The Organization of Somatosensory Area II in Tree Shrews

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ABSTRACT   Microelectrode multiunit recording methods were used to determine the somatotopic organization of the second somatosensory area, S-II, in tree shrews. Neurons were activated by light tactile stimuli, and receptive fields were located on the contralateral body surface only. The orientation of S-II was such that the top of the head adjoined S-I and the distal limbs pointed away from S-I so that the representation could be characterized as "erect." In general, the distortions of the body surface in S-II were similar to those found in S-I of the tree shrew (Sur et al., '80), with the exception that proportionately less cortex was devoted to the glabrous nose. The representation in S-II was more continuous than that in S-I. Finally, cortex bordering S-II caudally was found to be responsive to generally more intense somatosensory stimuli such as taps to the body surface.

The second somatosensory area, S-II, is a relatively small area of cortex that is often partly or in whole buried in fissures in gyrencephalic brains. For these reasons, it has been difficult to obtain detailed information about the organization and extent of the representation, and there have been questions about even such crude features as the orientation of the limb and trunk representations relative to the first somatosensory area, S-I. Thus, the first reports on the organization of S-II denoted only face, arm, and leg regions (Woolsey and Fairman, '46; Benjamin and Welker, '57). Later, a body surface orientation was portrayed for S-II as a homunculus with the feet pointing towards S-I and the back of the trunk distal to S-I (Lende and Woolsey, '56; Hamuy et al., '56; Woolsey, '58). These early reports were based on surface recordings. More recent microelectrode investigations suggested another organization. Haight ('72) first argued that S-II, at least in the cat, is reversed from the organization previously illustrated, so that the feet point away from S-I. Evidence supporting this "upright" or "erect" orientation for S-II has been presented for the sheep (Johnson et al., '74), a number of rodents (Campos and Welker, '76; Nelson et al., '79; Pimentel-Souza et al., '80), and the raccoon (Herron, '78). It now seems likely that the erect orientation of S-II represents a common mammalian plan. However, the documentation of the "erect" orientation of S-II in the above species has been limited, and it would be reassuring to have

additional evidence from species in other orders of mammals. More importantly, further detailed observations on the organization of S-II in different species of mammals could provide the background data necessary for the formulation of additional general rules of organization, as well as indicate if major variations in organization are possible. A related issue is whether or not S-II systematically differs from S-I in some features of organization. Such information might be helpful in suggesting functional roles for each area. However, accurate information on this issue is quite limited (see Nelson et al., '79; Pimentel-Souza et al., '80, for review). Finally, it is important to determine the organization of S-II in order to guide anatomical studies of connections. Such studies are underway in the tree shrew (Weller and Sur, '80; Sur et al., '80.

The goal of the present study was to use microelectrode recording methods to determine the organization of S-II in great detail in a species not closely related to those mammals already investigated. We chose the tree shrew, which has the advantages of a lissencephalic brain, a relatively large S-II, and an available detailed map of S-I (Sur et al., '80; '81).

An abstract of some of the findings was reported elsewhere (Weller et al., '80).

METHODS

The organization of the second somatosensory area of cortex, S-II, was investigated in nine adult tree shrews, *Tupaia glis,* using microelectrode mapping methods described previously (Sur et al., '78, '80; Nelson et al., '79). The tree shrews were anesthetized with an initial dose of 50 mg/kg of ketamine hydrochloride, which was supplemented as needed to maintain anesthesia. The S-II region of cortex was exposed, surrounded by an acrylic plastic dam attached to the skull, and covered with a pool of silicone fluid. The skull and dam were fixed to a metal bar which was held in a universal vise and rotated so that the lateral S-II region of cortex was nearly horizontal. Perpendicular electrode penetrations were made within and around S-II using glass-coated platinum-iridium microelectrodes or parylene-coated tungsten microelectrodes (Bak Electronics). Penetrations were cited on an enlarged (× 25 or more) photograph of the brain, and were usually placed 150–200 μm apart. Recordings were usually from unit clusters, and were conventionally amplified and displayed. Most recordings were obtained within or close to cortical layer IV, at depths of 500–800 μm. Receptive fields were defined for each recording site as the region of skin where light cutaneous stimuli produced consistent responses. Responses to other stimuli were also noted. In every experiment, an effort was made to reliably identify the border of the first somatosensory area, S-I, with the second, S-II, by carefully noting changes in somatotopic organization and receptive field sizes for rows of recording sites across the border. In the three most detailed experiments, 75–85 electrode penetrations were made within S-II, while an additional 100–120 penetrations were made in cortex around S-II. In most animals, anatomical tracers were injected into mapped areas of cortex; the results of these injections will be reported separately. At the end of each recording session, small electrolytic lesions (10 μA/ 10 sec) were made to mark boundaries and other locations of interest. Then the tree shrew was perfused intracardially with 0.9% saline followed by either 10% formalin or a paraformaldehyde-gluteraldehyde mixture. Brains were frozen and sectioned in the frontal plane at 50 μm thickness. Every fifth section or more was stained with cresyl violet and used for later identification of architectonic boundaries and marker lesions.

RESULTS

Using closely spaced multiunit microelectrode recordings, the somatotopic organization of S-II in tree shrews was defined in great detail. The representation was of the contralateral body surface only, and was organized mediolaterally from head to tail in an "erect" fashion (Nelson et al., '79). In over 400 recording sites within S-II, no ipsilateral or bilateral inputs were found. All recording sites were activated by very light tactile stimuli, and there was no clear evidence of input from "deep" body receptors, or from high-threshold receptors. S-II was bordered rostrally and medially by S-I, and elsewhere by cortex generally responsive to more intense somatosensory stimuli such as taps, but not light cutaneous stimuli.

