

# The Organization of the Second Somatosensory Area (SmII) of the Grey Squirrel

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**ABSTRACT** Microelectrode mapping methods were used to determine the organization of the second somatosensory representation, SmII, in grey squirrels. A systematic representation of the contralateral body surface was found in lateral parietal cortex adjoining the first somatosensory representation, SmI (Sur et al., '78a). The representation of the body in SmII was found to be much less distorted than in SmI. Under our recording conditions, almost all recording sites were activated from strictly contralateral body locations. The most important finding was that the basic orientation of the body representation in SmII is "erect" rather than "inverted." This orientation allows SmII and SmI to be adjoined along a common border representing the top of the head and face. This type of border has been called congruent (Allman and Kaas, '75; Kaas, '77), and it may have significance in the development of sensory representations.

Recently, the basic orientation of the body surface representation in the second somatosensory area, SmII, has become a matter of controversy. The issue of disagreement is shown schematically in figure 1. In the early summary diagrams of SmII organization by Woolsey and Fairman ('46), the sequence of representation of the face, arm, and leg was portrayed, while the orientation of these body parts within SmII was not an issue (fig. 1A). Later, the organization of SmII was summarized by Woolsey ('52, '58) and others (Hamuy et al., '56; Lende and Woolsey, '56; T. A. Woolsey, '67; Campos and Welker, '76) as an inverted "homunculus" adjoining the head representation of the primary somatosensory area, SmI (fig. 1B). In this conceptualization, SmII is a rotated serial replication of SmI. The "inverted" organization for SmII has been widely accepted, and it is commonly illustrated in reviews and textbooks (see Haight, '72 for references). A quite different view was first expressed by Haight ('72), and more recently by Johnson et al. ('74), Herron, ('75) and Campos and Welker ('76). These investigators suggest that the basic organization of the head, arm, and foot in SmII is the opposite of that commonly illustrated, and that when SmII organization is summarized as a "homunculus," the orientation is erect rather than inverted (fig. 1C). In the erect pattern,

SmII can be considered as a "mirror image" of SmI with a rotation from a parallel to a roughly perpendicular alignment.

It is not completely clear from the published reports if the orientation of SmII is upright, inverted, or variable. Because of its relatively small size, the large size of receptive fields for SmII neurons, and the problem that SmII is often completely buried in fissures, the basic organization of SmII has been difficult to determine. In some of the early mapping studies with surface recordings, only part of SmII was explored and data relevant to the orientations of SmII were not collected (Adrian, '40; Woolsey and Fairman, '46; Berman, '61). Some early investigations of SmII organization have been reported only in abstracts and reviews (Woolsey, '43, '52, '58; Woolsey and Wang, '45) without results supporting conclusions. Other studies in mammals have indicated that SmII is too small relative to the surface electrode for the method to indicate the orientation of SmII (Zeigler, '64; Lende and Sadler, '67; Woolsey, '67; Lende, '70; Saraiva and Magalhães-Castro, '75). However, at least two reports of SmII organization based on surface recordings illustrated receptive fields for progressions of recording sites that are clearly more consistent with the concept of an inverted orientation (Hamuy et al., '56; Lende and Woolsey, '56).

In principle, microelectrode mapping studies can explore SmII in much greater detail and provide more certain evidence as to the orientation of SmII. Yet, SmII is so small in the opossum that a recent detailed microelectrode study failed to reveal the orientation of the area (Pubols, '77). Other microelectrode mapping studies of somatosensory cortex failed to establish the location of SmII (Carlson and Welker, '76) or collected little data from SmII (Kaas et al., '70; Campos and Welker, '76; Welker and Carlson, '76). In two other microelectrode mapping studies of somatosensory cortex of the sheep (Johnson et al., '74) and the llama (Welker et al., '76), receptive fields were shown for a limited number of recording sites in SmII with locations that support the view that SmII is upright. However, the trunk and limb representations in SmI were not found in these studies, and the possibility remains that the receptive fields illustrated for these parts of the body for SmII were actually from recording sites in SmI (Welker et al., '76). There appear to be only two published microelectrode studies of the organization of SmII where enough data were collected to determine the orientation with certainty. After collecting data from a total of 421 electrode penetrations in the SmII region of cats, Haight ('72) concluded that the orientation of the area is upright. In a similar microelectrode study on SmII on the rat based on 173 electrode penetrations, Welker and Sinha ('72) concluded that SmII is inverted. Neither study illustrated recording sites and receptive fields to support their quite opposite contentions.

Given the uncertainty about the basic organization of SmII in mammals, we decided to investigate this issue in the grey squirrel where the smooth cortex and relatively large brain would facilitate mapping. We considered the issue of the orientation of SmII important for two reasons. First, we have been impressed with the evidence that many of the auditory, somatic, and visual sensory representations are at least partially matched along their common borders so that receptive fields for adjoining recording sites in two representations roughly correspond in location on the receptor surface (Kaas, '77). These types of borders have been termed congruent (Allman and Kaas, '75), and they are common enough to suggest that they are important for developmental or functional reasons (Kaas, '77). As can be seen from figure 1, an upright

SmII could have a congruent border with SmI along the representation of the top of the head, while an inverted SmII could not. A second reason for investigating the orientation of SmII is that the interpretation of data from other studies sometimes depends on knowing the correct orientation. For example, Jones and Powell ('68, '73) summarized the evidence for the distributions of callosal connections in SmII and, assuming an inverted orientation for SmII, concluded that the distal hand and foot areas of SmII are almost devoid of callosal interconnections. If one assumes that the orientation of SmII is upright, then one might come to the quite different conclusion that the distal forelimbs are densely interconnected in the two representations.

The results of our investigation support the view that SmII is upright. In addition, observations were made on the proportions of SmII devoted to various body regions and comparisons were made between SmII and the more specialized SmI in the squirrel (Nelson and Sur, '77; Sur et al., '78a). An abstract of some of these results has appeared elsewhere (Sur et al., '77).

#### METHODS

The procedures employed in the present experiments were basically those described more fully in our report of the organization of primary somatosensory cortex, SmI, in grey squirrels (Sur et al., '78a). In the present study, the somatotopic organization of the second somatosensory area, SmII, was explored with microelectrode mapping methods in 11 grey squirrels, *Sciurus carolinensis*. Platinum-iridium microelectrodes were used to record from small clusters of neurons, usually at depths of 600-1,000  $\mu$  from the cortical surface where the most easily driven neurons were found. The location of each electrode penetration was marked on a high resolution photograph of the brain surface and vascular pattern of the SmII region. Receptive fields were determined by light tactile stimulation of the body surface with hand-held fine glass probes. The boundaries of each receptive field were marked on line drawings of the appropriate body region. Although the surface area of SmII is only about 4 mm<sup>2</sup> (RESULTS), as many as 40 penetrations within SmII were placed in a single experiment. In addition, 40-60 electrode penetrations were usually made in tissue around SmII in order to define the adjoining parts of SmI, auditory, and non-re-

