

## Physiological and Anatomical Evidence for a Discontinuous Representation of the Trunk in S-I of Tree Shrews

MRIGANKA SUR, ROSALYN E. WELLER, AND JON H. KAAS

*Departments of Psychology (M.S., R.E.W., J.H.K.) and Anatomy (J.H.K.), Vanderbilt University, Nashville, Tennessee 37240*

**ABSTRACT** Microelectrode mapping methods revealed that the representation of the body surface in the first somatosensory area of cortex, S-I, of the tree shrew is unique in that only the ventral trunk was found in the usual location of the trunk representation in cortex of the dorsolateral surface of the cerebral hemisphere. Instead, the dorsal trunk was found as an extension of the representation of the posterior leg in cortex on the medial wall. The separation of the representation of the trunk occurs along a line that is counter to the orientation of the dorsal root dermatomes, so that S-I of the tree shrew clearly cannot be characterized as a serial representation of dermatomes. Anatomical studies of connections support the conclusion that the representation of the trunk is split in S-I. Both the representation of the dorsal trunk on the medial wall of the cerebral hemisphere and S-I of the dorsolateral surface were found to project to S-II when horseradish peroxidase was injected into S-II.

While the somatotopic organization of the first somatosensory cortical area, S-I, has often been portrayed for convenience as a continuous but distorted body surface representation, or homunculus, it has been recognized from the first investigations that major discontinuities in the representation occur. The most commonly found discontinuity is a separation of the representation of a posterior portion of the hindleg from an anterior portion by the representation of the foot. This has been reported for the S-I region of cortex for a number of species of primates (see Merzenich et al., '78, for review), as well as for cats and rabbits (Woolsey and Fairman, '46), squirrels (Sur et al., '78), and tree shrews (Sur et al., '80). Other notable discontinuities are the separation of the back of the head from the face by the representation of the forearm and hand found in some primates (the "splitting of the occiput") (Woolsey et al., '42, '43; Blomquist and Lorenzini, '65; Dreyer et al., '75; Nelson et al., '78, '80), and an anterior strip of forearm from the rest of the forearm by the representation of the hand in galagos (Sur et al., '80) and perhaps some other primates (see Pubols and Pubols, '71, for review). A common feature of these traditionally recognized discontinuities in the S-I representation is that they correspond to lines of disruption along the body surface in

dorsoventral directions, and therefore roughly align with the margins of somatosensory dermatomes. It is largely because such discontinuities in the cortical representations seem to correspond to the margins of dermatomes and sometimes seem to preserve the serial sequence of dermatomes that the hypothesis that cortical organization is somehow determined by dermatomal organization has been postulated and supported (Woolsey et al., '42; Woolsey, '52; Celesia, '63; Blomquist and Lorenzini, '65; Werner and Whitsel, '68; Whitsel et al., '71). We have argued elsewhere that there are many minor somatotopic disruptions in cortical maps that do not correspond to dermatomal lines, and have suggested, as others have (Pubols and Pubols, '71; Welker, '73), that the dermatomal pattern does not adequately describe or account for cortical organization (Merzenich et al., '78; Sur et al., '78; Kaas et al., '79; Nelson et al., '80).

In support of the thesis that the dermatomal pattern does not specify cortical organization, we present here evidence that a major discontinuity in the S-I map in tree shrews separates

---

Address reprint requests to J.H. Kaas, 134 Wesley Hall, Department of Psychology, Vanderbilt University, Nashville, TN 37240.

M. Sur is now with the Department of Neurobiology, State University of New York at Stony Brook, Long Island, NY 11794.

body parts along a line counter to dermatomal lines. Specifically, it appears that the representation of the dorsal trunk is separated from the representation of the ventral trunk in this mammal. This line of discontinuity, of course, crosses the dorsoventral dermatomal lines on the trunk.

In a previous study of the representation of the body surface in S-I of tree shrews (Sur et al., '80), the details of most of the body representation were determined and described. However, the major question of how the trunk was completely represented in S-I was left unresolved. It was noted that the representation of the trunk in the usual location in dorsolateral cortex, between the forelimb and hindlimb representations, was incomplete and included only the ventral trunk. In addition, in a few tree shrews where recordings were obtained from cortex on the medial wall of the cerebral hemisphere, the representations of the lateral hindlimb and dorsal trunk were found in a protrusion of cortex caudal to the representation of the posterior hindlimb and tail. We were uncertain as to the identity of this representation of the dorsal trunk and lateral hindlimb in such a unique location, and considered the possibilities that 1) the representation of the dorsal trunk on the medial wall was indeed the missing part of S-I; 2) that it was part of a higher threshold representation of the body that was found on the surface of cortex along the caudal border of S-I; or 3) that it was part of the classical "supplementary somatic area" of Penfield and Jasper ('54). We now present both anatomical and electrophysiological evidence that the representation of the dorsal trunk on the medial wall of the cerebral hemisphere is part of S-I.

#### METHODS

The goals of the present study were to use electrophysiological microelectrode mapping methods to see if the representations of the trunk in dorsolateral cortex and cortex of the medial wall in the tree shrew complete a single somatotopic pattern, and to see if both cortical regions have similar connections with the trunk region of the second somatosensory area, S-II. The electrophysiological methods and procedures for preparing the animals for recording were identical to those used previously for mapping S-I in tree shrews (Sur et al., '80). Recordings were obtained from nine adult tree shrews, *Tupaia glis*, anesthetized with ketamine hydrochloride. Responsive regions of the medial wall as well as substantial portions of

the skin representation on the dorsal convexity of the brain were explored with platinum-iridium or tungsten microelectrodes. Receptive fields were determined with light cutaneous stimuli for clusters of neurons and occasionally single neurons. Electrode penetrations on the dorsolateral surface of the brain were spaced 200–300  $\mu\text{m}$  apart. Vertical electrode penetrations down the medial wall were placed so that cortical layer IV was traversed, and receptive fields were determined for recordings at 200- $\mu\text{m}$  intervals. These recording sites were related orthonormally to the surface of the medial wall to form a reconstructed unfolded surface view of S-I. Small electrolytic lesions (10  $\mu\text{A}$  for 10 seconds) used to mark critical recording sites were later identified in brain sections and were used to aid the reconstruction of surface views.

In some of the animals used for electrophysiological maps of the responsive region of the medial wall, parts of the second somatosensory area, S-II, were mapped in the same cerebral hemisphere, and injections of anatomical tracers were made in S-II to see if the representations of the dorsal trunk on the medial wall and the ventral trunk on the dorsolateral surface of cortex had similar connections. Recordings in S-II were always used to localize the injection site. Injections of  $^3\text{H}$ -proline and horseradish peroxidase (HRP) were made either at the start of a 12–24-hour terminal recording experiment, or one or two days prior to a terminal mapping experiment. In the cases of the longer survivals, sterile precautions were observed during the initial recordings and injections, and after the injections the exposed region of S-II was covered with silastic or a small sheet of teflon, the temporal muscle sutured in place, the skin closed, and the animal given a prophylactic injection of 0.1 cc of bicillin.