Location and organization of S-II

The second somatosensory area, S-II, in tree shrews is an oval-shaped region of cortex a little over 4 mm² in area (Table 1) adjoining the first somatic area, S-I, laterally and caudally in the positions shown in Figures 1 and 2. In most animals, S-II lies immediately caudal to the emerging middle cerebral artery and largely dorsal to the major rostrocaudal branch of this artery. Typically, S-II is partially embedded in S-I, as shown in Figure 1, and part of S-I sometimes appears to cap S-II as illustrated for case 79-48 in Figure 2. In other cases, the posterior somatic field (see Sur et al., '80) forms the medial border of S-II (Figs. 1, 2C).
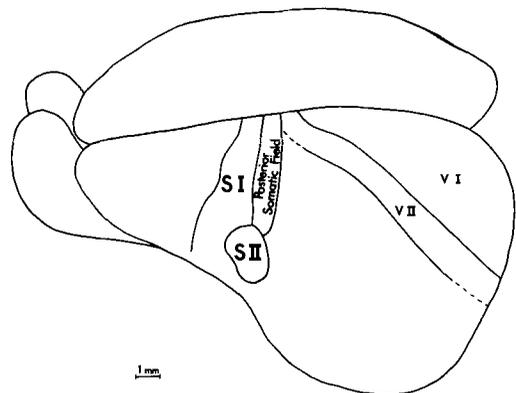

Fig. 1. The location of the second somatic area, S-II, on a dorsolateral view of the brain of a tree shrew. The posterior somatic field and first somatic area, S-I (Sur et al., '80), as well as the first and second visual areas, V-I and V-II, have been described elsewhere (Kaas et al., '72).
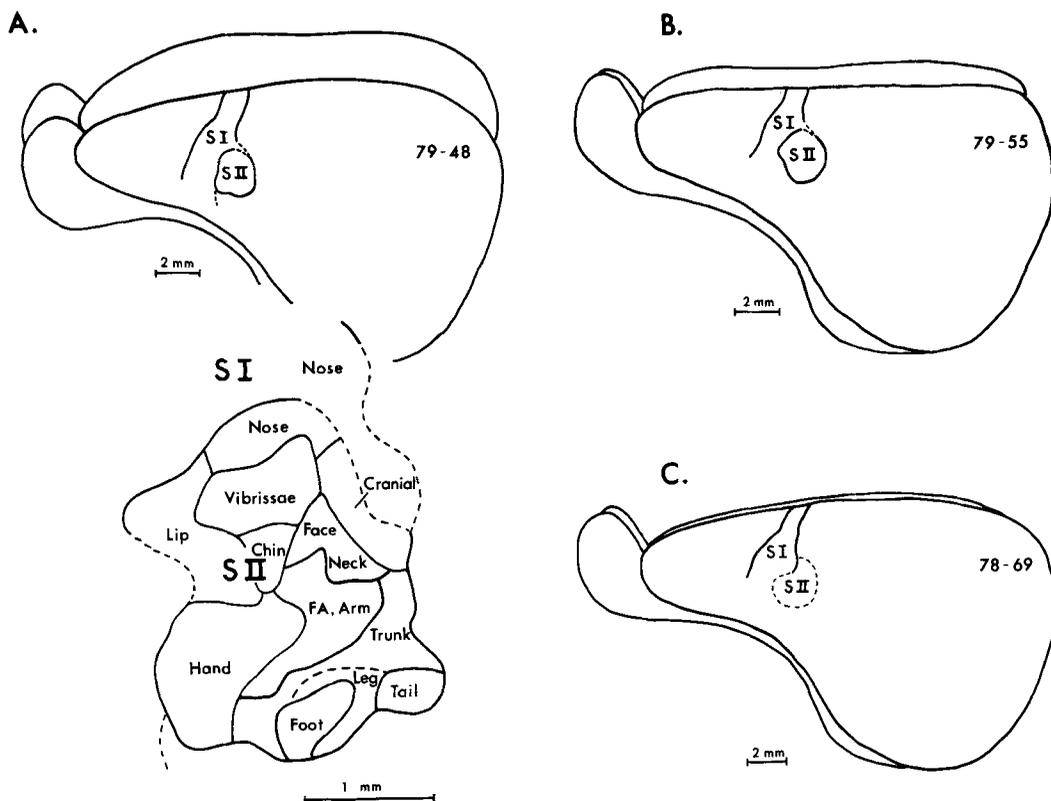
Fig. 2. The relation of S-II to S-I for three different cases, 79-48, 79-55, and 78-69. The organization of S-II is shown for case 79-48 at the lower left. S-I forms the rostral and medial borders of S-II to variable extents, depending on whether S-II is somewhat "embedded" in S-I, as shown for 79-48. FA, forearm.

Summary diagrams illustrating the somatotopic organization of S-II for three completely mapped cases are shown in Figures 2 and 3. For the summaries in Figure 3, the dots on the diagrams indicate the locations of electrode penetrations. For all three summaries, lines are drawn around all electrode penetrations with receptive fields centered on the designated body part. Thus, all electrode penetrations within the regions marked "hand" in the summary diagrams had receptive fields predominately, but not necessarily exclusively, on the hand or forepaw. Similarly, the penetrations related to the lower lip, upper lip, mystacial vibrissae, neck, foot, etc., are outlined. Many of the internal boundaries thereby indicated in S-II fail to include all neurons related to a given body part, and they depend on arbitrary, but conventional, distinctions between body parts. There is no real boundary between cortex representing the upper arm and cortex representing the trunk, for example, and receptive fields for neurons in the border region overlapped both skin surfaces. In contrast to boundary lines such as those separating trunk from limbs, other boundary lines were dictated by the internal organization of S-II. For example, the representation of the hand adjoins that of the face, but receptive fields for neurons along this border in S-II did not include both of these body parts.

