# The Representation of the Body Surface in Somatosensory Area I of the Grey Squirrel

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ABSTRACT    Microelectrode mapping methods were used to determine the organization of primary somatosensory cortex, SmI, in grey squirrels. A systematic representation of the contralateral body surface was found within somatic koniocortex. This primary representation differs from maps of SmI in other mammals in at least two significant ways. The first way in which SmI of squirrels differs from the organization reported for other mammals is that SmI of squirrels contains a double representation of the hand and parts of the forearm. The glabrous skin of the digits is represented twice in a mirror image fashion joined at the finger tips. The hairy skin of the digits, wrist, and parts of the forearm are also represented twice, once on each side of the joined representations of the glabrous skin. A second unique feature of SmI of squirrels is that there is a small region of cortex completely surrounded by SmI that was unresponsive to light cutaneous stimuli under our recording conditions. This unresponsive zone is easily identified in brain sections by architectonic features that deviate from sensory koniocortex and approach motor cortex. A third significant finding was that the back is rostral to the belly in the representation of the trunk in SmI of squirrels. This is the reverse of the orientation reported elsewhere for SmI of mammals, but corresponds to the orientation of the trunk representation in Area 3b of owl monkeys (Kaas et al., '76; Merzenich et al., '78). This similarity supports an earlier contention that the representation of the body in Area 3b of primates is the homolog of SmI in other mammals (Merzenich et al., '78).

The organization of the body surface representation in primary somatosensory cortex or SmI has been studied with surface recordings and microelectrodes in a number of mammalian species (more recent studies include Lende and Woolsey, '56; Hamuy et al., '56; Welker and Seidenstein, '59; Welker and Campos, '63; Lende, '63, '64, '69, '70; Zeigler, '64; Lende and Sadler, '67; Woolsey, '67; Werner and Whitsel, '68; Magalhaes-Castro and Saraiva, '71; Pubols and Pubols, '71; Rubel, '71; Paul et al., '72; Welker, '71, '76; Hall and Lindholm, '74; Johnson et al., '74; Saraiva and Magalhaes-Castro, '75; Campos and Welker, '76; Carlson and Welker, '76; Kaas et al., '76; Krishnamurti et al., '76; Welker and Carlson, '76; Welker et al., '76; Merzenich et al., '78; also see Woolsey, '52, '58, for review), and yet some important questions remain. One question has been raised by recent microelectrode studies in monkeys (Paul et al., '72; Kaas et al., '76; Merzenich et al., '78). These studies showed that the region traditionally designated as SmI contains two separate maps of the body surface, each activated by light cutaneous stimuli. One representation was found to occupy the architectonic field 3b, the other, Area 1. Both representations differed in detail from the accepted organization of SmI. For example, the posterior representation has the digit tips of the foot and hand oriented caudally, the opposite direction from that described for SmI. In the anterior map of the body surface, the back is represented rostrally and the belly caudally, the opposite trunk orientation from that accepted for SmI. Because the overall similarities of the anterior representation corresponded more with the traditional concept of SmI, we termed the anterior field in Area 3b "SmI Proper" to distinguish it from the older more inclusive SmI of primates. The Area 1 representation was called the "Poste-

rior Cutaneous Field." Because of differences in both of these fields with SmI as described in other mammals, we thought it would be reasonable to investigate the detailed organization of somatosensory cortex in a nonprimate. We chose the grey squirrel because this mammal has the advantage for mapping studies of a relatively large smooth surfaced brain with a well developed easily defined somatic koniocortex. Furthermore, the squirrel has been a reliable experimental animal in electrophysiological mapping studies of auditory (Merzenich et al., '76) and visual (Hall et al., '71) areas of neocortex. The goal of the present experiments was to further define the generalized features of SmI organization in mammals. The results support our contention that Area 3b of primates contains the homolog of SmI of other mammals. In addition, we also discovered some interesting and specialized aspects of SmI organization in the squirrel.

## METHODS

The organization of primary somatosensory cortex (SmI) was determined by microelectrode mapping experiments in 19 grey squirrels (Sciurus carolinensis). The recording results were related to cortical architecture by examining sections from the brains in which boundaries and other significant parts of the representation had been marked with small electrolytic lesions during the recording sessions.

### Preparation of the animals

At the start of each experiment, a squirrel was anesthetized with an initial intraperitoneal injection of a 25% solution of urethane (125 mg/100 gm body weight). Additional injections of one-tenth the initial dose were given throughout the course of the experiment as needed to suppress nocioceptive reflexes. After a suitable level of anesthesia was reached, the trachea was cannulated, and the animal was restrained with ear bars in a head holder while the brain was exposed. A large opening was made over somatosensory cortex in order to allow mapping of all parts of the representation and reduce brain movements. In some cases it was necessary to drain, collapse, and reflect one eye so that the opening in the skull could be enlarged to expose cortex along the rhinal fissure. The exposed brain was protected from dessication by a pool of silicone fluid contained in a dam of acrylic plastic around the opening in the skull. The

skull and plastic dam were then cemented to an iron bar which could be fixed in a vice to hold the head in a range of positions. The exposed brain was photographed, and the squirrel was positioned for recording with the body surface freely accessible for stimulation. During the experiment, the animal's body temperature was monitored and maintained at 37°C.

### Microelectrode mapping procedures

Somatosensory cortex was mapped with glass coated platinum-iridium microelectrodes with tip exposures large enough (impedance of 1-1.5 Megohm at 1 kHz) to favor recordings from small groups of neurons rather than single neurons. The indifferent electrode was a screw in the skull. The output of the recording electrode was amplified, displayed on an oscilloscope, and made audible through a loudspeaker. Electrode penetrations were usually normal to the brain surface and were placed from 200-500 $\mu$ apart or as closely as the vascular pattern would permit. In portions of cortex where much detail was desired, as many as 35 penetrations were made per mm$^2$ of surface. In each experiment, part of the SmI representation was mapped in detail, with an average of 120 penetrations per animal, while receptive fields were obtained for enough points surrounding the mapped region to determine its relationship to the remainder of the representation. Electrodes were positioned on the brain surface under observation through a dissecting microscope, and advanced by a microdrive unit while stimulating the body until the most effective recording depth was found. Most recordings were at depths of approximately 600 $\mu$. Each electrode penetration was marked on an enlarged photograph of the exposed part of the brain and later transferred to an enlarged photograph of the brain taken after the brain had been removed from the skull. During recording, a general receptive field area was first defined for each electrode penetration by tapping and stroking the appropriate area of the body. The precise extent and location of the minimal receptive field was then determined by using progressively finer and lighter cutaneous stimuli. Stimulators were made of dark glass probes, angled and drawn to fine blunt tips. The receptive field was defined as the skin surface over which a distinct response could be obtained from an extremely light tactile stimulus. In all instances, the receptive field was delineated with very light taps or strokes

on the skin surface, or movements of surface hairs. Thus, cutaneous rather than deep or joint receptors were activated. Care was taken to map the extent of the receptive field along different directions in order to accurately gauge its actual area. Mystacial vibrissae were stimulated by bending with small forceps. After a receptive field was delineated, it was drawn on a photograph or drawing made from a photograph of the appropriate body part. Boundaries of SmI were determined by penetrations that were unresponsive to cutaneous stimuli, or were judged by receptive field and response characteristics to be within the second somatic area, SmII. Usually, two consecutive unresponsive sites were determined at the anterior and posterior boundaries of SmI for each row of recording sites. Finally, the "map" of the body parts on the cortical surface was determined by relating receptive fields to electrode penetrations and recording sites. The body subdivisions of SmI were drawn on enlarged photographs of the brain and the surface areas of SmI and its subdivisions were estimated with an electronic planimeter.

### Histology

After the recording, the brain was either fixed by immersion in 10% formalin, which preserved the pattern of the surface blood vessels, or the animal perfused intracardially with 0.9% saline followed by 10% formalin. The brain was removed, placed in 10% formalin with 30% sucrose for several days and then sectioned on a freezing microtome in the sagittal or coronal plane at 50 $\mu$. In certain cases, the cortex was cut in special planes between horizontal and sagittal in order for the sections to be perpendicular to the surface in the portions of SmI of interest. Most cases also received injections of anatomical tracers during recording. The results of these studies of the connections of SmI will be reported elsewhere.

### RESULTS

Our microelectrode mapping experiments in grey squirrels have revealed a systematic representation of the body surface within a subdivision of cortex previously identified as koniocortex and as receiving projections from the ventroposterior nucleus of the thalamus (Kaas et al., '72). The overall somatotopic organization, location, and cytoarchitecture of the representation are characteristic of SmI,

and we conclude that the representation is the homolog of the primary somatic representation that has been described in many other mammals. However, the representation was found to differ from the organization reported for SmI of other mammals in three significant ways: (1) there is a double representation of the forepaw including palmar pads and the digits of the hand, as well as the wrist and forearm, within the single somatic koniocortical field; (2) there is a small region of architectonically distinct cortex within, and surrounded by SmI, that does not respond to light cutaneous stimulation and (3) the representation of the trunk of the body is reversed from the expected pattern with the dorsal midline of the trunk represented along the anterior edge and the ventral midline along the posterior edge of SmI.

### The location and overall organization of SmI

The location of SmI on the cerebral hemisphere is shown in figure 1. SmI is coextensive with the cortical subdivision labeled Pa or the anterior parietal area of an earlier architectonic study of neocortex in the squirrel (Kaas et al., '72). SmI extends mediolaterally on the surface of the cerebral hemisphere from near the midsagittal fissure to almost the rhinal fissure (fig. 1). SmI is narrow medially where it represents the trunk and hindlimb and wide laterally where it represents the forelimb and face. The frontal cortex immediately rostral to SmI has the architectonic characteristics of motor cortex, and electrical stimulation of this cortex with microelectrodes produced movements of different body parts. Cortex caudal to SmI has been described as corresponding to three architectonic fields: temporal anterior (Ta), parietal medial (Pm), and parietal lateral (Pl) (Kaas et al., '72). The Pm region was unresponsive to cutaneous stimulation in our experiments and the general significance of this cortical subdivision is unknown. The Pl region and perhaps some of the cortex along the Pa and Ta border responded to somatosensory stimulation in a pattern indicative of the second somatosensory area, SmII. The Ta region has been shown to contain two or more subdivisions of auditory cortex including AI or primary auditory cortex (Merzenich et al., '76). The spatial relations of SmI, SmII, and the auditory areas are shown in figure 1. The overall pattern of the body representation in SmII has been described elsewhere (Sur et al., '77).
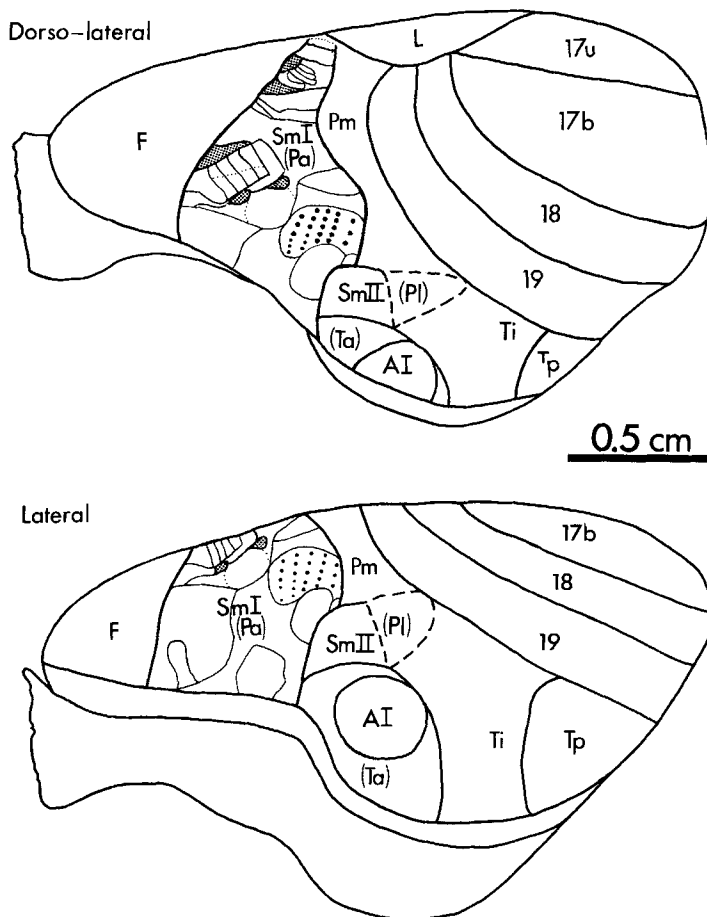
Fig. 1   The location of primary somatosensory cortex, SmI, in the grey squirrel (see fig. 2 for the significance of the subdivisions of SmI) relative to the architectonic subdivisions of Kaas et al. ('72) and the auditory fields of Merzenich et al ('76). SmI corresponds to the anterior Parietal Area, Pa. The frontal field, F, includes motor cortex and other areas. SmII occupies the rostral half of the lateral cortical field, Pl. A primary auditory field, AI, is distinguished within the temporal anterior region, Ta. Other subdivisions are the medial parietal Area, Pm, the intermediate temporal Area, Ti, and the posterior temporal Area, Tp. L indicates limbic cortex. Areas 17, 18, and 19 are based on Brodman's terminology; 17u, uniocular 17; 17b, binocular 17.

