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The Human Nervous System

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24. Somatosensory System

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While small shapes can be perceived with information solely from tactile receptors, discriminations of larger objects involve an active process with multiple contacts on the skin and an integration of cutaneous and proprioceptive information. This chapter outlines the organization of the parts of the somatosensory system in humans thought to be important in discriminations of shapes and textures. Thus, this review concentrates on pathways and centers for the processing of information from both low-threshold mechanoreceptors in the skin and deep receptors in muscles and joints, since these receptors are critical for object identification and discrimination. Conclusions are largely supported by evidence from studies on humans, but comparisons are often made with monkeys, where considerable progress in understanding the basic organization of the somatosensory system has occurred (see Kaas and Pons, 1988, for a review.) The important subsystems dealing with afferents coding pain and temperature have been reviewed elsewhere (e.g., Willis, 1985; Perl, 1984; Darian-Smith, 1984b).

The basic parts of the somatosensory system of humans are outlined in Figure 24.1. Peripheral neurons related to receptors in the skin, muscles, and joints send axons into the spinal cord and brain stem to synapse on second-order neurons in the spinal cord or dorsal column–trigeminal nuclear complex. These second-order neurons send axons to the thalamus largely over the spinothalamic and medial lemniscal pathways. The somatosensory thalamus has been divided in various ways by different investigators. Using recently proposed subdivisions for monkeys (see Kaas and Pons, 1988) the major cutaneous inputs

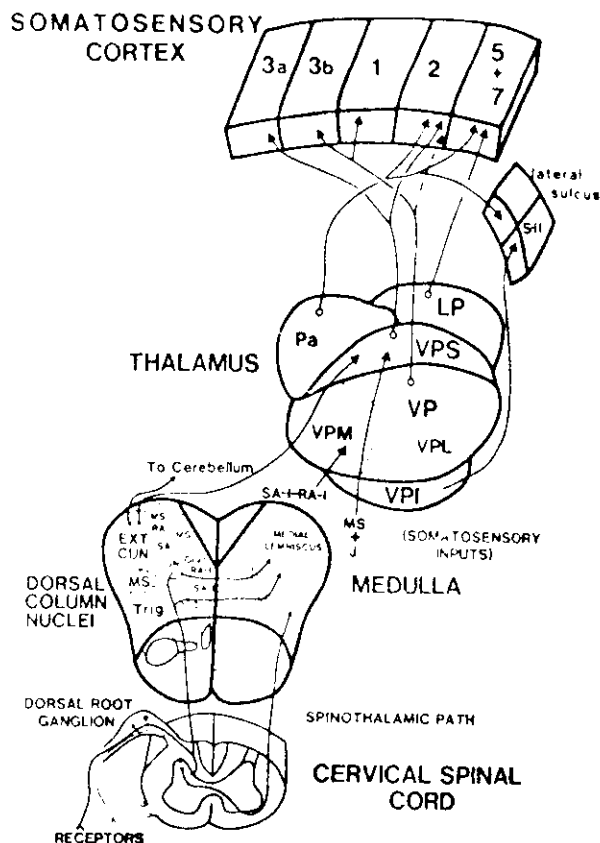


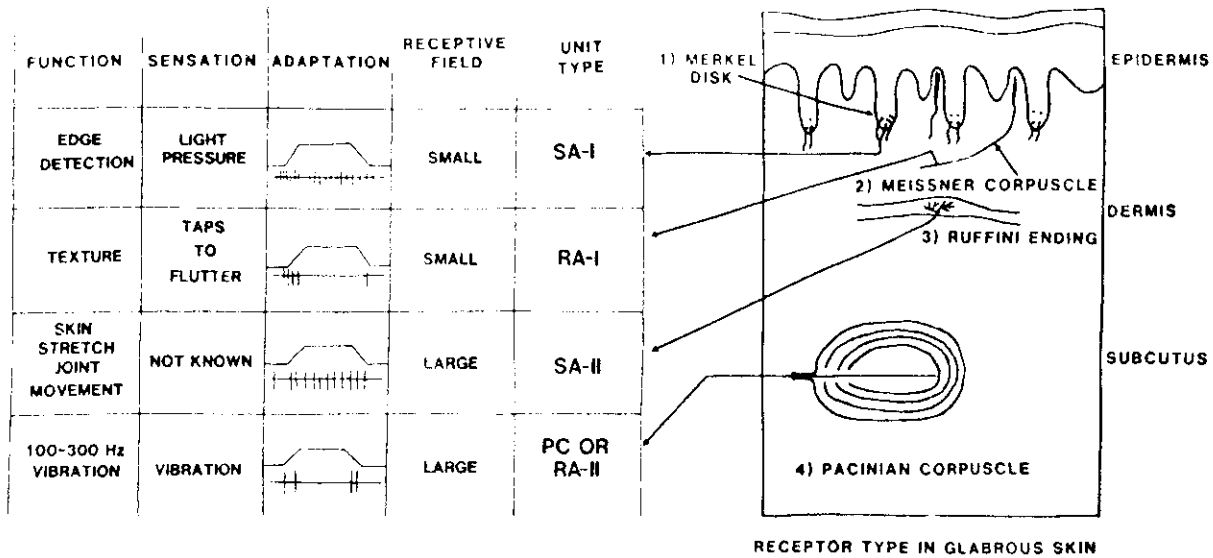
Figure 24.1. An overview of the human ascending pathways from receptors to cortex that are important for identifying objects by touch. Type I slowly (SA-I) and rapidly (RA-I) adapting cutaneous afferents, as well as afferents related to muscle spindles (MS), tendons, and joints (J), relay in the spinal cord or in the dorsal column-trigeminal complex in the medulla [including the cuneate nucleus (CUN), the gracilis nucleus (Grac), the spinal trigeminal nucleus (Trig), and the external cuneate nucleus (EXT CUN)]. Projections related to cutaneous receptors terminate in the ventroposterior thalamic nucleus (VP), which in turn projects largely to areas 3b and 1 of anterior parietal cortex. Ascending projections related to muscle spindles and other deep receptors, some of which arise in the external cuneate nucleus, terminate in a dorsal capping nucleus of the ventroposterior complex that has been termed the ventroposterior superior nucleus (VPS). VPS projects to areas 3a and 2 in monkeys and, presumably, in humans. Afferents activating the ventroposterior inferior nucleus (VPI) are uncertain but some evidence suggests the VPI receives inputs relayed from Pacinian receptors (PC). Recent studies in monkeys show that the major thalamic projection to the second somatosensory area, S-II in the lateral sulcus, is from VPI rather than VP. The anterior pulvinar (Pa) and lateral posterior complex (LP) are largely without sensory inputs, but they are interconnected with posterior parietal (or posterior somatosensory) cortex. Traditionally, posterior parietal cortex is subdivided into "areas" 5 and 7; however, the subdivisions of posterior parietal cortex which are related to somatosensation are not well understood. Lateral and insular somatosensory cortex includes S-II, the granular insular area, Ig, and the retroinsular area, RI. MS, Muscle spindle; RA, rapidly adapting fibers; SA, slowly adapting fibers; VPL, ventroposterior lateral nucleus; VPM, ventroposterior medial nucleus.