The overall order or arrangement of body parts in S-II is apparent from Figures 2 and 3. The medial (or dorsal) half of the representation was always devoted to the face and head, with the lower lip most rostral and the supraorbital and cranial skin most caudal. The hand, forearm, trunk, leg, foot, and tail occupied the rest of the representation in a roughly rostrocaudal cortical sequence. Figures 2 and
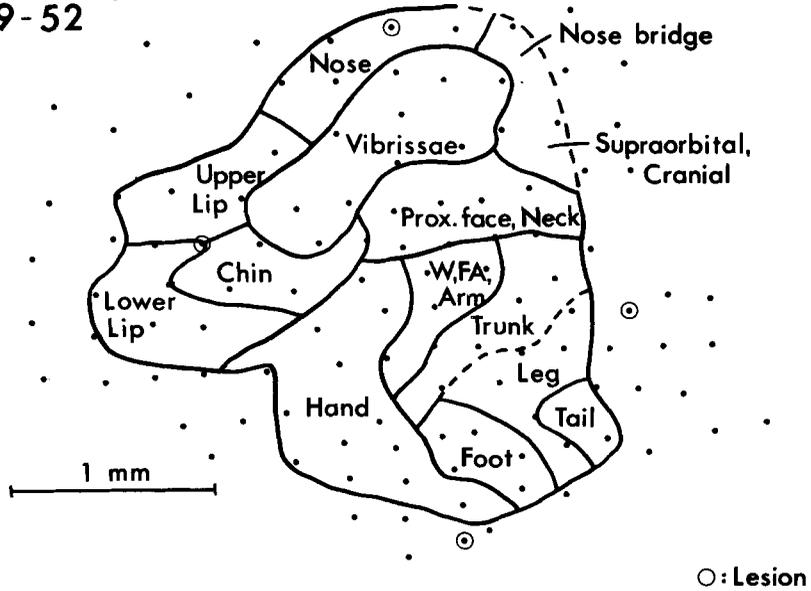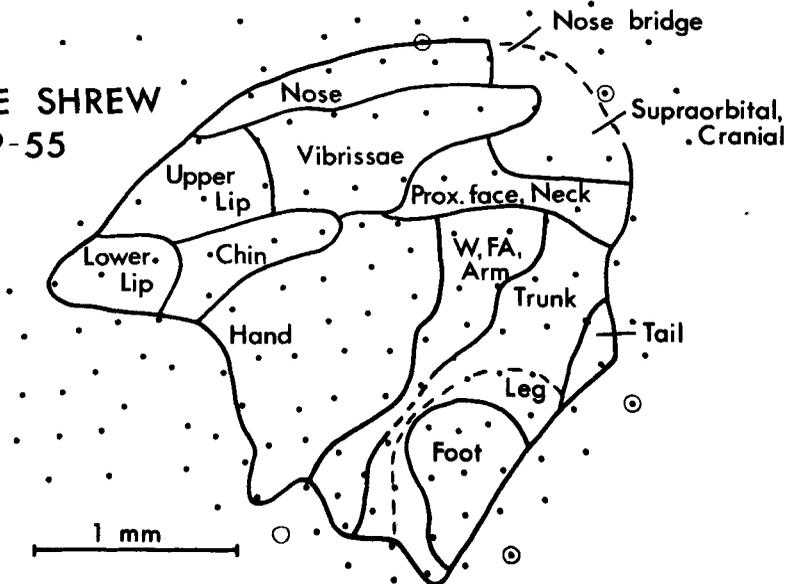
Fig. 3. Surface views of S-II in two tree shrews. Dots indicate the location of microelectrode penetrations, and lines separate clusters of electrode penetrations in S-II where responses to a given body part were recorded. Dashed lines indicate borders that were difficult to determine, either because receptive fields included two body regions or receptive fields for recording sites judged outside of S-II were similar to those inside of S-II. Circles indicate electrode penetrations where small electrolytic marking lesions were placed. FA, forearm; Prox., proximal; W, wrist.

3 also indicate some of the variability that is found in S-II from animal to animal. For example, the representation of the hand adjoins that of the foot in case 79-52, but not in cases 79-55 and 79-48. Other differences in the overall sizes and shapes of S-II and regions within S-II are apparent. Because of the high density of electrode penetrations in these cases, such variability, to a large extent, reflects real differences between cases rather than a sampling problem.

Although the diagrams in Figures 2 and 3 indicate the regions of S-II devoted to various body surfaces, they do not indicate the orderly progression of receptive fields for rows of recordings within the representations of these body surfaces, or the differences in receptive field sizes for different body parts. Observations relevant to the orientation of body parts within the representation, as well as the re-

lation of receptive field sizes to cortical magnification, follow for one typical case (79-52).

The representation of the face and head

Figure 4 illustrates that the representation of the head and face within S-II was highly topographic. The receptive fields for recording sites 1–4 show that the dorsal nose was caudal and medial, and the ventral nose rostral and ventral within S-II. The representation of the dorsal nose adjoined a continuous representation of the bridge of the nose and supraorbital and cranial skin. Thus, receptive fields for the sequence of recording sites 4–7 progressed from the dorsal glabrous nose to the proximal hairy nose, to the orbital skin, and to the cranial skin (the receptive field for penetration 7 is incomplete because part of the cranial skin was removed to expose cortex for mapping). The pattern of the vibrissae repre-
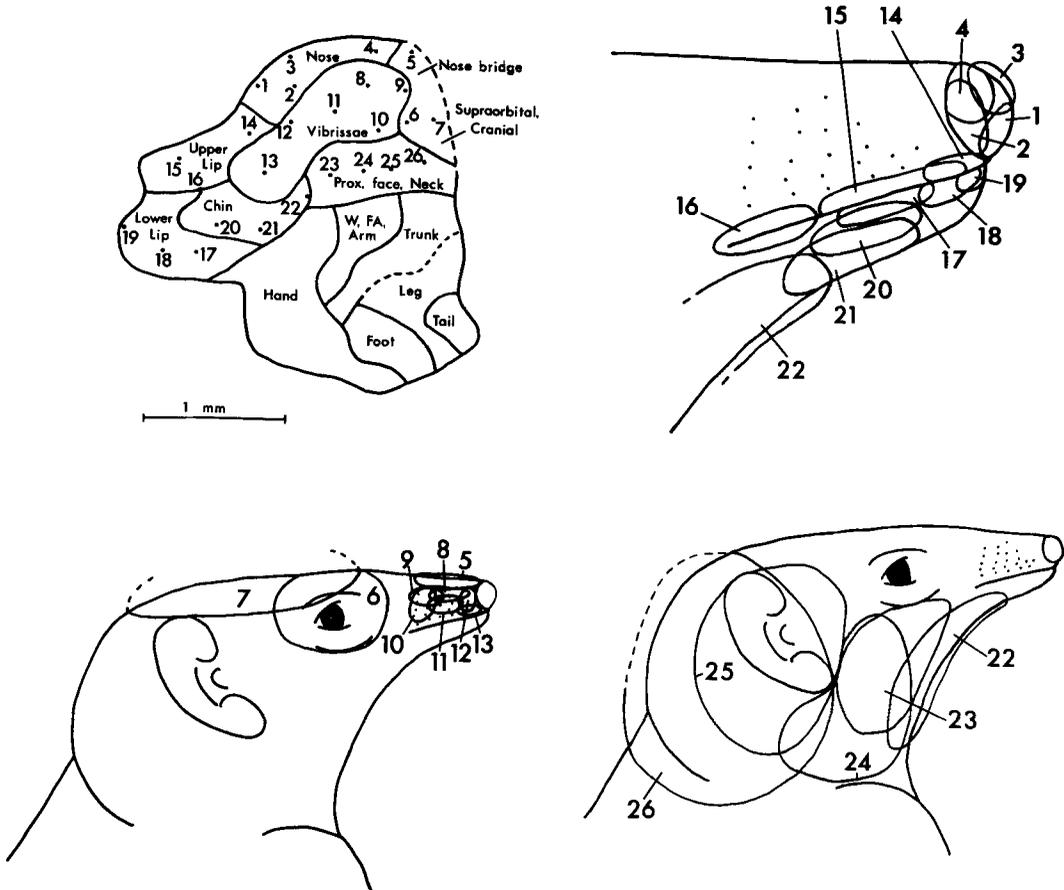

