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"The Somatosensory System of Primates"

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The Somatosensory System of Primates

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INTRODUCTION

This chapter describes the parts of the somatosensory system that are thought to be important in tactile discriminations. The emphasis is on the processing of information from low-threshold mechanoreceptors in the skin and deep receptors in joints and muscles, since these are the receptors that are likely to be critical in object identification and discrimination. We only briefly mention subsystems dealing with afferents coding pain and temperature and do not discuss spinal reflex mechanisms or the relay of somatosensory information to the cerebellum. Evidence is presented to support several main conclusions. First, there is a high degree of segregation and parallel processing of different classes of afferent inputs as they relay from the periphery to cortex. This point of view has been elaborated and discussed recently for mammals in general [Dykes, 1983], with much of the supporting data coming from studies on cats. Second, the somatosensory cortex and thalamus of monkeys and hominoids appear to have more processing stations, that is, areas and nuclei, than most other mammals including prosimian primates [see Kaas, 1983]. In addition, proportionately more of the total system is devoted to processing information from the hand in advanced primates. Finally, across different primate species, there are significant differences in how the somatosensory forebrain is organized.

The basic components of the somatosensory pathways from receptor to cortex for monkeys and, presumably, hominoids, are outlined in Figure 1. Receptors in muscles, joints, and skin send axons into the spinal cord or brainstem to synapse on second-order neurons in the spinal cord or dorsal column-trigeminal nuclear complex. These second-order (or higher) neurons send axons to the thalamus mainly through two well-known pathways, the spinothalamic tract and the medial lemniscus. Other spinal cord and brainstem terminations for second-order neurons [see Willis and Coggeshall, 1978, for review] are likely to be relatively unimportant for somatosensory discriminations.

The somatosensory thalamus of primates has been subdivided in several ways (see below). In the ventroposterior (VP) complex, we distinguish a ventroposterior "proper" nucleus with inputs relayed from two major classes of peripheral cutaneous receptors (rapidly adapting I and slowly adapting I; see Fig. 2). The ventroposterior inferior nucleus appears to relay information from pacinian receptors (PC) to cortex. Deep receptors in joints and muscles send information to a dorsal capping zone of VP that we term the ventroposterior superior nucleus (VPS). Inputs relayed from muscle receptors may also be segregated in a separate rostral nucleus capping VP, the ventroposterior oral nucleus (VPO). The anterior pulvinar (Pa) and the lateral posterior nucleus (LP) do not appear to receive any second-order somatosensory inputs, but an important role in somatosensory processing is suggested for these nuclei by their connections with cortical somatosensory areas.

As for the thalamus, the somatosensory cortex has been subdivided in various ways, and many questions of organization are not yet resolved. In monkeys and hominoids, there are four traditional subdivisions of anterior parietal cortex, areas 3a, 3b, 1, and 2 of Brodmann [1909]. These four architectonically defined fields have been conceptualized as subfields within a single functional area,

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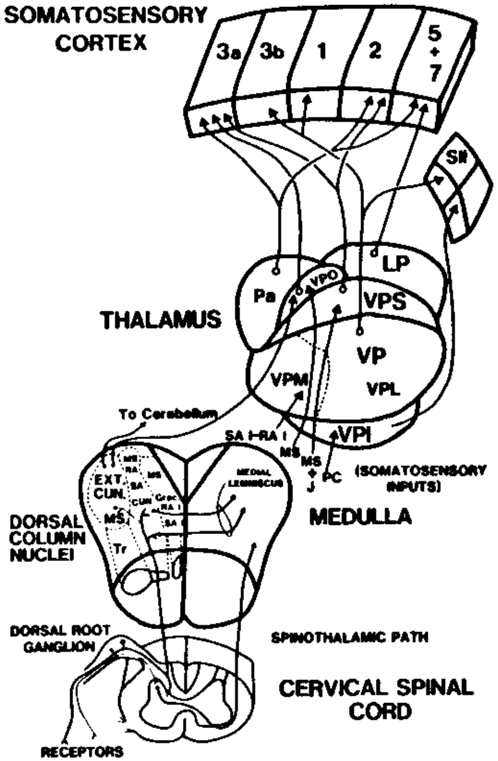
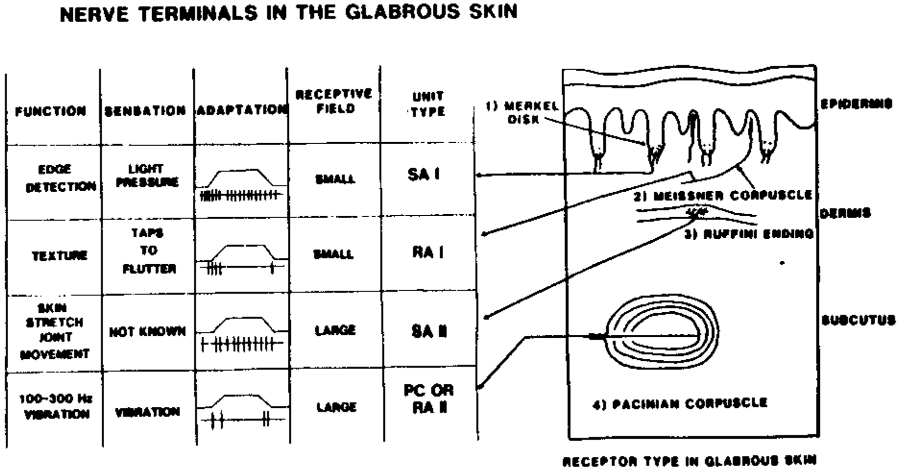


Fig. 1. An overview of ascending pathways in the somatosensory system important for tactile perception in monkeys and higher primates. See text for details. Relays in the medulla include the cuneate nucleus (CUN.), the gracilis nucleus (Grac.), the external cuneate nucleus (EXT. CUN.), and the spinal trigeminal nucleus (Tr). Inputs include those related to muscle spindle receptors (MS) and slowly adapting (SA) and rapidly adapting (RA) type I and type II cutaneous receptors. In the thalamus, ventroposterior (VP), ventroposterior superior (VPS), ventroposterior oralis (VPO), and ventroposterior inferior nucleus (VPI) are distinguished within the ventroposterior complex. VP includes the traditional ventroposterior medial (VPM) and ventroposterior lateral (VPL) subdivisions. Inputs include those from type I slowly adapting (SA) and rapidly adapting (RA) receptors, muscle spindles (MS), joint receptors (J), and pacinian (PC) receptors. The anterior pulvinar (Pa) and lateral posterior nucleus (LP) are not sensory relay nuclei, but project to somatosensory cortex. Areas 3a, 3b, 1, 2, 5, and 7 are traditional architectonic subdivisions of parietal cortex. S-II is the second somatosensory area. S-II or somatosensory cortex near S-II receives input from VPI.


NERVE TERMINALS IN THE GLABROUS SKIN

FUNCTION	SENSATION	ADAPTATION	RECEPTIVE FIELD	UNIT TYPE
EDGE DETECTION	LIGHT PRESSURE		SMALL	SA I
TEXTURE	TAPS TO FLUTTER		SMALL	RA I
SKIN STRETCH JOINT MOVEMENT	NOT KNOWN		LARGE	SA II
100–300 Hz VIBRATION	VIBRATION		LARGE	PC OR RA II

Fig. 2. Receptor types and characteristics of afferent fibers in the glabrous skin. Based on Johansson [1978], Johansson and Vallbo [1983], and Vallbo et al [1984]. RA, rapidly adapting; SA, slowly adapting; PC pacinian afferent. The ramp in the adaptation column indicates skin indentation.

primary somatosensory cortex, or S-I, since the landmark electrophysiological mapping studies of Marshall et al [1937] in macaque monkeys. However, each of these fields forms a separate representation of the body, and we consider only area 3b (or S-I "proper") as the homologue of S-I in other mammals [Kaas, 1983]. Areas 3b and 1 receive input from cutaneous receptors, while areas 3a and 2 are primarily activated by deep receptors. Of these four fields, only area 3b has been clearly identified in prosimians.

Posterior parietal cortex has somatosensory functions, but the subdivisions of this region of cortex are not clear. Traditionally, medial and lateral parts are distinguished as areas 5 and 7, respectively, after Brodmann [1909] and, more recently, subdivisions of areas 5 and 7 have been proposed.

Much of parietal cortex in the lateral fissure is also somatosensory, but again the basic subdivisions of this cortex have not been completely established. One of these subdivisions, the second somatosensory area, or S-II, is common to all mammals, and it appears to receive cutaneous information from VP and from anterior parietal cortex. Cortex near S-II, or perhaps S-II itself, receives pacinian receptor inputs from VPI. Cortex in the S-II region may be an important relay of information to a hippocampal and amygdala circuit that is critical for tactile memory [Mishkin, 1979].

RECEPTOR TYPES AND AFFERENT PATHWAYS

Afferent fibers sending somatosensory information to the central nervous system are traditionally divided into three groups [Dykes, 1983]: 1) those related to low-threshold cutaneous mechanoreceptors; 2) those serving deep receptors in muscles, tendons, and joints; and 3) those small-diameter fibers mediating sensations of cold, warm, pain, and crude touch. The receptors, afferent fibers, and possible functions of each group are reviewed briefly below [also see Iggo and Andres, 1982; Vierck, 1978].

Low-Threshold Mechanoreceptors of the Skin

Mammals vary in their arrangements of receptors in hairy and glabrous skin. In primates, the glabrous hand is an important tactile organ that is highly innervated. Four functionally distinct classes of low-threshold receptors sensitive to skin deformation have been described (Fig. 2). In the superficial skin, a class of slowly adapting afferents, SA-I, apparently terminate at receptor sites termed Merkel disks, while a class of rapidly adapting afferents, RA-I, end in Meissner corpuscles. Deeper in the skin, the Ruffini endings are probably the receptor organs of the slowly adapting SA-II afferents, while the pacinian corpuscles subserve the rapidly adapting PC or RA-II afferents. RA-I and SA-I afferents are densely distributed at the fingertips of the human hand, and they are undoubtedly important afferents for identifying objects. Both RA-I and SA-I afferents have small receptive fields with sharp boundaries. Each afferent subserves a number of endings, but the endings are grouped to provide a restricted receptive field with almost uniform sensitivity. SA-I neurons are especially sensitive to the edge or contour of objects pressed on the skin. When stimulated by a train of electrical pulses, single SA-I afferents in the human hand signal a sensation of light, uniform pressure at a particular skin location corresponding to the receptive field [see Torebjörk et al, 1984; Vallbo et al, 1984; Johansson and Vallbo, 1983; Johansson, 1978]. Single impulses are not felt, and increases in stimulation frequency increase the magnitude of the sensation. For RA-I afferents, a single electrical pulse often leads to a detectable sensation of a light tap at a location corresponding to the receptive field. Low-frequency stimulation produces a sensation of a series of taps, and this merges to a fluttering sensation at higher frequencies. However, no increase in the magnitude of the sensation follows increases in the frequency of stimulation. These observations support the view that RA-I and SA-I units are of great importance for discrimination of objects. RA-I units could be especially important in the discrimination of the texture of surfaces moved on the skin, while SA-I units would signal the edges of objects with maintained contact on the skin.

The PC or RA-II afferent is the only one capable of signaling higher frequency vibrations. Electrical stimulation of PC afferents in the human hand is not detected until stimulation trains are above 10–80 Hz, and then the sensation is of vibration or tickle. The sensation is felt in an area of skin that is often smaller than the rather large receptive field of the stimulated afferents [Torebjörk et al, 1984]. The SA-II afferent is extremely sensitive to skin stretch, and normal movements of digits and limbs are very effective in activating these neurons. Electrical stimulation of this afferent class has not produced sensations. Thus, information from this receptor may not reach consciousness. Because both SA-II and PC receptors are also widely distributed in deeper tissues such as joint corpuscles and tendons, both may be important sources of proprioceptive information, even when located in or near the skin.

Cutaneous Receptors of the Hairy Skin

As in glabrous skin, the hairy skin has receptors for SA-I, SA-II, RA-I, and PC afferents. One difference is that the Merkel cell receptors of the SA-I afferents are often concentrated in touch spots as domes of slightly raised skin of 0.2–0.5 mm in diameter. A single afferent subserves all Merkel disks in one touch dome. Merkel-type endings are also associated with the sheaths of hair follicles, so the SA-I afferents also relate to hairs. Other afferents are rapidly adapting, terminate on hair shafts, and include one or more RA types [see Dykes, 1983; Darian-Smith, 1984].

Deep Receptors

The deep receptors include those in muscles, tendons, and joints. Muscle receptors are of three types: the type Ia, or primary muscle spindle ending, which responds to muscle stretch; the type Ib, or Golgi tendon organ ending, which responds to muscle contraction; and the type II secondary muscle spindle ending, which responds to muscle stretch. Afferents from muscles have very specific reflex functions, but they also may provide much of the information for judgments of limb position [see Dykes, 1983].

Afferents from the joint corpuscle include the SA-II type from Ruffini endings, which signal that the joint is near the limit of its extension, and a slowly adapting Golgi-Mazzoni ending, which responds to compression of the corpuscle and signals pressure.

Small-Diameter Afferents Signaling Pain, Temperature, and Crude Touch

Present evidence indicates that there are mechanical nociceptors producing pricking pain, mechanothermal nociceptors (A-delta nociceptors) signaling pain, polymodal nociceptors (C-nociceptors) signaling burning pain, cold fibers signaling cooling, and warm fibers coding warmth [see Dykes, 1983]. There may be other afferents related to itch and tickle, and some small-diameter afferents, possibly including some polymodal afferents, may signal aspects of crude touch.

Afferent Pathways From Receptors

Afferents course from receptors in receptive field locations to join nerve fascicles that further combine and join with efferents to form the peripheral nerves. Peripheral nerves branch, segregate into sensory dorsal roots and motor-sensory ventral roots, and enter the spinal cord or brain stem. Single axons either terminate on neurons in the dorsal horn of the spinal cord, or enter the dorsal columns while giving off collateral branches to the spinal dorsal horn (Fig. 1). Axons in the dorsal columns ascend to terminate on neurons in the dorsal column nuclei, while afferents subserving the face enter the brainstem and descend to the trigeminal component of the medullary somatosensory complex.

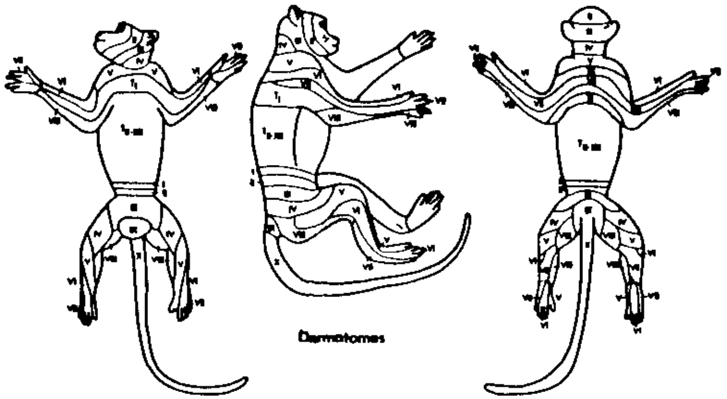


Fig. 3. The distribution of dermatomes on the body surface of a macaque monkey. Numerals for the upper extremities indicate the cervical segments of the spinal and the corresponding dorsal roots. Thalamic derivations (T_{II}-XII) are not indicated, but form narrow bands similar to the first lumbar dermatomes. Postthoracic dermatomes are numbered according to standard terminology [see Sherrington, 1939]. From Nelson et al [1980] after Sherrington [1939].

The axons of each dorsal root subserve receptors distributed over one segment of the body wall called a dermatome. Figure 3 shows the distribution of the dermatomes on the body of a macaque monkey as determined by Sherrington [1939]. The figure shows the striplike forms of the dermatomes, but does not indicate the extensive overlap of adjacent dermatomes. More recent research on dermatomes in green monkeys [Dykes and Terzis, 1981] indicates that there is considerable individual variability in the distribution and overlap of dermatomes. Dermatome patterns have also been defined in spider monkeys [Pubols and Pubols, 1969], squirrel monkeys [Werner and Whitsel, 1967], and humans [eg, Foerster, 1933], where they are basically similar to those shown for macaque monkeys.

The arrangement of afferents in each dorsal root reflects some somatotopic organization. In general, fibers with distal receptive fields tend to be caudal in the dorsal root, while fibers with proximal receptive fields tend to be rostral [Werner and Whitsel, 1967]. In addition, branches of these afferents ascending in fasciculis gracilis and fasciculus cuneatus tend to preserve their order of entry into the spinal cord so that axons from caudal spinal roots are medial to axons from rostral spinal roots [Whitsel et al, 1970, 1972]. Thus, the body surface is represented from lower to higher in a mediolateral sequence in the spinal cord. Pathways for muscle spindles include the cuneate fasciculus for the upper limb and apparently other pathways over second-order neurons for the lower limb [Whitsel et al, 1972].

Second-order neurons in the dorsal horn appear to contribute about 10% of the axons in the dorsal columns of macaque monkeys [Rustioni et al, 1979]. The response properties of these neurons have not been studied, but in cats the majority of such afferents are activated by convergent inputs from cutaneous and muscle afferents [see Mountcastle, 1984, for review].

