

# REGIONAL SEGREGATION OF NEURONS RESPONDING TO QUICKLY ADAPTING, SLOWLY ADAPTING, DEEP AND PACINIAN RECEPTORS WITHIN THALAMIC VENTROPOSTERIOR LATERAL AND VENTROPOSTERIOR INFERIOR NUCLEI IN THE SQUIRREL MONKEY (*SAIMIRI SCIUREUS*)

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**Abstract**—The ventroposterior nuclei and the ventroposterior inferior nucleus of the thalamus were mapped in squirrel monkeys (*Saimiri sciureus*) using low-impedance platinum-iridium microelectrodes. The body site and receptor category from which the optimum response was obtained was recorded every 50  $\mu\text{m}$  in orthogonal penetrations through these nuclei. The results suggest that the neurons are grouped according to submodality in this area and that discrete and spatially separate volumes of the thalamus are devoted to input from deep, Pacinian, cutaneous rapidly adapting and cutaneous slowly adapting receptors. The Pacinian responses were limited to the ventroposterior inferior nucleus and deep responses were limited to a region just above the ventroposterior nuclei. Within ventroposterior nuclei the cutaneous rapidly adapting and cutaneous slowly adapting volumes were interspersed in a pattern that could not be readily defined.

The results indicate that there is more than one representation of the body in this area of the thalamus. Discontinuities in receptive field sequences make it difficult to see how any representation can be a spatially continuous map of the body.

SINGLE unit studies of the primate thalamus have demonstrated that many neurons within the ventroposterior nuclei (VP) and the ventroposterior inferior nucleus (VPI) are specific for place and modality (ANDERSON, LANDGREN & WELSH, 1966; LOE, WHITSEL, DREYER & METZ, 1977; MOUNTCASTLE, POGGIO & WERNER, 1963; POGGIO & MOUNTCASTLE, 1963; PUBOLS & PUBOLS, 1966; WELKER & JOHNSON, 1965). These neurons are activated by stimuli applied within restricted receptive fields contralateral to the recording site and their responses indicate that they receive their major excitatory input from only one class of sensory receptors (i.e. from 'deep' or 'cutaneous' receptors (LOE *et al.*, 1977; POGGIO & MOUNTCASTLE, 1963; WELKER, 1978). Further, neurons driven by these two receptor classes are differentially distributed in the thalamus; neurons activated by deep receptors are situated dorsally and rostrally to neurons activated by cutaneous receptors. The deep input may be from Group Ia afferents, which have been shown to terminate in the anterodorsal part of the ventroposterior lateral nucleus (VPL) in the cat (ANDERSON *et al.*, 1966).

We have studied the detailed topology of the body representation in VP of the squirrel monkey to see whether restricted regions within VP receive a predominant input from specific kinds of cutaneous receptors.

## EXPERIMENTAL PROCEDURES

Adult squirrel monkeys (*Saimiri sciureus*) were anesthetized with ketamine hydrochloride, their skulls then fixed in a stereotaxic device and a craniotomy performed. Platinum-iridium microelectrodes were advanced through the thalamus along the cardinal axes of the Horsley-Clark coordinate system. Standard amplification and recording techniques were used to observe multiunit activity in closely-spaced penetrations within the thalamus. Although seven animals were used for this study, the results reported here were obtained primarily from two animals in which particular attention was given to the submodal character of the neural responses. Every 50  $\mu\text{m}$ , the multiunit response was characterized in terms of: (i) receptive field location; (ii) the traditional modality classes (deep or cutaneous: POWELL & MOUNTCASTLE, 1959); and (iii) probable receptor type within the cutaneous modality (i.e. slow or rapidly adapting or Pacinian). At the end of the experiment, each monkey was deeply anesthetized and perfused with 10% formol-saline. Fifty- $\mu\text{m}$  thick frozen sections were cut and stained with Cresyl Violet. All of the data presented were taken from electrode tracks whose trajectories were recon-

**Abbreviations:** VP, ventroposterior nuclei of the thalamus; VPI, ventroposterior inferior nucleus of the thalamus; VPL, ventroposterior lateral nucleus.

structed from histological sections using electrolytic lesions and evidence of cellular damage for reference.