Injections of a mixture of HRP (Sigma type IX, concentration of 20–30%) and  $^3\text{H}$ -proline (50  $\mu\text{Ci}/\mu\text{l}$ , specific activity 20 Ci/mole, New England Nuclear) in saline were made into mapped locations in the trunk representation of S-II in three tree shrews. In two of these animals, a fine gauge 1- $\mu\text{l}$  Hamilton syringe was used to inject 0.05  $\mu\text{l}$  of the mixture over a period of 15 minutes. In the other animal, a comparable injection was made iontophoretically through a micropipette. In addition, a larger injection was made in one animal which included most of S-II. In all four animals, the responsive region of the medial wall and portions of the dorsal S-I cortex were mapped in

detail, and marker lesions were suitably placed so that the anatomical results could be related to the electrophysiological data. These results were compared to those from one animal with an injection in the forearm region of S-II which did not involve the representation of the trunk.

At the end of the terminal recording experiments, animals were deeply anesthetized and perfused with 0.9% saline followed by a mixture of 1.5% paraformaldehyde and 0.5% glutaraldehyde in phosphate buffer. Brains were stored briefly in the perfusion solution and then transferred to a solution of 30% sucrose in phosphate buffer. After 24–48 hours, the brains were frozen and cut coronally in 50- $\mu$ m sections. Typically, 3 in 5 sections were reacted for HRP using three different reaction methods (DAB, LaVail et al., '73; O-dianisidine, modified from de Olmos, '77; TMB, Mesulam, '78); 1 section in 5 was processed for autoradiography following standard procedures (Cowan et al., '72); and 1 section in 10 was stained with cresyl violet for cortical cytoarchitectonics. In addition, the autoradiographic and some of the HRP-processed sections were also stained with cresyl violet. The injection sites, marker lesions, retrogradely labeled cells, and anterogradely labeled axons were drawn at appropriate magnifications using the light microscope, and the drawings were used for reconstructions of appropriate views of the brain surface for each animal so that the anatomical results could be related to the electrophysiological maps.

#### RESULTS

The goals of the present experiments were to see if the representations of the dorsal trunk on the medial wall of the cerebral hemisphere and the ventral trunk on the dorsolateral convexity complemented each other so that in each animal they combined to form a complete and systematic map of the total trunk, and to see if both representations connected in a similar manner with the second somatosensory area, S-II. The results argue that the representation of the dorsal trunk on the medial wall is part of S-I in that it completes the S-I representation, and has connections with S-II that correspond to those for the rest of S-I.

##### *Organizations of the separate representations of the ventral and dorsal trunk*

The locations and overall somatotopic organizations of S-I and S-II are shown in Figure 1, which is modified from previous maps of S-I (Sur et al., '80) and S-II (Sur et al., '81) to

include the representations of the lateral leg, dorsal trunk, and base of the neck and shoulder on the medial wall of the cerebral hemisphere. This summary map is unfolded so that these features as well as the previously reported representations of the posterior leg, gluteal region, and tail on the medial wall are shown continuous with the rest of S-I on the dorsolateral surface of the brain. Note that S-I forms a complete and systematic representation of the body surface, typical in basic features of S-I organization except for the separation of the representations of the dorsal and ventral trunk. The ventral trunk is in the usual position of the trunk in cortex on the surface of the brain, just lateral to the representation of the foot and anterior leg and medial to the representation of the forearm. The lateral leg, dorsal trunk, base of the neck, and some of the shoulder, however, adjoin the representation of the posterior leg on the medial wall. This location for the representations of these body parts has not been reported for S-I of any other animal.

The somatotopic organizations of the medial and lateral representations of the trunk are shown for a specific tree shrew in Figure 2. Recording sites are numbered for cortex of the dorsolateral surface and lettered for cortex of the medial wall. The corresponding receptive fields are shown on views of the body surface. The ventral trunk and anterior and medial leg were represented in dorsolateral cortex just lateral to the representation of the pads of the foot, medial to the upper arm, and caudal to the dorsum of the foot (shaded). (These and other parts of S-I were mapped in detail in the present experiment, but the results are not shown for reasons of space; however, the results correspond closely to those previously reported (Sur et al., '80) for S-I of the tree shrew.) By considering the receptive fields for penetrations 1, 2, and 3, it can be seen that the representation of the inner part of the upper arm (penetration 1) was continuous with the representation of the upper ventral trunk and chest (penetrations 2 and 3). More caudal parts of the ventral trunk were represented medially (penetrations 4 and 6). It is also apparent that the ventral midline of the trunk was found caudally (penetrations 3, 5, and 6), and the ventrolateral trunk was found rostrally (penetrations 2 and 4) in S-I.

The representation of the inner surface and anterior margin of the hindlimb was found in cortex immediately medial to that devoted to the ventral trunk. The representations of these

