

Connections of Areas 3b and 1 of the Parietal Somatosensory Strip with the Ventroposterior Nucleus in the Owl Monkey (*Aotus trivirgatus*)

CHIA-SHENG LIN,^{2,5} MICHAEL M. MERZENICH,⁴ MRIGANKA SUR^{1,3} AND JON H. KAAS^{1,2}

¹Department of Psychology, ²Anatomy, and ³Electrical Engineering, Vanderbilt University, Nashville, Tennessee 37240; and ⁴The Coleman Memorial Laboratory, University of California, San Francisco, California 94143

ABSTRACT Anatomical tracers were injected into electrophysiologically defined sites in somatosensory cortical Area 3b (SI proper) and Area I (posterior cutaneous field) of owl monkeys after these cortical subdivisions had been extensively explored in microelectrode mapping experiments. These mapping experiments revealed that both Areas 3b and 1 contain complete and separate representations of the body surface (Merzenich et al., '78). Restricted injections of the retrograde tracer, horseradish peroxidase (HRP), into either Area 3b or Area 1 labeled neurons within a band of cells in the ventroposterior nucleus (VP). The location of the labeled band in VP varied with the location of the injection site in both representations, and the labeled region of VP was overlapping for injections in corresponding body parts in the two representations. Neurons projecting to the hand and foot cortical representations were in architectonically identified subnuclei. Because injections into either Area 3b or Area 1 labeled over half of the neurons in the appropriate regions of VP, it appears that some neurons in VP project to both cortical representations. Finally, injections of HRP combined with the anterograde tracer, ³H-proline, indicate that VP neurons are reciprocally interconnected with both Areas 3b and 1.

In a previous paper, we presented evidence for a reinterpretation of the organization of somatosensory cortex in primates (Merzenich et al., '78; also see Kaas et al., '76). In brief, we argued that the four architectonic subdivisions of "SI" in primates (Areas 3a, 3b, 1, and 2) correspond to four representations. Two areas, 3b and 1, contain complete maps of the body surface, and neurons in these areas are responsive to light tactile stimuli. More limited evidence was presented for a systematic representation of input from deep body tissues in Area 2 caudal to the two cutaneous representations. In addition, observations on Area 3a were consistent with the concept that this strip of cortex represents muscle afferents and other deep receptors (Tanji, '75; Lucier et al., '75; Phillips et al., '71). Only the 3b representation was considered to be homologous with the primary somatosensory cortex, SI, of other mammals, and this cutaneous field was termed "SI proper" to distin-

guish it from the common use of "SI" in primates which, in our view, fails to distinguish the four complete representations comprising the "parietal somatosensory strip." The second cutaneous representation (Area 1) was called the "posterior cutaneous field." The two cutaneous representations, SI proper and the posterior cutaneous field, have been demonstrated not only in owl monkeys (Kaas et al., '76; Merzenich et al., '78), but also in squirrel monkeys (Nelson et al., '78) and macaque monkeys (Paul et al., '72a; Kaas et al., '78; Sur et al., '78).

If our reinterpretation of the organization of somatosensory cortex is correct, then it is obvious that it will be necessary to extensively reinvestigate the connections of somatosensory cortex in primates. Investigations that have considered "SI" as a single functional unit will require reevaluation, and studies of

⁵Present address: Department of Physiology, University of Virginia Medical School, Charlottesville, Virginia 22901.

the connections of individual areas will be needed. Even if results and conclusions of anatomical studies have been carefully related to Areas 3a, 3b, 1, and 2, our reinterpretation of the organization of somatosensory cortex means that, other than in a very general way, anatomical results have not been adequately related to somatosensory maps of the body surface.

In the present study, the connections of electrophysiologically defined parts of the two cutaneous fields with the ventroposterior nucleus of the thalamus are described. In individual monkeys, regions of SI proper and the posterior cutaneous field were extensively mapped with microelectrodes, and either the retrograde tracer, horseradish peroxidase (HRP), or a mixture of HRP with the anterograde tracer, tritiated proline, was injected at one or more precisely determined sites in the body surface representations. In addition, HRP was introduced into a defined body locus in the representation of deep body receptors in cortex caudal to Area 1 of one monkey. The results define slabs of cells of isorepresentation in the ventroposterior nucleus, and suggest that each slab is reciprocally interconnected with homotopic locations in both SI proper and the posterior cutaneous field. Major sensory input into the posterior cortical representation of deep receptors appears to be from neurons dorsal to the ventroposterior nucleus.

METHODS

The present experiments combined electrophysiological mapping studies of somatosensory cortex with the use of anterograde and retrograde tracers to determine thalamocortical connections. Injections of HRP or HRP combined with ^3H -proline were made in one or both cerebral hemispheres of eight owl monkeys, into cortical locations precisely defined by microelectrode mapping procedures (as described in detail elsewhere; see Merzenich et al., '78). To summarize relevant methods, monkeys were anesthetized with ketamine HCl and fixed in a headholder. The parietal cortex was exposed, and protected by a pool of silicone fluid within a dam of dental cement (methyl methacrylate) fastened about the skull opening. Microelectrode mapping procedures were then used to determine the details of the representations of body surfaces in a sector of Areas 3b and 1 of Brodmann ('09). These experiments revealed two separate orderly representations of the body sur-

face, one for each of these two architectonic fields, as described elsewhere (Merzenich et al., '78). After the organization of the representations of a given part of the body surface was determined in detail in one hemisphere, tracers were injected at defined locations in one or both of the representations. The mapping was then continued in the other hemisphere for another 12 to 24 hours. At the end of the microelectrode mapping of the second hemisphere, injections were made into the second hemisphere in some monkeys. Individual injections were approximately 0.1-0.2 μl of HRP (Sigma type VI, 30% HRP in saline) or a combination of HRP and tritiated proline (33 $\mu\text{Ci}/\mu\text{l}$). In all cases, small electrolytic lesions were made at key recording sites for later correlation of the mapping results with the cortical architecture. After survivals of 15 to 24 hours from the last injection, the anesthetized monkeys were perfused with saline followed by 8% formalin in saline. The removed brains were kept overnight in fixative and then changed to fixative with 30% sucrose and phosphate buffer for approximately an additional 24 hours. After photographing the brains, the thalamus and cortex were usually separated so that each could be cut in the most favorable plane. The thalamus was frozen and cut into 25 μ sections in the frontal plane. Separate sets of serial sections were stained with cresyl violet, reacted for HRP according to the procedure of LaVail ('75), or processed for autoradiography using the method of Cowan et al. ('72). If processed separately, cortex in the somatosensory region was cut in the parasagittal plane and processed in the same way. Injection sites, labeled neurons, and spread of label were later identified in these sections and related to architectonic divisions of the cortex (Merzenich et al., '78) or thalamus according to the atlas of Emmers and Akert ('63) for squirrel monkeys.

RESULTS

1. *Subdivisions of ventroposterior nucleus*

The ventroposterior nucleus of the thalamus (VP) in primates is commonly subdivided into several cell groups, including ventralis posterior lateralis (VPL), ventralis posterior medialis (VPM), ventralis posterior medialis pars parvocellularis (VPMp), and ventralis posterior inferior (VPI) (Walker, '38). These major subdivisions of the dorsal thalamus of owl monkeys are shown in figure 1, where they are distinguished by differences in cell sizes

