

# Representations of the Body Surface in Cortical Areas 3b and 1 of Squirrel Monkeys: Comparisons With Other Primates

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## ABSTRACT

Microelectrode multiunit mapping techniques were used to determine the somatotopic organization of postcentral parietal cortex in the squirrel monkey *Saimiri sciurus*. Recordings were largely confined to architectonic areas 3b and 1. Results were compared to those from similar studies of owl (Merzenich et al., '78) and macaque (Nelson et al., '80) monkeys. As in these previous investigations, separate representations of the body surface were found in areas 3b and 1 of squirrel monkeys. These representations were organized in parallel, so that both proceeded from the tail on the medial wall of the cerebral hemisphere, to the lips and oral cavity on the lateral margin of these areas along the sylvian fissure. The representations were also roughly mirror images of each other so that whatever skin surface was represented rostrally in area 3b was represented caudally in area 1, and similar skin surfaces were represented along the common border. However, the representations were not identical. For example, the split representations of the leg differed so that the distal leg was represented in cortex lateral to that devoted to the foot in area 1 and medial to the foot in area 3b. Remarkably, the representations of some body parts were reversed in orientation in both area 3b and area 1 in squirrel monkeys as compared to owl and macaque monkeys. The face, arm, trunk, and leg representations were all reversed in squirrel monkeys, while the orientations of the hand and foot representations were the same. For example, the dorsal trunk is represented rostrally in area 3b and caudally in area 1 and the ventral trunk is represented at the 3b/1 border in owl and macaque monkeys, while the ventral trunk is represented rostrally in area 3b and caudally in area 1 and the dorsal trunk is represented at the 3b/1 border in squirrel monkeys. These reversals of somatotopic organization in part but not all of the representations in areas 3b and 1 suggest that both fields are divided into sectors where the basic somatotopic orientation is independently determined, that the orientation of some of these sectors is subject to reversal in evolution, and that matching sectors in areas 3b and 1 are not independent in somatotopic organization.

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In a number of papers we have argued that the traditional "S-I" region of monkeys contains four separate representations of the body corresponding to the four classical architectonic fields, areas 3a, 3b, 1, and 2 (Merzenich et al., '78, '81; Kaas et al., '79; '81a,b). Separate mirror-image cutaneous representations were postulated for areas 3b and 1, while area 3a was related to deep body receptors, probably muscle spindles, and area 2 was related to deep receptors, probably muscles and joints, with some cuta-

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neous input as well. Evidence was obtained by microelectrode mapping procedures from New World owl monkeys and Old World macaque monkeys. Detailed maps were obtained only for the two cutaneous representations.

Our experiments on squirrel monkeys were motivated by the desire to demonstrate the existence of the two cutaneous representations in another species of monkey, and to consider species differences in the two representations. Comparisons of owl and macaque monkeys revealed that the organizations of the two representations were basically similar in the two species, but there were certain minor differences. For example, the area 3b and 1 representations of the hand adjoined along the palm in owl monkeys, and largely along the proximal digits in macaque monkeys. Because the area 3b and area 1 representations in a New World monkey and an Old World monkey were so similar, and because the 3b representation in both of these monkeys was very much like the homologous S-I representation in prosimian primates (Sur et al., '80a,b; Carlson and Welt, '80; Krishnamurti et al., '76), we expected the organizations of areas 3b and 1 in the squirrel monkey to be very much like those in owl and macaque monkeys. To our surprise, the results indicated that the representations of a number of body parts in both areas are reversed in somatotopic organization in squirrel monkeys. This dramatic species difference in cortical organization is of special interest because it reveals not only what can change, but also suggests what can not change. Thus, we can start to see what rules are followed in the developmental and phylogenetic constructions of cortical maps and have some information to support suggestions for the mechanisms of constructing cortical maps.

Some of the present results have been briefly presented elsewhere (Nelson et al., '78).

## METHODS

Experiments were performed on 12 adult squirrel monkeys (*Saimiri sciurus*). Methods of animal preparation and recording have been described in detail elsewhere (Merzenich et al., '78; Nelson et al., '80). Briefly, animals were initially anesthetized with ketamine hydrochloride (35 mg/kg, IM) and supplementary doses (1/10 initial dose) of ketamine were given as needed to maintain a surgical level of anesthesia. Body temperature was maintained at 37°C. Somatosensory cortex of one hemisphere was exposed, and silicone fluid held in an acrylic dam was used to cover the brain. The dura was excised and an enlarged photograph of the somatosensory cortex was made and subsequently used to mark electrode penetration sites. Glass coated platinum-iridium microelectrodes (1–2.5 Mohm at 1 kHz) were used to record from single neurons or small neuron clusters. The relatively shallow central sulcus was used to locate somatosensory cortex. Typically, recording sites were spaced 250–350  $\mu\text{m}$  apart. In penetrations that were normal to cortex, usually one receptive field was recorded at a depth of 700–1,000  $\mu\text{m}$ . Receptive field locations were found to be unchanged as a function of cortical depth in such penetrations. In penetrations down the back of the central sulcus or the medial wall, receptive fields were recorded at intervals of 200–300  $\mu\text{m}$ . Receptive fields were determined with fine hand-held glass probes, and were distinguished as cutaneous or noncutaneous. All cutaneous receptive fields were defined as the skin region from which a distinct response was determined with very light

tactile stimulation. These minimal cutaneous fields were drawn on outlines of appropriate body parts. After each experiment, electrolytic lesions (5–10  $\mu\text{A}$ , 5–10 seconds) were made at borders of areas 3b and 1 defined by mapping and at other recording sites of interest. Physiologically defined maps were later correlated with architectonic borders of areas 3b and 1.

Because of the large expanse of responsive cortex and the folding of cortex in the central sulcus, producing detailed maps of the organizations of areas 3b and 1 of somatosensory cortex of the squirrel monkey was a major undertaking. The summary map in Figure 1 is the result of combining partial summaries from individual experiments, and from "unfolding" results from the banks of the central sulcus to produce flattened summaries. In each experiment, the goal was to map completely the separate representations of one or more major body parts in both areas 3b and 1. Several such partial maps were then adjoined in overlap regions to form a single summary map. Thus, the summary map reflects data from several cases, but parts of the map are from individual monkeys, and results from different monkeys are not "averaged" in any way. Individual maps were constructed by associating each recording site with its receptive field location, and enclosing all recording sites with receptive fields on a given body region or subregion by lines. The manner of doing this and the typical densities of recording sites have been shown elsewhere (Kaas et al., '81a; Merzenich et al., '81). For practical reasons, all recording sites and receptive fields for individual experiments are not shown, and only selected points are documented by such data.

The procedures for unfolding recording results from electrode penetrations in the central sulcus have been illustrated previously (Nelson et al., '80). In electrode penetrations that were perpendicular to the cortical surface receptive field positions did not shift with progressively deeper recording sites, and single recording sites were typically made within each penetration within or close to layer IV. In penetrations down the banks of the central sulcus, recording sites were closely spaced, and an effort was made to determine every significant shift in receptive field location. Penetrations were usually made in rostro-caudal rows that were extended in both directions until cortex unresponsive to cutaneous stimuli was encountered.

## RESULTS

Multiunit microelectrode recording techniques were used to map body surface representations in areas 3b and 1 of parietal cortex of squirrel monkeys. As in macaque monkeys (Nelson et al., '80) and owl monkeys (Merzenich et al., '78), each of these cytoarchitectonic fields was found to contain a separate systematic representation of the contralateral body surface. Neurons at recording sites throughout both of these representations were activated by cutaneous stimuli, and no recording sites were activated by only deep receptors. The possibility of inputs from deep receptors is not ruled out, but none were detected.

The border between the separate representations in areas 3b and 1 was revealed physiologically, for the most part by a reversal in the receptive field progressions over a body part, as the electrode moved away from the 3b/1 border. For some body parts, such as the forearm, arm, and leg representations, which are complicated by discontinuities, complete reversals were sometimes evident only after extensive mapping. The border between area 3b and area 3a

was distinguished by a sharp decrease in the activation of neurons by cutaneous stimuli. Neurons could be driven by tapping and moving the body tissue. Much of the input to area 3a was judged to be from deep body tissues, possibly from muscle receptors, but some of the input, particularly in the parts of 3a devoted to the digits of the hand and foot, appeared to be cutaneous. The caudal border of area 1 with area 2 was also distinguished by a sharp change in the nature of the afferent driving. In deeply anesthetized monkeys, area 2 was poorly activated by cutaneous stimuli, although in one or two monkeys, possibly less deeply anesthetized, there was substantial cutaneous driving of neurons in portions of area 2. In these instances, it was apparent that the hand region of area 2 was organized at least roughly as a mirror image of area 1. Typically,

however, restricted cutaneous receptive fields could not be determined for neurons in area 2, and taps on the body and movements and rotations of joints were required to activate neurons. No attempt was made to map either area 2 or area 3a.

