

Representation of the Body Surface in Somatosensory Area I of Tree Shrews, *Tupaia glis*

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ABSTRACT Microelectrode mapping methods were used to determine the organization of the first somatosensory area, S-I, of tree shrews. Tree shrews were chosen for study because of their generalized body form, phylogenetic relationship to primates, and smooth, easily mapped cortex. A systematic representation of the contralateral body surface was found in an architectonically distinct zone identified as somatic koniocortex. Overall features of somatotopic organization were similar to S-I of other mammals, S-I of prosimian primates, and the Area 3b "S-I proper" representation of monkeys. Like Area 3b in monkeys and the somatic koniocortex in galagos, S-I in tree shrews is bordered caudally by cortex also responsive to somatosensory stimuli. Several aspects of S-I organization in tree shrews appear to be primitive and generalized. These include the representation of the trunk with the ventrum at the caudal margin of S-I, the restriction of the glabrous digits of the hand and foot to the rostral half of the representation and pointed rostralward, the representation of an anterior strip of the forelimb lateral to the hand, and a posterior strip of hindlimb medial to the foot representation. As in a number of other mammals, a large portion of S-I in tree shrews is devoted to the head. However, the proportion of S-I activated from the glabrous nose is greater in tree shrews than in any previously studied mammal. We conclude that S-I of tree shrews has both specialized and generalized features, and that the generalized features importantly relate to an understanding of the evolution of the primate somatosensory system.

One of the goals of comparative studies of mammalian brains is to determine the generalized or basic plan of organization and the major modifications or variations of this plan. Since all extant mammals have probably specialized to some degree, the basic plan is best determined by considering a large number of species, and looking for recurring and common features. However, when specific brain features are actually considered, it may be necessary to form at least preliminary hypotheses from studies on relatively few species because of the labor and time involved in each individual study. Under these all-too-common conditions, the selection of the particular species for study becomes critical, and factors such as availability, cost, and convenience become less important than phyletic position, evidence of specialized or generalized features, and ease of study.

Although the organization of the first somatosensory area, S-I, of mammals has been explored with electrophysiological mapping methods in a wide range of mammals, most of these studies have not specified the details of the representation, either for technical reasons, or because the studies were concerned with other goals (for review see Sur et al., '78). The results of such studies are usually summarized in terms of a distorted body image or "homunculus" on the brain surface, which can show the general body arrangement and distortion in cortex, but fails to indicate the exact boundaries of S-I, the precise locations of regions of cortex devoted to individual body parts, the accurate relationships of body parts

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to each other in the representation, and the disruptions in somatotopy that are common. In addition, incorrect orientations of skin surfaces within the representation are often implied. Detailed comparisons of somatotopic order and proportions of S-I are possible when the boundaries of cortical regions within the field that are devoted to specific body parts are obtained accurately and outlined on a surface view of the brain. Presently, this type of information about the location and precise extent of most body parts in S-I is available for only two nonprimates, the opossum (Pubols et al., '76) and the grey squirrel (Sur et al., '78). Partial information is available for other mammals. For example, the representations of the mystacial vibrissae in rodents (Woolsey et al., '75), and the representation of the glabrous hand in the raccoon (Welker and Seidenstein, '59) are well defined, and the locations of large regions of the body (head, hand, etc.) have been compared in several carnivores (Welker and Campos, '63). Additional comparisons can be made with the detailed outline maps of S-I in the prosimian primate, galago (Sur et al., '80), and the two cutaneous fields, S-I proper and the posterior cutaneous field, in the owl monkey (Merzenich et al., '78) and the macaque monkey (Nelson et al., '80). However, it is obvious that if we are to have a better concept of the generalized organization of S-I in mammals, and how this organization has been modified in primates, more nonprimates need to be studied. This conclusion seems especially valid in view of the distant phyletic relationship of opossums to primates and other eutherian mammals (McKenna, '75), and the unique specialization of a double representation of the forelimb in S-I of the squirrel (Sur et al., '78).

The tree shrew is an obvious selection for further comparative studies on the organization of S-I. Most importantly, it is a close relative of primates (McKenna, '75), and information about the tree shrew brain is more likely to be relevant to an understanding of the early stages of the evolution of primate brains than any other mammal. In addition, the overall body form of the tree shrew is highly generalized, as Romer ('67) has stressed. Thus, there are a priori reasons for supposing that S-I of tree shrews will be generalized and relatively free of specializations. Finally, tree shrews have a smooth and relatively large brain, so that microelectrode mapping procedures would be greatly facilitated. For these reasons, we investigated the somatotopic or-

ganization of S-I and adjacent regions of cortex in the tree shrew. Preliminary results have been briefly summarized elsewhere (Weller et al., '79).

METHODS

The organization of primary somatosensory cortex, S-I, was investigated in ten adult tree shrews, *Tupaia glis*, using microelectrode mapping methods similar to those described elsewhere (Merzenich et al., '78; Sur et al., '78). The tree shrews were first anesthetized with an initial dose of 50 mg/kg of ketamine hydrochloride and supplementary doses were given as needed to maintain a surgical level of anesthesia. A large region of cortex including S-I was exposed and the dura was excised. The exposed cortex was covered with a pool of silicone fluid retained in an acrylic dam around the skull opening. The skull and dam were fixed to an iron bar which was held in a universal vise so that any desired head position could be obtained. The portion of S-I to be investigated was then aligned perpendicular to the plane of the recording electrode.

Recordings were made with glass-coated platinum-iridium microelectrodes designed to record from small clusters of neurons. Electrode penetrations were made approximately 200 μm apart, and were marked with respect to the surface vasculature, as viewed with an operating microscope, on a magnified high-resolution photograph of the cortical surface. Recording depths were typically between 650–900 μm from the pial surface, in the region of layer IV. In electrode penetrations parallel to the cortical surface down the medial wall of the cerebral hemisphere, receptive fields were determined for recording sites every 150–250 μm . Cutaneous receptive fields were defined with a fine hand-held glass probe which was used to lightly stimulate the glabrous skin and displace hairs and vibrissae on the hairy skin. Responses to stronger stimuli such as tapping the skin and manipulations of joints and body parts were also noted. Over regions of skin where light cutaneous stimuli were effective, minimal receptive fields were defined and outlined on drawings of tree shrew body parts made from photographs. Boundaries of S-I were indicated by penetrations unresponsive to light tactile stimulation, or by a change in receptive field size and somatotopic organization when the second somatosensory area, S-II, or other adjoining somatosensory fields were entered. Typically, rows of recording sites were made in the rostrocaudal

dimension, and pairs of microlesions (10 μ amps/5–10 sec) were made at several medial-lateral levels at the rostral and caudal boundaries of the mapped cortex. These lesions aided comparisons of the recording results with the cortical cytoarchitecture.

Except for the lateralmost portion representing intraoral surfaces, S-I was completely mapped in two animals, with two additional animals having all of S-I except portions of the medial wall and the lateralmost portion entirely mapped. In six other tree shrews, more limited portions of S-I were explored in detail. In addition, other experiments on the organization of other somatosensory regions also involved parts of S-I so that features of organization were repeatedly confirmed. Up to 213 and more typically about 100–150 electrode penetrations were made in a single experiment. In most experiments, small amounts of anatomical tracers were injected into specific locations in S-I. The results of these injections will be reported separately.

At the end of recording sessions, the animals were deeply anesthetized and perfused through the heart with 0.9% saline followed by either 10% formalin, or, after horseradish peroxidase injections, with a paraformaldehyde-glutaraldehyde mixture. The brain was later sectioned on a freezing microtome or on a vibratome (Oxford) in the sagittal or occasionally the frontal plane at 50 μ m. Every fifth section was stained with cresyl violet for cell bodies. Additional sections were stained for myelin with hematoxylin, or processed for horseradish peroxidase or autoradiography.

The representation of the body surface in cortex was reconstructed by relating receptive field locations to recording sites. Sectors of cortex within the cutaneous representation receiving input from specific regions of the body surface were demarcated on the brain map. Results from penetrations down cortex of the medial wall were orthonormally related to the pial surface and illustrated as part of an "unfolded" representation.

RESULTS

Multiunit microelectrode mapping techniques were used to explore somatosensory cortex in tree shrews. A systematic and relatively unspecialized representation of the body surface, the first somatic area or S-I, was found in somatic koniocortex. Cortex caudal to the representation of the head contained a second cutaneous representation, S-II, and cortex caudal to S-I on the dorsal surface of

the brain responded to stronger somatic stimuli. The organization of S-I is described in this report.

Location and overall organization of S-I

The location of S-I on a dorsolateral view of the brain is shown in Figure 1. The electrophysiologically defined region is also coextensive with an architectonically distinct zone, somatic koniocortex (see histological results). The representation extends from tissue on the medial wall to near the rhinal fissure, a total distance of about 7 mm. The representation is as narrow as 1 mm or less medially and it widens laterally to about 3 mm. Motor cortex, identified by large layer V pyramidal cells, is rostral to S-I, but it is not shown in Figure 1. The boundaries of S-II and the higher threshold somatic region caudal to S-I are demarcated, and visual (Kaas et al., '72b) areas are shown for reference. Note that less than 2 mm of tissue separate the rostral extent of the first visual area, V-I, from the first somatic area, S-I.

The overall organization of S-I, as determined in a single extensively mapped case, is shown in Figure 2. The map was obtained by reconstructing 282 recording sites from 213 electrode penetrations. Electrode penetrations down the medial wall yielded recording sites at multiple depths.

It is apparent from Figure 2 that S-I of the tree shrew conforms to the usual pattern of S-I in nonprimates (see Sur et al., '78), prosimians (Krishnamurti et al., '76; Sur et al., '80; Carlson and Welt, '80), and the 3b field of monkeys (Merzenich et al., '78; Kaas et al., '79; Nelson et al., '80). The tail and gluteal region along with a strip of the posterior hindlimb are represented on the medial wall of the hemisphere. The glabrous foot is found in adjacent cortex on the dorsal surface of the hemisphere with digits 1–5 represented in sequence from lateral to medial along the rostral border of S-I. The glabrous pads and heel of the foot are caudal to the digit representation. The dorsal hairy surface of the digits and foot are found in cortex lateral and caudal to digits 1 and 2. Most of the leg, including the anterior, medial, and portions of the lateral surfaces, is represented lateral to the foot pads. A very small region of cortex devoted to the trunk of the body adjoins the representation of the anterior leg with the upper arm in more lateral cortex. In the relatively large representation of the glabrous hand, the digits are rostral and in order from

1-5 in a lateral to medial sequence. Cortex caudal to the digits is occupied by the pads of the hand, while the dorsum of the digits and hand relates to a lateral and caudal strip of cortex. The radial wrist, forearm, and arm are represented lateral to the hand in a way that seems to crudely maintain a continuity between the hand and face representations. A noticeable invagination of "high-threshold" cortex unresponsive to cutaneous stimulation but responsive to more intense stimuli on the contralateral forelimb is found at the rostral margin of S-I between the hand and face representations. The head occupies the lateral half of the representation in which the neck and proximal face are medial and caudal and the chin medial and rostral. The lower lip lies rostrally in cortex lateral to the chin while

the dorsal surfaces of the face including the vibrissae, upper lip, nose, and orbital skin are caudal. A large region of cortex is devoted to the glabrous nose. Teeth, gums, and other intraoral surfaces activate the most lateral portion of S-I. Because of difficulties in stimulating all parts of the oral cavity, the lateral margin of S-I was not precisely determined.