The Dorsolateral Fasciculus and the Spinocervical Tract

Other second-order neurons project in the dorsolateral fasciculus (Fig. 4) to components of the dorsal column nuclei. This pathway has been studied in cats where neurons activated by cutaneous mechanoreceptors project to both dorsal column nuclei and to small adjoining medullary nuclei

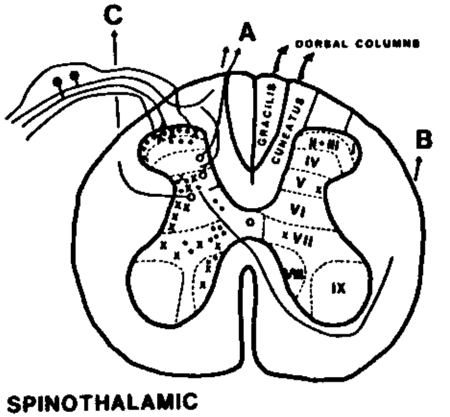


Fig. 4. First- and second-order somatosensory pathways in the spinal cord. First-order sensory afferents activate neurons contributing to the ascending dorsal column system (A), which also includes some second-order afferents. Other afferents ascend in the dorsolateral spinal cord (C) to contribute to the dorsal column nuclei, and other relay neurons (see text). A third ascending system is from neurons that cross the spinal cord and course in the lateral spinal cord to form the spinothalamic tract (B). The locations of spinothalamic cells projecting to the right lateral thalamus (●) and right medial thalamus (×) are based on Willis et al [1979]. The layers of the spinal grey are after Rexed [1952].

termed X and Y, which are relay centers for deep receptors from the hindlimb [see Mountcastle, 1984]. Similar systems may exist in monkeys and humans where nuclei X and Y have been described [Nijensohn and Kerr, 1975]. Another ascending system of somatosensory afferents is the spinocervical tract (Fig. 4), which is large in cats, but small in primates. Second-order neurons in the spinocervical tract send axons in the ipsilateral dorsolateral column to the lateral cervical nucleus of the ventrolateral dorsal horn spinal cord. Axons in the spinocervical tract respond to light touch, as well as other somatic stimuli [see Willis and Coggeshall, 1978]. Neurons in the lateral cervical nucleus cross the cord and ascend in the medulla to join the medial lemniscus.

Of course, another well-known pathway in the dorsolateral quadrant or funiculus of the spinal cord is the dorsal spinocerebellar tract, which is a direct source of mechanoreceptor information to the cerebellum [see Mann, 1973, for review]. Since this pathway does not contribute sensory inputs to the thalamus, it is not described here.

The Spinothalamic Tract

The spinothalamic tract neurons relay information largely concerned with temperature and pain as well as some aspects of touch. The locations of cells projecting from the spinal cord to the thalamus have been determined in macaque monkeys (Fig. 4). Most of the cells project contralaterally and are located in both layer I of the dorsal horn and more ventral layers. Cells projecting to the lateral thalamus, presumably relaying tactile information, and to the medial thalamus, presumably relaying pain and temperature inputs, differ in distribution. In monkeys, neurons in the spinothalamic tract have been found to respond to displacement of hairs, light pressure on the skin, stimulation of muscles, and more intense noxious stimuli. Neurons sensitive to low-threshold mechanoreceptive stimuli increase their responses with increased intensity of stimulation into the noxious range. Such neurons have been termed the wide-dynamic-range neurons, and they may have a role in nociception [Chung et al, 1979].

The Dorsal Column-Trigeminal Nuclear Complex and the Medial Lemniscus

The major components of the dorsal column-trigeminal complex are apparent in Figure 1. The gracile, cuneate, and external cuneate nuclei represent the body below the head, while the trigeminal nuclei represent the face and oral cavity. Within these major components, there are subregions or nuclei with specialized functions and histological structure. The basic organization appears to be roughly similar in most mammals [see Darian-Smith, 1973; Mountcastle, 1984], including monkeys [Rustioni et al, 1979] and prosimians [Albright, 1978; Albright and Haines, 1978].

The elongated gracile and cuneate nuclei are not uniform in structure and function. Recordings in cats [see Dykes, 1983] indicate that the central portions receive inputs from RA-I and SA cutaneous afferents; pacinian or RA-II afferents are concentrated more caudally where neurons are more scattered, while muscle and joint afferents relate to more rostral and deeper portions of these nuclei. A similar segregation of function may exist in primates, since different types of afferents are not uniformly distributed. The majority of neurons throughout the cuneate and gracilis nuclei project to the ventroposterior thalamus in macaque monkeys [Rustioni et al, 1979].

The external cuneate nucleus receives muscle spindle and tendon organ afferents from the upper limb and upper body via the cuneate fasciculus. At least in the cat [Nyberg and Blomqvist, 1984], and presumably in primates, the muscles are represented somatotopically in the external cuneate nucleus, with the hand medial to the chest and neck. "Nucleus Z" together with "nucleus X" (not shown in Fig. 1) form the equivalent relay for muscle afferents from the hindlimb, but these are almost completely second-order afferents. First-order afferents for muscle spindles of the hindlimb travel only partway in the gracilis fasciculus, and then leave to terminate on dorsal horn neurons that ascend in the dorsolateral fasciculus to nucleus Z and nucleus X. Neurons in the external cuneate nucleus, nucleus Z, and nucleus X relay to the lateral thalamus and to the cerebellum [Nijensohn and Kerr, 1975]. The relay to the lateral thalamus terminates near the dorsorostral margin of VP [Bovie and Boman, 1981], perhaps in VPS or VPO.

The lateral cervical nucleus can be considered part of the somatosensory complex of the lower brainstem in that second-order cutaneous neurons in the spinocervical tract terminate in the lateral cervical nucleus (not shown in Fig. 1), which in turn relays via the medial lemniscus to the ventrolateral thalamus [see Brown and Gordon, 1977]. The spinocervical system is present in primates, but it has been studied electrophysiologically only in cats, where it is well developed and dominated by low-threshold, velocity-sensitive receptors [Craig and Tapper, 1978].

The trigeminal complex includes the principal or main sensory nucleus and the spinal trigeminal nucleus. The principal sensory nucleus is analogous to the cuneate-gracilis nuclei, and the three together form one systematic representation of the body surface. The principal nucleus projects via the medial lemniscus to the ventroposterior nucleus. The spinal trigeminal nucleus has three subnuclei. Subnucleus caudalis is structurally similar to the dorsal horn, and is analogous to the spinothalamic system. As in the dorsal horn, a marginal zone is dominated by pain afferents, while deeper neurons relate to cutaneous and muscle receptors. Subnucleus caudalis projects to the ventroposterior nucleus and adjoining portions of the medial thalamus [Burton and Craig, 1979]. More rostrally, subnucleus interpolaris is distinguished by a lack of a substantia gelatinosa layer as well as other architectonic characteristics [see Darian-Smith, 1973]. Neurons project to the ventroposterior thalamus and to the cerebellum. Subnucleus oralis forms the rostral extent of the spinotrigeminal nucleus. Its neurons project to the ventrolateral thalamus via the medial lemniscus.

The dorsal column nuclei project to the thalamus and midbrain (see below). A minor projection, which has been described in monkeys and prosimians, as well as a range of nonprimate species (including tree shrews) is to the inferior olive [see Schroeder and Jane, 1976], which in turn projects to the cerebellum.

Somatosensory Inputs to the Midbrain

Some ascending somatosensory afferents terminate in subdivisions of the inferior colliculus, which is principally auditory in function, and the superior colliculus, which is mainly visuomotor in function. The inferior colliculus is generally subdivided into the central nucleus, which is a major auditory relay nucleus with dense inputs from the medial lemniscus, an external (lateral) nucleus with descending cortical inputs that are auditory and collaterals from ascending central nucleus projections, and a pericentral dorsal nucleus with auditory inputs via collaterals from the medial lemniscus. In cats and opossums, neurons have been found in the external nucleus that respond to somatic stimuli [see Morest and Oliver, 1984, for review], but such studies have not yet been extended to primates. However, the external nucleus has been shown to receive inputs from the dorsal column nuclei in prosimians and monkeys, and the pericentral nucleus has been found to receive spinal cord inputs in prosimians [Schroeder and Jane, 1976]. The functional significance of somatosensory inputs into these auditory structures is unknown, but Schroeder and Jane [1976] speculate that both systems may overlap in the detection of low-frequency vibratory stimuli, and thus overlap in connections in the inferior colliculus.

At least in rodents and cats, the deeper layers of the superior colliculus contain neurons activated by somatosensory stimuli, and these layers contain a systematic representation of the body, largely devoted to the face. Somatosensory inputs to these deeper layers have been reported from the spinal trigeminal nucleus, the dorsal horn of the spinal cord, the lateral cervical nucleus of the spinal cord, and the dorsal column nuclei [see Huerta and Harting, 1984, for review]. Less is known about the deeper layers of the superior colliculus in primates, but recordings in cebus monkeys have revealed neurons with somatosensory responses [Updyke, 1974]. Preliminary studies by M.F. Huerta in galagos (personal communication) indicate that the dorsal horn in the spinal cord, dorsal column nuclei, and the spinal trigeminal nucleus all contain neurons projecting to the superior colliculus. Thus, it seems likely that further research will indicate that neurons in the deeper layers of the superior colliculus of primates have somatosensory properties and connections that are similar to those demonstrated in nonprimate mammals. The presumed function of the somatosensory inputs, together with visual and auditory influences, is in directing eye and head movements toward objects of interest [see Meredith and Stein, 1985].

THE SOMATOSENSORY THALAMUS

The functional subdivisions of the primate thalamus are a matter of debate, and many uncertainties remain. Early researchers divided the thalamus on architectonic criteria into nuclei and groups of nuclei, largely using location as the principal guide for names [see Jones, 1984, 1985, for reviews]. However, different investigators have used different names and subdivisions within primates, and often quite different terminology was used for primates and nonprimates. Recent studies of connections, somatotopic organization, and neuron properties have contributed to a better understanding of how the somatosensory thalamus is subdivided, and some modifications of previous descriptions seem desirable. In brief, we attempt to describe the major functional subdivisions of the thalamus, and reserve the term "nucleus" for such subdivisions. As in cortex, each separate and complete representation of the body is considered a subdivision (a nucleus in the thalamus and an area in cortex), regardless of previous terminology. Subdivisions of a single representation are not considered to be separate nuclei, even though they may have been so distinguished by early investigators using architectonic criteria. We retain traditional terminology when possible, and introduce new terminology that is consistent with previous use. The same terms for primates and nonprimates are used where homologues appear obvious.

Some of the somatosensory nuclei of the primate thalamus are shown relative to other nuclei for a representative Old World monkey and New World monkey in Figure 5. Thalamic organization in the two groups of monkeys appears to be remarkably similar. The subdivisions indicated are standard, except that a ventroposterior superior nucleus is distinguished in tissue typically relegated to the ventroposterior nucleus (see below). Other relevant somatosensory nuclei are caudal and rostral to the thalamic level shown. The major somatosensory nuclei are described below.

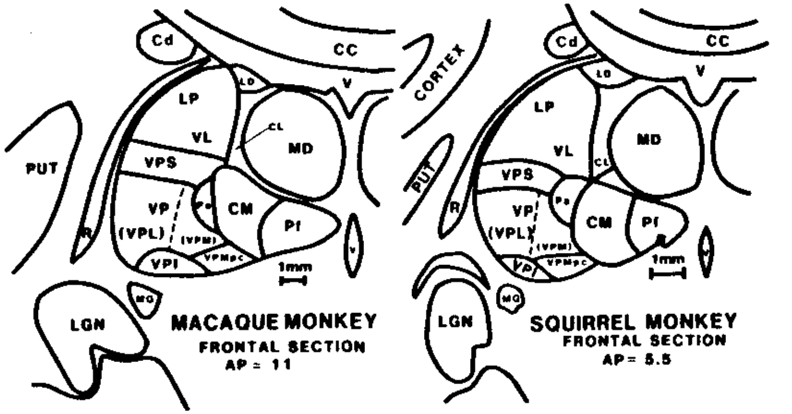


Fig. 5. Subdivisions of the thalamus at roughly equivalent rostrocaudal levels in macaque and squirrel monkeys. The ventroposterior complex includes the ventroposterior nucleus (VP), with ventroposterior lateral (VPL) and ventroposterior medial (VPM) subdivisions. The parvicellular ventroposterior medial nucleus (VPMpc) is involved in taste. Other ventroposterior complex nuclei are the ventroposterior inferior (VPI) and the ventroposterior superior (VPS). The lateral posterior nucleus (LP) and the anterior pulvinar (Pa) connect with subdivisions of somatosensory cortex. Other thalamic nuclei and forebrain structures are the central lateral nucleus (CL), the centromedian nucleus (CM), the corpus callosum (CC), the caudate nucleus (Cd), the lateral geniculate nucleus (LGN), the lateral dorsal nucleus (LD), the medial geniculate nucleus (MG), the parafascicularis nucleus (Pf), the medial dorsal nucleus (MD), the putamen (PUT), the reticular nucleus (R), the ventral lateral nucleus (VL), and the ventricles (V). Anteroposterior (AP) levels are in Horsely-Clark stereotaxic planes.

The Ventroposterior Nucleus

The ventroposterior nucleus (VP) is a basic subdivision of the mammalian thalamus [Welker, 1974; Jones, 1985]. VP is characterized by densely packed and darkly stained neurons in Nissl preparations, and it can be quite distinct in cytochrome-oxidase preparations, which reflect levels of metabolic activity. VP sometimes is called the ventrobasal nucleus or the ventrobasal complex. Traditionally, VP has been divided into "nuclei," the ventroposterior lateral "nucleus," VPL, and the ventroposterior medial "nucleus," VPM, but it has been obvious for some time that they are subdivisions of the same nucleus, with VPL representing the body and VPM representing the face. VP, in our terminology, corresponds to a single systematic representation of the body surface. Neurons are largely activated by slowly adapting or rapidly adapting cutaneous receptors. This VP is homologous to the VP generally described for nonprimate mammals, such as raccoons, cats, or rats [see Welker, 1974], but it does not include the more dorsal representation of noncutaneous receptors in VPS, which traditionally has been included in VP of monkeys [see Kaas et al, 1984, for review]. Thus, it may be necessary to distinguish the present VP from previous usage by the term VP "proper". Another complication is that many investigators use the thalamic divisions outlined in the atlas of Olszewski [1952] for macaque monkeys. Olszewski misidentified the ventroposterior thalamus by including parts of the ventrolateral thalamus. Modern studies of connections [eg, Berkley, 1983] indicate that Olszewski's oral division of VPL (VPL_o) is completely outside of the somatosensory thalamus and corresponds to part of VL, with cerebellar input and projections to motor cortex. Olszewski's caudal division (VPL_c) includes both our VPL and VPS. In our view, the continued use of Olszewski's terminology for the somatosensory thalamus unnecessarily complicates comparative statements.

Part of the evidence that VP or VP proper is a somatosensory nucleus is that it forms a systematic representation of the body surface. This has been demonstrated for VP of a number of nonprimate species [see Welker, 1984] and for VP of macaque monkeys, several species of New World monkeys, and prosimian galagos [see Kaas et al, 1984, for review]. Figure 6 shows the somatotopic organization of VP in the squirrel monkey as determined in a detailed microelectrode mapping study [Kaas et al, 1984]. For descriptive purposes, it is useful to divide VP into five subnuclei. The medial subnucleus, VPM, is partially separated from VPL by a narrow cell-poor zone, the arcuate lamina. VPM represents the face in a somatotopic manner with much of the subnucleus devoted to the lips and tongue (Fig. 6). The parvocellular ventroposterior medial nucleus, VPM_{pc}, ventromedial to VPM (Fig. 5), is not part of VP, but instead is a gustatory nucleus [see Beckstead et al, 1980]. VPL is partially divided into four subnuclei by cell-poor fiber bands. Narrow medial and lateral fiber bands separate subnucleus A of VPL, sometimes called VPL_m, from VPM and more lateral parts of VPL. Subnucleus A represents the hand in a systematic manner, with the digits represented from thumb to little finger (D1-D5) in a mediolateral sequence. More laterally, subnucleus B represents the foot in a similar manner, and over part of VP a small subnucleus C devoted to the tail can sometimes be distinguished by a narrow separating fiber band. Dorsally, subnuclei VPM, A, B, and C all fuse with subnucleus D, representing the limbs, trunk, neck, and caudal head. Although subnuclei may not always be obvious, the basic somatotopic organization of VP appears to be similar in all mammals. However, the proportional representation of body parts varies greatly according to species.

Differences and similarities within primates in overall VP organization become apparent when squirrel monkeys (Fig. 6), macaque monkeys (Fig. 7A), and galagos (Fig. 7B) are compared. While many details of the somatotopic organization of VP in prosimian primates are not known, the galago VP has a common form and organization [Pearson and Haines, 1980a,b] with much of the nucleus devoted to the hand (subnucleus A) and

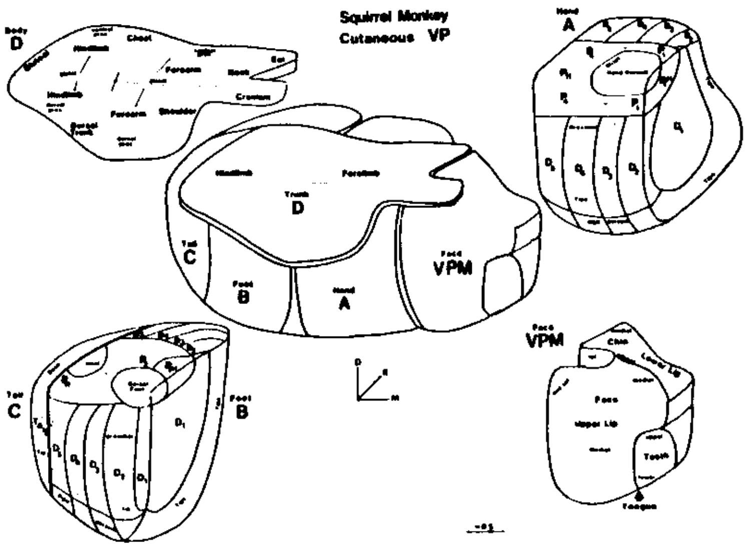


Fig. 6. The somatotopic organization of the ventroposterior nucleus in squirrel monkeys. The nucleus can be divided into two divisions, ventroposterior medial (VPM) for the face and ventroposterior lateral (VPL) for the body. VPL is further divided into subnuclei A for the hand, B for the foot, C for the tail, and D for the trunk. Digits and digital pads are numbered for the hand and foot. Ph, hypothenar pad; Pth, thenar pad. From Kaas et al [1984].

face (subnucleus VPM). In monkeys, the glabrous foot gains somewhat in proportional representation.

