

Representation of the Body Surface in Somatic Koniocortex in the Prosimian *Galago*

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ABSTRACT Microelectrode mapping methods were used to determine the organization of somatosensory cortex in galagos, a prosimian primate. A systematic representation of the contralateral body surface was found within somatic koniocortex with an organization comparable to that of Area 3b of parietal cortex of monkeys (S-I proper) and primary somatosensory cortex (S-I) of other mammals. Limited studies of the response properties of single neurons within the representation revealed further similarities with the 3b field of monkeys. We conclude that somatic koniocortex of galagos and Area 3b of monkeys are homologous, and suggest the term S-I proper for the representation in both prosimians and monkeys. Differences in the details of S-I proper in galagos and monkeys suggest a more primitive organization in galagos.

It is generally recognized that somatosensory cortex of monkeys consists of four distinct architectonic zones: Areas 3a, 3b, 1, and 2. Until recently, these four Areas have been considered to be a single representation of the body and a single functional division of cortex. Microelectrode mapping studies on owl, squirrel and macaque monkeys (Paul et al., '72; Kaas et al., '76, '79; Merzenich et al., '78; Nelson et al., '78b; Sur et al., '78b) have shown that each of Areas 3b and 1 contain a separate and complete map of the body surface, have revealed much of a third representation of deep and cutaneous receptors in Area 2, and have provided evidence for a fourth representation of predominantly deep receptor input in Area 3a. The conclusion of four separate representations within "primary somatosensory cortex" or "S-I" of monkeys is compatible with single unit studies showing a differential distribution of receptor types in the four architectonic zones, anatomical studies of the patterns of connections of each of the zones, and the behavioral deficits following lesions in separate zones (for review see Merzenich et al., '78). While multiple representations have been found in "S-I" of monkeys, only a single representation has been found in the S-I region of other mammals (for review see Sur et al., '78a).

The possibility of major differences in the organization of parietal cortex of monkeys and various non-primates suggested that we should

investigate the organization of parietal cortex in prosimian primates to see if they reflect the pattern found in non-primates or that in monkeys. However, establishing species differences is a difficult problem, and it might be first useful to simply review the contributions that might result from mapping studies of somatosensory cortex.

Perhaps the most important contribution of mapping studies is that they can be a critical first step in establishing the subdivisions of the brain of functional significance. Comparative architectonic studies have long suggested that the cortex of mammals is divided into a number of functionally distinct areas, but architectonic studies by themselves cannot establish the significance of perceived distinctions, and opinions on how to divide the cortex have varied greatly. However, careful microelectrode studies can clearly identify systematic sensory representations, and these representations can then be related to cortical architecture, patterns of connections, properties of neurons, and the behavioral effects of restricted lesions. The evidence to date overwhelmingly supports the view that each sensory representation is distinct in architecture, connections, overall neural response properties, and role in behavior.

A second contribution of mapping studies is that they can help identify homologous subdivisions of the brains of separate species with

relative ease and a high degree of certainty. If two representations in similar locations in two brains resemble each other in a vast amount of detail, it is reasonable to hypothesize that this detail reflects inheritance from a common ancestor, and that the areas are homologous. This hypothesis can then be supported by other similarities revealed by other types of investigation. For example, the similarities between S-I of the grey squirrel (Sur et al., '78a) and "S-I proper" (Area 3b) of monkeys (Merzenich et al., '78) led to the conclusion that the two representations are homologous. This contention is supported by similarities in relative position, connections with other parts of the brain, and cortical architecture (see Merzenich et al., '78), and it is open to further test.

A third and related contribution of mapping studies is that by defining homologous subdivisions that are responsive to sensory stimuli, a start can be made towards resolving the intriguing issue of how or if species differ in number of cortical areas. It is tempting to suppose that behaviorally advanced mammals have more cortical subdivisions than primitive mammals, but it can be difficult to establish the absence or presence of any cortical subdivision. While mapping studies are limited to cortex responsive to sensory stimuli, the identity of poorly responsive and unresponsive areas bordering sensory representations can subsequently be established by less powerful methods once the problem of identification is restricted. In parietal cortex of the grey squirrel (Sur et al., '78a), for example, the identification of only one subdivision, S-I, with certainty, does not necessarily mean that the other subdivisions of somatosensory cortex of monkeys do not exist in squirrels, but it does clearly limit the quest. Specifically, there is a suggestion of a narrow intermediate architectonic zone between somatic koniocortex (S-I) and the presumptive motor region. Anatomical, electrophysiological, and other approaches can now be directed toward the very limited question of whether or not cortex on the rostral border of S-I contains the homologue of Area 3a in monkeys. Likewise, these approaches can be used to determine if the "non-responsive" cortex immediately on the caudal border of "S-I" in squirrels is the probable homologue of the Area 1 (posterior cutaneous field) representation, or some other subdivision of cortex. Thus, mapping studies can be a critical step in attempts to identify species differences in numbers of areas.

The parietal cortex of prosimians invites all

these applications of the mapping method. We were first interested in establishing systematic representations of the body and relating these to cortical architecture on the assumption that such representations would be the functionally important subdivisions of parietal cortex. Secondly, it seemed possible that any or all of the representations of monkeys could be identified in prosimians by the detailed organization of the representations. Brodmann ('09) described only an "Area 1" in prosimians so one could argue that the Areas 3a, 3b and 2 representations might be missing. However, Sanides and Krishnamurti ('67) identified the same subdivision of cortex as somatic koniocortex and as the homologue of Area 3b in monkeys. They also considered a narrow bordering zone of cortex rostral to koniocortex as an "intermediate sensori-motor area" homologous to Area 3a. They were uncertain about the cortex caudal to koniocortex, although the possible presence of Areas 1 or 2 or both were discussed. Because we are greatly interested in identifying homologous areas in prosimians and simians, and in attempting to determine if differences in number of cortical areas relate to the behavioral advances seen in simians, we investigated the organization of somatosensory cortex with microelectrode mapping methods in two species of galagos, and related our results to the results of a similar study on the slow loris (Krishnamurti et al., '76), and a more limited mapping study of the hand representation in galagos (Carlson and Welt, '77). We conclude that the principal responsive zone, somatic koniocortex, is the homologue of Area 3b or S-I proper of monkeys. Furthermore, there is evidence for bordering zones rostral and caudal to the S-I representation that require more intense stimuli for activation than cells or cell groups in S-I.

Some of these results have been briefly described elsewhere (Nelson et al., '78a).

METHODS

The organization of anterior parietal cortex was determined by microelectrode mapping experiments conducted on 10 adult galagos (8 *Galago senegalensis* and 2 *Galago crassicaudatus*). The mapping results were later related to cortical architecture by examining sections from the experimental brains in which small electrolytic lesions had been made to mark significant recording sites, especially at the borders of cortex responsive to very light cutaneous stimulation. The procedures were basically the same as in our earlier studies (Merzenich et

al., '78; Sur et al., '78a) and will only be briefly stated here.

Galagos were anesthetized with ketamine hydrochloride (50mg/kg, IM) and maintained with supplementary injections at a surgical level of anesthesia throughout recording. Parietal and adjoining cortex was exposed and protected by a pool of silicone fluid retained in an acrylic dam constructed around the skull opening. Penetrations were made with glass-coated platinum-iridium microelectrodes with relatively low impedances so that recordings were most commonly from several neurons rather than a single neuron. In mapping studies, data from a large amount of cortex has to be collected in a relatively short time, requiring a large number of penetrations per animal. Multi-unit electrodes facilitate data collection because responses can be obtained immediately in each penetration in the vicinity of layer IV, rather than having to search for maximum amplitude spikes as is often the case with single-unit electrodes.

The surface vasculature of the exposed brain and electrode penetrations were observed with a dissecting microscope and penetrations were sited on a high resolution photograph of parietal cortex. Minimum cutaneous receptive fields were defined with light tactile stimulation with fine glass probes, and responses to other stimuli such as intense taps, pressure and joint movement were noted. Receptive field locations were outlined on drawings of galago body parts. Penetrations were usually made 200–300 μ apart. On the medial wall, receptive fields were recorded every 250–300 μ in depth penetrations. These data were reconstructed by "unfolding" such penetrations. Almost the entire body surface representation within S-I was mapped in two animals. In all other animals, representations of one or more body parts were mapped completely. Our results are based on 1929 recording sites in the 10 mapped animals.

Single unit experiments were conducted on two galagos (*Galago senegalensis*). Controlled stimuli were provided with an electromechanical stimulator (Chubbuck, '66). A PDP-8/a minicomputer was used for data collection and analysis.

After recording, the animals were perfused with saline followed by 10% formalin. The brain was later sectioned on a freezing microtome in the sagittal plane at 50 μ . Sections were stained with cresylviolet for cell bodies, or with hematoxylin (Lin and Kaas, '77) for fibers. Experimental brains were reconstructed from these sections so that mapping results could be

related to cortical cytoarchitecture with the aid of the marker lesions. Almost all lesions in all brains were identified later.

RESULTS

Most of the results are from the smaller galago species, *Galago senegalensis* and unless otherwise stated, results are reported for *Galago senegalensis*. However, more limited experiments on the larger *Galago crassicaudatus* revealed no significant differences in the organization of somatosensory cortex in the two prosimians. The major result is that there is a single systematic representation of the body surface within somatic koniocortex in galagos. Because of its similar somatotopic organization, this field is judged to be homologous to the 3b field (S-I proper) of monkeys. Therefore, the term S-I proper (Merzenich et al., '78) will be used to refer to the representation.

Location and overall organization of S-I proper

The location of S-I proper on the cerebral hemisphere is shown in Figure 1, and the overall organization of the representation is shown in Figure 2. The representation is just rostral to the caudal tip of the Sylvian fissure and extends from the medial wall to near the rhinal fissure. Parts of the representation on the medial wall were not explored because of limited accessibility, and the most lateral boundary of the representation was not determined rostrally because of difficulties in stimulating within the oral cavity, and caudally because the representation entered the Sylvian fissure. However, the representation as mapped is nearly complete and the medial and lateral ends of the summary diagram probably are very close to the actual borders of the area.