The overall features of the representation of the body parts in SmI of the squirrel are shown schematically in figure 2. The tail, genital region and postaxial leg are represented most medially where SmI is only slightly over 1 mm wide. Next, a sector of cortex is activated by stimulation of the foot. The digits project to narrow rostrocaudal strips of tissue with the large toe or hallux laterally and the other toes in order more medially. Strips of tissue along the rostral margin and lateral to the digits respond to the dorsal hairy surface of the foot. The digit tips point rostrally while foot pads and the heel are represented caudal-

ly. The projection of the foot is followed laterally by the preaxial leg and the trunk of the body. Although the trunk is represented in very little tissue, and we found receptive fields for recording sites within this subdivision of SmI to include relatively large areas of the body surface, the mapping data clearly showed that the dorsum of the trunk is found rostrally and the ventrum caudally within the trunk representation in the squirrel. The shoulder is represented in a wedge of cortex at the rostro-lateral part of the trunk. After the representation of the trunk, the width of SmI increases to 3-5 mm, and proportionately large
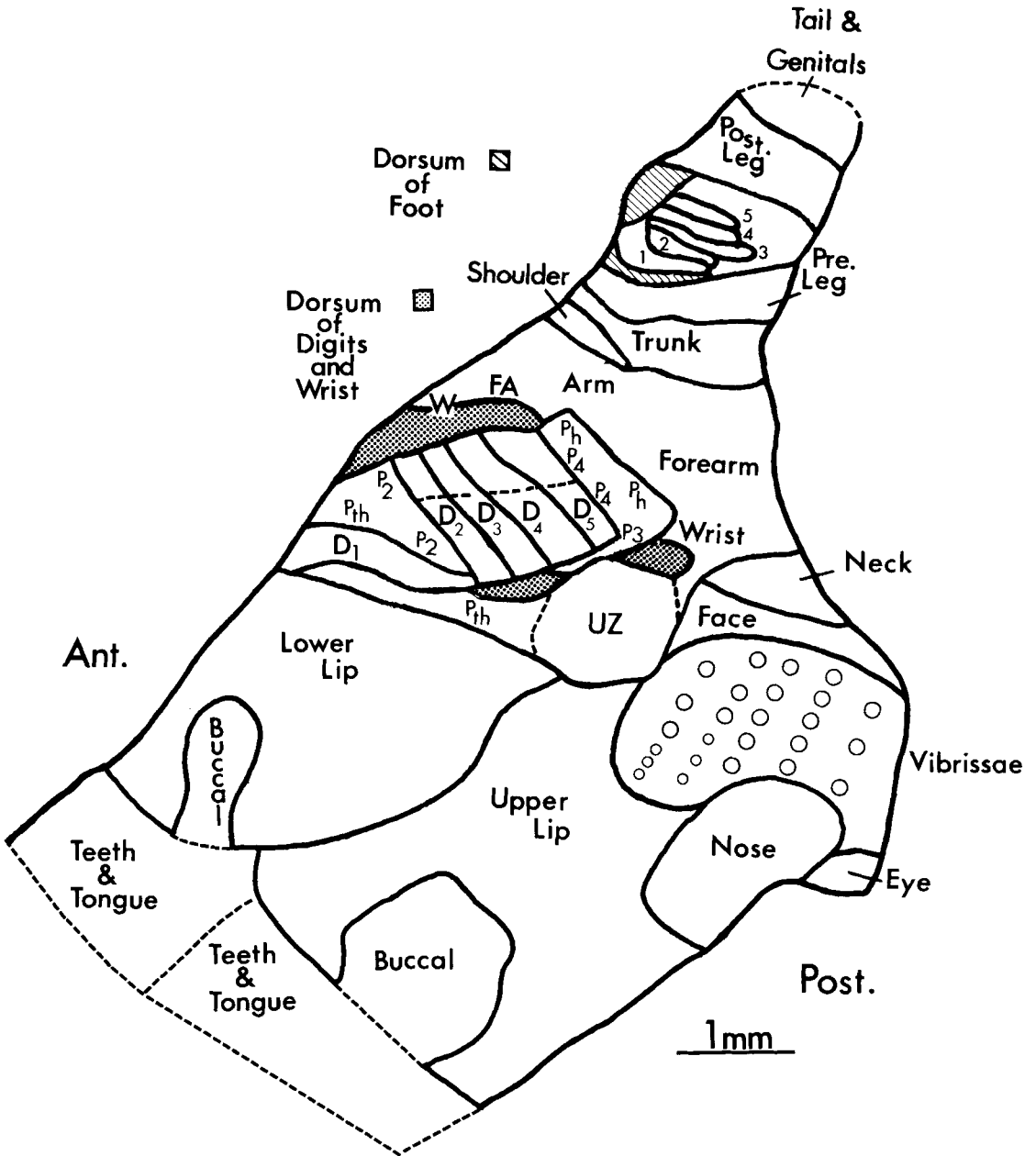
Fig. 2 The organization of SmI in the grey squirrel. See text and following illustrations for details. The digits, $D_1$-$D_5$ and pads, $P_2$-$P_4$, PH and PTh, of the forepaw are represented twice (see fig. 4 for nomenclature). The toes of the foot are numbered from the great toe, pre- and postaxial leg regions are indicated; W, wrist; FA, forearm; UZ, unresponsive zone.

amounts of tissue are devoted to the forearm, forepaw, and head. In a medial to lateral progression, the arm is followed by the forearm and wrist, and then digits 5 through 1 (digit 1 is a rudimentary pad on the forepaw of squirrels and other rodents) which are bordered medially and laterally by the palmar pads. The glabrous and hairy surfaces of the hand as

well as the wrist and forearm are represented twice within SmI, and the details of this dual representation are discussed below. The neck is represented at the caudal margin of SmI just lateral to the forearm and arm and caudal to a central unresponsive region about 1 mm wide (see below). The mystacial vibrissae project lateral to the neck region with the most proximal vibrissae relating to the most medial recording site and the most dorsal vibrissa relating to the most caudal recording sites. The nose, upper lip, and lower lip are more lateral in a caudal to rostral sequence. The skin around the eye is represented caudal to the nose representation. Intraoral parts are represented most laterally, with the upper buccal cavity and upper incisor caudal to the inside of the lower lip and lower incisor.

In summary, with some important differences, the overall pattern of SmI in the squirrel is similar to that found in other mammals with a medial to lateral progression that is *regionally somatotopic* and with roughly a caudal to rostral body sequence. A more detailed description of the representation of parts of the body follows.

### The representation of the head

A large part of the SmI region is devoted to the face. A small example of the extensive receptive field data used to reconstruct this part of the representation is shown in figure 3. A row of recording sites starts at the rostral margin of SmI and proceeds across the representation to the caudal border. The corresponding receptive fields form a systematic progression from the midline of the lower lip, to the corner of the mouth, across the upper lip to the midline, and then along the bridge of the nose to the skin over the eye. At each end of the row there were several unresponsive electrode penetrations that were judged to be outside SmI. In this and other experiments, there were other rows of recording sites across SmI with similar systematic progressions of receptive fields. Note that in the row illustrated, there is a single progression of receptive fields and there are no reversals or receptive fields out of sequence. This was the general finding within the lip region which can be described as somatotopic.

The representation of the snout is relatively large. The caudal snout is represented medial and caudal within the representation, adjacent to the vibrissae and skin above the eye. The rostral nose is represented laterally and

rostrally within the representation of the nose, adjacent to the medial upper lip. The small area of tissue caudal to the snout represents the supraorbital skin (see penetration 17: fig. 3). The overall pattern suggests that a small region of cortex along the caudal and the caudo-lateral border of the supraorbital area may represent the top of the head. However, this skin was removed to expose the brain and could not be stimulated in our experiments.

The inferior orbital region of the face, i.e., the skin below the eye including the cheek and proximal face skin, is represented medial to the vibrissae adjacent to the neck representation. Infraorbital receptive fields were seen to be much bigger than supraorbital fields, frequently covering the entire proximal face and extending to the neck.

The buccal cavity is represented laterally within the upper and lower lip representations. Most of the cortex lateral to the external upper lip representation is activated by the inside of the lip and cheek pouch. The cortex lateral to the external lower lip representation largely corresponds to the inside of the lower lip. The teeth and tongue are represented further laterally in the cortex along the rhinal fissure. The upper contralateral incisor is represented in tissue adjoining the upper lip, and the lower contralateral incisor in tissue adjoining the lower lip. Penetrations at the border of the upper and lower teeth representations are responsive to both upper and lower teeth. Other penetrations in this lateral cortex had receptive fields on the gums and tongue.

### The representation of the mystacial vibrissae

The mystacial vibrissae occupy a considerable portion of SmI in many rodents and this part of the representation has been related to a histological subdivision of somatic koniocortex, the "barrel" field (DISCUSSION). Because of the interest in the barrel field of rodents, we mapped this region in detail in several squirrels. Since the cortical "barrel" field reflects the organization of the mystacial vibrissae, it is useful to start with a description of the orderly arrangement of these facial hairs. The arrangement of the facial sinus hairs of the squirrel has been described by Woolsey et al. ('75) and is shown at the lower left in figure 3. The mystacial vibrissae are arranged along the side of the face in five rows of three to six hairs. For purposes of describing

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Fig. 3 The representation of the lips and mystacial vibrissae. The five rows of vibrissae, A-E, are represented caudal to rostral with the proximal vibrissae medial and distal vibrissae lateral in SmI. Receptive fields for a typical row of penetration sites across the lip and upper face region is also shown.

the cortical representation, the rows are numbered A-E from dorsal to ventral, and hairs are numbered from caudal to rostral; thus each hair is specified by a letter and number after the scheme of Welker ('71) for the rat.