While the summary diagram in Figure 2 is based on one individual tree shrew, there were minor variations from animal to animal. Most importantly, the representations of the trunk and adjoining leg extended to the rostral boundary of S-I in one case, the representation of forelimb medial to the hand did not always extend to the rostral border of S-I, and the intrusion of unresponsive tissue at the rostral margin of S-I between the head and hand

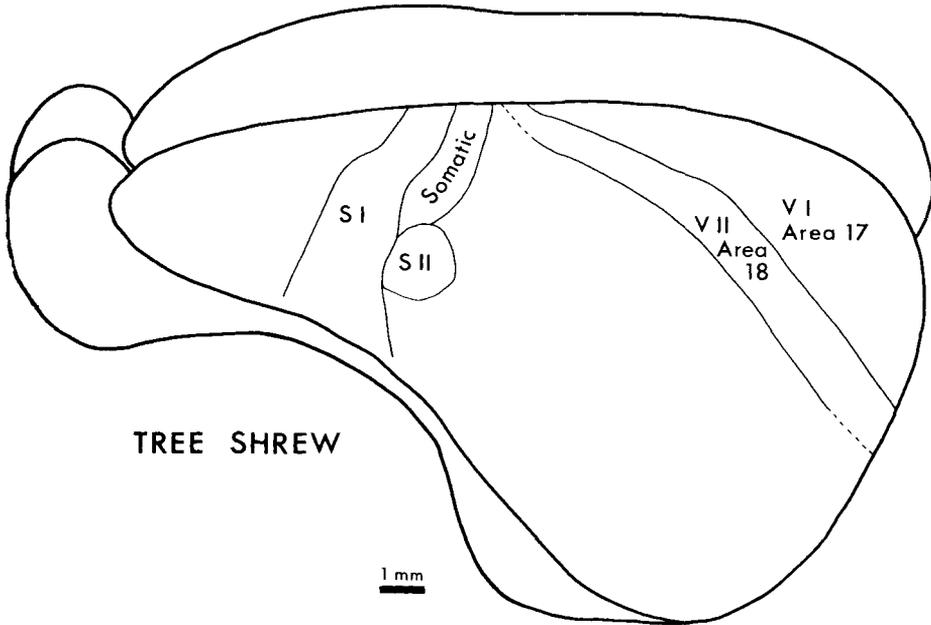


Fig. 1. The location of the first somatosensory area, S-I, on a dorsolateral view of the brain of a tree shrew. S-I also extends about 1 mm down the medial wall of the cerebral hemisphere. The precise lateral boundary of S-I was not determined. The locations of the second somatosensory area, S-II, and the zone of cortex caudal to S-I that is responsive to somatic stimuli, Somatic, are also shown. The visual Areas 17 and 18 were architectonically determined in the tree shrew illustrated, and they correspond to the first (V-I) and second (V-II) visual areas as previously determined (Kaas et al., '72b).

Fig. 2. The organization of S-I in the tree shrew. The heavy line marks the borders of S-I, as shown on a dorsal view of the brain on the upper left. Thinner lines demarcate subdivisions of S-I where all recording sites have receptive fields centered on the designated body part. Digits of the hand and foot are numbered from the thumb or great toe to the little finger or toe, D₁-D₅. The locations of the dorsal hairy surfaces of the hand and foot, the dorsoradial wrist and forearm and the dorsoulnar wrist are shaded. The pads of the hand are interdigital, P₁-P₄, the hypothenar, P_H, and the thenar, P_{TH}. H, hand; FA, forearm; Wr, wrist; r, radial; u, ulnar. Case 78-69.

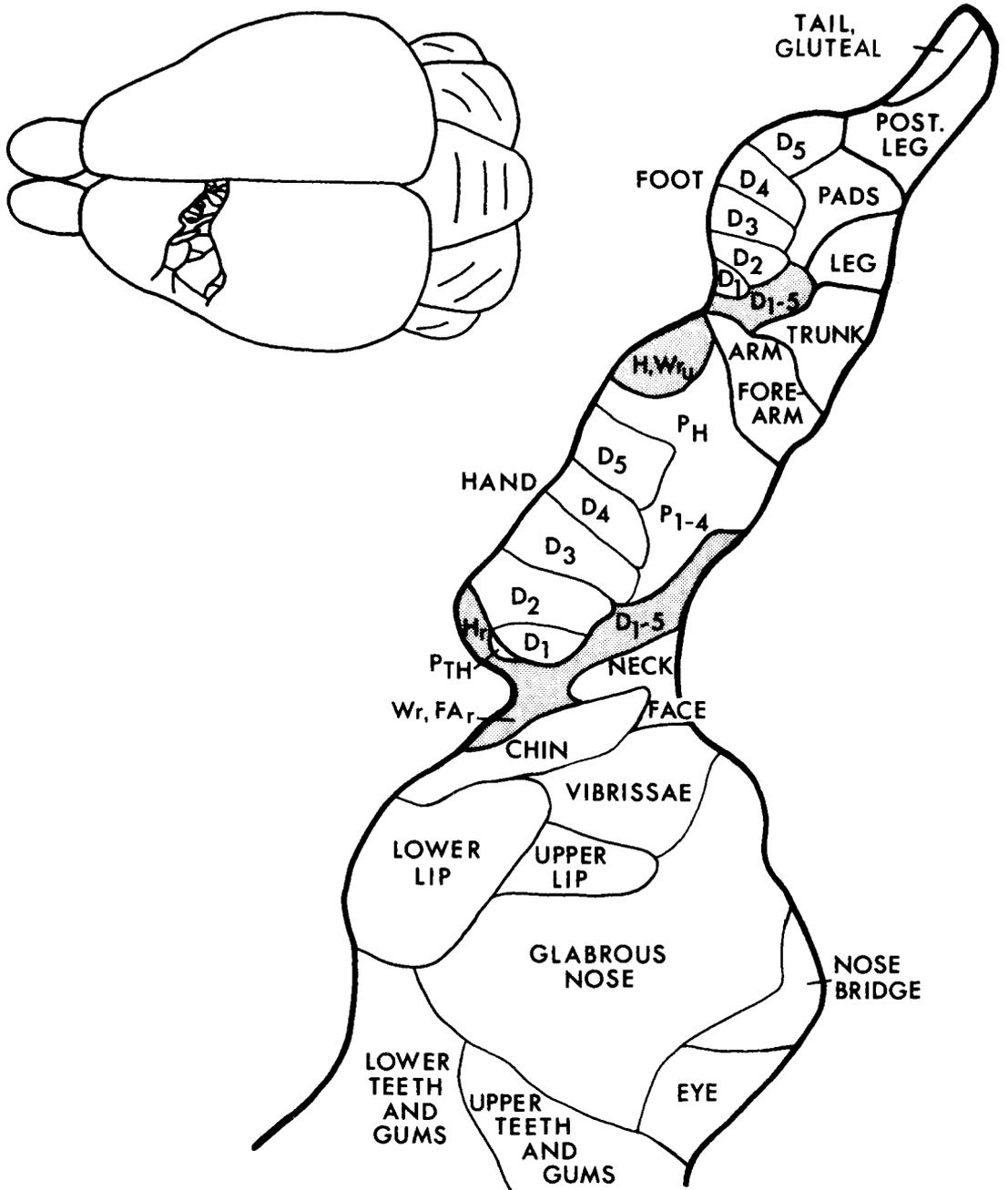


Figure 2

representations varied in extent from 0.5 to 1 mm. Such variations are discussed further below.

It is also apparent from Figure 2 that some body parts are disproportionately represented in S-I. The proportions of cortex devoted to various body surfaces are quantified and converted to magnification factors in Table 1. The overall area of S-I, about 8 mm², is small compared to the entire area of neocortex of tree shrews (Figs. 1 and 2). While the head occupies over half of S-I and the hand nearly a fourth, the remainder of the body surface is represented in the remaining fourth of S-I. Within the representation, magnification factors vary greatly, over four orders of magnitude from the gluteal region and tail to the glabrous nose. The glabrous nose has the largest magnification within the representation, perhaps reflecting its importance as a sensory surface for the tree shrew. At the other extreme, very little tissue per unit of skin area is devoted to the trunk, leg, gluteal region, and tail. The glabrous hand and foot exhibit moderately high magnifications.

Representation of the head

The general organizing feature of the cortex devoted to the head is that dorsal skin surfaces are represented caudally and ventral skin

surfaces are represented rostrally. The proximal face is medial in S-I, while the distal face and oral cavity are lateral. These conclusions are partially documented in Figure 3, where receptive fields are shown for three rows of recording sites. Conclusions supported by these illustrative rows are based on over 100 recording sites in the representation of the head in the case shown, and in similar numbers of recording sites in other cases. Receptive fields for some additional recording sites from another animal are shown in Figure 8.

Row A of Figure 3 illustrates a progression of receptive fields from the distal chin at the rostral margin of S-I (site 1) to the proximal chin (site 4) and onto the neck and face (sites 5, 6, and 7). Note that the progression is continuous, without disruption. Similarly, small changes in electrode position from the chin representation to the adjoining vibrissae representation result in receptive field movements across the corner of the mouth from the proximal jaw to the mystacial vibrissae (sites 8 and 9).

The region of cortex devoted to the mystacial vibrissae is proportionately smaller than that found in rodents such as squirrels (Sur et al., '78), rats (Welker, '71), and mice (Woolsey, '67), and single recording sites were usually activated by stimulating more than one vi-

TABLE 1. Areas, relative proportions, and magnification factors (cortical area/skin area) of different body surfaces within S-I of tree shrew 78-69

Skin region	Area within S-I, mm ²	Proportion of S-I, %	Magnification ($\times 10^{-4}$)
Head	4.47	55.0	36.65
(excluding intraoral)			
Glabrous nose	2.04	25.1	2965.1
Neck, proximal face	0.18	2.2	2.37
Ventral surfaces (chin, lower lip)	1.05	12.9	254.2
Dorsal surfaces (upper lip, vibrissae, nose bridge, supraorbital)	1.20	14.8	29.2
Hand	1.82	22.4	30.71
Glabrous	1.47	18.1	49.61
Dorsal (incl. lateral and medial reps.)	0.35	4.3	11.81
Forearm, arm (incl. lateral and medial reps.)	0.28	3.5	1.85
Trunk	0.23	2.8	0.51
Leg (incl. lateral and medial reps.)	0.46	5.7	1.05
Foot	0.76	9.4	10.01
Glabrous	0.65	8.0	17.02
Dorsal	0.11	1.4	3.01
Gluteal, tail	0.10	1.2	0.21
Total S-I	8.12	100.0	

brissae. Within the region, proximal vibrissae activate medial recording sites and distal vibrissae activate lateral recording sites. The dorsal rows of vibrissae are represented caudally and the ventral rows rostrally within the region.

Row B of recording sites illustrates the organization of the regions of cortex devoted to the upper and lower lips. The midlines of the lower and upper lips are at the rostral and caudal margins of the lip representations (sites 1 and 5) while the junction of the lip representations corresponds to the corner of the mouth. Medially within the lip region,

receptive fields include small groups of sinus hairs that line the lips; laterally, receptive fields usually are confined to the glabrous skin.

The most prominent feature of the representation of the head in S-I of tree shrews is the large expanse of cortex devoted to the glabrous nose (Table 1). The smallest receptive fields found anywhere on the body surface are located on the glabrous nose, where some of the receptive fields are 1 mm² or less in size, which approaches the limits of receptive field delineation by hand-held probes. The nose, from ventral to dorsal, is represented from