terminate in the ventroposterior nucleus (VP). A dorsal capping region we term the ventroposterior superior nucleus (VPS) is activated by inputs from muscle spindles and probably other deep receptors. Ventrally, the ventroposterior inferior nucleus (VPI) is possibly activated by Pacinian receptor inputs (see Dykes, 1983). The anterior pulvinar (Pa), the medial pulvinar, and lateral posterior complex (LP) apparently do not receive ascending somatosensory inputs, but these nuclei are related to the somatosensory system by being interconnected with somatosensory regions of parietal cortex. Research on monkeys indicates that anterior parietal cortex consists of four parallel representations of the body, and data from humans are largely consistent with this interpretation. Areas 3b and 1 represent cutaneous inputs, while areas 3a and 2 integrate cutaneous and deep receptor inputs. Thalamic projections to areas 3b and 1 are largely from VP, while VPS provides driving inputs for areas 3a and 2. Posterior parietal cortex is a higher-order region related to both somatosensory and visual functions. Functional subdivisions are obviously present, but the organization of the region is poorly understood, even in monkeys. Insular and other cortex of the lateral (Sylvian) fissure contain subdivisions of somatosensory cortex including the second area, S-II, which has inputs from VPI and from anterior parietal cortex (Pons *et al.*, 1987). S-II projects to adjacent areas as part of a laterally directed processing sequence related to object identification and memory (Mishkin, 1979).

I. Receptor Types and Afferent Pathways

Several general classes of afferent fibers send information to the central nervous system (see Dykes, 1983, for a review):

1. Four main types of afferents relate to low-threshold cutaneous mechanoreceptors in the skin. The afferent classes include two types of slowly adapting afferents and two types of rapidly adapting afferents. All of these types have been extensively studied physiologically in monkeys and related to receptor types. More recently, the response properties of these afferents have been characterized during recordings in humans and sensations have been evoked by electrical stimulation. These afferents are important in tactile discrimination, and they are described more fully below.



RECEPTOR TYPE IN GLABROUS SKIN

Figure 24.2. Receptor types and characteristics of afferent fibers from the glabrous skin of the human hand. 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. From Kaas and Pons (1988).

2. Muscle spindle receptors, perhaps aided by other deep receptors in joints and tendons, play a significant role in the position sense of limbs and fingers. This sense is critical in the ability to recognize the form of objects.

3. Afferents that are thin and slowly conducting relate to the sensations of cold, warm, pain, and crude touch. Other afferents may be related to the sensations of itch and tickle.

In humans, the hand is the most important tactile organ for object identification (Darian-Smith, 1984a). Receptors in the hand must convey information about texture and shape. This is done primarily from the fingerpads during active exploration, so that finger positions and temporal sequences are important. The glabrous skin of the hand has the highest innervation density and tactile acuity of any body surface (Darian-Smith, 1984a). Hairy skin is less important in object identification, and hairy skin is less sensitive to touch and vibration (Hamalainen and Jarvilehto, 1981). However, the hairs themselves provide an increased sensitivity to air movement and other stimuli that displace hairs (Hamalainen *et al.*, 1985).

A. Low-Threshold Mechanoreceptor Afferents from the Hand

Four types of low-threshold mechanoreceptors are found in the skin of primates and other mammals,

and afferents from these four types in the human have been studied electrophysiologically (Jarvilehto *et al.*, 1981; Johansson, 1976; 1978; Johansson and Vallbo, 1983; Johansson *et al.*, 1982a,b; Torebjork *et al.*, 1984; Vallbo, 1981; Vallbo *et al.*, 1984; Westling and Johansson, 1987). The major conclusions are summarized in Figure 24.2.

The SA-I Afferent In the superficial skin, the type I class of slowly adapting afferents. SA-I, apparently terminate at receptor sites termed Merkel disks (see Darian-Smith, 1984a). Each receptor site actually includes a specialized Merkel cell that is distinct from adjacent skin cells and a number of disklike nerve terminals originating from a myelinated (7–12 μm diameter) afferent fiber. SA-I receptors are densely distributed at the distal glabrous phalange of the human hand, and they constitute about one-fourth of the 17,000 tactile units of the hand (Johansson and Vallbo, 1979). Microelectrode recordings indicate that the SA-I afferents respond throughout the period of a skin indentation, even when the indentation is sustained for many seconds. Depending on the rate of the indentation, a large transient indentation response also occurs. The SA-I fibers have small, circumscribed receptive fields, and seem especially responsive when the edge of an object indents skin within the receptive field. When stimulated by a train of electrical pulses, a single SA-I afferent signals the sensation of light, uniform pressure at a skin location corresponding to the receptive field. Single impulses

are not felt, and increases in stimulation frequency result in feelings of increased pressure. Thus, SA-I afferents are thought to be very important in mediating sensations of static pressure and providing information about the locations of edges and textures of held objects. SA-I afferents best preserve information about moving Braille-like dot patterns on the skin (Johnson and Lamb, 1981). After correlating human discrimination of skin indentation with the response profiles of skin afferents in monkeys, Srinivasan and LaMotte (1987) concluded that static discriminations of shape are based primarily on the spatial configuration of the active and the inactive SA afferents. In addition, under static conditions, the SA afferents provide most of the intensity information.

