

ALS

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Somesthesia and the Neurobiology of the Somatosensory Cortex

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The organization of lateral somatosensory cortex in primates and other mammals

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Summary: The organization of lateral somatosensory cortex has been described for several primates including Old World, and New World simians as well as prosimians. While descriptions of SII for New World monkeys and prosimians are consistent, those for Old World macaque monkeys vary considerably. However, all data conform to the proposal that at least two mirror symmetric representations reside in the area traditionally considered as a single field. These include the second somatosensory area, SII, and the parietal ventral area, PV. Discrepancies in the descriptions of SII in primates, as well as non primate mammals may be the result of the two fields being confused. Because of the ubiquity of SII and PV in all mammals, it is proposed that these areas are part of a basic plan of somatosensory processing. The addition of new fields, such as VS, Ri, and 7b in the line which led to extant primates, may account for the increase in dexterity, bilateral coordination of the hands, and tactile recognition abilities that characterize primates.

Introduction

Early in this century new techniques for examining the brain, particularly the cortex, not only allowed us to develop more accurate descriptions of cortical architecture and cell morphology, but revolutionized our ideas regarding brain construction and function. Architectonic studies of Brodmann (1909), Von Economo (1929), and Vogt and Vogt (1919), demonstrated that the brain is composed of a number of separate parts, and work in the middle of this century by Woolsey and colleagues (1946; 1958), established that those parts defined architectonically, were coextensive with maps of the sensory epithelium in visual, auditory, and somatosensory cortex. Since then, our efforts have been directed at uncovering smaller units of brain construction, and the properties of the separate components that compose the brain. Very recent studies have described the organization of separate fields in the cortex, have elucidated details of individual cell function, dendritic arborization, synaptic specialization, and neurotransmitter distribution across cortical regions. Not surprisingly, our level of analysis has again shifted to even smaller units of processing. However, while the techniques have become more refined, and our view of neurophysiological properties and neuroanatomical construction more acute, it is still unclear how

all of these specific events or units of brain construction generate complex behaviors and perceptions. The following review on the organization of lateral somatosensory fields is an attempt to refocus our attention on more global aspects of somatosensory processing.

Early electrophysiological investigations in the somatosensory cortex reported that only a single primary area, SI, and a second somatosensory field, SII were present in parietal cortex (e.g. Woolsey and Fairman, 1946, Woolsey, 1958). Since then, SI has been further divided and found to contain separate representations coextensive with areas 3a, 3b, 1 and 2 of Brodmann (1909; e.g. Merzenich et al., 1978; Nelson et al., 1980; Pons et al., 1985), modules within SI related to segregated projections from slowly adapting and rapidly adapting inputs have been discovered (Sur et al., 1984), and specific patterns of connections for the different anterior parietal fields have been ascertained (e.g. Pons and Kaas, 1986). Recent work in which individual properties of neurons in areas 3b and 1 (e.g. Iwamura et al., 1983; Sinclair and Burton, 1991), area 2 and posterior parietal cortex (e.g. Iwamura et al., 1994) were investigated in awake monkeys allows us to appreciate the possible function of fields (see Kaas and Pons, 1988 for review). While our knowledge of anterior parietal and posterior parietal cortical organization and function has increased considerably in the last decade, only recently has cortex lateral to anterior parietal fields, in the SII region, been given attention. Work to date indicates that this region of cortex is involved in more complex discriminations, bilateral coordination of the hands, and discriminations made during active touch (e.g. Sinclair and Burton, 1993). Connections of this field with posterior parietal cortex (e.g. Cavada and Goldman-Rakic, 1989a; 1989b; Andersen et al., 1990), temporal lobe areas that are connected to the amygdala and hippocampus (e.g. Krubitzer and Kaas, 1990), and lesions along this pathway, indicate that areas here may be involved in tactile recognition and memory (Mishkin, 1979; Murray and Mishkin, 1984). Finally, this is the region of cortex where sensory modalities converge suggesting that fields in the lateral sulcus play a role in sensory integration across modalities. Thus, most data indicate that areas in this region are involved in more complex tactile discriminations than areas in anterior parietal cortex. Comparisons of this region in primates as well as non primate mammals demonstrate that this area is composed of at least two separate representations, the second somatosensory area, SII, and the parietal ventral area, PV, and that additional areas such as VS, Ri, and 7b may have evolved somewhat later, particularly in the lineage leading to extant primates. These areas may be responsible for the complex behavior associated with primates such as bilateral coordination of the hands, and precise tactile discriminations necessary for object identification and recognition.