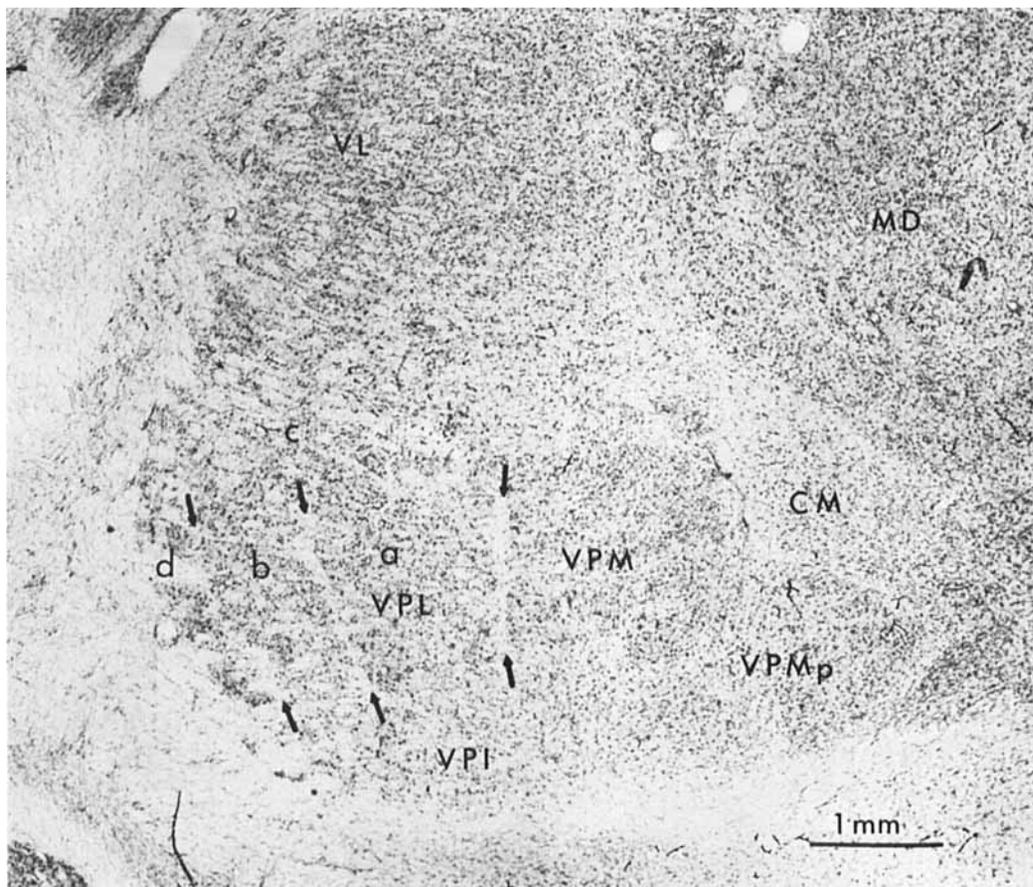


Fig. 1 The cytoarchitecture of the ventroposterior complex (VP) of the owl monkey. For reference in the text, subnuclei of nucleus ventralis posterior lateralis, VPL, are labeled a-d. Arrows mark bands of fibers separating subnuclei. Other nuclei are medialis dorsalis, MD; ventralis posterior medialis, VPM; ventralis posterior medialis pars parvocellularis, VPM_p; ventralis posterior inferior, VPI; centrum medianum, CM; ventralis lateralis, VL; Owl monkey 76-9, section 854.

and distributions. VPL is further subdivided by bundles of fibers. In the caudal two-thirds of VPL, two ventral blocks of neurons, roughly square in cross-section, are bordered medially, laterally and dorsally by bands of fibers. The medial group of cells (subnucleus a, fig. 1) is somewhat larger than the lateral group of cells (subnucleus b). Within both of these subnuclear groups neurons are unevenly distributed suggesting even further internal subdivision. A narrow strip of cells (subnucleus d) lateral to the two blocks lies along the lateral border of VPL. Cells in the dorsal portion of VPL are more evenly distributed; they form a fourth distinct subdivision (subnucleus c). These subdivisions are not apparent in the most rostral and extreme caudal aspects of

VPL. The relation of these aggregates of cells within VPL are noted here because they will be shown to relate to the representation of the body surface within the nucleus.

2. General features of the connections of the somatosensory thalamus with somatosensory cortical fields

In every experiment in which HRP was injected into Area 3b or Area 1, HRP-positive neurons were found within VP. With small, restricted injections at cortical sites representing skin surfaces of the hand or foot or body, labeled neurons were found largely or totally within one of the subnuclear divisions of VPL. The intensity of the reaction product resulting from an injection into Area 3b was

consistently greater than from an injection into Area 1. With small injections into either Area 3b or Area 1, groups of neurons were labeled in VPL which often extended over much of the rostrocaudal length of the nucleus. Combined injections of HRP and ³H-proline labeled similar regions of VPL showing reciprocal cortico-thalamic connections. With injections into an orderly representation of "deep" body structures in cortex caudal to Area 1, neurons dorsal to VP were labeled.

These results are described in more detail and documented by specific cases below.

3. Projections of VPL neurons to Areas 3b and 1

In one monkey (76-11R), an effort was made to determine if all of VPL projects to the body and limb representations in Areas 3b and 1. As shown in figure 2, HRP was injected into three locations in Area 3b corresponding to the sites of representations of prescribed sur-

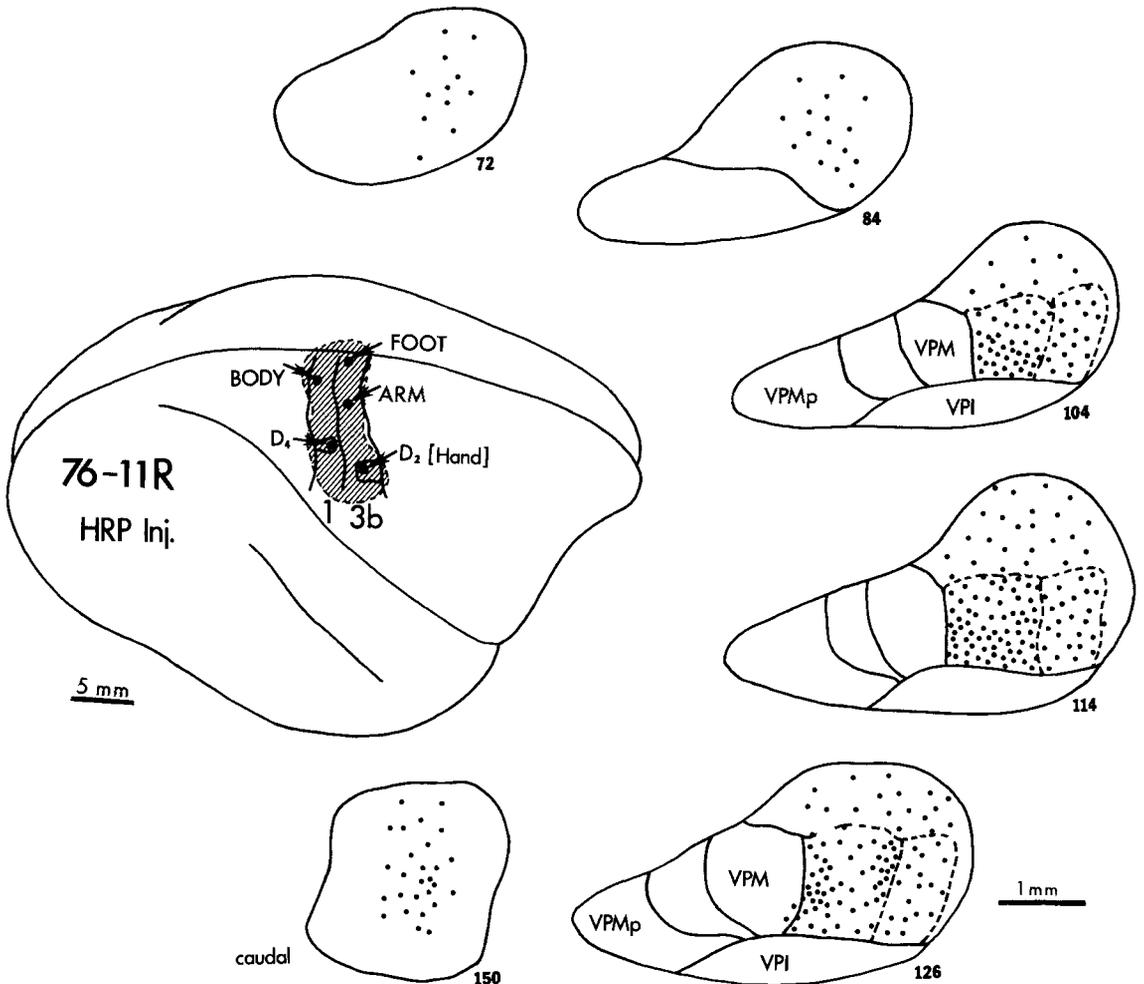
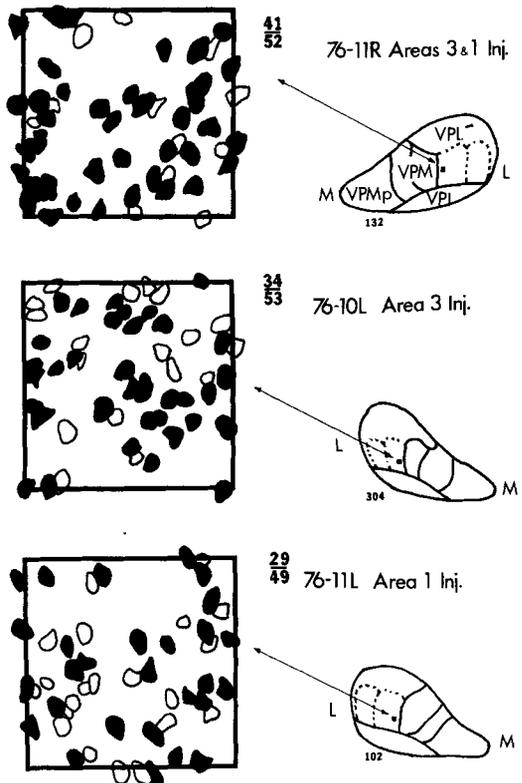


Fig. 2 The distribution of HRP-labeled neurons in VP after cortical injections into Areas 3b and 1. The drawing of the right cerebral hemisphere shows architectonic boundaries of Areas 3b and 1, the injection sites (arrows to dots) within electrophysiologically determined representations of body parts (D₂ and D₁ indicate the second and fourth glabrous digits of the hand), and the cortical extent of the HRP reaction product (hatching). Drawing of VP from numbered rostrocaudal serial 25 μ frontal sections indicate the resulting locations of HRP-labeled neurons with dots. Each dot represents approximately five labeled neurons. Abbreviations as in figure 1.

faces of the foot, arm, and second finger, and into two locations in Area 1 falling within the representations of the trunk and fourth finger. Examination of the reacted brain sections showed that the HRP diffused to extend over almost the entire region of the body and limb representations in Areas 3b and 1, with little spread outside these areas. Possibly, only portions of cortex on the medial wall representing the tail of the animal escaped exposure to HRP. As a result of these injections, neurons were labeled throughout the rostrocaudal extent of VPL. HRP-positive neurons were found in all four subnuclear groups of the nucleus, but only a few labeled cells were in the lateral strip of VPL (subnucleus d). The lack of labeled neurons suggests that subnucleus d of VPL projects to cortex on the medial wall of the cerebral hemisphere, and represents the tail and, perhaps, adjoining body parts. The lateral margin of the HRP-positive zone of cortex only minimally involved the face and head representations, and only a few labeled neurons were observed in VPM. A few labeled neurons were also found in the thalamus dorsal to VP. Since injections in Area 2 also labeled neurons in this region while injections clearly restricted to Area 3b or Area 1 did not, we attribute the few labeled neurons dorsal to VP in this case to the slight spread of HRP to Area 2. Labeled neurons were not seen in VPI.