Many features of the overall organization of S-I proper are apparent in Figure 2. These features are comparable to S-I proper of monkeys (Merzenich et al., '78; Sur et al., '78b; Nelson et al., '78b; Kaas et al., '79). The genitalia, tail and posterior part of the leg are represented on the medial wall, along with the lateral edge of the glabrous foot (parts of digits and the hypothenar pad). The rest of the foot occupies the most medial cortex of the dorsal surface. The glabrous digit tips of the toes are most rostral in this region, followed by the rest of the glabrous digits, the foot pads, and the hairy heel. (The sole of the hind foot of galagos consists of the glabrous pads rostrally and a caudal hairy heel.) The dorsum of the toes and foot is lateral to the glabrous foot representation, as is much

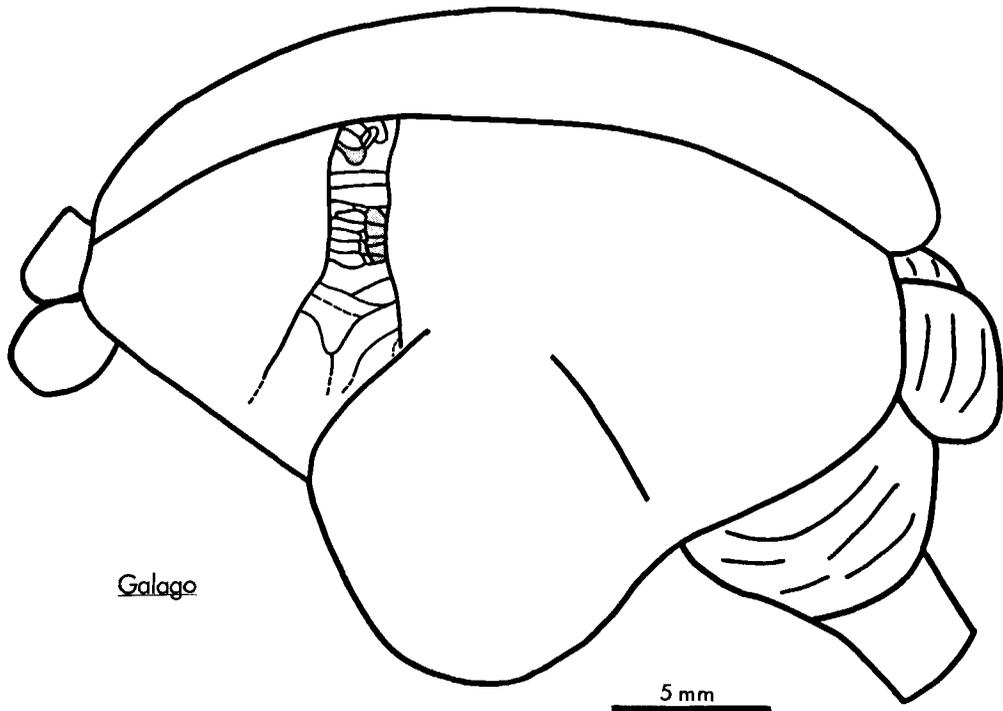


Fig. 1 The location of the body surface representation, S-I proper, on a dorsolateral view of the brain of a galago. See Figure 2 for details.

of the leg. The trunk is represented with the dorsum rostral and the ventrum caudal, as it is in Area 3b in owl and macaque monkeys. Most of the arm, forearm and wrist falls between the trunk and hand. Like the foot, the glabrous digit tips of the hand (as well as skin extending somewhat onto the dorsum of the digit tips) are most rostral in the representation, followed caudally by the rest of the glabrous digits, the pads of the palm and then the dorsal surfaces of the digits. This location of the dorsal digits differs from that in Area 3b in monkeys where the comparable skin surface is split laterally and medially to the glabrous digits in the representations. Another difference is that the dorso-radial edges of the wrist, forearm and arm are lateral to the hand in galagos, but not in monkeys. More laterally, the chin and neck representations are followed by the lower and upper lip regions and the oral cavity rostrally. The nose and orbital skin is caudal and lateral extending somewhat into the Sylvian fissure.

Receptive fields for selected recording sites from extensive experiments in single galagos will be used to illustrate conclusions. These conclusions are based on consistencies in organization revealed by many more recording

sites. In addition, observations made in one animal were repeated in two or more other animals.

Representation of the head

The locations of electrode penetrations for receptive fields on the neck, the chin, the upper and lower lips, the nose and the orbital skin are shown in Figure 3. The rostral to caudal row of recording sites, A through F, illustrates receptive fields that start out on the ventral midline of the chin, move laterally and caudally on the chin and then dorsally on the neck to end near the dorsal midline of the neck. The representation of the lower and upper lips is illustrated by recording sites 1–10. Sites at the rostral margin of the lower lip representation have receptive fields on the midline of the lower lip. As recording sites move caudally on cortex, receptive fields move laterally on the lower lip with the corner of the mouth being represented at the border of the lower and upper lip representations (penetration 6). Receptive fields then move from lateral to medial on the upper lip, with the midline of the upper lip being represented at the caudal margin of the representation (penetration 10).

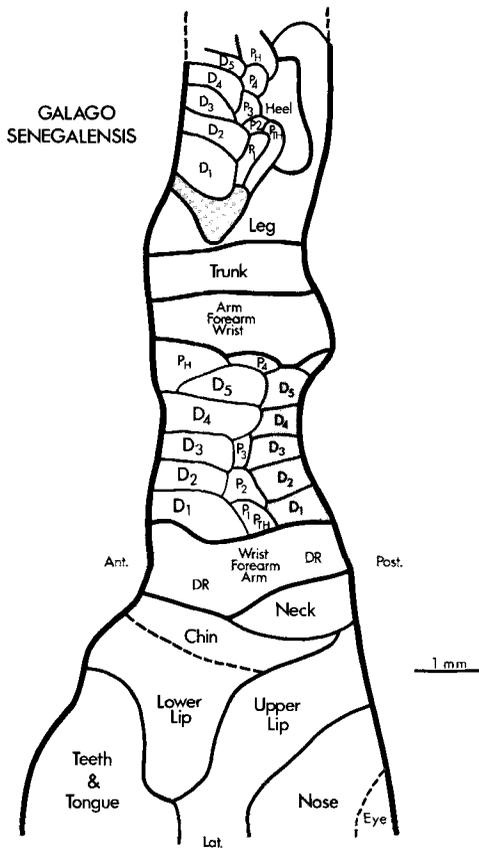


Fig. 2. A summary of the somatotopic organization of S-I proper of the galago. The digits (D₁-D₅) of the foot (upper) and hand (lower) and the interdigital pads (P₁-P₄) are numbered in the standard manner (see Merzenich et al., '78). Thenar (P_{Tn}) and hypothenar (P_H) pads are also indicated. The representations of the dorsal hairy surfaces of the digits are shaded. DR, dorso-radial. See Figures 3-8 for documentation.

The cheek and the proximal facial skin are represented between the neck and the upper lip representations. Receptive fields here are large and often extend onto the neck and the glabrous upper lip. Penetrations 11-14 in Figure 3 illustrate the representation of the nose and orbital skin. Distal parts of the nose are represented medially and rostrally within the nose representation while the bridge of the nose is represented laterally and caudally, adjacent to the representation of the orbital skin.

In two experiments, the cranial skin was found represented further laterally, bordering cortex judged to be S-II (the second somatosensory area). Experiments indicate that S-II lies largely caudal and lateral to the cranial and

orbital skin representation in S-I and abuts S-I along this common border of skin surface, in a similar manner to that in the squirrel (Sur et al., '77, Nelson et al., '79a).

Representation of the wrist, forearm and upper arm

One of the ways in which the S-I proper of galagos differs from that in monkeys is that in galagos, a narrow strip of dorso-radial forelimb is represented lateral to the hand, between the hand and head representations, while the rest of the forelimb is represented medial to the hand, between the hand and trunk representations. In monkeys, the entire forelimb representation lies medial to the hand, and the head is represented immediately lateral to the hand. This conclusion is supported by the recording sites and receptive fields on the wrist, forearm and arm from one mapped galago which are illustrated in Figure 4. The dorso-radial wrist and forearm lie immediately lateral to the hand representation (Figure 4, left; points 2 and 5). The dorsal radial hand lies adjacent to the dorsum of digit 1 (point 1). The dorso-radial upper arm lies lateral within the strip (points 3 and 6), adjacent to the chin and neck representation (point 4). Receptive fields 1-4 show a narrow zone of tissue representing a region of skin that bridges what would otherwise be a major discontinuity between the hand and head representations.

The main representation of the forelimb is medial to the hand. In this division of S-I proper, rostral to caudal rows of recording sites result in simple progressions of receptive fields around the circumference of the wrist, forearm and arm. Two such progressions are shown in Figure 4 (right). The receptive fields start on the dorsum of the arm, proceed to the ulnar side and then progress radially across the ventrum. The wrist and forearm are most laterally located in the representation, while the upper arm is most medial.

Representation of the hand

As in Area 3b in monkeys, the glabrous digits are successively represented, thumb to little finger, from lateral to medial in S-I proper of galagos. Likewise, the distal digits are rostral to the proximal digits, and the volar pads are caudal to the digits in both groups of primates (Fig. 5).

In galagos, the glabrous ulnar aspect of the hand, including pad 4 and the hypothenar pad, is represented medial to the representation of digit 5 (Fig. 5). Pad 4 is central, the hypothenar

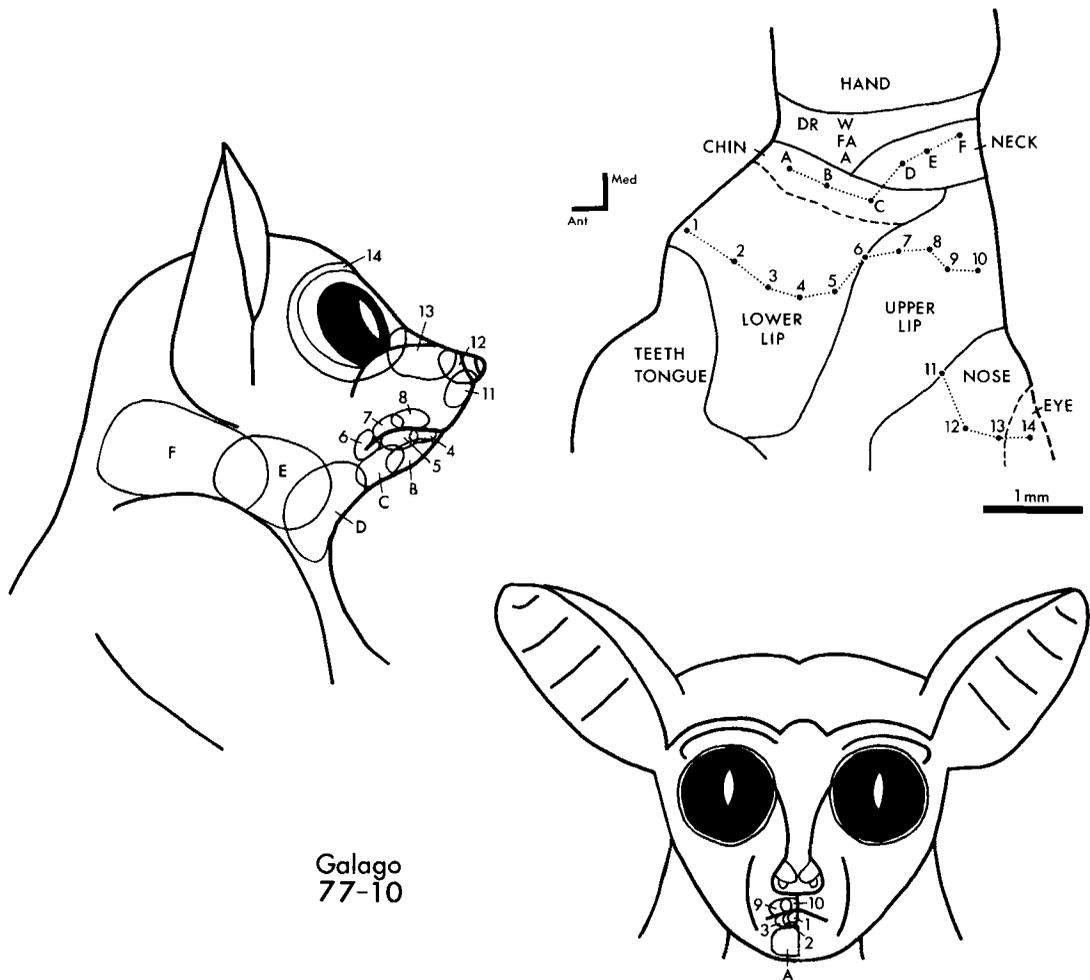


Fig. 3 Receptive field for recording sites in the head and neck regions of S-I proper. Note that the midline of the upper lip and the dorsal neck are at the caudal extreme while the midline of the lower lip and chin are at the rostral extreme of responsive cortex.

pad rostral, and the ulnar margin of the hand caudal within the representation.