The organization of lateral somatosensory areas in primates

The second somatosensory area, SII. The second somatosensory area, SII, has been described in a variety of primates including macaque monkeys (Whitsel et al., 1969; Robinson and Burton, 1980b; Pons et al., 1988; Krubitzer et al., 1995), marmosets (Krubitzer and Kaas, 1990); owl monkeys (Cusick et al., 1989), and galagos (Burton and Carlson, 1986). In Old world macaque monkeys, discrepancies exist in the size of SII, the position of SII, and the internal organization of SII (Fig. 1). However, recent electrophysiological as well as anatomical data have provided evidence for two separate fields in cortex traditionally defined as SII. It has been proposed that these discrepancies in the description of SII in Old World monkeys may be the result of the two fields being confused (Krubitzer et al., 1995). The internal organization, relative location, and architecture of SII in New World and prosimian primates is similar to recent descriptions of SII in macaque monkeys (Figs. 2 and 3). SII forms a complete representation of the body surface with the face, head and neck represented medially, the forelimb laterally or rostrally, and the hindlimb most laterally. The trunk is represented caudally or caudolaterally in SII. Within the limb representation, the representation of the distal limbs, including glabrous digits and toes occupies a large region of cortex rostral to the representation of the proximal limbs. SII is also distinguished by a heavily myelinated appearance relative to surrounding cortex, as well as a dense granule cell layer in cortex that has been cut coronally or parasagittally. In some experiments, bilateral receptive fields have been described for neurons in the SII region (e.g. Whitsel et al., 1969; Robinson and Burton, 1980b). Another feature of SII is that it is proposed to be a major recipient zone of connections from SI (e.g. Friedman et al., 1980). However, at the time most investigations were done, SI included fields 3a, 3b, 1 and 2, and we now appreciate that only 3b should be considered as SI as described in other mammals (Kaas, 1983). Also, the definition of SII was vague and somewhat circular, i.e. neurons responsive to tactile stimulation in cortex lateral to SI are in SII, and SII receives direct inputs from "SI". Recently, it has been shown that in marmoset monkeys (Krubitzer and Kaas, 1990) and macaque monkeys (Burton et al., 1995) there are a number of recipient zones of 3b projections in this region of cortex, several of which receive topographically matched inputs from 3b, and that a very large region of cortex lateral to anterior parietal fields, much larger than the traditional SII, contains neurons responsive to tactile stimulation. Thus, while neurons in SII respond to tactile stimulation, and while SII does indeed receive inputs from the primary somatosensory area, it is not the only field to do so. Finally,

recent experiments in which the cortical connections of SII were directly investigated (Friedman and Murray, 1986; Friedman et al., 1986; Krubitzer and Kaas, 1990), support the contention that additional fields, densely interconnected with SII, are present in the lateral sulcus of primates.