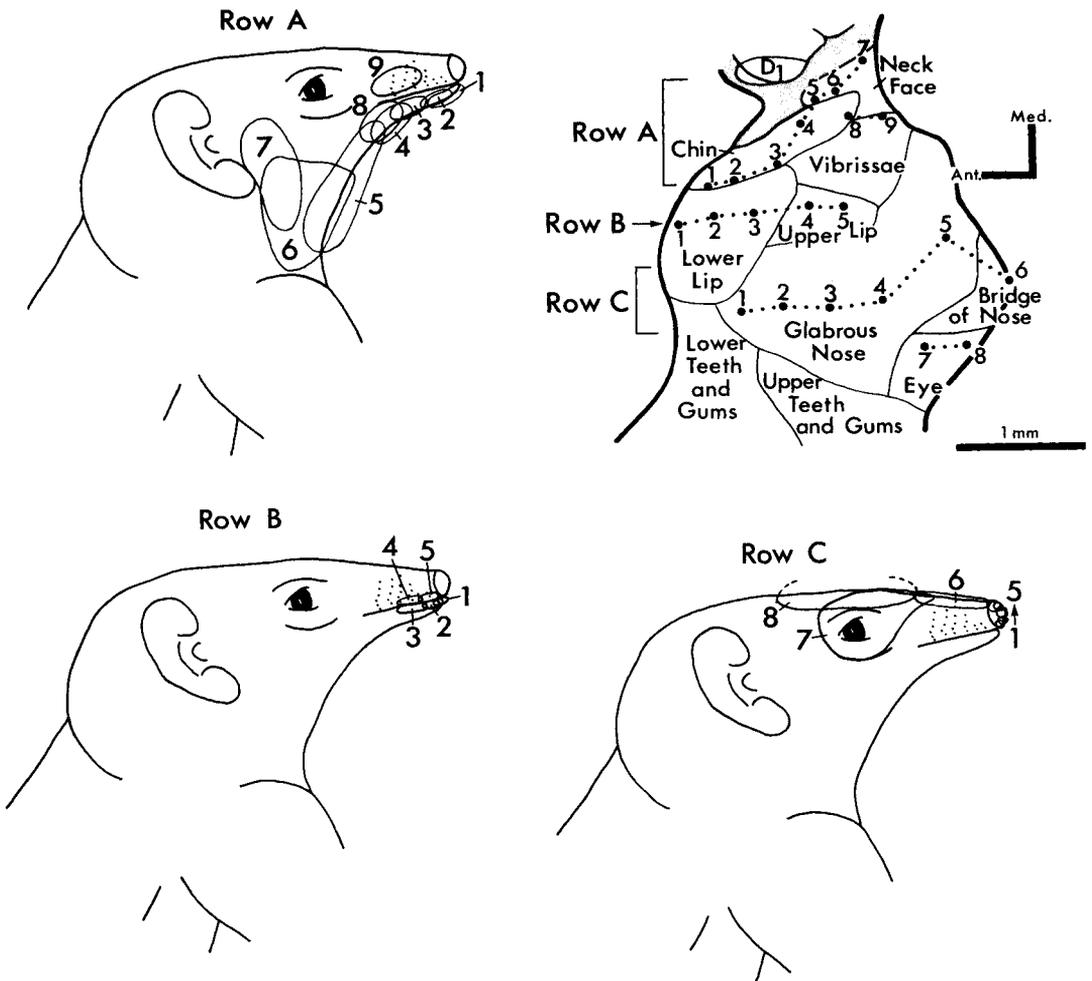


Fig. 3. Receptive fields for three rows of recording sites across cortex related to the head and face. Note that the ventral face is represented rostrally and the dorsal face caudally in S-I. Receptive field 8, Row C, extended to the margins of the skin removed to explore the cortex. As in other figures, the recording sites shown represent only a portion of those used to determine boundaries of subdivisions within S-I. Case 78-69. Conventions as in Figure 2.

rostral to caudal in cortex. The lateral surface of the nose is represented adjacent to the vibrissae, while the midline of the nose lies laterally (row C, sites 1-5). The proximal ventral nose is represented adjacent to the upper lip. The distal ventral surface of the nose is represented adjacent to the lateral part of the lower lip in cortex (row C, site 1). With successively more caudal recording sites, a clear progression of receptive fields occurs from ventral to dorsal on the nose (row C, sites 1-5). The most caudal recording sites (see site 6) enter a region of cortex devoted to the bridge of the nose and upper face. More laterally, in this caudal part of S-I, cortex is responsive to stimuli around the eye and on the forehead (sites 7 and 8).

Because part of the cranial skin had to be removed in order to expose cortex for recording, the representation of the top of the head was not determined. However, judging from the receptive field location and size for penetration 7 in row C of Figure 3, the top of the head would be expected to activate a very small region of cortex close to recording site 8.

The lateralmost part of the head representation responds to stimulation of the lower and upper teeth and gums. The lower teeth activate cortex rostral to that activated by the upper teeth. As with the representations of the upper and lower lips, the midline incisor teeth are represented at the rostral and caudal extremes of the teeth regions, while the back molars near the corner of the mouth are represented at the junction of the upper and lower teeth regions. Because of difficulties in carefully stimulating within the mouth, the representations of other parts of the oral cavity were not determined. Occasional recording sites indicate that the tongue and adjoining skin surfaces are lateral to the teeth representations.

Representation of the hand

The region of the cortex devoted to the hand was explored in detail in four tree shrews and the case illustrated in Figure 4 is typical. The glabrous digits are found in the rostral two-thirds of the hand region in an orderly medial to lateral sequence from digit 5 to digit 1. Digit tips are represented along the rostral margin of S-I and progressively more proximal portions of the digits activate progressively more caudal regions of cortex. These conclusions are documented in Figure 4 by the receptive field locations for five rows of recording sites, one for the representation of each digit.

Receptive fields on the proximal digits typically extended onto adjoining pads (see Figure 4). The hypothenar, insular, second, third, and fourth pads of the glabrous hand occupy cortex medial and caudal to the representations of the digits. The ulnar pads, P_H and P_4 , are found most medially in this area, and the other pads are found more laterally. The hypothenar pad activates a large region of cortex which typically extends across the complete rostrocaudal extent of the hand in cortex just medial to the representations of D_5 and P_4 . Further medially and rostrally within this region of cortex, some recording sites have receptive fields extending onto the ulnar margin of the hand and to the dorsal ulnar hand and wrist (H, Wr in Figure 4).

Receptive fields for recording sites lateral and sometimes caudal to the region of cortex activated by the first digit often extend onto the adjoining radial pads—pad 1 and the thenar pad. In general, the representation of the palmar pads seems to be split into two regions, with all pads except the thenar pad and usually pad 1 represented medial to the digits and extending to the caudal border of digit 3, while the radial pads occupy a narrow region lateral and caudal to digit 1.

The dorsoradial part of the hand is found in a narrow zone of cortex adjacent to the representation of the radial pads and digit 1 (see Figures 4 and 8). The central and ulnar dorsum of the hand and wrist is found medial to the glabrous hand at the rostral margin of S-I.

The dorsal hairy skin of the digits projects to a narrow mediolateral, usually continuous, zone of cortex along the caudal border of the hand region of S-I (Figures 4 and 5). Thus, the dorsal surfaces of the digits are represented caudal to the pads, except for the cortex immediately caudal to digit 2 and sometimes 1 where the dorsum of the digits appears to directly adjoin the glabrous digits. Receptive fields on the dorsum of the digits are large and usually include more than one digit (see Figure 4). However, a progression of receptive field locations was still evident, with medial recording sites activated by digit 5 and more lateral recording sites successively relating mainly to digits 4-1 (compare sites 3 of row D_1 and 5 of row D_4 of Figure 4).

Representation of the forelimb

The organization of the forelimb representation was carefully explored in five tree shrews. The most important conclusion is that

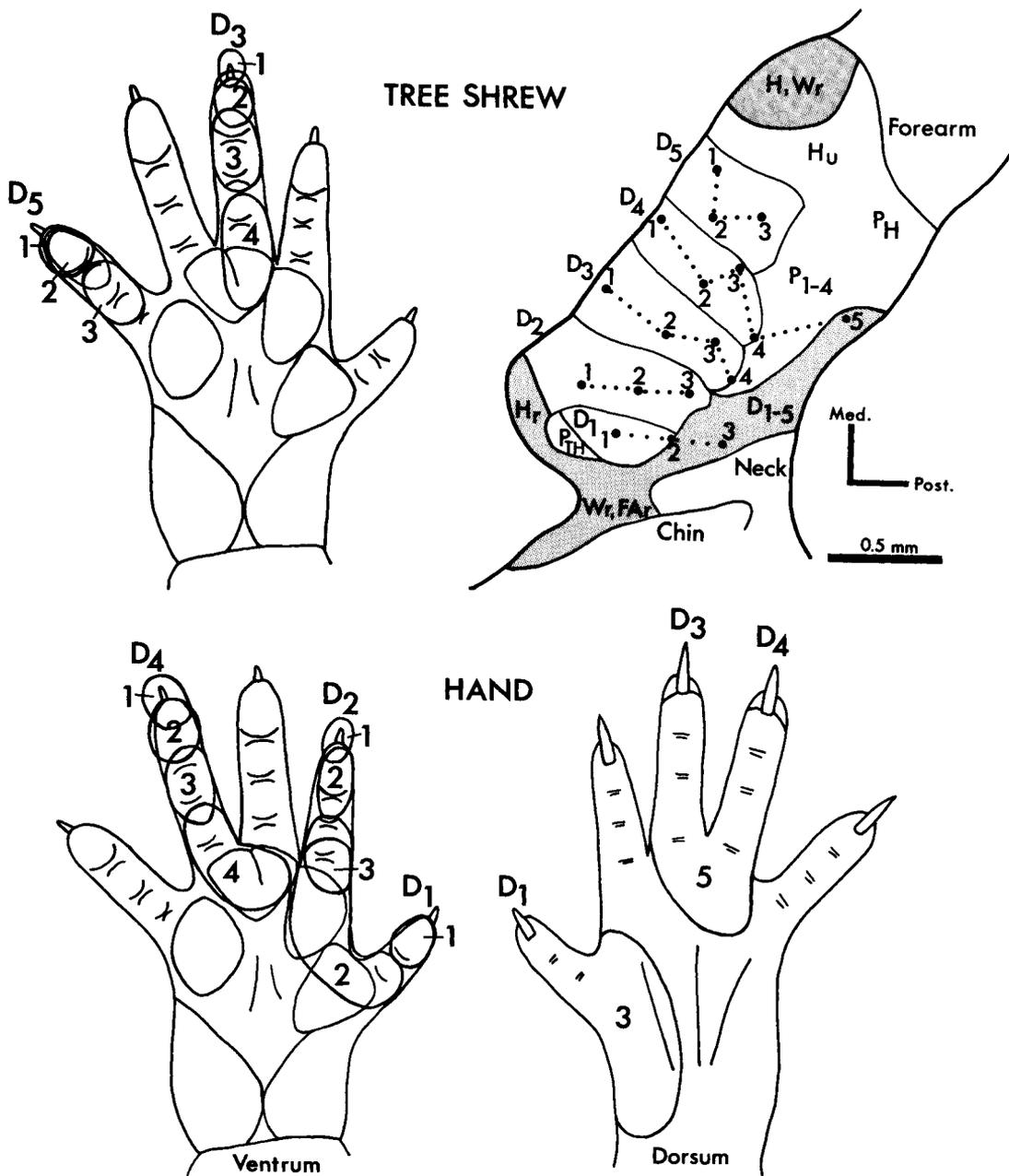


Fig. 4. Receptive fields for five rows of recording sites in cortex devoted to the hand. A rostral-to-caudal progression across cortex relates to a shift in receptive fields from distal to proximal parts of each glabrous digit, D₁-D₅. The pads of the hand are split into a large ulnar and central group, P_H and P₁₋₄, and a smaller radial group, P_{TH}. The dorsal hairy surfaces of the digits are represented separately behind the glabrous digits. Case 78-69. Conventions as in Figure 2.

parts of the forelimb are discontinuously represented on both sides of the hand. Most of the forelimb including the dorsal, ulnar, and ventral aspects of the wrist, forearm, and arm are found lateral to the trunk and medial to the hand in S-I. A narrow radial strip of the forelimb skin is found lateral to the hand where it joins the radial dorsal aspect of the hand with the ventral neck.

Both forelimb regions preserve somatotopic continuity with adjoining cortex. The larger medial region of cortex, which is activated by most of the forelimb, is organized to match the bordering cortex activated by the trunk.