When the somatotopic organization is considered in detail, VP is characterized by small volumes of tissue that are activated by stimulating a single receptive field location on the skin (zones of isorepresentation), discontinuities in somatotopic organization in the nucleus, and the separate representation of submodalities within the nucleus. In recording experiments where a microelectrode is pushed along a line through VP, one often encounters short sequences of neurons with nearly identical receptive fields. These sequences define lines of unchanging representation or isorepresentation. The orientation and lengths of lines of isorepresentation vary in different parts of VP, but it is obvious from Figure 6 that these lines would be extended in the dorsoventral and rostrocaudal planes, but not the mediolateral plane, for much of the representation of the digits, which occupy most of subnuclei A and B. This is in accord with the observation that many afferent axons entering VP to activate neurons have terminal ramifications that are elongated rostrocaudally [Jones, 1983], and the observations that zones of cells in VP that are typically elongated in the rostrocaudal and dorsoventral planes project to given locations in somatosensory cortex representing a small portion of a skin surface [see Lin et al, 1979; Jones et al, 1982; Nelson and Kaas, 1981; Pons and Kaas, 1985]. It is also apparent from Figure 6 that most recording sequences in VP would encounter discontinuities in the representation. For example, receptive fields for successive neurons can be on different fingers. In particular, mediolateral electrode penetrations produce neuron sequences with many jumps in receptive field locations. However, penetrations at other angles also produce such jumps, and many of them are not predicted by the summary map. Thus, there are details of the representation that are not yet completely understood. Such results suggest that there is some "folding" of a sheetlike representation in VP [see Kaas et al, 1984] but the nature of this folding has not been revealed.

All neurons along a line of isorepresentation are activated by the same skin surface, but all need not be activated by the same afferent axon, or even by the same class of afferent axons. In monkeys, neurons throughout VP appear to be activated by stimulating cutaneous receptors, and there appears to be no locations where neurons are not activated by cutaneous receptors. Other inputs may exist, but they are rare and certainly do not exclusively activate groups of neurons in VP. For example, in a recording study involving thousands of VP neurons in macaque monkeys [Kenshalo et al, 1980], only 73 were found that were responsive to noxious stimuli, and many of these also responded to light touch (the "wide-dynamic-range" neurons). However, there are clearly different types of cutaneous inputs in VP. Recordings in VP typically reveal short sequences where all neurons rapidly adapt to skin indentation, or where all neurons are slowly adapting [see Dykes et al, 1981]. These neurons appear to be activated by SA-I receptors or by RA-I receptors for glabrous skin and the equivalents for hairy skin. RA-II or pacinian inputs appear to be missing, as well as inputs from muscle receptors and joints. It is not yet clear if SA-II inputs are included. However, along any line of isorepresentation, sequences of RA and SA neurons alternate, but the pattern of alternation is not yet clear.

The sources of ascending inputs to VP (Fig. 8) have been studied extensively in macaque [Bovie, 1978, 1979; Kalil, 1981; Asanuma et al, 1983; Berkley, 1980, 1983; Mantyil, 1983] and squirrel monkeys [Berkley, 1980]. The major inputs are from the dorsal column nuclei and the main sensory trigeminal nucleus. Other inputs are from the contralateral cervical nucleus, which contributes ascending axons to the medial lemniscus, and the spinothalamic tract. Presumably, all these pathways include RA and SA cutaneous receptor information. Both the dorsal column and spinothalamic ascending systems contribute to the few wide dynamic-range neurons in VP [Kenshalo et al, 1980]. For reasons that are unclear, the three sources of input are unevenly distributed in VP [see Berkley, 1980]. The lateral cervical nucleus inputs are denser ventrally, the spinothalamic inputs are concentrated laterally, and the dorsal column afferents are dense throughout. These differences could relate to the somatotopic pattern, so that some skin surfaces are subserved more by one pathway than another, or to unknown differences in the distribution of submodalities in VP. As stated above, there is no clear evidence for any substantial submodality input to VP (or VP proper) other than RA and SA cutaneous receptors.

The cortical connections of VP are with anterior parietal cortex (Fig. 3) and apparently with S-II [Burton and Carlson, 1986; Burton, 1984]. In prosimian primates VP projects to area 3b (S-I) [Kaas, 1982] and S-II [Burton and Carlson, 1986], and no other cortical connection fields have been demonstrated. In monkeys, any given location in VP projects to somatotopically matched locations in both areas 3b and 1 [Lin et al, 1979; Nelson and Kaas, 1981; Kaas et al, 1984], and a proportion of neurons in VP, perhaps 20%, project to both areas 3b and 1 [Lin et al, 1979; Cusick et al, 1985]. In general, the axons and axon branches terminating in area 3b are larger in diameter than those ending in area 1 [Jones et al, 1979]. In macaque monkeys, minor projections of VP are to parts of areas 2 and 5 [Pons and Kaas, 1985].

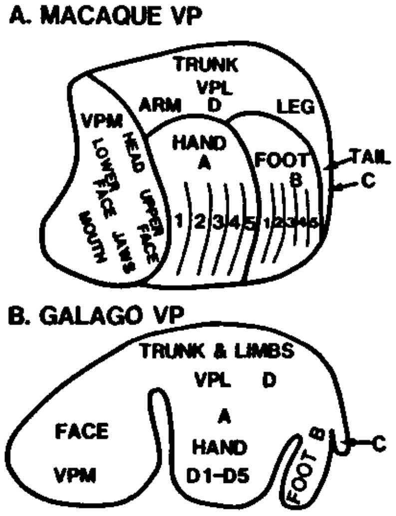


Fig. 7. The somatotopic organization of the ventroposterior nucleus in macaque monkeys and galagos. VP is divided into ventroposterior medial (VPM) and "A," "B," and "C" subnuclei as in Figure 6. Digits of the hand and foot are numbered. In the frontal brain sections, medial is to the left. The macaque thalamus is based on Jones and Friedman [1982]. The galago is from Kaas [1982].

The Ventroposterior Superior Nucleus

Our ventroposterior superior nucleus (VPS) corresponds to the well-known zone of activation from "deep" noncutaneous receptors in the dorsal part of the traditionally defined ventroposterior "nucleus" [Poggio and Mountcastle, 1963; Pubols, 1968; Loe et al, 1977; Pollin and Albe-Fessard,

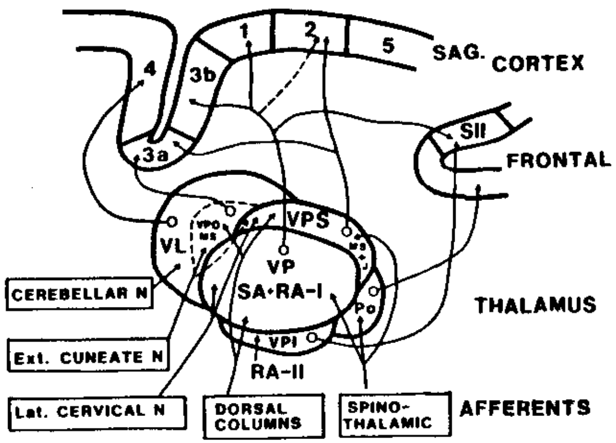


Fig. 8. Sensory inputs to the thalamus and the relay to somatosensory cortex. The ventroposterior nucleus (VP) relays slowly adapting (SA) and type I rapidly adapting (RA-I) cutaneous receptor information from the dorsal column-medial lemniscus pathway and the spinothalamic pathway to areas 3b and 1, with some involvement of area 2, and to S-II. The ventroposterior superior nucleus (VPS) receives information from receptors in muscles (MS) and joints (J) and relays to areas 3a and 2. A separate ventroposterior oral nucleus (VPO) relaying muscle spindle (MS) information to area 3a may also exist. The ventroposterior inferior nucleus (VPI) relays pacinian receptor (RA-II) information to cortex in the lateral fissure near S-II, and perhaps to S-II as well. Part of the posterior group of the thalamic nuclei (Po) relays somatosensory information to cortex in the region of S-II. The ventrolateral (VL) nucleus relays "sensory" information from the cerebellum to motor cortex. See text for further details. Ares 1-5 are indicated on a sagittal section of frontal and parietal cortex, while the S-II region is shown on a frontal section of parietal cortex.

1979; Dykes et al, 1981; Maendly et al, 1981; Jones and Friedman, 1982]. We distinguish VPS from VP (or VP proper) for the following reasons: 1) VPS is architectonically distinct, and it can be identified in Nissl preparations from VP by a change to slightly smaller cells and a more scattered distribution of cells. This change is much more obvious in squirrel monkeys [see Dykes et al, 1981] than in macaque monkeys [see Pons and Kaas, 1985]. In addition, VPS is less densely stained than VP when sections are reacted for cytochrome oxidase (Cusick, unpublished observations) or acetylcholinesterase [Pons and Kaas, 1985]. 2) VPS forms a separate representation of the body that parallels the representation in VP [see Kaas et al, 1984]. 3) The neurons in VPS are closely related to noncutaneous receptors, probably those in muscles and joints, although there apparently is some minor cutaneous activation as well (see references above). The change in response properties of neurons at the VPS-VP border is sharp. 4) The cortical connections, and apparently the subcortical sources of input, for VPS and VP are quite different (Fig. 8). Other investigators either fail to distinguish VPS, or distinguish it from VP as the shell or part of the shell of a VP core (our VP) [eg, Jones and Friedman, 1982; Berkley, 1980].

Afferents to VPS appear to include dorsal column, spinothalamic, and lateral cervical nucleus systems [eg, Berkley, 1980; Asanuma et al, 1983]. A likely source of some of the information from muscle spindle receptors is from the external cuneate nucleus [Bovie and Boman, 1981], although much or all of this input may be concentrated in a separate "ventroposterior oralis" nucleus (see below). There is evidence that a few afferent axons with terminations in VP send collaterals to terminate in VPS [see Jones, 1984]. These collaterals probably contribute some cutaneous receptor information. The significance of spinothalamic input is unknown, but some spinothalamic neurons are activated by muscle afferents [Foreman et al, 1979]. It is also possible that the dorsal column

nuclei contribute muscle afferent information [see Wiesendanger and Miles, 1982, for review].

Major cortical projections of VPS (Fig. 8) are to area 2 [Lin et al, 1979; Nelson and Kaas, 1981; Friedman and Jones, 1981; Jones and Friedman, 1982; Cusick et al, 1985; Pons and Kaas, 1985]. In macaque monkeys, sensitive methods also reveal a slight projection to part of area 1 [Pons and Kaas, 1985]. In addition, other major projections are to area 3a [Friedman and Jones, 1981; Jones and Friedman, 1982], and as many as 40% of VPS neurons may project via collaterals to both areas 3a and 2 [Cusick et al, 1985]. While clear evidence exists for VPS in both New World and Old World monkeys, its presence in prosimian primates is not yet certain.

The Ventroposterior Oralis Nucleus

There is some evidence that there is a separate group of cells on the rostral margin of VPS and VP (see Fig. 8) that receives information from muscle receptors and projects only to area 3a [see Wiesendanger and Miles, 1982, and Jones and Friedman, 1982, for review]. We have adopted the term "ventroposterior oralis" for this presumptive nucleus, after the use of Dykes [1983], although its existence as a separate nucleus is somewhat uncertain. The major input appears to be from the external cuneate nucleus [Bovie and Boman, 1981], and this nucleus may project only to VPO and not VPS. VPO also appears to be within the projection zone of dorsal column nuclei [see Wiesendanger and Miles, 1982]. In squirrel monkeys, a clearly separate VPO projection to area 3a was not revealed by matched injections in area 3a and area 2 [Cusick et al, 1985]. Thus, the conclusion that VPO and VPS are separate nuclei, at least in New World monkeys, remains tentative. However, Dykes [1983] reviews evidence that VPO is part of the ventroposterior complex in cats, and therefore it may be part of the basic mammalian thalamus.

The Ventroposterior Inferior Nucleus

The ventroposterior inferior nucleus (VPI) is one of the traditionally recognized subdivisions of the ventral thalamus [eg, Jones, 1984, 1985]. In Nissl preparations, it is easily recognized by the presence of smaller, lightly stained cells, which contrast with the larger and densely stained cells of VP. Microelectrode recording experiments indicate that pacinian (PC) or RA-II afferents provide a major source of activation [Dykes et al, 1981], and the nucleus appears to form a crude representation of the body that parallels the somatotopic organization of VP [Kaas et al, 1984]. Earlier studies suggested that VPI receives inputs from vestibular nuclei [eg, Lang et al, 1979; Deecke et al, 1975], but this input appears to only pass through VPI to VL [see Wiesendanger and Miles, 1982].

The source of PC activation in VPI is unknown, although the nucleus does appear to be within the dorsal column nuclei and spinothalamic projection zones [eg, Bovie, 1978; Berkley, 1980; Kalil, 1981]. Judging from experiments on cats, it is likely that PC information in primates is relayed to the thalamus over the dorsal column nuclei-medial lemniscus system [Dykes, 1983].

The major cortical projection target of VPI appears to be S-II, while sparser projections may terminate in cortical fields near S-II [Friedman and Murray, 1986]. Burton and James [1976] originally provided evidence that VPI projects to dysgranular insular cortex in the lateral fissure adjoining the second somatosensory area, S-II. More recently, several investigators have concluded that VPI is a major relay to S-II, and VP provides little or no input to S-II [Manzoni et al, 1984; Friedman and Murray, 1986]. Other investigators have provided further evidence of inputs to S-II from VP [Burton, 1984; Burton and Carlson, 1986]. S-II in monkeys appears to be dominated by rapidly adapting skin receptors, but a small number of neurons in S-II reportedly are pacinianlike in responsiveness [Robinson and Burton, 1980c]. The retroinsular field caudal to S-II has more pacinianlike neurons [Robinson and Burton, 1980c], and this cortex should be considered as a possible target of VPI.

The Medial Posterior Nucleus

A region of thalamus at the posterior pole of the ventroposterior nucleus is generally recognized as the posterior group of nuclei [see Jones and Burton, 1976; Jones, 1981], and at least one division, the medial posterior nucleus (Pom) is a component of the somatosensory thalamus. Pom is identified by having less densely stained and more scattered cells than VP. Pom receives spinothalamic terminations and has been implicated in pain systems [see Geisler et al, 1981; Jones, 1984]. A role in pain perception, however, seems unlikely since the apparent cortical target of Pom, retroinsular cortex on the border of S-II, has neurons that are activated by innocuous cutaneous stimulation [Robinson and Burton, 1980].

The Anterior Pulvinar and the Lateral Posterior Nucleus

The anterior pulvinar (Pa) is an obvious division of the thalamus rostrally where its scattered, small, pale-staining cells distinguish it from the adjoining VP (Fig. 5). More caudally, Pa merges with the medial pulvinar without a marked change in cytoarchitecture. The lateral posterior nucleus is a more dorsal and rostral region of scattered darkly stained cells (Fig. 5). Neither thalamic region receives direct spinal cord or dorsal column somatosensory afferents, but both nuclei are implicated in somatosensory functions by their patterns of cortical connections. The anterior pulvinar has long been known to project to posterior parietal cortex and to somatosensory cortex in the lateral fissure [see Cusick et al, 1985, for review], but recently it has been shown to have major projections (Figs. 1, 8) to area 2 [Pons and Kaas, 1985] and area 3a [Cusick et al, 1985]. Robinson and Burton [1980c] suggest that somatosensory information from the deep layers of the superior colliculus might relay in Pa, but clear evidence of this is not available. The lateral posterior nucleus has no known subcortical input, but it is interconnected with areas 5 and 7 of the posterior parietal somatosensory cortex [see Pons and Kaas, 1985].

Other Somatosensory Nuclei

Thalamic nuclei specifically concerned with pain and temperature receptors have not been identified in primates, but Craig and Burton [1981] have provided evidence in cats that the ventromedial nucleus is activated by cold-sensitive thermoreceptors and that nucleus submedius is the target of spinothalamic nociceptor afferents.

ANTERIOR PARIETAL CORTEX

In primates, much of the parietal lobe has somatosensory functions. Traditionally, this expanse of cortex is divided into three major regions, each containing several subdivisions. Until recently, the most rostral region, anterior parietal cortex, was considered as a single functional division, "primary" somatosensory cortex, but there is now clear evidence that each of the four classical architectonic fields in anterior parietal cortex is functionally distinct. Presently, there is fairly good agreement on the organization and subdivisions of anterior parietal cortex in monkeys, and there is considerable information for prosimians. Less is known about the divisions of posterior parietal cortex. The posterior parietal region is thought to have higher-order somatosensory functions, and parts mediate visual functions as well (see Yin and Medjbeur, this volume). Posterior parietal cortex has been divided in several ways, but it is common to refer to the architectonic fields 5 and 7 of Brodmann [1909] and subdivisions of these fields. The third major region of parietal cortex is located in the banks of the lateral fissure. Somatosensory cortex in the lateral fissure, because of its relative inaccessibility, has been studied the least, and this region is poorly understood. There is a systematic representation of the body surface, the second somatosensory area or S-II, which is part of the basic mammalian plan of cortical organization, as well as several adjoining cortical fields that are responsive to somatic stimuli and have connections with other somatosensory structures. Some of these fields have auditory, as well as somatosensory, inputs. We refer to cortex in and near S-II in the lateral fissure as the S-II region.

Background

Early attempts to divide anterior parietal cortex into functionally significant regions form the background for our current understanding. Concepts of how anterior parietal cortex in primates is organized have been strongly influenced by the architectonic studies of Brodmann [1909], Vogt and Vogt [1919], and von Economo [1929]. Brodmann's descriptions have had the most impact in that his numerical terminology is widely used for both subdivisions of somatosensory cortex and for other regions of cortex.

In anterior parietal cortex of macaque monkeys, apes, and humans, Brodmann distinguished a region of densely packed granule cells in cortical layer IV, a typical feature of sensory cortex, as area 3 (Fig. 9). Areas 1 and 2 formed architectonic strips caudal to area 3. In addition, Brodmann described a "transitional" field with both sensory (granule cells) and motor characteristics (pyramidal cells) in anterior area 3. Vogt and Vogt [1919] stressed the distinctiveness of this anterior portion of area 3 and subdivided area 3 into two fields, area 3a and 3b (Fig. 9). Von Economo [1929] also recognized four striplike architectonic fields in the anterior parietal cortex of humans, but used different terminology. Von Economo's most anterior parietal field, area PA, is associated with sensory (well-developed layer IV) and motor (large pyramidal cells) characteristics and is equivalent to area 3a. The adjacent field area PB, or sensory "koniocortex," was named for the powderlike appearance of the small granule cells that were densely packed in layer IV. Area PB corresponds to area 3b. Area PC, with a less distinct laminar structure, is equivalent to area 1 and, more caudally, area PD, with more distinct lamination, corresponds to area 2.