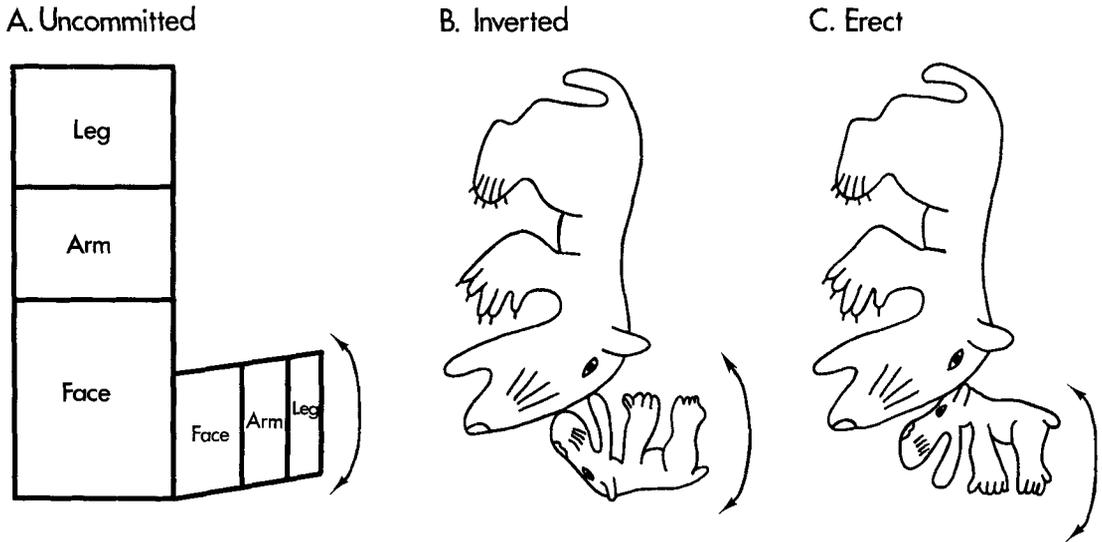


Fig. 1. A schematic portrayal of concepts of SmII organization. An early report (Woolsey and Fairman, '46) did not specify the orientation of the face, arm, and leg in the representation (A). Later, the distal portions of these body parts were shown as pointing toward SmI forming an "inverted" (B) image of the body (see text). Recently, several investigators (see text) have argued that the distal portions of the head, arm, and leg are orientated away from SmI so that SmII is "erect" (C). SmI and SmII body representations are represented as "homunculi" merely for illustrative purposes. The SmII representation may be rotated in the plane shown in various species (arrows).

sponsive cortex. At the end of each experiment, some recording sites, such as those judged to be at a border, were marked by passing a current of  $10 \mu\text{a}$  for five seconds to form small electrolytic lesions through the recording electrode. At the end of the experiments, the animals were perfused with saline followed by 10% formol-saline or a 1% paraformaldehyde-1.25% glutaraldehyde mixture. The brains were cut on a freezing microtome at  $25 \mu$  or  $50 \mu$ , and brain sections were stained for cell bodies with cresyl violet or for myelin by the Heidenheim method. These sections were examined for electrolytic lesions and electrode tracts so that the recording results could be related to cortical architecture. In some of the cases, anatomical tracers were injected during recording sessions, and then additional brain sections were processed for anatomical studies. These results will be reported elsewhere.

#### RESULTS

Even though SmII is small and occupies less than  $4 \text{ mm}^2$  of cortical surface in squirrels, we were able to determine receptive fields for 30-40 carefully spaced recording sites within SmII in some experiments. Observations were

made on the location of SmII relative to other subdivisions of cortex, the detailed somatotopic organization of SmII, the variability of SmII organization from squirrel to squirrel, the congruent border of SmII with SmI, the proportions of SmII devoted to various body regions, the responsiveness of neurons in SmII to ipsilateral as well as contralateral stimulation, and the architectonic distinctiveness of SmII cortex.

##### 1. The location of SmII

The location of SmII relative to other subdivisions of cortex is shown in figure 2. The rostral border of SmII is formed by the first somatosensory area, SmI. SmI has been previously defined by electrophysiological mapping methods (Sur et al., '78a) and related to an architectonic field, Pa, of an earlier report (Kaas et al., '72). SmII was distinguished from SmI by patterns of somatotopic organization, the larger receptive fields for neurons in SmII, and differences in the responsiveness of neurons in the two areas. The changes from SmII to SmI were abrupt and clear, and the distinction between the two fields could be made with assurance.

Other borders of SmII were also easily

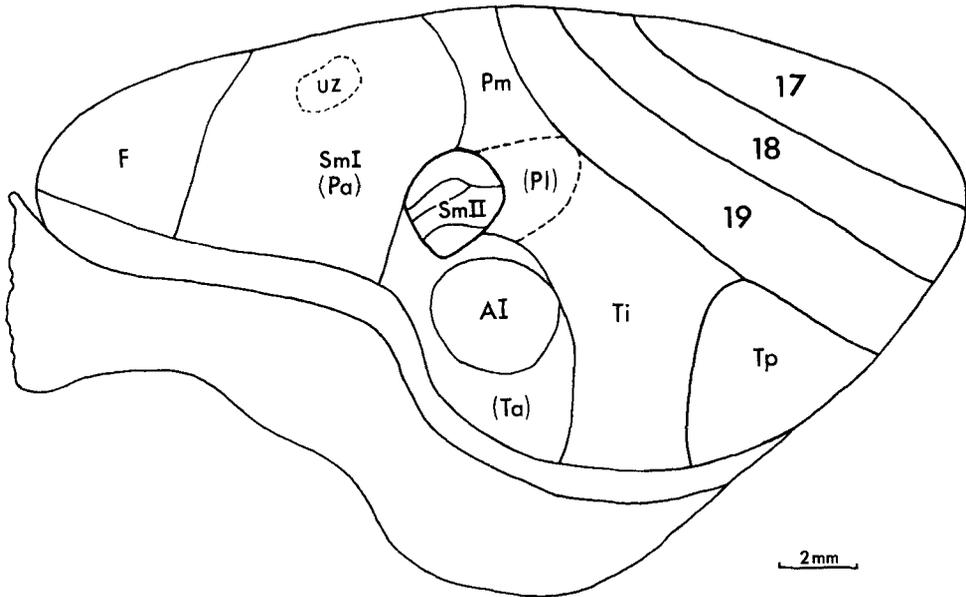


Fig. 2 The location of the second somatosensory area, SmII, in the grey squirrel relative to the architectonic fields of Kaas et al. ('72), the auditory fields of Merzenich et al. ('76), and the location of the first somatosensory area, SmI (Sur et al., '78a). See figure 3 for the significance of the subdivisions of SmII. 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 parietal region, Pl. The first auditory field, AI, is distinguished within the anterior temporal region, Ta. Other subdivisions are the medial parietal area, Pm, and the intermediate temporal area, Ti, and the posterior temporal area, Tp. Areas 17, 18, and 19 are based on Brodmann's terminology.

judged. Cortex ventral to SmII was responsive to auditory but not somatic stimuli. The tonotopic organization of the adjoining auditory cortex was not determined, but it probably included part of the second auditory field of Merzenich et al. ('76), rather than the first auditory area, AI. Cortex immediately caudal and dorsal to SmII did not respond to somatic or auditory stimuli, and therefore unresponsive recording sites were used to define these borders of SmII. Architectonically, the caudal and dorsal bordering regions correspond to part of the lateral parietal field (Pl) and the medial parietal field (Pm), respectively (Kaas et al., '72). In cats (Haight, '72) and macaque monkeys (Whitsel et al., '69), but apparently not in a number of other mammals, a field caudal to SmII is responsive to both somatosensory and auditory stimuli, and the field is without obvious somatosensory organization (see Pubols, '77 for review). In the present studies on the grey squirrel, we found no evidence for this "nonspecific" zone, which has been confounded with SmII in earlier studies on cats.