Thus, a rostral to caudal progression of recording sites relates to a shift of receptive fields from lateral to ventral on the arm in correspondence with a lateral to ventral shift in a similar row in the trunk representation. Documentation of this conclusion is presented in Figure 5. In row A, the receptive field for the rostral site 1 is on the dorsal or lateral arm and that for the caudal site 2 is on the ventral arm. Similar dorsum to ventrum progressions on the forearm and wrist are shown for rostral to caudal rows of recording sites in B and C of Figure 5. It is also apparent from these rows that the upper arm is represented

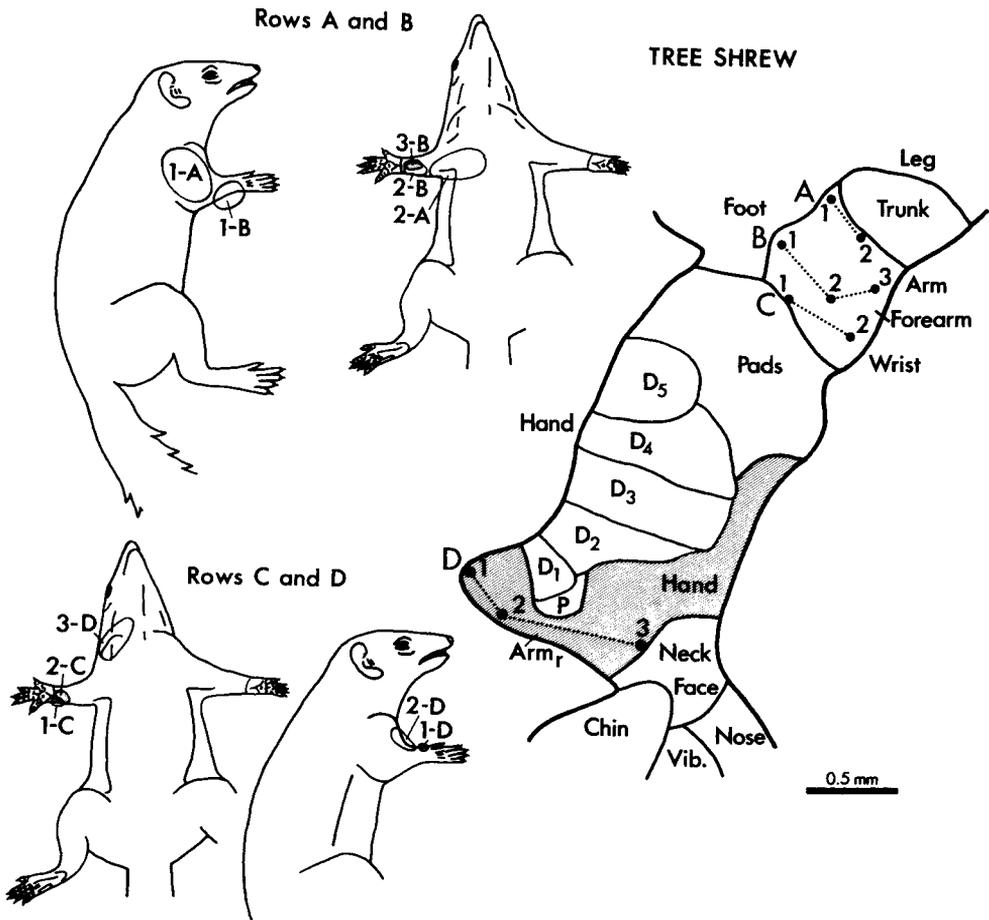


Fig. 5. Rows of recording sites in cortex representing the forelimb. Note that the radial surface of the forelimb is represented lateral to the hand (row D) while the rest of the forelimb is represented medial to the hand (rows A-C). A rostral-to-caudal progression of recording sites in the medial zone relates to a progression of recording sites around the forelimb from dorsal to ulnar to ventral. The distal parts of the radial forelimb are rostral to the proximal parts in the lateral zone of cortex. Case 78-70. P, pad 1 and thenar pad; other conventions as in Figure 2.

medially where it adjoins the trunk representation, and the lower forearm is found laterally where it borders the hand representation. Thus, an overall somatotopic continuity of hand, forearm, arm, and trunk occurs in S-I of the tree shrew.

The radial aspect of the forelimb is represented in cortex lateral to the hand. While the proportion of cortex devoted to the radial forelimb is small and appears variable in location and extent, it matches the somatotopic organization of the representations of the adjacent body parts. As can be seen from row D of recording sites in Figure 5, the distal parts of the radial forelimb are rostral in S-I while more proximal parts are more caudal so that the representation of the hand is joined to the representation of the neck.

Representation of the trunk

The representation of the trunk in S-I was investigated in six animals. The trunk in S-I of the tree shrew is located between the representation of the lateral, anterior, and medial surfaces of the hindlimb medially, and the dorsal, ulnar, and ventral aspects of the forelimb laterally (Figs. 2, 5). The trunk representation is widest caudally where it forms the posterior border of S-I, and it narrows rostrally so that it usually does not extend completely to the rostral border of S-I (Fig. 2). In cases where the trunk region does not extend to the rostral border of S-I, either the dorsal arm or the dorsum of the foot is found rostral to the trunk region.

Within the trunk region, the ventrum of the body is represented along the caudal border of S-I, and more lateral and dorsal skin surfaces are found more rostrally. The dorsal trunk is poorly represented or perhaps even absent in most cases. A few well-defined cutaneous receptive fields on the dorsal trunk were found for rostral recording sites in only one animal, and in this case the trunk representation extended to the rostral border of S-I. In five other tree shrews, receptive fields on the dorsal trunk and varying portions of the adjacent lateral leg, including the lateral proximal thigh, were not found, even though the S-I trunk region was mapped in fine detail. (However, these "missing" surfaces were found to be represented in cortex on the medial wall of the cerebral hemisphere; see Responsiveness and organization of cortex bordering S-I.) In contrast, the ventral belly was found to be represented in the caudal part of the trunk region in all six animals. Even though the

trunk representation usually appeared to be incomplete, caudal to rostral rows of recording sites consistently produced ventral to lateral (or dorsal) shifts in receptive field locations. It is also apparent from our recordings that the upper trunk and chest are represented laterally and the lower trunk and abdomen medially within the trunk region. Thus, the trunk region is somatotopically continuous with much of the adjoining leg and arm representations. Receptive fields on the trunk are generally larger than for any other skin surface except the tail. It is also apparent (Fig. 2) that very little cortex is devoted to this large portion of the body. However, if the trunk representation on the medial wall is included within S-I (see Discussion), the magnification factor for the trunk (Table 1) would be somewhat larger.

Representation of the foot

The foot representation was completely mapped in three animals, and partially mapped in three other animals. The glabrous digits of the foot are represented in order from 1 to 5 in a lateral to medial sequence in cortex with the tips of the toes at the rostral border of S-I and the proximal phalanges caudally, about in the middle of the width of S-I. The caudal part of S-I is occupied by the pads of the foot, and adjoining parts of the leg, while the dorsal hairy surface of the digits and foot relates to cortex lateral and caudal to that activated by digits 1 and 2.

Some aspects of the organization of the foot region are shown in Figure 6, where five rostral to caudal rows of recording sites illustrate the representation of each glabrous digit. In each row, it is apparent that recording sites with receptive fields on the digit tips are rostral to sites with receptive fields more proximal on the digits. Also, it can be seen from sites 4 and 5 of row D₄ of Figure 6 that distal pads of the foot are represented rostral to the proximal pads and heel. A typical receptive field for the dorsum of the digits is shown for site 3 of row D₁ of Figure 6. Receptive fields on the dorsum and heel of the foot were consistently larger than those on the glabrous digits and distal pads.

Representation of the hindlimb, gluteal region, and tail

The representation of the hindlimb in S-I is split by cortex devoted to the sole of the foot into a lateral region of cortex activated by the anterior, medial, and portions of the lateral

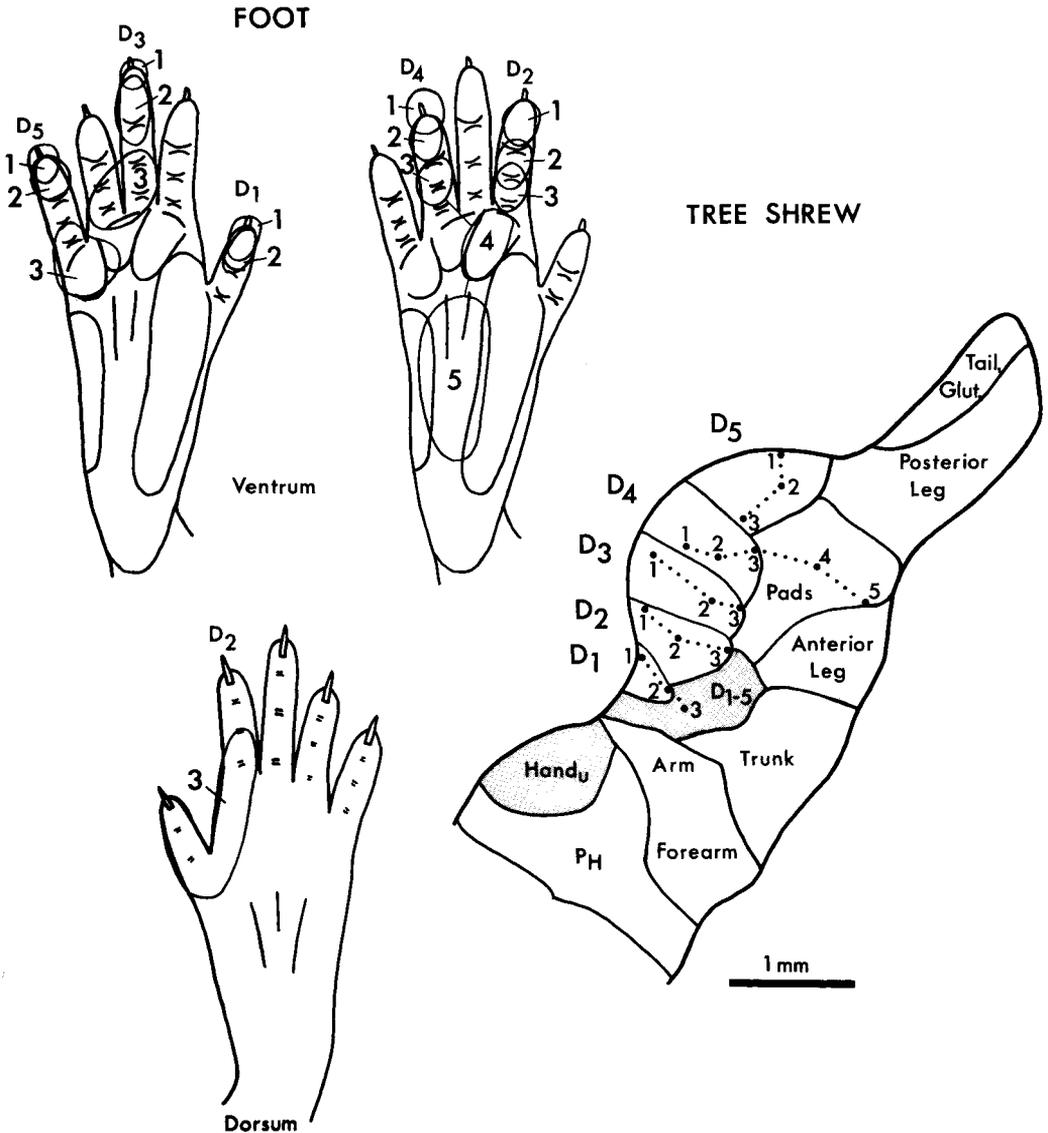


Fig. 6. Receptive fields for rows of recording sites in the representation of the foot. Receptive fields on the distal phalanges of the glabrous digits are for the most rostral recording sites. The dorsal surfaces of the digits are represented separately (shaded). Case 78-69. Conventions as in Figure 2.

leg, and a medial region extending onto the medial wall of the cerebral hemisphere, which receives projections from the rest of the leg, gluteal region, and tail. Results are based on recordings from only the lateral region in five tree shrews, and for both the medial and lateral regions in three tree shrews.