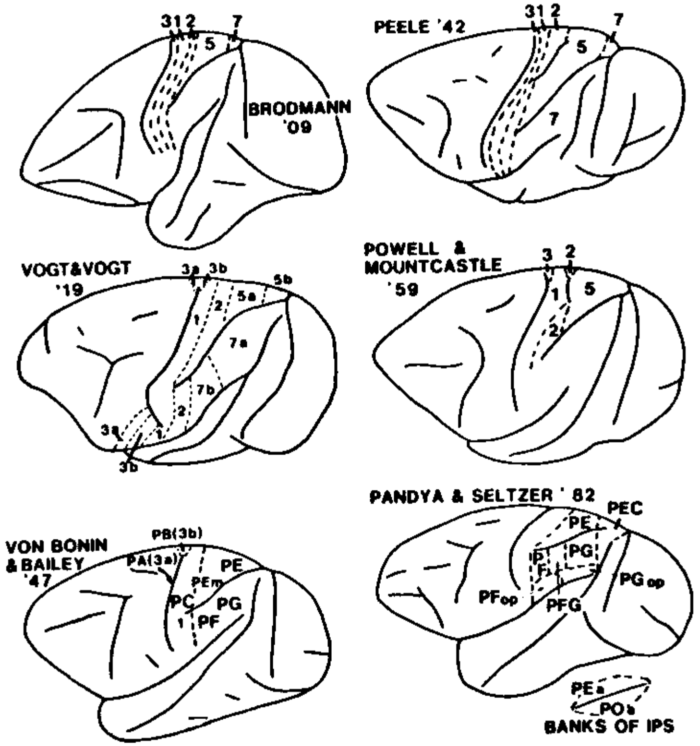


Fig. 9. Some proposed architectonic subdivisions of parietal cortex in Old World monkeys. See text for details.

Subsequently, not all investigators distinguished all four fields of anterior parietal cortex in higher primates. For example, von Bonin and Bailey [1947] argued that there was no justification for distinguishing areas 1 and 2 and illustrated only an area PC as the equivalent to area 1 or area 1 plus area 2 (Fig. 9). However, in general, there was remarkable agreement that four striplike fields subdivide anterior parietal cortex, and there were only minor disagreements about the locations of these fields, perhaps related in part to individual differences in the cases studied.

In regard to subdivisions of anterior parietal cortex in New World monkeys and prosimian primates, opinions have been more varied. Brodmann [1909] described only one anterior parietal field, 1 + 3, in marmosets (Fig. 10), implying that these monkeys had a single field that was differentiated into three fields in higher primates. Peden and von Bonin [1947] later recognized a narrow PA (3a), a wider PB (3b), and an extensive PC (1) in marmosets (Fig. 10). Von Bonin [1938] had denoted

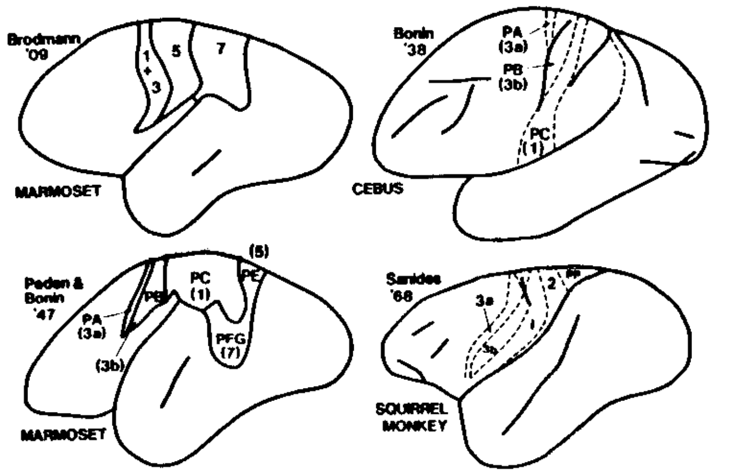


Fig. 10. Some proposed architectonic subdivisons of parietal cortex in New World monkeys. See text for details.

similar subdivisions in New World cebus monkeys, with the important difference that area PC (1) was restricted to an anterior strip that closely approximates recent architectonic and electrophysiological determinations of the location of area 1 in cebus monkeys [Felleman et al, 1983]. More recently, Rosahal [1967] divided anterior parietal cortex of squirrel monkeys into areas 3a, 1, and 2 while omitting area 3b. About the same time, Sanides [1968] recognized all four fields of anterior parietal cortex in squirrel monkeys, as have most subsequent investigators. By the 1970s, the consensus was that Old World and New World monkeys have the same four architectonic subdivisions of anterior parietal cortex. However, the significance of these four fields was not known.

There has been less final agreement regarding the subdivisions of anterior parietal cortex in prosimians (Fig. 11). Brodmann [1909] recognized only an area 1. Other investigators concluded that a single field was equivalent to three fields (1 – 3) in monkeys, while Sanides and Krishnamurti [1967] postulated separate 3a and 3b fields, and a combined 1 + 2 field. Current evidence supports the view that areas 3a and 3b are present, but an area 1, an area 2, or a combined field has not been identified with certainty (see below).

Architectonic arguments for the segregation of function in separate fields of anterior parietal cortex were greatly weakened by the conclusion of Marshall et al [1937] that a single representation of the body surface, the "primary somatosensory area" (S-I) occupied all of areas 3 (3a + 3b), 1, and 2 in macaque monkeys. S-I was described as a systematic topological (somatotopic), though distorted, representation of the body surface (Fig. 12), after the earlier homunculus described for anterior parietal cortex of humans [Penfield and Boldrey, 1937]. According to this formulation, different parts of the body would be represented in different architectonic fields, a very puzzling circumstance. The significance of the architectonic fields was brought into further question by the important electrophysiological study of Powell and Mountcastle [1959b]. These investigators reported that neurons in area 3 tended to be activated via cutaneous receptors and neurons in area 2 were activated via receptors in subcutaneous (deep) tissues, and that there was a gradient of change in activation from predominantly cutaneous to predominantly deep receptors across the three fields 3, 1, and 2, with no sharp changes from field to field. Thus, according to the single homuncular S-I concept, different parts of the body would not be subserved by all classes of receptor types. An alternative, suggested by Powell and Mountcastle [1959a] and subsequently by Werner and Whitsel [1967] and Whitsel and co-workers [eg, Whitsel et al, 1972], is that the representation of given body parts stretched across all three (or four) architectonic fields. This theory of "rostrocaudal bands" [see Kaas et al, 1981] allowed the architectonic fields to differ in neural properties without suggesting that given body parts necessarily differed in the types of cortical neurons devoted to them. Later, recording experiments by Paul et al [1972] led to extensive microelectrode "mapping" studies in a range of primate species that produced results that supported a "multiple representation" hypothesis [see Kaas et al, 1979; 1981], that each of the four architectonic fields of anterior parietal cortex contains a separate and complete representation of the body.

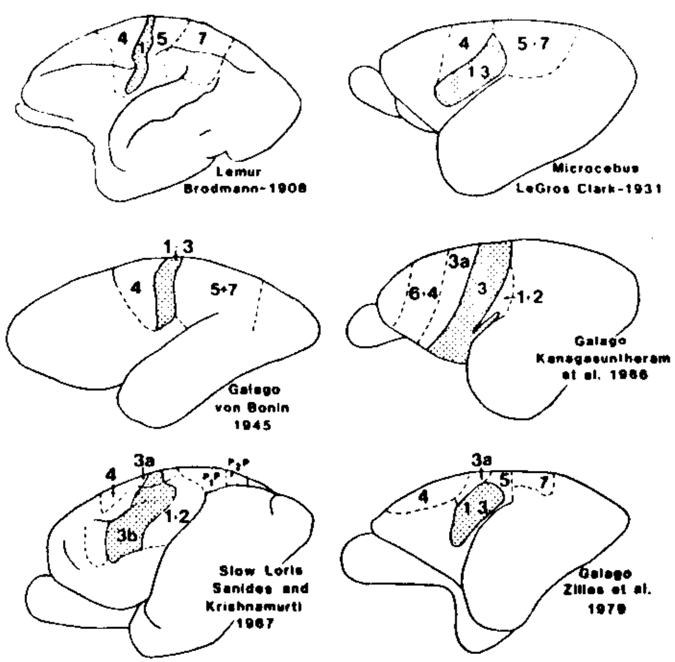


Fig. 11. Some proposed architectonic subdivisions of parietal cortex in prosimians. Zilles et al [1979] used other terminology, but gave equivalents in Brodmann's numbers, which are used here. See text for details.

Multiple Representations in Monkeys

Detailed microelectrode mapping experiments in monkeys produced data that challenged the whole concept of a single "S-I" representation in anterior parietal cortex. Instead, each architectonic field appeared to have its own representation. Results are summarized for owl monkeys in Figure 13. Owl monkeys were chosen for the initial investigations because this New World monkey lacks a central fissure; thus anterior parietal cortex is exposed on the brain surface, and it is easily accessible for electrode penetrations. The basic procedure was to record from hundreds of closely spaced cortical sites in or near layer IV in each monkey and note the receptive field locations and the type of stimuli that were effective in driving neurons at each site. Areas 3b and 1 were responsive to cutaneous stimuli throughout, and each of these fields contained a complete and separate map of the body surface. The two representations were in parallel and, while not identical, were approximately mirror reversals of each other (Fig. 13). Thus, both proceeded from foot to face in a mediolateral sequence across cortex, and the representation of digits of the hand and foot pointed in opposite directions. The mapping data for areas 3a and 2 were less complete, because in anesthetized owl monkeys these fields were largely driven by deep receptors in muscles and probably joints, and deep receptive fields were difficult to locate accu-

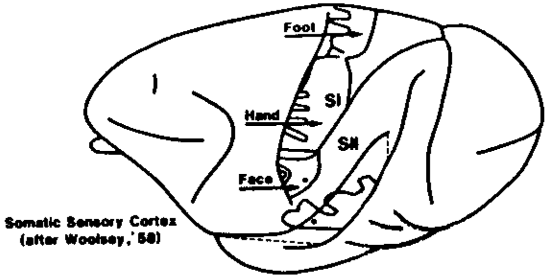


Fig. 12. The proposed organization of anterior parietal cortex as redrawn from Woolsey [1958]. A single representation (S-I) was thought to occupy all of anterior parietal cortex (areas 3, 1, and 2), and the somatotopic organization of this representation was summarized by a "homunculus." The second somatosensory area (S-II) is largely along the upper bank of the lateral sulcus, and the extent of the upper bank is indicated by a dashed line.

rately. However, the crudely determined organizations of areas 3a and 2 clearly paralleled those in areas 1 and 2 (Fig. 13). Basically, similar results were subsequently obtained for squirrel monkeys [Sur et al, 1982], cebus monkeys [Felleman et al, 1983], and macaque monkeys [Nelson et al, 1980; Pons et al, 1985a,b]. Thus, it became clear that the four architectonic fields in monkeys and, in all probability, higher primates in general, correspond to four functionally distinct fields, each representing the body. However, a complication of this generalization is that some body parts, fingers, for example, are represented twice in area 2 of macaque monkeys [Pons et al, 1985b]. This suggests that area 2 in some primates at least has a more complex organization than areas 3b and 1, or that area 2 has been inconsistently defined, and sectors of two functionally distinct fields have been included in area 2 of macaque monkeys.

Because the locations of cutaneous receptive fields for neurons in areas 3b and 1 can be determined rapidly and accurately, the most is known about the somatotopic organization of these representations. Some features of somatotopic organization in areas 3b and 1 are found in all monkey species investigated (cynomolgus macaque, rhesus macaque, cebus, owl, squirrel): 1) The area 3b and area 1 representations are roughly mirror reversals of each other at the common border; 2) the glabrous digits of the hand (Fig. 14) and, to a large extent, the foot, point rostrally in area 3b, and caudally in area 1; 3) the general medial-to-lateral progression across cortex is from tail, rump, posterior leg, foot, anterior leg, trunk onto neck and caudal head, arm, hand, face, and oral cavity; 4) the representations are somatotopic at local levels, but overall they are not. Discontinuities disrupt the maps so that adjoining skin surfaces are often represented at some distance from each other. For example, the posterior leg is separated from the anterior leg by the representation of the foot, the back of the head is separated from the face by the representation of the forearm and hand, and the pads of the hand are split into lateral and medial cortex by the representation of the digits.

Often such splits are highly variable within and across species. For example, the back of the hand and digits are discontinuously represented in scattered islands of cortex within the hand representation in a highly variable manner. Because of these discontinuities, the organization of areas 3b and 1 cannot be accurately portrayed by distorted surface views of the body (the "homunculus"), although this form of summarizing data does capture many major features of the somatotopic pattern. Another reason why the homunculus is inaccurate is that the orientation of the body parts in the representation often does not reflect the somatotopic pattern. For example, the back is represented rostrally and the belly caudally in area 3b of some monkeys (see below), and this is the opposite orientation from that predicted by the "homunculus" for S-I (see Fig. 12). Because representations are somatotopic for small regions, but not for all adjoining regions, they have been referred to as somatotopic composites [eg, Sur et al, 1980b].

There are also species differences in the features of organization in areas 3b and 1. An unexpected and puzzling difference is in the orientation of the representation of the trunk. In macaque monkeys (Fig. 16) and owl monkeys (Fig. 13), the back is represented rostrally in area 3b and caudally in area 1, while the belly is represented along the common border of the two fields. The opposite organization holds for squirrel and cebus monkeys. Apparently both types of cortical organization function equally well. Possibly such seemingly neutral traits could be used to help determine taxonomic relationships. Other species differences have to do with the relative proportions of each field that is devoted to given body parts and the resulting displacements of parts within maps. For example, the enlargement of the representations of the glabrous digits is so great in macaque monkeys that at some levels they occupy the complete width of areas 3b and 1 and thereby displace the representations of hand pads laterally and medially (Fig. 15) to a much greater extent than in squirrel or owl monkeys (Figs. 13, 14). In addition to variations in organization across species, variation occurs within species as well, especially in the amount of cortex devoted to given body parts [Nelson et al, 1980].

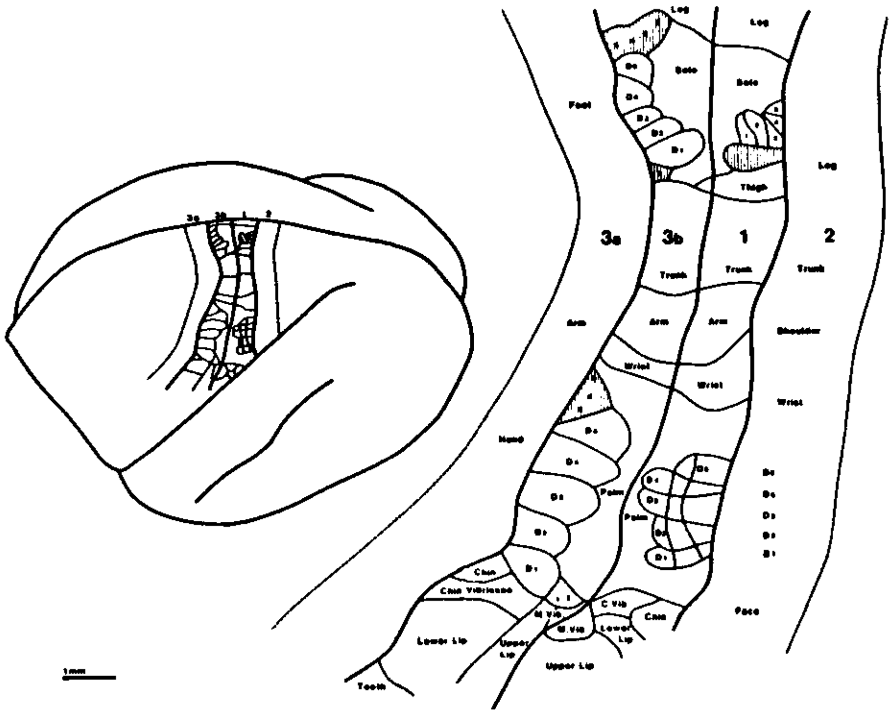


Fig. 13. The somatotopic organization of anterior parietal cortex in owl monkeys. Details are given for the cutaneous representations in areas 3b and 1. Areas 3a and 2 were responsive to the stimulation of deep receptors. Representations of the glabrous digits of the hand and foot are numbered. Shaded areas indicate the representation of the dorsal hairy surfaces of the hand and foot. Chin vibrissae, C.Vib.; mandibular vibrissae, M.Vib. Based on Merzenich et al [1978].