The vibrissae of the squirrel are represented in an orderly sequence on the brain in the relative positions shown in figure 3. The dorsal row A of vibrissae lies along the caudal margin of SmI and rows B-E occupy progressively more rostral strips of cortex. The most caudal vibrissa in each row activated the medial portion of the representation while progressively more rostral vibrissae in the sequence activated progressively more lateral cortical locations. Each recording site was generally maximally activated by a single vibrissa, although some recording sites were

activated by two or three vibrissae, especially by the smaller rostral vibrissae in rows A, B, and C. Since the responses were from groups of neurons, it was uncertain if single neurons responded to the movement of more than one hair. In rats both neurons responding to the displacement of a single vibrissa and neurons activated by two or more vibrissae are found in SmI (Simons and Sandel, '76).

### The double representation of the hand, wrist and forearm

One of the surprising findings in the present experiments was that parts of the forelimb are represented twice within what certainly appears to be SmI. Some of the evidence supporting our view that the digits are represented twice in SmI is included in figure 4 where receptive fields are shown for rows of recording sites across the cortex devoted to the glabrous skin of each digit. In the most lateral row of electrode penetrations, for example, the most rostral recording site corresponded to a receptive field on the glabrous skin of the most proximal portion of the second digit; the next recording site related to a receptive field on the middle phalanx of the digit, while the third site in the sequence was activated by stimuli on the tip of the digit. The receptive field for the next recording site, 4, was also on the digit tip, the receptive field for site 5 was on the middle phalanx, and the receptive field for the last recording site of the row was back on the proximal phalanx of the digit and even extended somewhat onto the second interdigital pad of the palm. Thus, the first three recording sites indicate the full extent of one orderly representation of digit 2, and the next three the full extent of a second orderly representation of digit 2. More rostral and more caudal recording sites in the row did not relate to the glabrous skin of digit 2, but were activated by the dorsum of the fingers. Similar progressions of recording sites with reversals of receptive field sequences are also shown for the other three digits. These and other results clearly indicate that the glabrous skin of digits 2-5 is represented twice in a mirror image fashion with the separate representations joined at the finger tips. The double representation is within the overall SmI map and within somatic koniocortex.

Other parts of the hand are digit 1, the glabrous palmar pads, and the dorsum or hairy surface. Digit 1 is a rudimentary stub in the squirrel. Because of its small size it was dif-

ficult to determine whether or not it is represented twice. However, stimulation of this stub does activate an unexpectedly large region of cortex, almost equalling that of the other digits. This cortex is almost completely split off from that devoted to the other digits by cortex activated by palmar pads.

Relatively little cortex was activated by stimulation of the hairy dorsum of the digits. With appropriate care, receptive fields on the hairy dorsum could be easily distinguished from receptive fields on the glabrous skin. A receptive field on the glabrous surface would respond to very light stroking or palpation within the maximally responsive zone. A response could be elicited from the corresponding dorsal skin only by using substantially harder taps. Similarly, receptive fields on the hairy skin could be defined by delicate stimulation of the hairs. Neurons with such fields would also respond to stimulation on the corresponding glabrous skin, but would require much harder stimulation than for the truly glabrous receptive fields. In addition, fields on the hand dorsum were much bigger, frequently covering two or more digits and large sections of the dorsal palm. Minimal receptive fields on the glabrous hand were much smaller, usually of the size of a phalanx. By carefully using light tactile stimuli, we were able to completely convince ourselves that both the double representations of the digits shown in figure 4 relate to the glabrous skin of the digits, and were true double representations and not separate representations of the dorsal and ventral surfaces of the fingers.

The palmar pads are represented in two groups, one lateral and the other medial to the representations of digits 2-5 (fig. 4). The representation pattern is as if the pads were split down the center of the palm into a radial group comprising the thenar eminence and pad 2, and an ulnar group comprising the hypothenar eminence, the insular pad, and pads 3 and 4. One group of pads, PTh and P2, is represented lateral to digit 2, and the other group, PH, PI, P3 and P4, medial to digit 5. The palmar pads also appear to be represented twice within SmI. The double representation is most clear for the thenar pad where two activation sites are separated by tissue related to digit 1 and pad 2, and for pad 4 where two activation sites are separated by cortex responsive to the insular and the hypothenar pads (fig. 4). The representations of the hypothenar pad and pad 2 could be divided

Anterior & Posterior
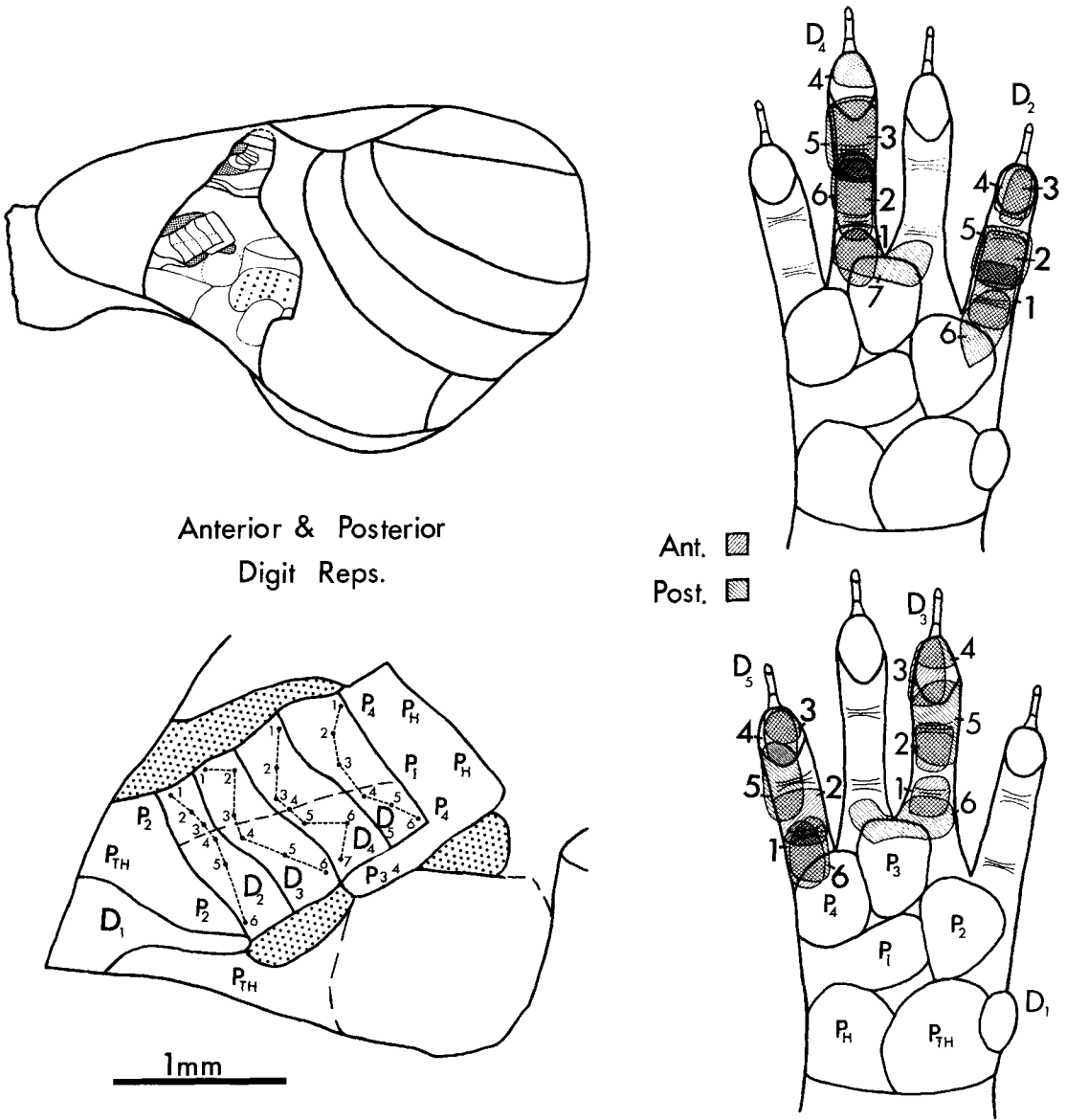Digit Reps.

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1mm

Fig. 4  The double representation of the glabrous hand. Receptive fields are shown for rows of recording sites across the double representations of the digits. Receptive fields progress in a proximal to distal and back to proximal sequence for each row indicating the double representation of each digit. P2-4, pads 2-4; $P_{Th}$, Thenar eminence; $P_H$, hypothenar eminence; $P_I$, insular pad.

roughly on the basis of their adjacency to the two representations of pad 4 and digit 2 respectively, although receptive fields were too large to demonstrate separate and double representations of these pads. Receptive fields on the palmar pads often extended entirely over one pad and sometimes over two or more pads.

Thus, portions of pad 3 and the insular pad were often included by receptive fields that were primarily over pad 4. There were few receptive fields confined to either pad 3 or I. Receptive fields primarily over pad 2 also included parts of pads 3 and I.
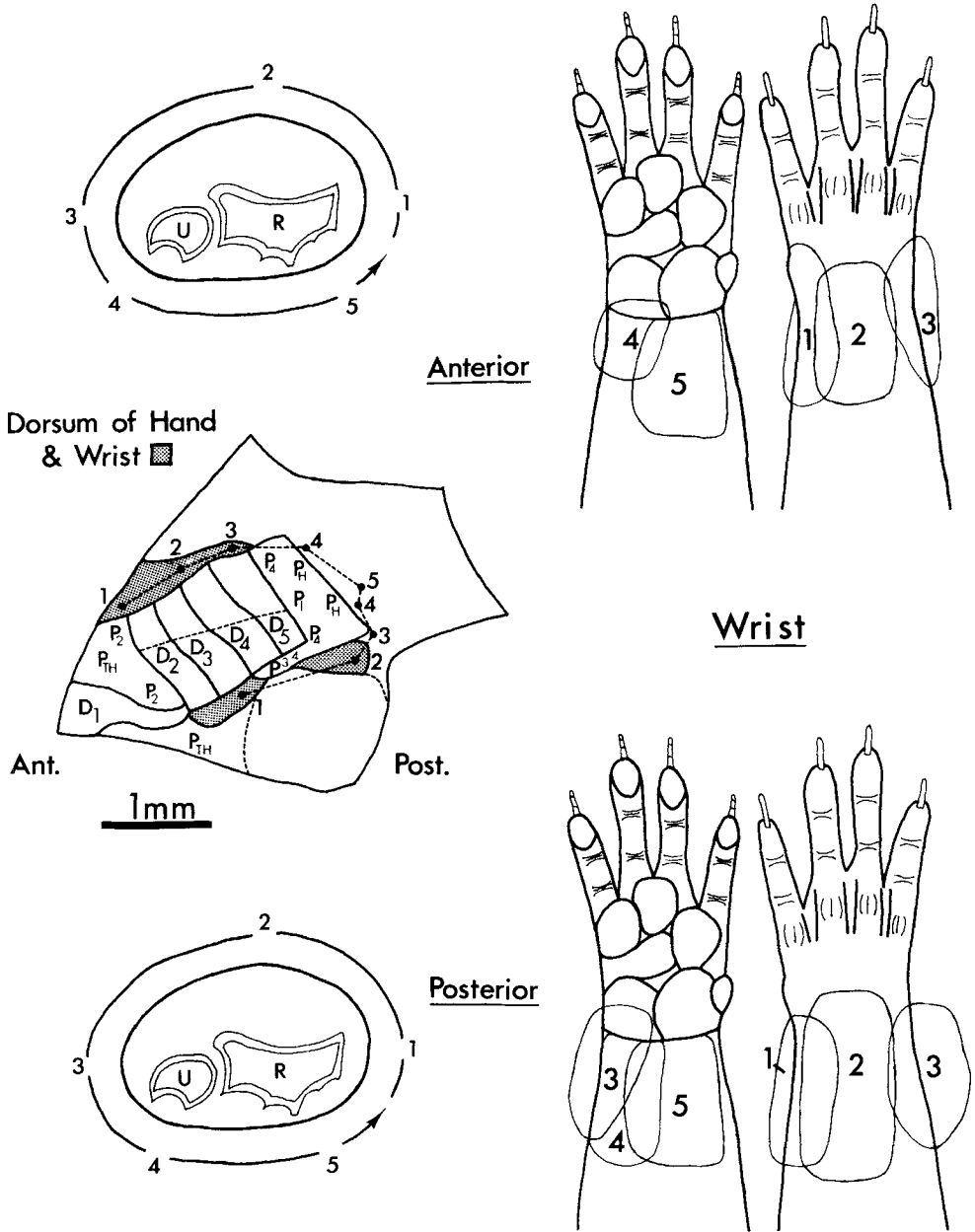
Receptive fields for neurons in the two

Fig. 5 The double representations of the wrist. Anterior and posterior rows of recording sites both yield similar sequences of receptive fields. R, radius; U, ulna. Other conventions as in figures 2-4.

glabrous skin representations did not vary significantly in size, and neurons in the two representations also responded similarly to light tactile stimuli. However, detailed studies of the characteristics of the two sets of neurons related to the glabrous skin are in progress.