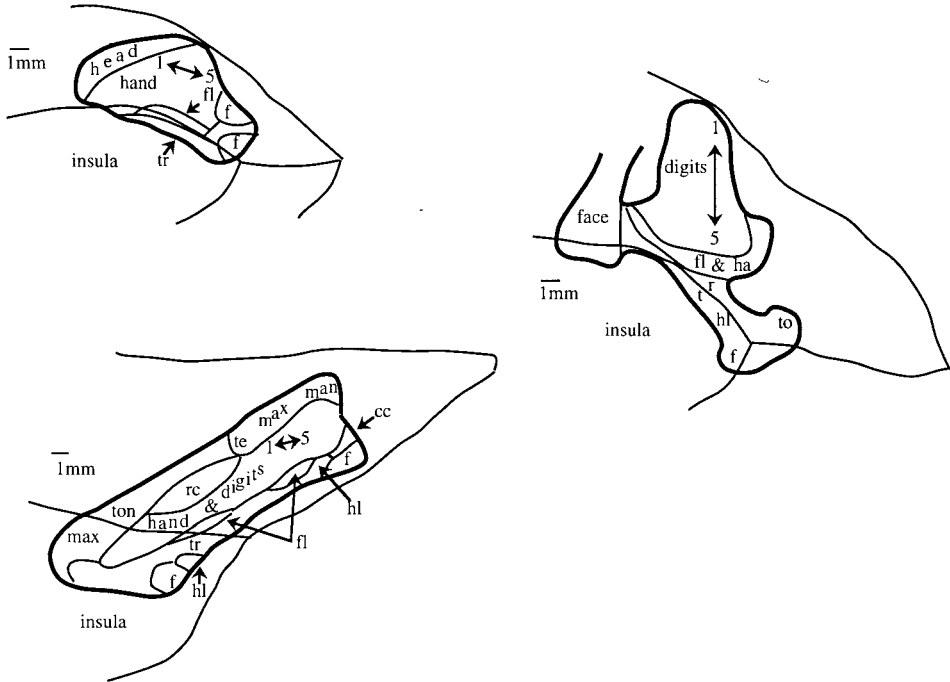


Figure 1. The organization of the second somatosensory area in the macaque monkey redrawn from Robinson and Burton, 1980 (top), Friedman et al., 1980 (middle), and Pons et al., 1988 (bottom). The top and bottom figures are based on results from electrophysiological mapping experiments and the middle figure is a summary based on results from connections from different body representations in SI. Note that the size, internal organization, and relative location of SII is different in the different studies. In this and the following figures, rostral is to the left and medial is to the top. Caudal complex, cc; foot, f; forelimb, fl; hand, ha; hindlimb, hl; mandibular, man; maxillary, max; teeth, te; tongue, ton; trunk, tr.

The parietal ventral area, PV. Single unit recording experiments in the early 1980's by Robinson and Burton, demonstrated that cortex surrounding the SII region contained neurons responsive to somatic stimulation (e.g. retroinsular, Ri, and granular insula, Ig), and were outside of the proposed boundaries of "SII". However, even within the region they defined as SII, multiple representations of similar body parts were described, suggesting that "SII" may contain separate fields. The notion that multiple representations exist in the lateral sulcus of primates has been

further substantiated in more recent studies in marmoset and macaque monkeys. The details of how cortex in the lateral sulcus of primates should be subdivided is still contentious, but the data across studies are consistent with the proposition that more than a single field resides here. There is clear electrophysiological and anatomical evidence for two mirror symmetric representations. Both early and recent studies of connections of anterior parietal areas with cortex in the lateral sulcus (Friedman et al., 1980; Burton et al., 1995) demonstrate that multiple target areas exist in the lateral sulcus. One of which is SII, the other of which is similar to PV. In accordance with this interpretation, our laboratory has termed these fields SII and PV, because we propose that they are homologous to similar fields described in other mammals (Fig. 3, see below). Like, SII, PV contains a complete representation of the sensory epithelium. The mediolateral organization of PV is much like that of SII with the head represented most medially (superficially in the sulcus), and the forelimb and hindlimb more laterally (deeper in the sulcus). However, the rostrocaudal organization of PV is mirror symmetric to that of SII with the distal limbs represented caudally and proximal limbs and trunk represented rostrally (Fig. 2, marmoset, Fig. 3).

The ventral somatosensory area, VS. Areas in addition to SII and PV have also been identified in primates using several different, although not always overlapping criteria. Based on connections from anterior parietal fields combined with electrophysiological mapping in owl monkeys, Cusick et al. (1989) described two separate representations in cortex lateral to 3b and 1 (Fig. 2). These fields included SII, similar in organization, position, and connections from 3b, to SII described in macaque monkeys, and a ventral somatosensory, VS, just ventral to SII. Although complete maps for VS have not been obtained in owl monkeys, the representation in VS appears to reverse off of the SII representation (Fig. 3; see the description of VS in flying fox). A partial map, similar in organization and position to VS described in owl monkeys has been generated in macaque monkeys (Krubitzer et al., 1995), and as in owl monkeys, has been termed VS.

Area 7b. Studies of connections, architecture, and physiology indicate that there is a region of cortex just caudal to SII and the lateral portion of area 1, which is termed area 7b (e.g. Robinson and Burton, 1980a). This region has interconnections with some subdivisions of the somatosensory cortex, and is also densely interconnected with subdivisions of frontal and posterior parietal cortex (Cavada and Goldman-Rakic, 1989a; 1989b; Anderson et al., 1990). Recent electrophysiological recording results indicate that neurons in this region respond to somatic stimulation, but that the type of stimulation needed to elicit a response is more complex than for

areas SII and PV (Krubitzer et al., 1995). Neurons in area 7b require a broader stimulus applied to a large region of the body, and often have a longer latency of response than neurons in other somatosensory regions. However, complete maps of this field have not been obtained, and studies of single neuron properties are needed to determine differences between 7b and surrounding fields.