The lateral region of cortex represents portions of the lateral, and the entire anterior

and medial surfaces of the leg. Within this region, the distal parts of the leg are represented rostrally and medially along the foot representation adjacent to the neighboring dorsal and glabrous foot. The proximal leg is represented caudally and laterally where it adjoins the representation of the trunk. This aspect of organization is illustrated by receptive fields for two rows of recording sites in

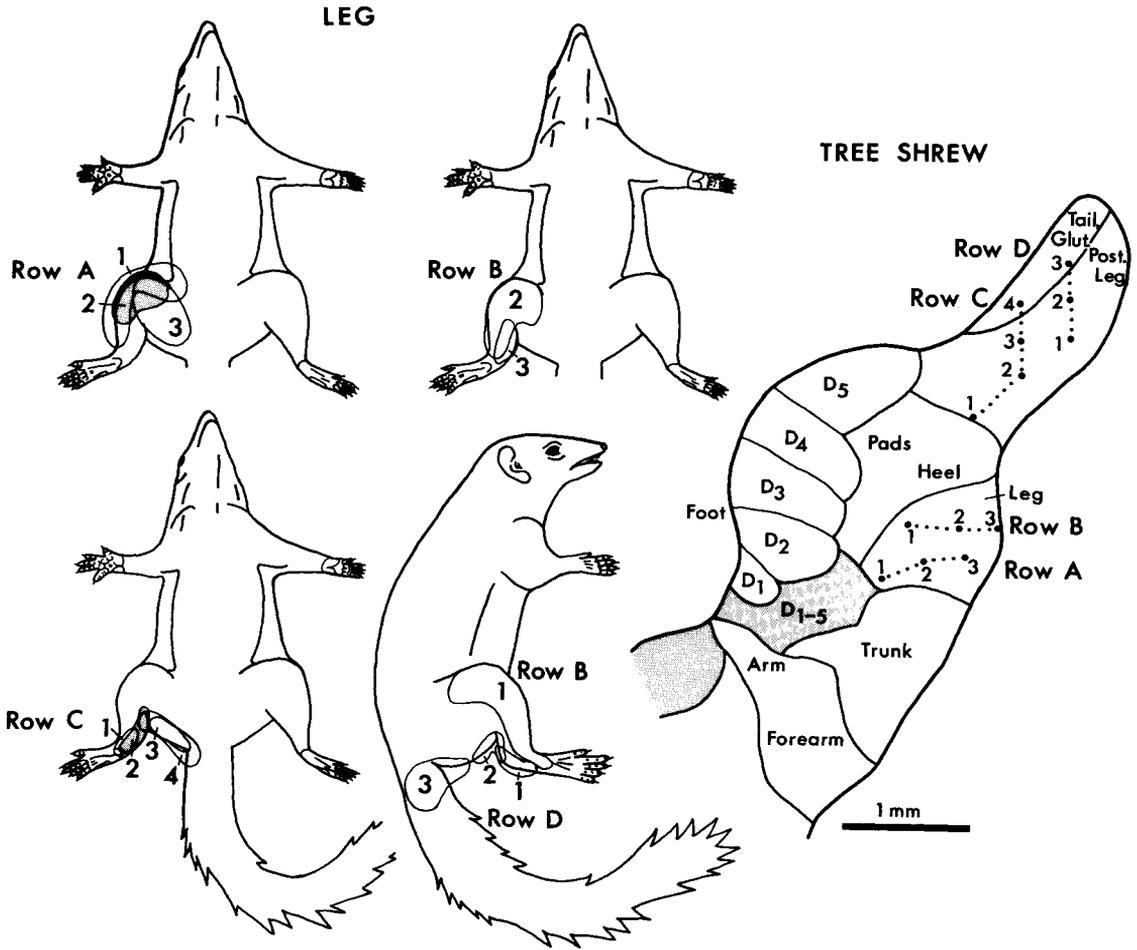


Fig. 7. Rows of recording sites in cortex related to the hindlimb and gluteal skin. A lateral region of cortex represents the anterior leg with the lateral leg rostral to the medial leg (rows A and B). A medial region of cortex extending down the medial wall of the cerebral hemisphere represents the posterior leg with the distal leg on the dorsal surface and the proximal leg on the medial wall (rows C and D). Case 78-69. Conventions as in Figure 2.

the lateral region in Figure 7. For each rostrocaudal row of sites, large receptive fields on the outer and anterior leg progress to those on the inner thigh (row A, site 3) and calf (row B, site 3). Thus, the shift in receptive fields is from the outer to inner leg rostrocaudally, and that from proximal to distal is essentially lateromedial. Since the ventral trunk and the inner thigh are found caudally in S-I while the lateral trunk and lateral thigh lie rostrally, continuity between the leg and trunk representations is preserved. Portions of the lateral leg, including the proximal thigh and sometimes more distal leg surfaces, appear to be poorly represented within the region (see

below). In addition, the lateral leg region, like the cortex devoted to the trunk, is variable in extent.

A narrow zone of cortex devoted to the heel separates cortex on the dorsal surface at the lip of the medial wall representing most of the lateral, anterior, and medial leg from cortex extending onto the medial wall representing the rest of the leg, gluteal region, and tail. Aspects of the organization of this medial zone of S-I are indicated by receptive fields for rows C and D of recording sites in Figure 7. The distal posterior leg and ankle project to cortex adjacent to the pads and heel of the foot, and more proximal parts of the leg extending to

the gluteal region and tail are found further from the foot representation in cortex down the medial wall of the cerebral hemisphere (more medially in the flattened summary diagram of Figure 2 and subsequent illustrations).

Few recording sites were found with receptive fields exclusively on the tail, and these sites were deepest on the medial wall. Large receptive fields including the genitals, gluteal region, and base of the tail were found for a few deep recording sites next to the posterior leg representation, and sites with small receptive fields restricted to the genitals were not found. Thus, the genital and gluteal skin surfaces appear to be poorly represented in S-I.

Responsiveness and organization of cortex bordering S-I

The present experiments provided evidence for at least four types of cortex adjoining S-I. First, recording sites along the rostral border of the representation were not responsive to light cutaneous stimulation, and were either unresponsive to somatosensory stimuli or required more intense stimuli, such as heavy taps or vigorous brushing. This high-threshold bordering region was narrow and consistently included an invagination into S-I between the representations of the hand and the face (Fig. 8). The invagination varied somewhat in rostrocaudal extent from animal to animal (Figs. 2 and 8), and it sometimes appeared to clearly separate cortex representing the dorsal radial hand and wrist from the cortex devoted to the medial chin. In other cases, the invagination of the high-threshold region did not appear to be extensive enough to complete this separation.

Another region of cortex bordering S-I was clearly identified as S-II (Fig. 1). Recording sites in this region of cortex caudal to the representation of the glabrous nose, snout, and cranial skin in S-I were also responsive to light tactile stimulation of the skin. The overall organization of this responsive zone, as well as its location, was typical of the second somatosensory area, S-II (see Nelson et al., '79). In addition, receptive fields were larger for most body parts for recordings in S-II in comparison with those in S-I. The change in receptive field sizes was most useful in distinguishing S-II from S-I along the representations of the nose, snout, and cranial skin, which adjoin in the two representations. The detailed organization of S-II is presented elsewhere (Weller et al., '80).

A third region of cortex bordering S-I was a moderate- to high-threshold somatosensory region caudal to S-I (labeled Somatic in Fig. 1). Neurons in this field were clearly responsive to somatic inputs, but they were activated by brisk taps on the body, rapid movements of hairs, or sustained pressure rather than light tactile stimulation. Some activation seemed to be from deep body tissues, although there was no clear evidence for joint receptor inputs. The responsive zone was about 1 mm in rostrocaudal width, and extended from the medial wall to the border of S-II.

Because neurons in the caudal somatic region required moderate levels of stimulation, and low-threshold cutaneous receptive fields could not be determined, receptive fields for recording sites were only roughly defined. In addition, receptive fields were much larger than those in S-I. Yet, consistent changes in receptive field locations were observed with changes in recording site locations, and a crude somatic topology was evident within the caudal somatic field. The body representation in the field paralleled that within S-I so that the trunk and hindlimb were medial and the forelimb and head lateral.

Recordings down the medial wall of the cerebral hemisphere continued through S-I into cortex that was unresponsive to somatic stimuli. In five tree shrews, penetrations on the medial wall were extended caudally beyond cortex representing the posterior hindlimb and tail. Portions of the lateral leg and dorsal trunk were found to be represented caudal to the representation of the posterior leg, in a small protrusion of cortex less than a millimeter in anteroposterior extent and about 0.5 mm dorsoventrally down the medial wall. The amount of skin represented varied from only the lateral proximal thigh and caudal dorsal trunk to much of the lateral surface of the hindlimb, the entire dorsal trunk, and the dorsal proximal upper arm. The lateral thigh and caudal trunk were found represented adjacent and caudal to the posterior leg, while more rostral parts of the trunk were represented further caudally on the medial wall. The dorsal midline of the trunk was represented at the most ventral extent of the region, and receptive fields on the dorsolateral trunk were found more superficially.

Architectonic features of S-I

The first somatosensory representation, S-I, was found to be coextensive with a distinct architectonic field, somatic koniocortex, as de-

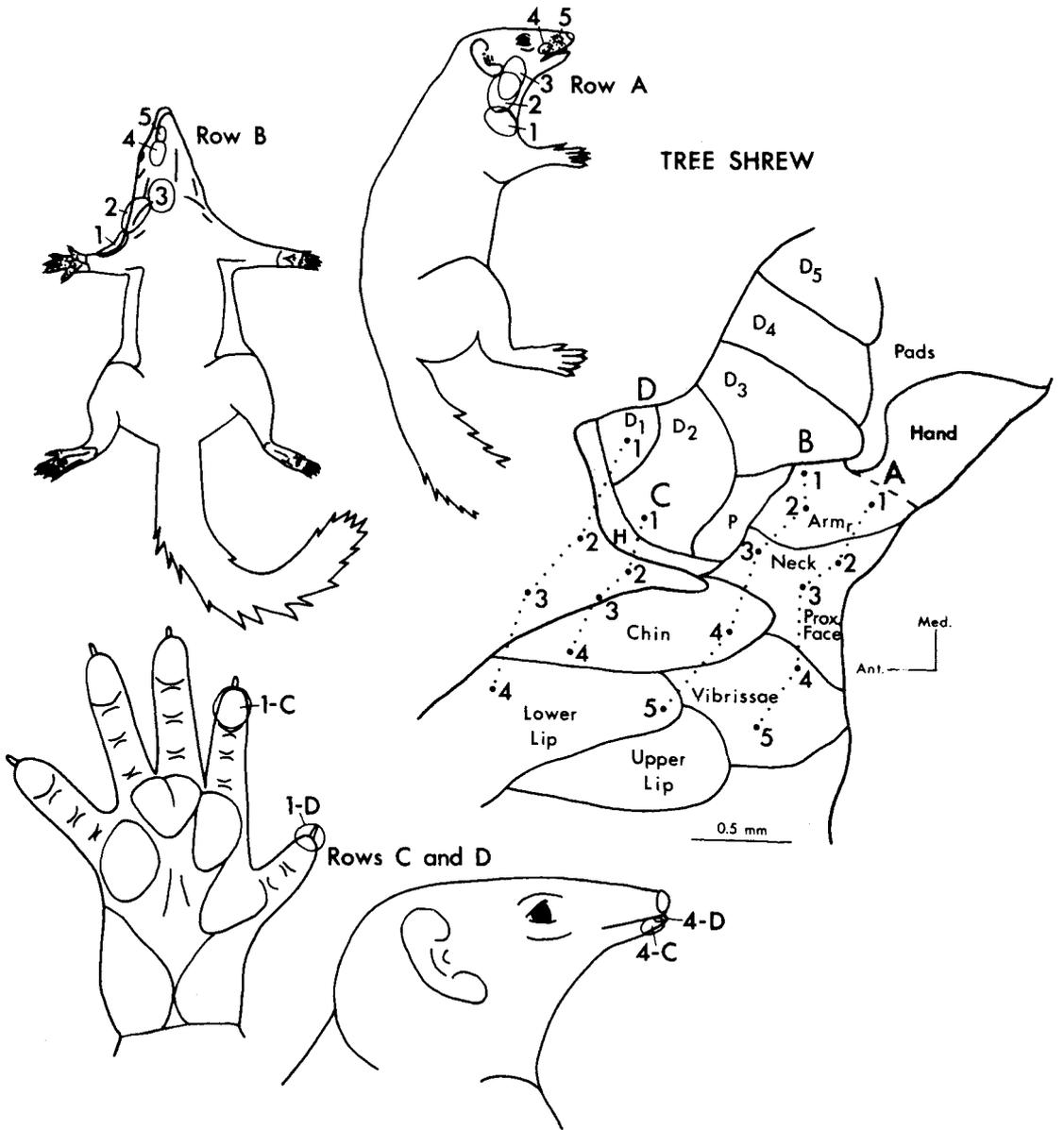


Fig. 8. Medial to lateral rows of recording sites demonstrating the location of an unresponsive or high-threshold invagination between the radial forelimb and face regions of S-I. Caudal rows A and B demonstrate uninterrupted progressions of receptive fields from arm to face. Rostral rows C and D contain recording sites (2 and 3) that were unresponsive to light cutaneous stimulation. Case 78-68. P, pad 1 and thenar pad; other conventions as in Figure 2.