Besides the glabrous skin, the dorsum of the hand, the wrist, and the adjoining parts of the forearm are represented twice in SmI. The double representation of the wrist is shown in figure 5 where an anterior row of five recording sites resulted in a progression of re-
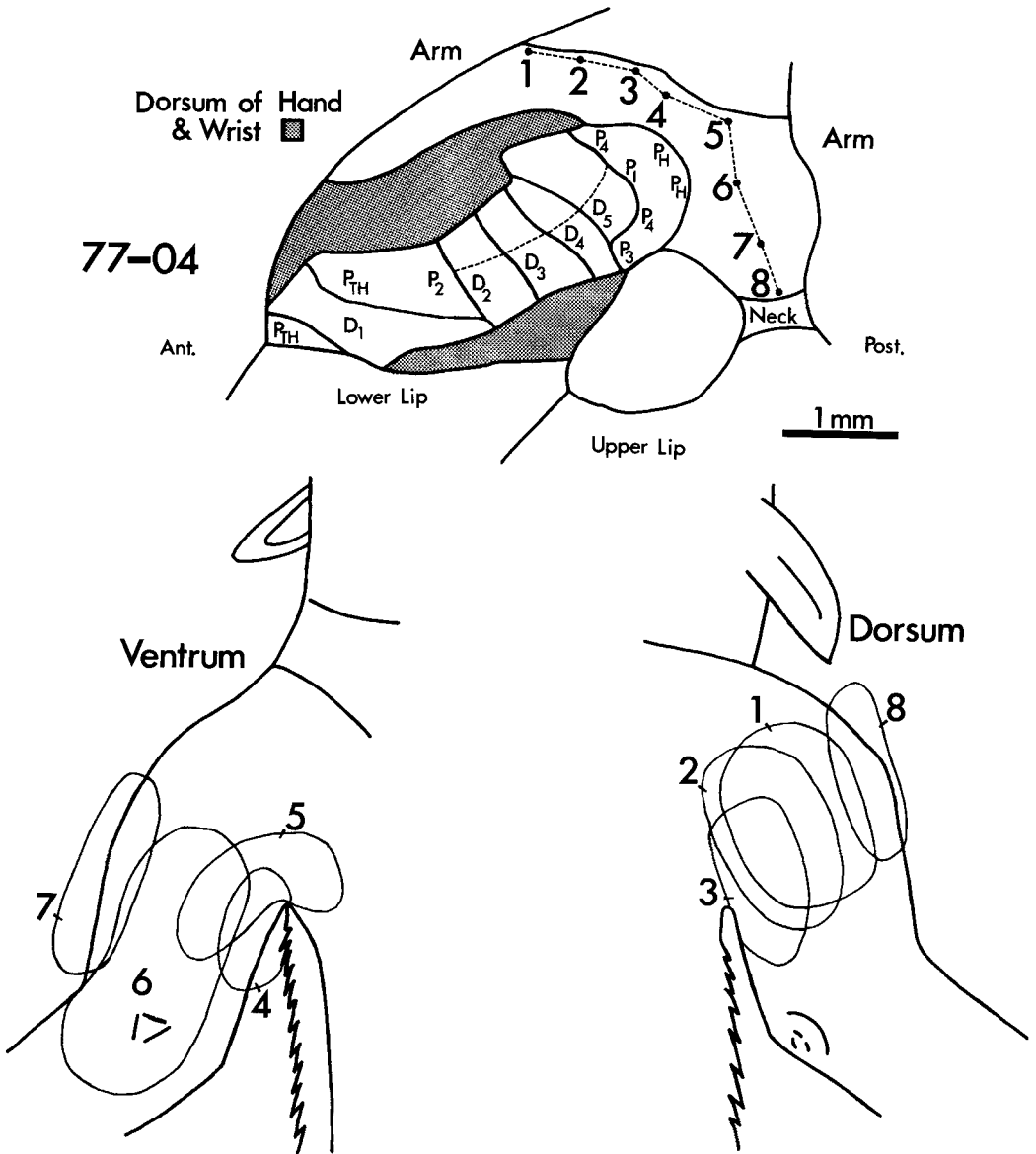
Fig. 6 The representation of the arm and receptive fields for a row of recording sites. Note that the progression of receptive fields circle the arm (fig. 12 illustrates the schematic unfolding of the arm surface on cortex).

ceptive fields from the radial side of the wrist, across the dorsum to the ulnar side, and then across the ventrum to the radial side again (fig. 5, upper). The same progression was found for a more posterior row of recording sites (fig. 5, lower). The two representations of the wrist are split apart by the representations of the glabrous skin, but they join medially at the representation of the ventral wrist.

The two representations of the wrist and forearm merge into a single representation of the arm. A row of recording sites and the corresponding receptive fields demonstrating the organization of the arm area of SmI is shown in figure 6. The receptive field for the most rostral recording site was centered on the dorsum of the upper arm. Successively more caudal recording sites resulted in a procession of
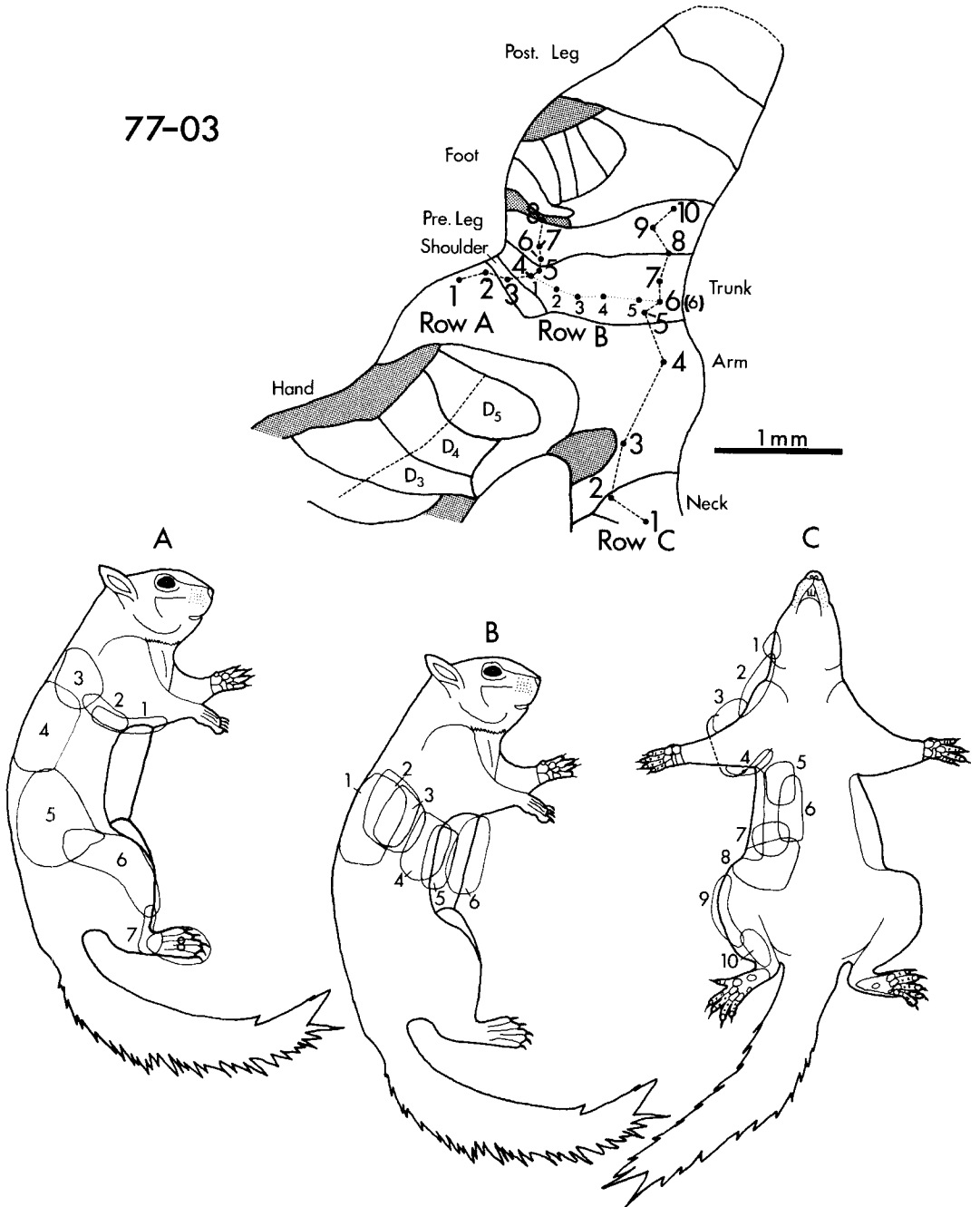
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Fig. 7   The representation of the trunk and receptive fields for three rows of recording sites crossing or within the trunk region. Note the representation of the back in rostral and belly in caudal SmI. Conventions as in previous figures.

receptive fields around the arm, first caudally across the dorsum and then rostrally across the ventrum to end with the radial skin represented adjacent to the neck representation.