The radial dorsum of the hand is represented largely lateral to the dorsum of digit 1 (point 1, Figure 4, left) while the central and ulnar dorsum of the hand is represented medial to the hypothenar pad (points 1 and 2, Figure 4, right). The hand representation in galagos has several distinct particularities. First, receptive fields at the rostral margin of the representation are found to be on the glabrous dorsum, around the nail bed of the distal phalanx of the digits. Second, the hairy dorsum of each digit is represented caudal to the digit's glabrous skin representation. Thus, rostral to caudal progressions of recording sites within a digit rep-

resentation lead to shifts of receptive field from distal to proximal along a digit ventrum and from proximal to distal on the digit dorsum. For digits 1, 2 and 3, the adjoining representation of pads 1-3 lead to a largely continuous transition from the representation of the ventrum to that of the dorsum. These pads at the bases of digits 1, 2 and 3 are fairly large and protrude between the digits (Fig. 5). Receptive fields on these pads, for recording sites caudal to the proximal digits, are large and include both ventral and "dorsal" aspects of the glabrous pads (sites 5 each for rows D₁ and D₃). Receptive fields for recording sites further caudal in the representation move from the dorsal pads to the proximal digit dorsums. For digits 4 and 5, the

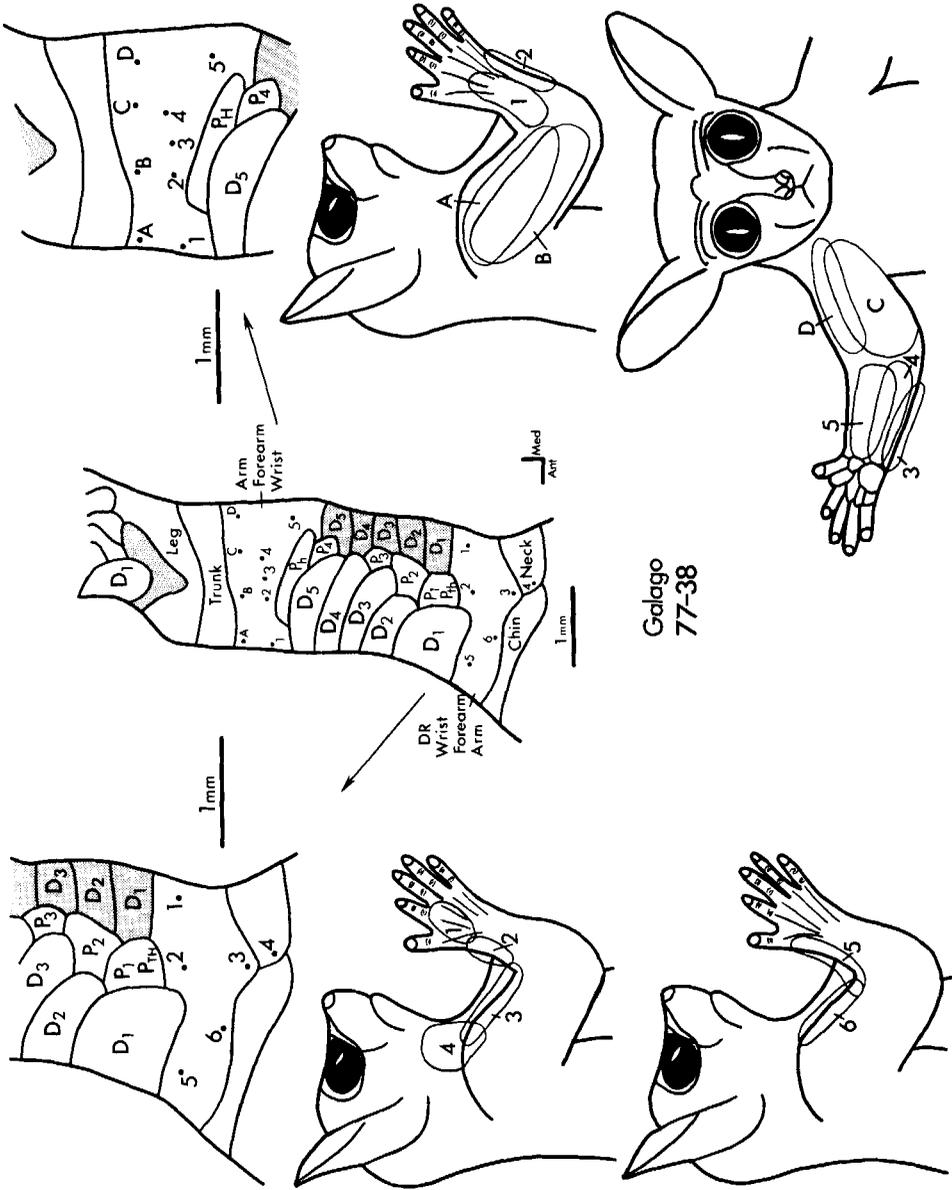


Fig. 4 Receptive fields for recording sites in the separate medial and lateral forelimb and limb representations in S-I proper. The lateral representation of the forelimb (left) includes only the dorsolateral skin and serves to join the hand and head representations. Most of the forelimb is represented medial to the hand (right). Note that the wrist and forearm adjoin the hand representation in both representations.

transition is from the ventral proximal phalanx to the adjoining dorsal proximal phalanx (Fig. 5, row D₃). A corollary to the fact that the glabrous dorsum of the distal phalanx of each digit is represented rostrally while the hairy dorsum of the proximal and middle phalanges is represented caudally in the hand representation is that adjacent receptive fields on the dorsum of the distal and middle phalanges are found at opposite ends of the representation. Such is the case with fields 1 and 7 in row D₁, and fields 1 and 8 in row D₃.

Representation of the trunk

The dorsal surface of the trunk is represented rostrally and the ventral surface caudally within the trunk representation. A typical row of recording sites in Figure 6 illustrates the progression of receptive fields from the dorsal midline of the back to the ventral midline of the rib-cage in a rostral to caudal sequence on cortex. Rostral parts of the trunk are represented laterally on cortex, adjacent to the arm representation, while caudal parts are represented medially, adjacent to the representation of the leg.

Representation of the leg

The representation of the trunk merges medially with the representation of the hindlimb, which is wrapped around the representation of the foot (Fig. 7). Most of the upper part of the leg that adjoins the trunk is found laterally in the leg region and receptive fields extend from the leg onto the trunk so that the dividing line, in Figure 7, indicates only where receptive fields are mainly on the leg rather than on the trunk. Both the dorsal midline of the trunk, and the lateral proximal leg are represented rostrally thus preserving the continuity of the trunk and the leg in the cortical map. Likewise, the skin under the proximal inner white fur of the leg is represented caudally, adjacent to the representation of the abdomen. Most of the lateral, anterior and medial surfaces of the thigh, knee and shin are represented lateral to the foot. Within this portion of cortex, medial recording sites adjacent to the foot representation have receptive fields on the distal leg while preserving the basic lateral to medial progression of receptive fields in rostral to caudal recording sites. The posterior leg is represented medial and somewhat caudal to the foot representation (receptive fields and recording sites 16–22, Fig. 7). Thus, the hindlimb representation is split around the foot representation. Recording sites lateral and medial to the foot representation

correspond to adjacent receptive fields on the leg (e.g., points 8 and 21 or 18; 10 and 19).

While there were only a few recording sites in cortex on the medial wall, these recording sites had receptive fields on the genitalia, gluteal region and tail. We propose that the medial representation of the posterior thigh serves to bridge an otherwise major discontinuity between the representations of the glabrous foot and extreme caudal body regions.

Representation of the foot

The basic organization of the cortex representing the foot is illustrated in Figure 8. The glabrous digits of the foot from the great toe or hallux to the little toe are represented in order from lateral to medial in the rostral half of the foot region. The digit tips are along the rostral border of S-I proper while more proximal parts of the digits are successively represented more caudally. Pads 1–4, which adjoin the digits of the foot, are represented in order from lateral to medial, and the thenar pad is lateral to the hypothenar pad. The hairy heel has a relatively large representation caudal to the pads. The dorsum of the foot is split off to a band of tissue lateral to the representations of digit 1, pad 1, and the thenar pad (Fig. 7 and 8).

Individual and species variations in the S-I proper map

As in all animals in which we have studied the organization of somatosensory cortex, there were minor differences in galagos in detail in the maps obtained from different individuals. For example, we can compare the hand representations in the two animals shown in Figures 4 and 5. The overall features of the two maps are very similar. However, the digit 5 representation in galago 77-38 (Fig. 4) extends up to the rostral margin of S-I proper but it does not in galago 77-53 (Fig. 5). The representation of the hypothenar pad is centrally located within the representation in galago 77-38 and pad 4 is represented almost entirely between glabrous and hairy digit 5. In galago 77-53, the hypothenar pad is represented rostrally and pad 4 medial to digit 5 centrally within the representation. Similar differences in detail within the foot representation in two galagos can be seen from Figures 6 (galago 77-12) and 7 (galago 77-38).