The body surface representations in areas 3b and 1 had both basic similarities and striking differences in somatotopic organization with those of owl and macaque monkeys. As in these other monkeys, the sequence of representation in area 3b and area 1 proceeded from tail and gluteal skin medially to the oral cavity laterally. This sequence is summarized in Figure 1 and supported with illustrations of receptive fields for rows of recording sites across areas 3b and 1 for lateral to medial sectors of cortex in Figures 2-8. The figures also demonstrate two impor-

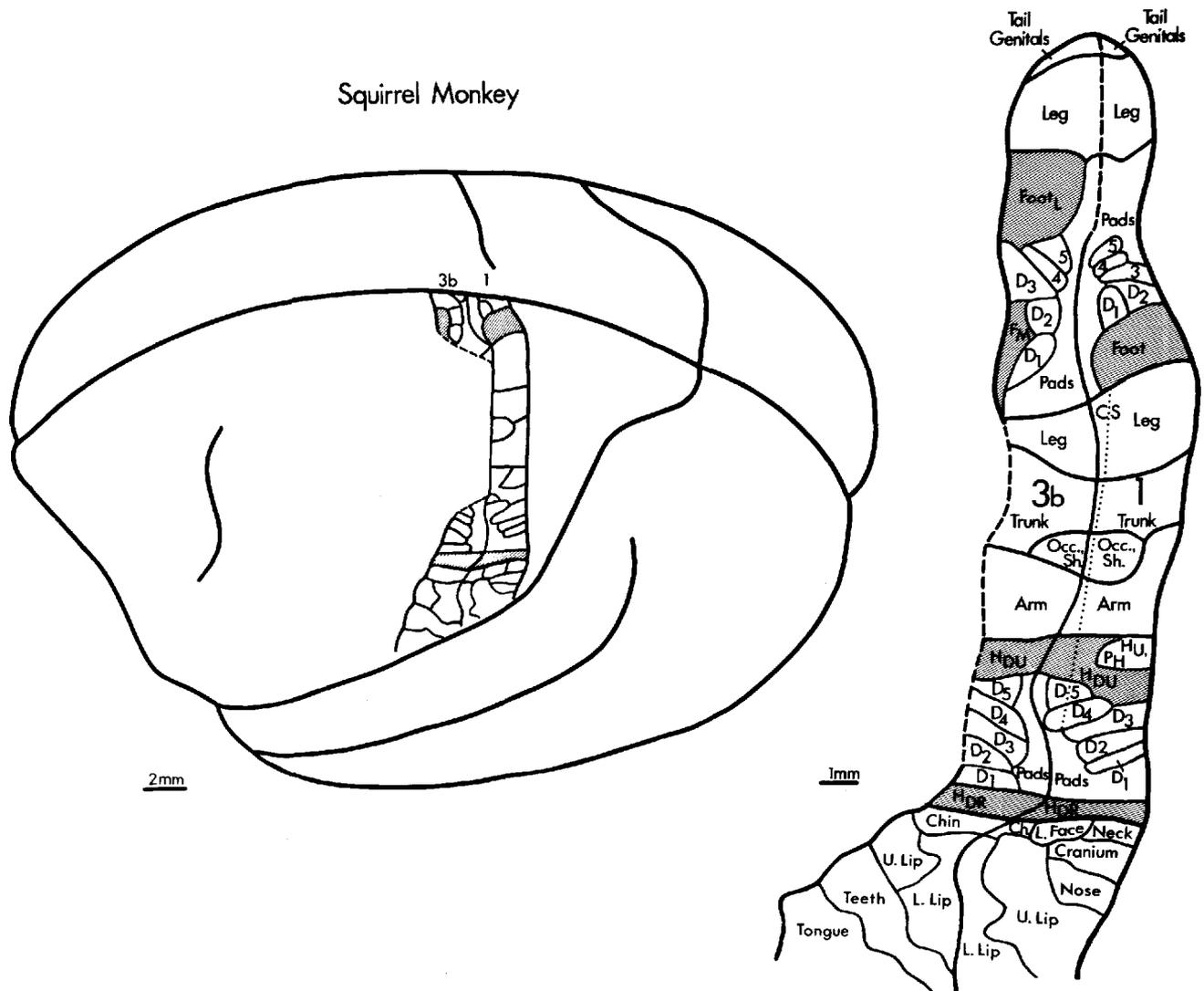


Fig. 1. Separate representations of the body surface in areas 3b and 1 of squirrel monkeys. The location of the representations on a dorsolateral surface view of the brain is on the left. The middle portion of area 3b is buried in the central sulcus. The details of the representation are shown on a flattened view of the surface on the right. Shaded areas correspond to dorsal hairy surfaces of the foot and hand. The dashed line along the rostral border of the 3b representation indicates where the precise margin was not determined because the central sulcus limited the spacing of re-

ording sites. The dashed line between areas 3b and 1 indicates where these fields are on the medial wall of the cerebral hemisphere and architectonic boundaries were estimated. The dotted line (CS) marks the central sulcus. Digits of the hand and foot, D<sub>1</sub>-D<sub>5</sub>, are numbered in order; UL, upper lip; LL, lower lip; Ch, chin; L Face, lateral face; HD<sub>r</sub>, dorsoradial hand; HD<sub>u</sub>, dorsoulnar hand; Occ, Occiput; Sh, shoulder; Fm, medial dorsal foot; Fl, lateral dorsal foot; Leg, hindlimb.

tant aspects of somatotopic organization. First, the illustrated data indicate the crudely mirror-image orientations of the two representations. This mirror reversal of somatotopic organization at the 3b/1 border was also noted in other monkeys, and it appears to be a consistent feature of the two representations. Second, the receptive field progressions reveal the orientations of skin surfaces in the representations. It is apparent from Figure 3, for example, that the glabrous digits surfaces of the hand are pointing rostrally in area 3b and caudally in area 1. It is in the orientation of some, but not all, body parts in the two representations that areas 3b and 1 differ in somatotopic organization in squirrel monkeys from owl and macaque monkeys. These differences in orientation are stressed in the detailed descriptions of the representations of given body parts below.

**The separate representations of the body surface in areas 3b and 1**

The somatotopic organizations of the two separate representations of the contralateral body surface in cortical areas 3b and 1 are summarized in Figures 1, 11, and 12. Figures 2–8 provided more details for the representations of given body regions. The two representations were organized in parallel with a lateral to medial cortical sequence of face, hand, arm, trunk, anterior leg, foot, posterior leg, genital region, and tail. The two representations were matched along the common border and progressed in opposite directions to form crude mirror images of each other. However, the two representations did not exactly mirror each other, and consistent differences in the organizations of the two areas were observed.

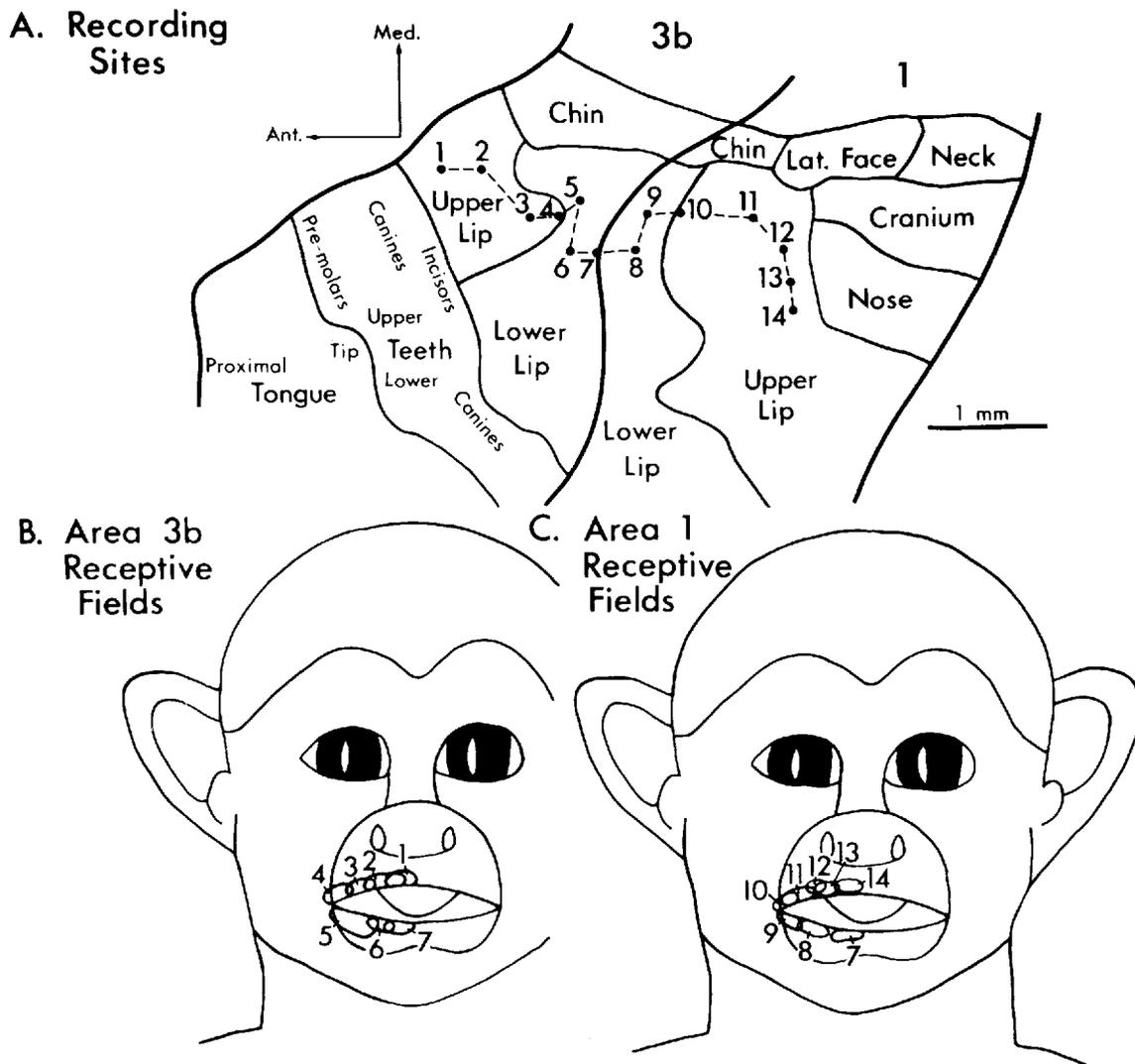


Fig. 2. The representations of the head and face in areas 3b and 1. The regions of cortex where neurons were activated by receptive fields centered on given body parts are outlined. A representative row of recording sites with receptive fields is included. The receptive field progression for re-

coding sites 1–7 is reversed and retraced for recording sites 8–14. Thus, there is a mirror-image organization of the 3b and 1 representations. Note also that the two representations differ. See Figure 1 for the cortical location of the map.

