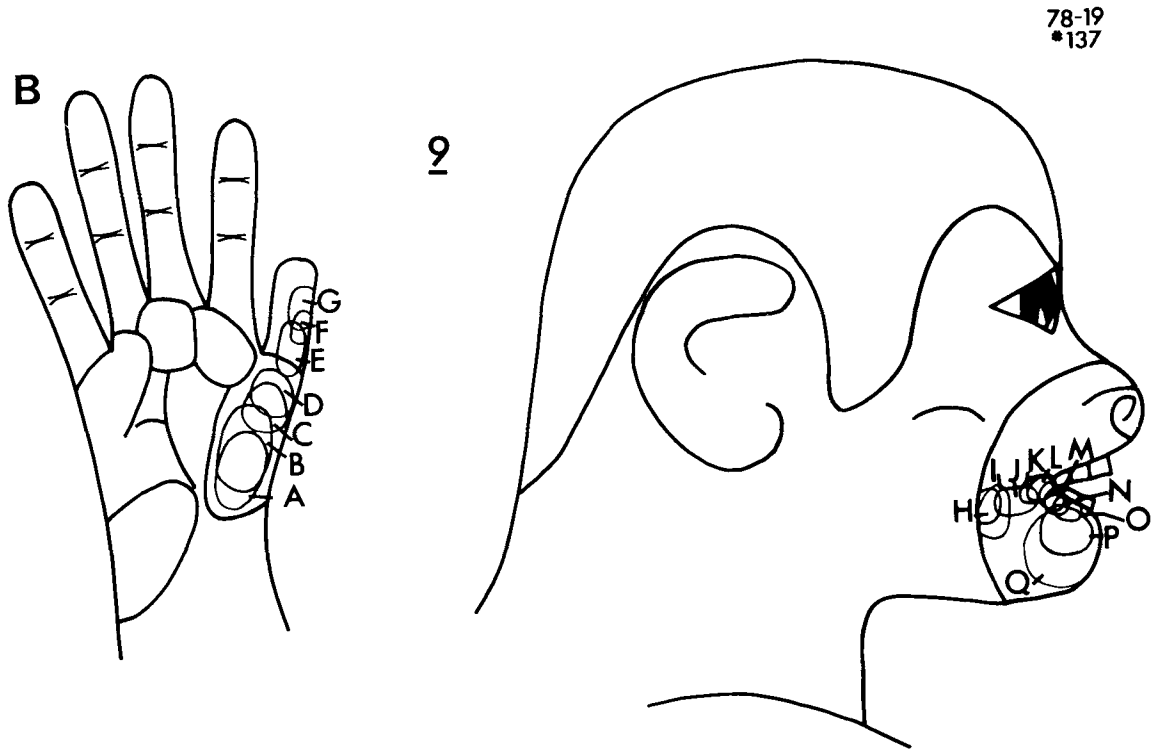

Figure 4 (continued)

sented ventrally. Note also that the representation of the dorsum of digit 2 was ventral in penetration 8 near VPM, that the receptive field sizes for the dorsum were about the same size as those for the palm, that the progression of receptive fields on the dorsum was from proximal to distal with successively more ventral recording sites, and that there was a discontinuity in the representation between sites D and E. Penetration 9 provided a continuous receptive field sequence on the radial hand for VPL and extended from VPL into VPM. The most dorsal recording sites in VPM corresponded to receptive fields on the lateral face near the corner of the mouth. With deeper recording sites, the receptive fields progressed toward the midline of the mouth and then down onto the chin.

Figure 5 shows results for electrode penetrations near the caudal end of VP. The most lateral penetration (unnumbered) missed the nucleus, although stimulation of the tail generated background responses as the electrode passed VP. Penetrations 10, 11, and 12 produced progressions of receptive fields that avoided the face, hand, and foot. Instead, the most caudal part of VP represented the limbs and upper head. Most of the recordings were from subnucleus D (Fig. 12), which curves ventrally to form the caudal cap of VP. Perhaps because of this curvature, receptive field progressions A–D for penetration 10, and A–K for penetration 11, proceeded from distal to proximal, the opposite direction from that observed for progressions more rostrally in the nucleus. Thus, receptive fields for the most dorsal recording sites in penetration 10 were near the knee, and receptive fields for successively deeper recording sites progressed up the thigh. Next, a series of unresponsive recording sites was encountered corresponding to a discontinuity in the representation, and the change from subnucleus D to subnucleus C. The deeper sequence of recording sites, E–H, produced a sequence of receptive fields from the middle to the base of the tail. Thus, the tail was represented laterally and caudoventrally in lateral VP. More medially, penetration 11 traced a sequence of receptive fields starting on the wrist for the most dorsal recording site and extending to the caudal shoulder for the most ventral recording site.

Penetration 12 encountered another major discontinuity in the representation. Receptive fields were on a fixed location on the wrist over a 700 μm distance for the most dorsal recording sites, but within 50 μm they switched suddenly onto the lateral head for the more ventral recording sites. Receptive fields for the most medial part of the nucleus in penetration 13 progressed from the ear to the rostral cranium. Thus, caudomedial VP represented the occiput and cranium.

Results from vertical electrode penetrations in other monkeys confirmed and extended the results illustrated in Figures 3–5. For example, in recordings from the right cerebral hemisphere in case 78-19 (not illustrated), the chin was found to be represented dorsorostrally and the tongue ventrorostrally with the lower lip in between in VPM. In the hand subnucleus of VPL, receptive fields again progressed from palm to distal digits and the dorsum of the digits was most ventral in some penetrations. More laterally in the foot subnucleus, the receptive field sequence began on the sole and progressed to distal digits. In the caudolateral extreme of VPL, the representation of the tail extended ventromedially under the leg representation.

One of the brains explored with vertical electrode penetrations was cut in the parasagittal plane, allowing rostrocaudal sequences of penetrations to be more easily compared

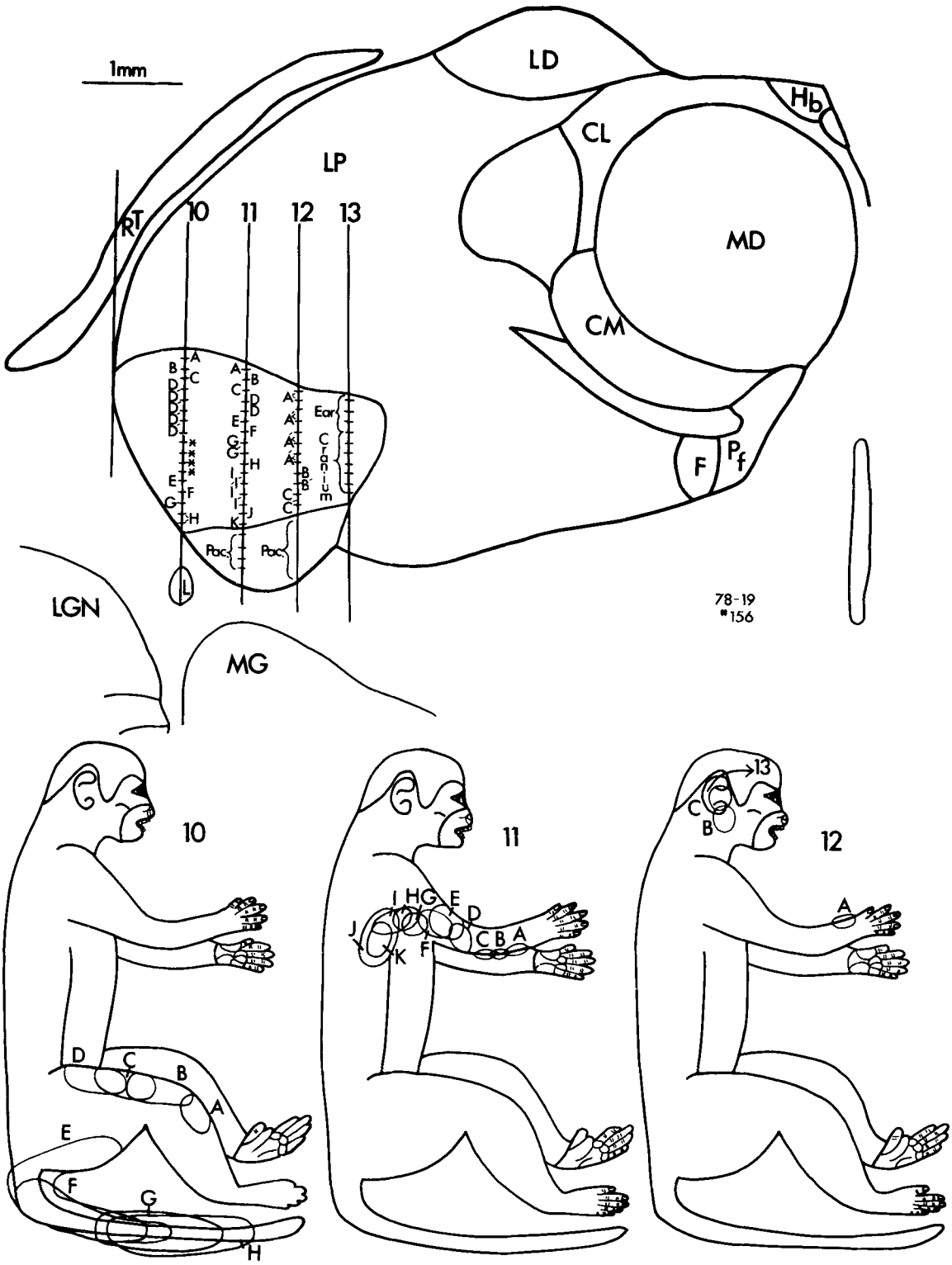

Fig. 5. Receptive fields for recording sites along electrode penetrations in caudal VP. Coronal section.

(case 78-54, not illustrated). The most lateral row of electrode penetrations resulted in one penetration rostral to VPL that produced a sequence of recording sites activated by deep receptors successively located on the foot, ankle, and leg as the electrode advanced. The most dorsal recording sites in the most rostral of the three penetrations through VPL had receptive fields on the dorsum of digit 5 and the adjoining lateral foot. Deeper recording sites had receptive fields on the glabrous surface of digit 5 where they progressed from the proximal phalanx to the tip. In the same parasagittal plane but about 220 μm caudal in VPL, the electrode encountered neurons in subnucleus D activated from the posterior leg and thigh, then from the lateral side of the dorsal foot, and finally from the lateral side of the ventral foot. The sequence in the next penetration 250 μm more caudal in VPL progressed from the dorsal foot, to the lateral ankle, then to the anterior leg near the knee, and finally to the anterior thigh and hip. These last recordings clearly demonstrated the distal to proximal sequence of representation in the caudal part of subnucleus D. In a more medial parasagittal plane, four penetrations passed through the part of VPL representing the hand and forearm. The results indicate that the radial hand and digits were represented at a single rostrocaudal plane across VPL, more proximal parts of wrist and hand were represented dorsally in the nucleus, and the dorsal surfaces of the hand and digits were represented at several locations in VPL. Small discontinuities in the representation occurred in the vertical plane, so that adjacent recording sites related to dorsal and ventral skin surfaces, and to the palm and the middle phalanx of a digit. Results from the most medial row of penetrations through VPM indicated that the lower lip was represented rostral to the upper lip, that the deepest recording sites produced receptive fields on the glabrous lips and the teeth, and that the upper head was represented caudally with the region of the ear dorsal to the cranium which, in turn, was dorsal to the upper face.

Lateromedial penetrations. The organization of VP was explored with lateromedial penetrations in two cases. The results from the two cases were very similar, and only case 78-20 (Figs. 6–8) is illustrated. The most rostral penetration (not shown) in the dorsal row only encountered the rostral margin of the more medial and dorsal extent of VPL where the receptive field sequence began on the forearm, moved to the hypothenar pad, and then to the thenar pad. In VPM the recording sites were activated by receptive fields around the ear, followed by fields around the eye and finally the nose. The next penetration (#1, Fig. 6) passed through the full lateromedial extent of VPL, and the recorded sequence of receptive fields shifted from the tip to the middle of the tail, then jumped to the posterior leg, to the anterior leg, and to the abdomen. Following this, the receptive fields shifted abruptly to the forearm and wrist, the anterior shoulder, and the lateral neck and ear. Between jumps in receptive field location, short advances of the electrode resulted in little or no change in receptive field location. The penetration ended medially in VPM in a region responsive to the lateral face. The most caudal penetration in the series (#2, Fig. 6) resulted in a sequence of receptive fields that began on the tip of the tail and remained there while the electrode moved 500 μm. For the next recording sites, the receptive fields moved to the caudal back, jumped to the lateral middle trunk, and then moved to the shoulder. Thus, there was a tail to head progression of representation from lateral to medial in the nucleus. The most dorsal aspects of VPL were largely devoted to the trunk and limbs, with the lower limbs rostral to the upper limbs and trunk. Perhaps the most significant observation in these penetrations was that adjoining blocks of tissue clearly represented separated regions of the body surface so that receptive fields remained in a similar location for a few recording sites, and then suddenly shifted to a different location.