## 2. The representation of the body surface in SmII

The locations of major body divisions in SmII and representative but partial data from a typical experiment are shown in figures 3 and 4. Although receptive fields for recording sites in SmII were large relative to SmI, a clear somatotopy exists. For each change in electrode position across the cortical surface a corresponding change in receptive field center was observed. The results indicate that the representation of the head is located dorsally in cortex immediately adjoining SmI. Tissue ventral to the face representation is devoted to the forelimb, and an adjoining ventrocaudal band of cortex is activated by the trunk. The most ventral portion of SmII is related to the hindlimb, tail, and genitals.

### a. The head, face, and neck

Almost half of SmII is devoted to the head, face and neck, and a number of recordings from this subdivision were obtained in all experiments. Receptive fields for recording sites

in the head representation of one squirrel are shown in figures 3 and 4. The observations are consistent with the view that the representation of the head is topologically organized and without major discontinuities. The overall arrangement of the head representation is such that the head is upright with the nose pointed rostrally. Thus, the dorsal midline of the head was represented dorsally along the SmI border (see receptive fields for penetrations 3, 4, 7, 8, 9, and 10), while the ventral midline of the lower lip projected ventrally to cortex adjoining the forelimb representation in SmII (penetrations 5 and 6); the proximal head near the neck was dorsal and caudal in SmII (penetrations 9 and 10) while the distal head and nose was ventral and rostral (penetrations 4 and 5). There was no evidence for a specialized area for the representation of individual mystacial vibrissae, as is found in SmI (Sur et al., '78a), and receptive fields for the upper face included both vibrissae and adjoining areas of skin (penetration 4).

#### b. The forelimb

The cortex representing the forelimb in SmII occupies a narrow rostrocaudal band lying just ventral to the lower lip and ventral face and neck. The basic organization of this region of SmII is apparent from the receptive fields illustrated in figure 5. Penetrations 1-5 indicate that the outer brown fur skin of the forearm is represented, from the dorsal shoulder to the distal forepaw, in a caudal to rostral sequence in cortex. It is important to note that the forelimb in SmII is therefore pointing ventrally and rostrally in cortex. Receptive fields for penetrations 7 and 8 show that the white skin of the underside of the forearm is more ventrally represented in SmII than the dorsal surface of the forearm.

#### c. The trunk

It is apparent from the receptive fields for recording sites shown in figure 6 (also see figs. 3, 4) that the dorsal midline of the body is represented along the caudal border of SmII in the grey squirrel. A dorsal to ventral row of recording sites along the caudal border of SmII produced a row of large receptive fields along the dorsal midline of the squirrel progressing from the head and neck dorsally within SmII to the base of the tail ventrally (penetrations 1-6). The ventral midline of the trunk is represented rostrally and toward SmI. Thus, a caudal to rostral row of recording sites in the

trunk representation resulted in a progression of receptive fields from the midline of the back to the midline of the belly (penetrations 4, 10, 11, and 12).

#### d. The hindlimb, tail and genitals

The medial and caudal region of the hindquarter representation in SmII was found to include the lower back, tail, and the lateral flank of the hindlimb (penetrations 21-23, fig. 4). The distal hindlimb including the foot was located ventrally in the representation (penetration 25). The most ventral and caudal part of SmII related to the tail and the adjoining gluteal and genital region (penetration 26). As in the forepaw region of SmII, the receptive fields for the hindpaw were large and included both the dorsal and ventral surfaces of the foot. Note that the orientation of the hindlimb representation in SmII is such that the distal foot is most ventral and rostral and thus parallels the forelimb representation.

### 3. Variations in the SmII map

Because of the small size of SmII, the limited numbers of penetrations we could place in SmII in each experiment, and the large receptive fields, we may have failed to detect some variations in the internal organization of SmII. However, overall variations in the proportions of separate parts of SmII were so marked from case to case that they were clearly apparent. The most noticeable variations were in the trunk region. For example, the representation of the trunk in cases 77-48 and 77-43 (figs. 4, 5) extended from the caudal to the rostral border of SmII, whereas this representation did not reach the rostral border in either case 77-07 (fig. 6) or 77-08 (not shown). In these cases the forelimb region was adjacent to the cranial representation medially and the representation of the leg laterally, as opposed to cases 77-43 and 77-48 in which the forelimb representation was not adjacent to the hindlimb region, but bordered the representation of the ventral trunk. The relative sizes and the orientations of other subdivisions of SmII also varied enough from case to case to be noticeable. We conclude from these cases that the overall somatotopic pattern in SmII is variable.

#### 4. The congruent border of SmII with SmI

SmII and SmI have a common border along which similar skin surfaces are represented in both areas. Thus, adjacent recording sites in

SmII and SmI have receptive fields with similar locations. An example is illustrated in figure 3 where receptive fields are shown for adjoining recording sites in SmII and SmI. The most medial extent of the common border corresponds to the skin between the eye and ear and the dorsal midline of the cranium. Receptive fields are found more and more distally along the upper face and nose with more and more lateral recording sites along the border. In all cases, receptive fields were approximately similar for matched recording sites on each side of the SmII and SmI border.

This correspondence in topological organization between the two abutting sensory representations defines the border as *congruent* (Allman and Kaas, '75).

5. Proportions of SmII and SmI

The maps of SmII allow us to make comparisons between the sizes and proportions of the major divisions of SmII with our earlier maps of SmI (Sur et al., '78a). These comparisons are made in table 1 and figure 7. First, it is apparent that SmI is about ten times as large as SmII. Second, SmII is not as