*The representation of the trunk*

The organization of the trunk region of SmI of the squirrel was found to be quite different
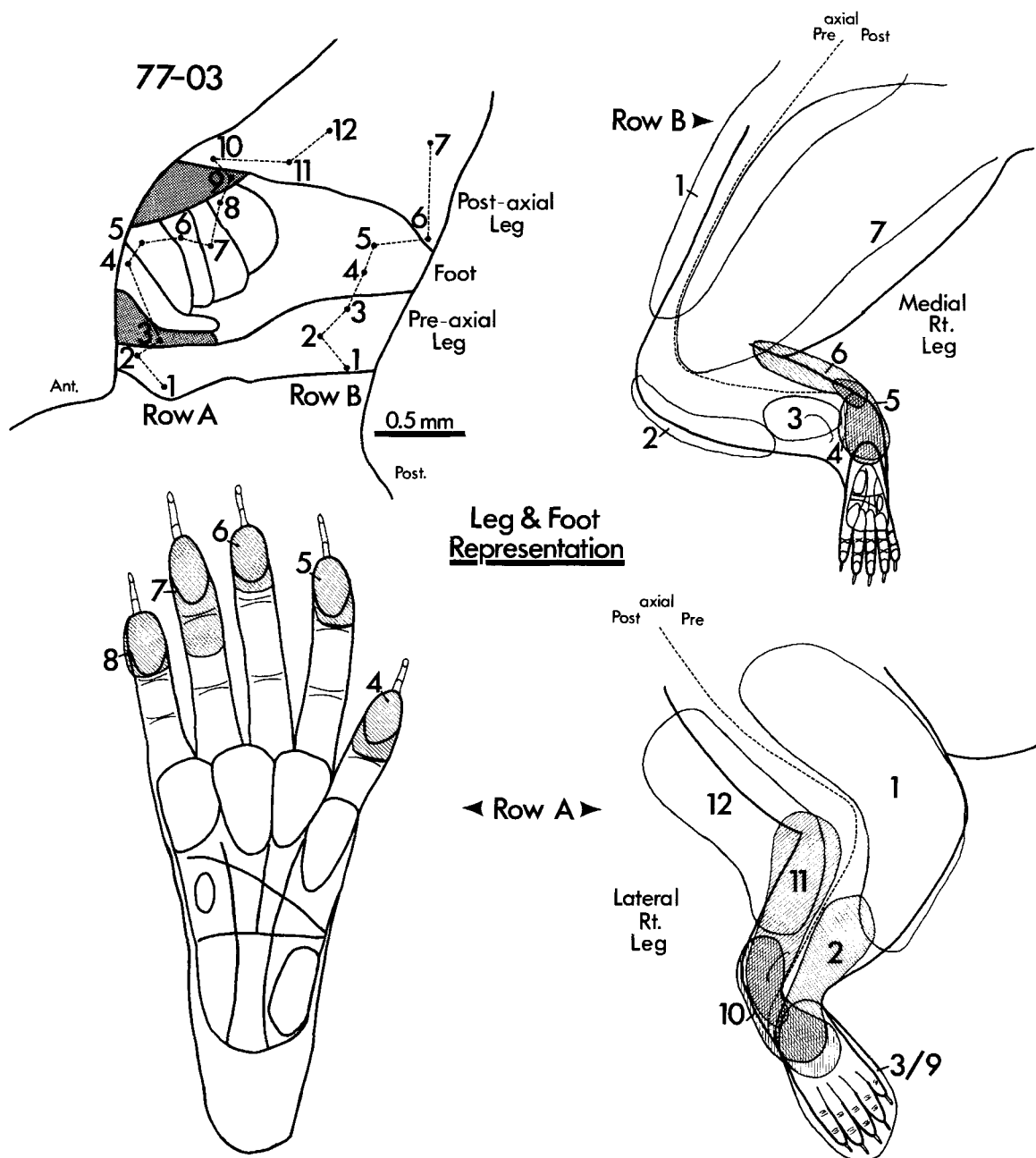
Fig. 8   The representations of the leg and foot and receptive fields for two rows of recording sites that demonstrate that the representation of the leg is split by the representation of the foot. Note also that the inner leg is caudal and the outer leg rostral in SmI. (The representation of the leg and foot is also shown schematically in figure 12.)

from that usually depicted for SmI. While we expected to find the ventrum of the trunk rostrally and the dorsum caudally in SmI, we actually found the reverse organization. Some of the evidence for this conclusion is shown in figure 7. The receptive fields for a rostrocaudal row of recording sites (row B) start at the midline of the back and progress ventrally across the contralateral trunk to end at the midline of the belly. Rows A and C in figure 7

show that the rostral portion of the trunk is represented laterally in SmI. In addition, results from these rows also indicate the representation of the back along the rostral border of SmI, and the belly along the caudal border of SmI. Although the amount of cortex devoted to the trunk is quite small (table 1), similar progressions were found in every case where the trunk region was extensively explored. In no case was there evidence of the back being represented caudally and the belly rostrally.

### The leg and foot

The organizations of the representations of the hind leg and foot are shown in figures 7 and 8. In the experiment illustrated in figure 8, for example, the glabrous tips of the digits 1-5 were represented successively along the rostral border of SmI (row A). The dorsum of the digits and foot activated two narrow zones of cortex just lateral and just medial to the representations of the glabrous digits. The pads of the foot were represented caudal to the digits in SmI (figure 8: row B). The pre-axial leg was found to be lateral to the foot and the post-axial leg medial to the foot in SmI (figure 8: rows A and B). Rostral recording sites in both of these subdivisions of the leg representation were activated by receptive fields that were lateral on the leg while progressively caudal recording sites were activated by more medial receptive fields on the skin surface (DISCUSSION).

### The unresponsive zone, UZ

Figure 2 shows the location of a zone of cortex completely surrounded by SmI that was unresponsive to our usual light cutaneous stimulation. In addition, except for the borders of the UZ, we were unable to clearly activate neurons in the UZ by even more vigorous somatosensory stimulation such as taps and rubbing, or by joint manipulation. The transition from SmI to the UZ was striking, and very similar to the transition between somatosensory and motor cortex. The architectonic features of UZ suggest that this is an island of tissue less specialized for sensory functions within SmI (see below). It is unlikely that the UZ was unresponsive because we failed to stimulate the appropriate body part. We stimulated all available body surfaces in an effort to activate neurons in the UZ. Of course, we could not stimulate the cranial skin because of the surgery required to expose the brain.

However, the representation of the top of the head within the UZ would be inconsistent with the overall topology of the map, would require an unexpectedly large representation of the cranial skin, and would not account for the distinct architectonic appearance of the UZ.

### Individual variations in the SmI map

Each body region was mapped a number of times in detail in different squirrels. These detailed maps showed that the amount of tissue devoted to a body part varies somewhat from squirrel to squirrel, and that the precise arrangement of skin surface is not the same in SmI of all squirrels. For example, figures 4, 6, and 7 show the proportions of tissue devoted to the glabrous and hairy surfaces of the hand digits in three different animals. The hairy skin occupies proportionately much more tissue in the case illustrated in figure 6 than the cases illustrated in figures 4 and 7.

As another example of individual differences, the representations of digit 1 and the palmar pads are not the same in the cases illustrated in figures 4 and 6. In the case of figure 4, the glabrous surface of digit 1 is represented in a strip between the caudal representation of the hairy dorsum of digit 1 and motor cortex. However, in the case illustrated in figure 6, the glabrous surface of digit 1 occupies a strip of cortex between the rostral and caudal representations of its hairy dorsum. Other differences in proportion and detail can be seen by inspecting the cases illustrated in this report. Such results lead to the conclusion that the overall organization of SmI is similar but not identical from squirrel to squirrel. Variations in the details, proportions, and shapes of the representations are found.

### The proportions of body parts of SmI

Proportions of SmI devoted to different body parts vary considerably. The surface areas of cortex devoted to the subdivisions of the body were estimated from photographs of the brain, and are shown in table 1. The photographs were normal to the surface of the brain where the particular body part was represented and included boundaries from experiments on that brain to determine the extent of the representation. The most complete mapping experiments, those used to construct the summary diagram shown in figure 2, were chosen for the measurement of the area devoted to each body

TABLE 1

*Areas and relative proportions of subdivisions within primary somatosensory cortex of the grey squirrel*

| Region | Estimated mm² | % of SmI |
|---|---|---|
| Head | 23.5 | 65.7 |
| Upper lip | 6.7 | 18.7 |
| Lower lip | 5.0 | 14.0 |
| Mystacial vibrissae | 3.0 | 8.4 |
| Nose and eye | 1.6 | 4.5 |
| Intraoral | 6.8 | 19.0 |
| Neck | 0.4 | 1.1 |
| Forelimb | 7.3 | 20.4 |
| Glabrous hand | 3.6 | 10.1 |
| Dorsal hand, wrist | 0.8 | 2.2 |
| Forearm, arm | 2.9 | 8.1 |
| Unresponsive zone | 1.0 | 2.8 |
| Trunk and shoulder | 0.8 | 2.2 |
| Hindlimb | 2.7 | 7.5 |
| Glabrous foot | 1.0 | 2.8 |
| Dorsal foot | 0.3 | 0.8 |
| Preaxial leg | 0.6 | 1.7 |
| Postaxial leg | 0.8 | 2.2 |
| Genitalia and tail | 0.5 | 1.4 |
| Total SmI | 35.8 | 100.0 |

part. From these measurements, we conclude that almost two-thirds of SmI represents the head with large proportions devoted to the lips and intraoral surfaces. Surprisingly, less than 10% of SmI is activated by the mystacial vibrissae. The forelimb occupies about 20% of SmI and about half of the total forelimb representation relates to the glabrous skin of the palm and digits. Together, the representations of head and forelimb constitute approximately 85% of SmI. Thus, little tissue is devoted to the hindlimb, the rest of the body, and the unresponsive zone. If the unresponsive cortex is excluded from the representation area of SmI, the proportion devoted to the head and forelimb become even larger (89%).

The neurons in SmI were activated by light cutaneous stimuli (METHODS), and receptive fields varied in size according to the location of the recording sites in the representation. Some recording sites from each of the body regions and corresponding receptive fields are illustrated in figures 3-8. In figure 3, for example, it can be seen that receptive fields for recording sites on the bridge of the nose and over the eye are as large as 1 cm or more in diameter, while receptive fields on the lower lip near the midline are about 1 mm in diameter. The largest receptive fields, up to 5 cm along the long axis, were found for neurons activated by stimuli on the trunk of the body and proximal leg. Thus, there was a clear correlation between the amount of tissue devoted to

representing different parts of the body and the sizes of the receptive fields of the neurons within each part of the representation.

### Architectonic characteristics of SmI

The architecture of the somatosensory region of cortex in squirrels has been described previously (Kaas et al., '72) and that terminology is used here. In the present experiments, the recording results were related to the cortical architecture by marking critical electrode penetrations with small electrolytic lesions in all mapping experiments. To aid in the identification of the rostral and caudal borders of SmI, most brains, or suitable blocks of cortex from the brains, were cut either in the parasagittal plane or a plane between the parasagittal and horizontal planes. Sets of brain sections were stained for fibers or cells and the SmI region was reconstructed from these sections. The electrolytic marker then allowed the recording results to be related to the histology of the region. This detailed study of the brain sections indicated that SmI is coextensive with the rostral field of koniocortex described as the anterior parietal area, Pa. Furthermore, a specialized region within Pa, distinguished by having less densely packed cells in layer IV, was found to correspond to the unresponsive zone, UZ.

The cytoarchitectonic characteristics of Pa are shown in figure 9. Pa is most readily identified by the densely packed granule cells in layer IV. Layer IV is also more densely packed with cells in comparison with adjoining cortical areas. In addition, distinct outer and inner bands of Baillarger are apparent in brain sections stained for myelin. These features make Pa easy to distinguish from adjoining areas. When microlesions were placed along the borders of SmI, they always were located along the borders of Pa. An example of one such lesion is shown in figure 10. The lesion marks an electrode penetration just rostral to SmI, and the lesion is located in cortex just rostral to Pa.