Cortical Organization in Prosimians

The organization of anterior parietal cortex has been anatomically and electrophysiologically studied in a number of prosimian primates, including slow loris [Krishnamurti et al, 1976; Carlson and Fitzpatrick, 1982], potto [Fitzpatrick et al, 1982], and lesser or greater galagos [Sur et al, 1980b; Carlson and Welt, 1980, 1981]. There appears to

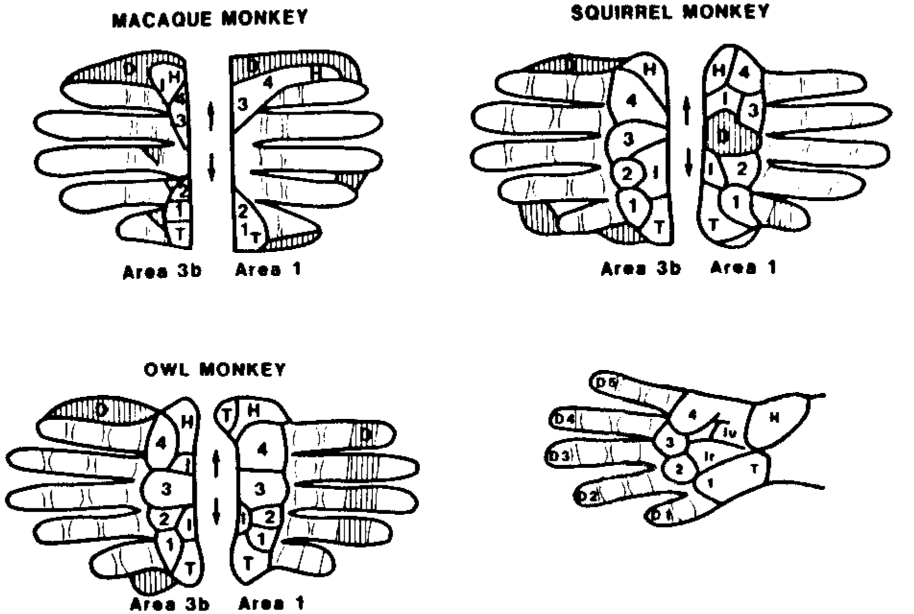


Fig. 14. A schematic to show how the hand is "split" and distorted in the representations in areas 3b and 1 of squirrel, owl, and macaque monkeys. Note that areas 3b and 1 differ somewhat in each monkey, and that a more extreme split of the palm from the digits occurs in macaque monkeys, allowing more cortex to be devoted to the digits. The representations of the dorsal hairy surfaces (D) of the hand are shaded. Digital pads are numbered. T, thenar pad; H, hypothenar pad; Ir, radial insular pad; Iu, ulnar insular pad; I, insular pad. Based on Merzenich et al [1978], Sur et al [1982], Nelson et al [1980], and Pons et al [1985a,b].

be at least three subdivisions of this cortex (Fig. 17). A large zone of koniocortex is coextensive with a single representation of the body surface. This representation appears to be the homologue of the area 3b representation in monkeys. In basic organization, the cutaneous representation resembles both area 3b of monkey and S-I of nonprimates. Other similarities in this "S-I" of prosimians, S-I of nonprimates, and area 3b of monkeys [see Kaas, 1983, for review] include histological structure (the field was identified as 3b by Sanides and Krishnamurti [1967]; see Fig. 11), neuronal response properties (both SA and RA cutaneous responses are present in cortical neurons in galagos, see Sur et al [1980b]), and dense connections with the ventroposterior nucleus [Kaas, 1982]. On the rostral border of S-I, a narrow zone of cortex responds to deep receptor inputs, possibly from muscle receptors, and this cortex has architectonic features that resemble area 3a [Sanides and Krishnamurti, 1967]. Because of these similarities in histological structure, responsiveness, and location relative to motor cortex and S-I, this rostral field is the probable homologue of area 3a in monkeys. Thus, at least two of the four fields of anterior parietal cortex in monkeys and higher primates appear to be present in prosimians. However, the identity of cortex caudal to S-I in prosimians remains uncertain.

A strip of cortex immediately caudal to S-I in prosimians (Fig. 17) is responsive to more intense stimulation of the body, which suggests either inputs from deep receptors or pathways from cutaneous receptors exist that are difficult to activate. Thus, the field does not obviously resemble area 1 of monkeys, which is generally highly responsive to cutaneous stimuli. However, the absence of low-threshold cutaneous driving for neurons does not, by itself, indicate that this field is not area 1. Tamarins and marmosets of the family Callithricidae are often considered to be the most primitive of New World monkeys. In keeping with this as-

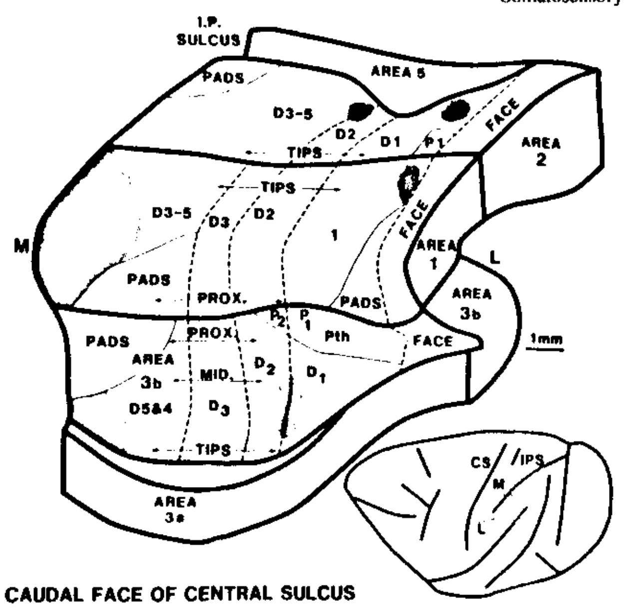


Fig. 15. The organization of hand representations in areas 3b, 1, and 2 of macaque monkeys. The block of cortex is a face-on view of the portion of the posterior bank of of the central sulcus that is devoted to the hand. The block of tissue comes from the location shown on the lateral view of the brain on the lower right. M, medial; L, lateral. Cortex activated from the dorsal hairy surface of the hand is shaded. IP, intraparietal sulcus, CS, central sulcus, Pth, thenar pad. Based on Pons et al [1987].

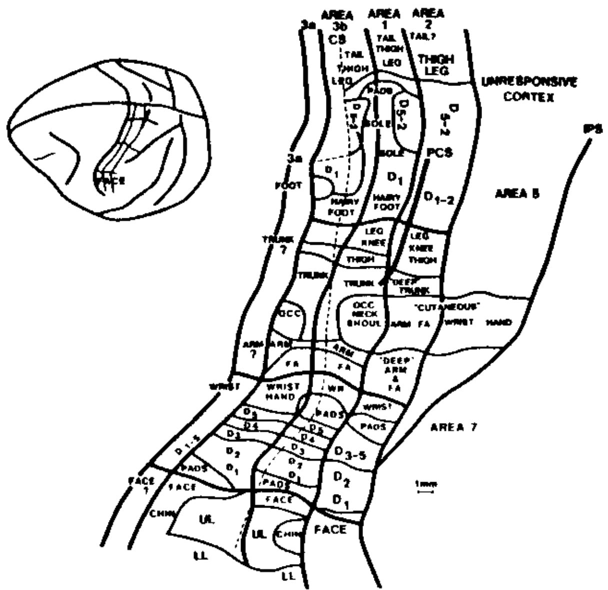


Fig. 16. The somatotopic organization of anterior parietal cortex in macaque monkeys. CS, central sulcus; IPS, intraparietal sulcus; FA, forearm; LL, lower lip; UL, upper lip.

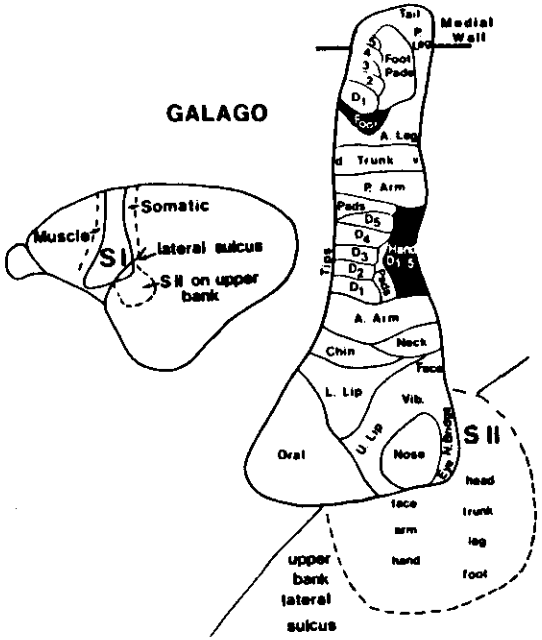


Fig. 17. The organization of anterior parietal cortex in galagos. Somatotopic organization of the primary field, S-I, is similar to that of area 3b of monkeys. Cortex rostral to S-I is activated by deep receptors and appears to be the homologue of area 3a. A strip of cortex caudal to S-I is somatosensory, but it does not appear to be area 1 (see text). A second somatosensory area is largely on the upper bank of the lateral sulcus (dashed lines in upper drawing). A region caudal to S-II responds to cutaneous stimuli and neurons with large bilateral receptive fields. Based on Sur et al [1980b], Carlson and Welt [1980], and Burton and Carlson [1986]. Conventions as in Figure 13.

sumption, these monkeys have only one highly responsive cutaneous representation in anterior parietal cortex [Carlson et al, 1986]. Thus, these monkeys resemble prosimians in this regard. Cortex caudal to S-I (3b) in marmosets and tamarins generally failed to respond to cutaneous stimuli under typical recording conditions, but sometimes responses to cutaneous stimuli were obtained, and then a somatotopic organization was apparent that resembles area 1 of monkeys. Thus, it seems likely that an area 1 exists in tamarins and marmosets, but it is not as well developed as in other monkeys. Furthermore, this area 1 could represent an intermediate level of development between the cutaneously unresponsive cortex caudal to S-I in prosimians and the highly responsive area 1 in monkeys. An important additional difference, however, is that the strip of cortex caudal to S-I in prosimians does not share the same connections as area 1 in monkeys. Thalamic input to the caudal strip (Cusick and Kaas, unpublished) is from part of the thalamus immediately dorsal to the ventroposterior nucleus (VP), as for area 2 of monkeys, rather than from VP, as for area 1 of monkeys (Fig. 8). Thus, for the present, the identity of cortex caudal to S-I in prosimians remains uncertain.

Features of the Cutaneous Maps: Magnification Factors, Modular Organization, and Dynamic Somatotopy

The representations of the body surface in areas 3b and 1 of monkeys have three features that are probably basic to other subdivisions of cortex as well. These features include the disproportionately large representation of some parts of the body, an uneven representation of receptor types, and ability of somatotopic organization to change.

Investigations of the organization of somatosensory cortex have consistently demonstrated that some body parts are represented in proportionately more cortex than others, and such distortions are reflected in the somatotopic composite summary maps (Figs. 13, 15, 17) and in earlier "homunculus" summaries (Fig. 12). As an example, a unit of skin surface on the glabrous hand is represented in nearly 100 times more cortical tissue than an equal unit of skin surface on the trunk in both areas 3b and 1 of owl monkeys [Sur et al, 1980a]. The magnification factor is a measure of the disproportionate representation of body parts, and magnification factors are shown for given body parts in areas 3b and 1 of squirrel monkeys in Figure 18 [Sur et al, 1982]. Very similar results have been obtained from owl monkeys [Sur et al, 1980a]. The magnification factors for both monkeys indicate that the glabrous hand and foot, and especially the lips, are greatly enlarged in the maps, and the distortions that occur in area 1 are almost identical to those that occur in area 3b. This suggests that the functions of areas 1 and 3b are closely related.

Another observation that has been made from the first recording studies is that receptive fields for neurons in the "magnified" parts of representations have smaller receptive fields than neurons in other parts of the representations. When the relationship was quantified in areas 3b and 1 of owl monkeys [Sur et al, 1980a], receptive field size was found to be proportional to inverse magnification over the entire representation. Furthermore, the relation between receptive-field size and inverse magnification appeared to be linear. As a result, the overlap of receptive fields for any two recording sites decreased with distance between the recording sites at the same rate for any locations in the representations so that receptive fields for recording sites 600 μm or more apart had little or no overlap. This observation indicates that, within a single area such as area 3b, a region of cortex 1.5 mm or so in diameter processes the information from a given skin location, regardless of where in the map that location is represented.

Another important observation is that area 3b is subdivided into sharply defined, and functionally distinct, processing modules [Sur et al, 1984]. Neurons in layer IV of cortex with direct input from the ventroposterior nucleus (VP) of the thalamus, like VP neurons, appear to be of two types, those that are slowly adapting (SA) to a maintained skin indentation and those that are rapidly adapting (RA). When the distributions of RA and SA layer IV neurons were determined by recording from neurons at hundreds of recording sites in a closely spaced grid in area 3b of owl and macaque monkeys, the RA and SA neurons were found to be distributed in alternating bands (Fig. 19) similar to the well-known "ocular dominance columns" of primary visual cortex in monkeys. For neurons above and below layer IV, which are at subsequent stages of processing, the sustained component of the response was lost, probably as a result of interneuron inhibitory mechanisms. Nevertheless, the results clearly indicated that thalamic inputs to area 3b are modularly segregated according to response type. We expect that other subdivisions of somatosensory cortex will be found to have similar types of modular organization.

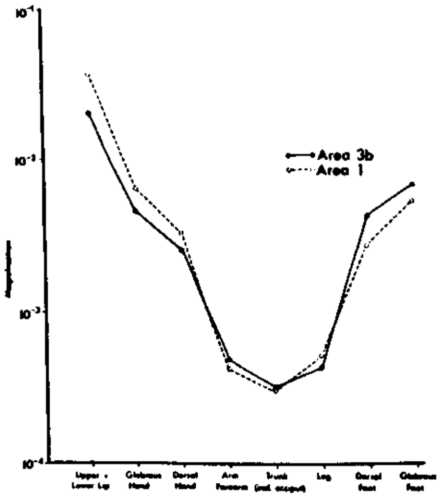


Fig. 18. A graph of the cortical magnification factors for different body regions in areas 3b and 1 of squirrel monkeys. Magnification is defined as the area of cortical surface for a given body part divided by the area of skin surface for the part. From Sur et al [1982].

While area 3b of somatosensory cortex has a very precise organization with very predictable somatotopy, SA and RA bands, receptive field sizes, and receptive field overlap with cortical distance, this organization is not completely "hardwired" or predetermined. Instead, this organization depends on dynamic adjustments to activity

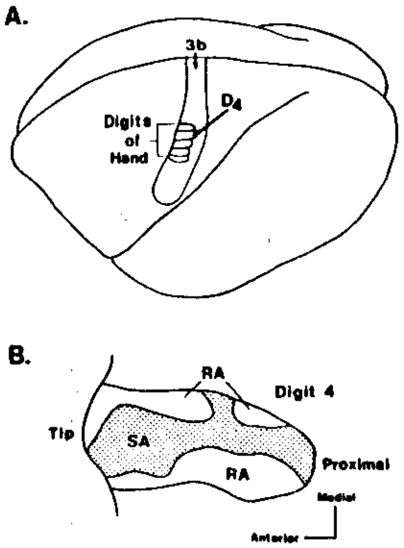


Fig. 19. A surface view of the shapes of slowly adapting (SA) and rapidly adapting (RA) bands of neurons in layer IV of area 3b of an owl monkey. Such a separation of the two types of inputs probably exists throughout the field, but the precise pattern, which is variable from animal to animal, has only been determined for the hand representation. The bands are narrow in width and appear to relate randomly to the borders of finger representations and other features of the somatotopic map. A. The location of the representation of the glabrous digits in area 3b. B) The arrangement of the RA and SA bands in the representation of a digit from a typical case. See text for details. Based on Sur et al [1984].

patterns [see Kaas et al, 1983, for review]. For example, when the normal source of activation for part of the hand representation in monkeys is removed by inactivating a nerve, this cortex ultimately becomes activated by other parts of the hand with intact nerves [Merzenich et al, 1983]. Initially, the altered cortical neurons are poorly driven and have large receptive fields. Later, normal responsiveness is restored, the sizes of receptive fields are reduced, and somatotopic organization prevails at the local level. Normal relationships between magnification and receptive field size and overlap also are reestablished. These changes are not necessarily permanent. If the functions of inactivated nerves are restored by regeneration, the previous normal map of the hand in cortex can be restored [Wall et al, 1983]. Thus, sources of activation for cortical neurons can change, and then the original sources can be restored. What activates cortical neurons at any given moment is dynamically determined in ways that are not clearly understood, but the selection process appears to be activity dependent.

The necessity for cortical neurons to select from the array of possible activating inputs is apparent when the distributions of single afferent axons in area 3b are considered [Pons et al, 1982; Conley and Jones, 1984]. The terminal arbor of a single thalamic axon includes synapses on neurons over a 0.5–1.0 mm or so of cortex (Fig. 20). Yet, within this amount of cortex, there is clear somatotopic organization. Thus, all inputs to cortical neurons are not equally effective in activating those neurons, and there must be some sort of cortical "filter" that reduces receptive field size and produces local somatotopic organization. This filtering is possibly achieved with inhibitory interactions in cortex. Reducing or removing the activity in some afferent neurons alters the filter, allowing previously ineffective inputs to become apparent. Further changes in the filtering mechanism eventually restores the normal relationship between receptive field size and cortical magnification.

Connections, Neuron Types, and Functions

The four divisions of anterior parietal cortex in monkeys have clearly different functional roles, which are reflected in patterns of connections, the response properties of neurons within these fields, and the behavioral effects of lesions or chemical inactivations. For more recent reviews of cortical connections, see Pons and Kaas [1986], Shanks et al [1985], Jones et al [1978], and Cusick et al [1985].

Area 3b. S-I proper or area 3b receives the major output of the ventroposterior nucleus (VP). At least 70% of the neurons in VP project to area 3b [Lin et al, 1979], and these projections include relays of both RAI and SA receptor types [Dykes et al, 1981; Jones and Friedman, 1982]. There is also the possibility of a relay of a small number of wide-dynamic-range neurons [Kenshalo and Isensee, 1983]. The microelectrode mapping studies indicate that, except for narrow "high-threshold" zones separating the representation of major body parts such as the hand from the face, neurons in all locations in 3b respond to low-threshold cutaneous stimuli. Although earlier reports varied in the proportion of neurons activated by cutaneous or deep receptors in area 3b, recent studies agree that 90–99% of studied neurons are activated from skin afferents [eg, Tanji and Wise, 1981; Dreyer et al, 1975; McKenna et al, 1982]. Given that there is some potential for error in assigning neurons to architectonic fields, or in defining response types, it is reasonable to suppose that close to 100% of the driving of area 3b is by RA-I and SA neurons in VP.