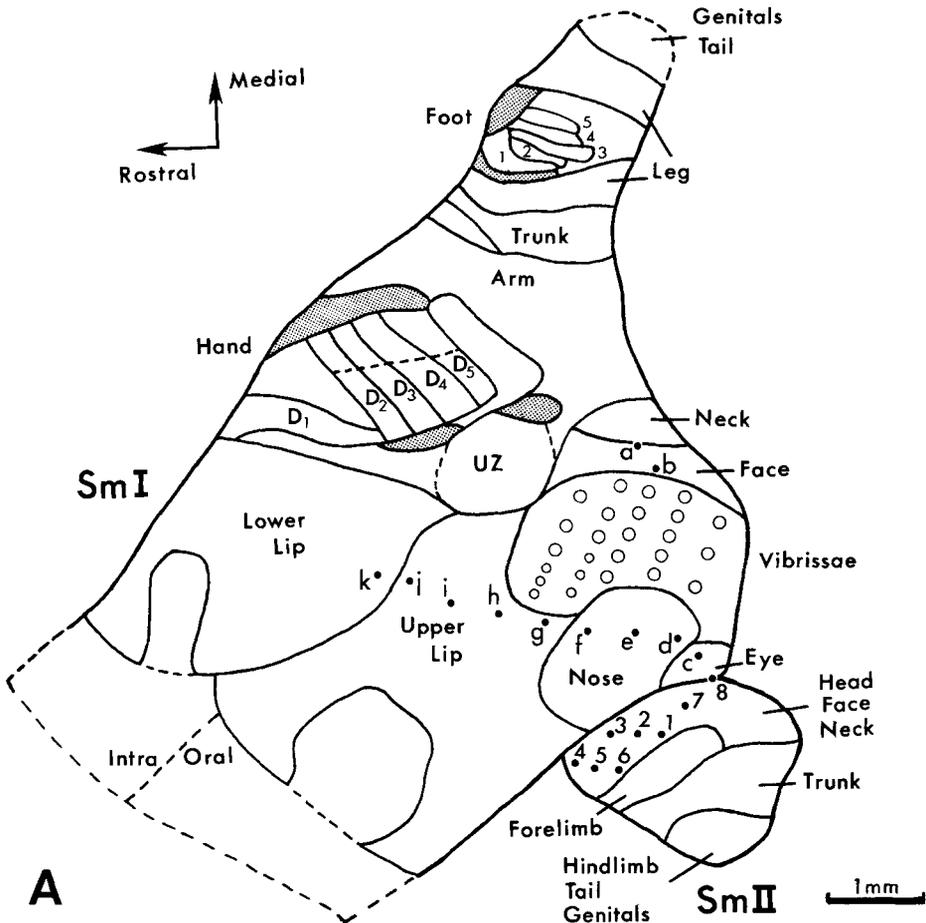
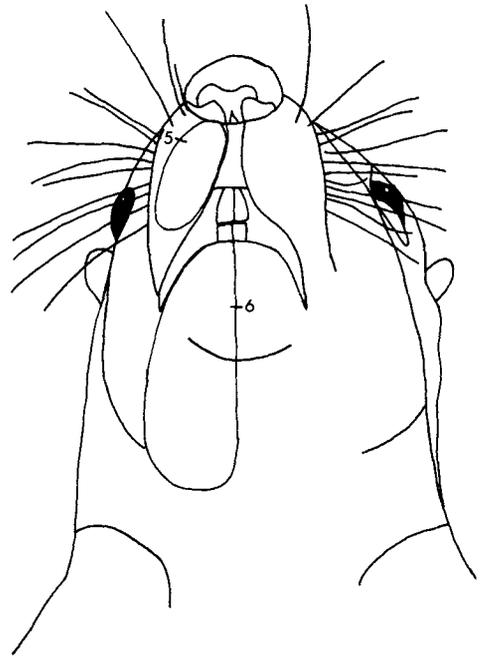
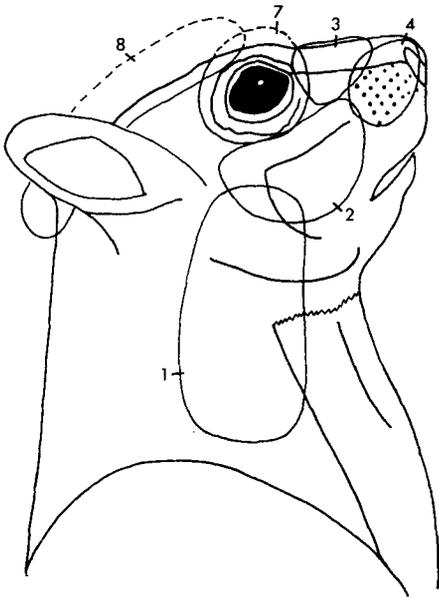
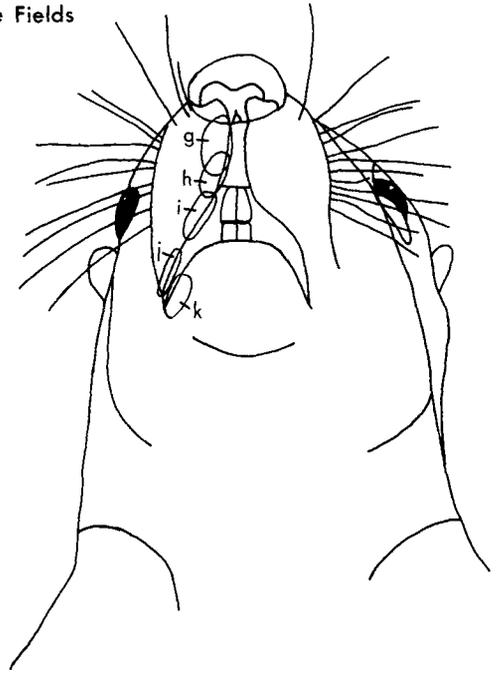
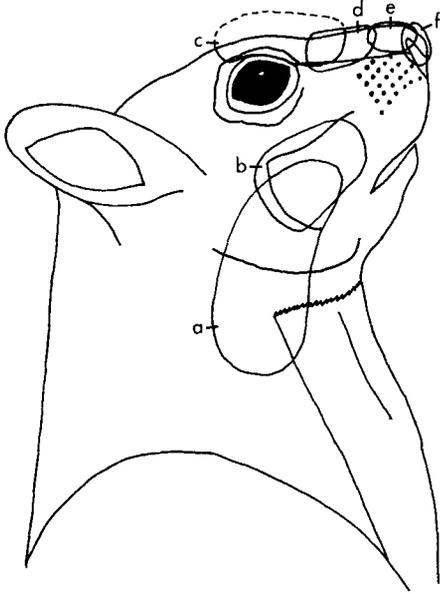


Fig. 3 Receptive fields for recording sites in SmI (a-k) and SmII (1-8) of grey squirrel 77-48. Note that receptive fields for similar body locations are larger in SmII, and that SmI and SmII adjoin along the representation of the dorsal midline of the head and face. The subdivisions of SmI in figure 3A are from Sur et al. ('78a). The dorsum of the foot and forepaw are shaded. D<sub>1</sub>-D<sub>5</sub> indicate the digits of the forepaw; UZ, an unresponsive zone. Receptive fields for the numbered and lettered recording sites are in figure 3B. Also see figure 4.