In the two experiments on greater galagos (*Galago crassicaudatus*) we concentrated on mapping the hand region in great detail. The features of the hand representation in these two *Galago crassicaudatus* were very similar to

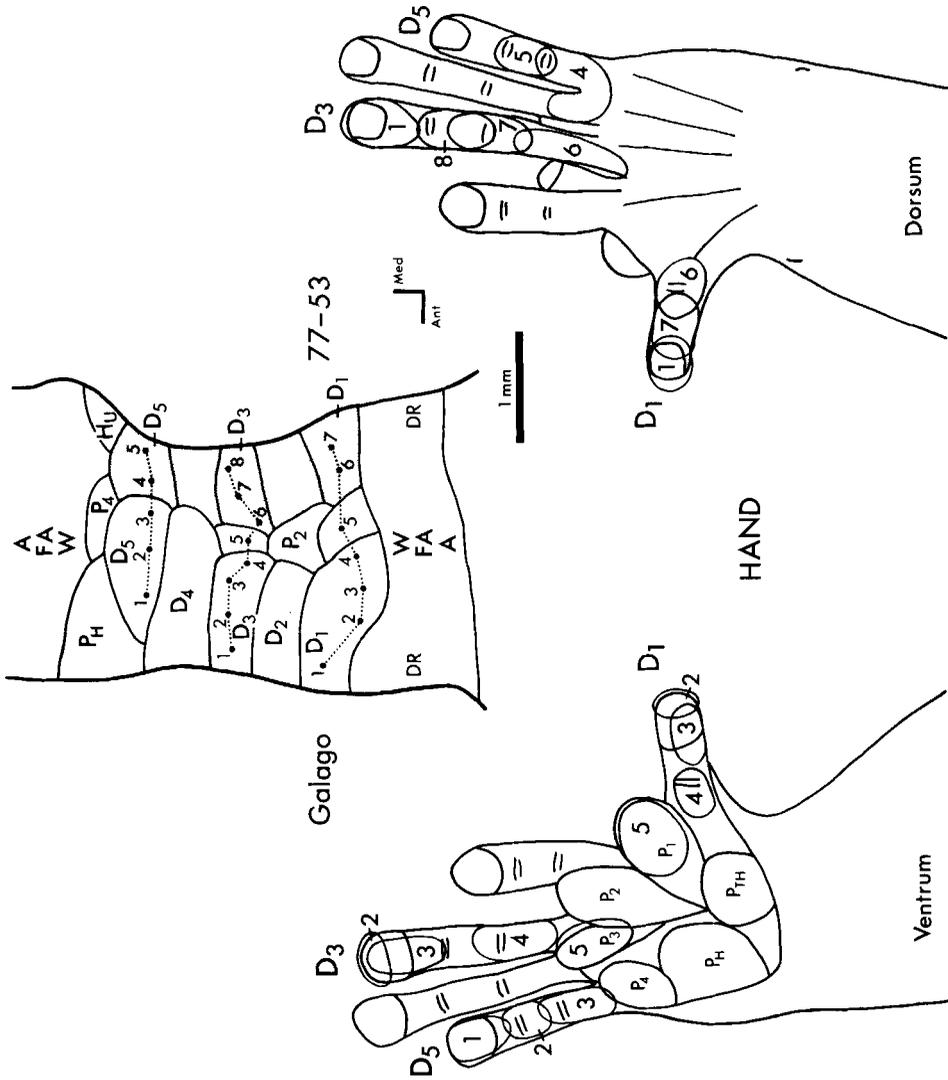


Fig. 5 Receptive fields for recording sites in cortex representing the digits of the hand in S-I proper. The hairless dorsum of the digit tips around the nail bed is most rostral followed by the distal to proximal glabrous digit surfaces followed by the proximal to distal hairy digit surfaces. Pads partially separate the representations of the hairy and glabrous surfaces of the digits.

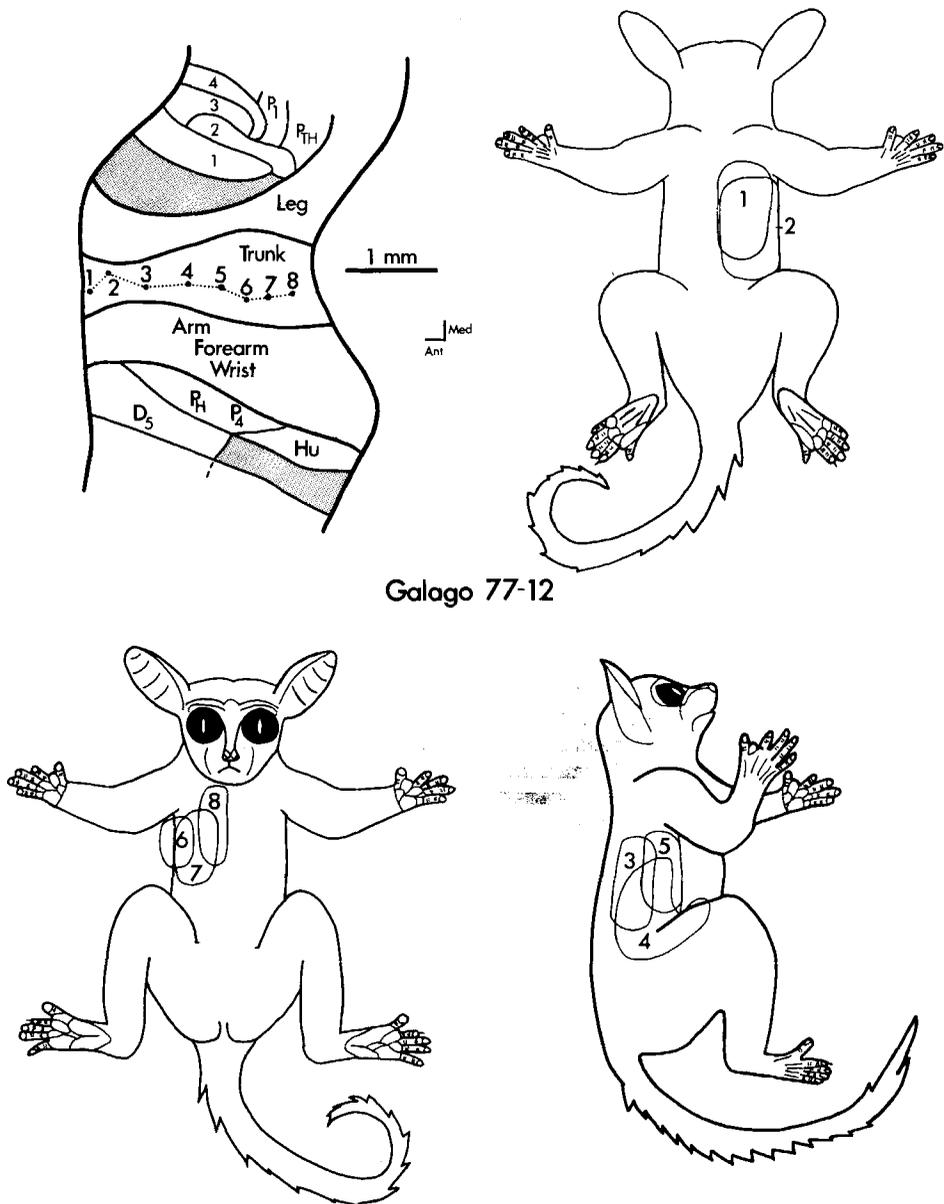


Fig. 6 Receptive fields for recording sites in the representation of the trunk in S-I proper. The dorsum is represented rostrally and the ventrum caudally.

those found in *Galago senegalensis*. Differences in these maps and those obtained from *senegalensis* were comparable to those noted between individual maps for *senegalensis*. Thus, as in *senegalensis*, the glabrous digit tips

and distal phalanges were located rostrally within S-I proper of *crassicaudatus*, the glabrous and hairy proximal phalanges were represented centrally, and the distal hairy dorsum of the phalanges were represented caudally. No

obvious species differences were noted in the hand representation in S-I proper of galagos.

Response characteristics of neurons in S-I proper

In the mapping studies, receptive fields were determined for small clusters of neurons or sometimes single neurons with light tactile stimuli. Neurons in all parts of S-I proper were sensitive to such cutaneous stimuli, and recording sites activated by only the stimulation of deep body tissues and joints were not found. Because of the sensitivity of neurons to light touch and hair movements, and because it was difficult to stimulate exclusively joints and deep body tissues, these studies did not determine if non-cutaneous receptor inputs activate neurons in S-I proper. However, limited quantitative studies of the responses of single neurons to tactile stimuli were made in two galagos to see if two obvious classes of neurons present in S-I proper of monkeys are also found in S-I proper of galagos.

The responses of a total of 37 neurons to a steady skin indentation were carefully studied. An electromechanical stimulator (Chubbuck, '66) produced a one second skin indentation in the center of the receptive fields of the studied neurons. Two types of responses to skin indentation were observed. These same two have been found in S-I proper of macaque monkeys (Sur, '79). The two types of neurons are termed slowly adapting (SA) and rapidly adapting (RA) because these two types of cortical neurons appear to receive inputs from slowly adapting and rapidly adapting peripheral receptors, respectively, and because our use of the terminology appears to be consistent with that previously used for classifying neurons in somatosensory cortex of macaque monkeys (Powell and Mountcastle, '59; Mountcastle et al., '69; Paul et al., '72). Typical examples of the two types of responses of neurons in S-I proper of galagos are shown in Figure 9. Both types of neurons exhibited high rates of discharge during stimulus onset and usually during stimulus offset. The offset discharge was usually less than the onset discharge. Both types of neurons showed brief (25–150 msec) periods of response suppression following peak discharge rates. However, the SA and the RA neurons differed in their responses to maintained skin indentations. The SA neurons fired at rates higher than the spontaneous rate during a maintained skin indentation while the RA neurons did not. As in macaque monkeys (Sur, '79), the SA neurons in galagos were much less numerous

than the RA neurons, and the SA neurons were largely within the region of layer IV of cortex. Of the 37 cells carefully studied for adaptation properties, only 7 were classified as SA. The recording depths of five of these neurons were between 800 and 900 μ , while one neuron was less deep (683 μ) and one more deep (1201 μ). The RA neurons were found over a wide range of depths of cortical recording, although the 30 carefully studied cells were obtained between the depths of 430 μ and 1654 μ .

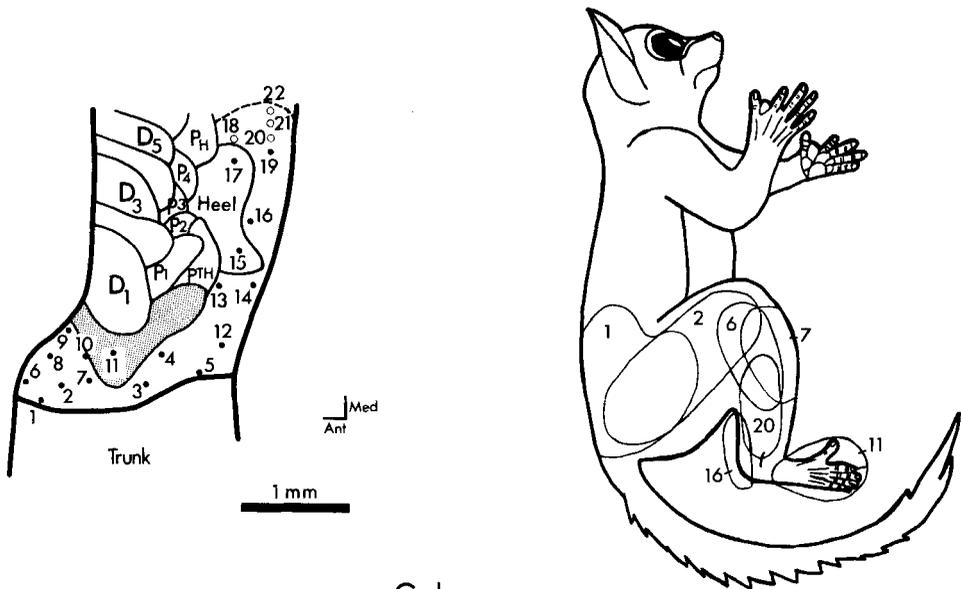
Responses outside S-I proper

Responses within S-I proper were obtained by light tactile stimulation of clearly defined regions of the skin surface. At the first penetration outside S-I proper, either rostrally or caudally and usually within 250 μ from the last penetration, cell groups could no longer be driven by cutaneous stimuli. Vigorous stroking and brisk taps were required on the appropriate body surface, which was always the same as that represented in adjacent S-I proper, to elicit a response. Such responses were usually weak and often barely discernible over the background. "Receptive fields" here were large and diffuse, often covering the entire body part. For example, if receptive fields within S-I proper were confined to portions of a digit, responses outside S-I proper would be obtained by moderate or hard taps over the entire hand. At levels corresponding to the arm, trunk and leg representations in S-I proper, responses outside S-I proper were often elicited by vigorous brushing of hairs on the trunk or limb. The rostro-caudal extent of these bordering zones from which weak responses were obtained was of the order of 0.5 mm. The longest extent of the rostral bordering field, of all mapped galagos, was 0.75 mm. The longest extent of the caudal bordering field was 1.25 mm. Medio-laterally, these zones bordered all of S-I proper except at the very lateral extent.