While the above characteristics hold for most of Pa, there is a specialized region within Pa where the cell packing in layers IV and VI is certainly much less pronounced. This is the unresponsive zone, UZ, identified in the upper part of figure 9 by the clear break in the cell density of layer IV in the cortex labeled B as compared to the cortex labeled A or the cortex lateral to B. The UZ cortex is shown enlarged in the lower part of the figure and compared
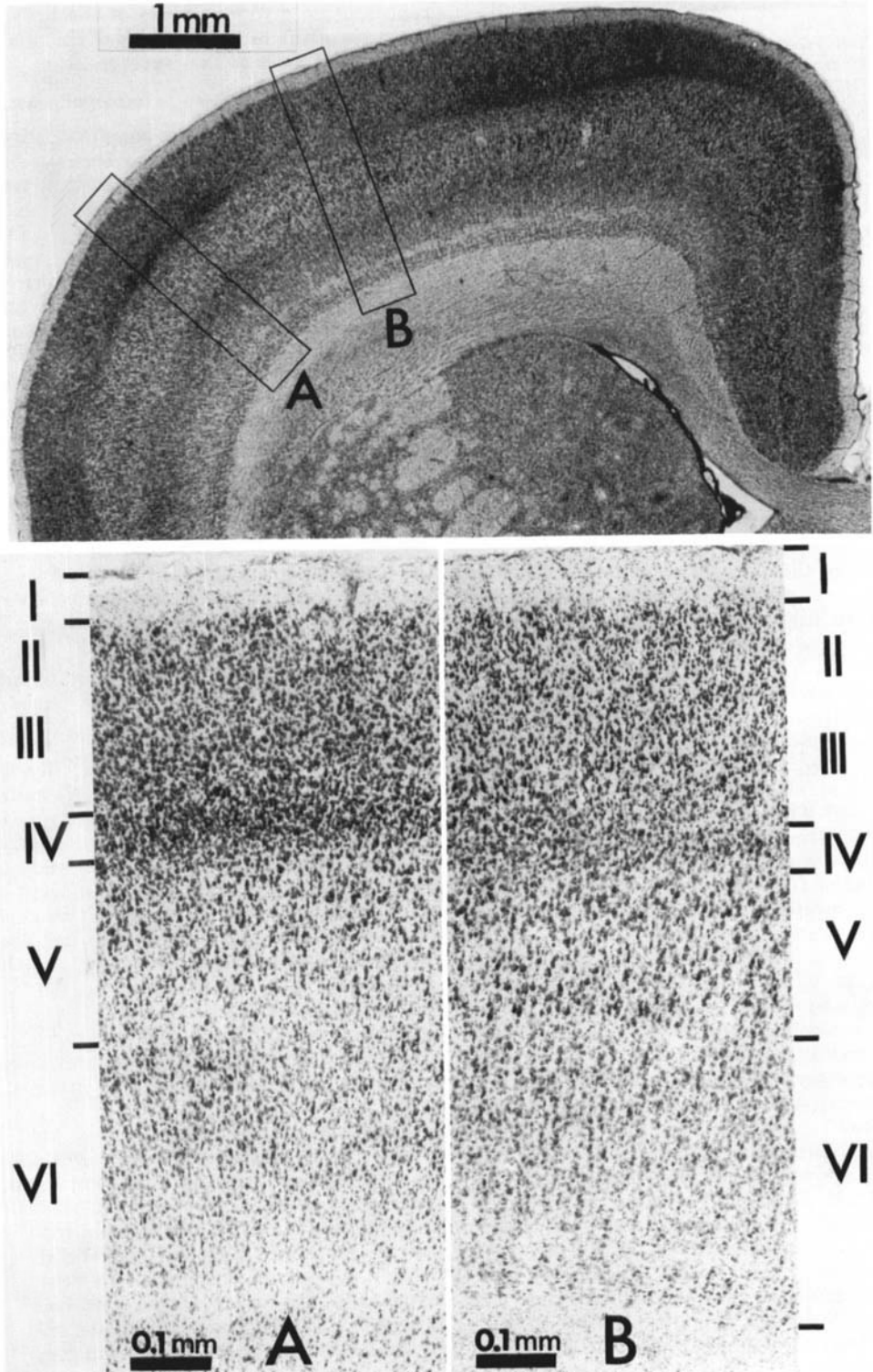
Fig. 9 A thionin stained coronal section through Pa of the grey squirrel.

    A   An enlargement of the cortex which responds to stimulation of the upper lip, representing the basic cytoarchitectural characteristics found in the majority of Pa.

    B   An enlargement of the zone which is unresponsive to cutaneous stimulation depicting the differing cytoarchitectonic features.
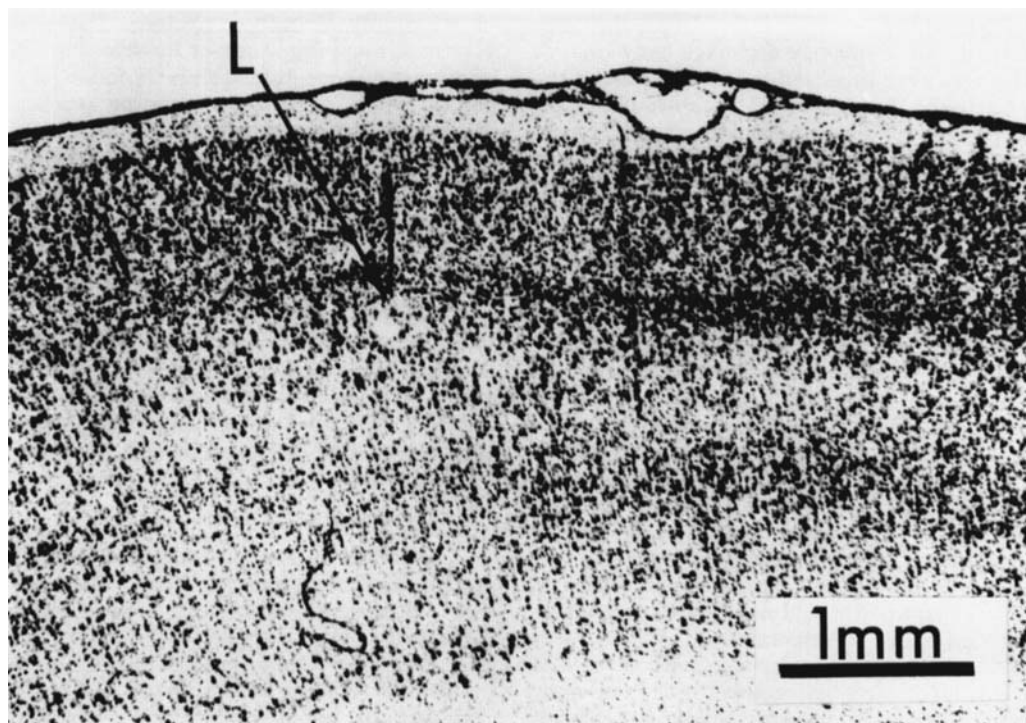
Fig. 10  A microlesion (L) marking a recording site just rostral to the architectonic field, Pa. The recording site was also just rostral to SmI. Parasagittal section. Pa is on the right and frontal (motor) cortex is on the left.

with cortex from a part of Pa representing the upper lip. The reduced cell packing in layer IV of UZ is obvious. In addition, more and somewhat larger and deeply staining pyramidal cells are apparent in layer V. In brain sections stained for myelin, the staining intensity of the inner and outer bands of Baillarger is significantly reduced from that in adjoining parts of Pa. In our experiments, microlesions identified the UZ cortex as the region that was unresponsive to tactile stimuli (fig. 2).

### DISCUSSION

The present study provides a detailed microelectrode map of SmI of the grey squirrel that reveals both specialized and generalized features. The overall organization of SmI is similar to that of other mammals. Spatial constraints result in disruptions in the topology of SmI so that the map is reasonably described as a composite of somatotopic regions. The trunk representation is reversed from the accepted pattern, but it is uncertain if this is a specialized or generalized feature. However, the squirrel is unusual in having a double representation of the forepaw and a large unresponsive zone within SmI.

### SmI as a "homunculus" or "regionally somatotopic composite"

The present results indicate the detailed organization of SmI in the grey squirrel. Such detail raises the important question of how to describe or characterize SmI in mammals. SmI is commonly portrayed as a single continuous map of the contralateral body surface in the form of a "homunculus" or the appropriate animal "unculus." In rodents alone, the organization of SmI has been drawn as a body figurine or "rodent-unculus" for rats (Welker, '71; Woolsey, '52), mice (Woolsey, '67), beavers (Carlson and Welker, '76), capybaras (Campos and Welker, '76), guinea pig (Campos and Welker, '76; Zeigler, '64), and porcupines (Lende and Woolsey, '56). The homunculus concept developed early in the history of mapping studies (see Merzenich et al., '78, for review), and this concept adequately summarized the gross organizational features of SmI at a time when surface recordings from small

or fissured brains often failed to provide adequate detail. The early distorted body surface diagrams were intended to only "represent the general arrangement of the somatotopical organization" of SmI and it was clearly recognized even from the early surface electrode maps that such diagrams were "inadequate to the actual facts" (Woolsey, '58). For example, such diagrams did not distinguish between dorsal and ventral surfaces of the limbs, and had difficulty in dealing with the major discontinuity between the representation of the forelimb and head noted in several animals (see below). However, the homunculus concept has persisted, perhaps because it so simply summarizes a vast amount of data, and there is a widespread opinion that, at least for small smooth-brained mammals, the representation of the contralateral body surface is roughly in the form of a homunculus with no major disruptions in the somatotopic pattern.

Our results on the organization of SmI in the grey squirrel would not be accurately represented by a "rodent-unculus." While many spatial relationships between parts of the body surface are preserved in the cortical map, others are not. To mention a few examples of disjunctive representations of adjoining body parts, the shoulder is represented far from the neck, the glabrous hand adjoins the lower lip, adjacent pads of the paw are separated by representations of the digits, the hairy dorsum of the digits is separate from the glabrous skin of the digits, and the leg representation is split into a preaxial portion lateral to the glabrous foot and a postaxial portion medial to the glabrous foot. Most importantly, the dorsal midline of the trunk is represented along the rostral border of SmI, and the ventral midline is represented along the caudal border (see below). Thus, the trunk is the opposite orientation from that consistent with the homunculus which portrays the back caudally and the distal limbs rostrally on the brain.

The grey squirrel is not the only mammal for which a "homunculus" has been found to inadequately portray the organization of SmI. We have shown that a "simian-unculus" does not reflect the organization of SmI in the owl monkey where both "SmI Proper" and a "posterior cutaneous field" were found to have disruptions and discontinuities similar to those in the squirrel (Kaas et al., '76; Merzenich et al., '78). Likewise, in a recent microelectrode mapping study of SmI of opossums, Pubols et al. ('76) illustrated the results as a composite

of regionally somatotopic sectors. The microelectrode mapping study of Pubols et al. ('76) is of particular interest since it followed two earlier surface electrode mapping studies of opossums that summarized SmI organization with a "homunculus" (Lende, '63; Magalhaes-Castro and Saraiva, '71). As a final example of organization not reflected by the homunculus, separate and adjacent representations of the glabrous skin and dorsal hairy surfaces of the paws of raccoons (Welker and Seidenstein, '59) and slow lorises (Krishnamurti et al., '76) have been noted. In view of the above results, it seems reasonable to suggest that SmI in many, if not all, mammals would be more accurately described as a "regionally somatotopic composite" (Merzenich et al., '78) than as a homunculus.

### SmI organization in the squirrel

Many of the generalized features of SmI organization such as the progression from tail to head with medial to lateral locations in the cortex have been reviewed by Woolsey ('58) and others (Welker and Seidenstein, '59; Lende, '69; Welker and Campos, '63; Welker, '71), and are not discussed further here. Instead, the unexpected and unusual aspects of SmI organization in the squirrel are considered. These include (1) the "reverse order" representation of the trunk, (2) the "split" representation of the post- and preaxial leg, (3) the double representation of the forepaw and adjoining forelimb, and (4) the unresponsive zone. In addition, the representation of (5) the mystacial vibrissae which have been extensively studied in rodents, is discussed.