**The face.** The face representations were incompletely mapped (Figs. 1, 2) due to the difficulty in gaining access to this most lateral region of cortex. While the representation of the oral cavity, including the teeth and tongue, was located largely on the dorsolateral surface of the brain for area 3b, the most lateral recording sites in area 1 were related to the lips. There were other obvious differences in the way face parts were represented in the two areas. For example, the neck, lateral face, nose and cranial skin were found caudally within area 1 just lateral to cortex devoted to the hand. However, within area 3b, the neck, lateral face, and cranial skin were represented, at least in part, by large receptive fields centered on the shoulder and occiput in cortex medial to that activated by the hand and arm. A representation of the nose was not found in area 3b, but it is possible that more complete mapping would reveal it.

The map of the face shown in Figure 2 was based on 172 electrode penetrations. Large amounts of cortex in both areas 3b and 1 were devoted to the upper and lower lips. Aspects of the somatotopic organization of this cortex are indicated by the receptive field progression for a rostrocaudal row of recording sites in Figure 2. This progression shows that the midline of the upper lip was rostral in area 3b (penetration 1), and that successively more lateral skin on the upper lip was represented in successively more caudal locations in area 3b until the corner of the mouth was reached (penetration 4). The representation then changed to the lower lip, and the sequence reversed so that the rostrocaudal progression was from the corner of the mouth (penetration 5) to the midline of the mouth (penetration 7). At the 3b/1 border, the sequence of representation reversed, and the progression was from the middle of the

lower lip (penetration 7) to the corner of the mouth (penetrations 9 and 10), and back along the upper lip to the midline of the upper lip (penetration 14). This sequence was seen in all rostrocaudal rows in the cortex activated by the lips in this monkey, and in other monkeys where the face region of cortex was explored. The upper lip was always rostral to the lower lip in area 3b and caudal to the lower lip in area 1. This observation is important, because the opposite arrangement of upper and lower lip representations was found in owl monkeys (Merzenich et al., '78). However, the mediolateral cortical sequence in squirrel monkeys was typical of other monkeys for the lip representations. Thus, the inner parts of the lips were lateral in cortex next to that devoted to the teeth, while the outer lips and adjoining face were related to more medial cortex.

The representation of the teeth in area 3b is of further interest in that the organization of this cortex is not well known for other monkeys. In the cortex indicated in Figure 2, all recording sites were activated by lightly tapping only contralateral teeth. The upper teeth activated cortex rostral to that related to the lower teeth, and the incisors were centered in the cortex with canines and premolars activating cortex rostral and caudal in area 3b. Typically, light taps on only one or two teeth were effective stimuli for a given recording site. Some recording sites were activated by matched upper and lower teeth. Cortex lateral to the teeth representation was devoted to the tongue, with the tongue tip represented next to the teeth.

**The hand.** The hand was found to be represented once in area 3b and again in area 1 in cortex just medial to that devoted to the face. A partial map based on 229 electrode penetrations in the hand and adjoining face regions

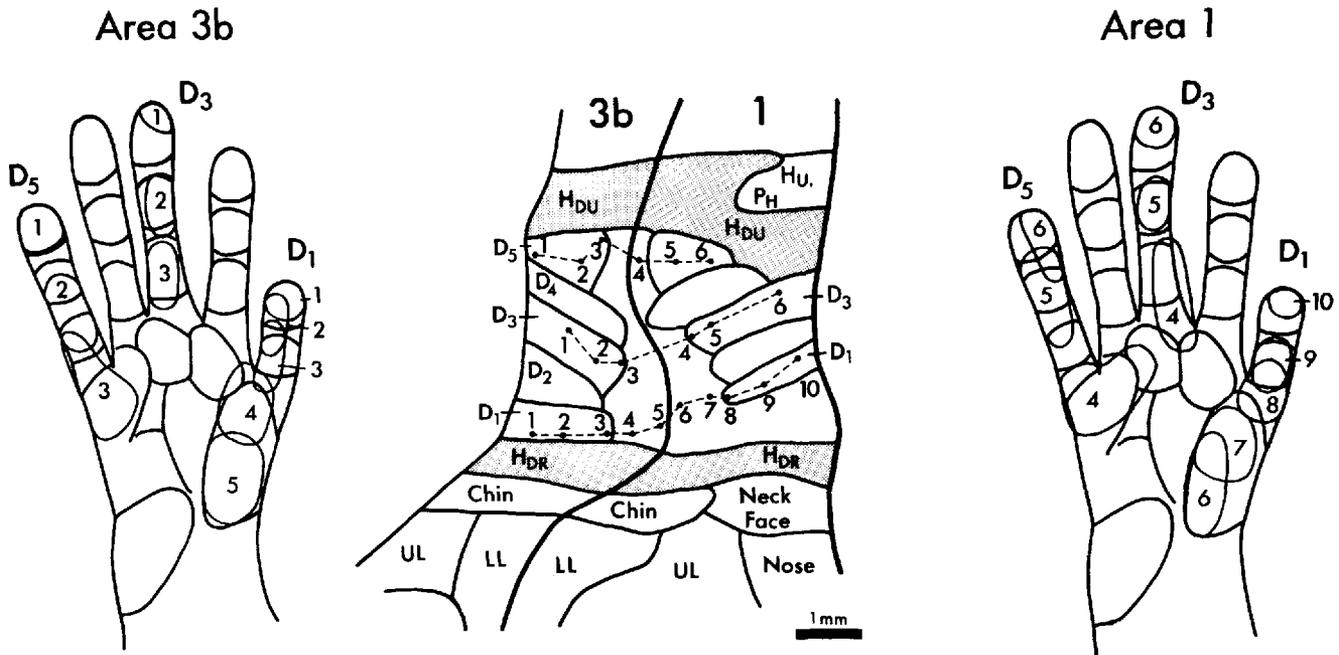


Fig. 3. The hand representations in areas 3b and 1. Receptive fields for three rostrocaudal rows of recording sites are indicated. Cortex devoted to dorsal hairy portions of the digits and hand is shaded and marked H<sub>DR</sub> dorsoradial hand, and H<sub>DU</sub>, dorsoulnar hand. Tissue devoted to each digit

is outlined; other unlabeled cortex represents the palm. The representation of the hypothenar pad, P<sub>H</sub> and adjoining glabrous ulnar hand, H<sub>U</sub>, was displaced caudomedially in area 1 in this case.

of cortex of one squirrel monkey is shown in Figure 3. In this case, a large central region of areas 3b and 1 was devoted to the glabrous surface of the hand, while the hairy dorsum of the digits and hand was split in both fields into the representation of the radial hand dorsum laterally next to the face and the ulnar hand dorsum medially next to the forearm and wrist. The dorsal digits were mostly caudal in area 1 and rostral in area 3b, while the dorsal hand was represented largely near the borders of the areas. Thus, these surfaces were represented twice, once in area 3b and once in area 1.

The glabrous surface of the hand was also represented twice, and the details of this double representation are indicated by receptive field progressions for rostrocaudal rows of recording sites in Figure 3. From these progressions, it is apparent that the digit tips were found rostrally in area 3b and caudally in area 1. The proximal digit surfaces were more caudal in area 3b and more rostral in area 1. Representations of the palm form the common border of the two areas. The mediolateral cortical sequence of representation for both areas was from radial to ulnar across the palm and digits. This was the basic organization

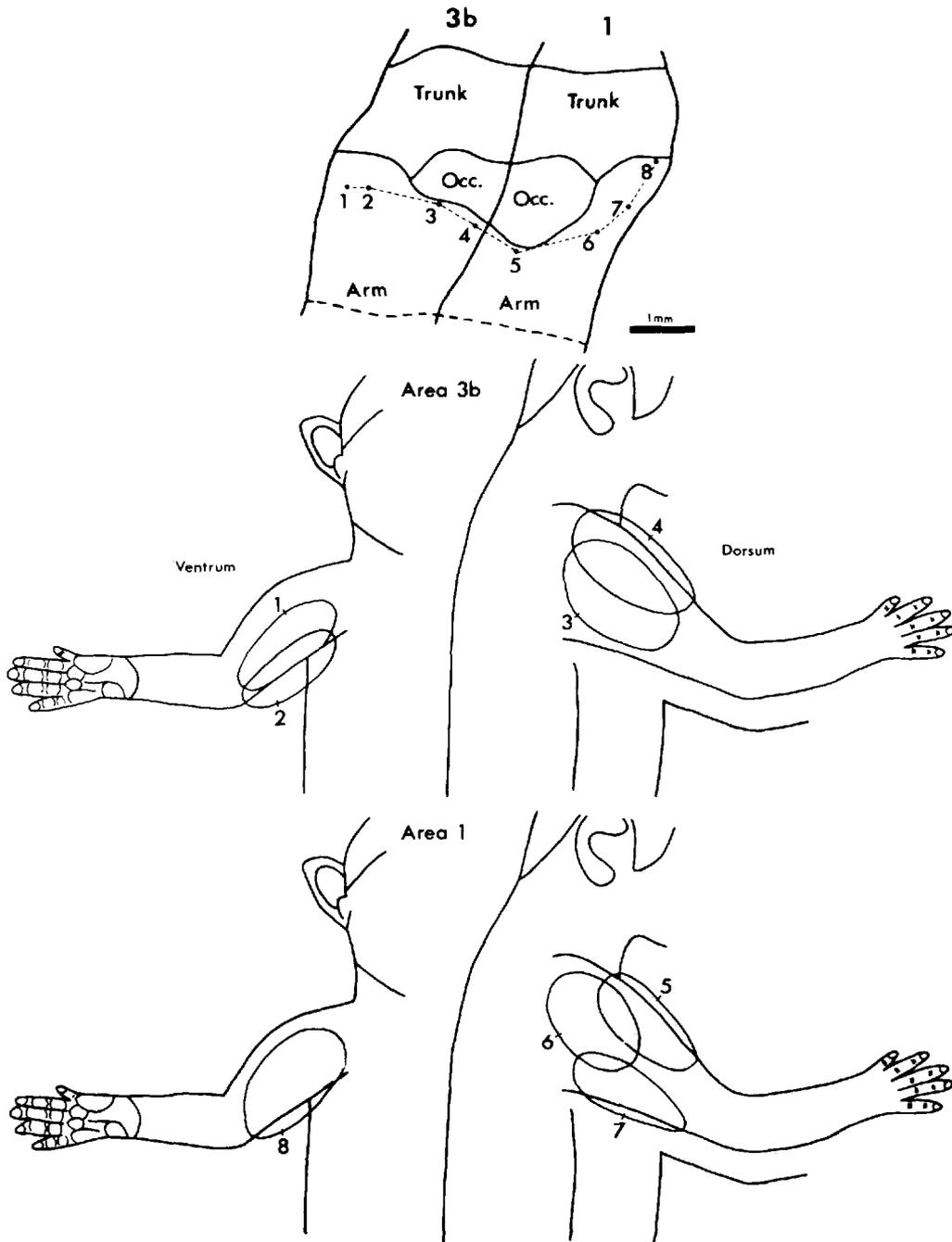


Fig. 4. Receptive fields for a row of recording sites across the representations of the upper arm. Occ., occiput.

found in other squirrel monkeys, although individual variations, especially in the representation of the dorsal hairy surfaces and in the representation of pads, were noted. Also, the relative amount of cortex devoted to various parts of the hand varied somewhat. These variations were studied in a number of monkeys, and they have been described elsewhere (Nelson et al., '80). It is important to note, however, that the basic pattern with the digits pointing in opposite directions in areas 3b and 1 was also found in other species of monkeys.