The SA-II Afferent A second class of slowly adapting afferents. SA-II, terminate in encapsulated endings called Ruffini corpuscles (see Darian-Smith, 1984a; Miller *et al.*, 1958), which are located somewhat deeper in the skin than the Merkel disks subserving SA-I afferents. Ruffini or Ruffini-like receptors are also found in deep tissues, including ligaments and tendons. Each Ruffini corpuscle contains an elongated ($500\text{--}1000\ \mu\text{m} \times 200\ \mu\text{m}$) capsule of four to five layers of lamellar cells covered with a membrane, and a core of nerve fiber branches and longitudinally aligned collagen fibrils. Movement of the skin results in stretching of the corpuscle because the corpuscle is attached to surrounding tissue. Such stretching results in deformation and activation of the innervating axon. Each Ruffini corpuscle is innervated by one A-beta myelinated fiber, which may also innervate several other adjacent corpuscles. In the human hand, the SA-II class of afferents constitutes about one-fifth of the tactile units (Johansson and Vallbo, 1979). SA-II fibers have large, poorly defined receptive fields (Figure 24.3), often located near the nail bed or near skin folds on the digits or palm. These afferents are extremely sensitive to skin stretch, and often they are sensitive to direction of skin stretch. Normal movements of digits and limbs are very effective in activating these neurons. Electrical stimulation of single SA-II afferents is apparently not felt, so uncertainty remains about the role of SA-II afferents in tactile perceptions. However, there is psychophysical evidence that SA-II channels participate in the sense of touch (Bolanowski *et al.*, 1987). In addition, inputs from these skin stretch receptors may combine with sensory inputs from muscles and joints to provide limb and digit position and movement signals (e.g., McCloskey, 1978). Some cu-

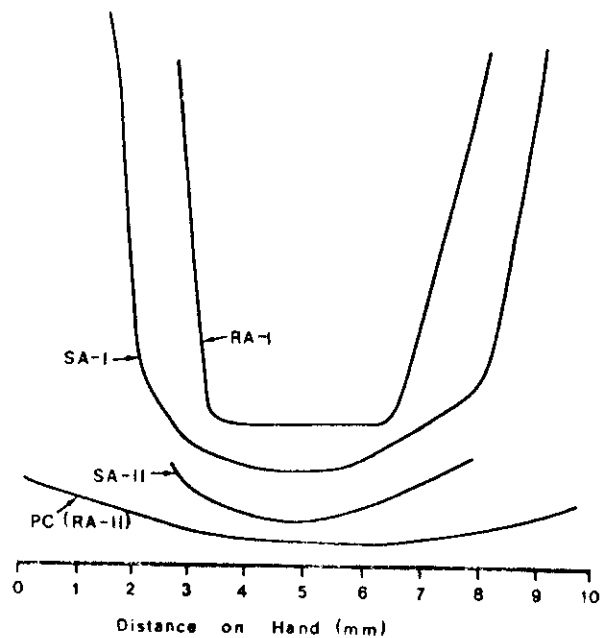


Figure 24.3. Changes in the sensitivity to tactile stimuli with distance across the receptive field for four classes of afferents from the glabrous skin of the human hand. Threshold levels on the vertical scale are arbitrary and do not indicate different thresholds. The rapidly adapting RA-I and the slowly adapting SA-I afferents have small receptive fields with sharp boundaries, while Pacinian (PC) or rapidly adapting RA-II and slowly adapting SA-II afferents have large receptive fields with poorly defined boundaries and a gradual change in sensitivity across the skin. Based on Johansson (1978).

taneous mechanoreceptors do appear to contribute to a movement sense, but not to an awareness of the static position of a joint (see Clark *et al.*, 1986). Also, SA-II units are sensitive to skin shearing, and thus they might provide information about the weight of objects (McCloskey, 1974). Finally, SA-II units seem well suited for a role in motor control (Westling and Johansson, 1987).

The RA-I Afferent The predominant receptor afferent of the digit skin is the rapidly adapting RA-I, type I, fiber (Darian-Smith, 1984a). Nearly half of the tactile afferents from the hand are of the RA-I type (Johansson and Vallbo, 1983). RA-I afferents innervate Meissner corpuscles, which are located in dermal papillae protruding into the epidermis. Meissner corpuscles are particularly dense in the glabrous skin of the distal phalanges; they are less common on the palm and are rare in hairy skin, being replaced by RA afferents related to hair shafts. The corpuscles consist of a core of nerve terminal disks and lamellae of Schwann cells surrounded by connective tissue ex-

tensions of the endoneurial sheath. Meissner corpuscles are elongated ($100 \times 50 \mu\text{m}$) perpendicular to the skin, and the outer collagen fibers of the corpuscles are linked with fibrils of adjacent epidermal cells which allow skin deformations to stretch the corpuscle. Most corpuscles are innervated by two to six myelinated axons, and each axon innervates a tight group, providing a small receptive field of almost uniform sensitivity and sharp boundaries (Figure 24.3). RA-I afferents respond only to changes in skin indentation, and not to steady indentation (e.g., Srinivasan and LaMotte, 1987). Thus, RA-I afferents are capable of providing shape and intensity information during active touch (see LaMotte and Srinivasan, 1987). Single electrical impulses on RA-I afferents from the human hand often result in the 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; at higher frequencies the taps merge into a fluttering sensation. No increase in the magnitude of the sensation follows increases in stimulation rate. These observations suggest that RA-I units are especially important in discriminations of textures moved across the skin, and of course in the sensation of flutter.