SmI Receptive Fields



**B**

SmII Receptive Fields

Figure 3

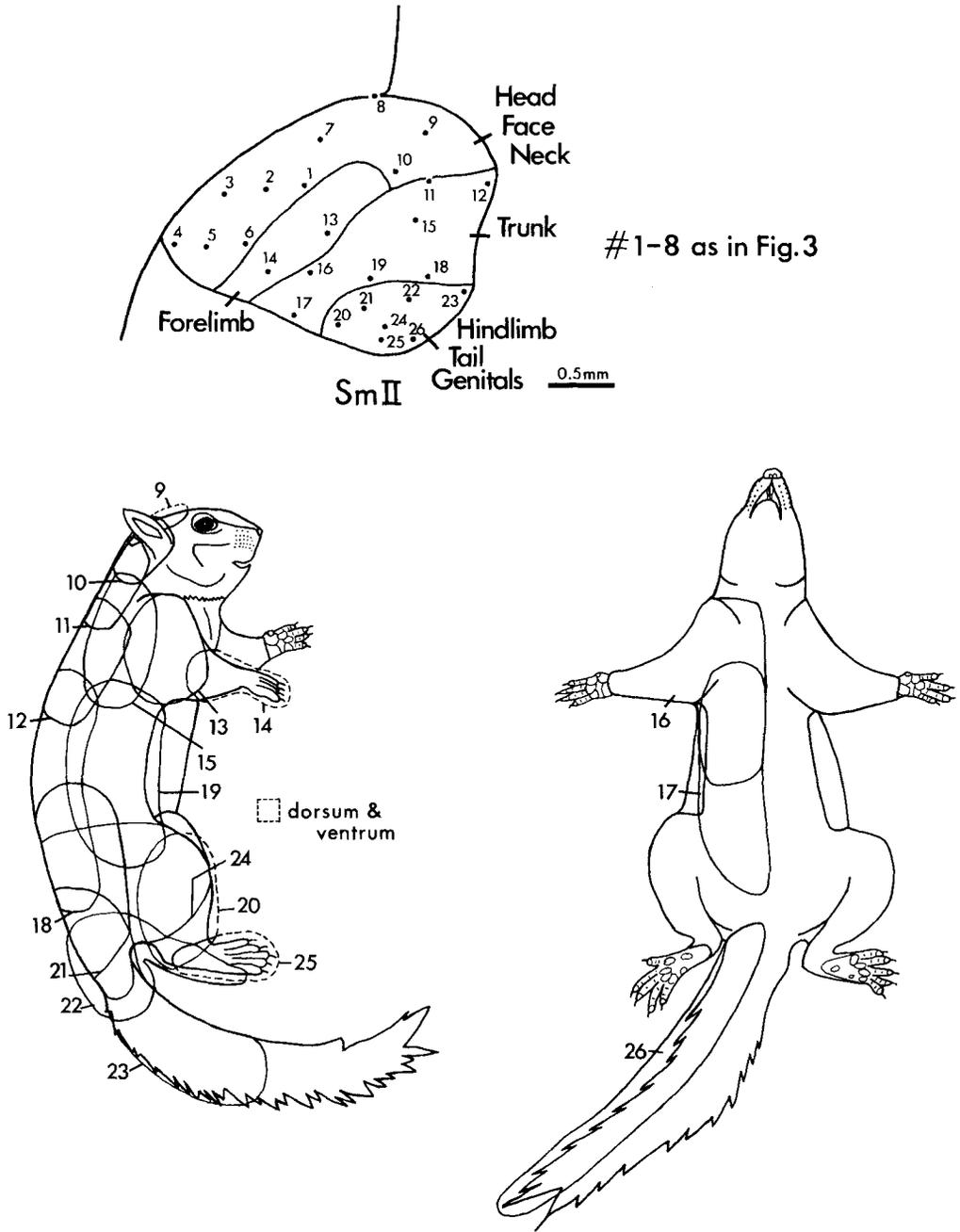


Fig. 4 Receptive fields for representative recording sites in SmII of grey squirrel 77-48.

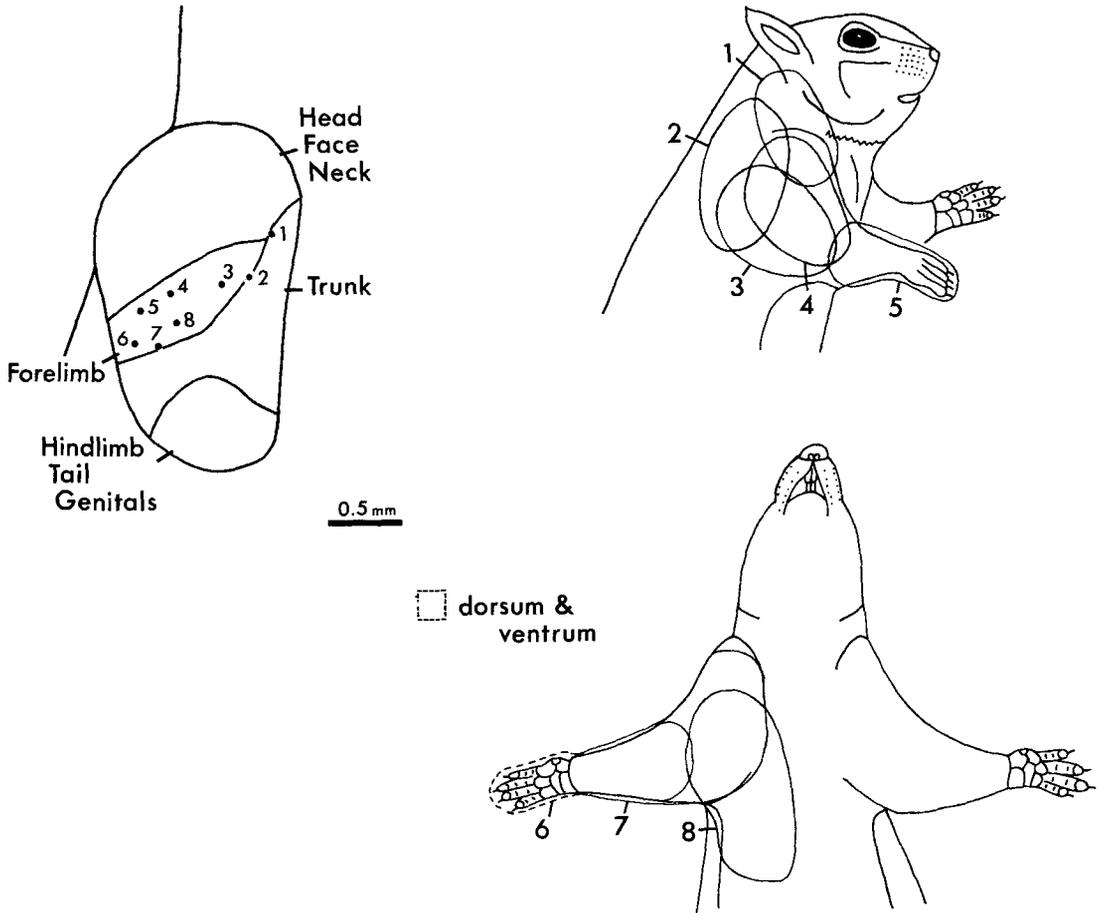


Fig. 5 Receptive fields for representative recording sites in the forelimb region of grey squirrel 77-43.

TABLE 1

Surface areas and proportions of SmII and SmI

Region	Body surface area mm <sup>2</sup>	SmII cortical area mm <sup>2</sup>	%	Magnification <sup>2</sup> × 10 <sup>-5</sup>	SmI cortical area mm <sup>2</sup>	%	Magnification <sup>2</sup> × 10 <sup>-5</sup>
Head, face, neck	6,499	1.55	39.7	23.9	23.5	65.7	361.6
Forelimb	12,403	0.58	14.8	4.7	7.3	20.4	58.9
Trunk	26,710	1.01	25.8	3.8	0.8	2.2	3.0
Hindlimb, tail, genitalia	22,419	0.77	19.7	3.4	3.2	8.9	14.3
Unresponsive zone <sup>1</sup>		3.91 mm <sup>2</sup>	100%		1.0	2.8	
					35.8 mm <sup>2</sup>	100%	

<sup>1</sup> Not observed in SmII.

<sup>2</sup> Magnification =  $\frac{\text{Cortical area}}{\text{Body surface area}}$ .