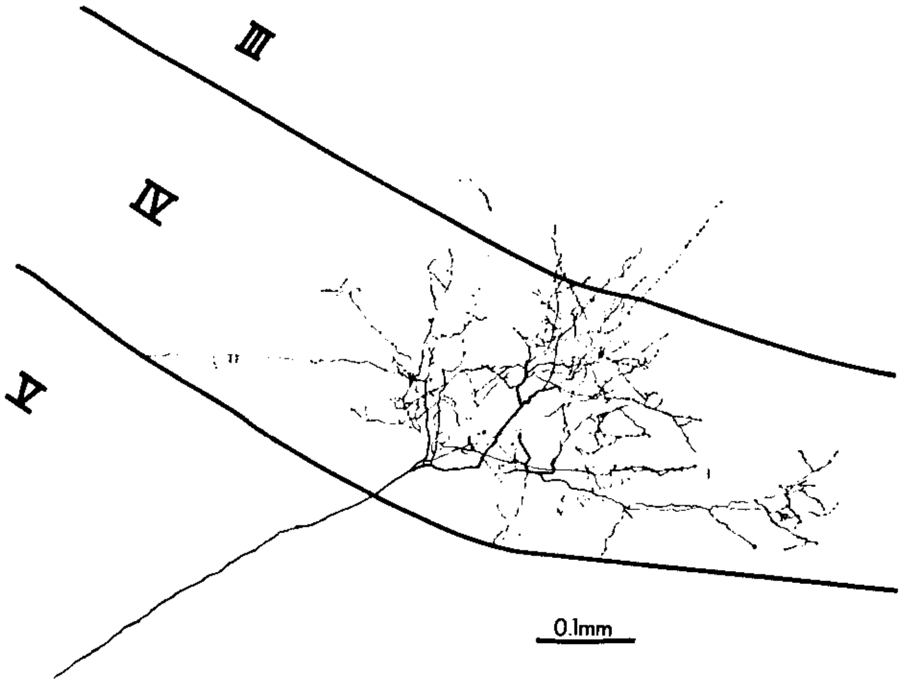


Fig. 20. A drawing of a typical single thalamocortical axon arborizing in layers IV and IIIb of area 3b of an owl monkey. Enlargements on fine axon branches are synaptic terminations. Based on Pons et al [1982].

Other inputs to area 3b are unlikely to provide any significant driving of neurons. Most or all of the inputs from S-II [see Friedman, 1983], area 1, and area 2 (Fig. 21) are of the feedback type, largely to layers I and II. Such "feedback" cortical projections have been discussed most frequently for connections of the visual system [see Cusick and Kaas, 1985], and the general consensus is that these inputs modulate the discharge pattern of neurons, but do not provide the source of driving. Cortical outputs from area 3b are of the driving or feedforward type. A major projection from layer III pyramidal cells in area 3b is to layer IV and inner layer III of area 1 [eg, Pons and Kaas, 1986]. Thus, area 1 can be considered the next station in a cortical processing hierarchy. Other feedforward projections are to areas 2 and 3a. Thus, area 3b provides cutaneous receptor information to these two fields which receive more direct muscle receptor information from the thalamus. Other feedforward projections are to the middle cortical layers of S-II.

Area 3b does have a significant callosal projection to area 3b, S-II, area 1, and area 2 of the opposite hemisphere [see Killackey et al, 1983; Cusick and Kaas, 1985, for review]. However, callosal inputs and outputs largely avoid the representations of the glabrous hand and foot, and callosal inputs do not result in bilateral receptive fields, except perhaps for neurons with receptive fields along the body midline.

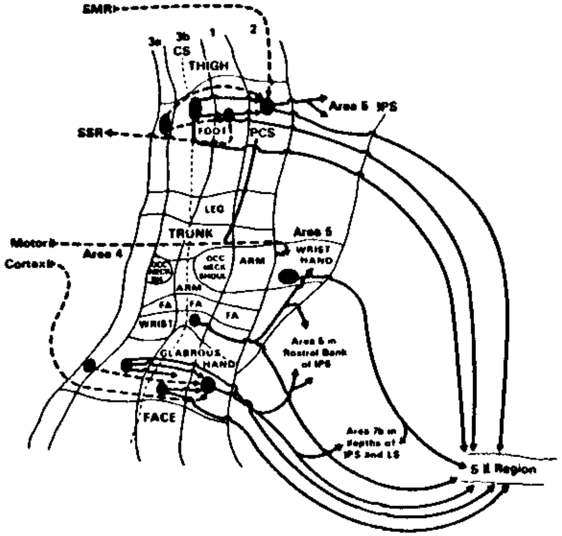


Fig. 21. Schematic of major interconnections of fields of anterior parietal cortex in monkeys. CS; central sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; PCS, postcentral sulcus; FA, forearm; SMR, supplementary motor region; SSR, supplementary sensory region. From Pons and Kaas [1986].

Inactivating area 3b by chemicals or lesions produces clear changes in somatosensory abilities in monkeys. As one might expect from removing the major cortical receiving station for SA and RA-I receptor information, lesions of area 3b severely impair monkeys on all but the crudest of tactile discriminations, including those involving texture and shape [Randolph and Semmes, 1970]. Chemical inactivation of area 3b in behaving monkeys results in small objects being unrecognized by touch and being ignored [Hikosaka et al, 1985].

Area 1. At least 50% of the neurons in VP project to area 1 [Lin et al, 1979], and perhaps 20% or more of the VP neurons project to both areas 3b and 1 [Cusick et al, 1985]. This input is not as dense as that from VP to area 3b, and it depends on smaller-diameter axons [Jones et al, 1979]. Judging from the sparseness of SA neurons in area 1 (see below), it seems probable that the thalamic input is largely from the RA-I rather than the SA neurons in VP. Dense terminations in the middle layers of area 1 also come from area 3b, and together, 3b and VP neurons probably provide nearly all of the driving inputs. The output neurons in layer III of area 3b are likely to provide largely or only RA types of driving [Sur et al, 1984]. A sparse input from VPS exists [Pons and Kaas, 1986], and this may provide some deep receptor input.

Feedback inputs to area 1 are from areas 2, 5, and S-II, and area 1 provides feedback to area 3b and to VP from layer VI neurons. A feedforward projection is to S-II or cortex in the region of S-II [Cusick et al, 1985; Pons and Kaas, 1986]. Callosal connections are more dense than those for area 3b, but again they are sparse in the representation of the hand and foot. The physiological functions of these callosal connections are unknown. The connections could contribute to bilateral excitatory receptive fields on the body midline, but the callosal connections are too widespread in area 1 to be limited to this role [Killackey et al, 1983].

As for area 3b, microelectrode mapping studies (see above) indicate that area 1 is activated by cutaneous stimuli throughout. Most of the neurons respond as if they were activated by RA-I cutaneous receptors, although there are both SA and pacinian (RA-II) types of responses as well. The proportion of neurons with pacinianlike responses in area 1 is not great, perhaps 5% [Hyvärinen and Poranen, 1978b]. The source of this pacinianlike activity in area 1 is unknown, since there is no clear input from VPI. Pacinianlike neurons tend to be grouped in area 1 [Merzenich et al, 1978], suggesting some type of modular organization, but the nature of this organization has not yet been revealed. Likewise, little is known about the areal distribution of SA-response-type neurons in area 1.

There is considerable evidence that most neurons in area 1 have more complex receptive fields and therefore, by implication, are "higher order" than neurons in area 3b. Receptive fields tend to be larger [Sur et al, 1985], and this difference undoubtedly reflects more convergence of inputs [see Iwamura et al, 1983; Merzenich et al, 1978 for supporting evidence]. Also, many area 1 neurons have complex receptive fields with antagonistic centers and surrounds [Sur, 1980], and some neurons in area 1 are selective for direction of stimulus movement on the skin [Hyvärinen and Poranen, 1978a]. A majority of area 1, but not area 3b, neurons appears to be influenced by not only the stimulus conditions, but by what motor behavior will follow the stimulus event [Nelson, 1984].

The effects of lesions in area 1 [Randolph and Semmes, 1970; Carlson, 1981] are consistent with the view that area 1 largely mediates information received from area 3b, but area 3b also projects to other cortical areas. Thus, area 1 lesions impair monkeys on discriminations of texture such as judging differences in surface texture or number of lines indented per centimeter of surface, while not providing impairments in judgments of shape. Such impairments are in keeping with the physiological evidence that area 1 is specialized for dealing with RA-I receptor information, since these receptors would be critical in texture discriminations (Fig. 1).

Area 2. A major thalamic input to area 2 is from VPS (Fig. 8), and this pathway presumably provides information from muscle receptors [Burchfiel and Duffy, 1972; Schwarz et al, 1973] and, to a lesser extent, from joint receptors. A small input from VP most probably provides some information from cutaneous receptors, either SA or RA or both. The significance of a dense input from the anterior pulvinar [Pons and Kaas, 1985] is unknown. Major feedforward cortical inputs (Fig. 21) are from areas 3a, 3b, and 1. Thus, area 2 receives cortically processed information from areas dominated by deep receptor (3a) and cutaneous receptor (3b and 1) information. Outputs are to S-II and/or the S-II region, to adjoining parts of areas 5 and 7, and to motor cortex [Cusick et al, 1985; Pons and Kaas, 1986]. Callosal connections are much more dense than for areas 3b and 1 [Killackey et al, 1983], and they include many projection neurons in the representations of the hand. However, neurons with bilateral receptive fields on distal body parts have not been found in area 2.

Mapping experiments in anesthetized monkeys have revealed that area 2 is complexly organized (see above) and uneven in responsiveness to cutaneous stimuli. Furthermore, there may be species differences so that there is little responsiveness to cutaneous stimuli in anesthetized owl monkeys [Merzenich et al, 1978], while several large zones are highly responsive to cutaneous stimuli in anesthetized macaque monkeys [Pons et al, 1985a,b]. In unanesthetized monkeys, most of the neurons in the hand representation in area 2 become responsive to cutaneous stimuli [eg, McKenna et al, 1982]. Thus, it appears that the information from skin receptors in area 2 largely depends on cortical pathways from areas 3b and 1 that are depressed by anesthesia. The complex response properties of neurons suggest that area 2 is a higher-order field, integrating information from deep receptors from VPS, with more complex information from areas 3a, 3b, and 1. The receptive fields are typically, but not always, large [see Iwamura et al, 1983; Pons et al, 1985b], many neurons are activated by both deep and cutaneous receptors, and many neurons are best activated by complex stimuli of certain shapes or direction of movement [Hyvärinen and Poranen, 1978a; Iwamura and Tanaka, 1978].

Lesions of area 2 in monkeys produce impairment in discriminations of object shape and size [Carlson, 1981; Randolph and Semmes, 1970], and chemical inactivation of parts of area 2 impairs finger coordination [Hikosaka et al, 1985]. These deficits suggest that area 2 functions as a center for integrating finger and limb position information with texture and edge information for accurate judgments of the shapes of objects, and that the output of area 2 to motor cortex is important for guiding skilled manipulations of objects. In these functions, area 2 resembles areas 5 and 7 more closely than areas 3b and 1.

Area 3a. The major thalamic inputs to area 3a are from VPS neurons activated by deep receptors, and perhaps by a more rostral nucleus, VPO, specialized for relaying muscle spindle information (Fig. 8). The anterior pulvinar provides an input of uncertain significance [Cusick et al, 1985].

Something in the range of 40% of the VPS neurons project to both areas 3a and 2 [Cusick et al, 1985], and these two fields project to each other (Fig. 21). Other projections of area 3a are to cortex in the S-II region [Friedman, 1983]. Callosal connections are slightly more dense for area 3a than those for area 3b, but less dense than for area 2 [eg, Killackey et al, 1983]. Hand and foot representations in area 3a have sparse callosal connections.

Almost all neurons in area 3a are activated by limb movements that would activate muscle receptors, and it is well established that muscle spindle afferents provide the major driving influence [see Phillips et al, 1971; Lucier et al, 1975; Maendly et al, 1981; Wise and Tanji, 1981]. Some neurons are also responsive to cutaneous stimuli [Tanji and Wise, 1981; Wise and Tanji, 1981], especially in the part of area 3a related to the digits of the hand. Neurons in area 3a appear to be strongly influenced in responsiveness by the "motor-set" or behavioral intentions of the monkey [Nelson, 1984].

Subcortical Pathways

Areas 3a, 3b, 1, and 2 all project to a number of subcortical structures, presumably in part to provide feedback to neurons relaying sensory information to cortex and in part to influence motor behavior directly. Each field projects back to its major thalamic relay nucleus, so that 3a and 2 project to VPS, and 3b and 1 project to VP. In addition, areas 3a and 2 project to VPS, and 3b and 1 project to VP. In addition, areas 3a and 2 project to the anterior pulvinar [Pons and Kaas, 1985; Cusick et al, 1985]. Presumably, these projections are largely from layer VI neurons [Jones, 1985]. Pyramidal neurons in layer V of all four fields project ipsilaterally but not contralaterally to the putamen [Jones et al, 1977]. Larger layer V neurons in these fields also project to the spinal cord [Coulter et al, 1976], pons [Wiesendanger et al, 1979; Brodal, 1978; Glickstein et al, 1985], and to the dorsal column nuclei [Weisberg and Rustioni, 1977; Cheema et al, 1985]. This last projection system would allow cortical modification of ascending sensory information.

POSTERIOR PARIETAL CORTEX

The posterior parietal region is a somewhat arbitrary subdivision of the brain that includes all of parietal cortex caudal to area 2, but little of the cortex buried in the lateral fissure. Most of posterior parietal cortex has been implicated in somatosensory functions, but lesions in this region do not produce simple sensory deficits. Furthermore, there is clear evidence that posterior parietal cortex is organized somewhat differently in humans than in monkeys, and this brain region undoubtedly accounts for some of the remarkable differences in mental capabilities between monkeys and humans. Major reviews of posterior parietal cortex include those by Mountcastle [1975], Lynch [1980], Hyvärinen [1982], Robinson and Petersen [1984], and Yin and Medjbeur (this volume).

Background

The evidence that posterior parietal cortex is organized differently in humans and monkeys comes from studies of the effects of unilateral damage. In macaque monkeys, unilateral lesions produce a number of impairments including mild neglect of tactile stimuli on the contralateral body surface, a reduction in spontaneous movements of the contralateral limbs, and errors in reaching to a target with the contralateral arm [see Mountcastle 1975 for review]. However, the impairments are basically the same regardless of the hemisphere of the lesion. In humans, similar but more severe impairments can result, but the clinical problems depend very much on the side of lesion. Contralateral neglect of visual and somatosensory stimuli is likely to follow lesions of the right but not the left posterior parietal lobe [see Hyvärinen, 1982]. Other problems associated with parietal lobe lesions in the right or "minor" hemisphere include a serious impairment in the ability to copy drawings and form designs with blocks, an inability to draw and follow maps of well-known regions, and difficulties in visually recognizing objects in unfamiliar views. Lesions of left posterior parietal cortex can cause disorders related to language and mathematical abilities and right-left confusion.

Architectonic Subdivisions

The subdivisions most commonly used for posterior parietal cortex of monkeys (Fig. 9) are areas 5 and 7 of Brodmann [1909] and the subdivisions of these fields (5a, 5b, 7a, 7b) introduced by Vogt and Vogt [1919]. Von Bonin and Bailey [1947] later applied the lettering system of von Economo [1929] to the brains of macaque monkeys and the terms PEm for 5a, PE for 5B, PG for 7a, and PF for 7b. More recently Pandya and Seltzer [1982b] have distinguished several additional fields (Fig. 8). However, stated architectonic distinctions between these fields are not marked, and many investigators use surface features of the brain to delineate their "architectonic" regions. An additional complication is that area 5 forms the caudal border of area 2 in most architectonic maps for New World monkeys (Fig. 10), while area 7 forms the lateral part of the area 2 border in proposals for Old World monkeys. There is no experimental evidence to justify this proposed species difference, and it appears to have little justification. To summarize, various subdivisions of posterior parietal cortex have been proposed. They have some usefulness in indicating the general region of cortex of concern, but the subdivisions, in all probability, do not correspond precisely with subdivisions of functional significance and certainly do not precisely identify homologues across major taxonomic groups.

Brodmann [1909] distinguished the additional fields 39 and 40 in posterior parietal cortex of humans, but considered areas 39 and 40 as merged or undifferentiated from area 7 in monkeys. However, Brodmann [1909] recognized areas 5 and 7 in all primates (Figs. 9-11). Thus, Brodmann [1909] believed that major changes that took place in the organization of posterior parietal cortex took place in humans, and it has been subsequently common to conclude that areas 39 and 40 exist only in humans. The large size of posterior parietal cortex in humans and the progressive enlargement of this region from prosimians to humans, together with the unique hemispheric specialization in humans, argues strongly that major changes in organization have occurred in posterior parietal cortex in primate evolution, but there is little understanding of precisely what types of changes have occurred. Thus, our discussion of this region will largely depend on macaque monkeys where the most experimental evidence is available.

Connections

The connections of subdivisions of posterior parietal cortex have been most investigated in macaque monkeys. Since the functionally significant subdivisions of this cortex have not been established, patterns of connections are incompletely known and understood. In general terms, subdivisions of anterior parietal cortex, especially area 2, project caudally into the rostral portions of posterior parietal cortex (Fig. 22A), providing indirect somatosensory inputs from both deep and cutaneous receptors. These inputs terminate in both 5a and 7b, suggesting that the architectonic distinction between these fields is not particularly meaningful. In New World monkeys, these fields have been defined differently, and area 7 does not border area 2 (Fig. 8), and only area "5" receives anterior parietal projections [eg, Jones et al, 1978]. By using connections rather than cortical architecture to subdivide posterior parietal cortex, Pandya and Seltzer [1982a] have divided posterior parietal cortex into a rostral half, the "proximal somatic parasensory association region" with input from anterior parietal cortex, and a caudal half, the "distal somatic parasensory association region," with input from the proximal association region. However, we now recognize that the distal association region receives some input from anterior parietal cortex [Pons and Kaas, 1986]. While it has been useful to consider two main divisions of posterior parietal cortex, this is a complexly connected region and it certainly contains a number of functionally distinct subdivisions.

The other major sensory input to posterior parietal cortex is visual. There may be several sources of visual input. In New World owl monkeys, for example, three visual areas, the middle temporal visual area, the dorsomedial visual area, and the superior temporal visual area, project to parts of the caudal half of posterior parietal cortex [see Weller et al, 1984]. In Old World macaque monkeys, visual input is relayed (Fig. 22B) most directly from area 17 to the middle temporal visual area (MT), and then to part of posterior parietal cortex, or less directly via another step in the middle superior temporal area (ST of owl monkeys). Other visual input, specifically to cortex named POa of the intraparietal sulcus, is relayed from a broad band of preoccipital cortex [Seltzer and Pandya, 1980; Siegel et al, 1985] that is more extensive than, but includes, "V4." Thus, parts of the caudal half of posterior parietal cortex have more direct visual than somatosensory inputs, and some of the cortex with bimodal influences is dominated by visual rather than somatosensory inputs.