The RA-II Afferent The PC (Pacinian) or rapidly adapting RA-II afferents terminate in Pacinian corpuscles. These corpuscles are much less common than other cutaneous receptor endings in the hand (10–15%), and they are found in other tissues (see Darian-Smith, 1984a; Johansson and Vallbo, 1979). Only about 200 corpuscles may be found in the human finger, where they are distributed within deeper skin, subcutaneous fat, and tendonous attachments of the ventral but not the dorsal finger. The PC corpuscles are large ($0.3\text{--}1.5 \times 0.2\text{--}0.7 \text{ mm}$) ovoids consisting of a central nerve fiber surrounded by an inner core of 60 or so layers of concentrically wrapped lamellar cells, a space filled with fluid, and an outer capsule of up to 30 less densely packed lamellae. The corpuscle acts as a mechanical filter, relaying high-frequency and attenuating low-frequency components of skin compression to the axon terminal. PC afferents are extremely sensitive to transient indentations of the skin over large areas such as a complete digit and part of the palm. Thus, information is transmitted in the tissue to the region of the receptor. Sensitivity gradually decreases with distance from the receptor, and receptive field boundaries are not sharp (Figure 24.3). PC units typically can be activated by gently blowing on the skin, and they respond to vibrations

produced by tapping the table surface on which a skin surface rests. PC afferents, like RA-I fibers, respond to the indentation and release of the skin produced by a probe (Figure 24.2), but fail to respond during steady indentation. The responses of Pacinian afferents follow the cycle of a sinusoidal vibratory stimulus. However, unlike RA-I afferents which respond with lowest thresholds in the 30–40 Hz range, PC afferents have lowest thresholds in the 250–350 Hz range. Thus, PC afferents appear to be the only afferents capable of subserving the sensation of high-frequency vibration. Electrical stimulation of PC afferents in the human hand are not felt at low stimulation rates, but a sensation of vibration or tickle occurs at high stimulation rates. Often, the sensation is restricted to a part of the large, diffuse receptive field. PC afferents poorly resolve moving texture patterns (Johnson and Lamb, 1981), and they are apparently unimportant in object identification. Their major role, therefore, seems to be in detecting and roughly locating sudden skin deformations produced by ground and air vibrations, and by skin contacts.

B. Cutaneous Receptors of the Hairy Skin

As in the glabrous skin, the hairy skin has SA-I, SA-II, RA-I, and PC afferents, and Merkel cell receptors, Pacinian corpuscles, and Ruffini endings are found; however, modifications in the receptor mechanisms exist. First, Merkel cell disks of the SA-I receptor are often aggregated in small (0.25–0.5 mm) diameter touch domes that are slightly elevated from surrounding skin and can be visualized with a dissecting microscope. The Merkel touch spot or *hauerscheibe* is innervated by a single, large (7–12 μm) myelinated fiber that branches to terminate in a number of disks associated with Merkel cells. Isolated Merkel cells are rare. Second, some RA-I and SA-I afferents relate to the shafts of hairs. The SA-I afferents seem to be activated by Merkel-type endings around hair follicles, and the RA-I afferents may be the equivalent of Meissner-type endings in glabrous skin.

C. Deep Receptors

As noted above, SA-II type afferents associated with Ruffini-like endings are not only found in the skin, where they signal stretch, but they are also found in deep tissues where they also signal stretch. The receptors are Ruffini corpuscles and Golgi tendon organs. SA-II afferents provide information about joint

extension and tissue compression, but it is not clear that SA-II afferents have any role in the conscious awareness of joint position (Burgess *et al.*, 1982). Part of the evidence against such a role is that joint position sense survives joint removal and replacement (Cross and McCloskey, 1973).

Other important deep receptors are the muscle spindle receptors, which were once thought to participate only in reflexes via spinal cord pathways, and motor control via a relay to the cerebellum. Muscle spindle afferents are now known to also relay to the cortex (Figure 24.1), and to contribute to a sense of posture and movement (Burgess *et al.*, 1982; Clark *et al.*, 1986; Goodwin *et al.*, 1971; McCloskey, 1978). For static limb position, Clark *et al.* (1986), for example, argue that the nervous system computes joint angles and thus limb position from muscle spindle information about the lengths of muscles that set the positions of joints.

D. Other Peripheral Nerve Afferents

Other afferents in the skin and deeper tissues relate to the sensations of temperature, pain, itch, and crude touch (see Dykes, 1983). In primates, including humans, specific low-threshold thermoreceptive fibers are found that are excited by either warming or cooling the receptive field in the skin while being unresponsive to tactile stimulation (see Darian-Smith, 1984b, and Sumino and Dubner, 1981, for a review). Other thermoreceptive units are polymodal or require heat in the painful range. Slowly adapting skin afferents (SA-I, SA-II) are also sensitive to temperature changes, but are not thought to play a role in temperature sensation.

Pain is signaled by several afferent classes (see Perl, 1984; Willis, 1985). There are two types of nociceptors: A-delta and C polymodal nociceptors. Pricking pain appears to be mediated by A-delta nociceptors and burning pain by C polymodal nociceptors. Mechanical nociceptors (A-delta) in the skin respond to pressure in the noxious and sometimes tactile range, with increased rates of action potentials with increased intensities of stimulation. These nociceptors can be sensitized to noxious heat. Receptive fields are restricted to a number of sensitive spots within a small skin area. A single myelinated axon from each nociceptor loses its myelin sheath as it branches to enter these sensitive locations (spots) in the epidermis. The thin, unmyelinated C polymodal nociceptors respond to noxious mechanical, thermal, and chemical stimuli. Receptive fields are generally either one or two small spots or a larger region of

more uniform sensitivity. Many of these receptors respond to nondamaging stimuli and increase in discharge rate with increases in stimulus intensity. Bradykinin, histamine, acetylcholine, acids, and potassium all activate C polymodal nociceptors.