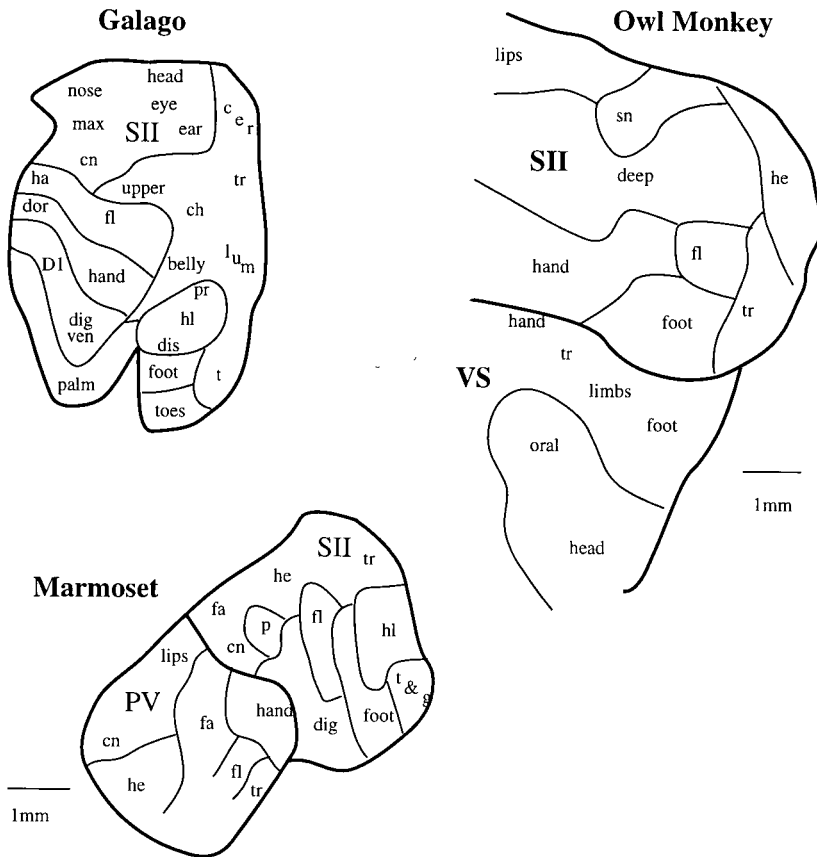


Figure 2. The organization of SII and surrounding fields redrawn from studies in galagos, marmosets, and owl monkeys. The internal organization of SII is very similar across these different species of primates. The panda representations. Cervical, cer; chest, ch; chin, cn; digits, dig; distal, dis; dorsal, dor; face, fa; genitals, g; head, he; palm, rietal ventral area, PV, shares a common border with SII at the representations of the lips and glabrous hands, and the ventral somatosensory area, VS, in owl monkeys shares a common boundary with SII at the foot and ha p; proximal, pr; tail, t; ventral, ven. Other abbreviations as in previous figures. (Galago: Burton and Carlson, 1986, Owl Monkey: Cusick et al., 1989; Marmoset: Krubitzer and Kaas, 1990).

Early studies in macaque monkeys identified regions outside of the area termed SII whose neurons were responsive to somatic stimulation, and neurons in these regions were related to architecture. These fields include the retroinsula, Ri, the granular insula, Ig and the post auditory Pa area (Robinson and Burton, 1980a). Similar subdivisions have been used in studies of connections of SII in macaque monkeys (Friedman et al., 1986). However, earlier studies in which these architectonically defined areas were related to electrophysiological recording results only sampled a small amount of cortex in any individual animal, and data was collapsed across animals to develop these subdivisions. Also, subdivisions such as Ig, Ri, and Pa do not appear to correspond with more recent electrophysiological recording results. Rather, it is likely that the relatively large region termed Ig is composed of more than a single field, and that the very small area Ri (approximately 1 mm x 1 mm) is part of a larger field.