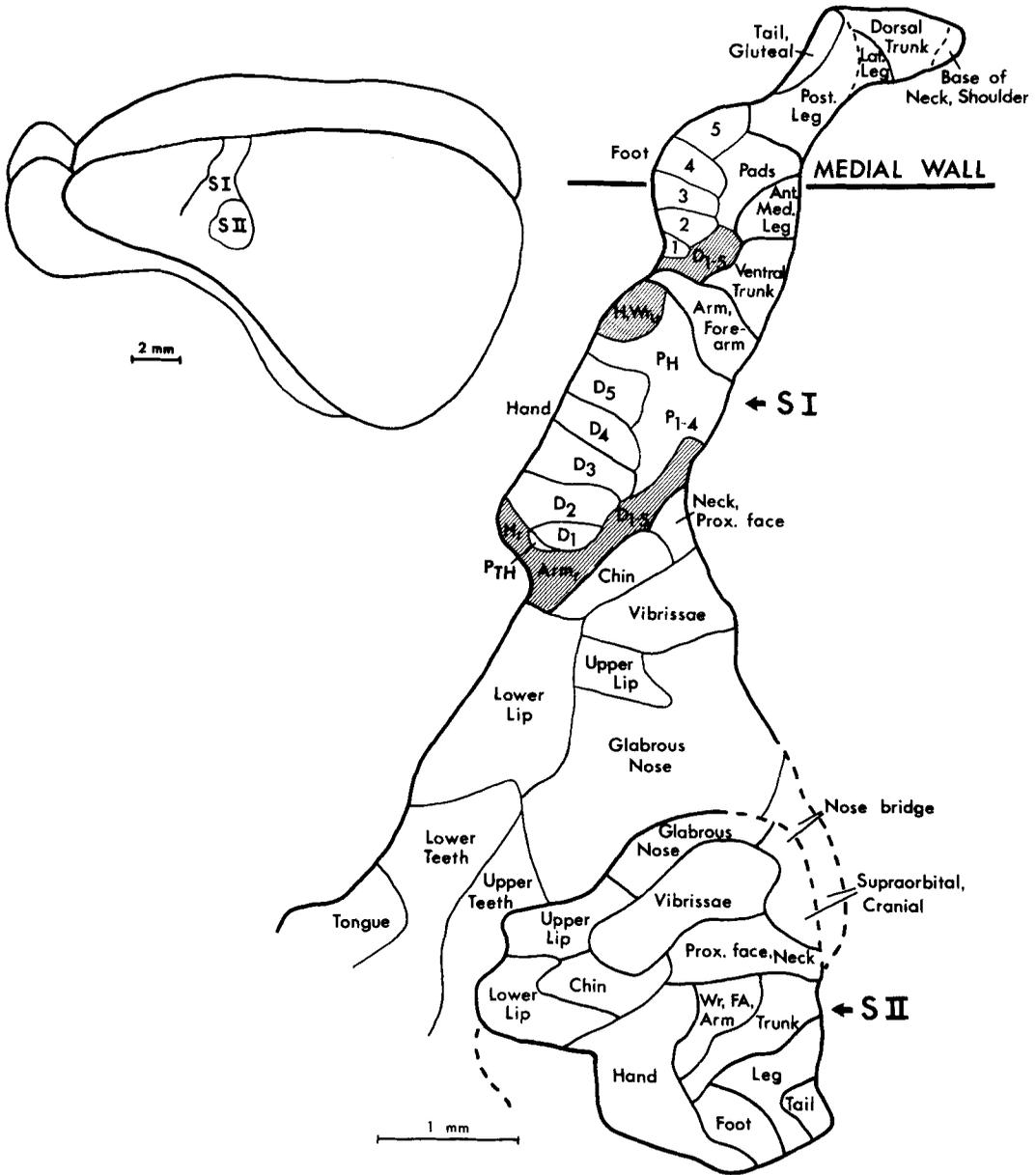


Fig. 1. The location and somatotopic organization of S-I and S-II in the tree shrew. The two areas are shown on a dorsolateral view of the brain on the upper left. Details of the body surface representations are shown in flattened views of S-I and S-II on the right. The medial wall part of the S-I map is from case 80-17, S-II, and the face representation of S-I from 79-52, and the rest of S-I is from 78-69. The part of S-I representing the posterior and lateral leg, the tail and gluteal region, the dorsal trunk, and the base of the neck and shoulder is folded out from the medial wall of the cerebral hemisphere along the marked line. Thick

lines mark the outer boundaries of S-I and S-II. Thin lines indicate subdivisions of the two areas where all included recording sites had receptive fields centered on the designated body part. Dashed lines mark uncertain boundaries. The locations of the dorsal surfaces of the hand and foot, dorsoradial wrist and forearm, and the dorsoulnar wrist are shaded. The pads of the hand are hypothenar,  $P_H$ , thenar,  $P_{TH}$ , and interdigital,  $P_1-P_4$ . The digits of the hand and foot are numbered  $D_1-D_5$ ; H, hand; FA, forearm; Wr, wrist; Prox., proximal.

two adjoining parts of the body were topologically continuous so that the line separating them on the illustration is artificial. Receptive fields for the most lateral recording sites, 7 and 8, overlapped receptive fields on the trunk, and the receptive field for the more caudal of the two recording sites, penetration 8, extended to the ventral midline of the body, further illustrating the principle that the ventral midline is represented along the caudal border of S-I. More medially, however, the caudal margin of S-I was devoted to the lower leg (penetration 10). This allowed the representation of the medial leg to be continuous, or nearly so, with the pads of the foot. The results also showed that the anterior margin of the hindleg was represented in cortex rostral (penetrations 7 and 9) to that of the inner leg (penetrations 8 and 10). Thus, the representation of the lower anterior margin of the leg adjoined that of the foot dorsum (shaded).

The posterior margin of the leg, the lateral leg, the tail, and the dorsal trunk were found represented in cortex on the medial wall of the cerebral hemisphere, just ventral and caudal to cortex devoted to the pads of the foot. Recording sites close to cortex activated by the pads were activated from skin on the lower leg, while more ventral and caudal recording sites related to the upper leg. The representation of the lateral leg (site K) was caudal to that of the posterior leg (sites O and N). The tail was represented most ventrally, where receptive fields usually included the gluteal region around the base of the tail (sites M and L). These features of the organization of S-I have been shown previously (Sur et al., '80).

The remaining recording sites in Figure 2 show that the dorsal and dorsolateral trunk were represented in cortex on the medial wall as a continuous extension of S-I. The dorsal midline of the body was represented most ventrally in this cortex (sites L, H, E, C, and A), corresponding to the rostral margin of S-I on the dorsolateral surface of the brain. More dorsal recording sites (J, F, G, and D) related to receptive fields displaced from the dorsal midline onto the dorsolateral trunk. The most rostral of these recording sites (H, I, and J) were activated from receptive fields on the caudal trunk extending onto the hindleg. The most caudal of these recording sites (A, B, C, and D) were activated from receptive fields on the rostral trunk extending onto the shoulder and base of the neck. Thus, the representation of the dorsal and dorsolateral trunk was topological and continuous with that of the leg.

It is important to note from the data presented in Figure 2 that the medial and lateral cortical representations of the leg and trunk were completely complementary, in that each region of cortex was devoted to areas of skin not found in the other region. Together they form a complete map of the leg and the trunk. Receptive fields for recording sites in the two cortical regions were centered on completely different regions of skin, and overlapped only slightly at the margins of the receptive fields, if at all. Although both the hindleg and the trunk were "split" in the representation into quite separate regions of cortex, an overall continuity in the representation was preserved so that adjoining recording sites always had adjoining or nearly adjoining receptive fields.