## RESULTS

The penetrations reconstructed in Figs 1 and 2 illustrate the major findings concerning segregation of receptor types. Frontal sections at two rostrocaudal levels of the thalamus are illustrated in Figs 1A and 2A.

Note the irregularities in cell density, cell size and cell distribution which cause the neurons to appear grouped within this large nucleus (cf. HAND & VAN-WINKLE, 1976). Heavy lines demarcate the major identifiable thalamic subdivisions. Modality changes were closely related to these boundaries. The receptive field sequences encountered in the penetrations shown in Figs 1A and 2A are illustrated in Figs 1B and 2B respectively.

In the penetration illustrated in Fig. 1A, a high threshold response from stimulation of the hand was first recorded about 1 mm dorsal to the nuclear boundary of VPL. These responses could not be classified by submodality. In the region extending about 500  $\mu\text{m}$  immediately above VPL (region A in Fig. 1A), responses could be elicited by manipulation of the hand in a manner suggesting that deep receptors (possibly in the thenar muscles) were the source-activating neurons in this region. Upon entering the VPL, the adequate stimulus changed abruptly (within 100  $\mu\text{m}$ ) to cutaneous and remained cutaneous until the electrode passed out of VPL near the end of the penetration. Initially, the receptive field of this cutaneously-driven neural response was located on the glabrous tip of the second digit (Fig. 1B). The nature of the adequate stimulus was unclear. When a vibrating biological stimulator (CHUBBUCK, 1966) was applied to the receptive field, a response was obtained for all low amplitude vibrations tested from 5 to 400 Hz, suggesting that inputs from several classes of fibers were converging on these cells. Responses of this nature were recorded over a penetration distance of 250  $\mu\text{m}$ . Then, within one 50  $\mu\text{m}$  step, the response changed so that the adequate stimulus, as verified with the biological stimulator, was static indentation of the skin. The receptive field also shifted at this point to a location on the thenar eminence. Slowly adapting responses were recorded over the next 450  $\mu\text{m}$  of the penetration.

The response character of thalamic neurons again shifted abruptly as the electrode entered region D in Fig. 1A and for the subsequent 200  $\mu\text{m}$  it was difficult to elicit responses (an unusual occurrence within VPL). When the electrode was advanced 50  $\mu\text{m}$  further, the low threshold cutaneous responses were again recorded, but they were not rapidly adapting. The receptive fields were located on the dorsum of the second digit. Tests with the mechanical stimulator indicated that the predominant input was from non-Pacian rapidly adapting fibers (HARRINGTON &

MERZENICH, 1970; MERZENICH & HARRINGTON, 1969). This rapidly adapting response was recorded over a penetration distance of 600  $\mu\text{m}$ ; when it disappeared, the threshold became elevated so that multiunit responses could only be activated by tapping the wrist as the penetration passed out of VPL.

The data from a second penetration, crossing VPL more rostral to the first, are illustrated in Figs 2A and 2B. After driving 1600  $\mu\text{m}$  through the dorsal aspects of the thalamus, where only strong taps of the hand elicited a weak response, the electrode entered the VLP nucleus. Within 100  $\mu\text{m}$ , a low-threshold cutaneous response, centered on the tip of the fourth digit, was identified. Subsequently (area B in Fig. 2A), the electrode encountered a cutaneous slowly adapting region activated by receptive fields on the same digit. After this, the responses changed to cutaneous rapidly adapting (region C) and the receptive fields moved progressively back towards the tip again. Tests with the mechanical stimulator suggested that the predominant input to this region was from cutaneous rapidly adapting fibers having frequency characteristics of afferent fibers serving Meissner corpuscles (TALBOT, DARIAN-SMITH, KORNHUBER & MOUNTCASTLE, 1968). After 500  $\mu\text{m}$  of cutaneous rapidly adapting responses, the responses weakened and disappeared in a distance of 150  $\mu\text{m}$  at a point later shown to correspond to the ventral margin of VPL.

Twenty-six penetrations were made in the two animals where modality and submodality were noted in detail. Of these, 18 passed through the VP region and encountered both deep and cutaneous responses. In 14 of these cases, the sequence of modalities and submodalities encountered were almost identical: first, high threshold taps (16 of 18 times) activated neurons above VPL as the nuclear region was approached. Then 15 of 18 times, deep responses were encountered in the region immediately above VPL. Fourteen times, cutaneous slowly adapting responses were encountered in the dorsal part of VPL, followed by cutaneous rapidly adapting responses. Eight times, Pacinian responses were encountered. Each time the Pacinian responses were the last-driven response in the penetration.