The second row of horizontal electrode penetrations in this animal was 500 μm more ventral in the nucleus (Fig. 7). For the most lateral recording sites in the most rostral penetration (#3), receptive fields were on the proximal tail. Subsequent recording sites had receptive fields on the pads of the foot, on pads of the hand, and, for the medial margin of VPL, on the tip of digit 1. The first recording site in VPM (J) was strongly driven by stimulating the midline of the chin under the lip, and weakly responsive, presumably from activity of adjacent neurons in VPL, to stimuli on the tip of digit 1. Subsequent receptive fields progressed along the lower lip to the corner of the mouth and back to the midline of the upper lip. A more caudal electrode penetration (#4) resulted in receptive fields first on the middle of the tail, then progressively on the outer pads of the foot, the posterior hindlimb, the chest, the forearm and hand, and finally the rostral cranium. A still more caudal electrode penetration (#5) in the row produced a discontinuous sequence of receptive fields that started near the base of the tail and included receptive fields on the base of the tail, jumped to the anterior leg and then the inner anterior knee, moved to the lateral trunk, moved to the forearm and dorsal wrist, and finally, for sites in the caudal bridge of tissue joining subnucleus D to VPM, on the neck, ear, and caudal cranium. The final electrode penetration located in the caudal aspect of VPL produced receptive fields on the lateral trunk. Overall, the results from these four penetrations emphasized the rapid caudorostral progression of receptive field loci, and the somatotopic discontinuities that occur in the lateromedial dimension of VPL and VPM.

One electrode penetration was placed at a third horizontal plane 600 μm deeper in VP. The results (Fig. 8) show quite clearly the lateromedial order of the representation of the digit tips of the hand from 5–1 (receptive fields A–F) along the rostral margin of subnucleus A. In adjoining VPM, the receptive fields were on the lower lip. Receptive fields were on the first three lower contralateral teeth and adjoining gums for the most medial recording sites in VPM.

In a fourth horizontal plane, 150 μm more ventral in VP, individual subnuclei were quite evident (Fig. 9). The most rostral electrode penetration (8) entered subnucleus B at the representation of the heel and moved to the digits of the foot. Next, the electrode crossed subnucleus A, and the recording sites produced an ulnar to radial progression of receptive fields across the forelimb digits with an interesting alternation of dorsal and ventral receptive fields. Receptive fields for neurons within VPM progressed from the corner to the midline of the upper lip. The next penetration (#9 in Fig. 9) first entered subnucleus C, representing the tail, and then passed through the caudal portion of subnucleus B, where neurons with receptive fields on the glabrous sole of the foot (C, shaded, Fig. 9B) were found, followed by receptive fields on the outer dorsum of the foot and digits. The next recording sites were in a bridge of tissue joining the caudal part of subnucleus D with the rostral part of subnucleus A. The receptive fields in this region were on the forearm. Next, while recording from tissue bridging subnucleus D to VPM, neurons were en-

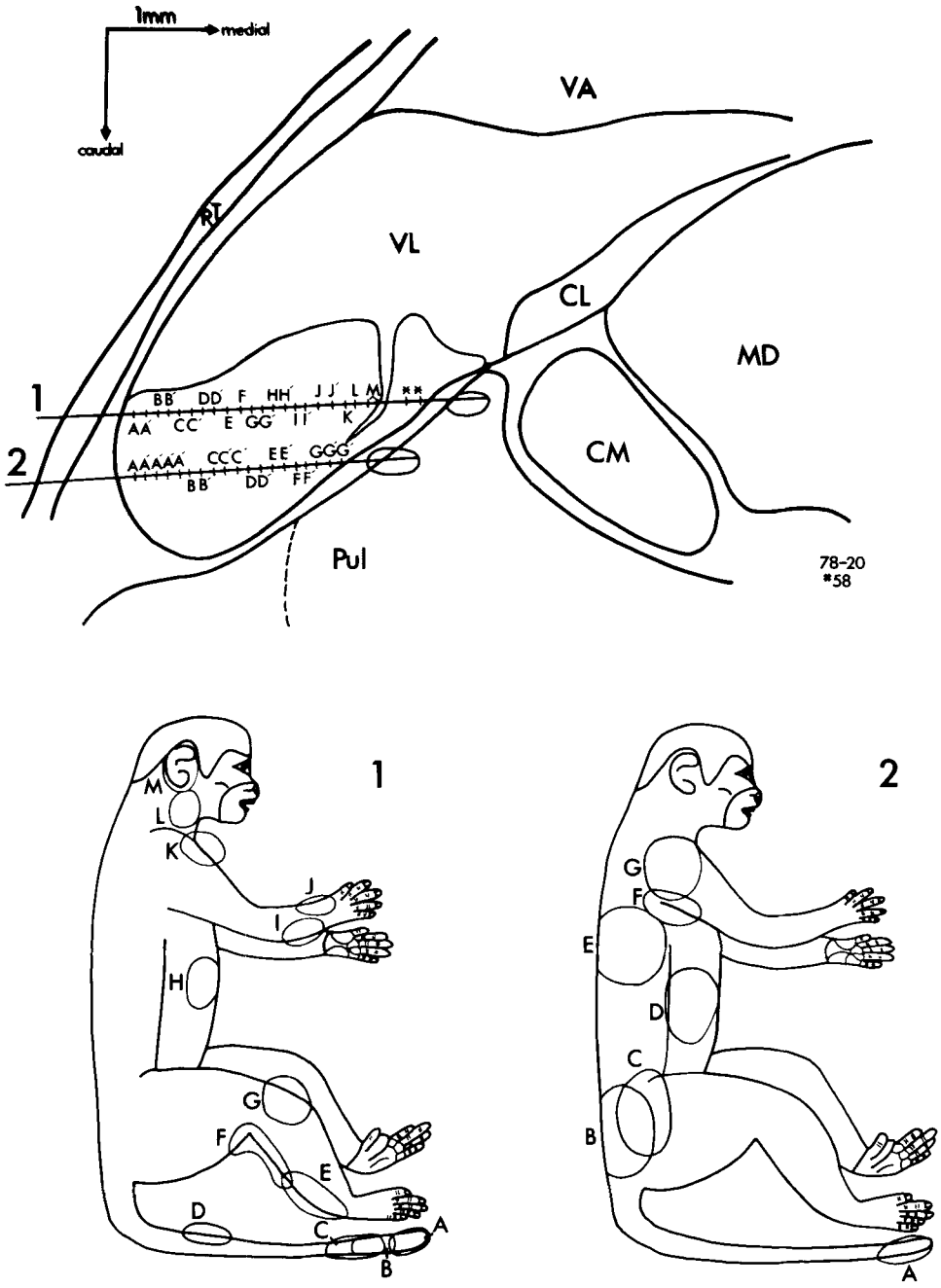

Fig. 6. Receptive fields for recording sites along electrode penetrations in dorsal VP.* weak response to lateral face onto corner of mouth. Horizontal section.

countered with receptive fields on the neck and lateral face, moving to just over the eye. The VPM receptive fields that are labeled M were located on the nose and they changed little in location (Fig. 9B, left) as the electrode advanced over several recording sites. The most caudal penetration in VPL (#10) passed through regions having receptive fields on the tail in subnucleus D, the base of the tail, genital region, and inner thigh in the cell bridge between subnuclei C and B, and on the knee and trunk in parts of subnucleus D. The most medial extension of subnucleus D was activated from the neck and ear.

Results from penetrations 9 and 10 showed that the tissue bridges between subnuclei represented parts of the body surface that joined the parts represented in the subnuclei. While there were many discontinuities in the lateromedial dimension of VP, small regions of continuity were evident, especially dorsally and caudally in the nucleus (Figs. 7, 8). In the ventral parts of the nucleus, the major discontinui-

ties in the representation were reflected by cell-poor bands separating subnuclei and parts of subnuclei (Fig. 9).

Rostrocaudal penetrations. Results from rostrocaudal penetrations were obtained in one experiment. Rows of electrode tracks in three separate planes passed through VPL. Results from the most dorsal plane are shown in Figure 10. The most lateral penetration in the dorsal row passed through parts of subnuclei D and C of VPL. The most rostral recording sites (A and B) were activated both from the tail (A), and from the lateral foot (B), suggesting that the electrode recorded the activity of neurons from two subnuclei. More caudal recording sites were activated only by the lateral foot, and the most caudal recording sites were activated by only the tail. This pattern can be explained by subnucleus C, devoted to the tail, curving laterally in the midportion of VPL. The second electrode penetration first encountered neurons activated by stimulating pad 1 of the ventral foot. As the electrode advanced, the receptive fields moved to the dorsal surface of the foot. More caudal recording sites in the penetration were activated by receptive fields located on the chest. The most medial penetration in this plane (#3, Fig. 10) passed through two parts of subnucleus D and its junction with subnucleus A so that the receptive fields of the first neurons encountered had receptive fields on the inner forearm. Subsequent recording sites produced receptive fields on the dorsal hand, and finally fields extending up the anterior arm.

Four penetrations in a horizontal plane 500 μm deeper in VP are shown in Figure 11. The most lateral of these, penetration 4, entered subnucleus B and encountered a region serving the foot. Neurons at most of the rostral recording sites in subnucleus B were activated by the glabrous digit tips. More caudal sites were activated by the dorsum of the digits, and then the lateral pads of the foot. Further caudal as the electrode entered subnucleus C, the receptive fields shifted to the tail. In penetration 5, located approximately 150 μm medially, the recording sites were all in subnucleus B. Their receptive fields were also located on the foot, first on the tip of digit 3, then on digit 4, and finally on the tip of digit 5. Thus, the serial representation of digit tips was angled rostrally, as well as mediolaterally. Receptive fields for more caudal recording sites jumped suddenly to the pads, and then to the heel. The most caudal recording sites were on the ankle and finally on the tail where subnucleus C curves medially at the caudal border of VPL. Receptive fields for a more medial penetration (#6) through subnucleus A jumped from the tip of digit 5 of the hand to ulnar pads of the hand, and finally shifted abruptly to the dorsal hand, wrist, and forearm. The receptive fields for the most medial electrode penetration (#7) started at the rostral border of VPL with receptive fields on the tip of digit 3 and progressed to adjoining pads of the palm. The most caudal recording sites were in the dorsum of the hand.

The most ventral row of electrode penetrations was placed 500 μm deeper (Fig. 12). Penetration 8 again showed the sequence of representation of digit tips of the foot in subnucleus B suggesting that each digit representation was oriented at a slight angle to the rostrocaudal axis. The most rostral recording sites were activated from the tip of digit 3, more caudal recording sites related to digit 4 and then digit 5. Most caudally in the penetration, recording sites were activated from the dorsal foot and lateral ankle, and then the tail. The most medial electrode penetration in the row entered the medial margin of subnucleus A, where recording sites were activated by stimulating the glabrous thumb, and then the tip of digit 2. The tissue bridging VPM to VPL was entered next, and receptive fields for these neurons were located around the eye and on the lateral face.

The rostrocaudal penetrations revealed minor somatotopic discontinuities in the rostrocaudal plane within subnuclei, and major somatotopic discontinuities across subnuclei. Thus, sequences of recording sites were encountered that produced receptive field shifts from the digit tips to the palm with no indication of intervening receptive fields for the middle and proximal phalanges of the digits. Somatotopic jumps from tail to foot, and from forearm to trunk, occurred across adjoining subnuclei. The rostrocaudal penetrations also indicated that the mediolateral sequence of representation of the digits was rotated somewhat for the foot as compared to the hand, so that the tips of lateral digits were somewhat caudal to the tips of medial digits in the nucleus. Finally, both short regions of isorepresentation and short regions of gradual topographic change were observed.

The response properties of neurons and the organization of the ventroposterior thalamus

In the present study, the goal of obtaining receptive fields for a large number of recording sites in each animal precluded a detailed analysis of receptive field properties of neurons in the ventral thalamus. However, mapping procedures were adequate to determine that all of VP (VPL and VPM) was responsive to cutaneous stimuli. In addition, it appeared that neurons at all recording sites in VP were of one of three types. The vast majority were either slowly adapting (SA) or rapidly adapting (RA) to cutaneous stimuli, with the suggestion of somewhat more RA than SA sites. Recording sites activated by RA or SA inputs were found in short sequences so that several recording sites in a row were typically classified as RA or SA. The background activity at recording sites was almost always of the same type as the isolated neurons. These results suggest the segregation of SA and RA inputs in separate clusters or bands of neurons. Neurons at a few sites were difficult to activate by light touch and required light taps for activation. These neurons were classified as "high threshold." In some instances, the higher-threshold recording sites were later found to have been recorded in the cell-poor zones that separated subnuclei or parts of subnuclei. Neurons activated by deep receptors and insensitive to cutaneous stimuli were not found.

Neurons ventral and caudal to VPL in VPI were typically driven by inputs classified as pacinianlike. In one experiment, neurons responding to low-amplitude high-frequency probe vibrations of 150–400 Hz were recorded throughout VPI. There was no evidence from these experiments for SA or low-velocity RA inputs. In other experiments, the probable activation of neurons in VPI by pacinian receptors was indicated by the presence of neurons sensitive to light tactile stimulation over large receptive fields, to puffs of air, and to vibrations produced by tapping the table supporting the animals. Some of the recording sites responsive to pacinianlike inputs are shown ventral to VP in Figures 3 and 5. Recording sites related to pacinianlike inputs that were caudal to VP are shown in Figure 9.