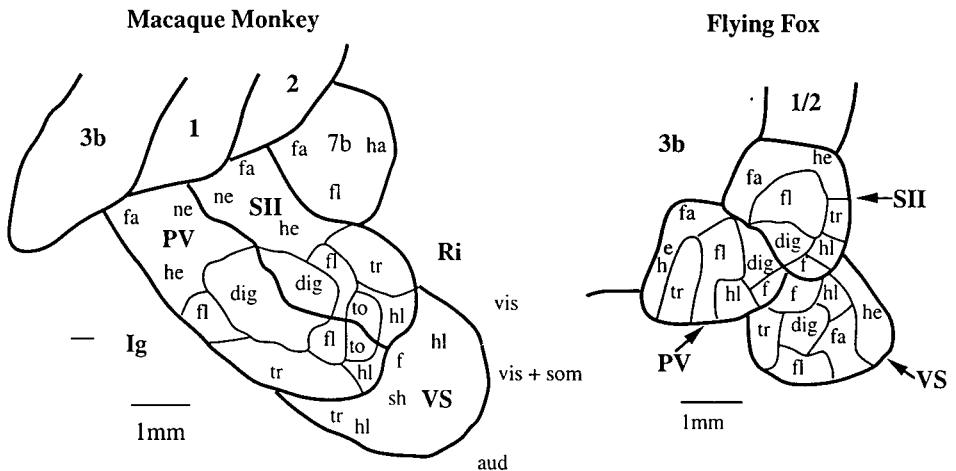


Figure 3. The organization of SII, PV, and VS, redrawn for the macaque monkey and flying fox. The internal organization, and relative location of these fields is similar in both species, although the location of SII and PV relative to anterior parietal fields is somewhat different. Neurons in cortex surrounding PV, SII and VS are also responsive to somatic stimulation and partial maps have been generated for at least one field, area 7b. Cortex in the region of Ri is responsive to visual and visual + somatosensory stimulation. Shoulder, sh; toe, t. Other abbreviations as in previous figures. (Macaque Monkey: Krubitzer et al., 1995; Flying Fox: Krubitzer et al., 1992).

Recently, studies in humans using imaging techniques such as positron emission tomography (PET, Burton et al., 1993; Ledberg et al., 1995) have also demonstrated that there are multiple areas in the lateral sulcus of humans, and that these areas have different roles in discriminating microgeometric and macrogeometric stimuli (e.g. Ledberg et al., 1995). How the multiple representations in this region in humans relates to the separate fields identified in monkeys is not known.

The organization of lateral somatosensory areas in other mammals

Although early studies in non primates described the second somatosensory area as a large inverted representation of the body surface (e.g. Lende and Woolsey, 1956; Woolsey, 1967; Fig. 4), microelectrode mapping studies in cats demonstrated that SII is an upright representation of the body surface (Haight, 1972), similar to that described above for primates. Subsequent microelectrode mapping studies in other mammals (Fig. 4) also described SII as a non inverted representation. The discrepancy in the orientation and internal organization of SII in different mammals is likely to stem from two problems. First, early studies used evoked potentials to describe the organization of SII, and these types of techniques are not as sensitive to defining details of organization within the fields as electrophysiological recording techniques. The second possibility is that more than one field exists in the SII region, and that SII and other fields were being confused. Despite these differences in description, most recent observations in a variety of mammals (see Johnson, 1990 for review) demonstrate that all mammals contain a small, non inverted representation of the body surface lateral to SI and often sharing a common boundary with the face representation of SI. This field is the second somatosensory area, SII.

Recently, a field in addition to SII has been described in rodents (Krubitzer et al., 1986; Fabri and Burton, 1991), megachiropteran bats (Krubitzer and Calford, 1992), and marsupials (Beck et al., 1993; Elston et al., 1993). This field is similar in location, internal organization, architecture, and connections to PV described in primates. We proposed that SII and PV are common features of organization in mammals, and their ubiquity in the various lineages investigated, including two species of primates, suggests that these fields are part of a common plan of organization in mammals, and may be present in humans as well. However, these fields have been evolving independently in the different lineages for tens of millions of years, it is unlikely that they are analogous (functionally similar).