*Variation and consistency in the representation of the trunk and hindlimb*

The "split" representations of the trunk and leg were mapped wholly or partly in nine tree shrews. Summary maps for three of these cases are shown in Figures 1, 2, and 3. In Figure 1, the organization shown for the representation of the leg and trunk on the medial wall was determined for tree shrew 80-17. Other parts of the illustration are based on tree shrew 78-69 (S-I) and tree shrew 79-52 (S-II and face of S-I). Figure 2 is based on data from case 80-5, and Figure 3 illustrates a summary based on case 80-79. It can be seen from these three summary illustrations that there is some variation in the shapes and amounts of cortex devoted to various body parts, but there is an overall consistency in the pattern. When details of the representations are considered, other features of variation and consistency are apparent. Most significantly, the exact proportion of ventral trunk represented laterally and dorsal trunk represented medially varied. The exact dividing border of the split was often along the white fur-dark fur line, as shown in a typical case in Figure 2, but sometimes more or less of the dorsolateral trunk was represented laterally. In one unusual case, almost all of the trunk was represented laterally. However, in all cases the pattern of somatotopic organization illustrated in Figure 2 prevailed. Thus, regardless of the amount of trunk represented laterally, the most caudal of the recording sites corresponded to the ventral midline of the body and the most rostral of the recording sites related to a receptive field that was displaced laterally from the ventral midline. Likewise, in cortex on the medial wall, the dorsal midline was always represented

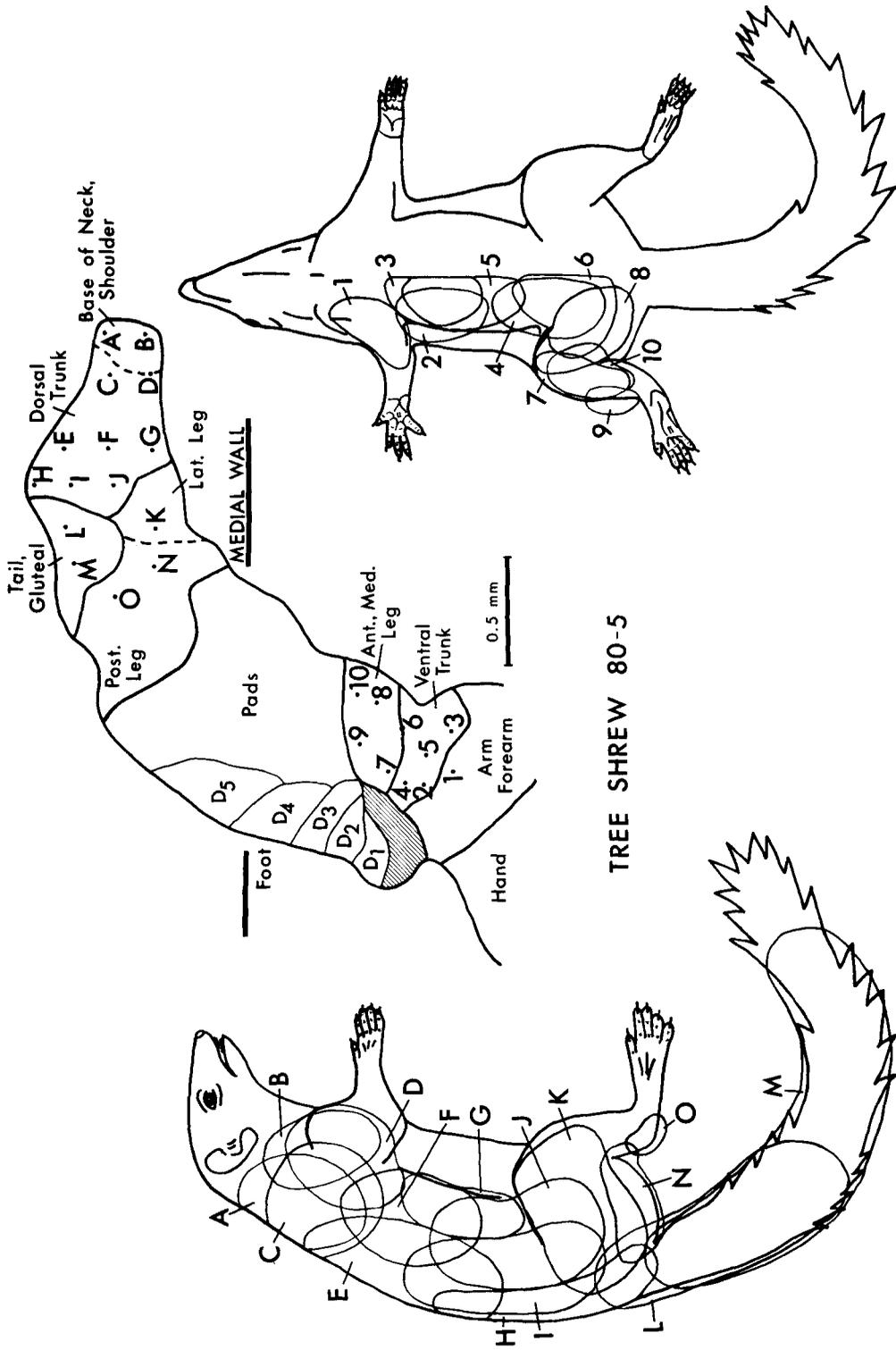


Fig. 2. Receptive fields for parts of S-I representing the trunk, tail, and leg. S-I is folded out from the medial wall of the left cerebral hemisphere along a line marked by the two horizontal bars. Shaded area represents the dorsum of foot digits. Rostral is to the left for the partial S-I map. Ant., anterior; Lat., lateral; Med., medial; Post., posterior. From case 80-5.