The experiments also indicated that the somatotopic organization of VPI was at least roughly parallel to that of adjoining VP. For example, in penetration 12 of Figure 5, the most ventral recording sites in VP responded to cuta-

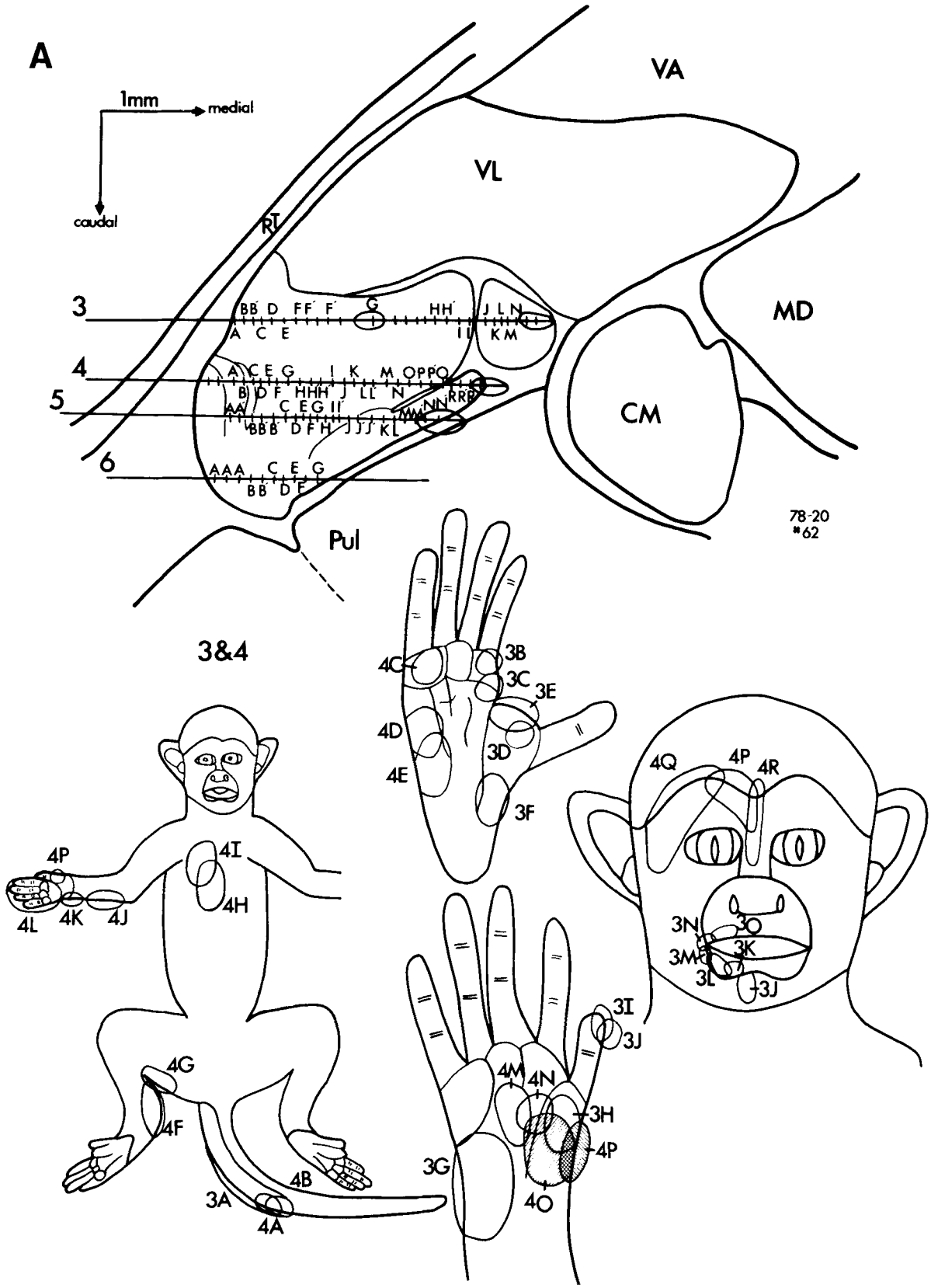

Fig. 7. Receptive fields for recording sites along electrode penetrations at a level ventral to that in Figure 6. Horizontal section.

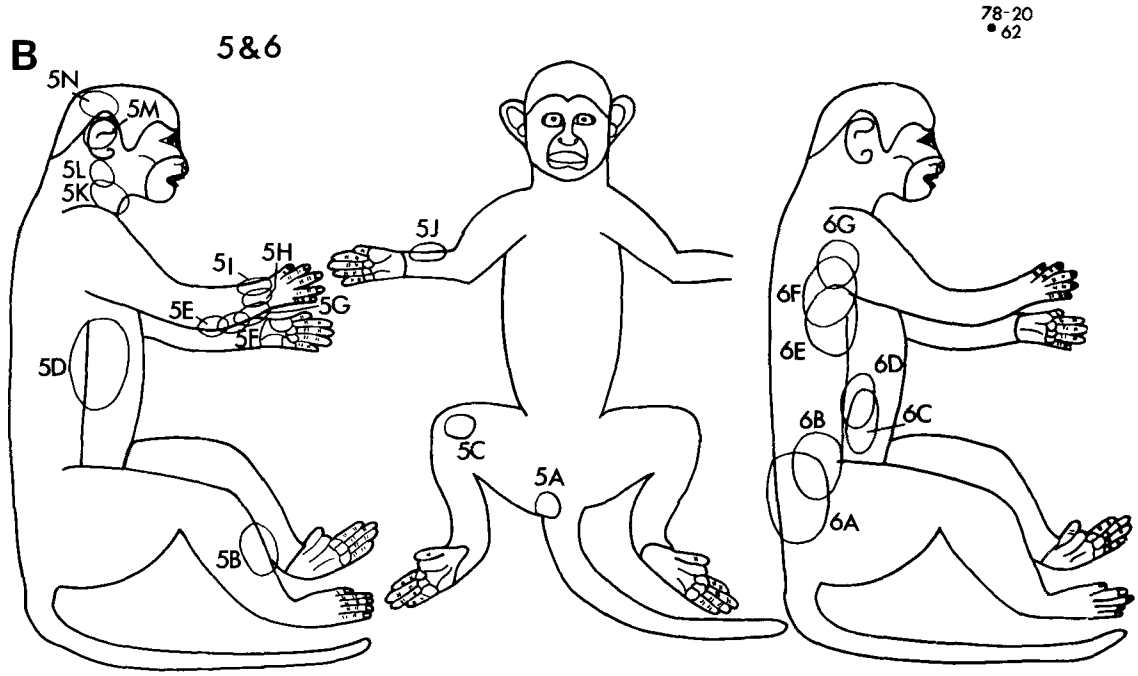

Figure 7 (continued)

neous stimuli on the ear. The first pacinianlike response in VPI was from skin around and including the ear. Deeper recording sites in VPI had receptive fields that progressed onto the shoulder, and finally the lateral chest. Similarly, the most ventral recording site in VP of penetration 11 of Figure 5 had a receptive field on the posterior shoulder, while the most dorsal recording site in VPI had a pacinianlike response with a very large receptive field on the posterior shoulder and adjoining lateral chest. Deeper recording sites in VPI had receptive fields on the caudal trunk, and the deepest recording site was activated from the lateral thigh. More rostrally in the ventral thalamus of the same case, pacinianlike responses were also found in penetrations into VPI (Fig. 3). In penetration 1, the deepest recording site in VP had a receptive field on the distal phalanx of digit 3 of the foot, and the pacinianlike responses from adjoining sites in VPI were from the foot and adjoining lower leg. In penetration 2, the receptive field changed from the tip of digit 5 of the hand in ventral VP to pacinianlike input from the forearm and elbow in VPI. In penetration 3, the receptive field changed from the tip of digit 2 of the hand in ventral VP to pacinianlike activity evoked from the hand in VPI. Thus, the somatotopic organization of VPI roughly paralleled that of VP, although receptive fields could shift some distance on the body with the change from recordings in VP to recordings in VPI. In addition, the rate of change in receptive field locations for sequences of adjacent recording sites in VPI suggests that the somatotopic organization, especially in the dorsoventral dimension, is coarse.

A region 1.0–1.5 mm in thickness immediately dorsal and rostral to VP was responsive to inputs that were typically higher threshold or appeared to be related to deep receptors. As in VPI, the organization of the responsive region that was dorsal to VP roughly paralleled the somatotopic organization of VP. Figures 3–5 illustrate one of the experiments (case 78-19) in which recordings were made dorsal to VP. Starting with the most lateral penetration in Figure 3 (unnumbered and marked with a lesion), over a recording distance of approximately 1 mm immediately dorsal to VP, neurons were responsive to manipulation and taps of the hind leg and foot, but no cutaneous receptive fields could be found. Neurons over a 1.5 mm distance just dorsal to VP in the next penetration (1) were also responsive to stimulation of deep receptors in the foot and leg. The more ventral recording sites in the penetration were activated by manipulation of the foot. Adjoining recording sites within cytoarchitectonically defined VP were activated by a light touch on the foot. More dorsally in the "deep" zone, neurons were activated by bending or tapping the knee. The most dorsal sites in the responsive zone were activated by moving the leg and hip. The relevant receptors were thought to be in muscles or the joint related to the hip. More medially in penetration 2, a 1.5 mm responsive zone dorsal to VP was first activated by moving the trunk. Deeper sites responded to movements of the upper arm. The sites just dorsal to VP responded to manipulation of the upper arm, forearm, wrist, and hand. There was no evidence of cutaneous input to any of these neurons. The first neurons encountered in VPL were activated by lightly touching the skin of the hand. Results from penetration 3 were similar. A 1.5 mm responsive zone dorsal to VPL was first activated by light taps on the anterior shoulder,next by stretching the arm and tapping the upper arm, and finally by flexing the wrist. Responses in VP were to stimulation of the skin of the hand. More medially (penetration 4), a 1.0 mm zone just dorsal to VPL first responded to wrist flexion and next to extension of the thumb and pressure on the hand as the electrode was advanced. Recordings in VP started with receptive fields on the chin, but it is relevant that the thumb representation adjoins that of the chin in VP. Most medially (penetration 5), few recordings were obtained, but several adjacent sites immediately dorsal to VPM were activated by taps to the lateral face.

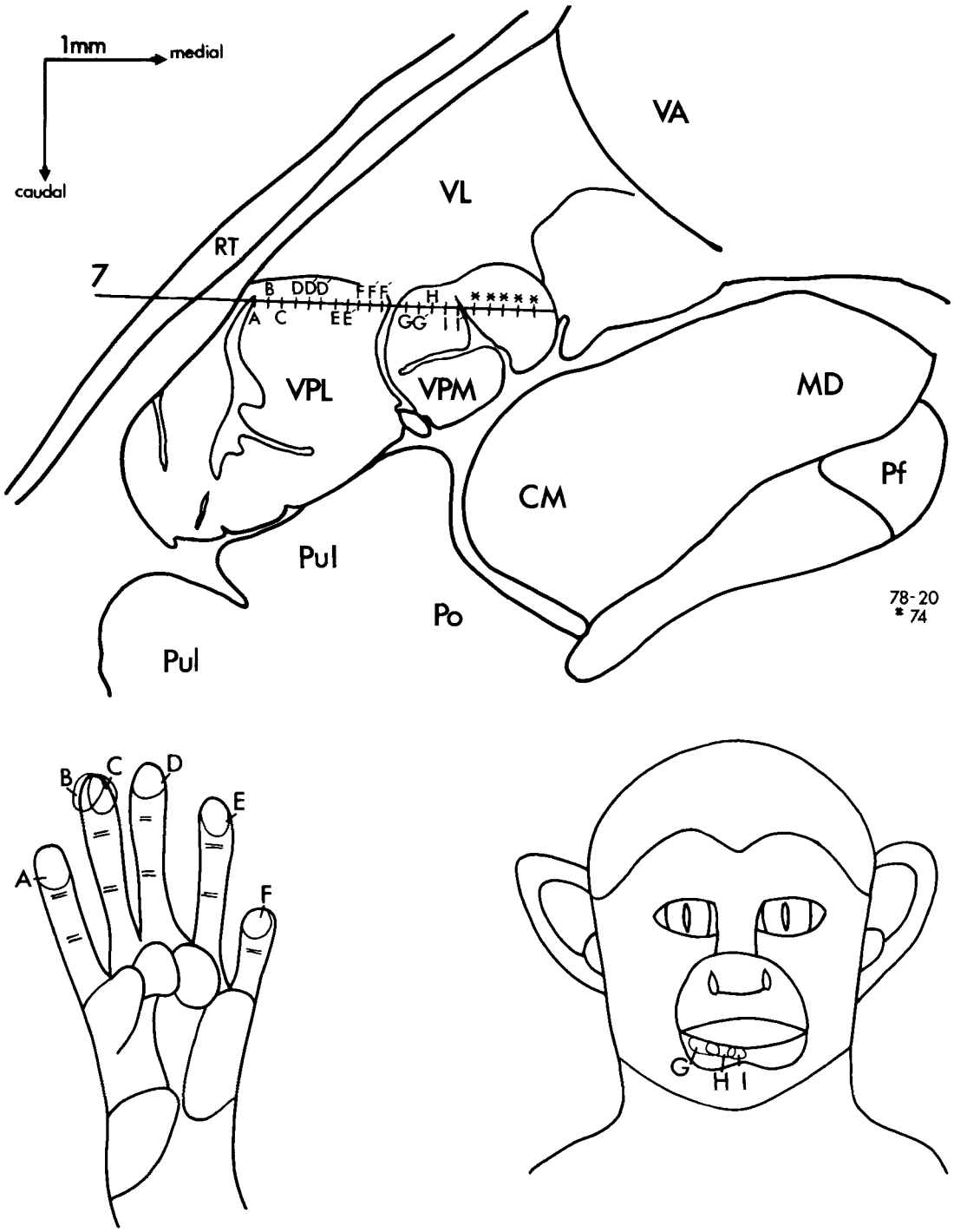

Fig. 8. Receptive fields for recording sites along an electrode penetration at a level ventral to that in Figure 7. Horizontal section*, response to lower teeth and gums.