There were only a few deviations from this pattern of tap, deep, cutaneous slowly adapting, cutaneous rapidly adapting and Pacinian. In two cases, no high-threshold tap was encountered; the responses immediately changed to deep. In four cases, the deep region was missed and the change was from tap to cutaneously-driven responses. Four times, a dorsal region of convergent rapidly adapting input was encountered (cf. Fig. 1). Each time this response class was encountered it was located between the deep and cutaneous slowly adapting region. In three penetrations, the cutaneous slowly adapting region was missed and the transition was from deep to skin rapidly adapting. When present, each response-type was encountered in the same order and the alterations in the sequences appeared to be due to the absence of

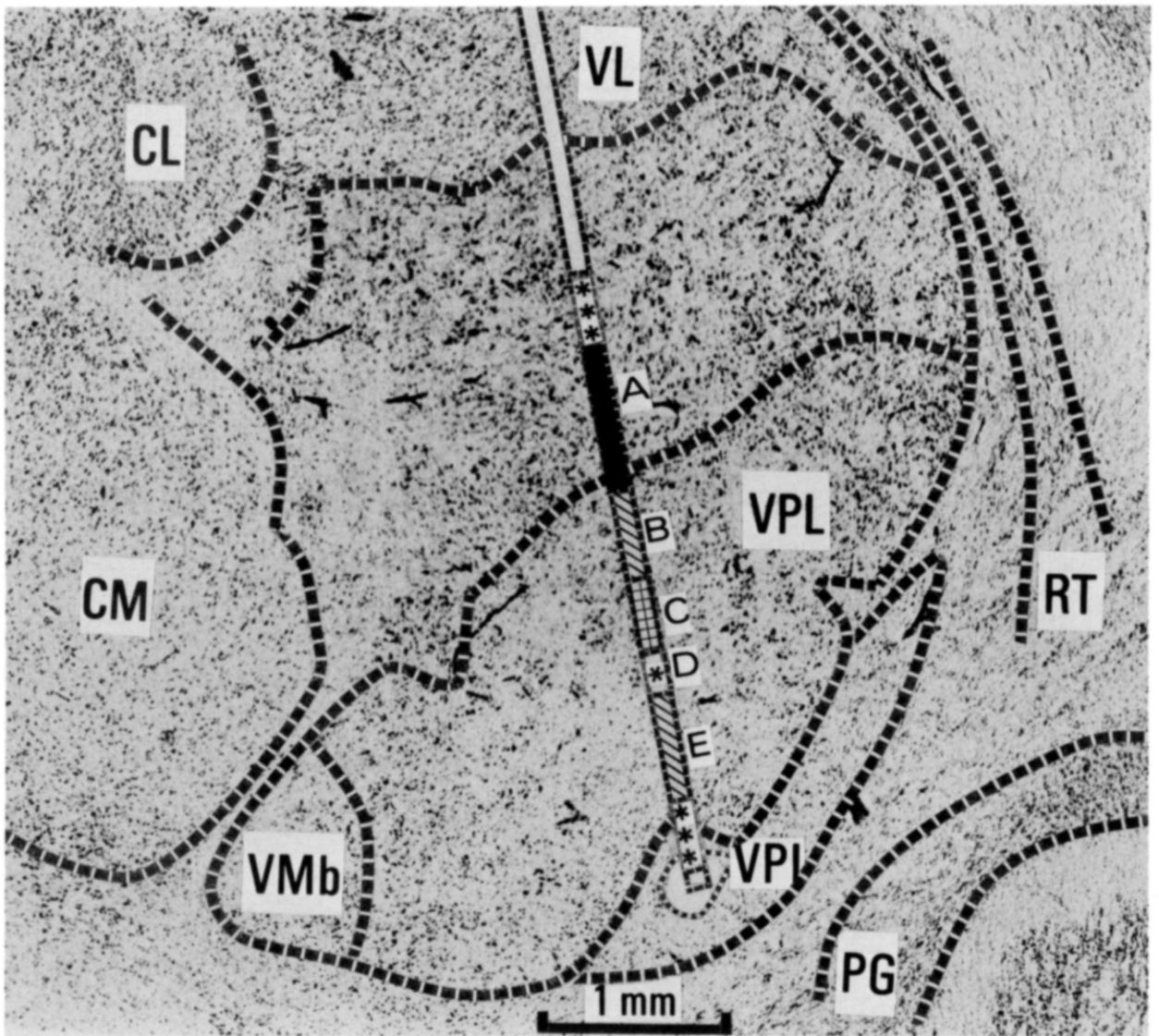