fined for the S-I field in prosimians (Sanides and Krishnamurti, '67; Sur et al., '80). In the present electrophysiological experiments, the rostral and caudal boundaries of S-I were marked with small electrolytic lesions made through the recording electrode at several

mediolateral levels. These lesions were later identified in brain sections cut in the parasagittal plane and stained for cell bodies. A typical marked section is shown in Figure 9 where the koniocortical field is obviously bounded rostrally and caudally by electrolytic



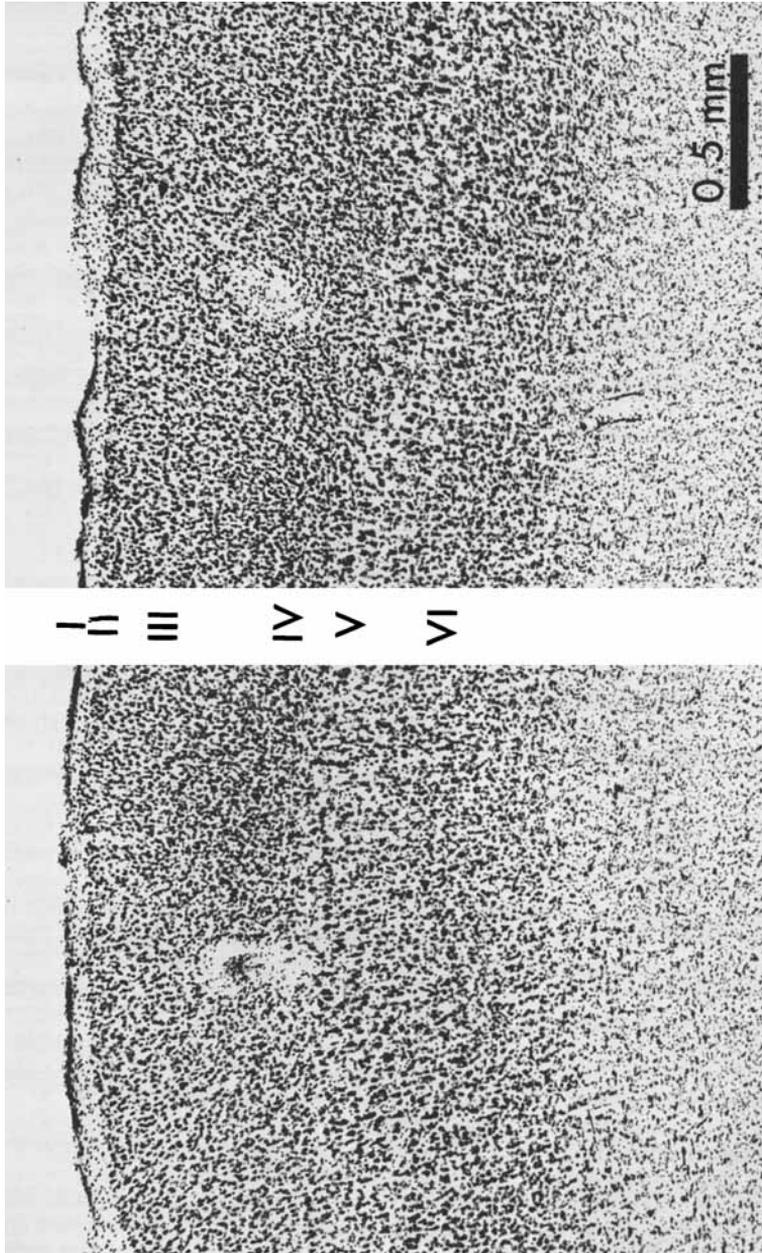


Fig. 9. The cytoarchitecture of S-I. A parasagittal brain section from tree shrew 79-13 is shown above. Microlesions mark the rostral (left) and caudal (right) boundaries of S-I as determined electrophysiologically. These lesions enclose somatic koniocortex which is characterized by a layer IV densely packed with cells. The abrupt change in this layer at the borders of S-I is shown at higher magnification below.

lesions. Like other koniocortical (sensory) fields (Sanides and Krishnamurti, '67), the dominant feature of somatic koniocortex is the dense packing of small granule cells in layer IV of cortex. This dense and thick layer IV is coextensive with S-I as electrophysiologically determined.

While somatic koniocortex can be distinguished from adjoining cortical areas by its dense layer IV of granule cells, the S-I field is not uniform throughout its extent. In particular, the lateral part of koniocortex representing the face has a somewhat thicker but less densely packed layer IV.

Layer IV is thinner and less densely packed with cells in cortex caudal to S-I (on the right in Fig. 9). However, layer IV is still relatively well developed for about 1 mm caudal to S-I, and this zone of moderate cell packing in layer IV appears to correspond with the caudal somatic region. Further laterally, S-II is also distinguished from S-I by a less densely packed, paler layer IV. Rostrally, the inner granular layer of cortex narrows abruptly at the border of S-I, but Area 4, characterized by large pyramidal cells, does not begin immediately. Instead, a narrow zone of cortex can usually be distinguished with a clear but greatly reduced layer IV and medium sized pyramidal cells in layer V. The high-threshold invagination at the rostral border of S-I has a similar appearance. In location and structure, this cortex suggests the intermediate sensorimotor area of Sanides and Krishnamurti ('67), possibly the homologue of the Area 3a field of monkeys.

DISCUSSION

The present report provides a detailed summary of the organization of the first somatosensory area, S-I, in tree shrews and documents many features of its organization. In addition, S-I is shown to be coextensive with a single architectonic field, somatic koniocortex. Other observations were based on the results of injecting anatomical tracers into S-I, and on recordings from cortex bordering S-I. The anatomical results show that S-I in tree shrews has many of the connections that typify S-I in other mammals, including reciprocal connections with the ventroposterior nucleus of the thalamus, S-II of the same hemisphere, and S-I of the opposite hemisphere. The recordings outside of S-I identified the location and organization of S-II and demonstrated a responsive zone of somatic cortex caudal to S-I and medial to S-II on the dorsal

surface of the cerebral hemisphere. In addition, a somatotopic low-threshold representation of portions of the lateral leg and dorsal trunk was found caudal to the posterior leg representation in S-I on the medial wall. The anatomical results, and the mapping data for the somatic regions bordering S-I, will be presented elsewhere.

Location of S-I and somatic koniocortex in tree shrews

The location of S-I on the surface of the brain is shown in Figure 1. All boundaries of S-I but the lateral boundary, which is close to the lateral extent of the map in Figure 1, have been carefully determined in a number of cases. There is some uncertainty about the precise location of the lateral boundary because the most lateral cortex responded to stimuli within the mouth, and seemingly unresponsive recording sites could have related to sensory surfaces that were relatively inaccessible. The location and extent of S-I, as shown in Figure 1, is completely coextensive with somatic koniocortex, which can be identified by a dense packing of small granule cells in layer IV.

The exact extent of S-I and its corresponding architectonic field were not previously known (Fig. 10). Lende ('70), using surface electrodes and evoked-potential mapping procedures, did demonstrate that a zone of parietal cortex was responsive to somatic stimuli, but the size of brain relative to the recording surface was so limiting in these experiments that the size of "S-I" was greatly overestimated and the overall organization was only crudely revealed. Clark ('24) published a study of the architectonic subdivisions of neocortex in tree shrews, but failed to subdivide parietal cortex at all. A similar architectonic map, failing to subdivide parietal cortex and without documentation, has been presented by Eliot Smith ('24). This map has been reproduced elsewhere with the complete parietal region designated as "somatic sensory" (Penfield, '75). In a later review, Clark ('59) altered his summary diagram of cortical areas in tree shrews and included a subdivision of parietal cortex termed "general sensory," which was thought to correspond to Areas 1-3 of primates. This "general sensory" region overlaps most of the lateral portion of S-I of the present study, but fails to include the dorsomedial and medial wall portions of S-I. In extent and location, this "general sensory Area 1-3" of the tree shrew, *Tupaia*, is similar to the "postcentral

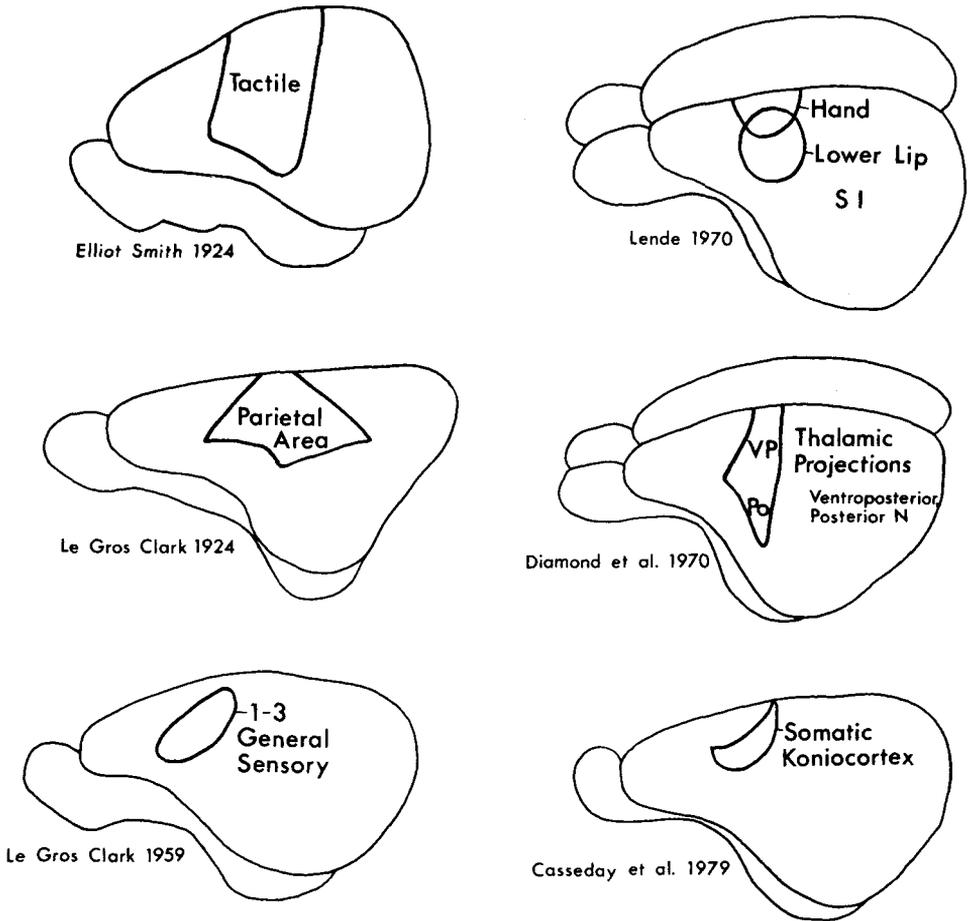


Fig. 10. Previous concepts of the location and extent of somatosensory cortex in tree shrews (*Tupaia*). Compare with Figures 1 and 2. Clark ('26) also described a "Postcentral Area 1" in the pen-tailed tree shrew (not shown) with a location and extent that is similar to the 1-3 general sensory field above in *Tupaia* (Clark, '59). See text.

Area 1" Clark ('26) described for the pentailed tree shrew, *Ptilocercus*. More recently, Diamond et al. ('70) published a retrograde degeneration study of thalamocortical projections in tree shrews in which a region of parietal cortex designated as receiving input from the ventroposterior nucleus roughly corresponds with much of the presently demarcated S-I. However, a current investigation of cortical projections in tree shrews, which includes a section on architectonic subdivisions, seriously underestimates the full extent of somatic koniocortex, as we define it, by including only what appears to be the body, arm, and leg regions of S-I within "koniocortex" (Casseday et al., '79; also see Diamond,

'79). The medial foot, leg, tail and gluteal regions of cortex, as well as the lateral hand and face regions, are largely or completely excluded (Fig. 10; cf. Fig. 2). This judgment is understandable in view of clear differences in the appearances of the medial, middle, and lateral portions of somatic koniocortex. Laterally, layer IV is less compact, and medially, koniocortex narrows rostrocaudally and has a thinner layer IV. However, layer IV is well developed in all parts of S-I in comparison with adjoining cortex, and the lack of uniformity should not detract from the electrophysiological arguments that S-I is a single field. Architectonic differences within a field can be quite marked. For example, the monocular

and binocular portions of striate cortex (Area 17) in squirrels are structurally quite different (Kaas et al., '72a), and the cortex corresponding to S-I is also variable in appearance. Furthermore, within somatic koniocortex of galagos, the densities of granule cells in layer IV and pyramidal cells in layer V vary across the mediolateral extent of the field (Sur et al., '80). Differences in the postulated extent of somatic koniocortex in tree shrews point out the usefulness of microelectrode mapping results as a guide in interpreting the significances of architectonic changes.