The multiple cortical injections in case 76-11R did not label all the neurons in VPL, and different portions of VPL were not equally labeled. Heaviest concentrations of labeled neurons were found in the two block-like subnuclear regions of VPL that other experiments identified as representing the hand and the foot. About 80% of the neurons in the most intensely labeled sectors of these subnuclear regions were HRP-positive (figs. 3, 12B). Labeled and unlabeled neurons were variable in size.

Injections restricted solely to either Area 1 or Area 3b always labeled neurons in VPL; the proportion of neurons labeled was less when only one cortical area was injected than when both were injected. The results of combined Area 3b and Area 1 injections are compared with Area 1 and with Area 3b injections in figure 3. Other details of these three comparison cases are shown in figures 2, 4, and 7. When the injection of HRP was restricted to Area 3b, labeled neurons were usually found across much of the rostrocaudal extent of



HRP Neurons

Fig. 3 Labeled (filled) and unlabeled (outlined) cells in VP following cortical injections of HRP in Areas 1 and 3, Area 3, or Area 1. The counts of the labeled and total number of neurons are from densely labeled parts of VP.

VPL. Case 76-10L is one example (figs. 3, 4). The injection was introduced at the site of the representation of the middle phalanx of the third digit of the hand in Area 3b. The detected spread of the tracer did not extend beyond the boundaries of the field. In the most densely labeled portion of VPL, approximately 66% of the neurons were labeled. In other cases with injections of Area 3b (figs. 5, 6), proportions of labeled neurons in VPL were comparable, and with injections into Area 1, similar proportions of neurons were labeled in the most intensely involved regions of VPL. In Case 76-11L, for example, an Area 1 injection labeled 60% of the neurons in the maximally affected region of VPL (figs. 3, 7). In this region, as with Area 3b injections, the labeled neurons were variable in size.

ly within subnucleus a of VPL. There were no labeled cells near the medial, lateral, and ventral extremes of the subnucleus. The zone of labeled cells was about 0.2-0.3 mm high and 0.1-0.2 mm wide, and was over 1 mm long. The column of neurons extended over the caudal two-thirds of VPL; as is evident in figure 5, it was more dorsally located in more rostral sections. These results indicate that the middle digits of the hand are represented in the middle of the mediolateral extent of subnucleus a.

In another case (76-12R), HRP was injected into the representation of the great toe in Area 3b (fig. 6). The HRP labeled cortex extended medially and laterally to include most or all of the Area 3b representation of the foot and some of the lateral representation of the leg. Some spread of label also extended into

adjoining Area 3a. Most of the resulting labeled neurons in VPL were in subnucleus b, identifying it as representing the foot. The few labeled cells in the lateral portion of subnucleus c may have resulted from the spread of cortical label to the representation of the leg.

These three Area 3b injection cases taken together suggest that subnucleus a is related to the digits of the hand, subnucleus b to the foot, and subnucleus c to the limbs and trunk. Cases with injections involving both Area 3b and Area 1 (figs. 2, 9) support these conclusions.

5. Topographic projections to Area 1

The topographic projections from VPL to Area 1 are similar to those to Area 3b. Two

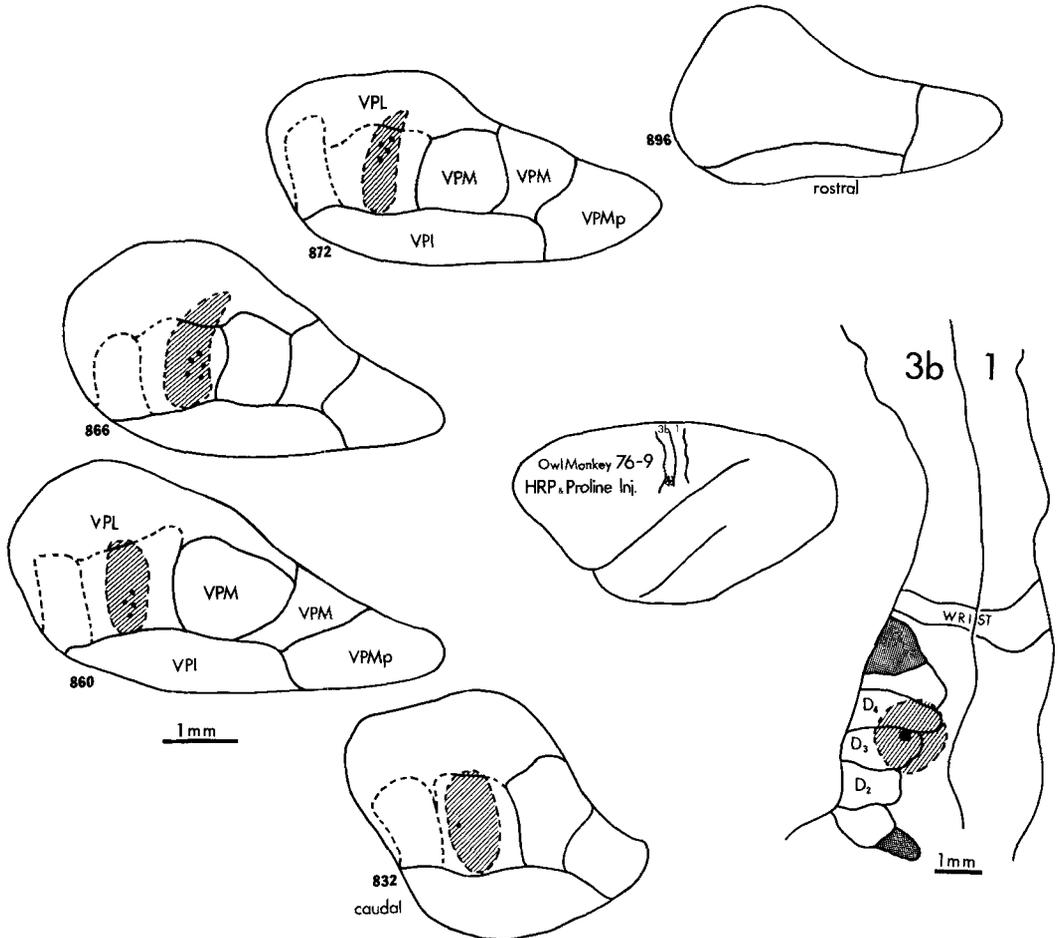


Fig. 5 The distribution of HRP-labeled neurons and silver grains after an injection of ³H-proline and HRP into the representation of the glabrous surface of the third digit in Area 3b. Conventions as in previous figures.