The pattern of activity recorded dorsal to VP at more caudal levels of the thalamus in case 78-19 was similar. Laterally, at the level of the mid-portion of VP (Fig. 4, penetration 6), a narrow 0.8 mm deep region just above VP responded to manipulation and pressure on the foot and ankle. Cutaneous responses were not noted until the electrode entered VP where the trunk and foot were represented. More medially in penetrations 7 and 8, in tissue just dorsal to the representation of the hand in VPL, responses to pressure and movement of the wrist, hand, and fingers were recorded. The neurons immediately dorsal to VP in penetration 8 were well driven by manipulations of digit 3. Here the noncutaneous zone was 1.25 mm thick. At the medial extreme of VPL (penetration 9), there were good

responses to wrist flexion in a 0.5 mm zone just above cutaneously driven activity related to the palm. Even more caudally in the thalamus (Fig. 5), as lateral electrode penetration (10) first encountered a 1.0mm zone that was activated by moving the foot, ankle, and knee, followed by responses in VP elicited by touching the skin of the knee. In penetration 11, the 0.8 mm. thick deep zone was related to the forearm and hand immediately over the part of VPL representing the forearm. In penetration 12, the responses from deep receptors were from the wrist and hand dorsally and the digits ventrally in a 0.9 mm zone dorsal to representation of the radial skin of the wrist. Most medially, penetration 13 encountered a 0.5 mm zone of neurons responsive to moving the hand and wrist, before entering the cutaneous representation of the ear.

Results from other cases were similar to this representative case. Our stimulation methods were not well suited for distinguishing the sources of activity as driven from muscle, tendon, or joint receptors, so it is uncertain from these experiments if there are separate muscle and joint receptor regions of the thalamus. However, it does appear from our results that inputs from deep receptors are largely or completely segregated from cutaneous inputs, and are located in a 1–2 mm thick region of the thalamus capping VP dorsally and to a lesser extent, rostrally.

DISCUSSION

The results of the present microelectrode mapping experiments indicate that there are at least three separate representations of the contralateral body in the ventral thalamus. Detailed information was obtained on the organization of one representation in the ventroposterior nucleus which contains neurons related to either rapidly adapting or slowly adapting cutaneous inputs. A separate representation dominated by pacinianlike inputs exists in the adjoining ventroposterior inferior nucleus. In addition, a 1.5 mm thick zone of thalamus immediately dorsal to VP is activated by noncutaneous somatic receptors in a pattern that may include one or more representations

The representation of the body surface in VP

A summary of the somatotopic pattern. The overall regional somatotopic organization of VP indicated by the present results is illustrated in Figure 13. The summary shows the representation of major body parts within the subnuclei. VP is traditionally divided into VPM, devoted to the representation of face and head, and VPL, devoted to the representation of the rest of the body. Using the subdivisions of Lin et al.('79) for VP of owl monkeys, we distinguish subnucleus A (representing the hand), subnucleus B (foot), subnucleus C (tail), and subnucleus D (trunk and limbs) within VPL. These subnuclei are largely separated from each other by narrow cell-poor zones, but they are also partially joined by cellular bridges.The recordings indicate that the cell-poor zones correspond to major discontinuities in the representation, while the cellular bridges provide representational continuities between subnuclei. Thus, the hand and foot subnuclei (A, B) are separated ventrally by a cell-poor zone but dorsally join the subnucleus for the limbs and trunk (D) where the representations of the distal limbs join those of the hand and foot. Likewise, the face representation in VPM is separated from the hand subnucleus, but it is continuous with subnucleus D in the region of the representation of the neck. Most of the tail subnucleus is also separated from the adjoining foot subnucleus, but the tail subnucleus is continuous with the pelvic region of subnucleus D. Within each subnucleus, narrower cell-poor regions are obvious, and these often could be directly associated with discontinuities in the representation. The tissue representing the teeth and gums, for example, is largely separated from the rest of VPM by a cell-poor sheet.

The most medial subnucleus, VPM, does not include the parvocellular part, VPM_p, which presumably is activated by taste receptors (see Burton and Benjamin, '71). However, VPM does contain a tactile representation of the tongue, which is located ventromedially next to the representation of the teeth and gums. While much of VPM is devoted to the hairy, glabrous, and inner surfaces of the upper and lower lips, the representations of these surfaces are joined laterally by the lateral and upper face dorsocaudally, and the lower chin and neck dorsally. The neck and caudal head and face are largely represented in tissue bridging VPM and subnucleus D, and this bridge could be considered as part of either subnucleus. The representations of the upper and lower lips join at the corner of the mouth along a mediolaterally oriented line in VPM. The precise orientation of this line appears to vary somewhat from case to case. In agreement with present results, an earlier partial map of VPM in squirrel monkeys (Bombardieri et al., '75) placed the upper teeth dorsal to the lower teeth followed by the tongue.

The "hand" subnucleus (A) is dominated by large disclike representations of the glabrous digits proceeding mediolaterally from D_1 to D_5 and dorsoventrally from proximal to distal on each digit. Typically, the representation of digit 1 is less extensive than digit 2, and does not cover the entire medial wall of the subnucleus. Thus, part of that surface is devoted to digit 2, and this part may adjoin the representation of the face. The representations of the digit tips occupy a large band of tissue that extends from the base of the nucleus to form its rostral wall. Thus, digit tips are found dorsorostrally as well as ventrally in VPL. Middle and proximal phalanges are represented more dorsocaudally in the nucleus. The representation of the palmar pads forms most of the dorsocaudal cap of subnucleus A, with ulnar pads laterally next to ulnar digits. The representations of hand dorsum and wrist in subnucleus A form a junction dorsally with the part of subnucleus D that is devoted to the forearm. The dorsal hairy surfaces of the digits occupy little tissue and are found in part caudoventrally and in part rostrodorsally near the representations of the glabrous distal phalanges. The exact location of the dorsal hand and dorsal digits appears to be somewhat variable from animal to animal, so that a summary diagram may not be accurate for any particular individual.

The representation of the foot in subnucleus B is much like the representation of the hand in subnucleus A, with the difference that the disclike representation of the digits of the foot are rotated slightly so that the rostral portion of each disc is medial to the caudal portion. Thus, receptive fields for rostrocaudal electrode penetrations are likely to progress from lateral to medial digits. Again, the dorsal surfaces of digits are represented both rostrodorsally and ventrocaudally. The representation of the foot dorsum and ankle joins subnucleus B to the leg representation in subnucleus D.

Subnucleus C is a narrow caudolateral region of VPL that is devoted solely to the tail. Much of the caudoventral extent of the subnucleus represents the tip of the tail, while the representation of the base of the tail joins subnucleus C rostrocaudally with subnucleus D. Part of subnucleus C extends behind the foot representation in subnucleus B.

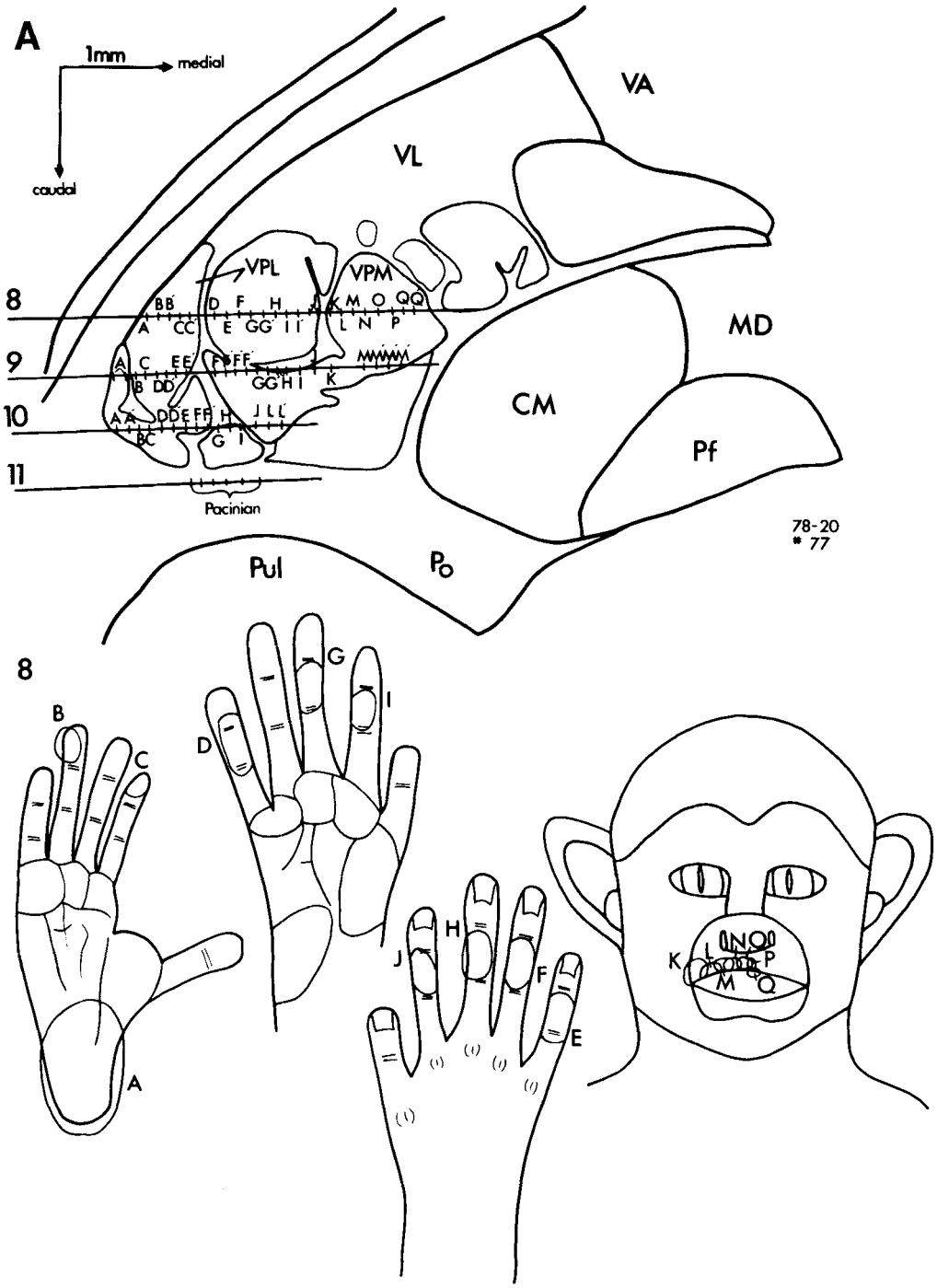

Fig. 9. Receptive fields for recording sites along electrode penetrations at a level ventral to that in Figure 8. Horizontal section.

Subnucleus D forms the dorsocaudal cap of VP. It represents the cranium, ears and lateral face medially as a bridge with VPM, the trunk and limbs centrally, and the gluteal region laterally. The subnucleus is dorsoventrally shallow, but there is a tendency for it to thicken in the representation of distal limbs.