Fig. 4. Receptive field locations for recording sites in S-II cortex representing the head in tree shrew 79-52. Compare with Figure 2. Receptive fields on the nose, lips, and chin are shown on an enlarged drawing of the snout at the upper right. As shown by dashed lines, receptive fields 7 and 26 probably extended onto skin removed to expose the brain. Abbreviations as in Figure 2.

sentation reflected the overall pattern of the face representation so that sites activated by ventral vibrissae were in cortex rostral and ventral to those activated by dorsal vibrissae. The proximal vibrissae (sites 9 and 10) were found caudal to distal vibrissae (sites 12 and 13). The overall continuity of the representation was maintained so that the side of the head (penetrations 25 and 26) was represented caudally in cortex next to the cranial skin dorsally and trunk ventrally. More rostrally, the proximal face (penetrations 23 and 24) joins the representation of the chin (penetrations 20–22), which joins the representation of the lower lip (penetrations 17–19).

It is apparent from Figure 4 that the receptive fields varied considerably in size over the representation of the head. Proportionally large receptive fields were determined for the back of the head, the neck, the side of the face, and the supraorbital skin, while the smallest receptive fields were found on the glabrous nose and the lips. Receptive fields for the mystacial vibrissae typically included five or more adjoining vibrissae.

The representation of the body

Next to the large representation of the head, proportionately more of S-II was found to be devoted to the glabrous hand than any other body part. The hand representation was laterally located in S-II, just caudal to the representation of the chin and lower lip (Fig. 4) and rostral to the dorsal hand, wrist, and forearm. Most of the region of cortex responsive to stimulation of the hand related to the glabrous hand, and the body part labeled "hand" in most of the illustrations refers to the representation of only the glabrous surface. Receptive fields for the dorsal hairy aspect of the hand occupied only a very small area of cortex, and were usually part of large fields also covering the wrist and distal forearm. For this reason, the small dorsal hand representation is usually included in the region of wrist, forearm, and arm in the figures. In one case (Fig. 3, case 79-55), the dorsum of the hand occupied a small part of cortex located medially and caudally within the hand area. Within the cortex activated by the glabrous hand, the digits were represented rostrally and the palmar pads, caudally. The radial aspect of the glabrous hand was found in cortex medial and rostral to cortex devoted to the ulnar aspect of the hand region (recording sites and receptive

fields 1–5, Fig. 5). Receptive fields were large relative to those for S-I (Sur et al., '80), and typically included more than one digit and often digits and pads.

Within cortex devoted to the forelimb, distal parts such as the wrist and dorsal hand were represented rostrally next to the glabrous hand, while the proximal skin on the upper arm was caudal next to the trunk representation; the ventral arm surfaces were found lateral to the dorsal arm surfaces (see receptive fields for sites 6, 7, and 8, Fig. 5).

The organization of cortex activated from the trunk continued the orderly somatotopy of S-II. The dorsal midline of the trunk was caudal and medial along the outer margin of S-II, while the ventral midline was rostral and lateral. Thus, recording sites 12, 13, and 9 in Figure 5 had receptive fields that progressed from dorsal to ventral on the trunk. The receptive fields for sites 11, 12, 14, and 17 indicate that the rostral trunk was represented in cortex medial to the cortex related to the caudal trunk.

Receptive fields for recording sites in the trunk region were large, and commonly continued onto the forelimb or hindlimb. Thus, the boundaries between the trunk and limbs only separate cortex where receptive fields were largely on the trunk from cortex where receptive fields were largely on the limbs. The hindlimb adjoined the trunk in S-II in a manner that continued the overall somatotopic patterns. Thus, recording sites with receptive fields on the inner thigh (e.g., site 16, Fig. 5) were found laterally in S-II next to recording sites with receptive fields on the belly (site 15, Fig. 5), while recording sites with receptive fields on the dorsal trunk and outer thigh were located more caudally in cortex (sites 14 and 17, Fig. 5).

Small regions of the most caudal and lateral portions of S-II were activated by stimulating the tail and foot. Receptive fields on the tail typically included most or all of the contralateral tail. Cortex between the representations of the foot and tail represented the back of the leg and the gluteal region. Within the representation of the glabrous foot, digits 1 (the hallux) through 5 appeared to be represented in cortex from rostromedial to caudolateral, although the receptive fields were large and covered more than one digit (Fig. 5). As for the hand, most of cortex representing the foot related to the glabrous foot (labeled "foot" in the

figures), and receptive fields on the dorsal hairy foot were usually part of larger fields which also included the ankle and distal leg.

The relation of S-II to S-I

Recordings along the border regions of S-II indicated that S-I forms a large portion of the medial and rostral border. Furthermore, the border between the two somatosensory fields appears to be largely congruent, since receptive fields for closely spaced recording sites on both sides of the border were overlapping on the body surface. Because of these similar receptive fields, defining the precise S-I and S-II border required a substantial amount of map-