FIG. 1A. Frontal section of the thalamus and corresponding electrophysiological data. The major nuclear regions are outlined with heavy dotted lines and identified with labels (Nuclei: VL = Ventrolateral, CL = Centralis lateralis, CM = Centralis medialis, VPL = Ventralis posterolateralis, RT = Reticularis, VPI = Ventralis posterior inferior, PG = Pregeniculate). The electrode track is coded according to the responses encountered and terminates in a lesion. (A = deep, B = cutaneous rapidly adapting, C = cutaneous slowly adapting, D = tap, E = cutaneous rapidly adapting).

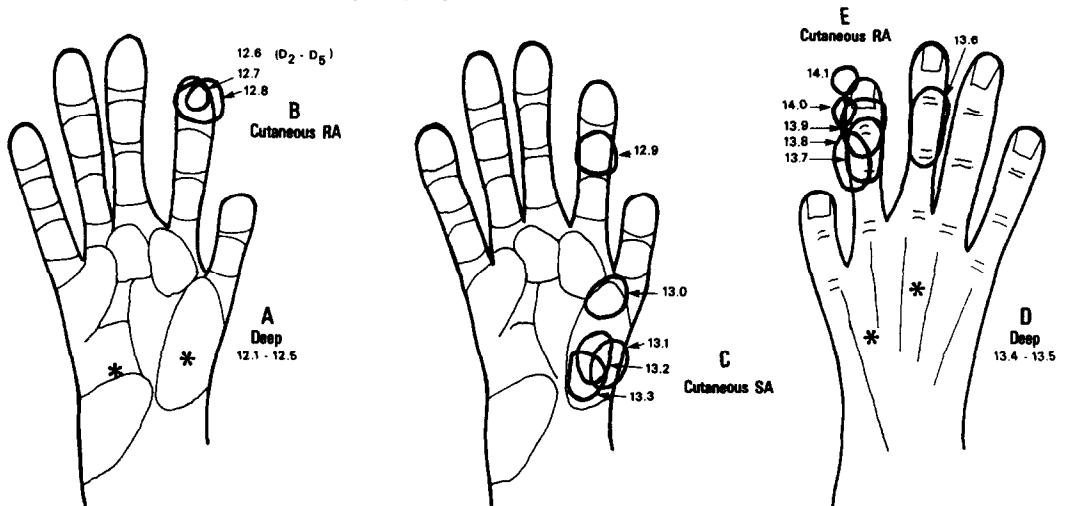


FIG. 1B. Loci of successively-encountered receptive fields observed during the trajectory shown in part A. Letters A through E correspond to the regions marked in part A. Note that the receptive field locus moved significantly with each change in response class.