Other major cortical connections of caudal regions in posterior parietal cortex are with cingulate cortex [Mesulam et al, 1977] of the limbic or "emotional" system (Fig. 22D). The region of cingulate cortex that is interconnected with poste-

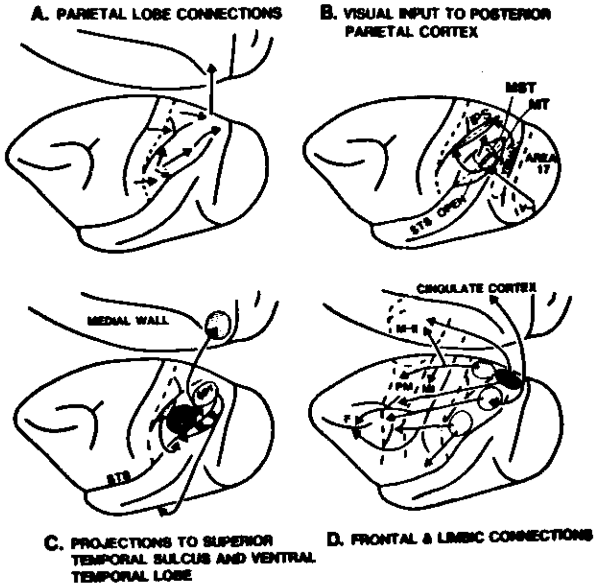


Fig. 22. Major ipsilateral cortical connections of posterior parietal cortex in macaque monkeys. Summaries are based on the indicated reports. A. Somatosensory inputs from anterior parietal cortex are largely to the rostral half of posterior parietal cortex, which relays to caudal posterior parietal cortex. B. Visual inputs from visual association areas including the middle temporal area (MT) and the medial superior temporal area (MST) in the superior temporal sulcus (STS) are largely to cortex in the intraparietal sulcus (IPS). C. Outputs are to possible polymodal cortex on the banks of the superior temporal sulcus. D. Interconnections are with cingulate cortex of the limbic system, and with motor (MI), supplementary motor (M-II), premotor (PM), and frontal cortex (F) fields.

rior parietal cortex is, in turn, interconnected with the amygdala. Mesulam [1981] has suggested that these limbic connections are the anatomical substrates for "motivational" influences on posterior parietal cortex activity. Thus, sensory events in the somatosensory and visual realms gain relevance via posterior parietal connections with the limbic system.

The dominant cortical outputs of posterior parietal cortex relate to subdivisions of motor cortex (Fig. 22A), visual and polysensory cortex in the superior temporal sulcus, and endstations in the ventral temporal lobe of an object vision processing sequence (Fig. 22C). More rostral portions of posterior parietal cortex project to primary motor cortex (MI), the supplementary motor area (MII), which is thought to play an important role in the intentional process [see Roland et al, 1980], and premotor cortex (PM), which has a high proportion of neurons related to voluntary limb movements [see Wise, 1985]. The cortex on the lateral bank of the intraparietal sulcus projects strongly to the frontal eye fields [Siegel et al, 1985]. Other projections are to higher-order somatosensory fields in the S-II region of the lateral fissure. More caudal portions of posterior parietal cortex avoid primary motor cortex in their projections, include premotor and supplementary motor fields, and also extend to frontal cortex [eg, Petrides and Pandya, 1984; Andersen et al, 1985]. Thus, the output of posterior parietal cortex to the frontal lobe involves systems that control and initiate movements, with a likely emphasis on hand and eye movements.

The significance of the outputs from posterior parietal cortex to visual and polysensory areas in the superior temporal sulcus [see Desimone and Gross, 1979] is uncertain. Many neurons in the polysensory cortex respond to somatosensory stimuli, and the posterior parietal connections may provide this source of somatosensory activation. In any case, these polysensory fields are considered among the "highest" of sensory processing stations [Desimone and Gross, 1979]. Likewise, the less-pronounced outputs to the ventral temporal lobe are to regions of cortex influenced by highly processed visual information and are related to complex functions in the "object vision" pathway [see Ungerleider and Mishkin, 1982].

Other connections of posterior parietal cortex are with subcortical structures [see Trojanowski and Jacobson, 1975; DeVito, 1978; DeVito and Simmons, 1976; Graham et al, 1979; Weber and Yin, 1984; Yeterian and Pandya, 1985]. Most or all of the region is interconnected with the pulvinar complex and the lateral posterior nucleus, and inputs from these structures can enhance or suppress neural activity in posterior parietal cortex [see Blum, 1984]. Connections of the anterior pulvinar tend to be more pronounced rostrally in posterior parietal cortex, while those of the medial pulvinar tend to project caudally in posterior parietal cortex [see Pons and Kaas, 1985]. Architectonically, the anterior and medial pulvinar nuclei tend to merge, so it would not be surprising if they have similar functions and connections. However, the medial pulvinar also has major connections with subdivisions of visual cortex, while the anterior pulvinar also projects to somatosensory fields in the S-II region and areas 3a and 2 of anterior parietal cortex. Because of connections with area 5, the lateral posterior nucleus has long been considered part of the somatosensory system. Portions of posterior parietal cortex also project to the central lateral nucleus, which may be involved in eye movements.

As for other regions of cortex, posterior parietal cortex projects to the reticular nucleus of the thalamus, which exhibits an inhibitory influence on the dorsal thalamus, and the caudate, putamen, and claustrum of the basal ganglia. The visual parts of posterior parietal cortex project to the pretectum and the superior colliculus [Graham et al, 1979; Lynch et al, 1985; Siegel et al, 1985], structures visual in function. Other descending projections terminate in the pons in regions that presumably are involved in visuomotor functions and, in part, relay to visual areas of the cerebellar vermis [see Glickstein et al, 1985]. Somatosensory influences seem important in the projections to the pons and area 5 may project more densely than area 7 to pontine nuclei [Weisendanger et al, 1979].

Neuron Properties and Effects of Electrical Stimulation

The response properties of neurons in posterior parietal cortex of macaque monkeys are varied, with more rostrally located neurons tending to be somatosensory, and more caudally located neurons, visual or visuomotor. Less is known about posterior parietal cortex in New World monkeys, but only the caudal half is responsive to visual stimuli in anesthetized owl monkeys [Allman and Kaas, 1971]. Some of the types of responses that characterize neurons in different regions of posterior parietal cortex in macaque monkey are indicated in Figure 23.

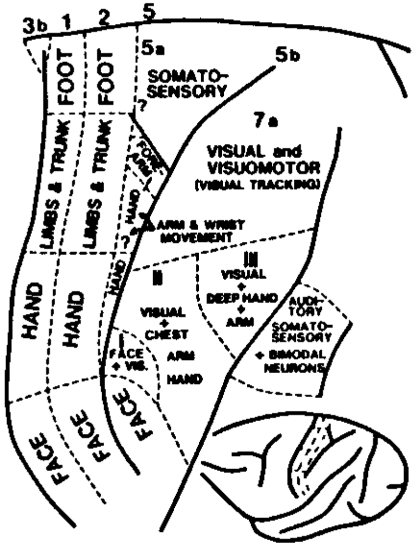


Fig. 23. Regional distributions of neuron types in posterior parietal cortex of macaque monkeys. The responsiveness of the cortex bordering area 2 to cutaneous somatosensory stimuli is from Pons et al [1985a]. Zones I-III are from Leinonen [1984]. See text for details.

In mapping studies that extend from areas 1 and 2 into adjoining portions of areas 5 and 7, two different observations were made according to the mediolateral level of the recordings [Pons et al, 1985a,b]. In two locations, indicated by question marks in Figure 23, neurons were unresponsive to sensory stimuli in anesthetized preparations. In awake animals, neurons in these regions apparently are driven by various manipulations of the body (see below). Other portions of this bordering cortex were highly responsive to cutaneous stimuli, even in anesthetized monkeys. In the portions of area 5 marked "forearm and hand" in Figure 3, for example, neurons were driven by low-threshold cutaneous stimulation, even though more medial and lateral regions of area 5 were unresponsive to such stimulation [Pons et al, 1985a,b]. Receptive field sizes and response properties were similar to those for neurons in adjoining parts of area 2, and the somatotopic sequence in area 5 was a continuation of that in area 2. Thus, these parts of area 5 seem closely related to area 2. Other parts of posterior parietal cortex were also highly responsive to light cutaneous stimuli. Cortex caudal to the parts of area 2 representing the hand (area 5) and face (area 7) responded to stimuli on the hand and face, respectively, and were somatotopically matched with the pattern of organization in the adjoining area 2 [Pons et al, 1985b]. The alternation of responsive with unresponsive zones to cutaneous stimuli under some anesthetic conditions indicates that this bordering cortex is not homogeneous in function. It is also important to note that there are at least two representations of the hand in area 5, and that injections of tracers into the hand representation in area 2 label more than one mediolateral level of area 5 [Pons and Kaas, 1985, 1986]. Of course, this also suggests that the region is functionally heterogeneous.

Studies of the properties of neurons in area 5 have not always been specific about recording locations and published descriptions of the response properties of neurons in area 5 may not reflect the characteristics of neurons in all parts of area 5. To briefly summarize previous reports [Duffy and Burchfiel, 1971; Sakata et al, 1973, 1978; MacKay et al, 1978; Seal et al, 1983; Chapman et al, 1984], neurons are predominately activated by deep receptors, but neurons are commonly activated by cutaneous stimuli also. Many neurons have both cutaneous and deep receptor sources of activation. Neurons also respond to passive or active manipulations of limbs. Because the vast majority of neurons respond after a movement starts, rather than before, the activity of area 5 neurons is unlikely to have a role in initiating movements.

More laterally in posterior parietal cortex, Leinonen [1984] has divided the region of area 7b into four zones (Fig. 24) on the basis of neuron response properties. Zone I [also see Leinonen and Nyman, 1979] contains neurons activated by touching and palpitating the face, passive hand movements toward the face, visual stimuli moving toward the face, or by movements of the lips and jaw and hand movements toward the mouth by the monkey. Some neurons respond to both visual and somatosensory stimuli. Neurons roughly in the same region have been described as having vestibular inputs in that they respond to optokinetic visual stimuli [Schwarz and Fredrickson, 1971; Schwarz et al, 1973]. Leinonen argued that this cortex constitutes a higher-order or associative face area. Neurons in zone II are activated by touching the hand, arm, and chest, often when stimulus movement is of a particular direction, and by visual stimuli moving toward the hand, arm, and chest. Neurons also respond during grasping, hand manipulation, and reaching. Zone III neurons tend to require noncutaneous somatic stimuli such as palpation of arm muscles, flexion of fingers and wrist, as well as visual stimuli moving toward the hand. Some of these neurons also respond during hand movements. Zone IV neurons in cortex adjoining zone III in the lateral sulcus are largely related to cutaneous stimuli on the head, shoulder, and back, rotation of the head, and visual stimuli in the peripheral visual field. These findings indicate that the region of area 7b is characterized by the convergence of higher-order somatosensory and visual inputs. Furthermore, different regions appear to have related but different functional roles concerned with the somatosensory and visual control of movements.

More medial portions of area 7 have been studied by Mountcastle and co-workers [Lynch et al, 1977; Yin and Mountcastle, 1977; Motter and Mountcastle, 1981; Mountcastle et al, 1975a, 1975b, 1981], as well as other groups of investigators [Hyvärinen and Poranen, 1978a,b; Robinson and Goldberg, 1978; Sakata et al, 1973, 1978, 1983, 1985; Kawano et al, 1984; Siegel et al, 1985]. Neurons in medial area 7 (7a) appear to be largely visual and visuomotor in function, and several classes of neurons have been distinguished. Visual tracking neurons respond during the visual pursuit of a small target. Generally, tracking neurons have large receptive fields, and they may have inputs related to eye movements and vestibular signals. Tracking neurons often fire during movements of one direction only, and they often start to respond before the onset of an eye movement. They also respond during eye movements in the dark. Another class consists of visual fixation neurons which are activated during the fixation of gaze on a visual target, whether the target is moving or stationary. These neurons respond to visual stimuli, but the response is enhanced by visual fixation. Some neurons respond during visually guided reaching movements with the hand and also respond to visual and somatosensory stimuli. Overall, neurons in the region of area 7a reveal strong visual influences, while somatosensory effects may be largely movement related. The results of electrical microstimulation studies in the region of area 7a support the view that this cortex has a major role in controlling eye movements. Stimulation typically is followed by saccadic eye movements or blinking, or both [Shibutani et al, 1984]. The eye movements may be mediated via direct and indirect (via the frontal eye field) projections to the superior colliculus, since removal of the superior colliculus abolishes the ability of posterior parietal cortex stimulation to evoke eye movements [Keating et al, 1983].

Functions

Many insights to the possible functions of posterior parietal cortex come from determining behavioral changes following damage. A major consequence of unilateral damage to the posterior parietal lobe in humans can be neglect of stimuli within the contralateral visual field and on the contralateral body surface [see Lynch, 1980; Mesulam, 1981; Hyvärinen, 1982, for reviews]. The neglect, most probable after right hemisphere lesions, can be so severe that a patient may fail to attend to one side of the body and fail to notice visual objects in the left visual hemifield. Other defects have been discussed above.

In monkeys, lesions of posterior parietal cortex produce two notable defects. First, there is contralateral neglect as in humans. This neglect is not as pronounced as in right (minor) hemisphere lesions in humans, but it can be revealed by presenting identical stimuli bilaterally. Under these conditions, there is a strong tendency to respond to the somatosensory or visual stimulus ipsilateral to the lesion. This neglect is also manifest in a "landmark" test [Ungerleider and Mishkin, 1982] in which a monkey is impaired by posterior parietal cortex lesions in the ability to select between two identical objects when a second "landmark" object is placed near the correct choice. The other major impairment observed after such lesions is reaching toward a target [LaMotte and Acuna, 1978]. After a unilateral lesion of much of 7a, misreaching to visual targets with either limb occurred in the visual hemifield opposite the side of the lesion.

In a recent review of posterior parietal cortex, Hyvärinen [1982] lists and discusses possible functions that are consistent with the extensive information that is available on connections, single neuron response properties, and the effects of lesions.

1) The caudal half or so of posterior parietal cortex is involved in visual functions, although many neurons in this cortex have higher-order somatosensory inputs as well. Hyvärinen [1982] reviews the suggestions of several other investigators and concludes that the visually dominated part of posterior parietal cortex (7a or PG) is an end station in the "ambient visual system" that functions through the extrapyramidal motor system. This cortex is sensitive to moving or changing stimuli, especially in paracentral and peripheral vision, and it allows attention to be changed, alterations in where foveal vision is directed, and adjustments in locomotion and posture. This part of posterior parietal cortex is the target of the pathway specialized for visual attention and visual localization in contrast to visually identifying objects, which is a temporal lobe function [Ungerleider and Mishkin, 1982].
2) The rostral half of posterior parietal cortex seems most closely related to somatosensory functions, and much of the evidence suggests that this cortex functions in mediating attention to somatosensory stimuli and in motivated or goal-directed movements related to somatosensory stimuli.
3) Many neurons, especially in the caudal half of posterior parietal cortex, are influenced by both visual and somatosensory stimuli, and there is evidence for vestibular influences as well. This cortex could be important in multimodal functions such as guiding and directing movements using both visual and somatosensory information.
4) It is clear that cortex in the region of 7a has motor functions such as having a role in controlling eye movements. A suggested motor role is in interrupting and redirecting fixation on the appearance of interesting new stimuli [Hyvärinen, 1982]. Posterior parietal cortex may also contain motor programs for the accurate guidance of reaching and other movements and for spatial learning. After review of the available data, Mountcastle [1975] postulated that neurons in posterior parietal cortex function as a "command" system for movements in "immediate extrapersonal space," that is, movements of limbs and head for reaching ob-

jects and surfaces within an arm's length distance. The difficulty with the "command system" hypothesis is that neural activity in posterior parietal cortex does not generally precede and predict movements, as does the activity of some neurons of frontal cortex [see Goldberg and Robinson, 1980]. Hyvärinen [1982] suggests that posterior parietal cortex is an earlier part of a command system where sensory and intentional factors converge before decision making, which occurs elsewhere.

5) The neglect and lack of attention following lesions of posterior parietal cortex indicate that this cortex is part of an intention, attention, or motivation system. Mesulam [1983] emphasizes the importance of the limbic cortex connections of posterior parietal cortex in providing the motivational component of posterior parietal cortex.

Summary. While posterior parietal cortex is not uniform in function, the region as a whole is thought to combine information about the body with largely visual information about nearby space. Hyvärinen [1982] concludes that the main task of posterior parietal cortex is to combine such information to guide behavior in changing situations.

The Supplementary Sensory Area

Because electrical stimulation of several sites in the medial parietal cortex of a human evoked sensations from the contralateral leg, arm, and face, Penfield and Jasper [1954] postulated the existence of a medial "supplementary sensory area" in an analogy to the supplementary motor area. Supporting evidence for the existence of a separate and complete representation of the body in medial parietal cortex of primates is extremely limited and has been reviewed recently by Murray and Coulter [1982]. In macaque monkeys, at least some neurons in medial parietal cortex respond to somatosensory stimuli, and there is some suggestion that anterior recording sites are activated by caudal body locations and posterior recording sites are activated by rostral body locations. Neurons in this cortex have large receptive fields and appear to have convergent inputs from deep and cutaneous receptors. Medial parietal cortex in the postulated location of the supplementary sensory area receives a major thalamic input from the lateral posterior nucleus of the thalamus [see Murray and Coulter, 1982]. Cortical inputs are from somatosensory areas 2 and 5, premotor cortex, and the region of supplementary motor cortex.

SOMATOSENSORY CORTEX OF THE LATERAL SULCUS

Much of the upper bank of the lateral sulcus and some of the cortex on the insula and the lower bank appear to be somatosensory in function. The most well-known subdivision is the second somatosensory area, S-II, but several other subdivisions have been proposed. Partly because it is difficult to study cortex buried in a fissure, the organization of cortex in the S-II region is not well understood, and most information comes from a few studies on macaque monkeys. Thus, there is little basis for comparative statements.