ping in both fields, and careful comparisons of receptive field progressions and reversals in progressions, as well as attention to receptive field sizes. Some of the differences between the adjoining parts of S-I and S-II are shown in Figure 4, which illustrates details of the representation of the head and face in S-II of tree shrew 79-52, and in Figure 6, which illustrates similar information for S-I of the same animal (for further details of the organization of S-I in tree shrews, see Sur et al., '80, '81). It is apparent from the two figures that receptive fields on the same surfaces of the head (i.e., the glabrous nose, cranial and supraorbital skin, upper and lower lips, vibrissae, chin, and prox-
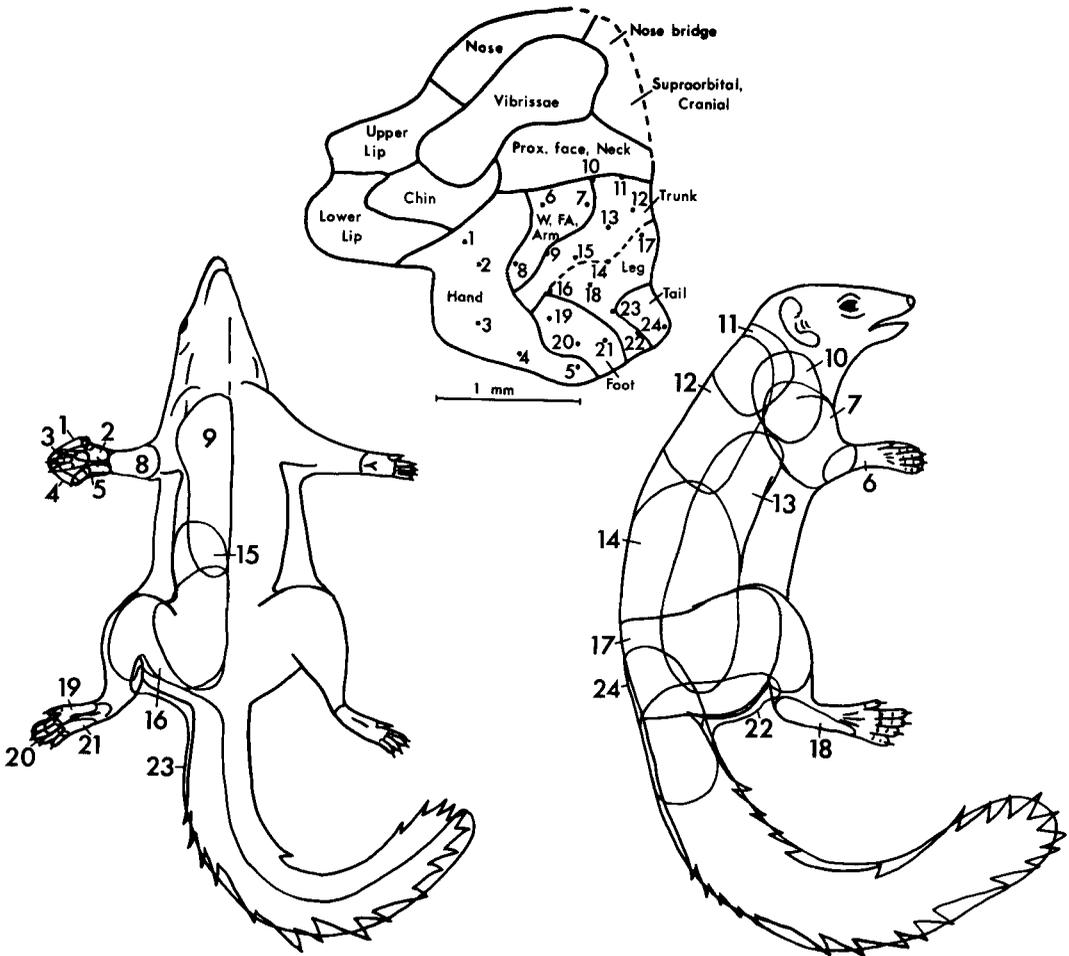

Fig. 5. Receptive field locations for recording sites in S-II cortex representing the body in tree shrew 79-52. Compare with Figure 2.

imal face) are separately represented in S-I and S-II. Each representation has its own pattern of organization, and the line that separates the two patterns defines the border between the two fields. However, in some locations, precise distinctions are difficult to make.

One region of difficulty is illustrated in Figure 6, where the bridge of the nose and the cranial skin were judged to be represented in a crescent of cortex extending caudally around

S-II (see receptive fields for sites 16 and 17). The primary reason for considering these recording sites to be within S-I is that they completed the head representation in S-I, and the bridge of the nose and cranial skin were not found elsewhere in S-I. If these recording sites are indeed in S-I, then S-I extends around even the caudal aspect of S-II in some cases, although this seems to be a variable feature. The relation of S-I and S-II, as judged from the electrophysiological data, is shown for three other
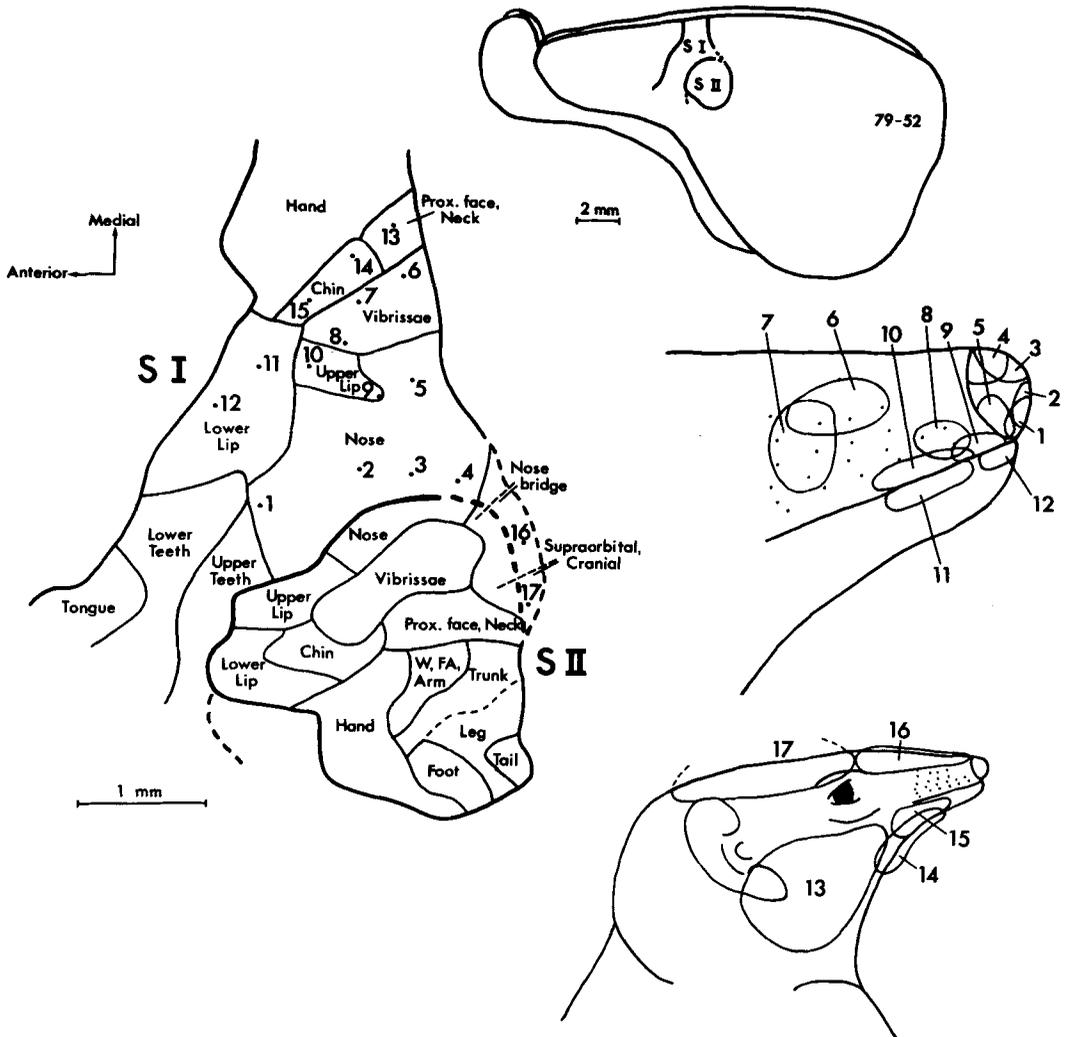