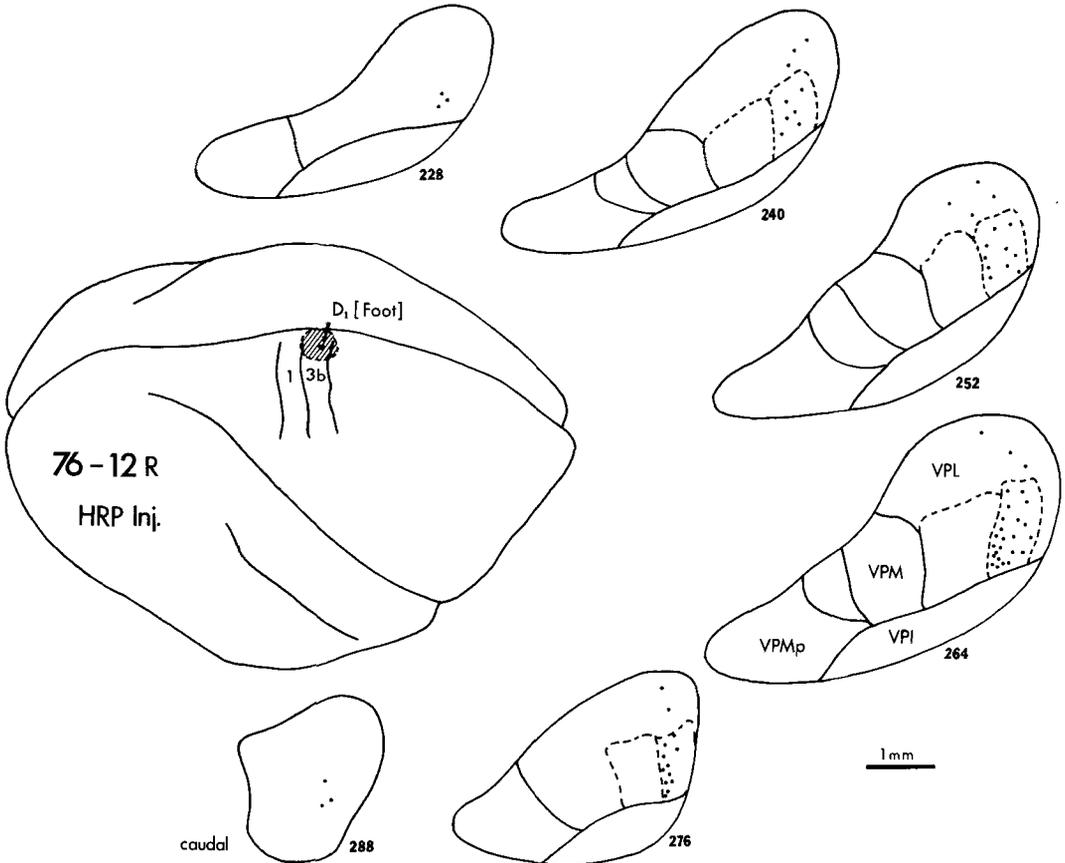


Fig. 6 The distribution of labeled neurons after an injection of HRP into the Area 3b representation of the glabrous surface of the great toe. Conventions as in figure 2.

examples are shown. In Case 76-11L (fig. 7), an Area 1 injection was in the representation of the hairy skin of the dorsum of the second digit of the hand. The label spread to the representations of the adjoining digits and part of the palm. The adjacent part of Area 2 was also affected. HRP-positive neurons were found in a 0.2-0.3 mm wide, 1.8 mm high, and 1.8 mm long slab in subnucleus a of VPL. Almost the complete rostrocaudal extent of VPL was labeled, and the most densely labeled region included about 60% of neurons (fig. 3). A few scattered HRP-positive neurons were also in subnucleus c. Thus, as with Area 3b injection, the label of subnucleus a of VPL follows the placement of HRP in the representation of the digits of the hand in Area 1.

In a second case (76-12L; fig. 8), an injection was placed in the part of Area 1 representing the base of the great toe. The HRP

spread to involve the representation of other digits, the sole of the foot, and perhaps part of the leg. The margins of the cortical label extended to the borders and possibly minimally involved Areas 3b and 2. Most of the labeled neurons in VPL were in subnucleus b with a few in subnucleus c. Thus, subnucleus b appears to project to the part of Area 1 representing the foot.

Since Area 1 and Area 3 injections corresponding to the same body part label similar regions in VPL, further information concerning the topological relation of VPL to cortex could be gained by injections including comparable parts of both Area 1 and Area 3b. In Case 76-10R (fig. 9), two injection sites were placed at the Area 1 border with Area 3b so that both areas were involved. One injection involved the representation of the foot in both Areas 1 and 3b, and the other injection spread

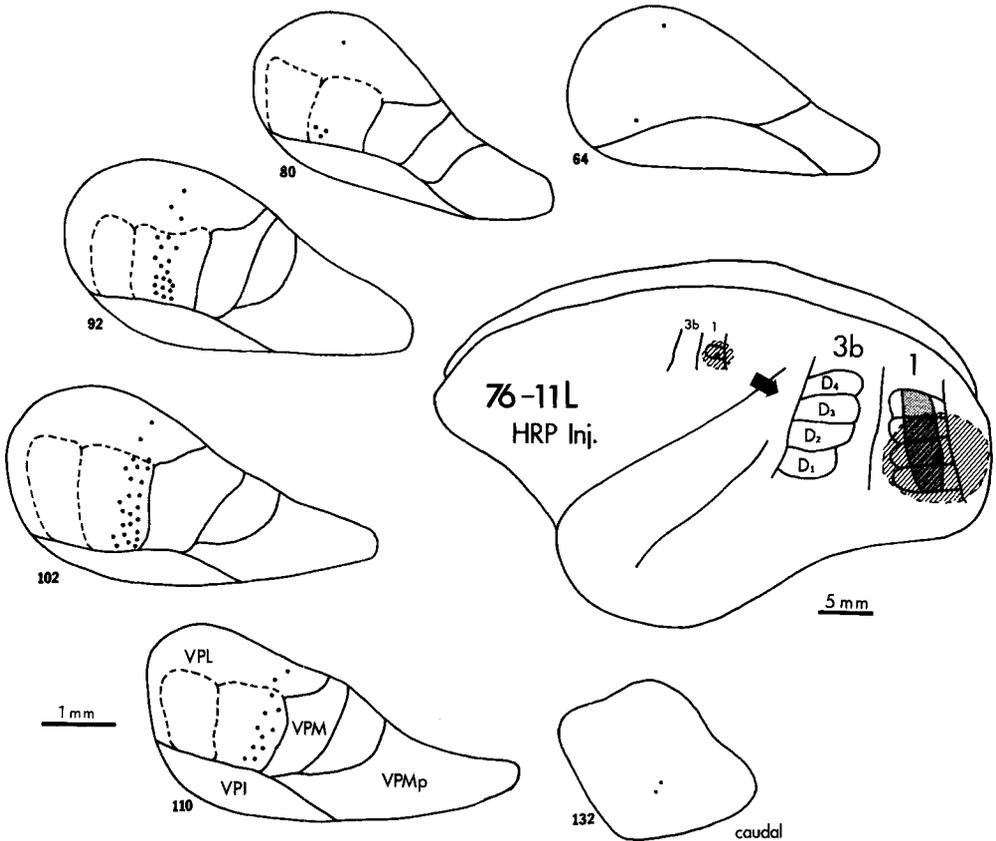


Fig. 7 The distribution of labeled neurons after an injection of HRP into the Area 1 representation of the second digit of the hand. Conventions as in figure 2.

to include both representations of the arm. For comparison, a third injection was confined to the region of the hand in Area 3b. As expected, labeled neurons were found in three distinct slabs in VPL. Thus, adjoining parts of Areas 3b and 1 do not appear to relate to separate slabs. Judging from previous cases (figs. 4, 5), the aggregation of labelled cells in subnucleus a was a result of the injection into the part of Area 3b representing the hand. Other cases (figs. 6, 8) indicate that the slab of cells in subnucleus b can be accounted for by the injection involving the foot region of both Area 1 and Area 3b. By the process of elimination, the slab of labeled cells in subnucleus c must be a consequence of the injection in the arm representations in Area 1 and 3b. These results suggest that single arrays of neurons in VPL project to corresponding body surface representational sites in Areas 1 and 3b. Also note that the zone of label in subnucleus c is

restricted in the rostrocaudal dimension compared to the zones in subnuclei a and b. This suggests that the arm representation occupies less of the length of the nucleus than the hand and foot representations.

6. Reciprocal projections from cortex

In some of the cases of injection of HRP into Areas 1 and 3b, ³H-proline was mixed with the HRP. These experiments demonstrated reciprocal connections between Area 3b or Area 1 with VPL. Three cases are shown.

In cases 76-9 (fig. 5) and 76-10L (fig. 4), combined injections were in the hand region of Area 3b. In each case, the resulting band of silver grains, indicating cortico-thalamic terminations, was in subnucleus a of VPL. The zone of silver grains was somewhat more extensive than the zone of cells labeled with HRP, suggesting that the cortical region of uptake of ³H-proline was larger than for HRP,