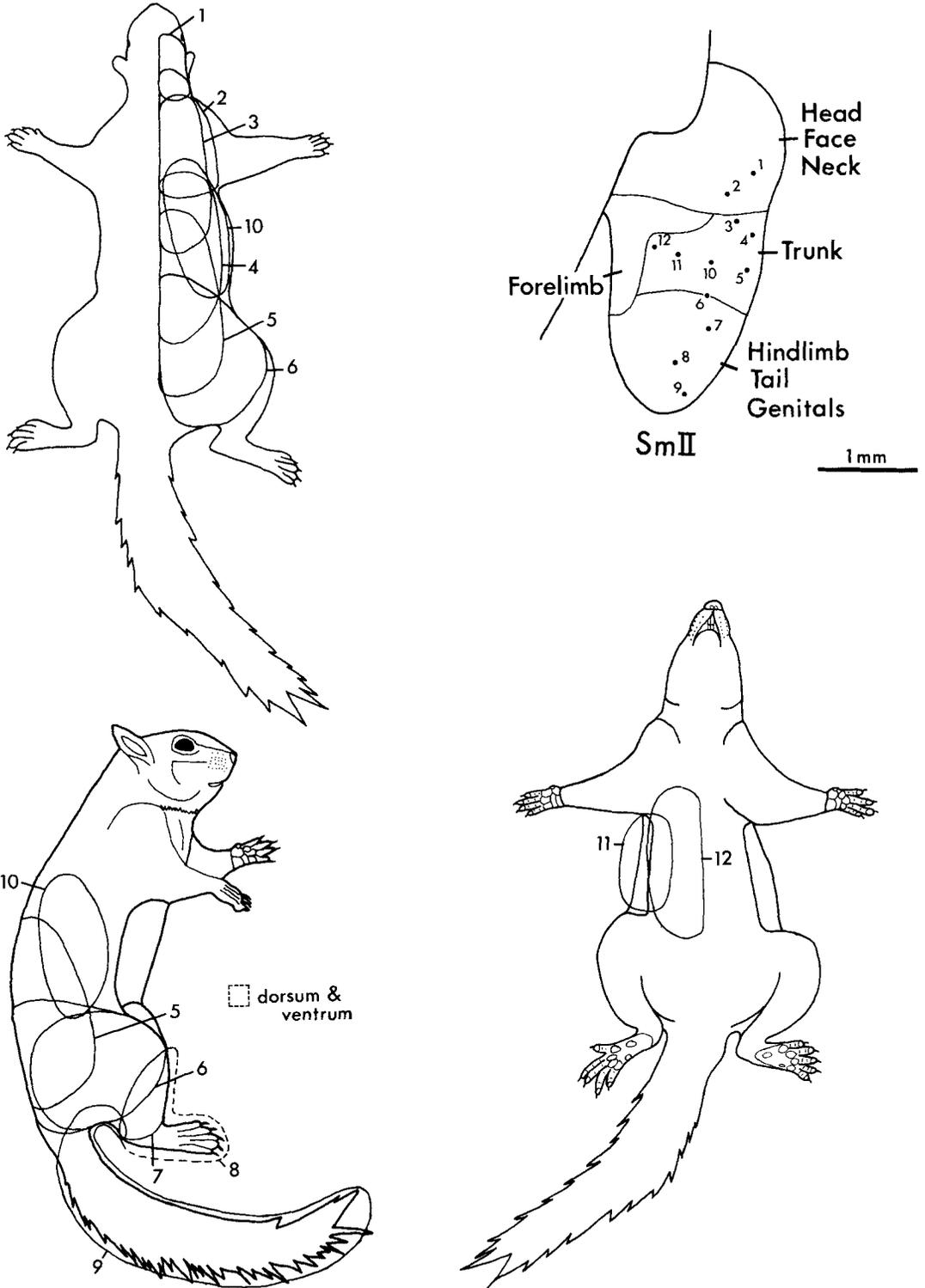


Fig. 6 Receptive fields for representative recording sites in the neck, trunk, and hindlimb regions of SmII of grey squirrel 77-07.

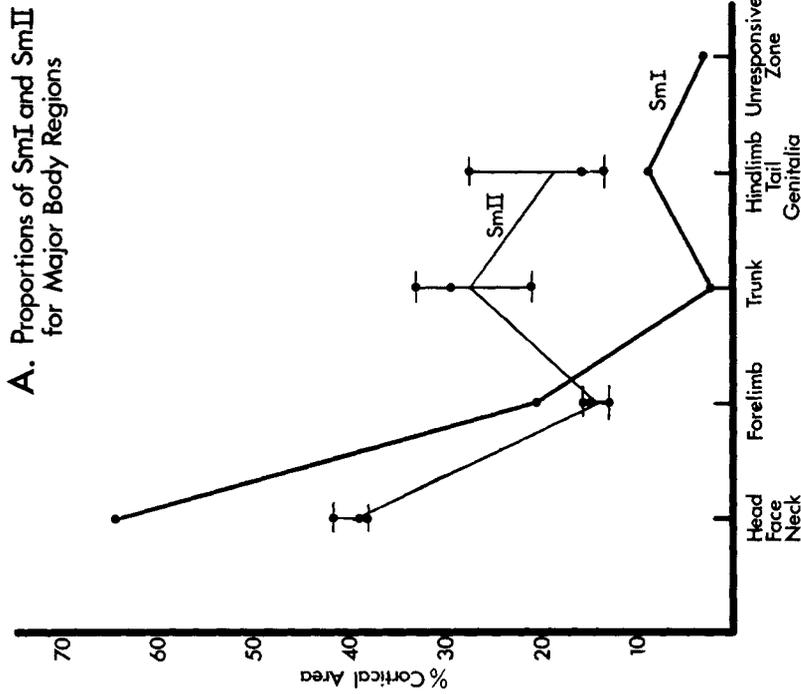
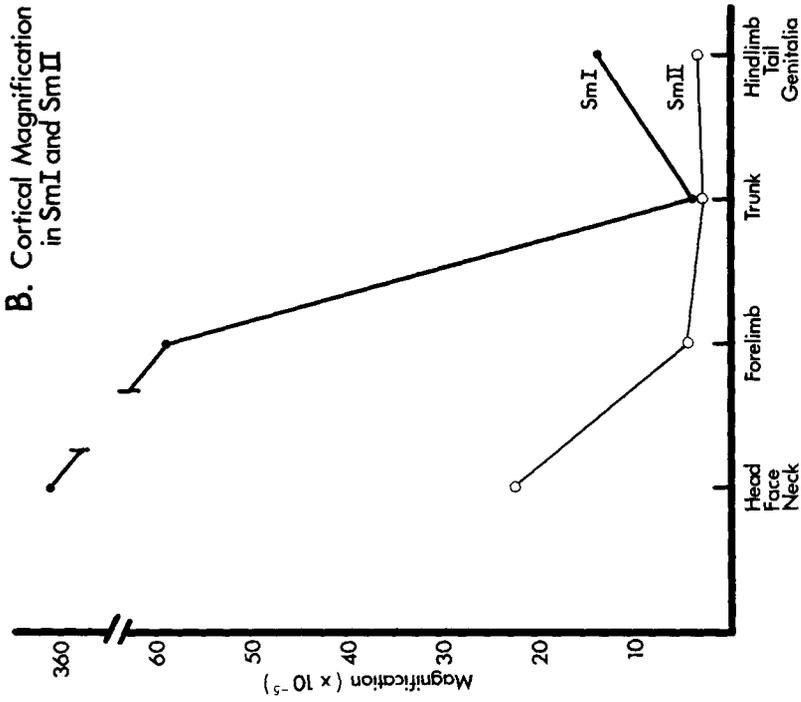


Fig. 7 Cortex devoted to body divisions in SmI and SmII. A. The percentage of the total cortical surface devoted to body regions. Data for three completely mapped cases (dots) are shown for SmI; the line connects the averages. Data for SmI is from the report of Sur et al. ('78a). B. Cortical magnification factors based on the average of three squirrels for SmII and one squirrel for SmI (fig. 7A).

distorted or disproportionate as SmI. The main differences in the two areas are in the parts representing the face and trunk. The head occupies two-thirds of SmI but less than half of SmII. In part, this difference reflects the larger representation of vibrissae in SmI. In contrast, the trunk representation is actually slightly larger in SmII than in SmI, and the relative proportions differ greatly. The trunk relates to about one-quarter of SmII, but only about 2-3% of SmI. Finally, the representation of the hindquarter occupies twice as much of SmII as of SmI. Thus, SmII has a much more equal representation of skin surfaces than does SmI.