**The forearm and arm.** All parts of the forearm and arm were represented in cortex medial to that devoted to the hand in areas 3b and 1, and there was no clear evidence for the representation of an anterior strip of arm in cortex lateral to the hand as in S-I of galagos (Sur et al., '80a). The wrist, forearm, and upper arm were represented as if the skin surface were a tube split along the ventral surface and unrolled across area 3b and again across area 1. Thus, the ventral arm was represented along the rostral border of 3b with the upper arm medial and the wrist lateral in

cortex. Caudal progressions of recording sites to the 3b/1 border resulted in progressions of receptive fields from the ventral arm to the posterior arm, to the dorsal arm, and finally to the dorsoanterior arm. A typical example for the upper arm is shown in Figure 4 (penetrations 1-4). A reversed organization was apparent in area 1, where the progression proceeded back to the ventral arm at the caudal border (penetrations 5-8). This somatotopic pattern was seen in all squirrel monkeys explored, and it appears to be reversed in rostrocaudal cortical sequence from that found in owl and macaque monkeys.

**The trunk and occiput.** The representations of the trunk and caudal head in areas 3b and 1 were just medial to cortex devoted to the upper arm. The orientations of the adjoined body parts in the maps allowed for overall continuity. Thus, the representation of the ventral upper arm in rostral 3b merged medially with the representation of the upper ventral chest in area 3b. Caudally in area 3b, the representation of the anterior shoulder merged with cortex related to the upper shoulder, the lateral and dorsal

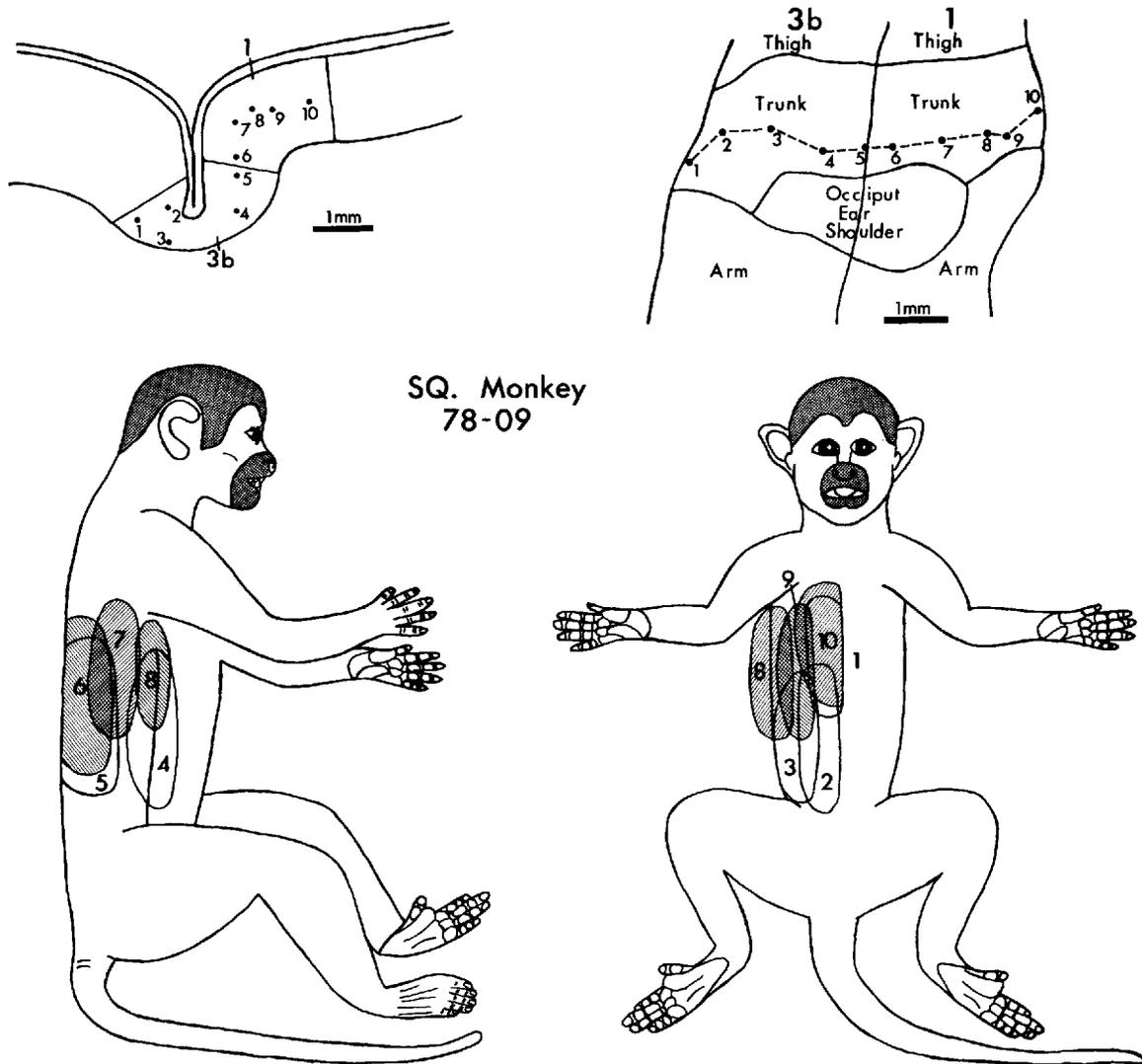


Fig. 5. Receptive fields for a row of recording sites across the representations of the trunk. Recording sites are related to a parasagittal brain section on the upper left and to a flattened summary map on the upper right.

neck, skin around the ear, and cranium. The dorsal midline of the neck and cranium was located along the 3b/1 border. The organization in area 1 was basically the reverse of that in 3b so that the ventral chest was caudal next to the ventral arm in area 1.

The somatotopic sequences in representations of the trunk matched the organization of the cortex devoted to the upper arm, shoulder, and occiput. Thus, as is shown in Figure 5, the midline of the ventral trunk projected to the rostral border of area 3b (penetration 1) and the caudal border of area 1 (penetration 10), while the midline of the dorsal trunk projected to the 3b/1 border (penetrations 5 and 6). The posterior trunk, near the thigh, was represented in more medial cortex and the anterior trunk was repre-

sented in more lateral cortex, so that the pattern of organization was as if the skin of the contralateral trunk were laid out as a continuous sheet, once in area 3b and once in area 1. The orientations of these two representations of the trunk in the rostrocaudal cortical plane were the reverse of the orientations in owl and macaque monkeys.

**The hindlimb.** The representations of the hindlimb in both areas 3b and 1 were split into two portions—a representation of the medial, anterior, and lateral hindlimb in cortex adjoining that devoted to the trunk and lateral to cortex activated from the foot, and a representation of largely the posterior hindlimb in cortex medial to the foot representation. In addition to this split, there was a major