*The trunk.* An unexpected finding was that the trunk region of SmI of the squirrel is organized in a reversed manner from the way it has been described for SmI in other mammals. Thus, we found the back of the squirrel to be represented rostrally and the belly caudally in SmI instead of the back caudally and the belly rostrally as has been illustrated and/or described for a wide range of mammals (see below). This unexpected finding allows us to reconsider our earlier mapping studies in a New World primate. Previously, we described a complete representation of the body surface within the architectonic field 3b of Brodmann ('09) of somatosensory cortex in the owl monkey (Kaas et al., '76; Merzenich et al., '78) which we considered to be the homolog of SmI of other mammals. In Area 3b, the back of the monkey was represented near the rostral

border and the belly towards the caudal border. Since this was the reverse from the accepted organization of SmI, we considered our arguments of homology weakened. Now, in view of the results in the squirrel, it seems reasonable to consider the possibility that the organization of the trunk region that is found in squirrels and owl monkeys is widespread in mammals, and perhaps even typical of SmI. The principal reason for seriously considering this possibility is that the organization of the trunk region of SmI is poorly documented. Proportionally little tissue is devoted to the trunk representation. For example, the trunk subdivision in five species of the family Procyonidae of the order Carnivora ranges from 3-5% of the surface area of SmI (Welker and Campos, '63). Furthermore, the receptive fields for the trunk are much larger than those for most other parts of the body (Welker, '73). Thus, it would be difficult to disclose the organization of the trunk representation especially with surface electrodes.

Typically, mapping studies have been unable to arrive at clear conclusions in regard to the organization of the trunk region of SmI. For example, Pubols et al. ('76) in a study of SmI of opossums, found the representation of the trunk "so small" that they were "unable to map it in any detail, even with closely spaced microelectrode penetrations." As a more extreme observation, Johnson et al. ('74) failed to find any representation of the trunk in SmI of sheep and speculated that it is either absent or very small. Likewise, Welker et al. ('76) did not find a representation of any part of the trunk in llamas. Many studies have simply failed to mention the organization of the trunk representation (Woolsey and Fairman, '46; Welker and Seidenstein, '59; Welker and Campos, '63; Lende and Sadler, '67; Rubel, '71; Saraiva and Magelhaes-Castros, '75; Krishnamurti et al., '76; Carlson and Welker, '76). Other investigations have described the traditional organization without presenting supporting data (Welker, '71; Hall and Lindholm, '74). However, a number of studies have included limited data supporting the traditional view (Hamuy et al., '56; Lende, '63, '64, '70; Zeigler, '64; Campos and Welker, '76; Welker and Carlson, '76). Perhaps the most extensive results supporting the contention that the back is represented caudally in SmI comes from the microelectrode mapping studies in the hyrax where belly to back progressions of receptive fields are shown for rostral

to caudal progressions of recording sites (Welker and Carlson, '76). We conclude that the representation of the trunk in SmI has not been extensively studied, that there may be species differences in the way the trunk is represented, and that further mapping studies are needed. Toward this end, we have recently mapped the trunk region of SmI of *Galago senegalensis,* a prosimian, and obtained results similar to those in owl monkeys and squirrels (Sur, Nelson, and Kaas, unpublished studies).

*The split leg.* A second unexpected finding was the split representation of the hindlimb in the squirrel so that part of the hindlimb was found medial and part lateral to the foot in SmI (figs. 2, 8, 12). The line of the split was variable, and difficult to accurately determine, but it appeared to roughly correspond with a division of the leg into pre- and postaxial surfaces. This result was unexpected in squirrels since a separation of two parts of the leg representation by the foot has not been reported for other rodents, and such a split has been specifically denied in a careful microelectrode mapping study of SmI in rats. However, a split leg representation has been commonly found in primates (see Merzenich et al., '78, for review) and has also been described for cats and rabbits (Woolsey and Fairman, '46) and suggested for dogs (Hamuy et al., '56). Since most mapping studies in nonprimates have failed to mention the details of the representation of the leg, it is not yet possible to determine if the split representation of the leg is a specialized or generalized feature of SmI organization. However, evidence of this split in Carnivores, Primates, Rodents, and Lagomorphs suggests that the split representation is a generalized feature.

*The double forepaw.* A specialized feature of SmI in the squirrel is the duplicated representation of the distal forelimb. Such a double representation of the forelimb in SmI has not been reported for any other mammal. The generalized type of representation of the glabrous forepaw is shown schematically in figure 11. The digits are oriented rostrocaudally with the thumb lateral and the little finger medial. The digit tips point rostrally. In squirrels, the small size of the structurally altered "thumb" made it difficult to determine the precise representation of the digit. However, the other four digits were clearly represented twice in the manner shown in figure 1B (also figs. 2, 4). In the more caudal representation the digits

point rostrally as in SmI of other mammals. In the rostral representation, the digits point caudally. Thus, the two representations of the digits have opposite orientations and are mirror images of each other joined at the finger tips. Perhaps as a consequence of the double representation of the digits the glabrous pads of the forepaw are largely discontinuous with the base of the digits in an atypical fashion. The pads of the palm and the wrist are also represented twice. The two representations of the glabrous surface of the hand along with those of the dorsum, wrist, and forearm are considered to be within primary somatosensory cortex for the following reasons: (1) Both representations are part of the larger somatosensory area responding to light cutaneous stimulation, having well-defined receptive fields and containing a complete map of the body surface. There were no unresponsive electrode penetrations between the two representations whereas boundaries of SmI were clearly obtained by nil penetrations along the rostral and caudal margins. (2) Both representations are within a single and distinct cytoarchitectonic field with a densely packed and myelinated layer IV. (3) Our studies have identified SmII, also representing the complete body surface and containing a separate map of the hand, as caudal and lateral to SmI (Sur et al., '77). (4) Stimulation of cortex with microelectrodes revealed the hand region of primary motor cortex, MsI, as rostral to the SmI hand area; thus, we have discounted the possibility that one of the hand representations might belong to MsI.

The functional significance of the double representation of the forepaw and the phylogenetic history of its development remain a matter of speculation. The orientation of the digits in the caudal representation is characteristic of other mammals, suggesting that this is the prototypical representation. Presumably, the double representation confers some advantage and occurred at some point in the evolution of squirrels or their ancestors. The results suggest that as a result of mutation, parts of sensory representations may replicate and assume functional significance. While double representations of the forepaw in SmI have not been found elsewhere, a double representation of the mystacial vibrissae is found in opossums (Pubols et al., '76). Thus, the replication of body parts within SmI is not confined to squirrels.

Quite different types of joined representations of the glabrous hand are found in primates as parts of two separate fields. The representation of the hand in SmI proper of the owl monkey is similar to that found in other mammals (Merzenich et al., '78). An adjoining representation in a second field, the posterior cutaneous field, contains a "mirror image" of the hand of SmI. These two representations are joined along the palm (fig. 11C). Recently we have obtained similar results for squirrel monkeys (unpublished). In Macaque monkeys, two representations of the glabrous hand in two separate fields have been reported (Paul et al., '72), but in both of these representations the finger tips point rostrally and the representations are serial (fig. 11D; Merzenich et al., '78). Thus, the double representation of the hand in primates differs from that in squirrels by (1) being in two separate cutaneous fields, and (2) having different orientations. These ways of joining double representations show that several patterns are possible when sensory representations are replicated. All types maintain roughly similar medial to lateral sequences of representation.

We have suggested that separate representations of sensory surfaces are required because the spatial constraints imposed by the requirements of local neural circuits restrict the number of functions that can be mediated by a single representation (Kaas, '77). Thus, separate representations are used to perform subsets of functions that can be interrelated over long interconnections. It seems likely that the dual representation of the forelimb in SmI of the squirrel also allows some separation of functions. While the overall architectonic, organizational, and neural characteristics of the two representations appear to be quite similar, we expect that differences will be revealed.

*The unresponsive zone.* The large unresponsive zone (UZ) of cortex within SmI of the squirrel (fig. 9) is another interesting feature of SmI of squirrels. Our inability to activate neurons in the UZ under our recording conditions suggests that this cortex is not involved in early stages of sensory processing. Perhaps the UZ is more involved instead in efferent activities. This possibility is suggested by the histological structure of the UZ as compared to the rest of SmI. The UZ has larger and more densely packed cells in layer V and few and less densely packed small cells in layer IV. Furthermore, our preliminary experiments with electrical stimulation of the UZ resulted
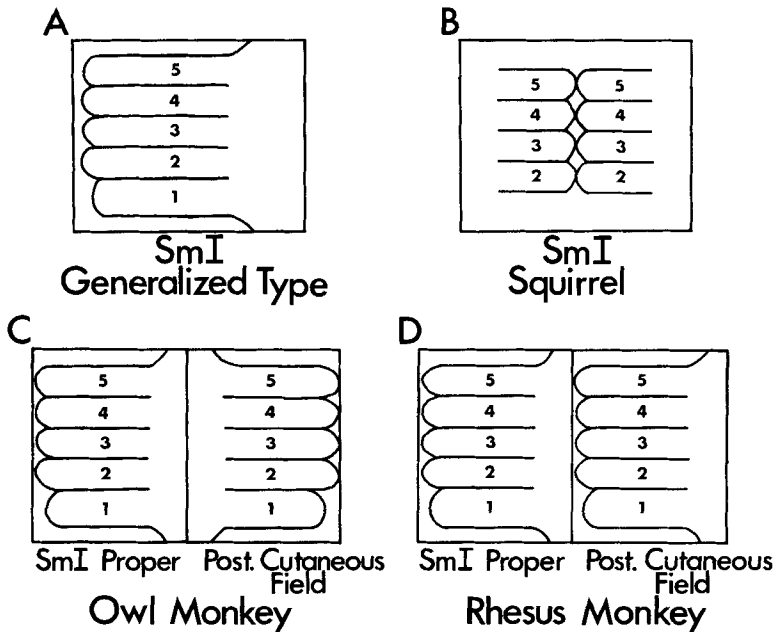
Fig. 11   A schematic illustration of the ways the glabrous digits are represented in somatosensory cortex of different mammals.

   A   The orientation of the digits and palm in SmI of most mammals. The digit tips are along the rostral border of SmI.

   B   SmI of the grey squirrel has two representations of the digits joined at the digit tips. The caudal representation of the digits has the orientation of the generalized tips.

   C   In owl monkeys (Merzenich et al., '78), the orientation of the digits in SmI proper (architectonic field 3b) is of the generalized type. The digits in the posterior cutaneous field (architectonic field 1) point in the opposite direction.

   D   In rhesus monkeys two serial representations of the hand have been reported (Paul et al., '72). The orientations of both representations are of the generalized type.

in hand movements. However, the levels of SmI stimulation were higher than those producing hand movements in motor cortex and the possibility that the UZ is a "motor island" surrounded by sensory cortex needs further investigation. Another possibility is that the UZ is a major source of callosal connections (see below).

While the large unresponsive zone with a poorly developed layer IV is the most obvious in squirrels, narrower zones with similar architectonic characteristics are also found within SmI (Kaas et al., '72). These zones appear to separate distinct body parts in the representation, although we have not established this contention with critically placed microlesions. However, cell-poor "septal regions" in SmI of rats have been identified with microlesions as being located between the representations of different body parts (Welker, '76). For example, such a cell-poor zone was found between the representations of the lower lip and

forepaw. As in the UZ, neurons usually "could not be isolated and driven" in these narrow zones. When activity was recorded, Welker ('76) suggested that it might be the activity of neurons in the adjacent cortex. Likewise, in an earlier study of SmI of racoons (Welker and Seidenstein, '59), narrow cell-poor unresponsive zones separated the representations of the digits. In rats, the cell-poor zones and the areas with densely aggregated cells have different patterns of connections. The aggregations of cells in layer IV appear to receive most of the thalamocortical input from the ventroposterior nucleus (Killackey and Leshin, '75; Killackey et al., '76) while commissural connections terminate largely in the cell-poor zones (Wise and Jones, '76). This evidence suggests that the UZ in squirrels may be an important source of callosal projections.