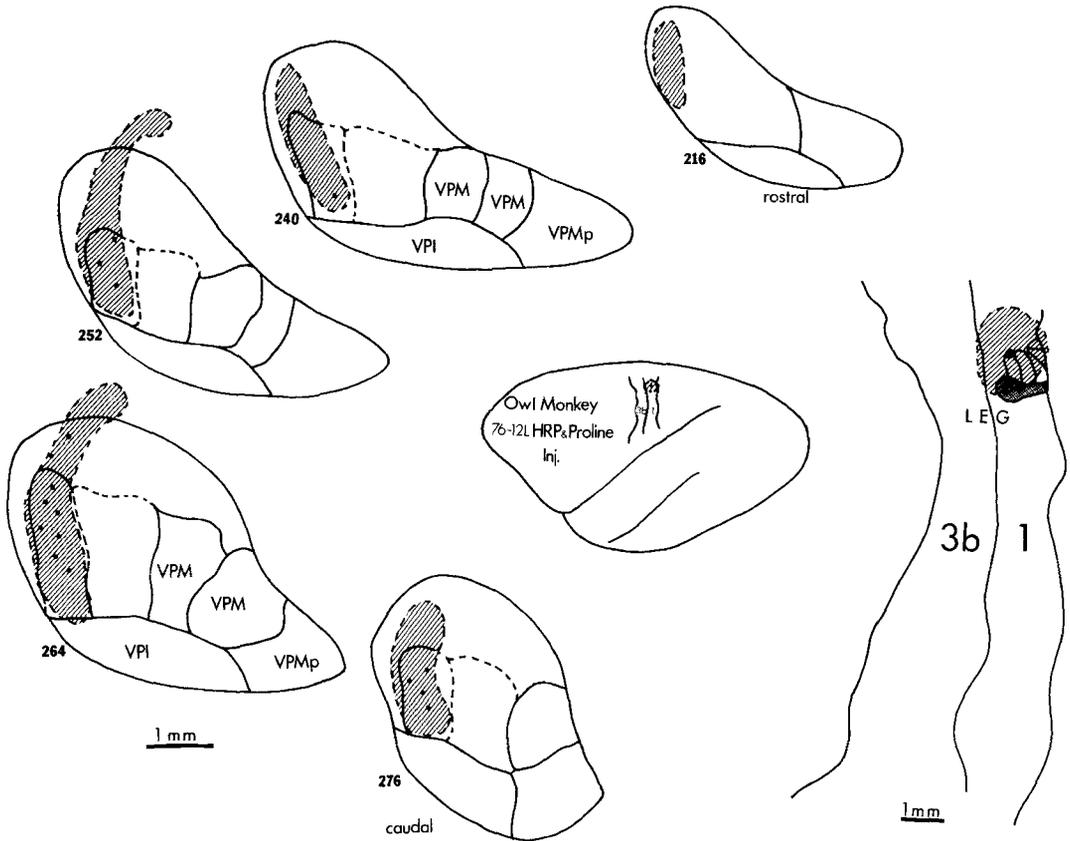


Fig. 8 The distributions of HRP-labeled neurons and silver grains after an injection of ^3H -proline and HRP into the representation of the great toe in Area 1. Conventions as in figures 2 and 4.

that thalamic cells lightly labeled with HRP were not detected, or that the cortico-thalamic projections are more diffuse than the thalamo-cortical projections. These two cases also labeled the dorsorostral portion of the posterior complex with silver grains. In a third case, ^3H -proline was combined with HRP in an injection within the region of representation of the digits of the foot in Area 1 (figs. 8, 12D). Silver grains were located in a zone including, and somewhat more extensive than, the zone of HRP labeled cells. The zone of silver grains was in subnucleus b and the lateral part of subnucleus c. Thus, both Area 1 and Area 3b appear to be reciprocally connected with VPL.

7. Projections to the caudal representation of deep body structures

Microelectrode mapping experiments revealed a systematic representation of deep body structures in cortex caudal to Area 1

(Merzenich et al., '78). In width, cytoarchitecture and location, this representation appears to correspond to Area 2 and perhaps part of Area 5 of Brodmann ('09). In case 76-14, an injection of HRP was placed in the portion of this representation that was found to respond to movement of the arm at the shoulder girdle (fig. 10). The cortical spread of HRP appeared to be confined to the "deep body" representation and did not extend into Area 1. Many labeled neurons were found in a restricted region of the thalamus just dorsal to VP (figs. 10, 12E). A few labeled neurons were also seen within the caudal aspect of the centrolateral nucleus. No labeled neurons were found in VP as defined here.

DISCUSSION

The present anatomical investigation is based on our reinterpretation of the organization of somatosensory cortex in primates. Pre-

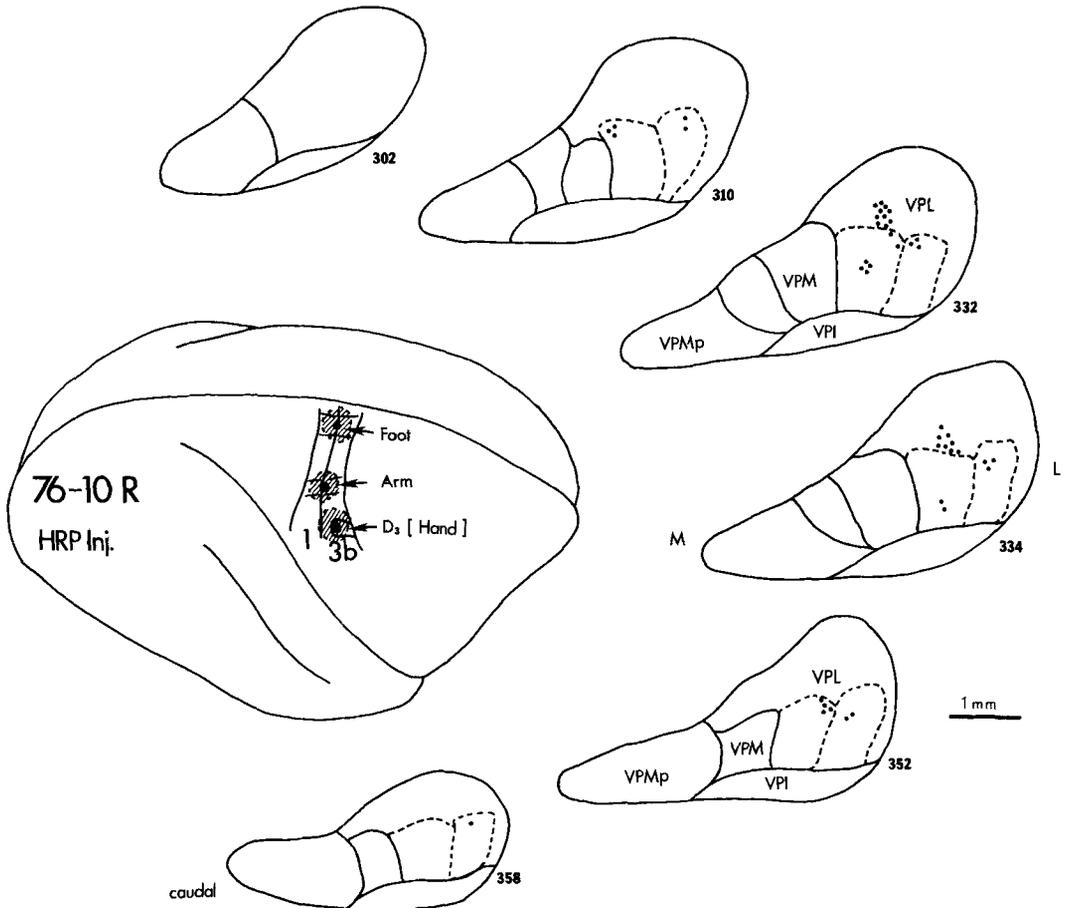


Fig. 9 The distributions of labeled neurons after injections of HRP into the representations of the glabrous surface of the proximal phalanx of the third digit in Area 3b, the arm at the Area 3b-Area 1 border, and the foot at the Area 3b-Area 1 border. Conventions as in figure 2.

viously, several architectonically distinct regions (usually Areas 3a, 3b, 1, and 2) were included in a single functional division of cortex, the first somatic area (SI) (see Merzenich et al., '78, for review and references). The organization of "SI" in primates has been defined in different ways by different investigators. The traditional hypothesis was that a single systematic and somatotopic representation of the contralateral body encompassed the four architectonic zones. Thus, no architectonic zone would include all body parts. Another view was that each body part was "represented" in a band extending across all four architectonic zones, a view that has been difficult to reconcile with the extensive evidence for regional somatotopy within "SI." Other theories combined aspects of both of these out-

looks in that a predominantly single body representation was partially replicated in the different architectonic zones. We have argued that both Area 3b and Area 1 have complete and separate representations of the body surface, and therefore must be considered as distinct subdivisions of somatosensory cortex (Merzenich et al., '78; Kaas et al., '76, '78; Nelson et al., '78; Sur et al., '78). Also, Areas 3a and 2 appear to be additional representations of the body devoted primarily to receptors in deep body tissues. Of course, the questions generated with regard to the connections of somatosensory cortex differ according to viewpoint. Previously, a major interest was in how "SI" or parts of "SI" connected with other subdivisions of the brain. We now ask how the different and distinct body repre-

sentations in the parietal somatosensory strip interconnect with other parts of the somatosensory system. Many useful studies are possible. This report was limited to a description of the connections of SI proper (Area 3b) and the posterior cutaneous field (Area 1) with the ventroposterior nucleus (VP) of the thalamus. While the connections of the architectonic fields 3b and 1 with VP have been studied (Clark and Powell, '53; Jones and Powell, '70; Jones, '75; Jones and Burton, '76), the connections of known body parts in the two representations have not. Finally, we have made preliminary observations on the possible thalamic source of input to the posterior representation of deep body receptors. Our basic conclusions stemming from the present studies are reviewed below and related to previous findings in primates.