Architectonic characteristics of S-I proper

In all experiments, small electrolytic lesions were made with the recording electrode at the rostral and caudal margins of the cortex responsive to light cutaneous stimulation (S-I proper). Such marking lesions are shown in Figure 10. These and other marking lesions clearly demonstrate that S-I proper is co-extensive with an architectonic field, somatic koniocortex, as defined in primates by Sanides and Krishnamurti ('67).

The architectonic features of S-I proper are the usual distinguishing features of konio-



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77-38

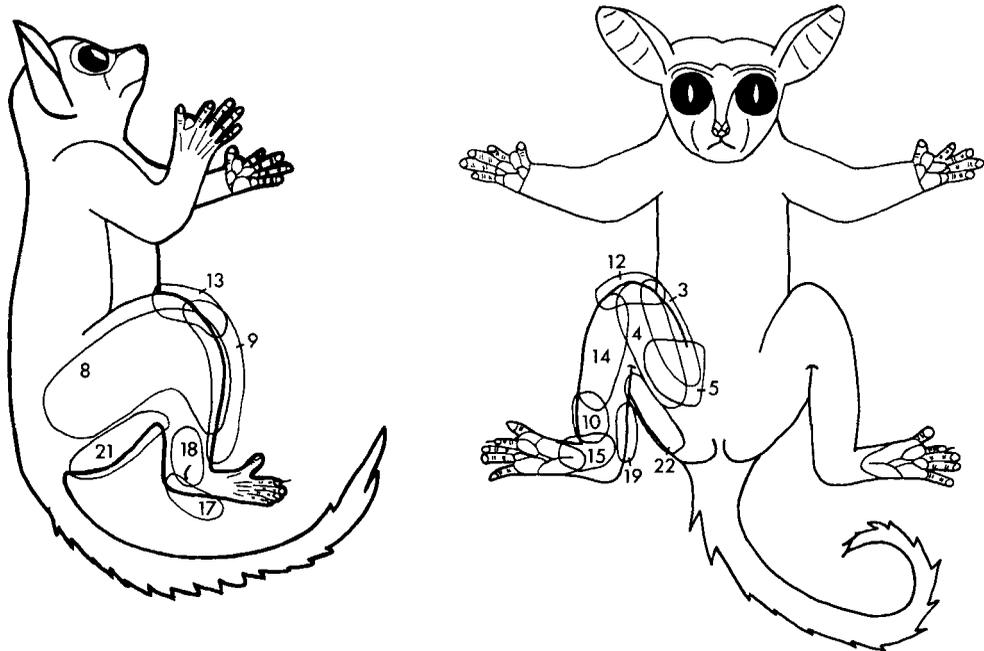


Fig. 7 Receptive fields for recording sites in the representation of the leg in S-I proper. The posterior hindlimb is represented caudal and medial to the foot while the rest of the hindlimb is lateral and caudal to the foot. Open circles indicate the locations of recording sites on the medial wall of the cerebral hemisphere folded out to join the dorsolateral view. The recording sites were reached by electrode penetrations from the dorsal surface.

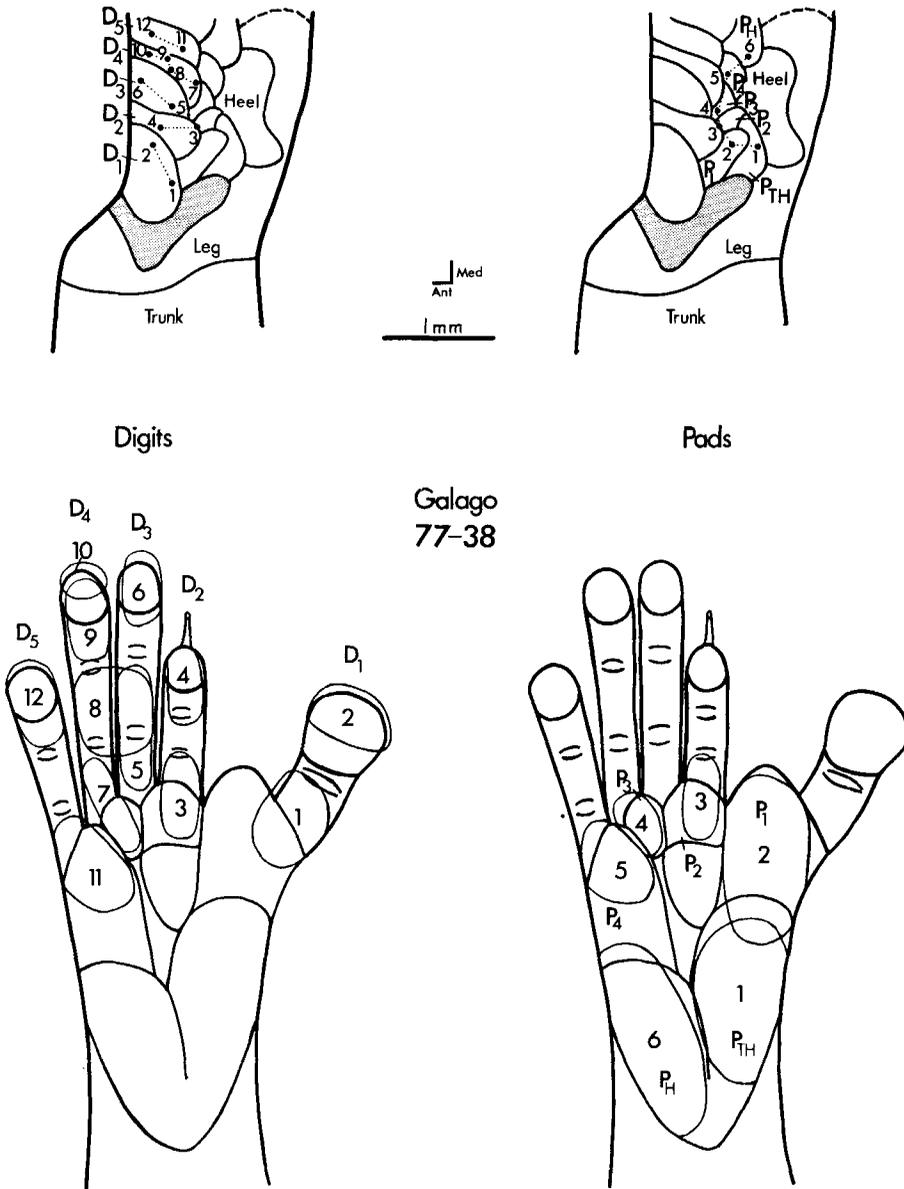


Fig. 8 Receptive fields for recording sites in the representation of the glabrous foot in S-I proper. Digit tips are rostral in the representation.

cortex in general and somatic koniocortex in particular (Fig. 10). Layer IV is densely packed with granule cells, and layer VI shows increased packing density with respect to surrounding cortex. One feature of somatic koniocortex more noticeable in galagos than in Area 3b of monkeys is the presence of medium and occasionally large sized pyramidal cells in

layer V. However, as noted by Sanides and Krishnamurti ('67) within somatic koniocortex in the slow loris, the number and size of pyramidal cells in layer V varies across the mediolateral extent of the field. As shown in Figure 10, pyramidal cells are more noticeable medially (Fig. 10A) than laterally (Fig. 10C) in somatic koniocortex. Also, the size of granule

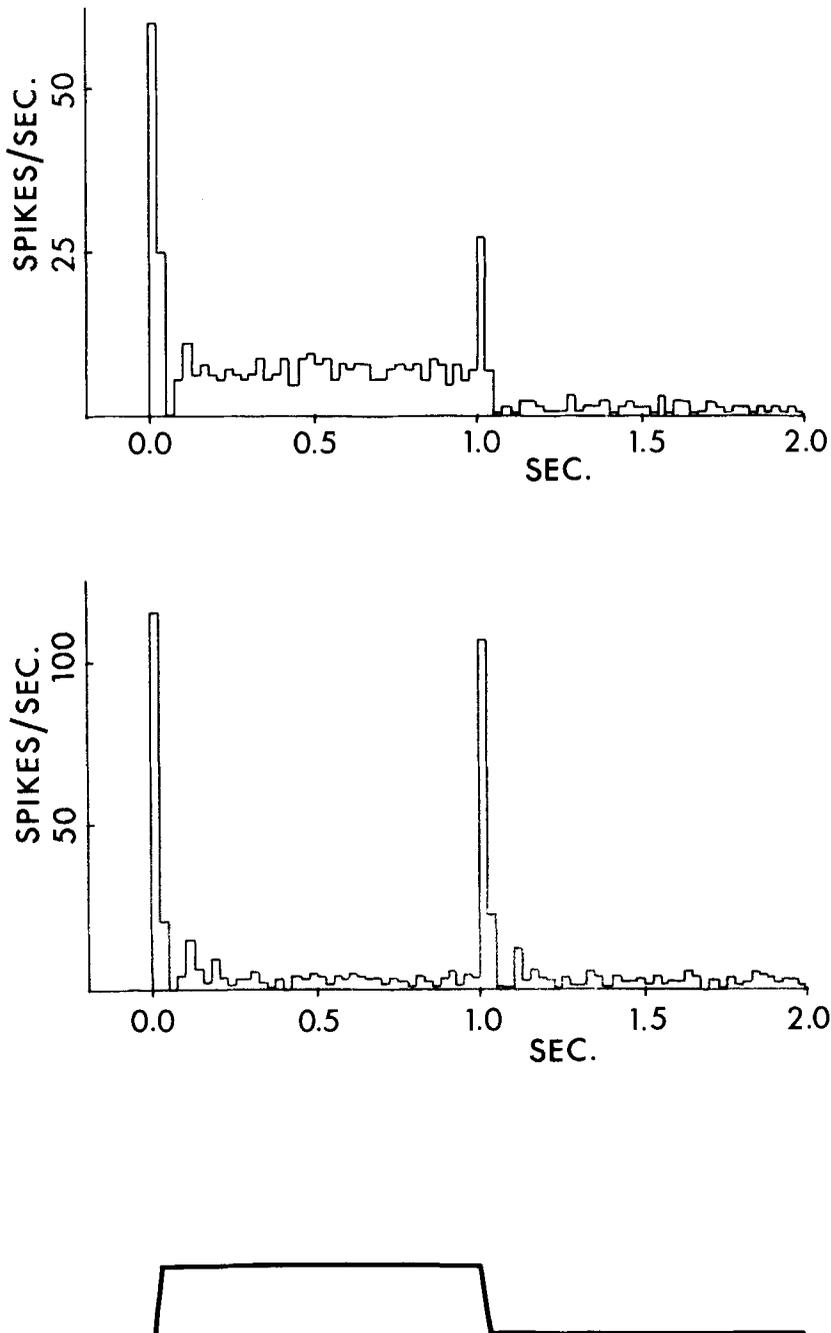


Fig. 9 Post-stimulus time histograms of the responses of two neurons in S-I proper. Above: Typical "slowly adapting" neuron (SA) isolated 683μ below the cortical surface with a receptive field on the distal phalanx of digit 3. Note a maintained discharge during skin indentation. Middle: Typical "rapidly adapting" neuron (RA) isolated 796μ below the cortical surface with a receptive field on the ulnar side of the distal phalanx of digit 3. Note the lack of a maintained discharge. Below: The stimulus waveform which was repeated for 50 cycles. A 1 mm diameter probe first indented skin for 1 sec and then was removed for 1 sec. Rise and fall times, 25.5 msec; indentation depth, 700μ ; bin width, 25 msec.