Organization of S-I in tree shrews and other mammals

The overall body surface map of S-I in tree shrews appears to be primitive and generalized, as one might expect from the tree shrews' generalized body form (Romer, '67) and phyletic position (McKenna, '75). Generalized features are judged by comparisons across species, and certain consistencies are seen in the S-I maps for several mammals that have been illustrated in enough detail for useful overall comparisons. These maps include the opossum (Pubols et al., '76), the grey squirrel (Sur et al., '78), the galago (Sur et al., '80), and the tree shrew (present study). More limited comparisons are possible with other mammals. A partial list of generalized features and some of the specializations follow.

1) In the generalized somatotopic order, the lower lip and teeth are rostral to the upper lip and teeth, and the nose and vibrissae of the upper lip are caudal and medial to the glabrous upper lip. This order appears to be modified in S-I proper of some monkeys (Nelson et al., '80).

2) The glabrous digits of the foot and hand are represented in order from digit 1 to 5 from lateral to medial along the rostral border of S-I. The pads of the hand and foot are largely caudal to the glabrous digits in cortex. The grey squirrel departs from this generalized scheme by a double representation of much of the forepaw, and a displacement of the digit tips from the rostral border of S-I.

3) Most of the arm is represented medial and caudal to the hand, but the radial arm is represented lateral and caudal to the hand where it joins the hand with the neck caudally. The degree of separation of the medial and lateral representations of the arm varies in different mammals in a manner suggesting that greater separation is a consequence of the enlarged hand representation—a common

specialization. In squirrels, the forearm representation is continuous behind the hand representation. In opossums, the wrist joins the medial and lateral arm regions in cortex caudal to the hand region. In galagos, the two arm regions are relatively separate, joined somewhat by the dorsal aspects of the digits and hand caudal to the glabrous hand. In tree shrews, the organization is similar, but the dorsal hand representation found caudally within the hand region does not often bridge the lateral and medial arm and forearm representations. The forearm regions in S-I proper of squirrel monkeys are separated by the glabrous hand (Nelson et al., '78), while the lateral arm representation is absent in S-I proper of owl monkeys (Merzenich et al., '78) and macaque monkeys (Nelson et al., '80).

4) The dorsal trunk is represented rostrally and the ventral midline at the caudal border. This organization has been established for the grey squirrel and the galago. In tree shrews, the lateral trunk is always found rostral to the ventral midline, and there are no well-documented nonprimate exceptions to this organization. The dorsal trunk is found rostral to the ventral trunk in S-I proper of owl monkeys (Merzenich et al., '78) and macaque monkeys (Nelson et al., '80), but the organization is reversed, with the back caudal in S-I proper of squirrel monkeys (Nelson et al., '78) and cebus monkeys (Felleman et al., '79).

5) The anterior leg, including most of the lateral and medial skin, is represented lateral and caudal to the foot, while the posterior leg is found medial to the foot. The two leg regions are joined by the hairy heel and ankle representation caudally in galagos, and by the glabrous heel in tree shrews and squirrels. In S-I proper of monkeys, the separation is greater due to an expanded representation of the foot, and the lateral representation of the leg is reduced in size in owl monkeys. The foot and leg region is very small in opossums, and the organization has not been established. However, it may be reasonable to suggest from the available evidence that the primitive organization of S-I was characterized by medial and lateral leg representations that were continuous caudally along the representation of the sole of the foot. In a number of lines of descent, enlargement of the glabrous foot representations then possibly separated the two leg regions.

6) Devoting a large proportion of S-I to the head seems to be a generalized feature. This representation of the head occupies about half

of S-I in both the tree shrew (Table 1) and opossum. In the grey squirrel, about 65% of the representation relates to the head. In carnivores, including the coatimundi, ring-tailed cat, lesser panda, and kinkajaw, the proportion of S-I representing the head ranges from 50 to 65% (Welker and Campos, '63). Large forepaw representations, such as in S-I of raccoons (Welker and Seidenstein, '59; Welker and Campos, '63) and in S-I proper of monkeys (Merzenich et al., '78), with the consequent reduction in the proportional representation of the head, are obvious specializations. Rats and mice (Welker, '71; Woolsey, '67; Woolsey et al., '75) have specialized to use the mystacial vibrissae as a tactile organ, and large parts of S-I are devoted to these vibrissae. The grey squirrel shows a less pronounced form of this specialization, and instead, more of S-I is activated by the lips. The glabrous nose representation is large in opossums, where it might reflect a primitive condition. However, the representation of the glabrous nose in tree shrews is so enlarged, with a magnification factor approximately 100 times that of the forepaw, that it is likely to be a specialization. Even the coatimundi, in which the glabrous nose is clearly a very important sensory surface, devotes proportionately less of S-I to this surface (Welker and Campos, '63) than the tree shrew.

Organization of S-I into blocks of partially discontinuous somatotopic sectors

The organization of S-I in tree shrews, as summarized in Figure 2, clearly cannot be adequately described as a simple distortion of the body surface or "homunculus." In addition, there are major disparities in the representation from an organization reflecting a serial lateral to medial sequence of dermatomes. The inadequacies of these descriptions of somatic representations have been discussed in several papers (Merzenich et al., '78; Sur et al., '78, '80; Nelson et al., '80) and need not be reviewed here. Instead, the organization can be described as a composite of sectors of cortex that are internally somatotopic, but sometimes partially discontinuous with each other. The discontinuities seem forced by the requirements of disproportionately representing some skin surfaces, and by the need for representing the three dimensions of the body surface on a two-dimensional cortical sheet. The locations and extents of discontinuities vary from species to species, and to a certain extent within a species, but they do not seem

to disrupt important sensory surfaces, such as the representations of the glabrous digits or the glabrous nose in tree shrews.

The internally somatotopic, but partially discontinuous, sectors in somatic cortex of tree shrews appear to be grouped into five general blocks (see Sur et al., '80). Within each block, skin surfaces that are adjacent on the body are largely adjacent in the cortex, and continuity is promoted by skin surfaces being represented in register. The five blocks of somatotopic sectors in cortex are 1) the head, 2) the hand, 3) the trunk and adjacent hairy forelimb and hindlimb surfaces, 4) the foot, and 5) the medial hindlimb, gluteal skin, and tail. Certain rules of organization apply to each block. Thus, the head is represented with the dorsal surfaces caudal and the ventral surfaces rostral. The hand is represented with the proximal surfaces caudal and the distal digit tips rostral. A similar organization is found in the block devoted to the foot. In between, the trunk and adjoining hairy limbs are represented with the dorsal skin rostral and the ventral skin caudal. Note that this is the opposite organization, as implied by a "homunculus." The medial "block" devoted to the posterior strip of leg is narrow and organized basically mediolaterally, with distal portions lateral and the proximal thigh, genitals, and tail medial.

There is considerable continuity across these blocks. The continuity between the head and hand blocks is maintained by a narrow strip of cortex representing the anterior surface of the arm in a manner that joins the hairy radial surface of the hand with the forearm, then upper arm, and finally neck in a rostral to caudal sequence. The blocks of cortex devoted to the hand and to the trunk and limbs are joined at the representation of the central and ulnar dorsal surface of the hand, which merges with the dorsal wrist and forearm at the rostral edge of S-I, and along the representation of the thenar pads and hypothenar pads which join the palm with the ventral wrist and forearm caudally in S-I. The trunk and limbs block joins the foot block rostrally along the lateral ankle and dorsal foot, and caudally along the medial ankle and the heel. The foot block and the posterior leg block join along the lateral and posterior margin of the sole.

The extent and types of continuities between blocks may play a role in preserving the somatotopic orientations of the blocks relative to each other. In squirrel monkeys (Nel-

son et al., '78) and cebus monkeys (Felleman et al., '79), the middle trunk block is reversed in orientation from the hand and foot blocks in S-I proper and in the posterior cutaneous field. Yet in each monkey there is an attempt at maintaining continuity across blocks within both the Area 3b and 1 representations. The patterns of continuity differ between owl and macaque monkeys, and squirrel and cebus monkeys. It may be that the hand and foot blocks become so enlarged in monkeys that the linked continuities between blocks are much more tenuous, possibly allowing variability in the orientation of blocks.

Disruptions of topology in the S-I map of tree shrews

There are two ways in which somatotopy is violated in the S-I map (Nelson et al., '80). First, adjacent recording sites in cortex may have widely separate receptive fields on the body surface. Second, adjacent receptive fields may relate to quite distant recording sites. Neither type of disruption necessarily follows from the other, and an analysis of discontinuities in the S-I map must consider both. Apart from the largely continuous progressions of receptive fields yielded by rows of recording sites along most parts of the map (Figs. 3-8), certain medial to lateral sequences of recording sites in the anterior part of S-I would produce sequences of receptive fields that jump from the dorsum of the foot to the dorsal arm, and from the radial hand to the chin. These are examples of where separated parts of the body are adjacent in the S-I map. In addition, there are three major places in S-I where adjacent skin surfaces are represented separately. These are the lines of discontinuity, in the cortical map, that split the posterior from the anterior leg, the anterior or radial arm and the neck from the rest of the arm and trunk, and the upper face (bridge of nose, orbital and cranial skin) from the lower face.

The disruptions in the topology of the S-I map appear to stem from the problem of accommodating the disproportionate enlargements of some body regions, and from the need to represent a three-dimensional body surface on a two-dimensional cortical sheet. The three skin regions represented discontinuously within S-I each relate to a part of the body that is greatly enlarged in the representation. Thus, the enlarged representation of the glabrous foot splits the hindlimb, the enlarged representation of the glabrous hand splits the forelimb, and enlarged representa-

tion of the glabrous nose splits the head (see Table 1 for magnification factors). The split of the upper from the lower face in S-I of tree shrews is not found in the same way in S-I of squirrels, where the upper and lower lips and, to some extent, the mystacial vibrissae are magnified rather than the nose, nor in monkeys, where the lips rather than the nose are enlarged in the representation.

At least the split representations of the hindlimb and forelimb appear to preserve connectivity in the S-I map. Given that the cylindrical surfaces of the limbs must have at least one line of discontinuity in a flat surface representation, separate locations for the anterior and posterior parts of the limbs in cortex seem to be a reasonable solution to the problem of connecting the distal limbs with the head, trunk, and gluteal skin. It can be seen that the lines of disruption appear to approximate lines separating dermatome distributions in mammals. However, whether or not the separations in the cortical map occur precisely along lines distinguishing dermatomes remains to be experimentally demonstrated. The separate representations of the anterior and posterior limbs are also seen in galagos (Sur et al., '80), and the anterior leg is represented separately from the posterior leg in S-I proper of monkeys, although the *exact* line of division varies from species to species. In owl monkeys (Merzenich et al., '78), considerably less leg surface is represented lateral to the foot than in macaque (Nelson et al., '80), squirrel (Nelson et al., '78), and cebus monkeys (Felleman et al., '79).

Relation of the single S-I representaton in tree shrews to the multiple "S-I" representations in monkeys

The "S-I" region of monkeys (Merzenich et al., '78; Kaas et al., '79; Nelson et al., '80), and probably of higher primates, appears to differ from that in most other mammals. In monkeys, four distinct architectonic fields form medial to lateral bands in "S-I." Two of these fields, Area 3b and Area 1, have been related to separate, complete, and systematic representations of the body surface, "S-I proper" and the "posterior cutaneous field." A third representation of predominantly deep body receptors, probably related to joints, has been partially revealed in Area 2. Recordings from Area 3a suggest a fourth representation of largely muscle afferents. These representations are parallel to each other within each field. At least the Areas 3b and 1, and Areas 1 and 2 representations also appear to be

roughly mirror images of each other. In contrast, the S-I region in nonprimates has been generally related to a single architectonic field, and a single systematic body surface representation, even in recent detailed microelectrode mapping studies (for review see Sur et al., '78; a notable exception is the "S-I" region of the domestic cat, where multiple architectonic fields have been described (Hasler and Muhs-Clement, '64), and the issue of single or multiple representations is unresolved (however, see Rasmusson et al., '79)). An obvious question is, how do the "S-I" regions of monkeys and non-primates correspond?