E. Afferent Pathways

Afferents course from skin receptor and deep receptor locations to combine in nerve fascicles that join other fascicles to form the peripheral nerves. The peripheral nerves branch and segregate into dorsal sensory roots and ventral motor-sensory roots. The afferents that enter the dorsal roots terminate on neurons in the dorsal horn of the spinal cord, or ascend to terminate on neurons in the dorsal column nuclear complex at the junction of the medulla and spinal cord (Figure 24.1).

A number of investigators have attempted to determine the skin regions subserved by the nerves in each spinal root in humans and other mammals (see Dykes and Terzis, 1981, for a review). Dissections have been used to reveal the gross patterns of these dermatomal distributions, but more accurate methods include using the zone of remaining sensibility after section of dorsal roots above and below the one studied, electrical recording or stimulation, interruptions of function produced by ruptured disks, and data from herpes zoster eruptions. For humans, the extensive dermatomal maps are those of Head (1920), based on skin regions affected by herpes zoster; Foerster (1933), from clinical cases where spinal roots were sectioned for the relief of pain; and Keegan (1943), from cases of local sensory loss subsequent to ruptures of intervertebral disks. Dykes and Terzis (1981) point out that these three maps of dermatomes differ considerably, and they suggest that none is accurate. However, the maps in humans, together with the results from other primates, allow several conclusions: (1) The field of each root is continuous, and tends to form a strip perpendicular to the spinal cord. (2) Adjacent dorsal root distributions overlap extensively. (3) There is little overlap at the ventral and dorsal body midlines. (4) There is considerable variability across individuals.

Within dorsal roots, studies in monkeys indicate that there is some crude organization of afferent fibers according to skin location, with distal receptive fields located caudal in the dorsal root, while fibers with proximal receptive fields tend to be rostral (Werner and Whitsel, 1967). These studies also indicate that ascending branches of axons entering the spinal cord in the dorsal columns (Figure 24.1) tend to pre-

serve their order of entry so that axons from lower spinal roots are medial to those from upper spinal roots (Whitsel *et al.*, 1972). In monkeys, inputs from muscle spindles branch and join the cuneate fasciculus for the upper limb, but terminate in the spinal cord for the lower limb.

Some afferent fibers with cell bodies in the dorsal root ganglion turn and enter the ventral root and spinal cord, while other afferents enter the ventral root and then turn and retrace a path back to the dorsal root, as if correcting an error (see Willis, 1985, for a review). These sensory fibers in the ventral root are largely unmyelinated axons and many are nociceptors.

F. Terminations in the Spinal Cord and Dorsal Column Nuclei

Figure 24.4 depicts sensory terminations in the spinal cord and relays to the medulla–spinal cord junction. Termination patterns of peripheral afferents have been investigated in monkeys and other mammals, and some rather consistent features can be assumed to apply to humans. Three general conclusions seem justified. First, the axons of specific types of afferents have characteristic termination patterns in the spinal cord. Second, afferents from different skin regions terminate separately in the spinal cord to form a somatotopic map. Third, afferents ascending to the dorsal column nuclei terminate somatotopically.

The termination patterns of individual axons that have been physiologically identified and labeled with horseradish peroxidase are known only for cats (see Brown, 1981). All the four types of cutaneous afferents bifurcate as they enter the cord to send rostral and caudal branches that further branch to form a sagittally arranged series of terminal arbors. Individual RA-I collaterals form a separate arbor of about 500 μm in the sagittal plane and 50–300 μm in the transverse plane in layers III and IV. Collaterals of PC or RA-II axons terminate in several sagittally elongated arbors (400–750 μm) that extend vertically from layers III and IV to layers V and VI. SA-I axon collaterals give rise to spherical arbors (250–700 μm) that distribute in layers II, III, IV, and the dorsal margin of V. SA-II axon collaterals terminate over layers III, IV, V, and part of VI in rostrocaudally thin sheets (100–300 μm). While all types differ in the details of distribution, the results indicate that inputs from single receptive fields on the skin relate to rostrocaudal rows of cells in the dorsal horn.

For a comprehensive description of Rexed's laminae in the human, see Schoenen and Faull (Chapter 2).

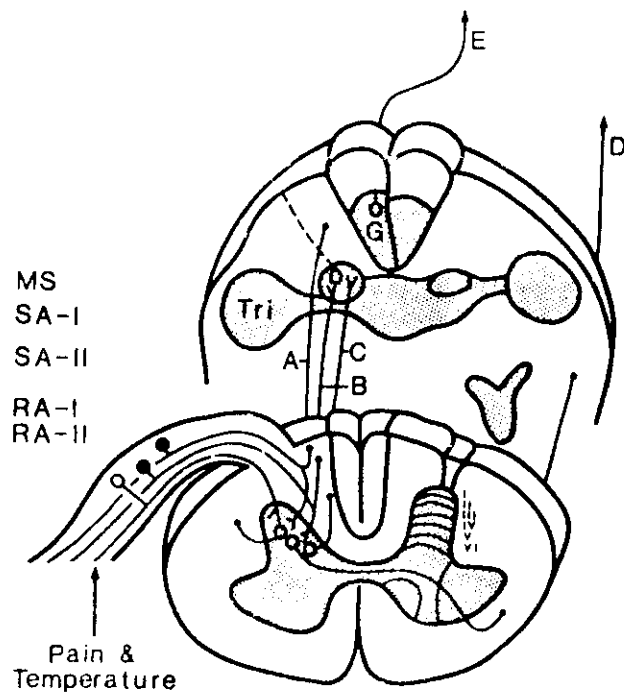


Figure 24.4. Sensory terminations in the spinal cord and relays to the medulla–spinal cord junction. Most large-diameter fibers related to muscle spindle (MS) and slowly adapting (SA-I and SA-II) and rapidly adapting (RA-I and RA-II) receptors enter the cord and send an ascending branch (A and B) to the ipsilateral dorsal column nuclei and another branch to terminate in the region of layer IV of Rexed of the dorsal horn. Second-order neurons then relay ipsilaterally (C) to the dorsal column nuclei or contralaterally (D) to form the spinothalamic tract. Neurons in the dorsal column nuclei relay contralaterally to form the medial lemniscus (E). Small-diameter axons related to pain and temperature terminate largely in layer I of Rexed, and second-order neurons project in various ascending ipsilateral and contralateral pathways. G, Gracile nucleus; Tri, spinal trigeminal nucleus. Redrawn and modified from Darian-Smith (1984a).