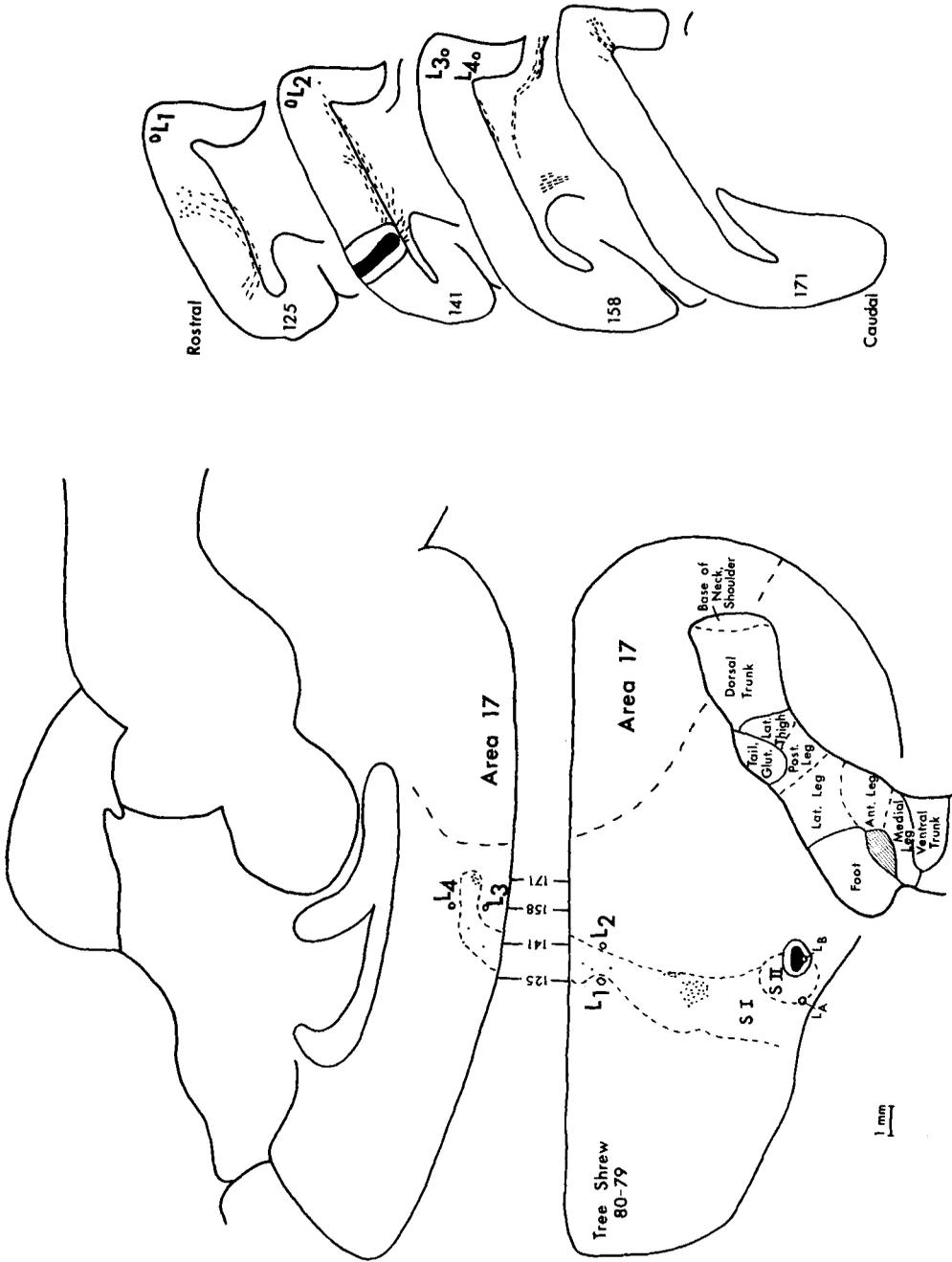


Fig. 3. The locations of labeled cells in S-I after an injection of horseradish peroxidase, HRP, into the representation of the dorsal trunk and adjoining neck in S-II. TMB sections. Dorsal and medial views of the brain are on the left. The inset shows the organization of the portion of S-I on the medial wall and the immediately adjoining dorsolateral surface as determined in detail in this tree shrew. Each dot indicates one retrogradely labeled cell. Marker lesions, L, are numbered for S-I and lettered for S-II. The zone of dense reaction product around the injection site is black; the lighter surrounding zone is outlined. The portions of the frontal brain sections shown on the right are indicated by numbered vertical bars on the views on the left. Dashed lines on the brain sections indicate axonal pathways labeled with HRP. From case 80-79.

most ventrally, while less ventral recording sites related to receptive fields dorsolateral to the midline. While both cortical regions devoted to the leg and trunk were not completely mapped in every case, there was never any evidence that parts of the body surface represented in the lateral cortex were also represented in the medial cortex. In addition, for recording sites in cortex on the medial wall, receptive fields were never found on the ventral neck, face, upper head, or any portion of the forearm other than the shoulder. Thus, the medial wall representation completes the S-I representation, and there is no evidence that it is part of a more extensive additional body surface representation.

#### *Response characteristics of cortex on the medial wall*

In all tree shrews, the cortex of the medial wall, including the representation of the dorsal trunk, was clearly cutaneous. Adequate stimuli included movement of body hairs and light touch of the body surface. The responsiveness of neurons to these stimuli was not notably different from that of neurons in S-I of the dorsolateral surface. In addition, the sizes of receptive fields related to the trunk and leg were similar for recording sites on the medial wall as for recording sites on the dorsolateral surface (Fig. 2).

Cortex outside the responsive region on the medial wall shown in Figures 1, 2, and 3 did not respond to cutaneous stimuli. Occasionally, recording sites dorsal to the cutaneous representation could be activated by vigorous stimulation of the body. Cortex immediately caudal to the cutaneous representation was activated by visual stimuli.

#### *Architectonic features of the medial wall*

The responsive region of the medial wall was identified in frontal brain sections by small electrolytic marker lesions. The responsive cortex showed a somewhat greater packing density of cells in layers III and IV, features of somatic koniocortex (S-I) in general, and of S-I in the tree shrew (Sur et al., '80). However, somatic koniocortex is not particularly well developed in tree shrews, and the cell packing in the responsive cortex of the medial wall is somewhat less developed than the more differentiated lateral parts of S-I. We conclude that the architectonic features of the medial representation of the dorsal trunk are consistent with those of S-I, but are not distinct enough to assign this cortex with certainty to S-I by architectonic criteria alone.

Cortex less than 1 mm caudal to the medial wall representation of the shoulder and base of the neck (Figs. 2, 3) is easily identified as striate cortex. The small amount of visually responsive cortex between striate cortex and somatic cortex is probably Area 18 (Kaas et al., '72).

#### *Connections with S-II*

From our ongoing studies of the connections of S-I and S-II in the tree shrew (Weller and Sur, '81), we know that these two fields are reciprocally and homotopically connected. S-I projects more strongly to S-II than S-II does to S-I. Neurons largely in cortical layer III project from S-I to S-II. Neither S-I or S-II appear to project to cortex caudal to S-I. By injecting the anterograde and retrograde tracers, <sup>3</sup>H-proline and horseradish peroxidase (HRP), into the representation of the trunk in S-II, we were able to determine that the connections of the trunk representation of the medial wall with S-II were similar to the connections between other parts of S-I and S-II.

Injections of combined tracers were made in S-II in five tree shrews. The sizes of the injections of HRP, as judged by the appearance of dense reaction product, ranged upward from 0.3 mm<sup>2</sup> in area and apparently restricted almost completely to the representation of the trunk in S-II, to about 4.0 mm<sup>2</sup> in area and including most or all of S-II. In all cases, the injection site in S-II was determined electrophysiologically, and enough of S-II was mapped so that the spread of the effective injection site in S-II could be estimated. The larger effective injection sites produced more extensive zones of label in S-I, and increased the number of labeled cells within these zones. The injection sites delimited when DAB was used as a chromagen were estimated as much smaller than when either O-dianisidine or TMB were used. The use of both the highly sensitive HRP reactants, TMB and O-dianisidine, and the less sensitive DAB, allowed valuable comparisons between different sizes of effective injection sites from the same injection.

The largest injection in S-II (case 80-89) included all or most of the area in sections reacted with O-dianisidine, and resulted in retrograde labeling of cells throughout most of S-I, including the region on the medial wall of the cerebral hemisphere representing the dorsal trunk. In all regions labeled, cells were largely confined to layer III.