cells in layer IV is not as different from the sizes of other cells as in Area 3b of monkeys. The result of these two aspects is that somatic koniocortex in galagos does not stand out as dramatically from the adjacent cortex as Area 3b of monkeys does.

Rostrally, between koniocortex and motor cortex, a narrow zone of cortex with intermediate architectonic characteristics is often apparent. In this strip of cortex, approximately 1 mm wide or less, both layer IV and layer VI are less densely packed with cells than in koniocortex, while layer V has intermediate and large pyramidal cells that are not quite as dense as in motor cortex. Caudal to somatic koniocortex, layers IV and VI are also less densely packed with neurons. Furthermore, layer III also has fewer cells and can be easily distinguished from layer IV. Some medium sized pyramidal cells appear in layer III. These bordering zones of cortex are probably included in the areas *Ism* and *parK* as defined by Sanides and Krishnamurti ('67) in the slow loris. Because we have not fully defined the extents of the bordering zones of cortex for somatic koniocortex in galagos, we are uncertain if the rostral and caudal bordering zones in galago fully correspond with areas *Ism* and *parK* of Sanides and Krishnamurti ('67).

DISCUSSION

The present study provides a detailed micro-electrode map of a single systematic representation of the body surface in rostral parietal cortex of a prosimian, galago. This representation was found to be coextensive with somatic koniocortex, and single neuron recordings have revealed two classes of neurons also present in S-I proper (Area 3b) of monkeys. The results support the view that somatic koniocortex in galagos is the homologue of Area 3b in monkeys, reveal a specialization of S-I proper in galagos, and suggest a theory of how the basic organization of S-I proper is specified.

Topography of the body surface representation in S-I proper of galagos

a. S-I proper is a composite of somatotopic regions. In previous discussions of the organization of S-I proper (Area 3b) of monkeys (Merzenich et al., '78; Kaas et al., '79) and of S-I in the grey squirrel (Sur et al., '78a), we have argued that the organizations of the representations are not adequately described by a "homunculus" or by a simple sequence or unfolding of dermatomes. Rather, the adjacent representations of non-adjacent body parts and

the non-adjacent representations of adjacent body parts are, in our view, best described by considering the cortical map as a composite of somatotopic regions. This concept also applies well to S-I proper of galagos where regions of continuous somatotopic representation are joined to form a complete representation with many contained lines of discontinuity. The following are examples of this concept: (1) the glabrous surface of digit 1 of the hand is represented next to part of the forearm; (2) the hairy dorsum of at least digits 1-3 of the hand does not adjoin the glabrous surface of these digits, (3) adjoining parts of the arm are completely separated by the hand representation, and (4) the dorsum of all the digits of the foot is represented lateral to the glabrous surface representation of digit 1.

b. S-I proper is more continuous in galagos than in monkeys. While the body surface map in S-I proper of galagos is a composite, it is less disconnected than in monkeys, i.e., there are fewer major discontinuities across the representations of adjacent body parts. Most notably (1) the dorsal hairy surface of the digits is represented in a continuous band caudal to the glabrous digits of the hand and medial to those of the foot in galagos (Fig. 2); in Area 3b of monkeys these hairy surfaces are split so that some of the hairy digits are lateral and some medial to the glabrous digits; (2) the narrow strip of wrist, forearm and upper arm joining digit 1 with the neck and chin as seen in galagos is not found in monkeys; (3) lateral and medial representations of parts of the leg are joined caudal to the representation of the foot in galagos but are separated in monkeys and; (4) in some monkeys part of the head is represented medial to the hand while other parts are represented lateral to the hand ("the splitting of the occiput" of classical descriptions) while this is not seen in galagos.

It seems likely that topological organization in somatic representations has been sacrificed in various ways as lines of descent evolve specialized sensory requirements, and body parts come to differ in their functional roles as sensory surfaces. Thus, the contention that the less distorted and disrupted representation in galagos reflects a generally more primitive organization than the representation in monkeys is a valid possibility. All of the above differences in S-I proper of galagos and monkeys appear to be consistent with the concept that features of a more primitive organization have been preserved in galagos. In the regions of the foot and hand, major discontinuities are

avoided in galagos by the representations of appropriate strips of skin. The lateral band of cortex representing a strip of the arm connecting the hand with the shoulder and neck representations perhaps is a remnant of forearm representation that was once joined caudally with the medial forearm representation but was subsequently isolated by the expansion of the hand representation. In S-I of the grey squirrel (Sur et al., '78a) and a number of other mammals, the representation of the hand is not so enlarged and it does not extend caudally across the complete representation. Thus, it is possible for a basically medial forearm representation to adjoin caudally and laterally with the representation of the neck and head. The representation of the foot in galagos does not extend to the caudal border of S-I proper as it does in monkeys. Therefore medial and lateral representations of parts of the leg, which serve to join the trunk with the foot laterally and the gluteal region and foot medially, are joined caudally behind the foot in galagos. This is similar to the organization found in S-I of squirrels (Sur et al., '78a) but not in S-I proper of monkeys where the representation of the foot is presumably so enlarged that it separates lateral and medial parts of the leg (Merzenich et al., '78). Thus, in several ways, the organization of S-I proper of galagos appears to be intermediate between that found in S-I of squirrels and other mammals and S-I proper of monkeys.

c. S-I proper in galagos differs from that in monkeys in at least one respect suggesting a specialization in galagos. In monkeys the most rostral recording sites in the hand representation corresponds to receptive fields on the glabrous finger tips. In galagos, receptive fields for the most rostral recording sites are found around the nail bed and often include the dorsal as well as the ventral tip of the finger (Fig. 5). This dorsal skin of the distal phalanx is hairless, and the inclusion of dorsal skin as a continuation of the map of the ventral digits suggests that these surfaces on the distal digits are used together as an important sensory surface in galagos but not in monkeys.

Properties of neurons in S-I proper of galagos

In our limited studies of the response characteristics of neurons in S-I proper of galagos, two basic types of neurons were described and termed slowly adapting (SA) and rapidly adapting (RA) neurons (see Fig. 9). Most neurons were of the RA type. Similar classes of neurons, and similar proportions of the two classes were noted in S-I proper (Area 3b) of macaque mon-

keys (Sur, '79), suggesting that S-I proper in monkeys and galagos has basically similar inputs and functions. Elsewhere, the existence of SA neurons in Area 3b of monkeys has been noted (Powell and Mountcastle, '59; Mountcastle et al., '69; Paul et al., '72) but their response properties, laminar locations, and numbers have been inadequately described and documented. In particular, the brief and complete suppression of activity following the high frequency onset and offset discharges have not been described. In this way, the SA (as well as RA) cortical neurons differ from the peripheral SA (and RA) neurons which show a sustained but adapting rate of discharge to a steady skin indentation (Burgess et al., '68; Pubols and Pubols, '76). The response profile of the cortical SA neuron suggests a strong recurrent inhibition that quickly disappears and is followed by a return to the adapting "envelope" rate of discharge of the SA receptor input (Sur, '78). Such inhibitory mechanisms also may account for the observation that most SA neurons were in the region of layer IV of cortex. Neurons in layer IV would be subject to the maintained activity of thalamic SA neurons, while cortical neurons in other layers would not be influenced by SA receptor activity unaltered by the powerful suppression of maintained activity. Suppression phenomenon such as that observed in both the SA and RA cortical neurons in galagos after onset and offset bursts has also been described for neurons in somatosensory cortex of cats (Hellweg et al., '77) and raccoons (Pubols and Leroy, '77).

Homology of S-I proper in prosimians and monkeys

We postulate that the mapped representation in galagos and the representation in Area 3b, S-I proper, are homologous, i.e., that the representation was present in a common ancestor. Furthermore, we believe that this representation evolved early in the phylogeny of mammals or even in reptiles, and that it is present in most, if not all mammals, where it has been commonly identified as S-I (for review see Sur et al., '78a). However, it is possible that in some mammals, such as the cat where separate architectonic fields have been described within S-I (Hassler and Muhs-Clement, '64), additional representations have been confounded with the S-I representation as they have been in monkeys (see Merzenich et al., '78). In such cases, a term such as S-I proper can be used to distinguish the S-I homologue from an older established, more inclusive, and we