We have previously suggested that S-I of most nonprimates is the homologue of the Area 3b representation in primates (Merzenich et al., '78; Sur et al., '80; Kaas et al., '80); hence the name, "S-I proper." Our basic contention is that S-I is a subdivision of the brain found in most, if not all, mammals, and that this field is Area 3b or S-I proper in higher primates. This conclusion stems from the remarkable number of similarities in somatopic organization, relative brain position, architectonics, anatomical connections, and neural response characteristics shared by S-I and S-I proper. These similarities are apparent when one compares S-I of tree shrews with S-I proper of monkeys. No other cutaneous field in monkeys matches in somatopic organization, position relative to motor cortex, and development of layer IV. The major connections of S-I and S-I proper are also similar, but it is not yet clear if patterns of connections of S-I are more like Area 3b or Area 1. Even without this additional information, the conclusion that S-I and S-I proper are homologous seems inescapable.

Recognizing the homology of S-I with S-I proper introduces a second question. Where do the other "S-I" fields in higher primates come from in evolution? A common assumption, since Brodmann's ('09) descriptions, has been that a single field, designated 1-3, gradually differentiated so that three or four separate architectonic fields could be distinguished. This assumption seemed reasonable when a single body representation was thought to occupy all four of the primate "S-I" fields. But how does a precisely organized single representation, S-I, gradually, over many generations, differentiate into several well-organized representations? (However, see Donoghue et al., '79 on sensory and motor cortex of the rat.)

Another possibility is that due to some ge-

netic change, cortex designated to be a single representation instead develops into two (or more) representations in a manner analogous to the observation that a cat with normal parents might be born with six instead of five digits on the paw. The point here is that there may have been a sudden rather than gradual replication of sensory representations. The sudden replication of body parts followed by gradual differentiation and specialization over generations has been a common mechanism in evolution (Gregory, '35) that has been largely overlooked as an explanatory factor in brain evolution. However, the large numbers of similarly organized sensory representations in higher mammals suggests that reduplication may have been common in the evolution of brain types (Allman and Kaas, '71; Kaas, '77, '78). In regard to the "S-I" region of monkeys, the posterior cutaneous field, Area 1, could have been a mirror replication of S-I proper, Area 3b, for example. In a general sense, then, the two representations would be serial homologues.

Another possibility is that the regions of cortex outside of S-I developed into the Area 3a, 1 and 2 fields in monkeys. If this is the case, we should be able to find evidence of these fields, though in a less developed form, in other mammals, and in particular in the close relatives of higher primates. This last possibility is strongly supported by the results of studies from the less developed prosimian primates, and by the present results for tree shrews, which are close relatives of primates (McKenna, '75). In prosimians, a single low-threshold cutaneous field is found in the "S-I" region and it corresponds in organization to S-I proper of monkeys and S-I of nonprimates (Sur et al., '80; Krishnamurti et al., '76; Carlson and Welt, '80). The representation is coextensive with a single architectonic field, somatic koniocortex, which Sanides and Krishnamurti ('67) have homologized, on architectonic grounds, with Area 3b of higher primates. Narrow regions of cortex rostral and caudal to the representation also respond to somatic stimuli, but inconsistently and at higher levels of stimulation, so that details of organization have not been determined. Sanides and Krishnamurti ('67) suggested that the rostral architectonic field is Area 3a of monkeys, and that the caudal region may correspond to Areas 1 and 2. Thus, the mapping results for prosimian primates are *basically like those for nonprimates*, but there are enough similarities with monkeys to support the conclusion that poorly developed Area 3a, Area 1, and perhaps

Area 2 fields may exist.

The tree shrew seems to occupy a position intermediate between monkeys, where multiple representations have been found, and most nonprimates, where only a single S-I representation has been found. Most notably, a higher threshold somatosensory region of cortex was found along the caudal border of S-I, and enough recordings were obtained to determine that it is at least roughly in parallel in somatotopic organization with that of S-I. Thus, both tree shrews and prosimians have more than one somatosensory field in the "S-I" region of cortex, and the possibility that some of the responsive cortex caudal and rostral to the S-I representation corresponds to less developed Area 3a, Area 1, and Area 2 fields seems supported.

Representation of the dorsal trunk on the medial wall of the cerebral hemisphere

One of the unexpected results of the present study was the finding of the representation of the dorsal trunk, and often, adjoining skin surfaces, on the medial wall of the cerebral hemisphere in cortex between the representation of the foot and leg in S-I and visually responsive cortex. We are presently uncertain of the identity of this somatosensory zone. There are at least three possibilities that need to be considered for the proper assignment of the representation of the dorsal trunk on the medial wall. The first possibility is that part of S-I is placed in a highly unusual position. Though a split leg representation lateral and medial to the foot has been commonly reported, a split trunk representation within S-I has not been reported for primates or nonprimates. However, the possibility that the medial trunk representation is part of S-I is supported by the fact that in four of the animals the dorsal surface of the brain was also mapped, and the dorsal trunk and portions of the lateral leg appeared to be poorly represented or absent in cortex lateral to the foot. In all studied animals, input to the medial wall region was cutaneous, and receptive field sizes were of the same order of magnitude as in the trunk and leg representation lateral to the foot. The second possibility for the medial wall region is that it is a part of the caudal high-threshold somatic region, but receives more cutaneous input from some body parts than others. Such input is present within the hand representation in Area 2 in macaque monkeys (Kaas et al., '79), for example, while the rest of the body surface map seems less strongly driven by cutaneous stimuli. In position, the wedge

of dorsal trunk representation lies medial and ventral to the high-threshold somatic region on the dorsal surface, and it can be seen as an extension of the dorsal region. However, the medial wall cutaneous zone does not correspond to the apparent somatotopic order of the dorsal region. A third possibility is that the medial wall region corresponds at least in part to the supplementary sensory area (Penfield and Jasper, '54; Blomquist and Lorenzini, '65). Its location on the medial wall caudal to cortex that is unequivocally S-I, and the orientation of the skin surface represented, is identical to that described classically for the supplementary somatic area. The architectonic features of the small posterior medial wall representation are not outstanding enough to permit a clear choice between these possibilities, and further studies of the anatomical connections and response properties of cells in the medial wall region are needed before the issue may be resolved.

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LITERATURE CITED

- Allman, J.M., and J.H. Kaas (1971) A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res* 31:85-105.
- 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.
- Brodmann, K. (1909) *Vergleichende Lokalisationslehre der Grosshirnrinde* Barth, Leipzig.
- Carlson, M., and C. Welt (1980) Somatic sensory cortex (Sml) of the prosimian primate *Galago crassicaudatus*: Organization of mechanoreceptive input from the hand in relation to cytoarchitecture. *J. Comp. Neurol.*, 189: 249-271
- Casseday, J.H., D.R. Jones, and I.T. Diamond (1979) Projections from cortex to tectum in the tree shrew, *Tupaia glis*. *J. Comp. Neurol.* 185:253-292.
- Clark, W.E. Le Gros (1924) On the brain of the tree-shrew (*Tupaia minor*). *Proc. Zool. Soc. (Lond.)* 70:1053-1075.
- Clark, W.E. Le Gros (1926) The anatomy of the pen-tailed tree shrew. *Proc. Zool. Soc. (Lond.)* 77:1179-1309.
- Clark, W.E. Le Gros (1959) *The Antecedents of Man*. Edinburgh University Press, Edinburgh.
- Diamond, I.T. (1979) The subdivisions of neocortex: A proposal to revise the traditional view of sensory, motor, and association areas. In: *Progress in Psychobiology and Physiological Psychology*, vol. 8, J.M. Sprague and A.N. Epstein, eds. Academic Press, New York, pp 1-43.
- Donoghue, J.P., K.L. Kerman, and F.F. Ebner (1979) Evidence for two organizational plans within the somatic-motor cortex of the rat. *J. Comp. Neurol.* 183:647-664.
- Felleman, D.J., R.J. Nelson, M. Sur, and J.H. Kaas (1979) Organization of the somatosensory cortex in cebus mon-

- keys. *Neurosci. Abstr.*
- Gregory, W.K. (1935) Reduplication in evolution. *Q. Rev. Biol.* 10:272-290.
- Hassler, R., and K. Muhs-Clement (1964) Architectonischer aufbau des sensorimotorischen und parietalen cortex der katze. *J. Hirnforsch.* 6:377-420.
- 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. (1978) The organization of visual cortex in primates. In: *Sensory Systems of Primates*, C. R. Noback, ed. Plenum Press, New York, pp. 151-179.
- Kaas, J.H., W.C. Hall, and I.T. Diamond (1972a) Visual cortex of the grey squirrel (*Sciurus carolinensis*): Architectonic subdivisions and connections from the visual thalamus. *J. Comp. Neurol.* 145:273-306.
- Kaas, J.H., W.C. Hall, H. Killackey, and I.T. Diamond (1972b) 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 primary somatosensory cortex of primates. *Science* 204:521-523.
- Krishnamuriti, A., F. Sanides, and W.I. Welker (1976) Microelectrode mapping of modality-specific somatic sensory cerebral neocortex in slow loris. *Brain Behav. Evol.* 13:267-283.
- Lende, R.A. (1970) Cortical localization in the tree shrew (*Tupaia*). *Brain Res.* 18:61-75.
- McKenna, M.C. (1975) Toward a phylogenetic classification of the mammalia. In: *Phylogeny of the Primates*, W.P. Luckett and F.S. Szalay, eds. Plenum Press, New York. pp 21-46
- 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.
- 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.
- Nelson, R.J., M. Sur, D.-J. Felleman, and J.H. Kaas (1980) Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. *J. Comp. Neurol.* 192: 611-643
- Penfield, W. (1975) *The Mystery of the Mind*. Princeton University Press, Princeton, New Jersey.
- Penfield, W., and H. Jasper (1954) *Epilepsy and the functional anatomy of the human brain*. Little, Brown, Boston.
- Pubols, B.H., L.M. Pubols, D.J. DiPette, and J.C. Sheeley (1976) Opossum somatic sensory cortex: A microelectrode mapping study. *J. Comp. Neurol.* 165:229-246.
- Rasmusson, D.D., R.W. Dykes, and P.B. Hoeltzell (1979) Segregation of modality and submodality in SI cortex of the cat. *Brain Res.* 166:409-412.
- Romer, A.S. (1967) Major steps in vertebrate evolution. *Science* 158:1629-1637.
- Sanides, F., and A. Krishnamuriti (1967) Cytoarchitectonic subdivisions of sensorimotor and prefrontal regions and of bordering insular and limbic fields in slow loris (*Nycticebus coucang coucang*). *J. Hirnforsch.* 9:225-252.
- Smith, G. Elliot (1924) *The Evolution of Man*. Oxford University Press, London.
- 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.J. Nelson, and J.H. Kaas (1980) Representation of the body surface in somatic koniocortex in the prosimian Galago. *J. Comp. Neurol.* 189:381-402.
- Welker, C. (1971) Microelectrode delineation of fine grain somatotopic organization of SmI cerebral neocortex in albino rat. *Brain Res.* 26:259-275.
- Welker, W.I., and G.B. Campos (1963) Physiological significance of sulci in somatic sensory cerebral cortex in mammals of the family Procyonidae. *J. Comp. Neurol.* 120:19-36.
- Welker, W.I., and S. Seidenstein (1959) Somatic sensory representation in the cerebral cortex of the raccoon (*Procyon lotor*). *J. Comp. Neurol.* 111:469-501.
- Weller, R.E., Sur, M., and Kaas, J.H. (1979) Representation of the body surface in SI of the tree shrew. *Anat. Rec.* 193:716.
- Weller, R.E., Sur, M., and Kaas, J.H. (1980) The representation of the body in the second somatosensory area, S-II, of the tree shrew, *Tupaia glis*. *Anat. Rec.* 194.
- Woolsey, T.A. (1967) Somatosensory, auditory and visual cortical areas of the mouse. *Johns Hopkins Med. J.* 121:91-112.
- Woolsey, T.A., C. Welker, and R.H. Schwartz (1975) Comparative anatomical studies of the SmI face cortex with special reference to the occurrence of "barrels" in layer IV. *J. Comp. Neurol.* 164:79-94.