Figures 2.8–2.14 depict dendritic morphology of various laminae. Schoenen and Faull also describe the chemoarchitecture of the spinal cord (Chapter 3).

How axons from specific skin regions terminate in the spinal cord is known for a range of mammals, including monkeys. Similarities across species suggest that the termination pattern in humans is similar. Figure 24.5 shows that the terminations from the skin of the digits of the hand are arranged in a rostrocaudal row in the medial dorsal horn of the cervical spinal cord of macaque monkeys (see Florence *et al.*, 1988, 1989). More proximal parts of the limb are represented more laterally in the dorsal horn, and inputs from the foot demonstrate a similarly orderly arrangement. Schoenen and Faull report a reduction of substance P immunoreactivity in the ipsilateral dorsal horn following limb amputations in humans. Sub-

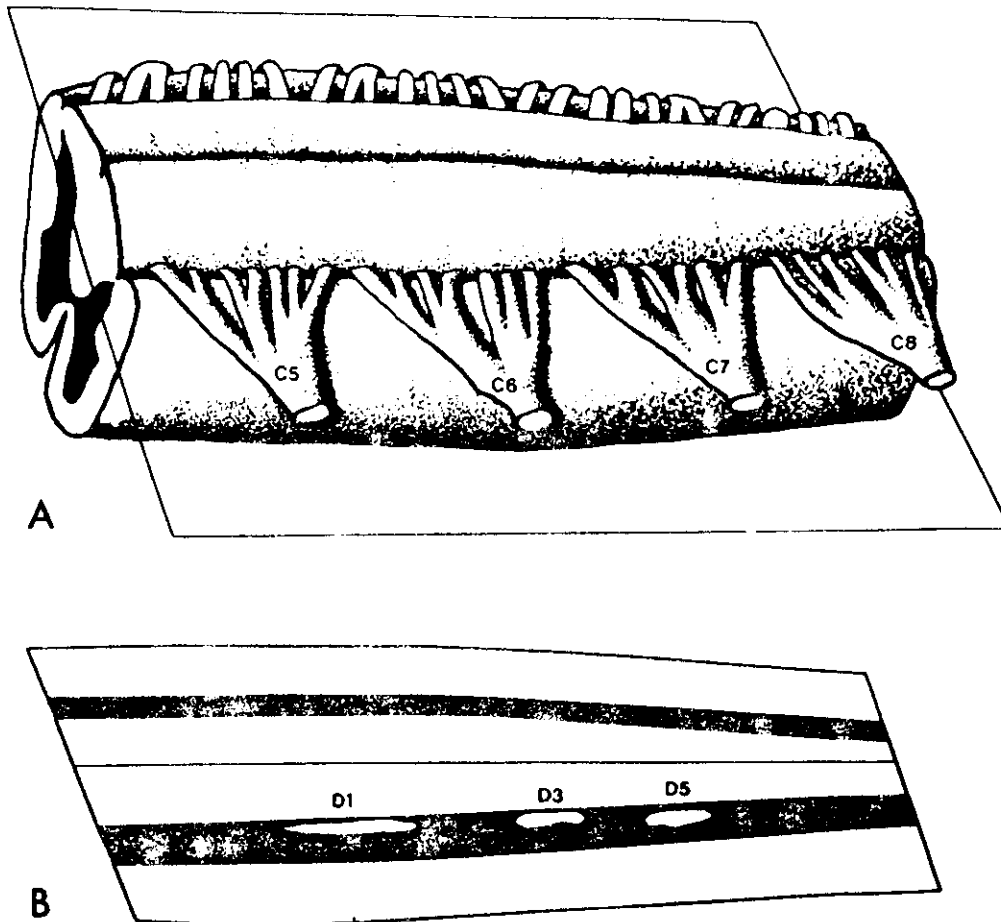


Figure 24.5. The terminations of inputs from the digits of the hand in the dorsal horn of the cervical spinal cord of macaque monkeys. (A) A dorsolateral view of part of the cervical spinal cord and cervical dorsal roots 5–8 shows the plane of the spinal cord section shown in B. The inputs from the skin of digits 1–5, as

demonstrated, in this case, by the transganglionic transport of horseradish peroxidase for digits D1, D3, and D5, are in a rostrocaudal somatotopic pattern in the medial dorsal horn. A similar pattern probably exists in the dorsal horn of humans. Based on Florence *et al.* (1988).

stance P depletion was most pronounced in layers I and II, especially in the medial part of these layers. The mediolateral extent of substance P depletion was proportional to the deafferented territory. It was greatest in the case of below hip amputation (Figure 3.10) and restricted to a narrow medial part of the dorsal horn in the case of a thumb amputation. As for the single axons, groups of axons from a limited skin region terminate in rostrocaudally elongated zones. Thus, body parts are represented in rostrocaudal slabs of cells. While different classes of afferents activate different groups of spinal cord cells, the single zones of label for each digit indicate that the dorsal horn cells activated from a given skin region are grouped together. For further details on sensory nerve terminations in the spinal cord see Schoenen and Grant (Chapter 4).

G. Ascending Spinal Cord Pathways

Traditionally, the ascending somatosensory pathways from the spinal cord include the dorsal column pathway and a ventrolateral pathway. The dorsal column pathway comprises the axons of first-order dorsal root ganglion neurons coursing ipsilaterally to the dorsal column nuclei. The ventrolateral pathway (see below) originates from second-order neurons of the dorsal horn, crosses to the opposite ventrolateral white matter of the spinal cord, and ascends to brain targets, including the ventroposterior nucleus of the thalamus. The ipsilateral dorsal column system was thought to deal with epicritic functions such as position sense and light touch, while the crossed spinothalamic system was thought to mediate protopathic sensibilities of crude touch, pain, and temperature.