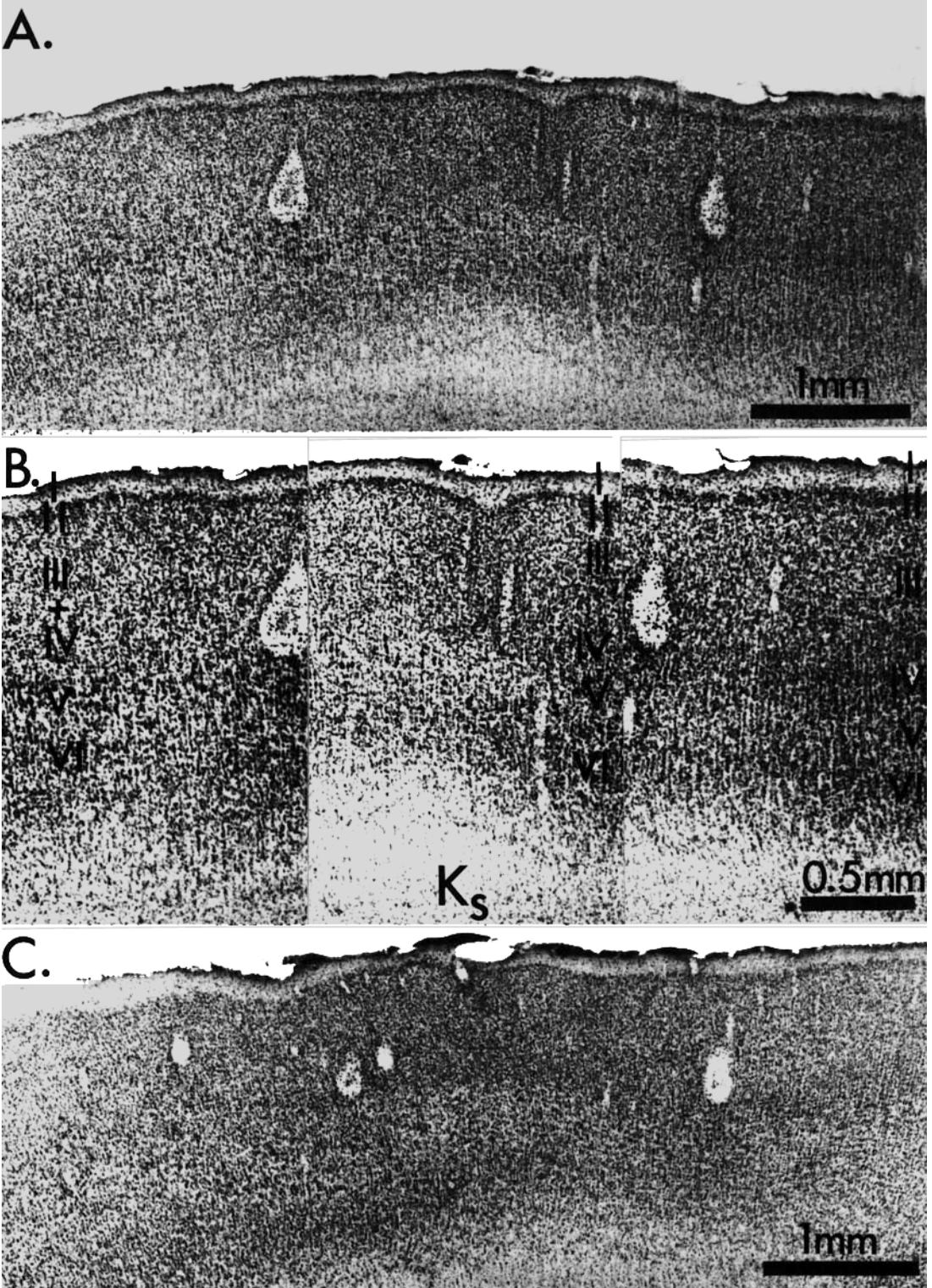
would argue, incorrect application of the term, S-I. In galagos, we use the term S-I proper rather than S-I, not because other representations have been confounded in "S-I" as they have in monkeys, but because we want to both stress the homology of the representation across primates, and we want to allow for the possibility that one or more of the additional "S-I" representations of monkeys will be revealed in prosimians.

The homology of the representation in galagos with S-I proper of monkeys might seem so obvious that there is no need to belabor the issue. However, at least two other possibilities need to be considered. One possibility is that the mapped representation in galagos is the homologue of one of the other representations in monkeys, i.e., the Area 1 posterior cutaneous field, the Area 2 "deep body field," or even Area 3a with the deep receptor input. The other possibility is that the single representation in galagos is a composite of the several "S-I" representations in monkeys. Both possibilities, as well as the possibility that the region in prosimians corresponds to region 3b of monkeys, have been suggested by previous investigators (see below).

Until recently, conclusions regarding the identity of subdivisions of cortex in prosimians have been based on architectonic studies. Because motor cortex (Area 4) is characterized by large pyramidal cells, it has been easy to identify in various mammals, and it serves as a useful reference subdivision of cortex. Brodmann ('09) identified the cortical strip immediately caudal to Area 4 as Area 3 in most primates, and Area 3 was later subdivided into Area 3a and 3b (Vogt, '19). Area 3 (3b) of monkeys was described by Brodmann as having a well developed layer IV of small tightly packed granule cells merging with the densely packed layer III, layer V with relatively few cells, and a layer VI of densely packed cells. These characteristics were also apparent in Area 1, but they were less pronounced. In appearance, the cortex corresponding to the S-I proper of the present study looks more like Area 1 of monkeys than Area 3b. However, in position relative to motor cortex (Area 4), it corresponds to Area 3b. Brodmann ('09) apparently favored the similarities in appearance in identifying the cortical strip in prosimians and labeled it Area 1 (while omitting Areas 3 and 2 from the subdivisions of parietal cortex in prosimians). Brodmann also considered the possibility that "Area 1" of prosimians was a composite of Areas 3, 1 and 2 of monkeys, and this alterna-

tive was clearly preferred by Clark ('31). More recently, in a detailed and extensive examination of the architectonics of parietal cortex in the prosimian slow loris, Sanides and Krishnamurti ('67) renamed the Area 1 field of Brodmann (the Area 1-3 field of Le Gros Clark) in prosimians as *somatic koniocortex* and suggested that the probable homologue in monkeys was field 3b of the Vogts. In reaching this conclusion, Sanides and Krishnamurti apparently were more influenced by the position of somatic koniocortex relative to motor cortex, and the finding of an "intermediate sensorimotor Area" (which they homologized with Area 3a) between koniocortex and motor cortex, rather than the appearance of koniocortex in prosimians. They remind us that J. Rose ('49) pointed out that sensory fields differ greatly in appearance from "lower mammals" to humans, and note that there is an overall more homogenous cytoarchitectonic picture in slow loris than in humans. The structural similarities of koniocortex in prosimians with Area 1 in monkeys may be because both are less specialized sensory areas than koniocortex (Area 3b) in monkeys, rather than the similarities in appearance being a consequence of homology.

Our argument that the koniocortical field of prosimians and Area 3b of monkeys are homologous is based most directly on the similarities in the body representations in these two cortical subdivisions. Most importantly, the glabrous digit tips of the foot and hand point rostrally in the representations in both S-I proper of monkeys (Merzenich et al., '78; Nelson et al., '78b; Sur et al., '78b; Kaas et al., '79) and in koniocortex of prosimians. This feature of "S-I proper" of prosimians is apparent from results presented here on two species of galagos, which agree with the conclusions of a detailed microelectrode investigation of the hand representation in *Galago crassicaudatus* (Carlson and Welt, '77) and those of a pioneering microelectrode mapping study on slow loris first reported in 1965 (Krishnamurti and Welker, '65) and more fully in 1976 (Krishnamurti et al., '76). Other features such as the representations of the back rostral to the abdomen and the lower lip rostral to the upper lip in respective positions in the maps also correspond between the Area 3b representation in owl and macaque monkeys and the koniocortex representation in galagos. In contrast, the koniocortical representation of galagos and the Area 1 representation of monkeys differs in all these features, since the Area 1 representation



approximates a mirror reversal of the Area 3b representation. Thus, on the bases of somatotopic organization as well as relative position, the representation mapped in galagos must be considered the homologue of the Area 3b representation of monkeys. This conclusion is also supported by what is known about the connections and response characteristics of S-I proper in prosimians. Our unpublished studies in galagos and the retrograde degeneration study of Krishnamurti et al. ('72) in the slow loris indicate that somatic koniocortex is connected with the ventroposterior nucleus as are Area 3b and Area 1 of monkeys. Furthermore, both somatic koniocortex in galagos and Area 3b of monkeys have about the same proportions of slowly adapting (SA) and rapidly adapting (RA) neurons (present study and Sur, '78, '79).

The conclusion that Area 3b of monkeys is homologous to somatic koniocortex of prosimians does not rule out the possibility that both Areas 3b and 1 of monkeys are homologous with somatic koniocortex of galagos in the special sense of "serial" homology. A viewpoint that is often seen in comparative studies, including our own, is that single subdivisions of the brain somehow give rise to two or more subdivisions in the course of evolution. When a part existing at one point in the course of evolution replicates so that two parts exist where there was one, both "new" parts can be considered "serial" homologues of the original part (Gregory, '35). It is uncertain how useful the concept of "serial homologues" is when applied to brain parts, but we have previously suggested that the sudden replication of brain structures followed by gradual divergences in organization and functions may have been a common method of brain evolution (Allman and Kaas, '71; Kaas '77). The replicated parts might have, for unknown reasons, taken the form of mirror images as representations of sensory surfaces, thus accounting for the prevalence of approximate mirror image organizations in adjoining sensory representations (Kaas, '77). While such possibilities deserve consideration, we do not now propose that a single somatosensory representation was retained in the primates leading to present day prosimians, while this Area was replicated one or more times in the primates giving rise to monkeys. The negative evidence for the Area 1

and Area 2 representations of monkeys in prosimians from three electrophysiological studies should not be considered conclusive. Many features of homologous cortical areas might be quite variable across different mammalian species. As a particularly relevant example, we found the Area 2 "deep body representation" of owl monkeys to be almost completely insensitive to light cutaneous stimulation under our recording conditions (Merzenich et al., '78), while the Area 2 representation was easily activated by such stimulations in macaque monkeys (Sur et al., '78b; Nelson et al., '79b, Kaas et al., '79). Our findings that cortex caudal to koniocortex of galagos, together with the similar findings in slow loris by Krishnamurti et al. ('76), is responsive to more intense somatic stimuli, suggests the possibility of a "less responsive" Area 1 homologue of monkeys in prosimians. However, it is important to remember that given the clear uncertainty of conclusions based solely on cortical architecture, there is no compelling evidence for or against the existence of Areas 1 and 2 (as well as many other areas) in prosimians. Given the failure of electrophysiological mapping methods to reveal the organization of cortex immediately caudal to "S-I proper" of prosimians, the most logical next step would seem to be to examine the efferent and afferent connections of this cortex and compare the results with those from Area 1 of monkeys. Such studies could help establish the existence or absence of Area 1 in prosimians.

The cortical "block" as an organizing feature of S-I proper

Details of the map in S-I proper of the galago can be used to support the argument that the representation consists of several discrete, separately specified, cortical "blocks." As mentioned above, the trunk, forelimb, and hindlimb are represented in register so that continuities are maintained. The dorsal trunk or back is represented rostrally in S-I proper and is adjacent to the rostral representations of the outer or dorsal leg and upper arm; the ventral trunk or belly is represented caudally next to the caudal representation of the ventral arm and inner thigh (Fig. 4, 6, 7, 11). We consider the cortex representing the leg, trunk, and arm between the foot and hand as one of the blocks

Fig. 10 Parasagittal brain sections showing cytoarchitectonic features of somatosensory cortex in galagos. In A and C, small electrolytic lesions mark recording sites just rostral (left) and caudal (right) to cortex responsive to light cutaneous stimulation but within cortex responsive to moderate taps. The low threshold responsive zone is in somatic koniocortex or K, (after Sanides and Krishnamurti, '67). In B, cortical regions between (middle), rostral to (left), and caudal to (right) the marker lesions are shown at greater magnification (taken from A).