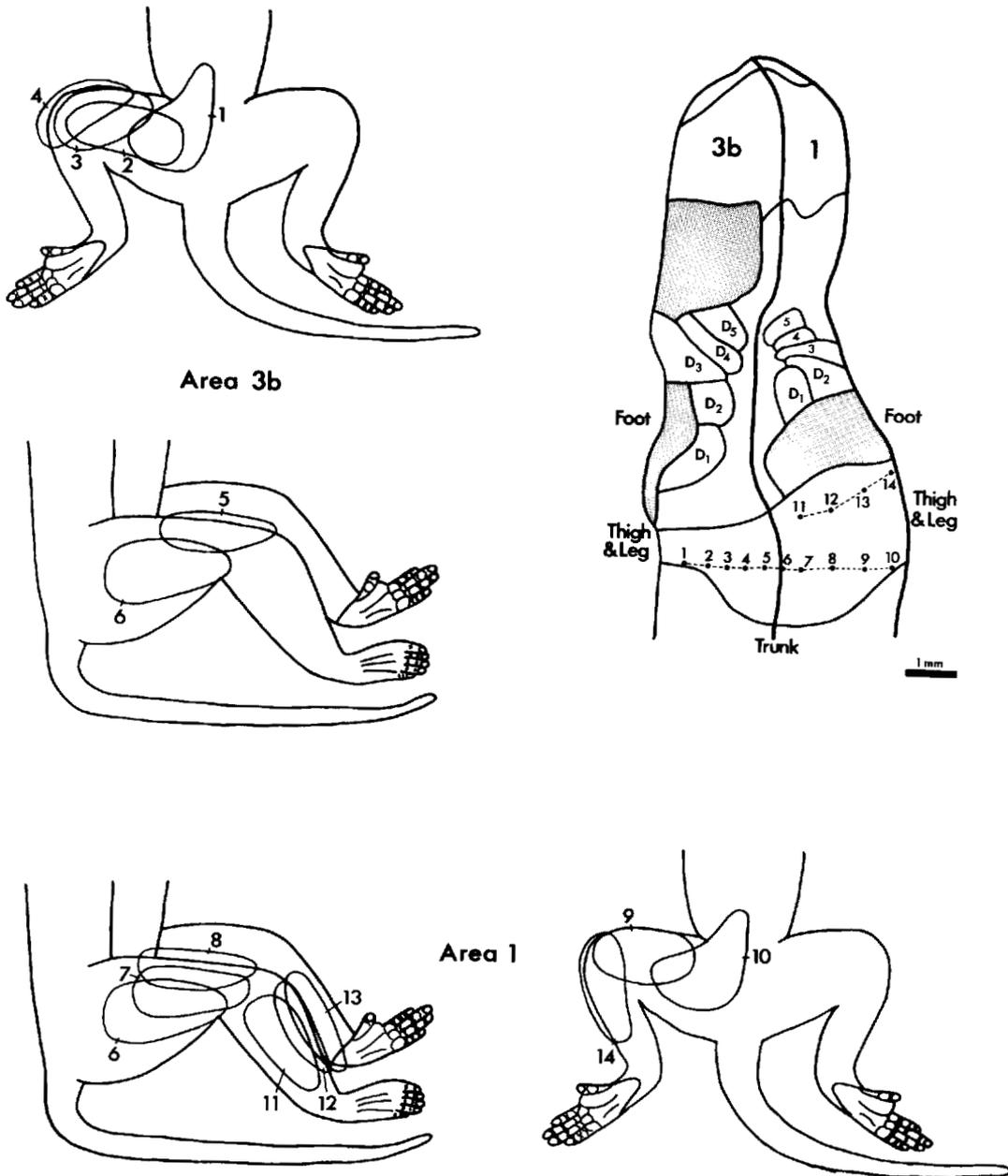


Fig. 6. Receptive fields on the leg for rows of recording sites in cortex lateral to the foot representations. The distal leg (receptive fields 11-14) was found only in area 1.

difference in the way the hindlimb was represented in area 3b and in area 1. Cortex lateral to the foot representation in area 3b contained inputs from only the thigh and proximal hindlimb above the knee, while both the proximal and distal hindlimb were represented in area 1. The cortex medial to the foot representation completed the two hin-

dlimb representations so that the complete distal hindlimb was found in area 3b, while area 1 was limited to the posterior hindlimb.

Receptive fields for recording sites in the lateral representations of the hindlimb are shown in Figure 6. The inner thigh was represented rostrally in area 3b (pene-

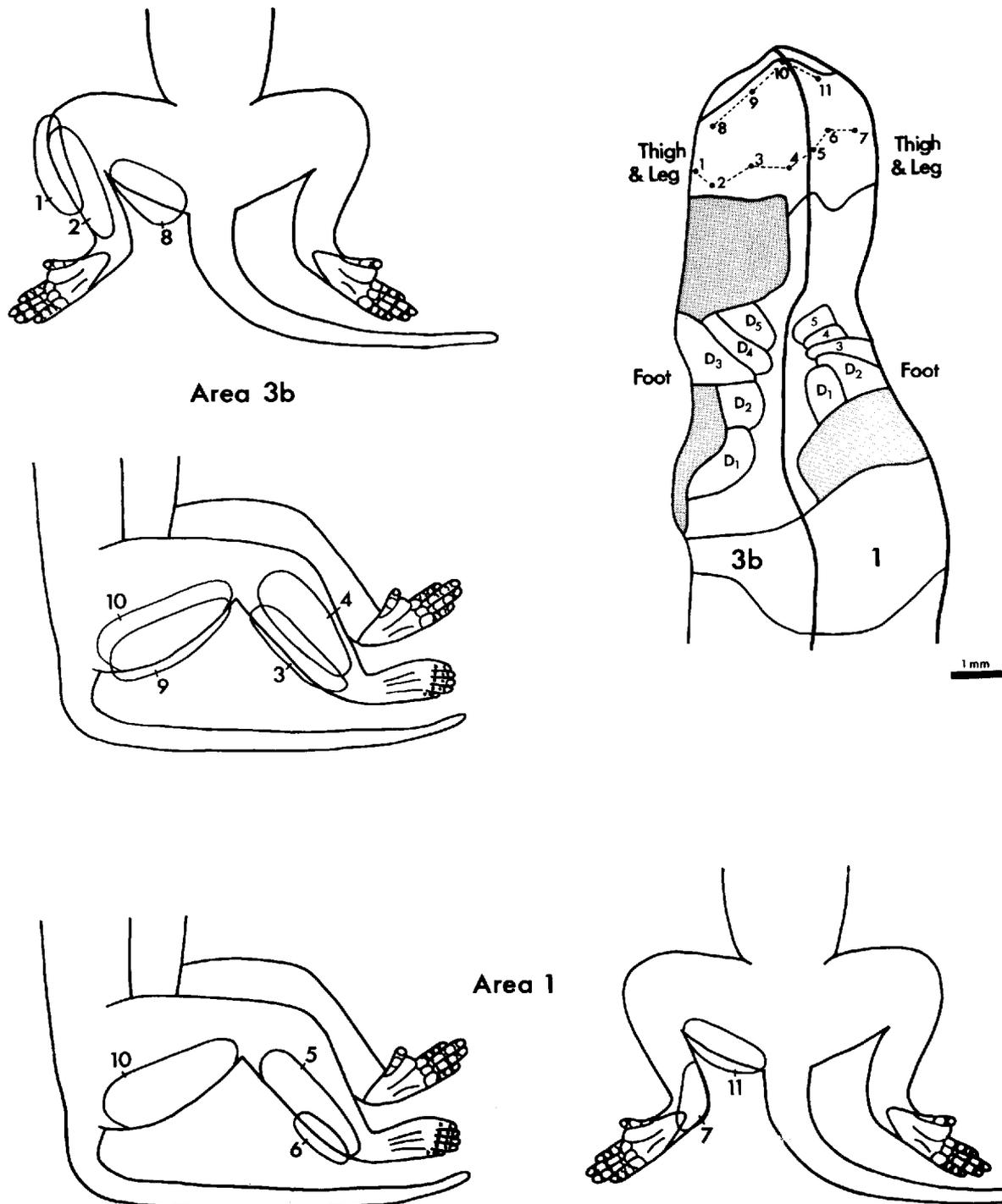


Fig. 7. Receptive fields on the leg for recording sites in cortex on the medial wall of the cerebral hemisphere. On a flattened view of the area 3b and area 1 representations (upper right), the recording sites are in cortex "medial" to that devoted to the foot. Thus, some of the leg is "medial" and some lateral (Fig. 6) to the foot representations.

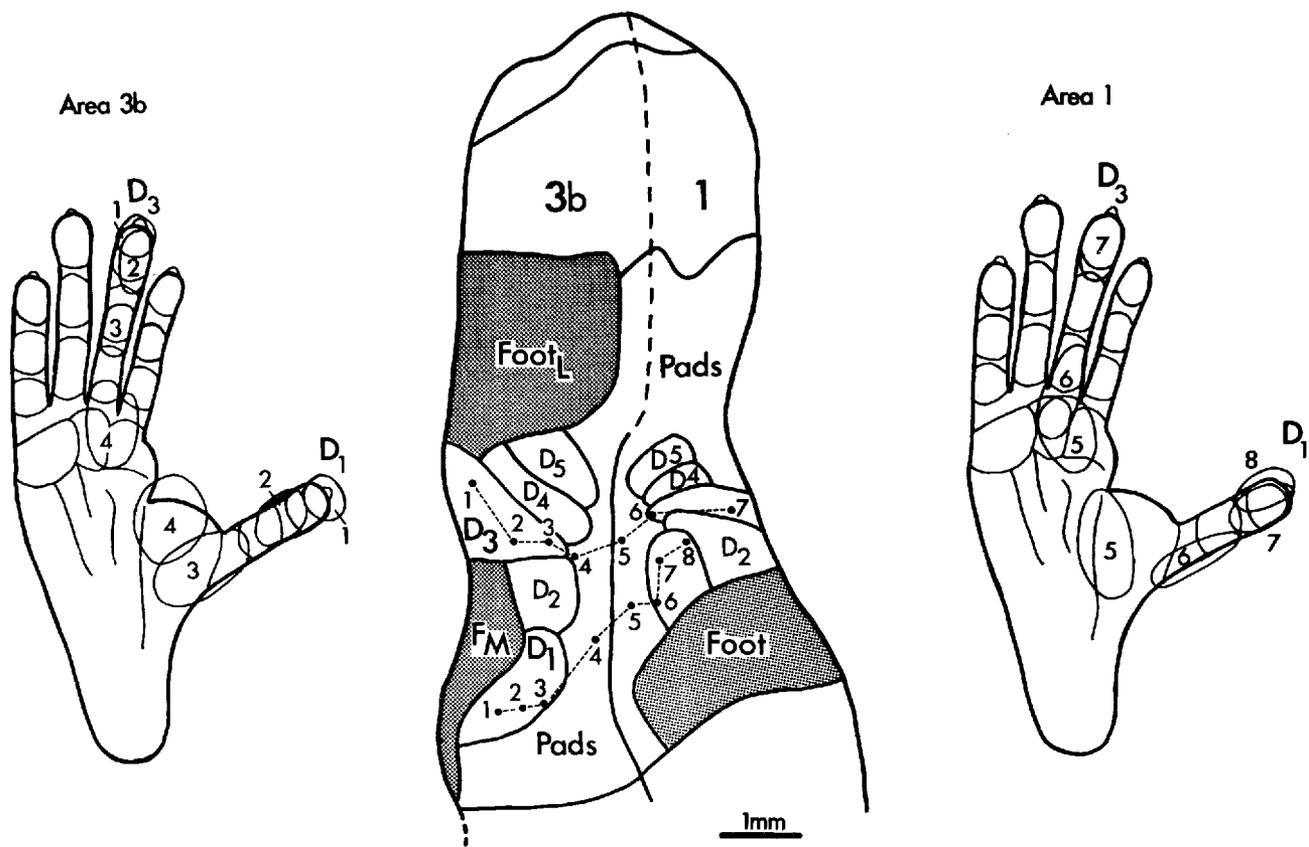
tration 1) and caudally in area 1, thus preserving continuity with the trunk representations. The lateral hindlimb projected to the border region of 3b and 1, with the upper hindlimb lateral in cortex (penetration 6) to the lower hindlimb (penetration 11) in area 1. In cortex medial to the representation of the foot, the lower hindlimb was represented in area 3b from the anterior margin of the hindlimb across the inner surface to the posterior and outer hindlimb in a rostrocaudal cortical sequence (Fig. 7, penetrations 1-4). The more medial representation of the upper hindlimb in area 3b was limited to the posterior thigh (penetration 8-10). The representation in area 1 medial to the foot was limited to the posterior hindlimb with the lower leg closer to the cortex devoted to the foot (penetrations 5-7, 11). The most "medial" cortex on the flattened map, and actually along the medial wall of the cerebral hemisphere, was devoted to the gluteal, genital, and tail regions in both areas 3b and 1.