The more restricted injections centered on the representation of the trunk in S-II resulted

in more restricted regions of label in S-I. Figure 3 illustrates results from one of these smaller injections. The electrode recordings indicated that the injection was centered on the representation of the dorsal trunk in S-II. Other portions of S-II were mapped, and marker lesions,  $L_A$  and  $L_B$ , were placed at the rostral and caudal margins of S-II. By comparing the HRP-dense region of the injection site with the limited mapping results in the experiment, and the previously determined detailed maps of S-II (Sur et al., '81), it appears that the injection included more than the representation of the dorsal trunk in S-II, and probably also involved the adjoining representation of the neck and proximal face, along with portions of the proximal forelimb and leg (see Fig. 1). The caudal portion of the injection site extended outside of S-II.

As a result of the injection illustrated in Figure 3, two separate groups of cells in more medial cortex were labeled. One group of cells was in S-I of the dorsolateral surface. This location in S-I corresponds to the location of the representation of neck and proximal face (Sur et al., '80, Fig. 1), a region of the body that is represented next to the dorsal trunk in S-II but not in S-I. A second group of cells was found in cortex on the medial wall devoted to the dorsal trunk and the base of the neck, which was extensively mapped in this case. Marker lesions  $L_3$  and  $L_4$  were made in an electrode penetration denoting the location of the representation of the dorsal trunk. It is apparent from the brain sections on the right of Figure 3 that the labeled cells were slightly caudal to the lesions and within the representation of the dorsal trunk and base of the neck and shoulder. A few scattered labeled cells were also found elsewhere in the medial portion of S-I, probably due to injection spread within S-II. Lesions  $L_1$  and  $L_2$  were made at the borders of the ventral trunk representation in S-I.

The labeled cells were located largely in layer III in all locations in S-I. The injection was too small to produce pronounced anterograde label, but silver grains slightly above background levels were noted in the autoradiographs in both locations. Other cases with restricted injections also demonstrated that the region of the medial wall devoted to the representation of the dorsal trunk is interconnected with S-II in a manner similar to the interconnections of other parts of S-I and S-II.

Because the dorsum of the trunk is represented along the caudal border of S-II, injections of neuroanatomical tracers centered in this region of S-II tended to spread and also

involve cortex caudal to S-II, as for the case illustrated in Figure 3. However, there was no evidence that cortex caudal to S-II was connected to either S-I on the dorsolateral surface or the somatosensory region on the medial wall. The somatotopic locations and amounts of label in both of these regions appeared to be solely related to the extent and location of the injection site in S-II.

#### DISCUSSION

In a previous study of the organization of the first somatosensory cortical area, S-I, in tree shrews, the representation was found to be incomplete in that the dorsal trunk and portions of the lateral leg were missing from their expected locations in cortex of the dorsolateral surface of the cerebral hemisphere (Sur et al., '80). The main findings of the present report are that these parts of the body are represented on the medial wall of the cerebral hemisphere, continuous with the representation of the posterior leg in S-I, and that both this previously missing part and the rest of S-I have similar connections with the second somatosensory area, S-II.

#### *Is the medial wall representation part of S-I?*

In our view, the only reasonable conclusion based on the electrophysiological and anatomical evidence is that the representation of the dorsal trunk on the medial wall is part of S-I. The electrophysiological results indicate that the medial wall region completes the S-I representation. Parts of the body surface missing from S-I of the dorsolateral surface are found on the medial wall, and there is no duplication in that skin surfaces are not represented in both places. The representation of the dorsal trunk and lateral leg on the medial wall is continuous with the typical representation of the posterior leg in S-I on the medial wall (Figs. 1-4). Although the medial wall representation includes the dorsal trunk up to the shoulder, it is incomplete and does not include the majority of the body surface. The caudal border of the responsive region on the medial wall, where the representation of the head and forelimb might be expected for a "homuncular" organization, is not responsive to somatic stimuli, but is responsive to visual stimuli instead. Anatomically, the medial wall region connects with S-II in a manner typical of the connections of S-I (Akers and Killackey, '78; Jones and Powell, '68; White and De Amicis, '77). As in other mammals, S-II in the tree shrew is homotopically interconnected with S-I; cortical regions caudal to S-I do not appear to project to

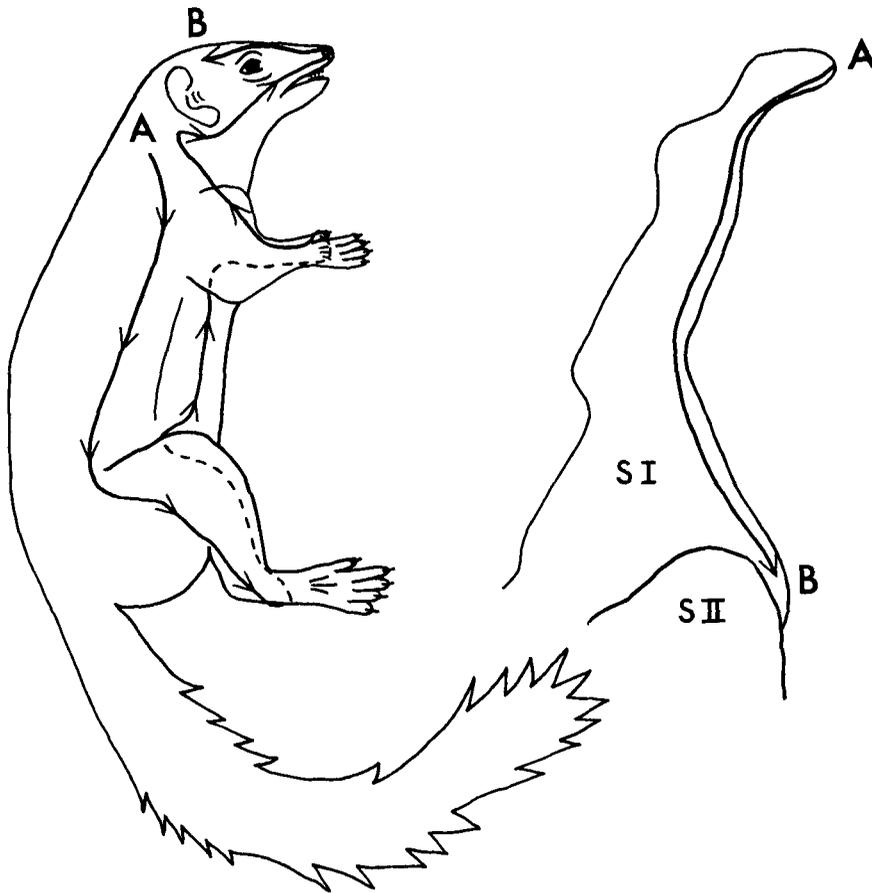


Fig. 4. Continuity in the representation along the caudal border of S-I. Although the representations of the upper and lower portions of the trunk are separated in S-I, these adjoining skin surfaces are connected by the representations of other skin surfaces along the caudal border of S-I. A sequence of recording sites along the line marked A-B in S-

I would produce a sequence of receptive fields along the line marked A-B on the lateral view of the tree shrew. Dashed lines travel along the hidden inner surfaces of the limbs. A similar sequence along the rostral border of S-I would, however, contain several "jumps" or discontinuities (see Fig. 1).