Fig. 6. The relation of S-I to S-II in tree shrew 79-52 and receptive field locations for recording sites in cortex representing the head in S-I. Dashed lines denote regions with uncertain borders (see text). Receptive fields for the nose, lips, and vibrissae are shown on an enlarged snout at central right.

cases in Figure 2. Note that S-II is largely embedded in S-I in cases 79-48 and 79-55, but this is not so in case 78-69.

Responsiveness of cortex lateral and caudal to S-II

The cortex immediately caudal to S-II was unresponsive to light tactile stimulation under our recording conditions. However, recording sites within a narrow 0.5-mm fringe of cortex along the caudal border of S-II occasionally could be activated by moderate taps on the skin or by vigorous brushing of the body hairs. The receptive fields for these poorly driven sites were large, usually encompassing the trunk and limbs. Cortex lateral to S-II was less accessible to mapping, particularly as the cortex curves sharply inward. Some recording sites were unresponsive to tactile stimulation. Other sites yielded higher threshold responses on the nose and on the rostral face that were difficult to localize adequately. It is possible that some of the cortex lateral to S-II, particularly the rostral part, is part of S-I representing hard-to-reach portions of the inside of the mouth such as the gums. It is also possible that we were recording from parts of a higher-threshold representation of the body surface in cortex lateral to S-II. The medial border of S-II was usually formed by S-I. However, in two tree shrews, a portion of S-II appeared to be adjoined by the "posterior" somatic field, a strip of cortex lying caudal to S-I and responsive to high threshold and possibly noncutaneous somatosensory stimuli (Sur et al., '80).

Architectonic features of S-II

The architectonic structure of S-II is more typical of general areas of cortex than that of S-I. Therefore, layers IV and VI in S-II are less densely packed with cells and appear substantially lighter in Nissl preparations than in S-I. Other cortical layers do not differ markedly between the two areas. Along most of the common border between S-I and S-II, as judged electrophysiologically, the architectonic change between the two fields is marked and easily distinguished. However, such a marked border is not apparent caudally where a narrow lip of S-I may curve around part of the caudal border of S-II (Fig. 3). Thus, the architectonic evidence does not unequivocally resolve the issue of whether or not to include this narrow band of cortex in S-I or S-II, or perhaps even in the posterior somatic field (Fig. 1).

Other fields bordering S-II have less cell packing in layers IV and VI than either S-I or

S-II. In addition, the posterior somatic field can be distinguished from S-II by the presence of more medium-to-large pyramidal cells in layer V.

The proportional representations of body regions in S-II and S-I

The detailed microelectrode maps of S-II in the tree shrew allowed measurements of the total surface area of S-II as well as the surface areas and proportions of S-II devoted to the major body parts. Measurements were made from three completely mapped cases, 79-52 (Fig. 3), 79-55 (Fig. 3), and 79-48 (Fig. 2). The results are shown in Table 1, where similar measurements from a previously described map of S-I in the tree shrew (Sur et al., '80) are included for comparison. The values for S-I differ slightly from those previously listed, because we have included a small representation of part of the trunk and adjacent leg and neck on the medial wall of the cerebral hemisphere as part of S-I. The arguments for including this cortex in S-I are presented elsewhere (Sur et al., '81).

One should use some caution in interpreting the data included in Table 1. While the consistency of the measurements across the three cases suggests that the criteria for assigning recording sites to S-I or S-II did not vary, it is possible that some recording sites belonging to S-I or S-II were misassigned. Since the common border region represents the upper face and nose, any consistent misassignment of recording sites would lead to an over- or underestimate of the amount of cortex in S-II that is devoted to the upper head. The present values suggest that S-II devotes proportionately less cortex to the glabrous nose but proportionately more to the upper face than S-I. We regard these differences as valid, but the possibility that they are partly artifactual cannot be eliminated without ways of unequivocally determining if recording sites are in S-I or S-II.

Another factor that complicates comparisons between S-I and S-II is the difference in receptive field sizes for the two fields. In S-I, separate regions for the glabrous and hairy portions of the hand and foot could be distinguished. In S-II, receptive fields for the forearm and foreleg typically extended distally to include the hairy dorsal surfaces of the hand and foot, and separate cortical regions were not included in the summary diagrams. The regions denoted "hand" and "foot" in Figures 2 and 3 can be regarded as largely or wholly devoted to the

TABLE 1. Areas, relative proportions, and magnification factors (cortical area/skin area) of different body surfaces within S-II of tree shrews 79-48, 79-52, and 79-55, in comparison with values within S-I of tree shrew 78-69

Skin region	Area within S-II (mm²)			Area within S-I (mm²)	Proportion of S-II (%)				Proportion of S-I (%)	Magnification (× 10⁻⁴), S-II				Magnification (× 10⁻⁴), S-I
	79-48	79-52	79-55	78-69	79-48	79-52	79-55	mean	78-69	79-48	79-52	79-55	mean	78-69
Head (excluding intraoral)	1.95	2.47	2.08	4.51	45.9	56.8	46.0	49.6	53.4	16.0	20.2	17.0	17.7	37.0
glabrous nose	0.33	0.30	0.30	2.04	7.8	6.9	6.6	7.1	24.2	479.6	436.0	436.0	450.5	2965.1
neck, proximal face	0.23	0.39	0.27	0.22	5.4	9.0	6.0	6.8	2.6	3.0	5.1	3.6	3.9	2.9
ventral surfaces (chin, lower lip)	0.39	0.62	0.44	1.05	9.2	14.2	9.7	11.0	12.4	94.4	150.1	106.5	117.0	254.2
dorsal surfaces (upper lip, vibrissae, nose bridge, supraorbital)	1.00	1.16	1.07	1.20	23.5	26.7	23.7	24.9	14.2	24.3	28.2	26.0	26.2	29.2
Glabrous hand	0.81	0.73	1.02	1.47	19.1	16.8	22.5	19.4	17.4	27.3	24.6	34.4	28.8	49.6
Hairy forelimb (dorsal hand, forearm, arm)	0.48	0.23	0.43	0.63	11.3	5.3	9.5	8.7	7.4	2.6	1.3	2.4	2.1	3.4
Trunk	0.46	0.32	0.41	0.45	10.8	7.3	9.1	9.1	5.3	1.0	0.7	0.9	0.9	1.0
Hairy hindlimb (dorsal foot, foreleg, leg)	0.17	0.29	0.21	0.64	4.0	6.7	4.7	5.1	7.6	0.4	0.6	0.4	0.5	1.3
Glabrous foot	0.24	0.21	0.30	0.65	5.6	4.8	6.6	5.7	7.7	6.3	5.5	7.9	6.6	17.0
Gluteal, Tail	0.14	0.10	0.07	0.10	3.3	2.3	1.6	2.4	1.2	0.3	0.2	0.2	0.2	0.2
Total	4.25	4.35	4.52	8.45	100.0	100.0	100.0	100.0	100.0					