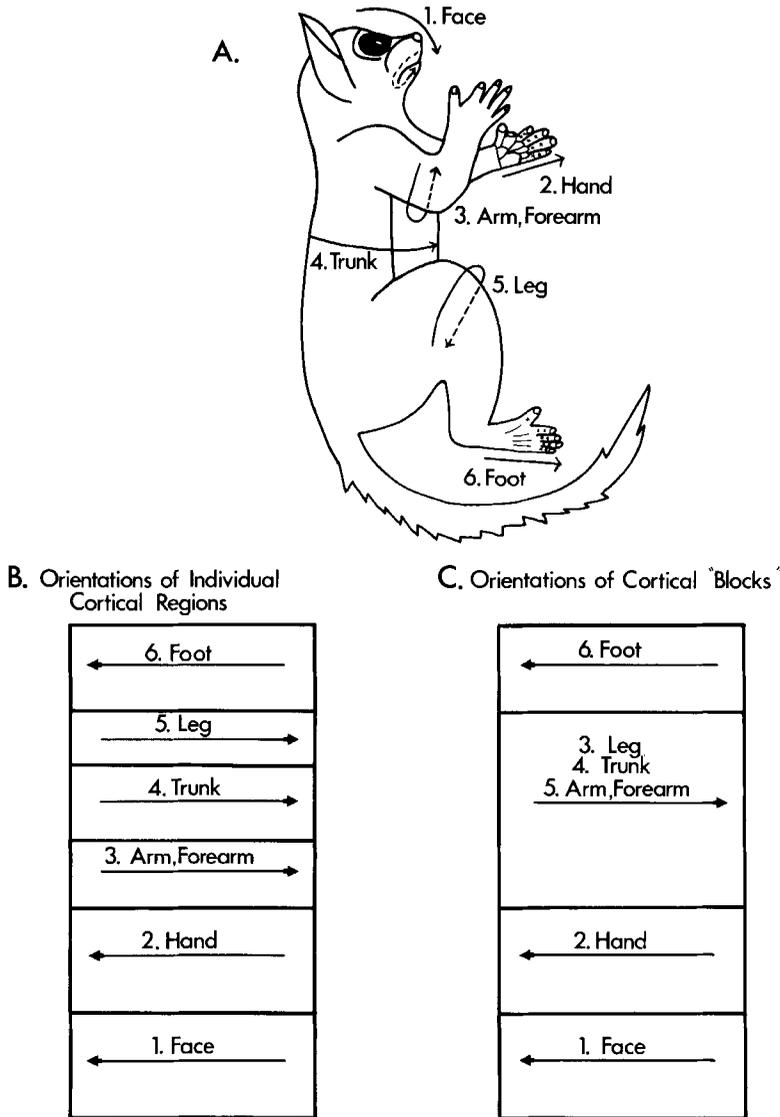


Fig. 11 A. Arrows depict the orientations in which different regions of the body surface are represented in S-I proper, as shown in B. C. Adjoining sectors of cortex with similar orientations. The leg, the trunk, the arm and the forearm can be combined into a single "block" within which topography is maintained. The foot, hand and face blocks are also internally somatotopic. Orientations of representational surfaces need not be maintained across blocks.

of somatotopic regions of S-I proper. The greatly enlarged hand and foot representations are considered as two separate blocks of cortex. Finally, the head representation including the neck, chin, lips, and orbital skin forms another block (Fig. 11). There is somatotopy within this block and contiguous skin regions are largely in register. Thus, the dorsal skin surfaces (the dorsal neck, the midline of the upper lip, the bridge of the nose, the orbital and cranial skin)

are represented caudally. Ventral regions of the head (the chin and midline of the lower lip) are represented rostrally.

While somatotopic contiguity is largely preserved within blocks, the separate blocks need not be aligned with each other, as seen in Figure 11. Thus, a single body surface orientation, such as in a homunculus, does not describe the organization of S-I proper. The central trunk, arm, and leg block is in a "reversed" orientation

from that in the foot, hand, and head blocks. In addition, major discontinuities occur across blocks. For example, the neck and chin, which adjoin the trunk on the body surface, are represented in a block lateral to the hand representation and in opposite orientation to the trunk block which is medial to the hand. Thus, the back of the neck is caudal and the adjoining back of the trunk is rostral.

Perhaps less obviously, the hand block and the block representing the trunk and limbs are also reversed in orientation with respect to each other. The wrist and forearm are represented medial to the hand with the same orientation as the trunk, that is with the dorsum rostrally and the ventrum caudally. In laterally adjacent cortex, the hairy dorsum of the hand digits is caudal and the glabrous ventrum of the pads and digits is rostral. In the foot block, the orientation is rotated somewhat so that the ventrum is largely medial to the dorsum. Yet the basic orientations of the glabrous surfaces are similar in the hand and foot blocks so that the digit tips are rostral.

In S-I proper of galagos, then, there are hand and foot blocks within which the digits point rostral, the trunk block with one orientation and the head block with the opposite orientation. Possibly there is some intrinsic functional advantage in the glabrous digit tips being represented closer to motor cortex.

While the foot, hand and head blocks have essentially a similar orientation in the cortical representation, it is not clear why the trunk block in galagos is reversed in orientation. Each of the blocks, however, seems to be a combination of one to several individual regions which are internally somatotopic and are aligned in somatotopic orientation.

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LITERATURE CITED

- Allman, J.M., and J.H. Kaas (1971) Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*). *Brain Res.*, 35:89-106.
- Brodmann, K. (1909) Vergleichende Lokalisationslehre der Grosshirnrinde. Barth, Leipzig.
- Burgess, P.R., D. Petit, and R.M. Warren (1968) Receptor types in cat hairy skin supplied by myelinated fibers. *J. Neurophysiol.*, 31:833-848.
- Carlson, M., and C. Welt (1977) Single representation of the hand in somatic sensory cortex (SI) of prosimian, *Galago crassicaudatus*. *Neuroscience Abstr.*, 3:478.
- Chubbuck, T.G. (1966) Small-motion biological stimulator. *APL Tech. Digest*, May-June, 18-23.
- Clark, W.E. Le Gros (1931) The brain of microcebus murinus. *Proc. Zool. Soc.*, 101:463-486.
- Gregory, W.K. (1935) Reduplication in evolution. *Q. Rev. Biol.*, 10:272-289.
- Hassler, R., and K. Muhs-Clement (1964) Architektonischer aufbaudes sensorischer und parietalen cortex des katze. *J. Hirnforsch.* 6:377-420.
- Hellweg, F.C., W. Schultz, and O.D. Creutzfeldt (1977) Extracellular and intracellular recordings from cat's whisker projection area: Thalamo-cortical response transformation. *J. Neurophysiol.*, 40:463-479.
- 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., M.M. Merzenich, C.-S. Lin, and M. Sur (1976) A double representation of the body in "primary somatosensory cortex" ("SI") of primates. *Neurosci. Abstr.*, 2:914.
- Kaas, J.H., R.J. Nelson, M. Sur., C.-S. Lin, and M.M. Merzenich (1979) Multiple representations of the body within "SI" of primates: A redefinition of "primary somatosensory cortex." *Science*, 204:521-523.
- Krishnamurti, A., R. Kanaguntheram, and W.C. Wong (1972) Functional significance of the fibrous laminae in the ventrobasal complex of the thalamus of slow loris. *J. Comp. Neurol.*, 145:515-524.
- Krishnamurti, A., F. Sanides, and W.I. Welker (1976) Microelectrode mapping of modality-specific somatic sensory cerebral neocortex in slow loris. *Brain, Behav. Evol.*, 13:267-283.
- Krishnamurti, A., and W.I. Welker (1965) Somatic sensory area in the cerebral neocortex of slow loris (*Nycticebus coucang coucang*). *Fed. Proc.*, 24:140.
- Lin, C.-S., and J.H. Kaas (1977) Projections from cortical visual areas 17, 18 and MT onto the dorsal lateral geniculate nucleus in owl monkeys. *J. Comp. Neurol.*, 173:457-474.
- 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.*, 181:41-73.
- Mountcastle, V.B., W.H. Talbot, H. Sakata, and J. Hyvarinen (1969) Cortical neuronal mechanisms in flutter-vibration studies unanesthetized monkeys. Neuronal periodicity and frequency discrimination. *J. Neurophysiol.*, 32:452-484.
- Nelson, R.J., M. Sur., and J.H. Kaas (1978a) The representation of the body surface in somatic koniocortex of a prosimian primate, *Galago senegalensis*. *Anat. Rec.*, 190:491-492.
- Nelson, R.H., M. Sur, and J.H. Kaas (1978b) Multiple representations of the body surface in postcentral parietal cortex ("SI") of the squirrel monkey. *Neurosci. Abstr.*, 4:556.
- Nelson, R.J., M. Sur, and J.H. Kaas (1979a) The organization of the second somatosensory area (SmII) of the grey squirrel. *J. Comp. Neurol.*, 184(3):473-490.
- Nelson, R.J., M. Sur, D.J. Felleman, and J.H. Kaas (1979b) Representations of the body surface in postcentral somatosensory cortex of *Macaca fascicularis*. In preparation.
- Paul, R.L., M.M. Merzenich, and H. Goodman (1972) Representation of slowly and rapidly adapting cutaneous mechanoreceptors of the hand in Brodmann's areas 3 and 1 of *Macaca mulatta*. *Brain Res.*, 36:229-249.

- Powell, T.P.S., and V.B. Mountcastle (1959) Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey. A correlation of findings obtained in a single unit analysis with cytoarchitecture. *Bull. Johns Hopkins Hosp.*, 105:133-162.
- Pubols, L.M., and R.F. Leroy (1977) Orientation detectors in the primary somatosensory neocortex of the raccoon. *Brain Res.*, 129:61-74.
- Pubols, B.H., and Pubols, L.M. (1976) Coding of mechanical stimulus velocity and indentation depth by squirrel monkey and racoon glabrous skin mechanoreceptors. *J. Neurophysiol.*, 39:773-787.
- Rose, J.E. (1949) The cellular structure of the auditory region of the cat. *J. Comp. Neurol.*, 91:409-440.
- Sanides, F., and A. Krishnamurti (1967) Cytoarchitectonic subdivisions of sensorimotor and prefrontal regions and of bordering insular and limbic fields in slow loris (*Nycticebus coucang coucang*). *J. Hirnforschung*, 9:225-252.
- Sur, M. (1978) Some principles of organization of somatosensory cortex. Ph.D. Thesis, Vanderbilt University, Nashville, Tennessee.
- Sur, M. (1979) Somatosensory cortex in macaque monkeys: Columnar organization of slowly and rapidly adapting neurons and receptive field organization. *Fed. Proc.* 38:898.
- Sur, M., R.J. Nelson, and J.H. Kaas (1977) The representation of the body surface in SmII of the grey squirrel. *Neurosci. Abstr.*, 3:492.
- Sur, M., R.J. Nelson, and J.H. Kaas (1978a) 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 (1978b) Postcentral somatosensory cortex in macaque monkeys: multiple body representations and neuronal properties. *Neurosci. Abstr.*, 4:559.
- Vogt, O. (1919) Allgemeiner Ergebnisse unserer Hirnforschung. *J. Psychol. Neurol. (Lpz.)*, 25:279-462.