S-II nor receive from S-II (Weller and Sur, '81). Large injections of anatomical tracers in S-II label both the medial wall region and the rest of S-I. Small injections avoiding the dorsal trunk and hindleg portions of S-II fail to label the medial wall region, while small injections including the dorsal trunk in S-II label the medial wall region. Finally, the architectonic characteristics of the medial wall region are consistent with those of S-I.

Another alternative to the conclusion that the medial wall representation of the dorsal trunk is part of S-I is that the responsive region on the medial wall is part of a separate sensory region referred to as "Penfield's supplementary sensory area." The evidence for the existence of such an area is limited and confined to primates. Penfield and Jasper ('54) reported that

electrical stimulation of cortex on the medial wall caudal to "S-I" evoked somatosensory experiences in patients. Blomquist and Lorenzini ('65) found that electrical stimulation of the dorsal roots for some parts of the body in three of a number of investigated squirrel monkeys evoked responses in cortex caudal to "S-I." Mechanical stimulation of the skin was ineffective in activating this region. More recently, Murray and Coulter ('77) used HRP injections into the spinal cord of macaque monkeys to demonstrate a projection from medial posterior parietal cortex, which they attributed to the supplementary sensory area.

We do not consider the presently reported medial region to be part of a "supplementary sensory area" or any sensory representation other than S-I because it is an incomplete rep-

resentation by itself, it completes the S-I representation, and because of the anatomical and architectonic evidence. Given our definition of S-I, there is, in fact, reason to question the existence of a supplementary sensory area in tree shrews. The expected location of the supplementary sensory area caudal to S-I is responsive to visual, rather than somatic, stimuli, and probably is part of Area 18 (Kaas et al., '72).

The conclusion that part of S-I actually borders visual cortex should not be too surprising. The number of cortical areas appears to be fewer in "primitive" or generalized, as compared to advanced, mammals (Kaas, '77), and the first visual area, V-I, appears to directly adjoin part of S-I in the hedgehog (Kaas et al., '70). The supplementary sensory area could be an additional sensory representation in higher primates. Conversely, the limited electrophysiological evidence for the supplementary area in primates might be due to a displaced part of one of the "S-I" representations, such as the displaced dorsal trunk representation in tree shrews. The "S-I" region of monkeys has been recently shown to consist of several separate representations of the body, including separate cutaneous representations in Areas 3b and 1 (Merzenich et al., '78; Kaas et al., '79). Neither representation has a displaced dorsal trunk representation. However, a more caudal body representation in Area 2 has been only incompletely mapped, and it is possible that some of the responses attributed to a supplementary area could be part of a caudally extended "Area 2" representation.

#### *The "unique" organization of S-I in the tree shrew*

We started our investigations of the organization of S-I in tree shrews with the expectation that its rather generalized body form (Romer, '67) would be reflected in a generalized somatotopic pattern in S-I. While S-I of tree shrews has many generalized features, there are also specializations. Most notably, the representation of the glabrous nose was found to be larger than that reported for any other mammal (Sur et al., '80), resulting in a discontinuous face representation. We now add another previously unreported feature, the displacement of the representation of the dorsal trunk and adjoining skin to the medial wall of the cerebral hemisphere.

While the displacement of regions of the trunk representation to the medial part of S-

I has not been reported for any other mammal, it may not be unique to the tree shrew. The trunk has been described as "missing" from S-I of some mammals, most notably in the sheep (Johnson et al., '74), the llama (Welker et al., '76), and the slow loris (Krishnamurti et al., '76). The possibility remains that the trunk representations are not missing, but are in unusual locations. The results from the tree shrew show that S-I organization is more variable across species than previously thought, and locations of body parts within the representations may not be where they are expected.

#### *Factors related to the somatotopic organization of S-I*

S-I of mammals is characterized by both somatotopic continuities and disruptions of continuity. Without these discontinuities, S-I might be reasonably described as either a "homunculus" or a dermatomal sequence, since a dermatomal sequence is largely somatotopic. It is the nature of some of these disruptions that suggested that the organization of S-I is somehow related to the segmental organization of the dermatomes (see Introduction). The major discontinuities that have been observed in the "S-I" representations in some primates, the back of the head from the face, the anterior leg from the posterior leg, and, more rarely, the anterior arm from the posterior arm, all approximate the segmental lines of the dorsal root dermatomes. Thus, there was some evidence that when disruptions in somatotopy occur, they follow dermatomal lines. However, we (Merzenich et al., '78; Sur et al., '78; Kaas et al., '79; Nelson et al., '80) and others (Pubols and Pubols, '71; Welker, '73) have previously pointed out that the dermatomal sequence poorly describes the organization of S-I. There are many somatotopic discontinuities of S-I that are not predicted by an understanding of the dermatomal sequence. However, no discontinuity so dramatically separates parts of dermatomes as the split trunk representation described here for S-I of the tree shrew; the dorsal parts of the thoracic and the first two or three lumbar dermatomes are represented on the medial wall of the cerebral hemisphere, while the ventral parts of those same dermatomes are represented in a completely separate cortical zone some distance away on the dorsolateral surface of the brain.

Considerations of the details of the S-I maps that have been obtained for various species support the conclusion that there are at least two factors that are important in determining

cortical organization. Both factors relate to the overall goal of preserving somatotopy. Given the restrictions of flattening the three-dimensional configuration of the skin surface on the two dimensions of the cortical surface, certain adjacent skin surfaces, at least on the limbs, cannot be adjacent in the representation (see Nelson et al., '80). Other discontinuities are imposed by the differential enlargements of the body parts in the representation. The large representation of the glabrous nose in the tree shrew, for example, forces a separation of the upper from the lower face in S-I (Sur et al., '80). Discontinuities in S-I do not seem to occur in the representations of important sensory surfaces, and disruptions appear to be restricted to the representations of the least important sensory surfaces. Thus, the glabrous foot, hand, and nose are represented in a continuous manner in S-I of the tree shrew, while major disruptions occur on the upper face above the vibrissae, the arm, the leg, and the trunk. Such observations lead to the conclusion that somatotopy is often preserved in S-I for functional reasons. Another conclusion is that there is continuity in the map that is not obviously related to function. Some of the evidence supporting this second conclusion is summarized in Figure 4. The figure emphasizes an observation that has not been sufficiently stressed: Discontinuities in somatic maps are usually incomplete, and there are generally at least token points of continuity. In the tree shrew, a line of complete or nearly complete somatotopic continuity exists along the caudal border of S-I (Fig. 4). Shorter lines of continuity generally exist perpendicular to this line, joining all major body regions in the representation. It is away from the caudal border of S-I that the major disruptions in the somatotopic sequence are seen. Thus, it appears that it is important to preserve lines of continuity so that, to whatever extent is possible, all parts of S-I are ultimately continuous and joined. Since the lines of continuity are so narrow, it is difficult to suggest that they exist solely for functional reasons. More logically, these lines might be important in generating the representation during development. Perhaps the generation of orderly sequences in cortical representations depends on some minimal level of continuity.