[1] From Sur et al., '80, with medial wall values for lateral leg, dorsal trunk, and base of neck added from Sur et al., '81.

glabrous surfaces (except for a small zone medial and caudal within the "hand" region of case 79-55 that contained receptive fields confined to the dorsal hand). Areas of cortex representing the glabrous hand or foot in S-II may be compared in Table 1 with similar areas in S-I, while the hairy forelimb and hindlimb values for S-I and S-II include the dorsal hand and foot areas, respectively. Finally, the larger receptive fields for neurons in S-II made the distinction between cortex devoted to the arm or leg and cortex devoted to the trunk less certain than in S-I.

The measurements included in Table 1 indicate that S-II occupies 4–4.5 mm² of cortical surface in the tree shrew. Thus, S-II is about half the size of S-I in this mammal. About half of S-II is devoted to the head, and another 20% or less represents the hand. These body parts are represented by very similar proportions of S-I, and it is only when parts of the head such as the nose and upper face are considered that differences appear. Like S-I, S-II devotes little cortex to the trunk, leg, foot, and tail.

DISCUSSION

In the tree shrew, the second somatosensory area, S-II, is relatively large and is exposed on the smooth surface of the cerebral hemisphere. These features allowed us to use microelectrode mapping methods to reveal the organization of S-II in more detail than has been achieved previously. These details demonstrate that S-II in the tree shrew is "erect" in orientation, highly topographic, largely devoted to the head, and activated by the contralateral body surface. Comparisons with a previous map of S-I in tree shrews (Sur et al., '80, '81) indicate that both areas have generally similar cortical magnification factors, but certain skin surfaces are less expanded in S-II so that S-II is somatotopically less distorted than S-I. In addition, S-II is somatotopically more continuous than S-I. Cortex caudal and lateral to S-II is also responsive to somatosensory stimulation, suggesting the possibility of other somatosensory cortical fields.

The organization of S-II

Under our recording conditions, all recording sites in S-II were activated by contralateral or midline body locations. This result differs from the traditional finding with surface electrodes that recording sites in S-II often respond to mirror-symmetrical discontinuous locations on both sides of the body (e.g., Woolsey and Fairman, '46), but corresponds to the results

of microelectrode recordings in squirrels (Nelson et al., '79), rats (Welker and Sinha, '72), cats (Haight, '72), and raccoons (Herron, '78). The different observations might be related to differences in both anesthetics and recording methods. The reported proportion of bilaterally activated neurons in S-II of cats varies greatly with the anesthetic state of the animal (see Nelson et al., '79), and studies reporting bilateral activation often recorded evoked slow-waves rather than unit responses. In a recent microelectrode study of S-II in the agouti, Pimentel-Souza et al. ('80) recorded slow waves, and defined S-II recording sites as those activated from both sides of the body. Because bilateral inputs were not detected in the activation patterns of the S-II neurons in the present study, we have described S-II as a representation of the contralateral body surface.

The representation of the input from the contralateral body surface in S-II of the tree shrew is topographic and oriented in an "erect" manner. Because S-II is highly topographic and relatively free of discontinuities, it can be more reasonably characterized by a homunculus than S-I, and such characterizations have been depicted as "erect" or "inverted" (see Nelson et al., '79, for review). In the "erect" representation, tops of the head adjoin along the common border of S-I and S-II, forming a congruent border. In the inverted conceptualization of S-II, the lower part of the head of S-II borders the upper head of S-I. The present results support the conclusion that the "erect" organization is the predominant, if not the only, form of organization for S-II at least in non-primates (the organization of S-II recently described for macaque monkeys (Robinson and Burton, '80) also can be described as "erect").

The detailed maps in the tree shrew allowed us to determine the surface areas and proportions of S-II devoted to various regions of the body (Table 1). S-II in the tree shrew is between 4 and 4.5 mm² in surface area, and is about half the size of S-I (Sur et al., '80, '81). It appears from these estimates that S-II is proportionately larger relative to S-I in the tree shrew than in any mammalian species examined to date. Microelectrode mapping methods have been used to estimate the sizes of both S-I and S-II in the grey squirrel, opossum, and rat, and the combination of the smooth cortical surfaces in these mammals and the use of microelectrode mapping methods can be expected to yield reasonably accurate values in these studies (see Pimentel-Souza et al., '80, for additional comparisons of S-I and S-II sizes). In

the grey squirrel, S-II was judged to be about 4 mm² in surface area (Nelson et al., '79), while S-I was approximately 36 mm² in size (Sur et al., '78). In the rat, the estimated sizes for S-II (Welker and Sinha, '72) and S-I (Welker, '71) were 3 mm² and 45 mm², respectively. For the opossum, S-II was judged to be between 2.5 and 3.5 mm² (Pubols, '77), while S-I was about 32 mm² in size (Pubols et al., '76). It appears from these values that S-I is commonly from 8–15 times the size of S-II, and the estimate of S-I being only twice as large as S-II in the tree shrew represents an unusual ratio. However, it is largely S-I rather than S-II that varies in size so that S-I is much larger in the squirrel, with a somewhat larger brain, than in the tree shrew, and larger yet in the rat with a somewhat smaller brain.