**The foot.** The representations of the foot in areas 3b and 1 of squirrel monkeys were very much like those found in other monkeys. The glabrous digits were represented from 1 to 5 in a mediolateral cortical sequence in both fields, and the digits pointed in opposite directions so that digit tips were rostral in area 3b and caudal in area 1 (Fig. 8). The proximal digits and foot pads were located near

the 3b/1 border. The medial pads of the foot were in cortex lateral to that devoted to the digits in both fields. The representation of the dorsal foot was split in area 3b so that the medial dorsal foot and the dorsum of digits 1 and 2 were lateral and rostral in the foot region of cortex, while the rest of the dorsal foot was medial. All of the dorsal foot including the digits was lateral to the glabrous digits in area 1.

### The relation of the body surface maps to cytoarchitecture

In all of the experiments, small electrolytic lesions were placed with the recording electrode at selected recording sites, typically at the rostral and caudal borders of the cutaneous representations and at the point of reversal in the two maps. These lesions were always at or very close to the architectonic borders of areas 3b and 1, supporting our contention that the two cutaneous representations are coextensive with the two architectonic fields. Given that the experimental brains were cut in the parasagittal plane, the relation of the mapping results to cytoarchitecture was most obvious for cortex on the dorsolateral surface of the brain. Parts of the two representations on the medial wall and close to the sylvian fissure could not be related with



Squirrel Monkey

77-55

Fig. 8. Receptive fields for rows of recording sites crossing the glabrous foot representation. Foot<sub>L</sub>, lateral foot; F<sub>M</sub>, medial foot. Dorsal areas of the foot are shaded in the flattened reconstruction.

complete assurance to cytoarchitecture in these experiments.

The identifying features of the relevant architectonic fields, areas 3a, 3b, 1, and 2, have been described in some detail for squirrel monkeys by Sanides ('68) and by Jones et al. ('78). These features also are apparent in Figure 9, which shows a parasagittal section of somatosensory and motor cortex in the region of the central sulcus (see Fig. 1) from an experimental brain (77-33) embedded in celloidin and cut at 50  $\mu\text{m}$ . Other experimental brains were cut frozen. In brief, area 3b is most easily identified by a broad layer IV densely packed with cells, and a dense layer VI. At the border with area 1, layer VI becomes much less dense, and layer IV is less broad and less dense. The border between areas 3b and 1 in Figure 9 is marked by a small lesion, which was placed during the recording experiment to mark the border between the two cutaneous representations. Other lesions (not shown) marked the transition from area 3b to area 3a, which is identified by a conspicuous thinning of layer IV. A second lesion in Figure 9 indicates the caudal border of the posterior cutaneous field and the border of area 1 with area 2. Area 2 is distinguished by a slight increase in cell packing density in layers IV and VI.

#### Magnification factors in the maps

It is obvious from the summary illustration that some body parts, such as the lips and hand, have large cortical representations, while others, such as the trunk, do not. The relation between the amount of cortex devoted to any given sector of skin can be expressed quantitatively in terms of area of cortex per unit area of skin. Magnification

factors were determined for the representations of the major body parts in area 3b and area 1 by dividing cortical regions from the summary map (Fig. 1) by measurements of skin surfaces. This procedure does not account for individual differences in the sizes of body parts in different adults and the amounts of cortex devoted to those parts, but these individual differences are small in comparison to the considerable variation in cortical magnification for different body parts.

The calculated magnifications for body parts in area 3b and area 1 are shown in Figure 10. The major conclusions are that the same body parts have similar magnifications in areas 3b and 1, and that there is considerable variation in cortical magnification for different skin surfaces. The small differences between the area 3b and area 1 magnification factors should be considered with caution, since minor errors in measurement could have easily occurred, especially for the extent of representations in the central sulcus. However, the results do show that the representation of the lips and glabrous digits have the greatest magnification, while those of the arm, trunk, and leg have the least magnification. It is of interest that the glabrous hand and foot have similar magnification and that the magnification for the dorsal hand and foot are higher than that for other hairy skin surfaces.

#### DISCUSSION

Microelectrode mapping methods were used to reveal in detail the somatotopic organizations of areas 3b and 1 of postcentral somatosensory cortex in squirrel monkeys. The results led to two major conclusions. First, the concept that

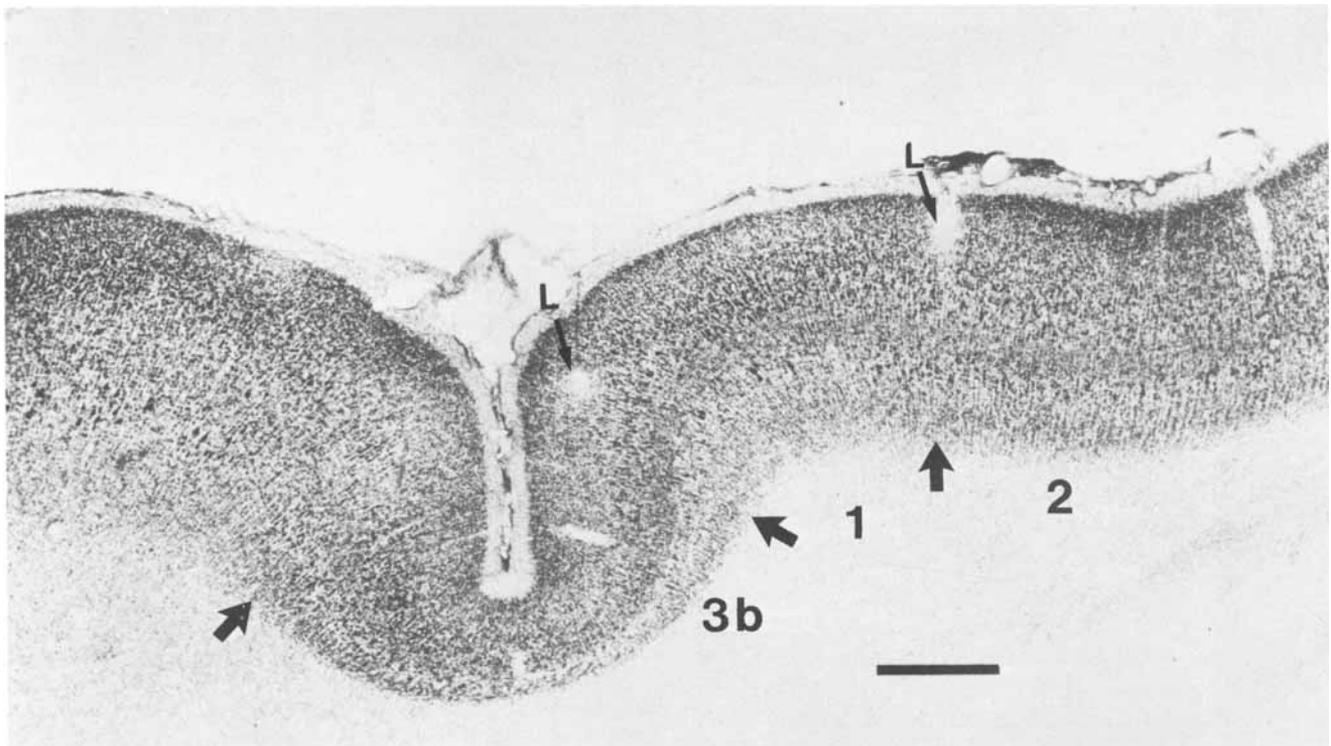


Fig. 9. A parasagittal brain section through areas 3b, 1, and 2 of squirrel monkey. Small arrows mark electrolytic lesions (L) placed at the borders of the area 1 cutaneous representation as determined by electrophysiological mapping. The lesions correspond closely to the borders of area 1 as judged from cytoarchitecture. In this and other experiments, the borders

of the two cutaneous representations and the architectonic borders of areas 3b and 1 were consistently in close agreement. Large arrows indicate the borders of areas 3b and 1. Marker bar equals 500  $\mu\text{m}$  in this celloidin-embedded section which has undergone considerable shrinkage. Other brains were frozen and sectioned (see text).

areas 3b and 1 each form separate complete or largely complete parallel and roughly mirror-image body surface representations was fully supported by the present results. This concept was developed in a series of mapping experiments on other species of monkeys (Merzenich et al., '78; Kaas et al., '79; Felleman et al. '79; Nelson et al., '80) and it is now supported by results from four different species of monkeys. The second major conclusion is that the basic somatotopic organization of these fields was subject to remarkable alterations in primate evolution. In brief, the representations of certain body parts, but not others, are reversed in somatotopic orientation in both area 3b and area 1 in squirrel monkeys as compared to owl and macaque monkeys. Furthermore, any representation that is reversed in area 3b is also reversed in area 1, thereby maintaining the mirror-image relation of these two fields. Finally, a high degree of continuity is maintained in the areas 3b and 1 maps despite these reversals. Thus, certain rules are followed in these cortical maps even when major changes occur. This consistency suggests that there are mechanisms promoting somatotopic order in cortical maps, and that the orders in adjoining maps are not independently determined. The remarkable reversals of parts of the maps indicate that the mechanisms determining the orientation of major body parts in the maps are at least partially independent. In addition, normal function would not appear to depend on a particular organization.