Isorepresentation. Recordings along electrode tracts in VP often encountered short sequences of neurons with nearly identical receptive fields. Such sequences define lines of isorepresentation (see Kaas et al., '72). In somatosensory cortex, true lines of isorepresentation appear to occur only across the thickness of the cortex. Thus, the lengths and directions of isorepresentation lines are easily established. In the thalamus, the organization may be more complex. The lateral geniculate nucleus of most mammals, representing the flat retinal surface, seems relatively simple,

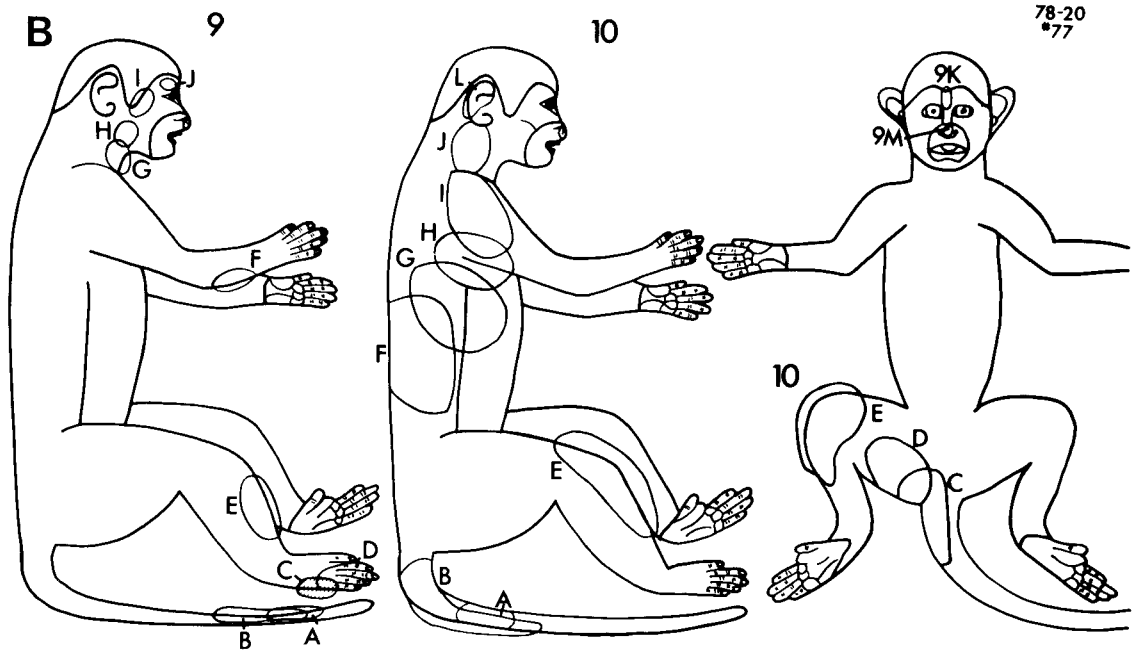

Figure 9 (continued)

with lines of isorepresentation coursing perpendicular to the layer from one to the other side of the nucleus (see Kaas et al., '72). Presumably, the representation of the skin, as a "two-dimensional" sheet, has some similarities in VP to the representation of the retina in the lateral geniculate nucleus. However, the observation that isorepresentation sequences occurred in all three stereotaxic planes indicates that the representation of the skin is not as simple as that of the retina. These results suggest that the lengths of lines of isorepresentation that result from the thickening of a sheetlike representation may vary for different skin surfaces, thus contributing to the differences in magnification factor, and that the directions of isorepresentation lines may vary as a consequence of bending and folding in the nucleus.

Although Figure 13 is intended to indicate only the overall organization of VP, relative lengths and orientations of lines or regions of isorepresentation can be deduced from the summary. The figure, for example, indicates that lines of isorepresentation for the representations of the digits of the hand and foot must be extremely limited in the mediolateral dimension, and extend largely in the rostrocaudal and dorsoventral dimensions, with emphasis on one axis or the other depending on position in the nucleus. Thus, lines of isorepresentation for the finger tips would largely extend dorsoventrally in the rostral part of subnucleus A, and continue largely in the rostrocaudal plane in the ventral part of subnucleus A. Similar conclusions apply to the representations of the tips of the toes in subnucleus B. For other parts of VP, the expected orientations of lines of isorepresentation are less obvious, but the recordings indicate that they typically are not in the lateromedial plane. Extended sequences of isorepresentation in the mediolateral plane were seen only medially in the representation of the face, laterally in the representation of the tail, and dorsally in the representation of the limbs.

Figure 13 also indicates that lines of isorepresentation vary in length. This conclusion is apparent from the proportions of the nucleus devoted to various body parts. Thus, the representations of finger tips extend across the length and most of the depth of VP, while the representations of the hand dorsum, proximal digits, and palmar pads are restricted to dorsal portions of the nucleus. Variations in the lengths of lines of isorepresentation, that is, in the thickening of different portions of the map, may be the major mechanism in VP for increasing the magnification of important receptor surfaces, such as the digit tips.

Discontinuities. The representation in VP is also characterized by disruptions of somatotopic sequences. Such disruptions could be the result of actual complete discontinuities in the somatotopic map in the thalamus, or of "folds" in the map so that the electrode passes from one part of a continuous representation to another. For example, the representation of the face next to the hand in area 3b of monkeys (e.g., Nelson et al., '80a,b) appears to be a true discontinuity in most species, since no representation of the arm and neck can be detected that joins the representation of the hand and face. In contrast, the representations of the forepaw and hindpaw in S-I of rats, for example, are closely approximated so that it is possible in a row of closely spaced electrode penetrations to jump from receptive fields on the hindpaw to those on the forepaw, but when the complete representation is considered, it becomes clear that the representations of the paws are joined caudally in S-I by the representation of the leg, trunk, and arm (Welker, '71; Kaas, '83). Thus, the disruption of the sequence of receptive fields for the row of recording sites is a result of crossing a "fold" in a relatively continuous representation, rather than from a major discontinuity in the representation.

In the ventroposterior nucleus, it is more difficult to distinguish between complete discontinuities and disruptions of sequences due to partial approximations. However, there is obviously some gross "bending" of representation in VP in a manner analogous to that observed in S-I of rats. This "bending" is indicated in Figure 13, and the figure predicts where a number of discontinuities in the representation

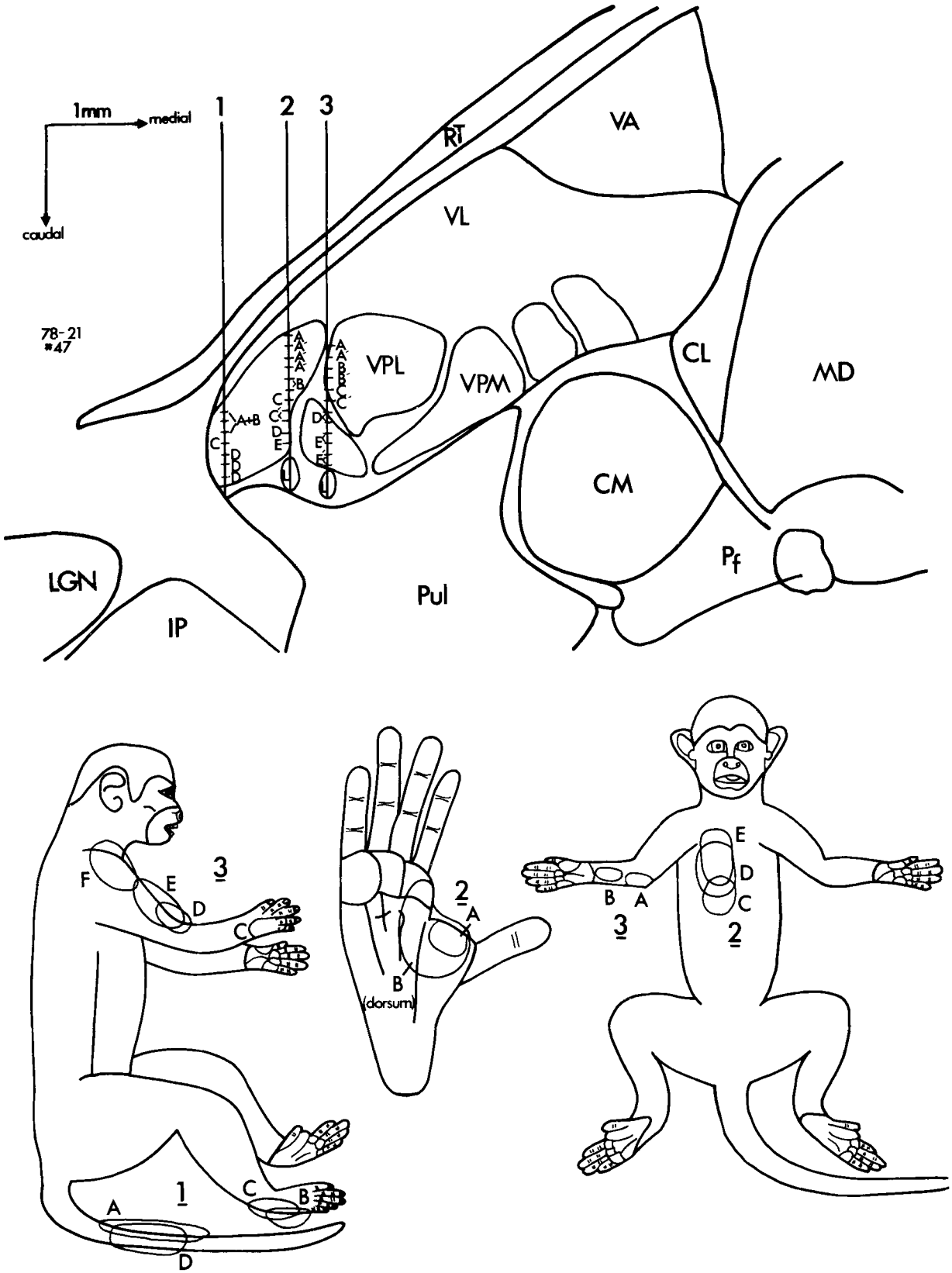

Fig. 10. Receptive fields for recording sites along electrode penetrations in dorsal VP. Horizontal section.

occur. Thus, subnuclei A and B for the hand and foot are approximated even though the hand and foot are not continuous skin surfaces. These approximations are marked by limiting fiber bands in VP so that subnuclei VPM, A, B, and C are narrowly separated in the rostrocaudal plane over the ventral two-thirds of the nucleus. The representations of the glabrous surfaces of digits can also be considered as approximations of separate skin surfaces, and there are suggestions in some brain sections of fiber bands separating the representations of digits in VP of squirrel monkeys as well. In raccoons, where the hand representation in VP is especially developed (e.g., Welker and Johnson, '65), vertical fiber bands clearly mark the edges of finger representations. When the representations of the digits are included, dorsoventral discontinuities extending largely in the rostrocaudal plane partially isolate at least 12 cell groups in VP (tail, foot D_5–D_1, hand D_5–D_1, face). These vertical discontinuities obviously account for many of the observed disruptions in receptive field sequences and indicate why long sequences of receptive field continuity are not observed in the mediolateral plane in the ventral two-thirds of VP.

The subdivisions of VP indicated in Figure 13 do not predict all of the discontinuities that were observed in the present experiments. Disjunctive receptive field sequences were also observed in dorsoventral and rostrocaudal electrode penetrations and in lateromedial electrode penetrations in subnucleus D. One possible explanation for such observations is further folding in the nucleus. For example, folding could largely account for the data illustrated in Figure 14. Figure 14 shows disrupted sequences of receptive fields for a vertical electrode penetration in VP. The marked dorsal and ventral borders of VP, the recording sites along the electrode track, and the receptive field locations are redrawn from penetration 5 of monkey 78-22. Receptive fields were first found at position A on the palm and they gradually shifted to position B with deeper recording sites. Then, the receptive field location suddenly changed to position C on the middle of digit 2 as the electrode advanced to the next recording site. After seven recording sites with little or no apparent change in receptive field location, receptive fields suddenly changed to the distal phalanx of the digit where they remained for the rest of the penetration. Thus, the penetration shows regions of gradual change in somatotopic organization, regions of little or no change (isorepresentation), and locations of sudden change. Vertical electrode penetrations through the hand subnucleus typically reveal one or more of these features of organization. The location of change appears to be variable, and our present understanding is incomplete and does not predict their occurrence . If subnuclei have small folds, something like shallow fissures in cortex, sudden change would occur as the electrode crosses the folds. Hypothetical folds are included in Figure 14 that could account for the recording results. Folding and bending of the subnucleus could result in sequences of gradual change, no change, and sudden displacements. While folding could account for the results, true discontinuities in the representation are another possibility. The nature of the folding, if it occurs, could be revealed by anatomical studies of thalamocortical relations.

The representation of RA and SA inputs. One of the important observations of the present study was that almost all neurons in VP could be characterized as responding to slowly adapting (SA) or rapidly adapting (RA) inputs, and that neurons of one type or another were grouped so that over short 100–200 μm recording distances neurons tended to be of one type or the other (also see Dykes et al., '81). The shapes and sizes of the SA and RA clusters of cells are not yet known. However, in the digit representations of area 3b of somatosensory cortex, SA and RA neurons appear to form alternating narrow bands (Sur et al., '81). The probable requirement of any segregation of groups of neurons by type within VP, or area 3b, is that the groups are integrated into the overall map in a manner that allows all body parts to be subserved by both types of neurons. Thus, for VP, all of the body parts indicated in Figure 12 would require separate groups of cells of RA and SA types. The representation of each digit tip, for example, would require at least one RA and one SA cluster. The size of any particular cluster of RA or SA cells could not be so large as to completely occupy the representation of any body part in the map. In order to subserve all body parts, RA and SA groups would alternate once or more along isorepresentation lines. However, they could join across isorepresentation lines to form bands, as they appear to do in cortex.

Related concepts of VP organization. The summary of VP organization includes many features that have been emphasized in previous reports. There is general agreement from earlier mapping studies in primates (Mountcastle and Henneman, '52; Poggio and Mountcastle, '60; Pubols, '68; Loe et al., '77; Pollin and Albe-Fessard,'79; Jones and Friedman, '82; Jones et al., '82) and other mammals (see Welker, '73, for review) that a tail, foot, hand, face progression exists in the lateromedial dimension of VP, and that the digit tips are ventral to the proximal limbs and trunk. In addition, fiber laminae separating VP into tail, foot, hand and face subnuclei have been noted for a number of mammals (see Welker, '73; Johnson, '80, for reviews). We have found subnuclei useful in describing thalamocortical connections in owl (Lin et al., '79) and macaque (Nelson and Kaas, '81) monkeys. Recently, Batton and Kutyna ('81) have described similar neuronal aggregates in VP of squirrel monkeys and used patterns of connections to relate them to specific body parts.