The differences in SmII and SmI are even more obvious when cortical magnifications, i.e., the ratios of cortical surface area to body surface area, are considered. While slightly more tissue in SmII is devoted to the trunk than the forelimb or hindlimb, the amount of cortical surface per unit of body surface is about the same for these three body regions. Only in the region representing the head is there an increase in cortical magnification, and this increase is very slight in comparison to that for the head in SmI. The differences in cortical magnification in SmI and SmII of the squirrel indicate that relatively more tissue in SmI is devoted to body parts with high receptor densities, especially the face and forepaw, while SmII relates more equally to all body parts.

#### 6. Lack of bilateral receptive fields

Given the reports of mirror symmetrical bilateral receptive fields for recording sites in SmII, we consistently stimulated both sides of the body to determine if neurons were activated bilaterally under our recording conditions in the squirrel. Of 252 carefully studied receptive fields for recording sites in SmII, 245 (97%) were completely confined to the contralateral body surface. The receptive fields for seven recording sites extended across the midline of the animal and included both contralateral and ipsilateral skin surfaces. The extension of these receptive fields onto the ipsilateral side of the body was far enough in each case to be sure that the tactile stimulus was not spreading to the contralateral body surface. All bilateral receptive fields were extremely large and continuous across the midline. Those on the trunk included portions of the legs of one or both sides. No mirror symmetrical disjunctive bilateral receptive

fields were found. Thus, SmII, like SmI, was almost exclusively activated by the contralateral body surface.

#### 7. Architecture of SmII

In our recording experiments, we routinely marked the borders of SmII with electrolytic microlesions with the recording electrode. Later, these lesions were noted in serial brain sections stained for cells with cresyl violet or for myelin by the Heidenhein method. Two of these sections at low and high magnifications are shown in figure 8. The sections are adjacent, showing fibers or cells, and two lesions mark the recording sites immediately dorsal and immediately ventral to SmII. The second somatic area occupies the rostral portion of lateral parietal cortex, Pl, of an earlier report (Kaas et al., '72). The cortex of SmII is less "sensory" or "koniocortical" in appearance than SmI. SmII can be distinguished from the cortex of SmI by a marked reduction in the packing density of cells in layers IV and VI. However, it is apparent from figure 8 that SmII does have a moderately developed granule cell layer. The packing of cells in layer IV of SmII drops off markedly and abruptly at the physiological borders of SmII with the adjoining medial parietal, Pm, and anterior temporal, Ta, areas. In sections stained for fibers, SmII is less easily distinguished. The myelination of the cortex is somewhat greater than the tissue of the immediately adjoining Pm and Ta regions, but less than Pa (SmI). As can also be seen in figure 8, the distinction between the inner and outer bands of Baillarger is less apparent than in adjacent cortex.

#### DISCUSSION

The major goal of the present study was to determine the orientation of SmII with respect to SmI in the squirrel. We conclude that the SmII representation is erect rather than inverted. This erect orientation allows the

Fig. 8 The architecture of SmII of the grey squirrel. A Nissl preparation of a frozen cut frontal section from an experimental brain is shown at the upper left and at higher magnification at the lower left. These are matched on the right by corresponding views of a fiber stained adjacent brain section. In all sections, small electrolytic microlesions can be seen. These lesions mark recording sites just dorsal and just ventral to SmII and they can be seen to be just outside an architectonic field characterized by an accumulation of small granular cells in layer IV (marked at each boundary by arrows in the lower left) and a moderately dense outer band of Baillarger (arrows, lower right).

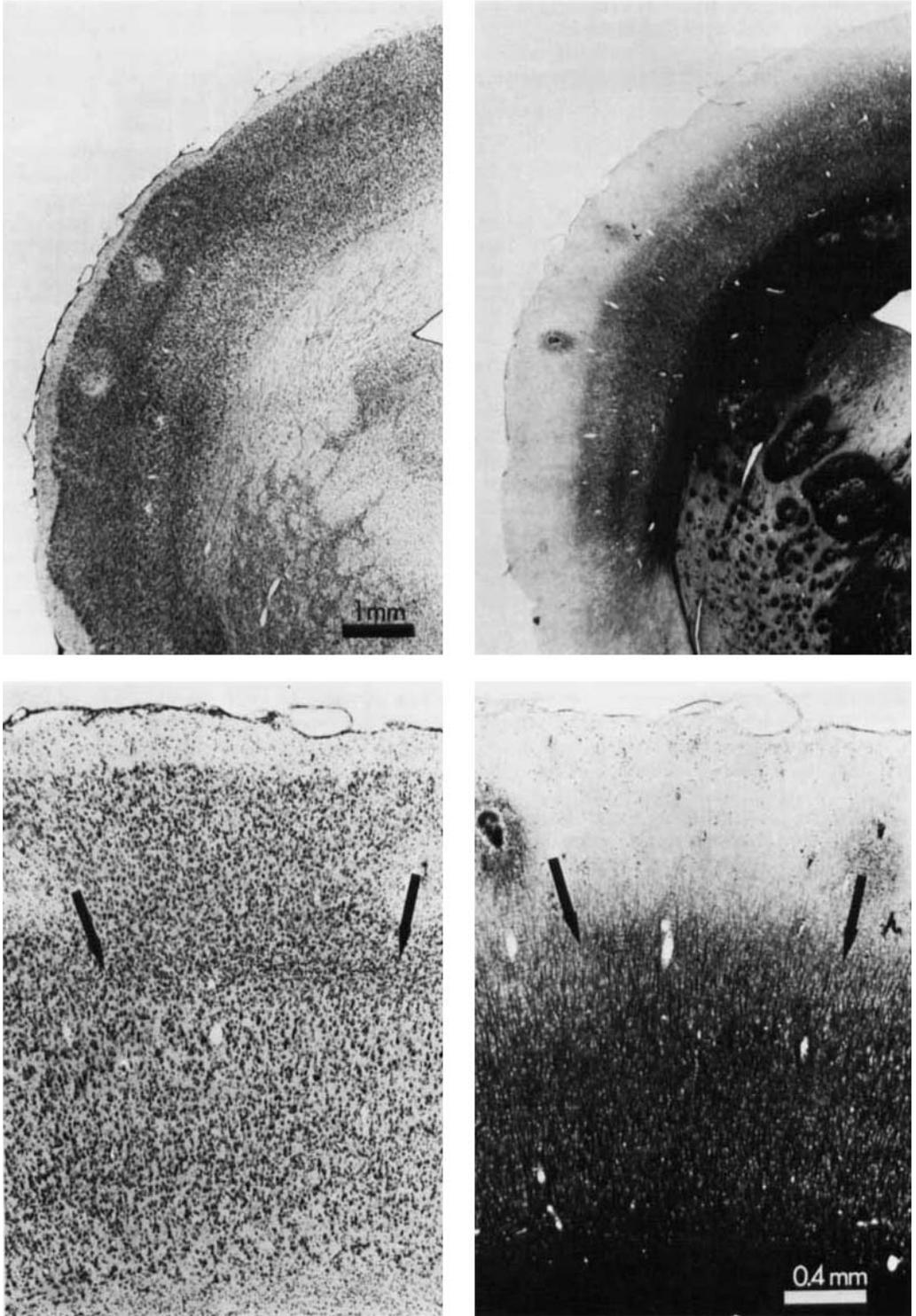


Figure 8

border between SmI and SmII to be congruent. Other observations were made on the somatotopic organization of SmII and the proportion of recording sites with bilateral receptive fields.