*The representation of the mystacial vibrissae.* Stimulation of the mystacial vibrissae has been found to activate a large proportion

of SmI in both mice (Woolsey, '67) and rats (Welker, '71), and the vibrissae region has been related to a subfield where cells in layer IV form identifiable groups termed "barrels" (Woolsey, '67; Woolsey et al., '75). In squirrels, the mystacial "barrel" field is both absolutely and proportionately smaller than in rats (Welker, '71) where it occupies 9.0 mm² of surface area and 20% of SmI compared to 3.0 mm² and 8.4% in squirrels (table 1). The barrel field is difficult to recognize architectonically in squirrels and other sciuromorphs (Woolsey et al., '75), and it is possible that the mystacial vibrissae are behaviorally less significant in the highly visual squirrels than in rats (Welker, '64) and some other rodents.

### Determinants of the cortical map in SmI

Once the topography of the cortical map in SmI has been characterized, it is possible to ask why the map is organized the way that it is. One long standing view is that the map is a consequence of the order of sensory input into the spinal cord and brain stem (see Merzenich et al., '78, for review). An extreme form of this concept would argue that the cortical map is nothing more than a lateral to medial overlay of successive dermatomes. Thus, the organization of SmI would be determined by the organization of the peripheral nervous system and it would be pointless to speculate about the functional significance of the resulting cortical map. Others have argued that the cortical map does not closely correspond to the dermatomal order and that other factors must be important in generating the central representation (Pubols and Pubols, '71; Merzenich et al., '78).

Our data on the grey squirrel are extensive enough to allow us to address the issue of how closely the cortical organization of SmI follows the sequence of the peripheral input. Although the arrangement of the dermatomes has not been determined for squirrels, the boundaries of dermatomes appear to be consistent enough across mammals to permit a generalized plan to be extended to the grey squirrel. When the cortical map and the dermatomal patterns are considered, it is obvious that there are numerous instances where the cortical map does not follow the dermatomal sequence and where discontinuities in the map do not fall along dermatomal boundaries. Some of these instances follow: (1) The opthalmic, maxillary, and mandibular branches of the trigeminal nerve are not part of a medi-

al to lateral sequence in cortex; instead the representation of the face and head is basically rostrocaudal in orientation. Thus, the lower lip is most rostral, the upper lip is caudal to the lower lip, and the nose, periorbital skin and mystacial vibrissae are most caudal in SmI. (2) The head and hand representations do not follow a dermatomal sequence. The glabrous hand adjoins the lower lip while the proximal upper face is bordered by the neck. (3) The dual representation of the hand is not a consequence of the dermatomal sequence. (4) The unresponsive zone disrupts the sensory sequence. (5) A single representation of the arm joins a dual representation of the wrist and distal forearm in a manner that is unrelated to dermatomes. (6) The trunk representation is reversed with respect to the orientation of the face and the foot. (7) The boundary between hairy and glabrous foot regions does not follow dermatomal lines to any appreciable extent. The dorsum of the foot is represented in a strip of cortex adjoining the glabrous digit tips. Thus, it is not possible to account for the organization of the SmI map solely in terms of the orderly arrangement of peripheral input into the spinal cord and brain stem. This does not mean that the dermatomal arrangement does not have a bearing on the SmI map. For much of the skin surface, following the dermatomal sequence in cortex would preserve an order that would be functionally significant too, and it is therefore impossible to determine whether functional or dermatomal factors are important in these parts of the cortical map. In addition, the split repre-

Fig. 12   Schematic illustrating the two different ways in which the cylindrical arm and leg skin are represented on the cortex of the grey squirrel. *Above:* the leg surface has two lines of discontinuity and is represented in separate preaxial and postaxial regions lateral and medial to the foot. The lines separating the two regions curve substantially on the leg, as shown by the arrow orientations at three representative levels on the leg from proximal to distal. Reconstruction of the 3-dimensional surface from its 2-dimensional representation clearly identifies it as equivalent to the cylindrical leg surface. The leg (upper left) is simplified as a cylinder (below). One segment of the surface of the leg (thick arrows), is represented lateral to the foot (middle right); the other segment (thin arrows) is represented medial to the foot (upper right). The numbered arrows on the right indicate the three numbered levels on the leg. Compare with figure 8. *Below:* the arm surface has only one line of discontinuity, which is necessary whenever a 3-dimensional cylindrical surface has to be laid over a 2-dimensional plane. The split separates the lateral from the anterior arm skin. Receptive fields that are adjacent to each other on the arm but on two different sides of the split are represented far apart on cortex. Compare with figure 6. A, anterior; L, lateral; M, medial; P, posterior.
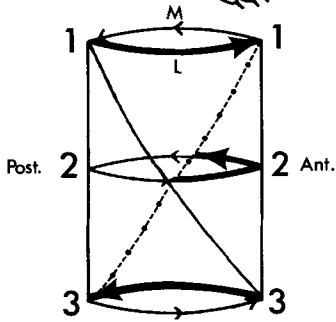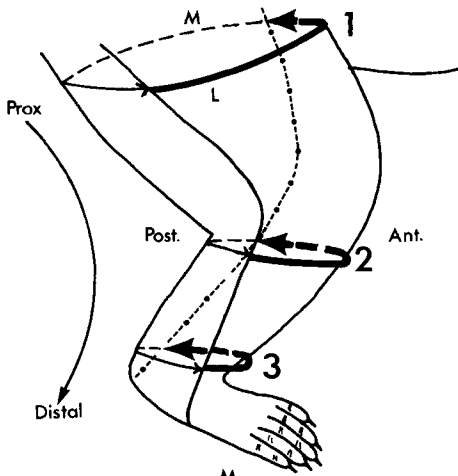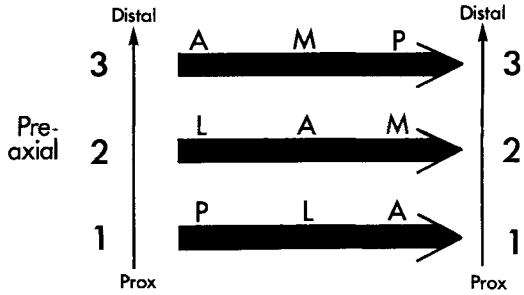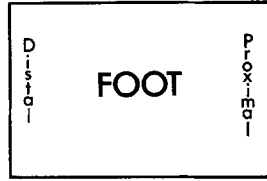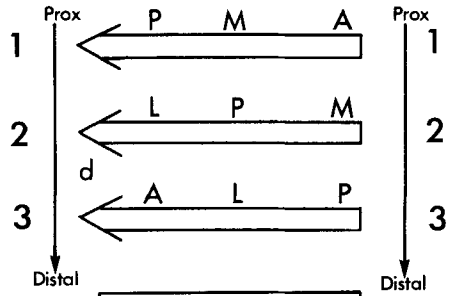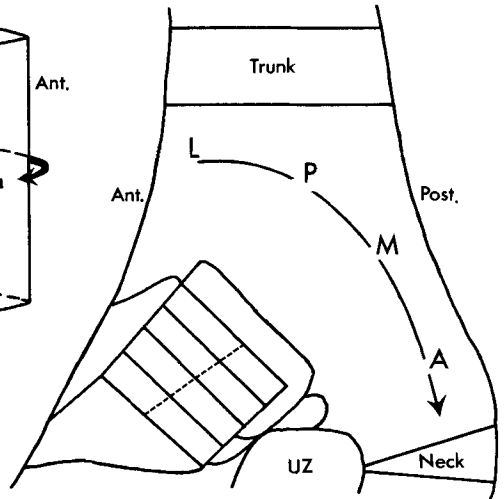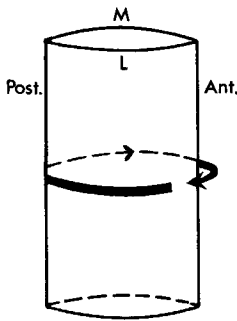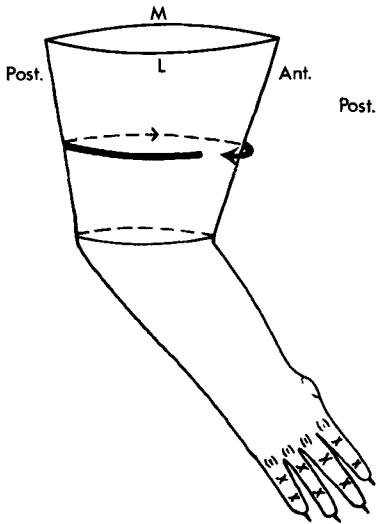
Figure 12

sentations of the neck and shoulder and the split representations of the leg approximately along pre- and postaxial lines argue for a dermatomal influence on the cortical map. However, it is clear that the cortical map does not closely resemble the dermatomal pattern, and therefore, anatomical reorganization of sensory input must occur.

Given the considerable constraints imposed by the distortions of body parts within SmI and the necessity of fitting the contralateral body surface into a two dimensional array on the brain, the major consideration in the formation of the SmI map appears to be to preserve somatotopy for the representation of functionally related skin surfaces, and when disruptions are required, to have these disruptions occur along lines or surfaces that are functionally unimportant. For example, in the arm representation the skin is in effect split along the dorso-radial surface and laid out along the hand, wrist, and forearm representation on cortex (fig. 6). Adjacency relationships across the two sides of the split are lost due to the unfolding; however, the split takes place along a line separating the dorsal and ventral arm or dark and white fur regions rather than through the middle of the dorsal or ventral surfaces. Likewise, the enlarged representation of the forelimb in SmI forces the separation of the representations of the neck and shoulder, and this separation also is along a line of little apparent functional significance. The principle of functional topography is further illustrated by the difference in the representations of the leg and arm. For purposes of discussion both of these skin surfaces can be simplified into the curved surface of a cylinder (fig. 12). Since the forelimb representation in SmI is relatively large (table 1), the arm can be arrayed and matched along the wrist and forearm representation with only a single split in the "cylindrical" arm surface. Since the hindlimb representation is relatively small, the entire leg surface cannot be arrayed topographically around the foot. Thus, the leg representation is split into two separate portions — a representation of largely the preaxial surface lateral to the foot representation and a representation of largely the postaxial surface medial to the foot representation. Both the arm and leg representations can be considered as topologically equivalent to split cylindrical surfaces, although the arm representation requires only one split,

and the leg requires two. It is not necessary to consider the hindlimb representation of the squirrel as a more complex transformation of the skin surface such as a Klein bottle as described for the rhesus monkey (Werner, '70). A Klein bottle is a non-orientable, three-dimensional surface that eliminates distinctions between the inside and outside of the surface, and it is not topologically equivalent to the hindlimb of the squirrel.

The findings on SmI in the squirrel presented in this study emphasize that maintaining topography is an important attribute of cortical somatosensory representations. Splits or discontinuities are required in SmI topography in order for the parts of the map to fit together. However, the splits occur where they least disrupt the representations of functionally significant skin surfaces. Thus, the dual requirements of form and function appear to determine the organization of the cortical map.

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