In our experiments, sequences of isorepresentation, sequences of gradual change, and points of sudden change were observed in VP along microelectrode penetrations in three stereotaxic planes. Using vertical electrode penetrations in macaque monkeys, Loe et al. ('77) concluded that progression of gradual change predominated, but they also found that neurons in close proximity received input from nonadjacent body regions, and many microelectrode penetrations encountered long sequences of neurons with similar receptive fields. More recently, Jones et al. ('82) and Jones and Friedman ('82) reported that vertical electrode penetrations in macaque monkeys were typically characterized by short jumps in receptive field location from one body region to another. Caudorostral electrode penetrations through the hand and face representations also produced short recording sequences of little or no change in receptive field position, followed by jumps to a nearby body location. In electrode penetrations angled from anterolateral to posteromedial, short 200 μm progressions of little change were disrupted by sudden large changes in receptive field locations. These observations in Old World monkeys are very similar to those made here in New World monkeys.

Two interesting concepts relate to the present portrayal of VP organization. One concept is that VP is described by a mediolateral sequence of curved "lamellae" extending dorsoventrally in the nucleus. In the description of Loe et

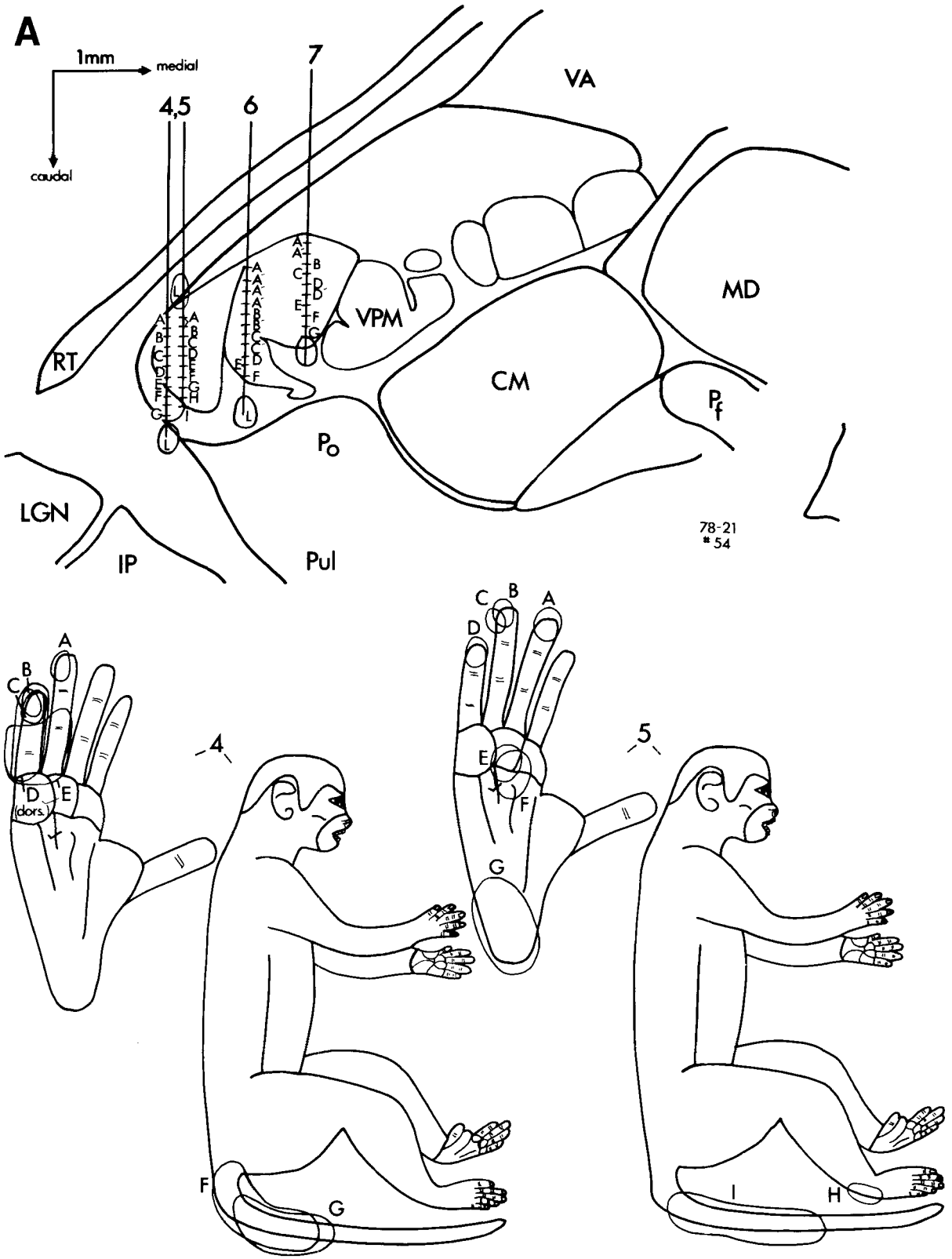

Fig. 11. Receptive fields for recording sites along electrode penetrations in middle VP. Horizontal section.

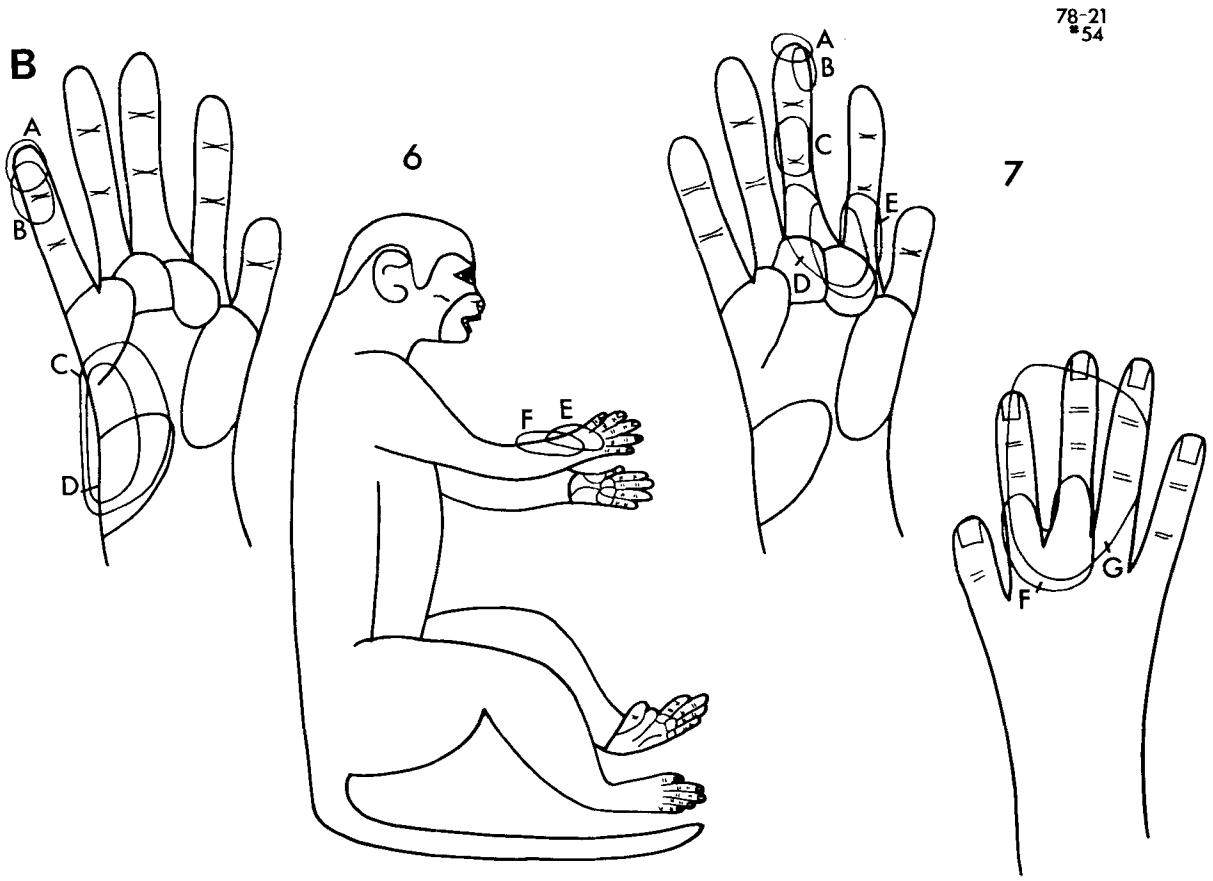

Figure 11 (continued)

al. ('77), each "lamella" in the sequence has a population of neurons with similar receptive field locations, and therefore each lamella represents a given body part. Lamellae extend from the dorsal to the ventral margins of the nucleus, but have various anteroposterior extents. Another closely related concept (Jones et al., '79) is that VP incorporates a series of curved "lamellae," each extending through the dorsoventral and anteroposterior dimensions of the nucleus, and each projecting to an anteroposterior sector of "S-I"; each lamella would represent a sequence of adjoining, nearby body parts, but not a single body location. Furthermore, lamellae were seen as a descriptive convenience without reality in terms of definable borders.

These two somewhat different concepts of "lamellae" in VP receive support from the repeated electrophysiological observations that directions of little or gradual somatotopic change tend to be in the vertical and rostrocaudal directions in the nucleus rather than the mediolateral directions (e.g., Loe et al., '77: Jones and Friedman, '82), and the anatomical observations that restricted injections of HRP in area 3b or area 1 of somatosensory cortex tend to yield a disc-shaped region of VP that is extended dorsoventrally and rostrocaudally (Jones et al.,'79; Lin et al.,'79; Nelson and Kaas, '81). In addition, axons entering VP from the brainstem have terminal regions that are restricted mediolaterally rather than dorsoventrally or rostrocaudally (Jones, '83). Finally, thalamic labeling with 2-deoxyglucose following restricted somatic stimulation is dorsoventrally and rostrocaudally extensive in VP (Juliano et al., '83). Thus, the concept of "lamellae," even given the somewhat different definitions, is consistent with a large number of observations. However, the lamellae may be no more than the partially distinct 12 or more cell groups indicated in Figure 13. As we stressed earlier, VP is dominated by a mediolateral sequence of at least 11 dorsoventrally oriented discontinuities that are almost in the parasagittal plane. These discontinuities appear to form real borders separating tail, toe, finger, and face representations. Sudden representational change always occurs across these borders, and thus, over much of VP, extended regions of gradual or little representational change can occur only in the parasagittal plane. In other parts of VP, subnucleus D and VPM, there is no obvious predominance of dorsoventral discontinuities. Thus, the "lamellae" in VP may be alternatively described as the sequences of cell groups with real borders that characterize the ventral two-thirds of VPL, but not all of VP.

Another concept of VP organization is the "thalamic rod." Jones et al. ('82) propose that a small focal zone in somatosensory cortex receives input from an elongated rodlike aggregation of cells in VP. Thus, a thalamic rod corresponds to an isorepresentation line or column. Rods are seen as extending in the anteroposterior dimension over much but not necessarily the entire length of VP. This concept is similar to one proposed for owl monkeys in which we concluded that "slabs" of cells in VP represent single loci on the body surface and project to somatotopically matched locations in areas 3b and 1 of cortex (Lin et al., '79). We

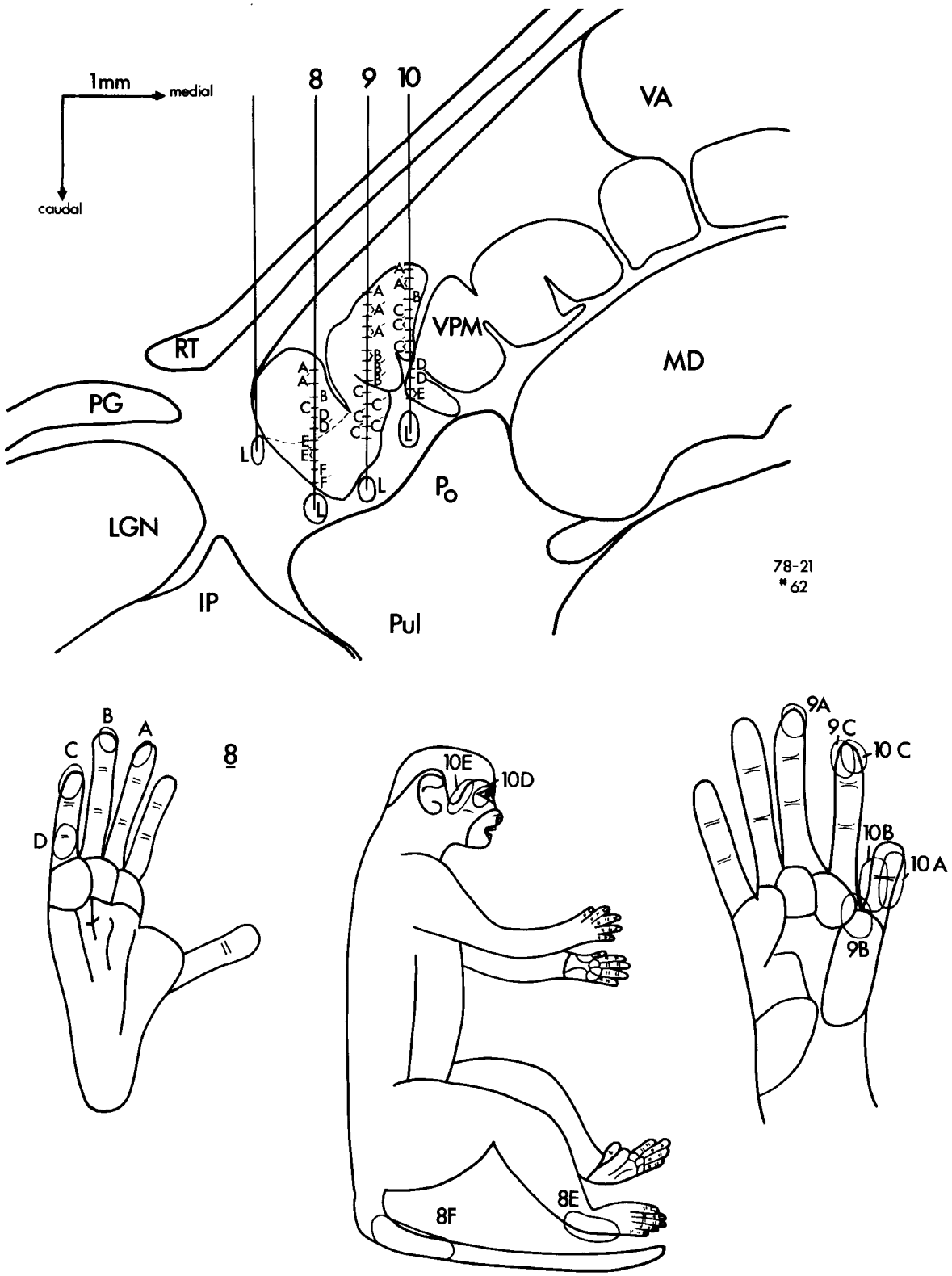

Fig. 12. Receptive fields for recording sites along electrode penetrations in ventral VP. Horizontal section.