Recent research has complicated this story by indicating that (1) second-order neurons also contribute to the ipsilateral dorsal columns; (2) additional ipsilateral pathways from second-order neurons exist, including a phylogenetically reduced spinocervical system; (3) pathways from the upper and lower limbs differ; (4) crossed spinothalamic pathways vary in location; and (5) descending axons are mixed with ascending axons. Of course, these refinements are based on anatomical studies in nonhuman primates and other mammals, but findings are general enough that they are likely to apply to humans.

The Dorsal (Posterior) Column System The extremely large dorsal column afferent pathway in humans occupies over a third of the spinal cord at high cervical levels (Wall, 1970). The two major divisions are the more medial gracile tract subserving the trunk and lower limb and the cuneate tract for the upper limb and associated trunk and neck. Inputs from the face and head via the trigeminal system descend in an analogous tract in the brainstem. The axons in the dorsal columns are largely myelinated dorsal root fibers that branch to ascend to the dorsal column nuclei, send descending collaterals for several segments in the dorsal columns, and emit a number of local collaterals to terminate on neurons in the dorsal horn. Other axons originate from spinal cord neurons and ascend over several segments to terminate in the spinal cord on local circuit neurons or on neurons that project to the brainstem. Some of these sensory neurons project via the dorsal columns to the dorsal column nuclei. Thus, both first- and higher-order axons are found in the dorsal column pathway. A few descending fibers may also travel in the dorsal columns. Entering fibers from each dorsal root form a narrow layer at the lateral margin of fibers from lower levels, but some mixing of levels occurs as the axons ascend.

Most of what is known about the types of information conveyed by the dorsal columns comes from microelectrode recordings in monkeys (Whitsel *et al.*, 1969), although limited recordings in humans revealed nerve fibers activated by pressure and limb movement (Puletti and Blomquist, 1967). The gracile and cuneate tracts differ at high spinal cord levels in the classes of axons they contain. The gracile tract at lower levels contains a mixture of cutaneous afferents, largely rapidly adapting afferents (probably RA-I), and muscle afferents that leave to terminate in Clarke's nucleus, which projects in turn to the cerebellum and other structures via the dorsal spinocerebellar tract. Clarke's nucleus is described by Schoe-

nen and Faull (Chapter 2, Figures 2.5–2.6). The remaining axons that travel to nucleus gracilis are almost completely RA cutaneous afferents. The cuneate tract contains a mixture of RA cutaneous and muscle afferents, but the cutaneous inputs terminate in the cuneate nucleus and the muscle afferents separate to innervate the external cuneate nucleus. Thus, lesions of the dorsal columns deactivate RA neurons, regardless of level, but muscle afferents from the lower body terminate on neurons that relay outside of the gracile tract. Presumably, the dorsal columns of monkeys and humans contain SA-I, SA-II, and PC afferents, as in other mammals (see Willis and Coggeshall, 1978), but evidence is presently lacking. Lesions of the dorsal columns in humans have little effect on many simple tactile abilities, but major defects occur in the abilities to detect the speed and direction of moving stimuli and to identify figures drawn on the skin (Nathan *et al.*, 1986; see Mountcastle, 1984, and Wall and Noordenhos, 1977, for reviews). These changes obviously can be attributed to the loss of inputs from RA cutaneous afferents. Other defects in the control of forelimb movements (Beck, 1976) may relate to disruption of muscle afferents.

Second-Order Axons of the Dorsolateral Spinal Cord (The Spinomedullothalamic System) In monkeys, all of the muscle afferents for the lower body apparently leave the gracile column and synapse on neurons that send axons in the dorsolateral (posterolateral) spinal cord to the dorsal column nuclear complex (Whitsel *et al.*, 1972). In humans, lesions of both the dorsal columns and the dorsolateral spinal cord result in severe defects in proprioception, but it is not certain that all proprioceptive axons from the lower limbs are in the dorsolateral pathway rather than the dorsal column pathway (Nathan *et al.*, 1986).

Many or all mammals have other inputs to the dorsolateral pathway, including a spinocervical pathway from second-order neurons in the dorsal horn that project ipsilaterally to the lateral cervical nucleus. A comparatively reduced lateral cervical nucleus has been described for humans (Truex *et al.*, 1970), but the types of inputs activating this nucleus are known only from studies on other mammals, especially cats (see Mountcastle, 1984, and Willis and Coggeshall, 1978, for reviews). Neurons projecting into the spinocervical tract have receptive fields on both the hairy and glabrous skin in monkeys (Bryan *et al.*, 1974). Peripheral inputs activating these neurons are cutaneous rapidly adapting afferents, and

there is an apparent lack of slowly adapting cutaneous and deep receptor influences.

The Spinothalamic Pathway Many second-order somatosensory neurons have axons that cross in the spinal cord to ascend in the ventrolateral white matter. Many axons in this pathway terminate before reaching the thalamus, but others branch to reach several thalamic nuclei. In monkeys, spinothalamic tract neurons have been found to respond to tactile stimuli and movement of hairs, stimuli ranging from tactile to noxious (wide dynamic range neurons), noxious stimuli, and temperature (see Willis and Coggeshall, 1978). In humans, some capacity for mechanoreceptive sensibility remains after large lesions of other ascending pathways, but electrical stimulation of the ventral quadrants of the spinal cord has produced sensation of only pain and temperature (Sweet *et al.*, 1950; Tasker *et al.*, 1976).

II. Relay Nuclei of the Medulla and Spinal Cord

Several groups of neurons in the spinal cord and medulla are important in relaying information to higher brain centers. These include the dorsal column nuclear complex, the dorsal nucleus of the spinal cord (Clarke's column), and the lateral cervical nucleus. The trigeminal nuclear complex adds analogous pathways for information from the head.