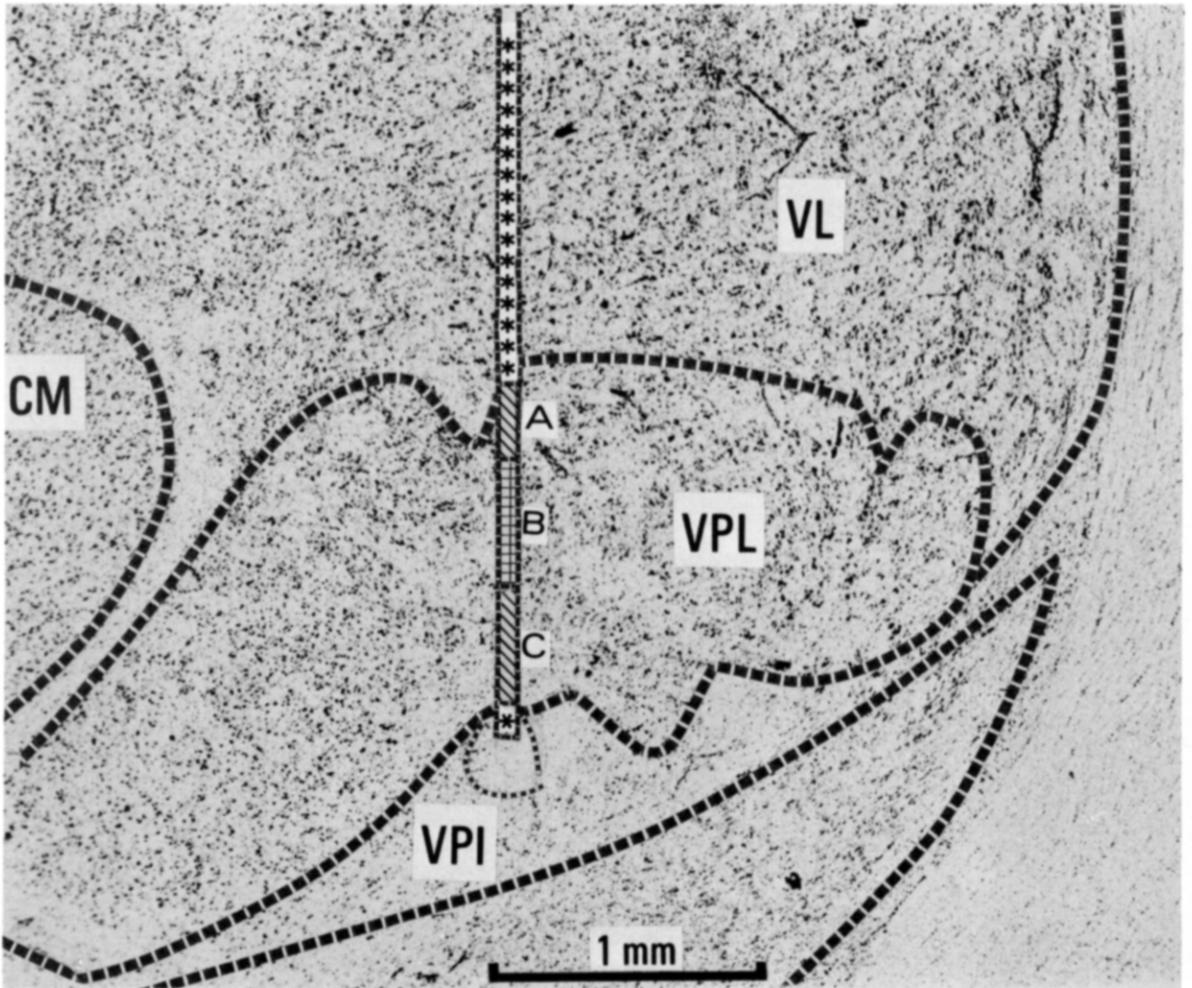


FIG. 2A. Frontal section through the thalamus and the corresponding electrophysiological data. Labeling conventions are the same as those shown in Fig. 1A. A = cutaneous rapidly adapting region, B = cutaneous slowly adapting region and C = cutaneous rapidly adapting region. The end of the electrode track is marked by a lesion.

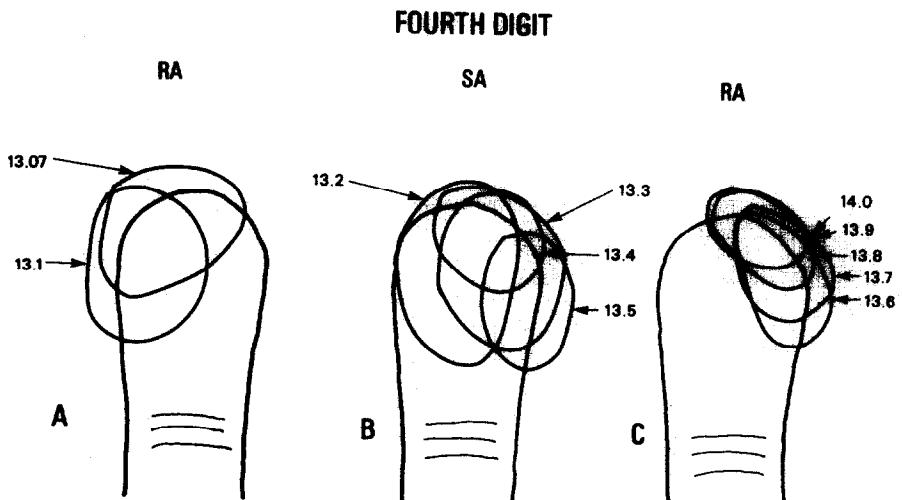


FIG. 2B. The sequence of receptive fields encountered during the trajectory illustrated in part A. Observe that the receptive fields cover the tip of the digit three times, once for each response class encountered.