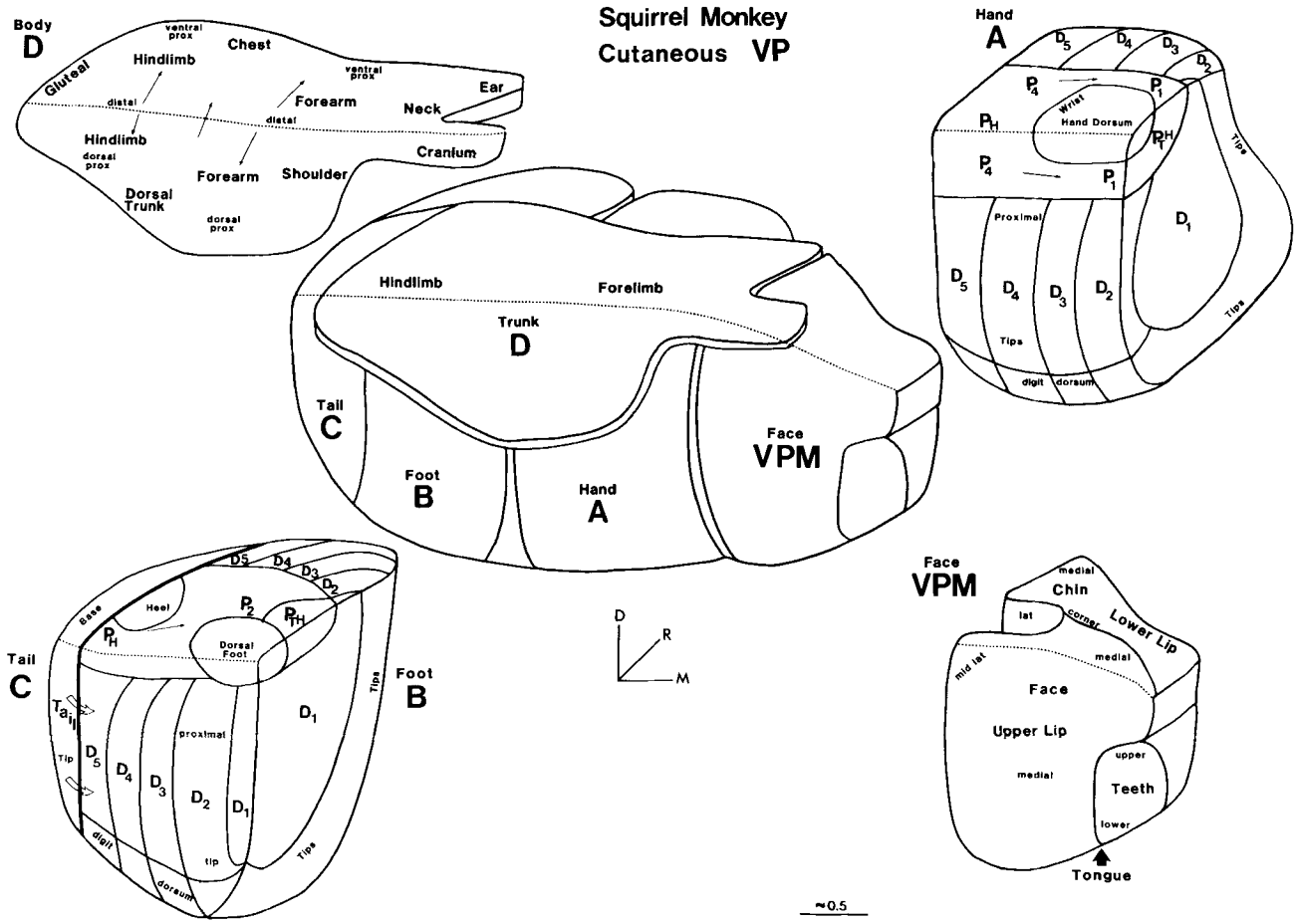

Fig. 13. Summary of VP organization. The nucleus is divided into two divisions, VPM and VPL. VPL is further divided into subnuclei A for the hand, B for the foot, C for the tail, and D for the trunk. VPM represents the face. The subnuclei are shown joined to form VP in the middle, and separately in more detail on the sides. Part of subnucleus C extends behind subnucleus B in the manner suggested by arrows, but this is not shown on the lower left because the extension of C would hide D_5 of B. The broken line indicates the upper margin of the caudal surface of VP and subnuclei. See text for further description.

proposed that each slab is most narrow in the mediolateral plane, intermediate in the dorsoventral plane, and longest in the rostrocaudal plane. The difficulties with the concepts of "rods" or "slabs" are the unintentional suggestion that functionally distinct boundaries exist for each elongated group of cells with overlapping receptive fields—something for which there is no clear evidence—and the failure to fully indicate that isorepresentation lines vary in length and orientation. Given the organization portrayed in Figure 13, within the representations of the glabrous hand and foot and perhaps elsewhere, rostrocaudal orientations would predominate. But for the rostral parts of VP representing digit tips, dorsoventral extensions are expected, and other orientations would occur elsewhere, including some mediolateral extensions in VPM. Isorepresentation lines would vary in length in a manner related to magnification factor. Long lines would exist ventrally in VP for digits, and short lines would exist dorsally for most hairy body parts. Finally, the concept of aligned, somewhat curved, similarly oriented isorepresentation rods does not suggest the frequency of the minor discontinuities that are found in rostrocaudal and dorsoventral (Fig. 14) electrode penetrations. However, the concept of rods or slabs does reflect the considerable evidence (Lin et al., '79; Jones et al., '82) that groups of thalamic cells with a common input from a given location on the body and a common restricted cortical target form shapes that are elongated in one plane. Thus, a complete understanding of VP organization must incorporate a detailed description of isorepresentation lines or rods, including lengths, widths, and bends, for different parts of the body representation. Anatomical approaches to this description would probably be productive.

Comparisons of thalamic and cortical maps

Both the ventroposterior nucleus and the cortical targets of VP, areas 3b and 1, have been mapped in squirrel monkeys. Thus, it is possible to compare thalamic and cortical maps. Such comparisons indicate that thalamic and cortical maps have major differences in organization. Therefore, the organization of any particular map is not a simple reflection of the arrangement of peripheral nerves and must depend on other factors for its ultimate arrangement.

The ventroposterior nucleus provides the inputs for the two somatotopic representations of the body surface in cor-

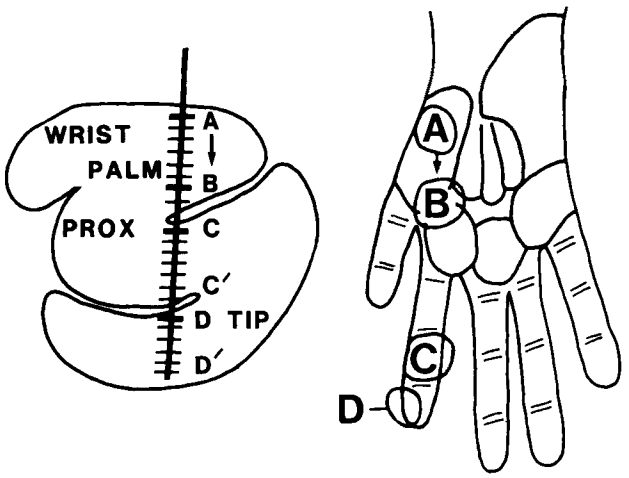

Fig. 14. Actual receptive fields for a recording sequence as related to hypothetical folding in the ventroposterior nucleus. As commonly observed in single vertical electrode penetrations, a short series of successive recording sites result in receptive field sequences that sometimes gradually shift in location, change very little in location, or suddenly jump to a new location. Thus, receptive fields gradually shifted from A to B on palm of the hand for the A to B series of recording sites, jumped suddenly to the digit and remained unchanged for the C to C′ series of recording sites, and then jumped more distally and remained unchanged for the D to D′ series of recording sites. These observations suggest that folding of a continuous representation occurs so that recordings are sometimes along sequences of continuous somatotopic change, sometimes along lines of isorepresentation, and, sometimes move abruptly across folds from one to another part of the representation.

tical areas 3b and 1, respectively (Lin et al., '79; Nelson and Kaas, '81, Jones and Friedman, '82). The organizations of the area 3b and the area 1 maps have been described in squirrel monkeys (Sur et al., '82), and they are basically similar to those found in other monkeys. The two cortical maps are not identical, but the differences are not great. The area 3b and area 1 representations form parallel mediolateral sequences of representation proceeding from tail to tongue. The two representations are roughly mirror images of each other so that, for example, pads of the palm adjoin along the 3b/1 border and digit tips are found rostrally at the 3b/3a border and caudally at the 1/2 border. Thus, the expected projection patterns of VP to areas 3b and 1 would form similar parallel mediolateral cortical sequences, but reversed rostrocaudal sequences.

There are several major and obvious differences between the thalamic and the cortical maps. In the thalamus, the tail, foot, and hand representations adjoin mediolaterally, and these representations are continuous with limb and trunk representations dorsally. The representation of the caudal head and neck bridges that of the trunk in subnucleus D with that of the face in VPM. Thus, major separations of adjoining skin surfaces are avoided in VP. In both the 3b and 1 maps, the organization is quite different, and a number of major separations occur. For example, the anterior and posterior leg are represented separately on each side of the representation of the foot. The posterior leg separates the tail from the foot in cortex. The anterior leg, trunk, and arm separate the foot from the hand. The back of the hand is separated from the face by the arm and hand. The dorsoradial hand and wrist are separated from the dorso-ulnar hand and wrist by the glabrous hand. These major differences in the thalamic and cortical maps mean that there can be no simple relation between the thalamus and cortex. The cortical maps cannot result from a simple "unfolding" of the projections from the thalamic map.

Patterns of thalamocortical connections can be predicted from the organization of the thalamic and cortical maps. Detailed comparisons of the thalamic and cortical maps can be obtained by considering the receptive field sequences for recording sites along electrode tracks in VP from the present study, and then plotting hypothetical recording site sequences in cortex that would produce the same receptive field progressions using the summary cortical maps of Sur et al. ('82). When that is done for vertical electrode penetrations in VP, sequences of thalamic recording sites across the complete nucleus often relate to a cluster of hypothetical recording sites in either area 3b or area 1 that are confined to a given 2–3 mm region of cortex. This is particularly the case for rostral penetrations through thalamic representations of the hand and foot, but it can occur caudally in the nucleus for the arm and medially in the nucleus for the face. However, other vertical sequences in the thalamus might include receptive fields that relate to quite distant cortical sites. For example, receptive fields on the anterior and on the posterior leg could be obtained within the same vertical electrode penetration in VP (Fig. 5), and yet could be found in cortical sites 8 mm or more apart in cortex (Sur et al., '82). Thus, a given vertical sequence of cells in VP often appears to project to only a limited location in area 3b and a matched, limited location in area 1. However, sometimes a given vertical sequence appears to relate to two or more separate locations in each cortical area. If the cortical maps reflect thalamocortical connections, a restricted injection of HRP in cortex could label most of a vertical thalamic sequence, or only part of it, depending on the location and extent of the cortical injection.

When receptive fields for actual VP recording sequences in a rostrocaudal direction are matched with hypothetical cortical sequences, the result is similar to that obtained for vertical electrode penetrations. Commonly, the cortical sites corresponding to a rostrocaudal thalamic sequence cluster within a 2–4 mm region of cortex in either the area 3b or area 1 map. However, quite separate cortical regions are contained in some rostrocaudal thalamic sequences. For example, many rostrocaudal thalamic sequences contain receptive fields on both the tail and foot—surfaces that are separated by the representation of the posterior leg in cortex (Sur et al., '82). A dorsal, rostrocaudal thalamic sequence could also include receptive fields on the trunk and on the pads of the foot. These skin surfaces are separated by the representation of the anterior leg in cortex. Thus, a limited injection of HRP in cortex could label all of the cells along a rostrocaudal line across VP, or only part of such a sequence of cells depending on the location of the cortical injection.