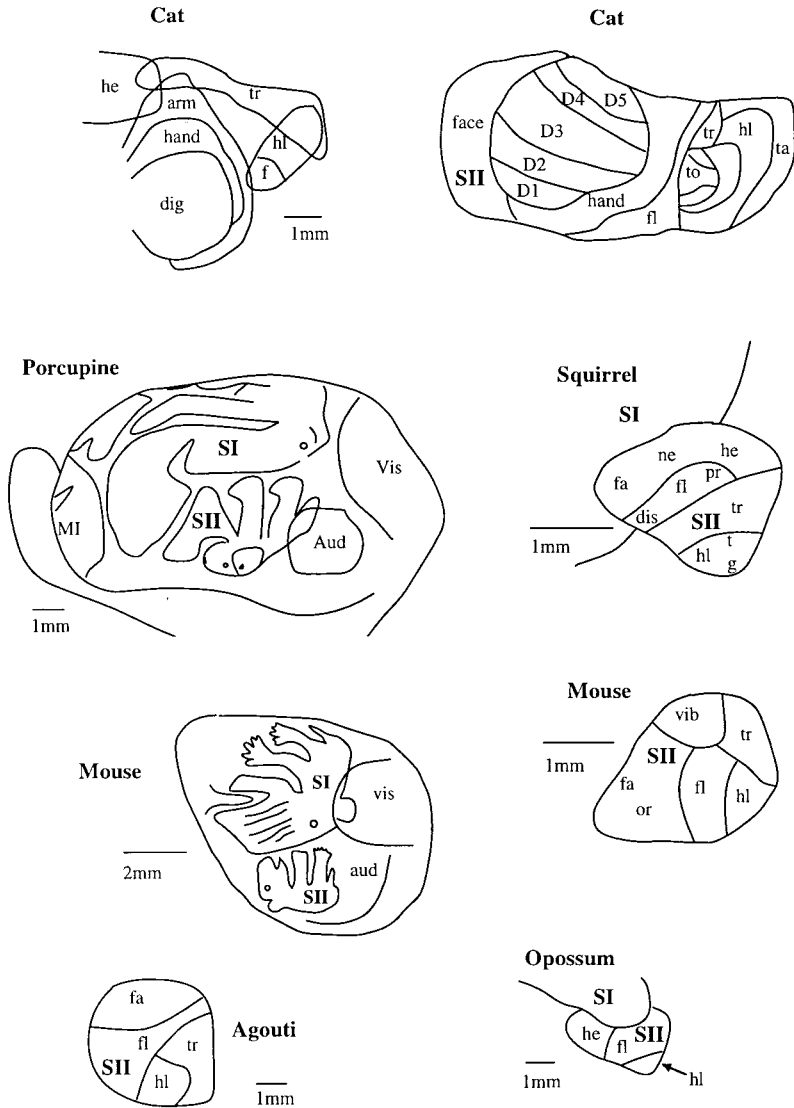


Figure 4. The organization of SII redrawn for a number of species including cats, porcupines, squirrels, mice, agoutis and opossums. The internal organization of SII differs in some investigations. In some investigations SII has been described as an inverted representation of the body surface and in other studies it has been described as a non inverted representation. Even in some studies in which the same species was examined (e.g. mouse), SII has been described as inverted (Woolsey, 1967) as subsequently as non inverted (Carvell and Simons, 1986). Abbreviations as in previous figures. (Cat (top, left): Haight, 1972; Cat (top, right): Burton et al., 1982; Porcupine: Lende and Woolsey, 1956; Squirrel: Nelson et al., 1979; Mouse (left): Woolsey, 1967; Mouse (right): Carvell and Simons, 1986; Agouti: Pimentel-Souza et al., 1980; Opossum: Pubols, 1977)

Work in cats demonstrates that at least two complete representations exist in this region, and that each of these separate regions is coextensive with a unique architectonic appearance and pattern of connections (Burton et al., 1982; Clemo and Stein, 1982; Burton and Kopf, 1984). The fields are termed SII, and SIV. The fourth somatosensory area, SIV, has some similarities with PV described in primates and other mammals (see below), but its relative location, internal organization, and patterns of connections, do not appear to be similar to PV.

In extensive electrophysiological mapping and studies of connections in the megachiropteran bat, at least four separate representations of the body surface have been identified and proposed to be involved in the processing of somatic inputs (Krubitzer and Calford, 1992; Krubitzer et al., 1993). These include, SII, PV, VS and the lateral somatosensory area, LS. These studies in the flying fox contain the first detailed description of the ventral somatosensory area in any mammal (Fig. 3). In the flying fox, VS shares a common boundary with both SII and PV. Although the organization of VS is less precise than that of SII and PV, VS clearly contains a complete representation of the body surface.

Conclusions

Based on comparisons of internal organization, patterns of connections, and architectonic distinctions, it is proposed that at least two complete representations of the body surface exist in all, or most mammals investigated, SII and PV. While other fields such as VS and SIV have been identified, their presence does not appear to be widely distributed across mammals, and is limited to only a few lineages. The presence of SII and PV in all mammals suggest that these areas form the basic building blocks of cortical organization of this regions of cortex, and that other fields were added independently in different lineages later in evolution. While some mammals appear to have an additional field, in primates, this region of cortex has expanded substantially, and contains at least four representations of the body. We propose that these additional fields compose networks that generate both perceptual and behavioral abilities directly associated with the extensive use of the glabrous, opposable digits in primates, and are involved in tactile exploration, object identification, and tactile recognition.

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