The proportions of S-II devoted to different body parts largely paralleled observations made previously for S-I in the tree shrew (Sur et al., '80). A major difference was that much less of S-II appears to be related to the glabrous nose than for S-I in the tree shrew. However, the enlarged representation of the glabrous nose in S-I of the tree shrew was regarded as a specialized feature related to discontinuities in the S-I map. Even without this specialization, S-II devotes proportionately almost as much area to representing the head as does S-I (both around 50%). Both representations also represent the glabrous hand in equal proportions (20%), and proportions for other parts of the body are not much different for the two fields (Table 1). Whatever different functions S-I and S-II have in the tree shrew, they do not appear to depend on grossly different distortions of the body representation. However, S-II has an oval rather than a strip-like shape, and does not have the conspicuous discontinuities in the representation as found in S-I (Sur et al., '80).

For most mammals, parts of the face are an important sensory surface, and the enlarged head representation found in S-II of the tree shrew appears to be a common feature. Thus, about half of S-II is also related to the head in grey squirrels (Nelson et al., '79) and opossums (Pubols, '77). In the grey squirrel, less of S-II is devoted to the head than for S-I, and Pimentel-Souza et al. ('80) have suggested that in general the face representation occupies a smaller proportion of S-II than of S-I. However, it is important to remember that S-II adjoins S-I along the common representation of the upper head, and the misassignment of a few S-II electrode penetrations to S-I could lead to an incorrect conclusion.

Responsiveness of cortex adjoining S-II

Regions of cortex bordering S-II caudally were found to respond to higher threshold somatic stimuli, and cortex lateral to S-II often responded to cutaneous stimuli. We regarded these responsive regions as outside S-II because of the clear differences in adequate stimuli, or because receptive field locations did not correspond to the somatotopic pattern found in S-II. All recording sites in S-II responded to light cutaneous stimuli, and there was no evidence for completely noncutaneous regions within S-II. It is, however, possible that "deep" receptor or other inputs converge on tissue activated by cutaneous input in S-II, since the cutaneous input could mask other inputs. We did not systematically test for auditory responses, but no neurons in or immediately around S-II were found to respond to sound. Thus, tree shrews may be like other mammals where additional somatosensory areas have been found to surround S-II. These additional somatosensory areas clearly exist in cats (Clemo and Stein, '80) and primates (Robinson and Burton, '80) where the organizations of somatosensory areas bordering S-II have been described.

LITERATURE CITED

Benjamin, R.M., and W.I. Welker (1957) Somatic receiving areas of cerebral cortex of squirrel monkey. J. Neurophysiol. 20:286–299.

Campos, G.B., and W.I. Welker (1976) Some physiological and anatomical comparisons between the brain of capybaras (Hydrochoerus) and guinea pigs (Cavia). Brain Behav. Evol. 13:243–266.

Clemo, H.R., and B.E. Stein (1980) Somatotopic organization in the anterior ectosylvian sulcus in the cat. Soc. Neuroscience Abstr. 6:652.

Hamuy, T.P., R.B. Bromiley, and C.N. Woolsey (1956) Somatic afferent areas I and II of dog's cerebral cortex. J. Neurophysiol. 19:485–499.

Haight, J.R. (1972) The general organization of somatotopic projections to S-II cerebral neocortex in the cat. Brain Res. 44:483–502.

Herron, P. (1978) The organization of somatotopic projections to S-II cerebral neocortex in the raccoon (Procyon lotor). J. Comp. Neurol. 181:717–728.

Johnson, J.I., E.W. Rubel, and G.I. Hatton (1974) Mechanosensory projections to cerebral cortex of sheep. J. Comp. Neurol. 158:81–108.

Kaas, J.H., W.C. Hall, H. Killackey, and I.T. Diamond (1972) Visual areas of the tree shrew (Tupaia glis): Architectonic subdivisions and representations of the visual field. Brain Res. 42:491–496.

Lende, R.A., and C.N. Woolsey (1956) Sensory and motor localization in cerebral cortex of porcupine *(Erethizon dorsatum)*. J. Neurophysiol. *19:*544–563.

Nelson, R.J., M. Sur, and J.H. Kaas (1979) The organization of the second somatosensory area (Sm II) of the grey squirrel. J. Comp. Neurol. *184:*473–490.

Pimentel-Souza, F., R.M. Cosenza, G.B. Campos, and J.I. Johnson (1980) Somatic sensory cortical regions of the Agouti, *Dasyprota Aguti*. Brain Behav. Evol. *17:*218–240.

Pubols, B.H. (1977) The second somatic sensory area (Sm II) of opossum neocortex. J. Comp. Neurol. *174:*71–78.

Pubols, B.H., L.M. Pubols, D.J. Di Pette, and J.C. Sheely (1976) Opossum somatic sensory cortex: a microelectrode mapping study. J. Comp. Neurol. *165:*229–246.

Robinson, C.J., and H. Burton (1980) The organization of somatosensory receptive fields in cortical areas 7b, retroinsular, postauditory, and granular insular of *M. fascicularis*. J. Comp. Neurol. *192:*69–92.

Sur. M., R.J. Nelson, and J.H. Kaas (1978) The representation of the body surface in somatosensory area I of the grey squirrel. J. Comp. Neurol. *179:*425–450.

Sur, M., R.E. Weller, and J.H. Kaas (1980) Representation of the body surface in somatosensory area I of tree shrews, *Tupaia glis*. J. Comp. Neurol. *194:*71–95.

Sur, M., R.E. Weller, and J.H. Kaas (1981) Physiological and anatomical evidence for a discontinuous representation of the trunk in S-I of tree shrews *(Tupaia glis.)*. J. Comp. Neurol. *201:*135–147

Welker, C. (1971) Microelectrode delineation of fine grain somatotopic organization of Sm I cerebral neocortex in albino rat. Brain Res. *26:*259–275.

Welker, W.I., and M.M. Sinha (1972) Somatotopic organization of Sm II cerebral neocortex in albino rat. Brain Res. *37:*132–136.

Weller, R.E., M. Sur, and J.H. Kaas (1980) The representation of the body in the second somatosensory area, S-II, of the tree shrew, *Tupaia glis*. Anat. Rec. *196:*254A.

Woolsey, C.N. (1958) Organization of somatic sensory and motor areas of the cerebral cortex. In: Biological and Biochemical Bases of Behavior. H.F. Harlow and C.N. Woolsey, eds. Univ. of Wisconsin Press, Madison, pp. 63–81.

Woolsey, C.N., and D. Fairman (1946) Contralateral, ipsilateral and bilateral representation of cutaneous receptors in somatic areas I and II of the cerebral cortex of pig, sheep and other mammals. Surgery *19:*684–702.