1. *Aggregations of cells in VP project to homotopic body part locations in SI proper (Area 3b) and the posterior cutaneous field (Area 1).*

Our major result (shown schematically in fig. 11) is that injections into the representation of the same body part in the two cutaneous fields label columns or slabs of cells in the same region of VP. Furthermore, comparison of the two cortical somatosensory maps in the owl monkey (Merzenich et al., '78) with the maps of VP in other primates (Pubols, '68; Mountcastle and Henneman, '52; Loe et al., '78) indicate that these thalamocortical projections connect similar body regions in the two cortical and the thalamic representations. While it is well established that VP projects to both Areas 3b and 1 (Clark and Powell, '53; Jones, '75; Jones and Burton, '76) the conclusion that single slabs of cells project to homotopic locations in the two cutaneous representations could only have been appreciated after the two representations were disclosed.

Injections of HRP into restricted locations in either Area 3b or Area 1 result in columns or slabs of labeled cells that are usually narrowest in the mediolateral plane, of intermediate size in the dorsoventral plane, and longest in the rostrocaudal plane. Thus, it is reasonable to conclude that many restricted skin locations are represented in cell aggregates with a predominantly rostrocaudal orientation. However, it is unlikely that single restricted body surface locations are repre-

sented across the full extent of the nucleus, and some body parts, the arm for example, appear to occupy only limited extents of the nucleus. This proposed organization is generally consistent with concepts of the generalized organization of VP in mammals (Welker, '73; Welker and Johnson, '65), and with the conclusions of most of the electrophysiological mapping studies (Mountcastle and Henneman, '52; Poggio and Mountcastle, '63; Pubols, '68), and with the results of retrograde degeneration studies (Clark and Powell, '53; Jones and Powell, '70; Krishnamurti et al., '72) conducted in primates. However, a predominantly dorsoventral orientation of isorepresentation slabs is suggested by patterns of retrograde label after HRP injections in somatosensory cortex of macaque monkeys (Jones and Leavitt, '74; Kievit and Kuypers, '75; Loe et al., '75; Strick, '76; Pearson et al., '78; Whitsel et al., '78) as well as by a recent electrophysiological mapping study of VP in macaque monkeys (Loe et al., '78). Perhaps, the orientation of VP is somewhat rotated in macaque monkeys as compared to owl monkeys. Another possibility is that the complete dorsoventral columns of label in VP of macaque monkeys are the result of injection sites including more body parts. In the owl monkey, an injection site including much of the foot representation and part of the leg representation labeled the full dorsoventral extent of VP (fig. 8), while an injection largely within the representation of the glabrous digits labeled an aggregation of cells in the ventral half of VP (fig. 4). Such results lead us to believe that in the owl monkey the dorsoventral dimension of the labeled slabs in VP increases with the spread of the injection site.

There is an important implication for the development of sensory systems inherent in the conclusion that there is a single representation of the body surface in VP which provides input to two body surface representations in somatosensory cortex with many very different features in their specific patterns of representation of the skin. To cite one of the

Fig. 10 The distribution of labeled neurons in the presumptive nucleus ventralis intermedius, VI (see text), after an injection of HRP into the representation of the shoulder and arm in the posterior representation of "deep" receptors. CM, centrum medianum; LGN, lateral geniculate nucleus; PG, pregeniculate nucleus; VL, ventral lateral nucleus; LD, lateral dorsal nucleus; LP, lateral posterior nucleus; R, reticular nucleus; ZI, zona incerta. Other conventions as in previous figures.

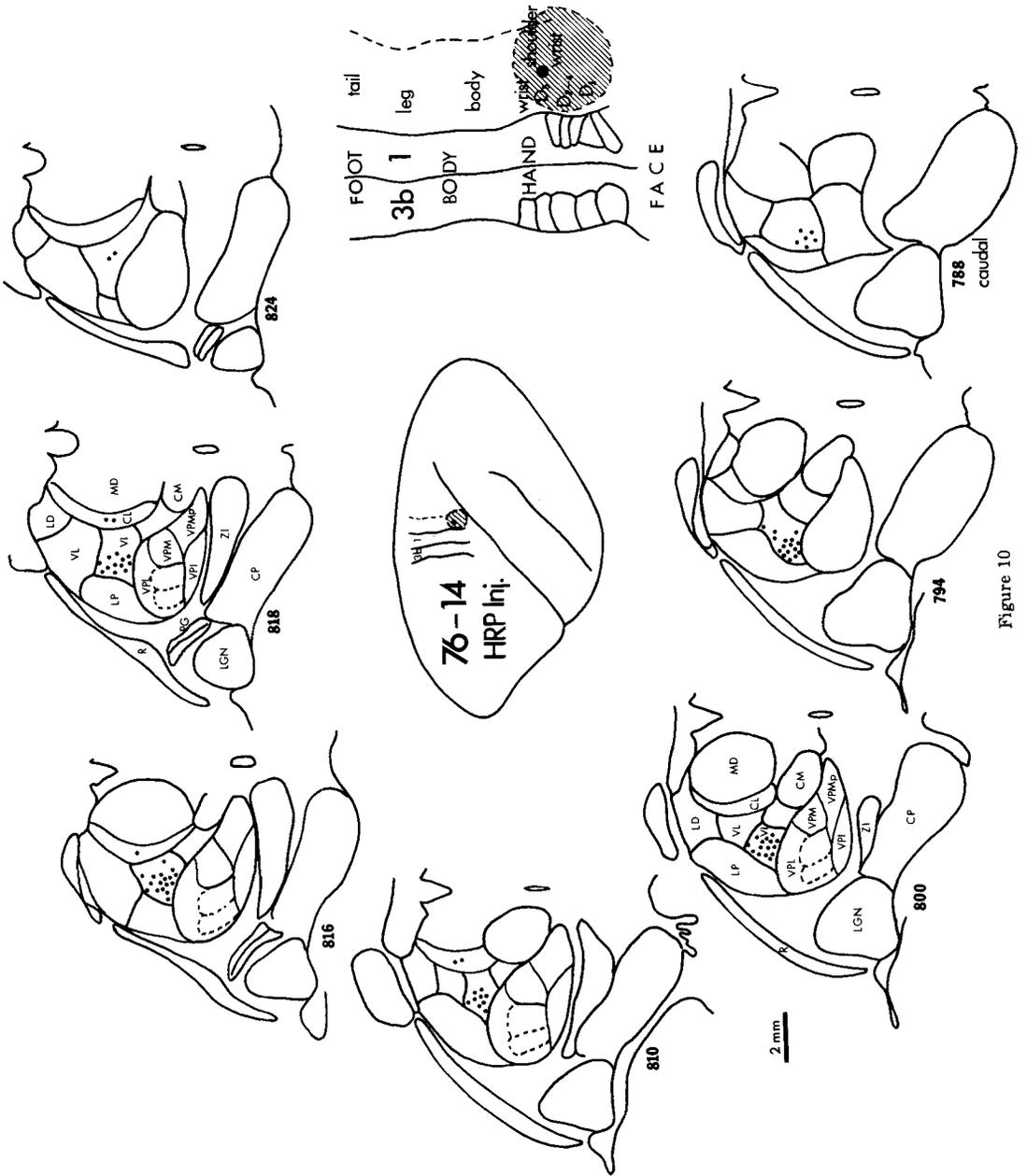


Figure 10

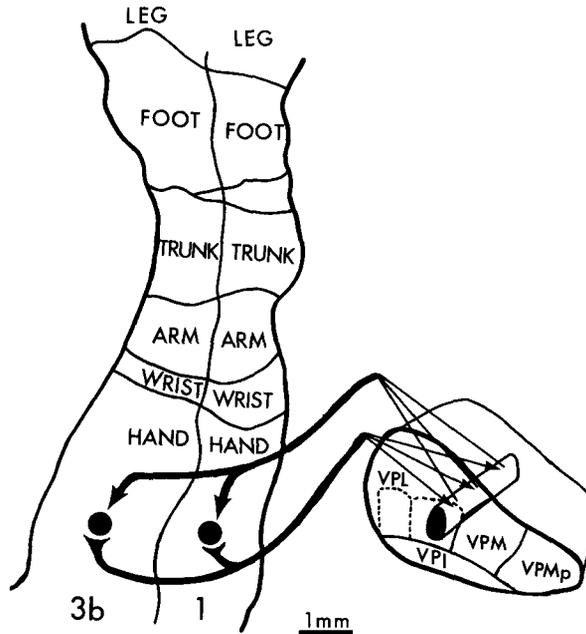


Fig. 11 A diagrammatic summary of conclusions. Separate loci corresponding to the same body part in the Area 3b and Area 1 cutaneous representations are reciprocally interconnected with a slab of cells in VP.

many examples (Merzenich et al., '78), the pattern of representation of the hairy and glabrous surfaces of the hand are very different within Area 3b and Area 1. Thus, the different destinations of separate and partially collateral axons from the overlapping neuronal populations in VP must be specified for each cortical field. The differences in connections cannot be explained by any developmental scheme in which there is some simple geometric and serial establishment of connections from VP to the two cortical fields.