When cortical sites are matched with sites along lateromedial electrode penetrations in the thalamus, the result is quite different. Typically, only one to three cortical sites matched for a thalamic sequence would be close together in cortex. The next thalamic site or sites would relate to another location in cortex, often at some considerable distance. These small clusters of sites would jump from medial to lateral across the cortical maps. However, short reversals sometimes occur so that a jump to a more medial cortical location results. A clustering of more than three cortical sites, corresponding to over 150 μm in the thalamus, occurs

for only very specific regions of the cortical map; i.e., for the representations of the trunk, hindlimbs, or pads of the hand and foot, which are represented dorsally in VP, and for parts of the face, which are represented in VPM. Thus, a restricted injection of HRP in the cortical map would seldom label more than a few adjacent cells in a lateromedial sequence in VP, except dorsally in subnucleus D, and medially in VPM, where limited lateromedial extents of labeled cells would sometimes occur.

The thalamocortical projection patterns predicted above assume that the cortical maps reflect terminations from thalamic neurons. Since hidden or subthreshold inputs can be revealed by removing dominant input of part of a cortical representation by sectioning a peripheral nerve (Kaas et al., '83; Merzenich et al., '83a,b), this assumption may not be fully warranted. Nevertheless, the predictions appear to conform well with known results from studies of thalamocortical relations in monkeys (Whitsel et al., '78; Lin et al., '79, Jones et al., '79; Jones et al., '82; Nelson and Kaas, '81; also see Juliano et al., '83). HRP cortical injections of limited size typically result in groups of labeled cells that are extended dorsoventrally and rostrocaudally, and limited mediolaterally. The labeled region may include part or all of the depth and length of the nucleus, or it may be discontinuous. Foci of label that are limited in dorsoventral extent are found dorsally in VP, where short mediolateral extensions of label sometimes occur.

Evidence for a pacinianlike representation in VPI and "deep" receptor representations dorsal to VP

We observed an orderly representation of pacinianlike receptors in VPI and of "deep" receptors in tissue dorsal to VP. These additional body representations were roughly parallel with the cutaneous representation in VP, so that all proceeded from tail to head in a lateromedial direction in the thalamus. In addition, there was some suggestion of partially congruent borders between the representations so that matched body parts tended to adjoin along the borders. Cortical representations tend to be both parallel and have congruent or matched borders (see Kaas et al., '81). Such patterns are seen in the auditory (see Anderson et al., '80) and visual (see Symonds and Kaas, '78) thalamus as well. Because adjoining thalamic nuclei are not directly interconnected, the parallel and congruent patterns of representation are probably not basic to thalamic function, but reflect developmental mechanisms.

Outside our preliminary report (Dykes et al., '81), the segregation of pacinianlike inputs in VPI in monkeys have not been noted before. However, recently Herron and Dykes ('81) have recorded pacinianlike responses in VPI of cats. The finding of pacinian input to VPI in cats is consistent with the observation that VPI projects to cortex activated by pacinian receptors (Herron and Dykes, '81; also see Dykes, '83; however, see Fisher et al., '83).

The segregation of inputs from "deep" receptors in parts of the thalamus dorsal to the cutaneous zone has been a common observation (Poggio and Mountcastle, '60; Pubols, '68; Loe et al., '77; Pollin and Albe-Fessard, '79; Dykes et al., '81; Maendly et al., '81; Jones and Friedman, '82). The main point of uncertainty has been whether the change from deep to cutaneous receptor activation is sudden or gradual. Our results (also see Dykes et al., '81) and those of Jones et al. ('82) and Jones and Friedman ('82) indicate that the change from deep to cutaneous activation is abrupt. Furthermore, the region activated by deep receptors is dorsal to the region we architectonically identify as VP in squirrel monkeys. However, our mapping of the dorsal "deep" receptor region was too limited to be able to reveal the separate rostral and caudal nuclei for deep receptors that are suggested by other evidence (see below).

A theory of thalamocortical organization

A wide range of physiological and anatomical observations has led to a revision of concepts of thalamocortical organization in the somatosensory system of primates. Some of these ideas have been reviewed elsewhere (e.g., Merzenich and Kaas, '80; Dykes, '83; Kaas, '83). In brief, evidence has accumulated for the separation of submodalities into parallel processing channels from the skin to the cortex. At the thalamocortical level, there are distinct areas and nuclei related to different information pathways, rather than a single, multimodal VP map relaying to a single, multimodal S-I map. Major interactions between submodalities appear to be postponed until cortex. Our concept of thalamocortical organization of the somatosensory systems of monkeys is summarized in Figure 15. This summary divides the ventroposterior thalamus into four nuclei: VP proper, VPS, VPO, and VPI.

The VP nucleus. In the scheme in Figure 15, VP includes VPL and VPM and corresponds to the single map of the body surfaces in the present study, and the "cutaneous core" of the ventroposterior or ventrobasal thalamus of some investigators (i.e., Jones and Friedman, '82; Loe et al., '77). Most of the input to this nucleus is from the dorsal column-trigeminal system (Boivie, '78; Kalil, '81; Berkley, '80; Asanuma et al., '83). VP contains separate aggregates of cells related to SA and RA receptors, and this information is relayed to cortical areas 3b, 1 and possibly S-II, each of which forms a separate representation of the body surface (for representations in 3b and 1, see Merzenich et al., '78; Kaas et al., '79; Nelson et al., '80a,b; Sur et al., '82; Felleman et al., '83; for S-II, see Cusick et al., '81; Friedman et al., '80; Robinson and Burton, '80). Because VP, areas 3b and 1, and S-II all contain separate maps of the body surface, it is logical to assume that all parts of VP project to all parts of each of its three cortical targets. Thus, some neurons in an isorepresentation group must logically project to each cortical area to complete the maps, and all isorepresentation groups must project to each cortical area. However, individual neurons in each isorepresentation group may project to only one representation.

Jones and Friedman ('82) have recently suggested that the inner part of the "central cutaneous core" (the core of the core) projects only to area 3b, while the outer area projects to both area 3b and area 1. Given the organization of VP summarized in Figure 13, we would argue that such a projection pattern is unlikely since the outer part of VP fails to represent all body parts. A tendency for such a pattern could result from the dominance of VP by the large hand and foot subnuclei with elongated isorepresentation lines. Perhaps the central portion of these lines projects only to area 3b. However, injections of HRP in locations matched for body part representation in area 3b and area 1 appear to label the same regions of VP (Lin et al., '79; Nelson and Kaas, '81), suggesting that the neuron populations projecting to the two fields are largely overlapping.

The physiological evidence for SA and RA bands in area 3b (Sur et al., '81) argues that both SA and RA cell clusters in VP project to area 3b. Something in the range of 20% (Sur et al., '81) to 55% (Paul et al., '72) of area 3b appears

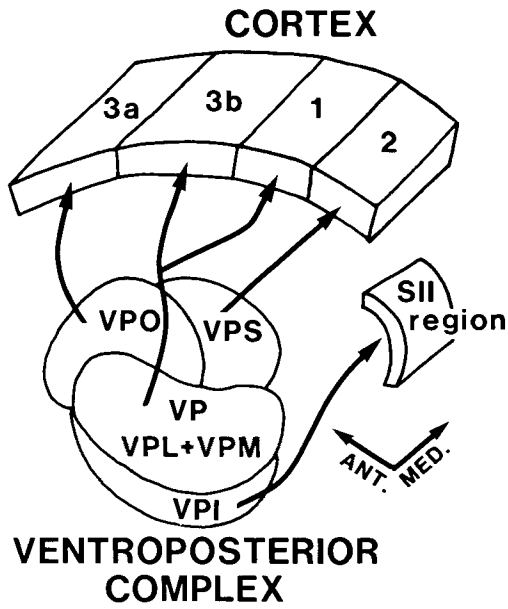

Fig. 15. Suggested subdivisions of the ventroposterior thalamus in monkeys. A ventroposterior nucleus (VP), including VPL and VPM as traditional subdivisions, projects SA and RA cutaneous inputs to areas 3b and 1 and possibly to S-II (not shown). The ventroposterior oral nucleus (VPO) relays muscle receptor information to area 3a, while the ventroposterior superior nucleus (VPS) relays inputs from noncutaneous receptors to area 2. The ventroposterior inferior nucleus (VPI) is responsive to stimuli that would activate pacinian receptors, and it projects to the region of S-II. See text for further details.

to be activated by SA inputs. Both RA and SA cell types are also found in area 1 (Paul et al., '72; Sur, '80), but the proportion of area 1 activated by SA inputs may be 5% or less (Paul et al., '72). Thus, it is likely that few of the SA neurons in VP project to area 1. According to Robinson and Burton ('80), neurons in S-II are rapidly adapting to hair or skin stimulation. Therefore, any projections to S-II from VP (Jones and Powell, '70; Burton and Jones, '76; however, see Friedman et al., '83) are likely to be from RA neurons.

The VPS nucleus. While it was once thought that a single body representation in VP projects to a single body representation across cortical areas 3a, 3b, 1, and 2 (see Merzenich and Kaas, '80 for review), it is now apparent that areas 3b and 1 receive inputs from the cutaneou representation in the ventral thalamus (VP or "VP core"), while area 2 receives from a separate thalamic region that we term the ventroposterior superior nucleus (VPS) after Diamond ('82). VPS is equivalent to much of the VPL shell of Jones and Friedman ('82), and it corresponds to the dorsocaudal portion of the "deep zone" of the present recording experiments. VPS is activated by joint and probably other deep receptors including those related to muscles. Injections of HRP in area 2 label this portion of the ventral thalamus (Lin et al., '79; Nelson and Kaas, '8l), and injections of anterograde tracers into the dorsal "deep" zone (VPS) label area 2 (Friedman and Jones, '81). The precise details of the inputs to VPS are not well understood, but it appears that VPS receives less-dense inputs from ascending somatosensory pathways than do other parts of the VP complex (Boivie, '78, '79; Kalil, '81; Berkley, '81, '83; Asanuma et al., '83). Indirect evidence suggests that joint receptor information is relayed to area 2 via dorsal column input to VPS (see Dykes, '83, for review), whereas the relay of cutaneous information to area 2 (see Kaas, '83, for review) is most likely dependent on a projection from area 1 (Vogt and Pandya, '78; Jones et al.,'78).

The VPO nucleus. Our mapping experiments were not detailed enough in the "deep" zone of the thalamus to reveal a separate map related to muscle spindle afferents shown as VPO in Figure 5. However, the rostrodorsal "cap" or "shell" of "VP" projects to area 3a (Friedman and Jones, '81; Kalil, '78), this capping region is activated by muscle stretch (Wiesendanger et al., '79; Maendly et al., '81), and area 3a is activated by muscle receptors (Phillips et al., '71; Tanji and Wise, '81). Thus, it seems likely that VPO contains a map of muscle receptors. In cats, Dykes ('82) has referred to the muscle receptor region of thalamus with projections to area 3a as the ventroposterior oral nucleus (VPO), and we use the same term here.

The VPI nucleus. The region responsive to pacinianlike inputs (VPI) is the ventroposterior inferior nucleus (Dykes et al., '81). Our VPI may include a part of the architectonically similar and caudally adjacent "medial posterior" nucleus (Pom) of some investigators. Pacinian receptor information is likely to come from a restricted portion of the dorsal column nuclei (see Dykes, '83), and it appears to be relayed from VPI to retroinsular cortex adjoining S-II "proper" (Burton and Jones, '76) or to S-II itself (Friedman et al., '83).

Are VPO, VPS, VP, and VPI separate nuclei or subdivisions of a single nucleus?

The regions we have designated as VPO and VPS in Figure 15 are in a region of the thalamus that has been described as the VPLc-VPLo "transition region," and the part of VP "shell" (see Berkley, '83). Architectonically, the shell region is characterized by a lower cell density (Berkley, '80). The difference in appearance between the "shell" and the "core" is more apparent in New than Old World monkeys, and we believe this difference corresponds to the distinction commonly made between VP and surrounding thalamus in a variety of mammalian species (see Welker, '73). As reviewed above, VP, VPI, and the two subdivisions of the shell appear to differ in neural properties, inputs, and projections. Such observations are consistent with the concept that VP, VPI, VPO, and VPS are separate nuclei. However, the argument also could be made that "layers" within a nucleus, like the magno- and parvocellular layers of the lateral geniculate nucleus, sometimes have different appearances, neural properties, and connections. Therefore the regions we term VPO, VPS, VP and VPI could be considered as "layers" of a single nucleus. For the "layers" to comprise a single nucleus, however, it would seem to be necessary for them to encompass only one map, as is the case for the lateral geniculate nucleus where lines of isorepresentation course perpendicular to the layers to unite the nucleus (Kaas et al., '72). The present results indicate that there are separate maps in VPI, VP, and VPS, and further studies, we suggest, will reveal a separate map in VPO. Furthermore, all layers in the lateral geniculate have a common cortical target, area 17, while VPO, VPS, VP, and VPI do not. The distinction between "layers" and nuclei is not trivial since ideas are shaped by language, and a consistent terminology can usefully influence the development of future knowledge.

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