### Organizations of areas 3b and 1 in squirrel monkeys

The basic organizations of areas 3b and 1 in squirrel monkeys are summarized in Figures 1 and 11. Figure 1

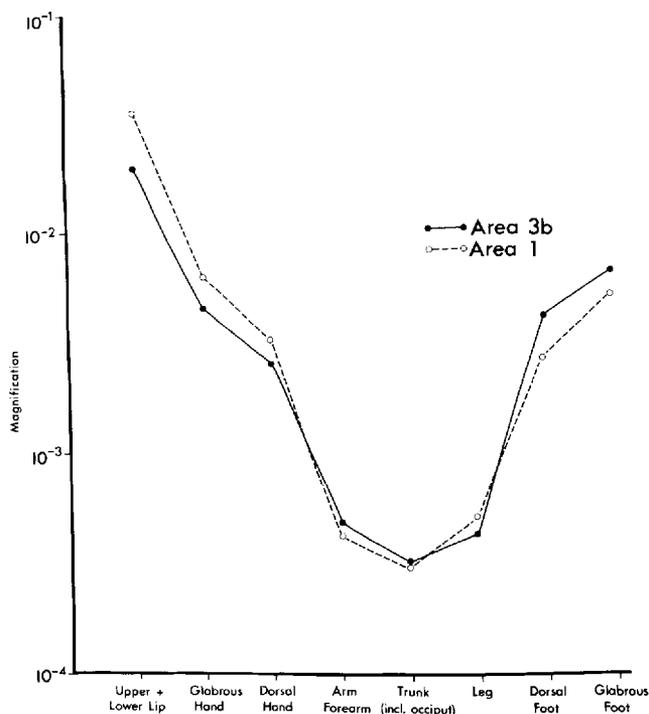


Fig. 10. Graph of cortical magnification factors for different body regions represented in area 3b and area 1. Magnification is defined as the cortical surface area for a given body part divided by the skin surface area for that part.

shows where the major body surfaces are located in the two representations, and Figure 11 indicates the orientations of the representations of these parts in the two maps. The salient features apparent in these summaries are that the two representations are indeed very similar, that they are in parallel with a common border that is congruent or matched for body location, and that they are roughly mirror imaged. It is also apparent that, while there are many partial discontinuities in the two maps, long lines of continuity can be drawn. Most notably, a single progression of representation from tail to hand exists along the 3b/1 border. The only obvious gap in this progression is from the hand to the face.

While the maps in areas 3b and 1 are similar, there are two major differences in somatotopy. The first is the way the leg is represented medial and lateral to the foot within the two areas. Most of the anterior thigh and distal leg is represented lateral to the foot in area 1, whereas only the anterior thigh lies lateral to the foot in area 3b (Figs. 6, 7). There is, therefore, a discontinuity between the thigh and foot representations within area 3b but not in area 1. The second difference in topography between the maps in the two areas is that much of the cranial skin and the proximal face and neck are represented along with the occiput representation in area 3b but not in area 1. Within area 1, these parts of the head are represented laterally, along with the rest of the face (Fig. 2).

Separate representations of the body surface in areas 3b and 1 have not been distinguished in previous maps of the "S-I region" in squirrel monkeys. However, important observations have been made that are consistent with the present interpretation. An extensive map of the S-I region of squirrel monkeys was first made by Benjamin and Welker ('57). In this study, evoked slow waves were recorded with surface electrodes. While this procedure apparently obscured the mapping details necessary to reveal the double map, the general medial to lateral cortical sequence found in the two parallel maps of the present study was apparent in the earlier "single" map. Thus, the separation of the posterior and anterior leg in cortex by the foot (Figs. 1, 6, 7) was determined, as well as the split of the back of the head from the face by the representations of the hand and

TABLE 1.

Body part	Cortical area (mm <sup>2</sup> )		Ratio 3b/1
	3b	1	
Lips	4.75	8.4	0.56
Upper lip	1.7	5.2	0.33
Lower lip	3.05	3.2	0.95
Glabrous hand	4.6	6.5	0.71
Digits	3.2	3.2	1.0
Pads	1.4	3.3	0.42
Dorsal Hand	2.6	3.3	0.79
Arm & forearm	3.6	3.1	1.16
Trunk & occiput	4.3	4.0	1.08
Leg	6.0	7.2	0.83
Lateral representation	2.4	5.1	0.47
Medial representation	3.6	2.1	1.71
Glabrous foot	6.4	5.1	1.25
Digits	3.1	1.7	1.82
Pads	3.3	3.4	0.97
Dorsal foot	4.1	2.6	1.58
Tail	.5	.15	3.33
Total <sup>1</sup>	36.85	40.35	

<sup>1</sup>Not including portions of areas 3b and 1 that lie very laterally.

arm. A more recent study using microelectrodes, but limited to cortex devoted to the trunk and hindlimb, was that of Werner and Whitsel ('68). Again, a major point of agreement is in the split representation of the posterior and anterior leg by cortex activated by the foot. However, separate cutaneous representations in areas 3b and 1 were not postulated, and the organization of the medial portion of somatosensory cortex was summarized in a manner quite different from the present summary. A final relevant paper on the organization of somatosensory cortex in squirrel monkeys was that of Zimmerman ('68). In this study two independent foci of evoked activity were found in somatosensory cortex after stimulating the tip of digit three of the hand. While Zimmerman ('68) interpreted one focus to be within "classical granular cortex" and the other to be in "intermediate" cortex (area 3a), the locations of these two foci correspond very closely to the area 1 and area 3b finger tip representations of the present study (see Fig. 3).

**Reversed orientation of some body parts in areas 3b and 1 of squirrel monkeys**

A major conclusion of the present study is that the rostrocaudal cortical sequence of the representation of some

body parts in areas 3b and 1 of squirrel monkeys is reversed from that of owl and macaque monkeys. While it is not completely certain how much of the body surfaces representations are reversed in squirrel monkeys as compared to owl and macaque monkeys, the simplest hypothesis that is consistent with most of our observations is that the representations of all hairy body surfaces are reversed in squirrel monkeys, while the representations of the glabrous hand and foot are not (Fig. 12).

The reversal of somatotopic order in squirrel monkeys is most obvious for the trunk representations. In both owl and macaque monkeys, the ventral midline of the trunk is represented along the 3b/1 border and the dorsal midline is found caudally in area 1 and rostrally in area 3b; in squirrel monkeys, however, the dorsal midline of the trunk is found along the 3b/1 border while the ventral midline is found rostral in area 3b and caudal in area 2 (arrow 4, Fig. 11).

Although the data are complicated by the split representation, the recording evidence also indicates that the separate anterior and the posterior sectors of the hindlimb are represented in opposite rostrocaudal cortical sequences in squirrel monkeys (arrows 1 and 3, Fig. 11). The posterior

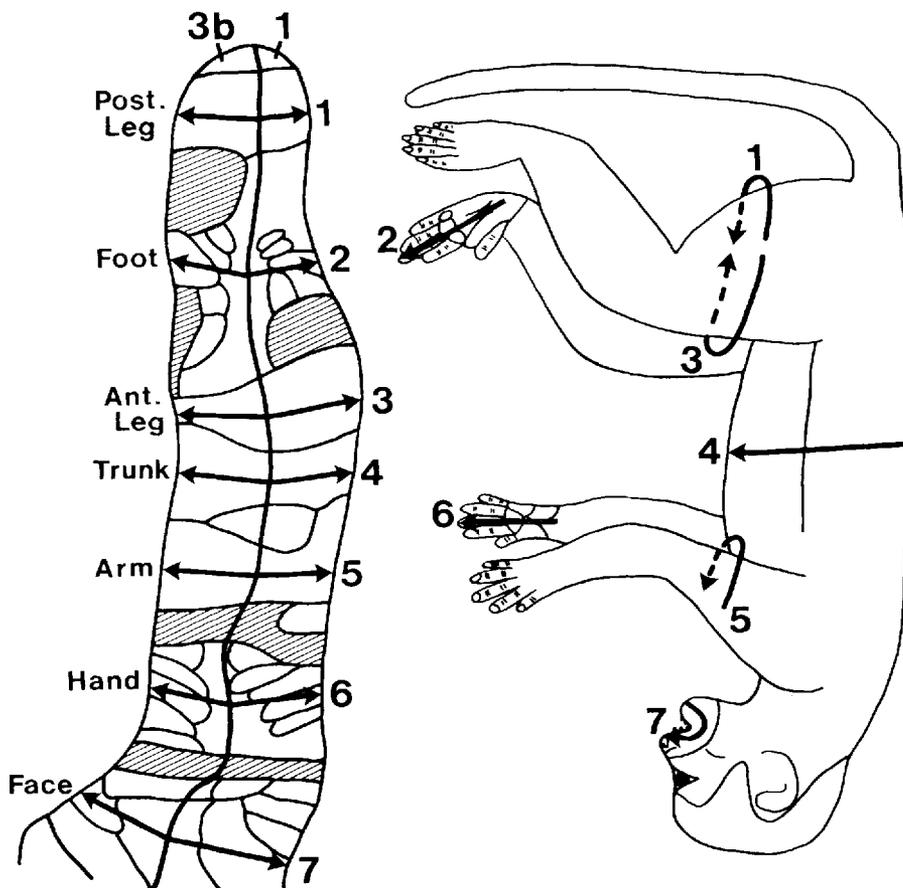


Fig. 11. The orientations of the representations of body surfaces in areas 3b and 1 of squirrel monkeys. Numbered arrows on the body surface (right) indicate somatotopic sequences that correspond with arrows marking the mirror-reversal sequences that progress rostrally in area 3b and caudally in area 1. From the 3b/1 border, for example, the trunk (arrow 4) is represented from the back to the belly in a caudorostral sequence in area 3b and in a rostrocaudal sequence in area 1. The locations of body parts in

areas 3b and 1 are explained further in Figure 1. Dashed portions of arrows in the right indicate hidden inner surfaces of the limbs. For convenience, arrows 2 and 6 are shown on the visible glabrous surfaces of the left hand and foot. The cortical representations in the left cerebral hemisphere are actually of the right side of the body, as indicated by the arrows on other body parts.

hindlimb is represented medial to the foot in both areas 3b and 1 of squirrel and macaque monkeys, where the outer leg surface is found at the 3b/1 border in squirrel monkeys, and the inner leg surface is found at the 3b/1 border in macaque monkeys (Fig. 12). In cortex lateral to the foot, a similar species difference in the representation of the anterior leg is found, again with the outer leg surface at the 3b/1 border in squirrel monkeys, and the inner leg surface at that border in macaque monkey. Comparisons with owl monkeys are more complicated. In area 1, the anterior and posterior leg surfaces are split by the foot as in macaque and squirrel monkeys, but little or none of the leg is found lateral to the foot in area 3b of owl monkeys. The lateral representation of the anterior leg in area 1 of owl monkeys is like that of macaque monkeys in basic orientation, but the orientations of leg representations medial to the foot have not been determined.