Background

After the early discovery of the first systematic representation of the body surface, S-I, in cats and other mammals, Adrian [1940] noted a second representation of the feet lateral to S-I in cats, and soon thereafter Woolsey [1943] demonstrated that a second complete representation of the body, S-II, exists lateral to "S-I" in cats, dogs, and monkeys. This second representation has now been demonstrated in a wide range of mammals [see Nelson et al, 1979, for review]. In most mammals, S-II is in the range of one-half to one-third the size of S-I, and S-II borders S-I along a common representation of the midline of the face and head, with the representations of the forelimb, trunk, and hindlimb progressively more distant from S-I. Early evoked potential studies suggested that neurons in S-II are activated bilaterally by stimulating either side of the body, rather than just on the contralateral body surface as in S-I. Mirror-symmetrical discontinuous receptive fields were commonly reported for recording sites in S-II. However, more recent studies have interpreted S-II as a single systematic representation of the contralateral body surface and have reported receptive fields that are confined to the contralateral body surface. Neurons with bilateral receptive fields have been found in cortex bordering S-II, and these regions were probably included in early definitions of S-II. In addition, inputs from ipsilateral body parts that are not always apparent in single neuron recordings could have been detected in earlier recordings of summed evoked neural activity. The evoked spike activity recorded with microelectrodes in S-II seems to largely depend on contralateral stimulation. There is evidence for additional somatosensory areas bordering S-II of nonprimates [eg, Clemo and Stein, 1982; Krubitzer et al, 1985] and monkeys [Burton and Robinson, 1981].

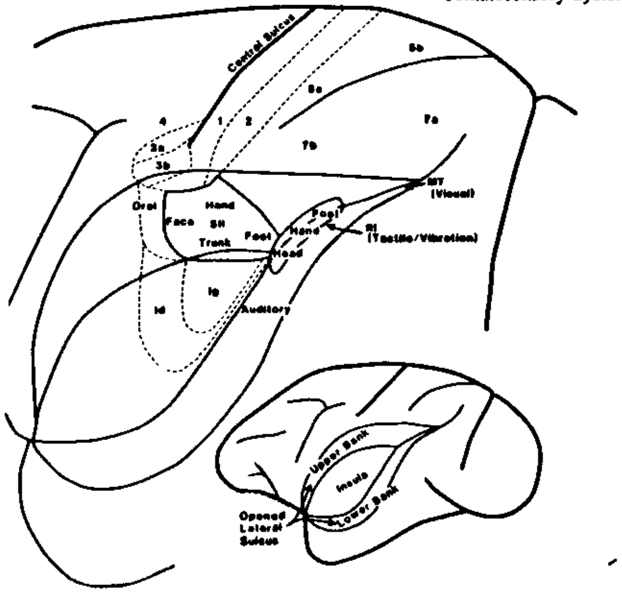


Fig. 24. Subdivisions of cortex in the S-II region of macaque monkeys. Based on Friedman et al [1981], and Robinson and Burton [1980a,b]. Id, dysgranular insular field; Ia, agranular insular field; RI, retroinsular area; MT, middle temporal visual area. See text for details.

The Second Somatosensory Area

Basic features of the second somatosensory area (S-II) have been determined for Old World macaque monkeys, New World owl and squirrel monkeys, and several species of prosimians. The somatosensory organization appears to be complex, but the hand and foot representations are found in sequence moving away from anterior parietal cortex, as originally described by Woolsey and co-workers [1942].

The location and somatotopic organization of S-II in macaque monkeys (Fig. 24) has been determined by projection patterns from anterior parietal cortex [Friedman et al, 1981] and by microelectrode mapping studies [Robinson and Burton, 1980a]. Conclusions from these two approaches appear to differ somewhat. Using injections of anterogradely transported tracers in anterior parietal cortex, Friedman et al [1981] conclude that areas 3b, 1, and 2 all project to S-II, and these projections converge. By injecting the representations of different body parts in anterior parietal cortex, the differing locations of label in S-II led to the conclusion that the face and head representations lie rostrally, the digits, hand, and arm are caudal to the face, and the trunk, leg, and foot are deepest in the lateral sulcus and extend onto insular cortex.

A more detailed understanding of the organization of the S-II region has been obtained from microelectrode recordings in awake monkeys [Robinson and Burton, 1980a]. Neurons with receptive fields on the face and mouth were found rostrally in S-II, and some of these neurons had receptive fields crossing the midline and thus were bilateral. More caudally, the largest portion of S-II was activated from receptive fields on the digits, and these and other receptive fields were confined to the contralateral body. Other parts of the body were represented in more caudal cortex. A complication in the map was that parts of the face, thumb, and foot were represented both superficially and deep within the sulcus. These additional representations may be part of S-II or may be parts of other fields.

The basic organization of S-II appears to be similar in New World monkeys. In owl monkeys [Cusick et al, 1981], S-II adjoins the representations of the face in areas 3b and 1 near the lip of the lateral sulcus. Both the trunk and forelimb representations lie near the banks of the lateral sulcus, with the forelimb and hand representations rostral to the trunk representation. The foot representation lies caudal to the hand region in the lower bank of the lateral sulcus. Receptive fields are mainly contralateral and larger than those in areas 3b and 1.

For prosimian primates, S-II has been described for slow loris [Krishnamurti et al, 1976] and for galagos [Carlson and Burton, 1983; Burton and Carlson, 1986] where the organization is similar to that of monkeys and many nonprimate mammals (Fig. 24).

Neurons in S-II of macaque monkeys [Robinson and Burton, 1980c], owl monkeys [Cusick et al, 1981], and prosimians [Krishnamurti et al, 1976; Carlson and Burton, 1983] are driven by cutaneous stimuli with almost all of the receptive fields on the contralateral body surface. Response characteristics of neurons in S-II have been most fully described by Robinson and Burton [1980c] in macaque monkeys. In this study, the vast majority of neurons in S-II were rapidly adapting to touch or movement of hairs. A related study demonstrated that these rapidly adapting neurons discharge for each cycle of low-frequency (20–80 Hz) vibrotactile stimuli [Sinclair and Burton, 1984]. A small proportion of neurons seem to be activated by deep receptors, and a small number of neurons with pacinianlike responses were found throughout S-II.

The connections and response properties of S-II suggest that it is a higher-order processing station with some parallel thalamic input. The major thalamic input has been described as from the ventroposterior nucleus [eg, Burton, 1984; Burton and Jones, 1976], but there is impressive evidence that the overwhelming thalamic input is from VPI [Friedman and Murray, 1986; Manzoni et al, 1984]. However, few neurons in S-II have pacinianlike responses, and neurons in VPI appear to be activated mainly by pacinian receptors (see above). Thus, VPI does not seem to provide the dominant input to S-II. The proposed projections from VP, of course, are consistent with the responsiveness of neurons in S-II to lightly touching the skin or bending hairs. The observation that most neurons in S-II are rapidly adapting suggests that any relay from VP to S-II would be largely from rapidly adapting neurons.

Other inputs to S-II are of the feedforward type from S-I in prosimians (Kaas, unpublished studies), and areas 3b, 1, and 2 in monkeys [Friedman, 1983; Friedman et al, 1981; Cusick et al, 1981, 1985] and probably other primates. Another source of dense feedforward input to layers IV and III of S-II is from the retroinsular area in monkeys [Friedman, 1983; Friedman et al, 1986]. These inputs probably account for some of the activations related to cutaneous receptors, and the few neurons apparently related to deep receptors could be activated from area 2. Callosal connections of S-II are dense and include inputs from S-II and anterior parietal cortex of the opposite hemisphere [Manzoni et al, 1984]. These inputs apparently do not activate neurons by themselves, and thereby do not produce bilateral excitatory receptive fields, but they may contribute to the evoked slow waves recorded with surface electrodes.

The projection pattern of S-II in primates has been most studied in macaque monkeys [Friedman et al, 1986]. Feedback projections have been demonstrated to the sources of major inputs, areas 3b, 1, and 2, and retroinsular cortex [Friedman, 1983]. Mishkin [1979; also see Murray and Mishkin, 1984] proposes that S-II is a station in a processing hierarchy that proceeds from anterior parietal fields to S-II and then to other fields related to tactile learning and memory. More specifically, a major output of S-II is to granular insular cortex (Ig, Fig. 24) [Schneider et al, 1984; Friedman et al, 1986]. According to the theory, Ig and the adjoining Id field form the next links in a somatosensory pathway to the amygdaloid complex and hippocampus that is critical for tactile memory.

Robinson and Burton [1980a] have described an "S-II proper" as well as two "S-II complex zones" on the rostral and caudal boundaries of S-II. Within these zones neurons differ in response properties from "S-II proper," and one might question whether they should be considered part of S-II or additional fields. Neurons within the complex zones were more varied in response characteristics than in S-II proper. Approximately one-fourth of the neurons sampled did not appear to be somatosensory, while one-third of the somatosensory neurons responded only when the monkey voluntarily moved the relevant body part during stimulation. Many of these neurons had bilateral receptive fields. Most somatosensory neurons were activated by cutaneous stimuli, but some required deep palpation or vibration of muscles.

The Retroinsular Area

Outside of S-II, little is known about somatosensory cortex in the lateral fissure of primates. The neural properties of the retroinsular area (Ri) (Fig. 24) have been studied only in macaque monkeys [see Robinson and Burton, 1980b]. Most neurons in Ri respond to cutaneous stimuli, and many respond in a rapidly adapting pattern to light touch and low-frequency vibration, and some discharge to follow high-frequency vibrations (over 100 Hz), suggesting pacinian receptor input. Thalamic input appears to be from parts of the posterior group [Burton and Jones, 1976; Friedman and Murray, 1986] and perhaps VPI [Friedman and Murray, 1986]. Cortical inputs are not well established, but a major feedforward projection is to S-II, with feedback input from S-II [Friedman, 1983; Friedman et al, 1986]. Ri also appears to project to Ig in insular cortex [Mesulam and Mufson, 1982; Friedman et al, 1986].

The Granular Insular and Dysgranular Insular Areas

Much of the insular cortex is activated by stimulating the hand or face [Juliano et al, 1983]. Cytoarchitectonically, cortex adjoining S-II on the insula of the lateral fissure can be divided into a "granular" portion (Ig) with a well-developed layer IV of "granule" cells and a more rostral "dysgranular" portion (Id) with a poorly developed layer IV (Fig. 24). Cortex in the Ig region forms a second representation of the body surface in the lateral sulcus, and receptive fields in Ig are similar in size to those in S-II in both macaque [Robinson and Burton, 1980b] and owl monkeys [Cusick et al, 1981], with the difference that many neurons in Ig have bilateral symmetrical receptive fields [Schneider et al, 1984]. The rostral portion of Ig represents the face and mouth, while caudal portions are devoted to the trunk and limbs. The representation of the hand is rostral to that of the foot, and there seems to be some matching of body parts along the S-II border. Most neurons in Ig respond to cutaneous stimuli, with a smaller proportion related to deep receptors.

There is evidence that Ig receives thalamic input from part of the posterior group of nuclei [Burton and Jones, 1976; Friedman and Murray, 1986], but such an input would not account for the responsiveness of neurons to cutaneous stimuli. A likely source of cutaneous activation is from S-II, since the response properties of neurons in S-II and Ig are very similar. Projections from Id to the amygdala and perirhinal cortex have been reported [Turner et al, 1980; Friedman et al, 1986]. The bilateral receptive fields of neurons in Ig may result from the dense callosal connections that occur in cortex of the lateral sulcus [see Cusick and Kaas, 1985].

The significance of Id is uncertain. It is not known to respond to somatosensory inputs, and its connections have not been extensively studied. Burton and Jones [1976] provide evidence that Id is interconnected with the ventroposterior inferior (VPI) nucleus of the thalamus. If so, neurons in Id should respond to vibratory stimuli, since VPI is thought to be a relay for pacinian receptors (Fig. 8). Friedman and Murray [1986] suggest that, in addition to VPI, the basal ventromedial nucleus and parts of the posterior group project to Id.

CONCLUSIONS

Principles

In this chapter, we described the organization of the parts of the somatosensory system concerned with object recognition and identification, rather than parts related to pain and temperature and sensory control of reflexes and cerebellar function. The relevant information starts in receptors in the skin, muscles, and joints, and relays over parallel afferent pathways to the spinal cord and medulla and then to the ventroposterior complex in the thalamus. In monkeys, the ventroposterior complex has been subdivided into a ventroposterior nucleus that represents both rapidly adapting and slowly adapting receptors of the skin in a somatotopic manner, a dorsally adjoining ventroposterior superior nucleus that represents muscle and probably joint receptors of the body, and the ventroposterior inferior nucleus that relates to pacinian receptors. These three thalamic nuclei appear to exist in all primates. The possibility exists of a separate ventroposterior oralis nucleus devoted to muscle receptors, but there is no clear supporting evidence. The lateral posterior nucleus and the anterior pulvinar, while not receiving a second-order relay of somatosensory information, do have interconnections with subdivisions of somatosensory cortex and are part of the somatosensory thalamus.

The somatosensory cortex of monkeys includes three large regions. One region, anterior parietal cortex, includes the four traditional architectonic subdivisions, areas 3a, 3b, 1 and 2. Each of these fields appears to contain a systematic representation of the body, although the representation in area 2 of macaque monkeys is complex and represents at least some parts of the body twice. Area 3b receives information from rapidly adapting and slowly adapting afferents from the skin that are relayed from separate clusters of cells in the ventroposterior nucleus. The slowly adapting and rapidly adapting inputs activate separate groups of cells or processing modules in area 3b. The ventroposterior nucleus and some of the cells that project to area 3b also project to area 1. Area 1 represents rapidly adapting receptors of the body surface. Some neurons in area 1, but not area 3b, appear to be activated by pacinian receptors (sensitive to high frequency vibration), but the anatomical pathways for this activation are unknown. Area 1 also receives a major input from area 3b, and therefore is, in part, a higher-order cortical station. Area 3a is activated by muscle receptor information that is relayed in the ventroposterior superior nucleus and to a lesser extent by cutaneous receptor information relayed from other subdivisions of anterior parietal cortex. Area 2 also receives inputs from the ventroposterior superior nucleus including many of the same cells that project to area 3a. Area 2 relates to noncutaneous receptors in muscles and joints via the thalamic relay, cutaneous receptors via a sparse and apparently species-variable ventroposterior nucleus input, and major cortical inputs from areas 3b and 1. Thus, area 2, to some extent, is a third level of cortical processing. Of the four fields, areas 3b and 3a appear to exist in all primates, and area 3b appears to be the homologue of primary somatosensory cortex, S-I, of nonprimates. Areas 1 and 2 may not be present in prosimian primates, but they appear to be present in all higher primates.

The organization of posterior parietal cortex is less well understood. Traditional subdivisions include architectonic areas 5 and 7 of monkeys and areas 5, 7, 39, and 40 of humans. The region has been divided further by recent investigators and obviously it contains a number of functionally distinct regions. Cortical somatosensory inputs are from anterior parietal cortex. In addition, part of posterior parietal cortex receives visual inputs from subdivisions of extrastriate visual cortex. Connections with the limbic system and the frontal lobe suggests motivational and motor control functions. Recordings reveal neurons with complex response properties related to somatic and visual modalities and behavioral intentions. Lesions result in sensory neglect and errors in reaching movements. Posterior parietal cortex appears to be important in guiding body and eye movements toward objects of interest.

A third region of somatosensory cortex is in the lateral fissure. Since much of somatosensory cortex in this region is occupied by the second somatosensory area, S-II, we refer to this cortex as the S-II region. The second somatosensory area, S-II, appears to be present in all mammals and therefore all primates. It forms a systematic representation of at least rapidly adapting cutaneous receptors, probably in part directly relayed from the ventroposterior nucleus of the thalamus. S-II also receives convergent inputs from all four fields of anterior parietal cortex and perhaps subdivisions of posterior parietal cortex and motor cortex as well. Thus, S-II has the inputs that would allow it to perform its suggested role as a higher station in a cortical series related to object identification and memory. Other somatosensory fields that have been identified in the S-II region of monkeys include the retroinsular area, the granular insular area, and the dysgranular insular area. The functional roles of these fields are uncertain, but at least one field near S-II is thought to be important in relaying somatosensory information from S-II to limbic structures important in memory.

Trends

Although there are certainly specializations within each group, in a general way prosimian primates, New World monkeys, apes, and humans can be considered as representing successively higher levels of behavioral and neural development. The most impressive difference in brain organization across these primate groups is at the cortical level. In prosimian primates, a single field in anterior parietal cortex responds to low-intensity cutaneous stimuli, and this field is justifiably termed the primary somatosensory area or S-I. This S-I is bordered rostrally and caudally by narrow fields that respond to more intense stimuli possibly related to deep receptors. Anterior parietal cortex of marmosets, which can be considered the most primitive of New World monkeys, resembles that of prosimians in that only one anterior parietal field, area 3b or S-I, is highly responsive to cutaneous stimuli [Carlson et al, 1986]. However, a caudal field with architectonic characteristics of area 1 is somewhat responsive to light cutaneous stimuli. In other New World monkeys (*Cebidae*), two fields, area 3b (S-I) and area 1, are fully responsive to cutaneous stimuli, while two other fields, area 3a and area 2, largely relate to inputs relayed from deep receptors (muscle spindles). In macaque monkeys, parts of area 2, especially those parts related to the hand and face, are highly responsive to cutaneous stimuli and even more caudally located cortex in areas 5 and 7 of posterior parietal cortex are easily driven by low-threshold cutaneous stimuli. Thus, there is a clear trend toward more fields being dominated by inputs from cutaneus receptors across these primate groups. Perhaps this trend, which appears to be reflected by changes in thalamic and cortical connections, continues into apes and humans, so that cutaneous receptors, especially those of the hand and face, dominate even larger regions of cortex.

Another trend appears to be an expansion of posterior parietal cortex, but little is known about the organization of posterior parietal cortex except in macaque monkeys, so the nature of this trend cannot be specified. It is also likely that the somatosensory cortex of the lateral fissure has increased in proportional size and perhaps the number of distinct fields, but again comparative information to support this conclusion is sparse.

Research Needs

Research on the somatosensory system of primates has concentrated on Old World macaque monkeys, and relatively little is known about the organization of the total system in prosimians, New World monkeys, apes, and humans. This lack of basic information greatly limits the development of theories of the evolution and specialization of the somatosensory system in primates.

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