a particular response, not to the re-arrangement of the sequence. For example, Pacinian responses were never found dorsal in the nucleus, and cutaneous slowly adapting responses were never found below the Meissner-like cutaneous rapidly adapting responses.

## DISCUSSION

From this data it is apparent that modality and submodality-specific responses occur in two patterns. The first pattern follows the traditional nuclear boundaries; around the VP there are other regions which contain at least partial representations of the body, each characterized by input predominantly from one modality or receptor class. The segregation of input from cutaneous and deep receptors has been established by previous investigators (ANDERSON *et al.*, 1966; LOE *et al.*, 1977; MOUNTCASTLE *et al.*, 1963; POGGIO & MOUNTCASTLE, 1960; POGGIO *et al.*, 1963; POGGIO *et al.*, 1966; WELKER, 1973; WELKER & JOHNSON, 1965). Our data confirm this separation and we note here the remarkable abruptness with which the transition from deep to cutaneous occurs at the top of VPL. The existence of the region driven by Pacinian input has not been reported previously. In our data it was always found ventral or posteroventral to VPL in a region identified as VPI. The second submodality pattern occurs within the VPL itself. The ventroposterior lateral nucleus appears to receive only cutaneous input. However, this nuclear region is divided into zones of slowly adapting responses and topographically continuous zones of rapidly adapting responses. We believe that there may be a dorsal rapidly adapting region in VPL which differs from the other rapidly adapting region by receiving its input from several different types of receptors. However, it was encountered in only four penetrations and thus not as well studied as the deeper rapidly adapting region, which appeared to have its major input restricted to only one class of rapidly adapting fibers.

Further, we have observed: (i) abrupt shifts of receptive fields (Fig. 1B), (ii) long sequences of receptive fields serving one body site (Fig. 2B), and (iii) regular, gradually shifting sequences of receptive fields within VP (not illustrated here). We interpret these data to mean that there are submodality-specific regions within VP which are topographically organ-

ized. However, the topography is far more complex than earlier studies have suggested, and is related to submodality. HAND & VAN WINKLE (1976) and JONES, WISE & COULTER (1979) have observed small groupings of cells in VPL projecting to punctuate zones in the first somatosensory area of the cortex which they proposed are the thalamic equivalent of cortical columns.

Some implications of these observations must be discussed. First, it is clear that there is more than one representation of the body in the thalamus. Two representations of the body have been reported previously in the context of thalamic projections to the first and second somatosensory cortical regions. EMMERS (1965) suggested that a thalamic relay region for the second region existed separately from the relay region for the first region in the rat. TASKER & EMMERS (1969) and TASKER, RICHARDSON, RENEWCASTLE & EMMERS (1972) also reported a double body representation in the human thalamus and RABIN (1974) reported a similar dual organization in the cat. In each case, the location of the thalamic region projecting to the second somatosensory cortex was ventral and posterolateral to the region projecting to the first somatosensory cortex. Perhaps these reports have identified the area which corresponds to our data from the VPI nucleus.

Second, because of the discontinuities of receptive fields observed in our data, it is difficult to see how any of these representations can be a spatially-continuous map of the body. Third, our data suggest that these representations are not easily reconciled with a representation based upon dermatomes. Fourth, the segregation of responses by submodality in the VP thalamus has major implications for its relationship to the cortex. For example, is there a clear separation of cutaneous slowly adapting and rapidly adapting responses in the 3b region of cortex as is apparent in the cat (RASMUSSEN, DYKES & HOELTZELL, 1979), or are there rules governing a recombination of these response classes when they reach the cortex? Similar questions must be asked for the cortical projections of each of the submodality-specific regions.

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