The surface of the arm also appears to be represented in opposite rostrocaudal cortical sequences in squirrel and macaque monkeys. In these monkeys most or all of the arm is represented medial to the hand in both areas 3b and 1. In squirrel monkeys the rostral outer arm is represented at the 3b/1 border and the representations proceed caudally across the outer arm and then rostrally across the inner arm for mirror progressions of recording sites toward the rostral border of area 3b and toward the caudal border of area 1 (arrow 5, Fig. 11). The opposite sequence is seen in owl monkeys (Merzenich et al., '78; unpublished studies). However, part of the anterior arm is sometimes represented in cortex lateral to the hand representation for area 1 of owl monkeys.

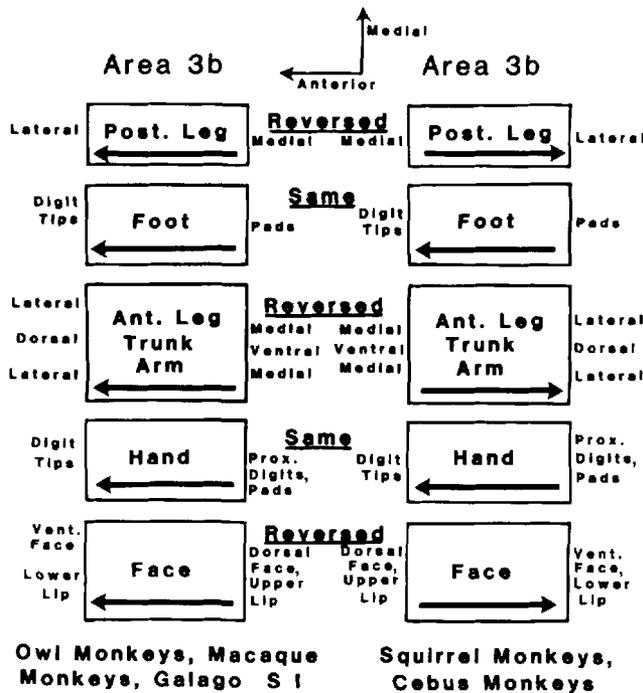


Fig. 12. A schematic summary of the differences in the organization of area 3b in primates. The body surface representation is portrayed in five blocks each devoted to a portion of the body (see Sur et al., '80a). The orientation of the body sector in each block is indicated, and two distinct patterns appear to exist. Compared to owl monkeys, macaque monkeys, and galagos, the posterior leg, the leg-trunk arm, and the face blocks appear to be reversed in squirrel and cebus monkeys (see text).

Because the face and head regions, especially in area 1, have not been fully mapped, it is difficult to determine how similar or different the organization of these representations are in squirrel monkeys. Nevertheless, the representations of the lips appear to be reversed in squirrel monkeys as compared to owl monkeys (arrow 7, Fig. 11). In owl monkeys, the upper lip midline is found at the 3b/1 border, while the lower lip midline is found at this location in squirrel monkeys.

The evidence indicates that the rostrocaudal orientation of the representations of many body parts, but not that of the hand or foot, are reversed in squirrel monkeys as compared to owl and macaque monkeys. The full extent of this difference is not completely clear, since the pattern of organization found in macaque monkeys appears to vary somewhat from that in either owl or squirrel monkeys, and the orientation of body parts in the area 3b and area 1 maps have not been completely determined in any of these monkeys. While Figure 12 specifies rather precisely the hypothetical orientations of a number of body parts for three species of monkeys, the diagram fails to incorporate the individual differences that were observed from experiment to experiment, or to indicate where some uncertainty exists about the exact orientation of a represented body part. Thus, we stress the conclusion that the representations in squirrel monkeys have major reversals from those in owl monkeys and macaque monkeys, while being unsure about the certainty of this reversal for some body parts, in particular the forearm and face. It is possible that further study will suggest modifications in the summary diagram, but the general conclusion seems clear.

Because owl monkeys and macaque monkeys are not closely related, it is logical to suppose that the similar patterns of cortical organization seen in these monkeys represent the generalized organization that is characteristic of monkeys, and, most likely, higher primates. This supposition is strengthened when the organizations of area 3b in these monkeys is compared with the organization of S-I in other mammals. Elsewhere we have argued that S-I is usually described in nonprimates and even in prosimian primates as the homologue of area 3b of monkeys (Kaas et al., '81a; Kaas, '82, '83). The organization of S-I (3b) in the prosimian galago has been previously summarized in a manner similar to that of Figure 11 of the present report (see Fig. 11: Sur et al., '80a). The orientations of the representations of the foot, anterior hindlimb, trunk, hand, posterior forelimb, and face in galagos all correspond with the orientations of the representations of these body parts in area 3b of owl monkeys and, with the possible exceptions of the forearm and face, with the orientations in area 3b of macaque monkeys (Fig. 12). Furthermore, the orientations of body parts in the area 3b representation of owl monkeys, macaque monkeys, and galagos are in close agreement with the orientations of the representation of these body parts in S-I of squirrels (Sur et al., '78) and tree shrews (Sur et al., '80b). Thus, the generalized and prototypical organization of area 3b in monkeys appears to be that found in owl and macaque monkeys, while the organization found in squirrel monkeys seems to be a dramatic modification of that organization.

If the organization found in squirrel monkeys is an alteration of the basic somatotopic pattern, it is logical to assume that owl monkey patterns will be found in most monkeys, and that the squirrel monkey pattern will be

found only in squirrel monkeys and perhaps in monkeys closely related to squirrel monkeys. While the phylogeny of New World primates remains an issue of debate, a close *Cebus-Saimiri* association has been postulated (e.g., Chiarelli, '79). This postulated relationship is supported by the finding that the trunk representations, at least, are reversed in areas 3b and 1 in cebus monkeys (Felleman et al., '79) as they are in squirrel monkeys.

### Implications of the partial reversals of the area 3b and area 1 maps

The observation that the representations of some body parts are reversed in areas 3b and 1 of squirrel monkeys has several important implications: (1) Since the representations of most or all of the hairy surfaces of the body are reversed, while the representations of the glabrous foot and hand are not, it is obvious that the cortical specification of the glabrous hand and foot can take place separately from the rest of the body surface in monkeys. This does not mean that an independence of body parts is a general feature of somatotopic maps. Rather, we have argued elsewhere (Sur et al., '80a) that the greatly enlarged representations of the glabrous hand and foot in primates has led to major disruptions in the overall continuity in the area 3b and area 1 maps so that the representations are divided into a mediolateral sequence of cortical "blocks" each possessing a large degree of somatotopic isolation. Thus, foot and hand blocks enclose a trunk-arm-leg block, and the hand block isolates the face block. Given the limited continuity between blocks, reversals of blocks are possible without greatly altering the extent of this continuity. Thus, some limited continuity is maintained between blocks in both normal and the reversed patterns of organization. If one of the organizational features of cortical maps is to maintain continuity in the representation of sensory surfaces, it is only in highly specialized maps, such as in areas 3b and 1 of monkeys, that major reversals of the representation of some parts relative to others can occur without greatly altering the overall continuity.

(2) Quite different patterns of organization appear to be capable of maintaining the functions of somatosensory cortex. Squirrel monkeys are not obviously impaired in any way in somatosensory abilities, and the fact that they are well adapted to their natural environment suggests that they have normal abilities. Thus, reversing the orientation of many, but not all body parts in the cutaneous maps, apparently results in no serious functional impairments. This conclusion is not surprising in that intrinsic cortical connections are probably minimal between cortical blocks in the maps (Shanks et al., '78) and therefore reversals would have little effect on the intrinsic processing in the fields. Connection patterns with other cortical and sub-cortical centers might be normal, especially if other maps besides the ones in areas 3b and 1 have matched reversals, or they might be altered to compensate for the reversals. Research on the visual system of Siamese cats shows that the altered retinotopic cortical maps in these animals result in altered and retinotopically appropriate patterns of cortical connections (e.g., Shatz and LeVay, '79).

(3) The organizations of the somatosensory maps in areas 3b and 1 do not appear to be independent. Wherever reversals in somatotopic organization occur in area 3b of squirrel monkeys, they are matched by similar reversals in area 1. Thus, areas 3b and 1, which are roughly mirror

reversals of each other in somatotopic organization in other monkeys, remain mirror reversals of each other in squirrel monkeys. One possibility is that the organizations of the two areas are induced along the common border during development. Developing two maps from a common reference line would produce roughly mirror-image representations, while allowing other factors to modify the detailed organizations of the two maps (Kaas, '82). This suggestion is consistent with the fact that adjoining cortical sensory representations are commonly mirror imaged in organization (Kaas, '77). Furthermore, mirror-image retinal maps in the tectum of frogs have been experimentally produced by rotating part of the thalamic precursor in embryos to the middle of the tectal precursor (Chung and Cooke, '78).

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