#### ACKNOWLEDGMENTS

Supported by N.I.H. grant NS 16446.

#### LITERATURE CITED

- Akers, R.M., and H.P. Killackey (1978) Organization of corticocortical connections in the parietal cortex of the rat. *J. Comp. Neurol.* 181:513-538.
- Blomquist, A.J., and C.A. Lorenzini (1965) Projection of dorsal roots and sensory nerves to cortical sensory motor regions of squirrel monkey. *J. Neurophysiol.* 28:1195-1205.
- Celesia, G.G. (1963) Segmental organization of cortical afferent areas in the cat. *J. Neurophysiol.* 26:193-206.
- Cowan, W.M., D.I. Gottlieb, A.E. Hendrickson, J.L. Price, and T.A. Woolsey (1972) The autoradiographic demonstration of axonal connections in the central nervous system. *Brain Res.* 37:21-51.
- de Olmos, J.S. (1977) An improved HRP method for the study of central nervous connections. *Exp. Brain Res.* 29:541-551.
- Dreyer, D.A., P.R. Loe, C.B. Metz, and B.L. Whitsel (1975) Representation of head and face in postcentral gyrus of the macaque. *J. Neurophysiol.* 38:714-733.
- Johnson, J.I., E.W. Rubel, and G.I. Hattton (1974) Mechanosensory projections to cerebral cortex of sheep. *J. Comp. Neurol.* 158:81-108.
- Jones, E.G., and T.P.S. Powell (1968) The ipsilateral cortical connections of the somatic sensory areas in the cat. *Brain Res.* 9:71-94.
- Kaas, J.H. (1977) Sensory representations in mammals. In: *Function and Formation of Neural Systems*. G.S. Stent, ed. Dahlem Konferenzen, Berlin. pp. 65-80.
- Kaas, J.H., W.C. Hall, and I.T. Diamond (1970) Cortical visual areas I and II in the hedgehog: Relation between evoked potential maps and architectonic subdivisions. *J. Neurophysiol.* 33:595-615.
- Kaas, J.H., W.C. Hall, H. Killackey, and I.T. Diamond (1972) Visual cortex of the tree shrew (*Tupaia glis*): Architectonic subdivisions and representations of the visual field. *Brain Res.* 42:491-496.
- Kaas, J.H., R.J. Nelson, M. Sur, C.-S. Lin, and M.M. Merzenich (1979) Multiple representations of the body within the primary somatosensory cortex of primates. *Science* 204:521-523.
- Krishnamurti, A., F. Sanides, and W.I. Welker (1976) Microelectrode mapping of modality-specific somatic sensory cerebral neocortex in slow loris. *Brain Behav. Evol.* 13:367-383.
- LaVail, J.H., K.R. Winston, and A. Tish (1973) A method based on retrograde intraaxonal transport of protein for identification of cell bodies of origin of axons terminating within the CNS. *Brain Res.* 58:470-477.
- Merzenich, M.M., J.H. Kaas, M. Sur, and C.-S. Lin (1978) Double representation of the body surface within cytoarchitectonic areas 3b and 1 in "SI" in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* 181(1):41-74.
- Mesulam, M.M. (1978) Tetramethyl benzidine for horseradish peroxidase neurohistochemistry: A non-carcinogenic blue reaction-product with superior sensitivity for visualizing neural afferents and efferents. *J. Histochem. Cytochem.* 26:106-117.
- Murray, E.A., and J.P. Coulter (1977) Corticospinal projections from the medial cerebral hemisphere in monkey. *Soc. Neurosci. Abstr.* 3:275.
- Nelson, R.J., M. Sur, and J.H. Kaas (1978) Multiple representations of the body surface in postcentral cortex ('SI') of the squirrel monkey. *Neurosci. Abstr.* 4:556 (abstr.).
- Nelson, R.J., M. Sur, D.J. Felleman, and J.H. Kaas (1980) Representation of the body surface in postcentral parietal cortex of *Macaca fascicularis*. *J. Comp. Neurol.* 192:611-643.

- Penfield, W., and H. Jasper (1954) *Epilepsy and the Functional Anatomy of the Human Brain*. Little, Brown, and Co., Boston.
- Pubols, B.H., and L.H. Pubols (1971) Somatotopic organization of spider monkey somatic sensory cerebral cortex. *J. Comp. Neurol.* 141:63-76.
- Romer, A.S. (1967) Major steps in vertebrate evolution. *Science* 158:1629-1637.
- 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 (1978) The 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) The organization of somatosensory area II of tree shrews. *J. Comp. Neurol.* 201:121-133.
- Welker, W.I. (1973) Principles of organization of the ventrobasal complex in mammals. *Brain Behav. Evol.* 7:253-336.
- Welker, W.I., H.O. Adrian, W. Lifschitz, R. Kaulen, E. Caviedes, and W. Gutman (1976) Somatic sensory cortex of llama (*Lama glama*). *Brain Behav. Evol.* 13:284-293.
- Weller, R.E., and M. Sur (1981) Some connections of S-I and S-II in the tree shrew, *Tupaia glis*. *Anat. Rec.* 199:271A.
- Werner, G., and B.L. Whitsel (1968) Topology of the body representation in somatosensory area I in primates. *J. Neurophysiol.* 31:856-869.
- White, E.L., and R.A. DeAmicis (1977) Afferent and efferent projections of the region in mouse Sm I cortex which contains the posteromedial barrel subfield. *J. Comp. Neurol.* 175:455-482.
- Whitsel, B.L., D.A. Dreyer, and J.R. Roppolo (1971) Determinants of body representation in postcentral gyrus of macaques. *J. Neurophysiol.* 34:1018-1034.
- Woolsey, C.N. (1952) Patterns of localization in sensory and motor areas of the cerebral cortex. In: *The Biology of Mental Health and Disease*. Milbank Memorial Fund, Hoeber, New York.
- 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.
- Woolsey, C.N., W.H. Marshall, and P. Bard (1942) Representation of cutaneous tactile sensibility in the cerebral cortex of monkeys as indicated by evoked potentials. *Bull. Johns Hopkins Hosp.* 70:399-441.
- Woolsey, C.N., W.H. Marshall, and P. Bard (1943) Note on organization of tactile sensory area of cerebral cortex of chimpanzee. *J. Neurophysiol.* 6:287-291.