2. Some neurons in VP project to both cutaneous representations

Since over half of the neurons were labeled in the same region of VP following either a restricted Area 3b or a restricted Area 1 injection, we conclude that some neurons in VP project to both cutaneous fields. Clark and Powell ('53) earlier noted the proportions of degenerated neurons after separate lesions of Area 3 or Area 1 and also concluded that neurons in VP project to both fields. The exact percentage of cells projecting to either area is difficult to determine from the present experiments, since the HRP injections were small in an attempt to limit the cortical spread of the

label. It is likely, therefore, that we never maximally labeled any sector of VP. Our present observations suggest that as many as one-third of the neurons in VP project to both cutaneous fields. However, it also appears that significant populations of neurons in VP project exclusively to one or the other of these two fields.

While the results suggest that the inputs to neurons in Areas 3b and 1 are partly from the same neurons in VP, the organization of the projections from VP to the two areas are likely to be fundamentally different. This conclusion is supported by at least two types of evidence. First, Paul et al. ('72b) noted earlier that the ultimate convergence of input from primary afferents to cortical "columns" was much greater to Area 1 than to Area 3b. They examined the consequences of nerve section and regeneration on the reorganization of Area 3b and Area 1 hand representations in the macaque monkey. They found that from two to seven receptive fields could be defined for all neurons within any vertical penetration into Area 1, while neurons within Area 3b usually had only one (often displaced) receptive field. We have recently repeated these experiments on owl monkeys, and likewise have

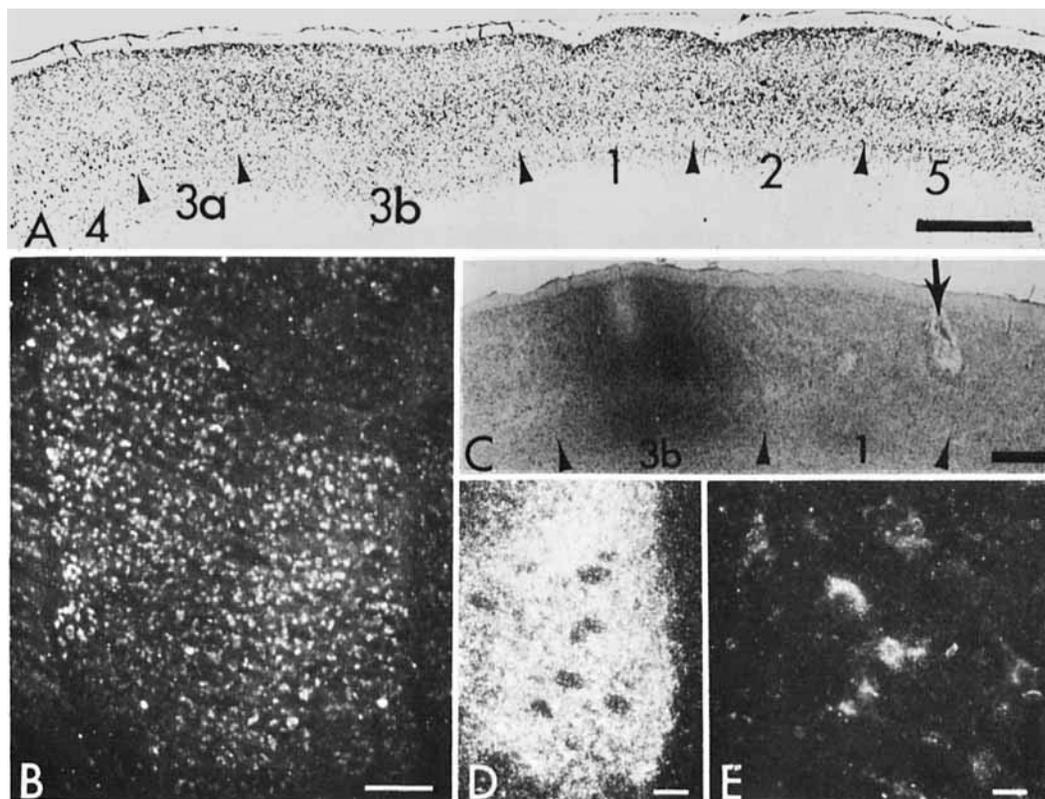


Fig. 12A A parasagittal brain section showing cytoarchitectonic areas in the owl monkey. Marker bar = 1 mm.

B A darkfield photomicrograph of neurons labeled with HRP in subnucleus a of VPL after injections in Areas 3b and 1 in owl monkey 76-11R (fig. 2). Marker bar = 0.25 mm.

C A parasagittal brain section showing the injection site in Area 3b of owl monkey 76-9 (fig. 5). The borders of Areas 3b and 1 are marked. An arrow indicates an electrolytic lesion made at the caudal border of the posterior cutaneous field as defined by electrophysiological mapping methods. Marker bar = 0.5 mm.

D A darkfield photomicrograph of silver grains in subnucleus b of VPL of owl monkey 76-12L after an injection into the foot representation in Area 1. The sharp border of silver grains on the right corresponds with the border with subnucleus a (section 264, fig. 8). Marker bar = 0.25 mm.

E Scattered neurons labeled with HRP in a darkfield photomicrograph of VI after an injection in the posterior representation of "deep" receptors in owl monkey 76-14L (fig. 10, section 800). Marker bar = 25 μ .

found a greater average number of distinctly separate receptive fields for Area 1 than Area 3b neurons. The greater number of separate receptive fields suggest that the projections to Area 1 are more convergent than those to Area 3b. More convergence of thalamic input would also account for the observations that receptive fields are consistently larger for neurons in Area 1 than in Area 3b (Merzenich et al., '78). Second, our finding that neurons in VP were generally more intensely labeled after Area 3b than Area 1 injections is also consistent with the concept that there are basic differences in the projections from VP to the two cutaneous representations.

3. Connections between SI proper and VP and between the posterior cutaneous field and VP are topological and reciprocal

This study demonstrates reciprocal connections between VP and both Areas 3b and 1 using combined anterograde and retrograde tracers. Restricted combined injections of HRP and ^3H -proline in Area 3b or Area 1 labeled overlapping regions of VP. Previous investigations established projections from VP to both Areas 3b and 1 (Jones, '75; Clark and Powell, '53; Jones and Powell, '70; Jones and Burton, '76; Pearson et al., '78; Whitsel et al., '78) and projections from Area 3b and from

Area 1 to VP (Coulter and Jones, '76). In addition, HRP injections in postcentral somatosensory cortex are known to label cells in VP (Pearson et al., '78; Whitsel et al., '78; Loe et al., '75; Kievit and Kuypers, '75; Strick, '76; Jones and Leavitt, '74). Topographic relations indicated by these studies of connections are consistent with the view that VP-Area 3b and VP-Area 1 thalamocortical interconnections are somatotopically reciprocal. Topologically reciprocal thalamocortical connections have also been demonstrated in the visual (e.g., Symonds and Kaas, '78) and auditory (e.g., Colwell and Merzenich, '75) systems.

4. Subnuclei in VP represent major body divisions

Fiber laminae in VP of the owl monkey separate VPM from VPL and also subdivide VPL. The patterns of thalamocortical connections indicate that the ventral subnucleus immediately lateral to VPM (subnucleus a) represents the hand and the laterally adjoining subnucleus b represents the foot. The results also suggest that the dorsal portion of VPL (subnucleus c) represents the trunk and limbs, while the narrow band of cells lateral to the foot (subnucleus d) represents the tail. By default, VPM can be expected to represent the head. Similar subnuclei have been identified and related to body parts in the prosimian, slow loris (Krishnamurti et al., '72), and subnuclei of VP related to body parts have been found in other mammals as well (Welker, '73; Welker and Johnson, '65). In addition, the general somatotopic organization of VP indicated by the present results is consistent with basic mammalian organization (Welker, '73), and conclusions based on electrophysiological mapping (Bombardieri et al., '75; Loe et al., '78) and studies of connections in primates (Roberts and Akert, '63; Benjamin et al., '68; Krishnamurti et al., '72; Jones and Powell, '70; Pearson et al., '78; Whitsel et al., '78).

5. The posterior representation of deep body receptors receives input from neurons outside VP

Area 2 of primates has been repeatedly described as receiving projections from VP (Jones, '75; Jones and Burton, '76; Jones and Powell, '70; Clark and Powell, '53), and there has been no clear evidence for input from other "relay" nuclei (Jones, '75). Our injections of HRP into the posterior representation of deep body tissues in the owl monkey

(Merzenich et al., '78), which is caudal to Area 1 and includes Area 2 and possibly some of Area 5, labeled neurons in a thalamic region dorsal to VP rather than within VP. By position and cytoarchitecture these neurons appear to be within the thalamic regions designated as nucleus ventralis intermedius (VI) by Walker ('38) after the earlier description of Vogt ('09). VI is not always recognized and the region might be considered by other investigators as part of the lateral posterior nucleus or part of what Olszewski ('52) called the oral division of the ventroposterior nucleus. However, the validity of VI as a functionally distinct nucleus is supported by evidence that it receives a somatotopically organized input from receptors located in muscle tissue (Poggio and Mountcastle, '63; Liegren et al., '76). The relay of input from deep receptors from VI is compatible with the responses of neurons in the deep body representation in owl monkeys, and it is tempting to suppose that VI is a major relay nucleus for this representation. However, more extensive studies are clearly needed.