1. *The orientation of the body region representation in SmII of squirrels*

The present results indicate that the orientation of the body representation in grey squirrels is erect (fig. 1) and similar to the orientation suggested for SmII of cats by Haight ('72), for raccoons by Herron ('75), for sheep by Johnson et al. ('74), and for llamas by Welker et al. ('76). This orientation is contrary to the inverted orientation commonly portrayed in reviews, textbooks, and journals for a wide range of mammalian species. It is difficult to account for the discrepancy in the two interpretations of SmII organization. We have suggested (see the beginning of the article) that the orientation of SmII has been poorly documented in experimental reports. Furthermore, it appears that the inverted orientation of SmII has often been assumed from rather ambiguous data. While it remains possible that species differ in the basic orientation of SmII, or that even mixed orientations<sup>4</sup> of different body regions occur in some species, we believe that it is more parsimonious to assume that SmII is erect in orientation in all mammals until unequivocal evidence for inverted or mixed orientations is presented.

If the basic orientation of SmII is upright rather than inverted, then at least some of the former conclusions on the topological connections of SmII are open to question. For example, a prevailing conclusion is that only the trunk, head, and proximal limb regions of SmII are interconnected by callosal fibers, while the distal limb regions "neither send nor receive commissural fibers" (Jones and Powell, '73; also see Jones and Powell, '68; Powell, '77). This conclusion seemed reasonable when inverted SmII body orientations were compared with callosal termination patterns. However, the upright orientation of SmII suggests instead that the distal limbs of SmII are the most densely innervated by commissural axons (Innocenti et al., '74). In fact, recent electrophysiological studies in cats suggest that the distal limbs of SmII are callosally interconnected since many corpus callosum fibers are activated by stimulating the paws, and at least some of these fibers ap-

pear to terminate in SmII (Innocenti et al., '73a,b, '74; Robinson, '73). However, the point here is not to argue for or against any view on SmII connections, but only to state that conclusions based on the assumption that SmII is inverted need to be reappraised.

The erect SmII has further significance in that this orientation permits a congruent border of SmII with SmI, while an inverted orientation does not (fig. 1). A congruent border is one that separates two precisely aligned representations so that adjoining points on each side of the border always relate to matching locations on the relevant sensory surface (Allman and Kaas, '75; Kaas, '77). Most adjoining sensory representations have at least partly congruent borders. Examples are the first and second visual areas that are matched point for point along the zero vertical meridian (Allman and Kaas, '74), the reversal in the "best frequency" sequence across the first and rostral auditory cortical areas in cats (Merzenich et al., '75), the precisely aligned skin locations along the border between the Area 3b and Area 1 cutaneous representations in primates (Kaas et al., '76; Merzenich et al., '78; Nelson et al., '78; Sur et al., '78b), and the continuous isorepresentation lines that join the hemifield representations in the inferior and the superior pulvinar in primates (Holländer, '74; Spatz and Erdman, '74; Ogren and Hendrickson, '76; Symonds and Kaas, '78). It is tempting to speculate on why congruent borders are so prevalent. Between certain representations such as the first and second visual areas, congruent borders may have functional significance in that they permit short interconnections between two adjoining representations (Allman and Kaas, '74). However, SmII and SmI have only a restricted common border, matched along the representations of the top of the head and face. Thus, the congruent border of SmII and SmI is unlikely to significantly reduce the length of most interconnections between the two areas. Another possibility is that congruent borders are somehow the consequence of developmental sequences in the formation of sensory representations (Kaas, '77). Perhaps, for example, the specification for orderly sensory input starts at the common border in development and proceeds in different directions so that

<sup>4</sup> Body regions do not always maintain their relative orientations to each other in cortical representations; SmI of the squirrel, for example, reverses the orientation of the trunk relative to the head and limbs (Sur et al., '78a).

border regions of adjoining representations are similarly specified. While the reason why borders are matched remains in question, the present results indicate that the border between SmII and SmI in the squirrel is congruent, and is not an exception to the common observation that adjoining sensory representations have congruent borders.

### 2. *The somatotopic organization of SmII*

While the basic orientation of body parts in SmII of the squirrel was apparent in the present experiments, the small size of the area, the limited number of recording sites, and the large receptive fields (that are probably the result of reduced cortical magnification due to small brain area) restrict the conclusions that are possible about the detailed somatotopic organization. It is apparent that the organization is largely topological in that skin regions that are adjacent on the body remained adjacent in the representation. Thus, rows of recording sites corresponded to progressions of receptive fields without clear discontinuities. There was no evidence for a split representation of the forelimb or hindlimb in the form of "dermatomal strips" as reported for cats (Haight, '72), and there was no suggestion of a double representation of the glabrous forepaw as was found in SmI of the squirrel (Sur et al., '78a). The representation in SmII of the squirrel is clearly more continuous than the one in SmI, and this is perhaps possible because the SmII representation is less distorted. SmII does not devote as much of the representation to the functionally important glabrous forepaw and mystacial vibrissae receptor surfaces as does SmI. In SmI, it appears that the disproportionate enlargement of parts of the representation result in splits that sacrifice some adjacency relationships in order to preserve other more critical adjacency relationships (Sur et al., '78a), and thus allow short interconnections between functionally significant cortical representations of certain body parts.

### 3. *Bilateral representation in SmII*

One of the traditional characteristics of SmII has been that recording sites respond to stimuli on both sides of the body often with mirror-symmetrical discontinuous fields (Woolsey, '43, '52; Woolsey and Fairman, '46; Hamuy et al., '56; Welker and Seidenstein, '59). Yet we found that 97% of the receptive fields for recording sites in SmII of the squirrel

were completely confined to the contralateral body surface, and the 3% that included the ipsilateral body surface were continuous across the dorsal midline with the contralateral body surface. These results do not lead us to the conclusion that SmII in squirrels is unusual. Microelectrode recording on other mammals such as the rat (Welker and Sinha, '72), cat (Haight, '72), and raccoon (Herron, '75) have produced similar results. However, comparable microelectrode studies of SmII in cats strongly suggest that the amount of bilateral activation is dependent on the anesthetic state of the animal. In unanesthetized cats, 63% of the recording sites were bilaterally activated (Robinson, '73); this percentage dropped to 12% in a study using chloralose anesthesia (Morse and Vargo, '70) and to 3% in a study using pentobarbital or nitrous oxide anesthesia (Haight, '72). Curiously, surface recordings indicate that evoked potentials activated by stimuli on the ipsilateral body surface are maintained under anesthesia (Woolsey, '43, '52; Lende, '70; Woolsey and Fairman, '46; Hamuy et al., '56, Lende and Woolsey, '56; Welker and Seidenstein, '59).

We are not willing to conclude, however, that species differences in the amount of ipsilateral input to SmII neurons do not occur. Under similar unanesthetized recording conditions, Whitsel et al. ('69) found that 90% of the recording sites in SmII were bilaterally activated in monkeys compared to 63% in cats (Robinson, '73). Furthermore, over 60% of the recording sites in SmII of opossums anesthetized with pentobarbital sodium were responsive to bilateral stimuli. These results suggest that some species differences in the amount or types of bilateral activation do occur.

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*Note added in proof:* Since submission of this paper, data supporting the conclusion that SmII is "erect" have been published for the raccoon [Herron, P. 1978 Somatotopic organization of mechanosensory projections to SII cerebral cortex in the raccoon (*Procyon lotor*). *J. Comp. Neur.*, 181: 717-728.]