ACKNOWLEDGMENTS

Histological materials were prepared by Laura Symonds. Supported by NSF Grant BNS 76-81824 and NIH Grant NS-10414.

LITERATURE CITED

- Benjamin, R. M., E. Emmers and A. J. Blomquist 1968 Projection of the tongue nerve afferents to Somatic Sensory Area I in squirrel monkey (*Saimiri sciureus*). *Brain Res.*, 7: 208-220.
- Bombardieri, R. A., J. I. Johnson and G. B. Campos 1975 Species differences in mechanosensory projections from the mouth to the ventrobasal thalamus. *J. Comp. Neur.*, 163: 41-64.
- Brodmann, K. 1909 Vergleichende Lokalisationslehre der Grosshirnrinde. Barth, Leipzig.
- Clark, W. E. Le Gros, and T. P. S. Powell 1953 On the thalamocortical connections of the general sensory cortex of Macaca. *Proc. Roy. Soc. (London)*, B, 141: 467-487.
- Colwell, S. A., and M. M. Merzenich 1975 Organization of thalamocortical and corticothalamic projections to and from physiologically defined loci within primary auditory cortex in the cat. *Anat. Rec.*, 181: 336.
- Coulter, J. D., and E. G. Jones 1976 Subcortical projections from cytoarchitectonic fields of the somatic sensory cortex in monkeys. *Soc. Neuroscience Abst.*, 2: 906.
- Cowan, W. M., D. I. Gottlieb, A. E. Hendrickson, J. L. Price and T. A. Woolsey 1972 The autoradiographic demonstration of axonal connections in the central nervous system. *Brain Res.*, 37: 21-51.
- Emmers, R., and K. Akert 1963 A stereotaxic atlas of the brain of the squirrel monkey (*Saimiri sciureus*). Univ. Wisconsin Press, Madison, Wisconsin, 102 pp.
- Jones, E. G. 1975 Lamination and differential distribution of thalamic afferents within the sensory-motor cortex of the squirrel monkey. *J. Comp. Neur.*, 160: 167-204.

- Jones, E. G., and H. Burton 1976 Areal differences in the laminar distribution of thalamic afferents in cortical fields of the insular, parietal, and temporal regions of primates. *J. Comp. Neur.*, *168*: 197-248.
- Jones, E. G., and R. Y. Leavitt 1974 Retrograde axonal transport and the demonstration of non-specific projections to the cerebral cortex and striatum from thalamic interlaminar nuclei in rat, cat, and monkey. *J. Comp. Neur.*, *154*: 349-378.
- Jones, E. G., and T. P. S. Powell 1970 Connections of the somatic sensory cortex of the rhesus monkey. III. Thalamic connexions. *Brain*, *93*: 37-56.
- Kaas, J. H., M. M. Merzenich, C. S. Lin and M. Sur 1976 A double representation of the body in "primary somatosensory cortex" ("SI") of primates. *Neuroscience Abst.*, *2*: 914.
- Kaas, J. H., M. Sur and R. J. Nelson 1978 Features of somatosensory cortex organization in primates. *Cajal Club, 33rd Annual Meeting*.
- Kievit, J., and H. G. J. M. Kuypers 1975 Subcortical afferents to the frontal lobe in the rhesus monkey studied by means of retrograde horseradish peroxidase transport. *Brain Res.*, *85*: 261-266.
- Krishnamurti, A., R. Kanagasuntheram and W. C. Wong 1972 Functional significance of the fibrous laminae in the ventrobasal complex of the thalamus of slow loris. *J. Comp. Neur.*, *145*: 515-524.
- La Vail, J. H. 1975 The retrograde transport method. *Fed. Proc.*, *34*: 1618-1624.
- Liegren, S. R. C., A. C. Milne, A. M. Rubin, D. W. F. Schwarz and R. D. Tomlinson 1976 Representation of vestibular afferents in somatosensory thalamic nuclei of the squirrel monkey (*Saimiri sciureus*). *J. Neurophysiol.*, *39*: 601-612.
- Loe, P. R., D. A. Dreyer, C. B. Metz, A. Rustioni and B. L. Whitsel 1975 Thalamocortical projections and body representation in the ventroposterior nucleus of the macaque thalamus. *Neuroscience Abst.*, *1*: 126.
- Loe, P. R., B. L. Whitsel, D. A. Dreyer and C. B. Metz 1978 Body representation in ventrobasal thalamus of macaque: a single-unit analysis. *J. Neurophysiol.*, *40*: 1339-1355.
- Lucier, G. E., D. G. Függe and M. Wiesendanger 1975 Responses of neurons in motor cortex and in Area 3a to controlled stretches of forelimb muscles in cebus monkeys. *J. Physiol. (London)*, *251*: 833-853.
- Merzenich, M. M., J. H. Kaas, M. Sur and C. S. Lin 1978 Double representation of the body surface within cytoarchitectonic Areas 3b and 1 in "SI" in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neur.*, *181*: 41-74.
- Mountcastle, V. B., and E. Henneman 1952 The representation of tactile sensibility in the thalamus of the monkey. *J. Comp. Neur.*, *97*: 409-440.
- Nelson, R. J., M. Sur and J. H. Kaas 1978 Multiple representations of the body surface in postcentral parietal cortex ("SI") of the squirrel monkey. *Neuroscience Abst.*, *4*: 556.
- Olszewski, J. 1952 *The Thalamus of the Macaca mulatta*. Karger, Basel.
- Paul, R. L., M. Merzenich and H. Goodman 1972a Representation of slowly and rapidly adapting cutaneous mechanoreceptors of the hand in Brodmann's Areas 3 and 1 of *Macaca mulatta*. *Brain Res.*, *36*: 229-249.
- Paul, R. L., H. Goodman and M. M. Merzenich 1972b Alterations in mechanoreceptor input to Brodmann's Areas 1 and 3 of the postcentral hand area of *Macaca mulatta* after nerve section and regeneration. *Brain Res.*, *39*: 1-19.
- Pearson, R. C. A., P. Brodal and T. P. S. Powell 1978 The projection of the thalamus upon the parietal lobe in the monkey. *Brain Res.*, *144*: 143-148.
- Phillips, C. G., T. P. S. Powell and M. Wiesendanger 1971 Projection from low threshold muscle afferents of the hand and forearm to Area 3a of baboon's cortex. *J. Physiol.*, *217*: 419-446.
- Poggio, G. F., and V. B. Mountcastle 1963 The functional properties of ventrobasal thalamic neurons studied in unanesthetized monkeys. *J. Neurophysiol.*, *26*: 775-806.
- Powell, T. P. S., and V. B. Mountcastle 1959 Some aspects of the functional organization of the postcentral gyrus of the monkey: a correlation of findings obtained in a single unit analysis with cytoarchitecture. *Bull. Johns Hopkins Hosp.*, *105*: 133-162.
- Pubols, L. M. 1968 Somatic sensory representation in the thalamic ventrobasal complex of the spider monkey (*Ateles*). *Brain Behav. and Evol.*, *1*: 305-323.
- Randolph, M., and J. Semmes 1974 Behavioral consequences of selective subtotal ablations in the postcentral gyrus of *Macaca mulatta*. *Brain Res.*, *70*: 55-70.
- Roberts, T. S., and K. Akert 1963 Insular and opercular cortex and its thalamic projection in *Macaca mulatta*. *Schweiz. Arch. Neurol. Neurochir. Psychiat.*, *92*: 1-42.
- Strick, P. L. 1976 Anatomical analysis of ventrolateral thalamic input to primate motor cortex. *J. Neurophysiol.*, *39*: 1020-1031.
- Sur, M., R. J. Nelson and J. H. Kaas 1978 Postcentral somatosensory cortex in macaque monkeys: multiple body representations and neuronal properties. *Neuroscience Abst.*, *4*: 559.
- Symonds, L. L., and J. H. Kaas 1978 Connections of striate cortex in the prosimian, *Galago senegalensis*. *J. Comp. Neur.*, *181*: 477-512.
- Tanji, J. 1975 Activity of neurons in cortical Area 3a during maintenance of study postures by the monkey. *Brain Res.*, *88*: 549-553.
- Vogt, C. 1909 La myeloarchitecture du thalamus du cercopitheque. *J. Psychol. Neurol.*, *12*: 285-324.
- Walker, A. E. 1938 *The Primate Thalamus*. University of Chicago Press, Chicago, Illinois, 319 pp.
- Welker, W. I. 1973 Principles of organization of the ventrobasal complex in mammals. *Brain Behav. and Evol.*, *7*: 253-336.
- Welker, W. I., and J. I. Johnson 1965 Correlation between nuclear morphology and somatotopic organization in ventrobasal complex of the raccoon's thalamus. *J. Anat. (London)*, *99*: 761-790.
- Whitsel, B. L., A. Rustioni, D. A. Dreyer, P. R. Loe, E. E. Allen and C. B. Metz 1978 Thalamic projections to S-1 in macaque monkey. *J. Comp. Neur.*, *178*: 385-410.