A. Dorsal Column–Trigeminal Nuclear Complex

The dorsal column–trigeminal nuclear complex consists of groups of cells in the lower brain stem and upper spinal cord that receive inputs from ipsilateral low-threshold mechanoreceptors and project to the ventroposterior complex of the thalamus (Figure 24.1). The part of the system originating in dorsal root ganglia and coursing in the dorsal columns terminates in the gracile nucleus for the lower body, and the cuneate nucleus for the upper body. The trigeminal complex receives inputs from cutaneous mechanoreceptors in the face and head. The gracile, cuneate, and trigeminal "nuclei" form a somatotopic map from hindlimb to head in a mediolateral sequence in the lower medulla.

The gracile and cuneate nuclei (see Olszewski and Baxter, 1954) are elongated in the rostrocaudal dimension (Figure 24.5). The overall appearance of the

nuclei in humans is quite similar to that observed in macaque monkeys (Florence *et al.*, 1988, 1989). In both, the middle regions contain discrete clusters of neurons outlined by bands of myelinated fibers. Stains for the mitochondrial enzyme cytochrome oxidase (CO) show that the cell clusters have more of the enzyme and, presumably, higher metabolic activity than the surrounding fiber regions. The details of the parcellation pattern of the nucleus in humans and monkeys are quite comparable, suggesting the significance of the parcellation is the same. In monkeys, specific cell clusters in the central cuneate nucleus correspond to inputs from specific digits of the hand. Thus, the parcellation reflects the somatotopic organization of the nucleus. The rostral and caudal poles of the cuneate nucleus have more convergent terminations from afferents of the digits. Thus, the nucleus appears to segregate inputs into a discrete somatotopic map in the central part of the nucleus and into less precise maps in the rostral and the caudal poles of the nucleus in monkeys, and probably in humans, judging from the close match in appearance. There is evidence from studies in cats (Dykes *et al.*, 1982) that RA-I and SA classes of cutaneous afferents activate neurons in the central zones of the dorsal column nuclei, while SA, joint, and muscle afferents relate to the rostral parts of these nuclei. Pacinian receptor afferents are concentrated caudally.

The projection neurons of the dorsal column nuclei send axons into the contralateral medial lemniscus, where they course to the ventroposterior complex (Rasmussen and Peyton, 1948). In humans, as in other mammals, some axons probably send collaterals to the inferior olive, which, in turn, projects to the cerebellum (see Schroeder and Jane, 1976). In monkeys and other mammals, the dorsal column nuclei, especially the rostral poles, receive inputs from the contralateral somatosensory cortex that may modulate the relay of sensory information (see Cheema *et al.*, 1985, for a review).

The trigeminal complex includes the principal or main sensory nucleus and the spinal trigeminal nucleus. The principal nucleus is thought to be analogous to the cuneate and gracile nuclei, and the three together form one or more systematic representations of cutaneous receptors of the body. The principal nucleus projects via the medial lemniscus to the medial subnucleus of the contralateral ventroposterior complex (VPM). The spinal trigeminal nucleus is analogous to the dorsal horn of the spinal cord. As in the spinal cord, a marginal zone receives pain and temperature afferents and deeper neurons are acti-

vated by cutaneous and muscle receptors (e.g., Price *et al.*, 1976). Second-order neurons in the spinal trigeminal nucleus form a relay that joins the contralateral spinothalamic tract to terminate in the ventroposterior nuclear complex and the more medial thalamus (see Burton and Craig, 1979). The dorsal column–trigeminal nuclear complex is depicted in the plates of Paxinos *et al.* (Chapter 7). These authors, on the basis of acetylcholinesterase distribution and degeneration following therapeutic cordotomies, have changed boundaries of the complex given by Olszewski and Baxter (1954).

B. Lateral Cervical Nucleus, Nuclei X and Z, External Cuneate Nucleus, and Clarke's Column

Second- and third-order relay neurons are found in several structures in addition to the dorsal column–trigeminal complex and the dorsal horn of the spinothalamic system.

Lateral Cervical Nucleus A long column of neurons outside the gray matter proper that extends from C4 to the caudal part of the medulla composes the lateral cervical nucleus. Rapidly adapting afferent fibers serving hairs and other tactile afferents enter the dorsal horn to relay on neurons forming the spinocervical tract in the dorsolateral white matter. These second-order neurons terminate on neurons in the ipsilateral lateral cervical nucleus (Figures 24.1 and 24.4). A subset of multimodal neurons with a convergence of nociceptive afferent inputs has been reported in the lateral cervical nucleus as well (see Boivie, 1978, for a review). The lateral cervical nucleus appears to relay touch, pressure, and vibration information, largely from the hairy skin, to the contralateral thalamus, inferior olive, and midbrain. In humans, the lateral cervical nucleus may be a rudimentary structure, since it is only well defined in some individuals (Truex *et al.*, 1970). In such humans, the nucleus contains up to 4000 neurons, while nearly double that number may exist in cats (Boivie, 1983).

Nuclei X and Z Other second-order axons of the dorsolateral fasciculus, possibly collaterals of spino-cerebellar axons, terminate in two small medullary nuclei, termed X and Z by Pompeiano and Brodal (1957). Muscle spindle afferents for the hindlimb relay via the dorsolateral funiculus to nucleus Z, located just rostral to the gracile nucleus. Nucleus Z, which has been identified in the human brain stem (Sadjadpour and Brodal, 1968), projects to the con-

tralateral thalamus. In monkeys, muscle spindle receptor afferents related to the forelimb relay over neurons projecting within the dorsal columns (Dreyer *et al.*, 1974). This probably also occurs in humans, since lesions of the dorsal columns impair motor control for the upper limbs (Nathan *et al.*, 1986). A separate nucleus X, not clearly present in humans, forms a second group of neurons receiving mostly second-order muscle spindle afferents related to the lower limbs.

External Cuneate Nucleus The muscle spindle afferents of the upper limbs and body course in the cuneate fasciculus to terminate in the external cuneate nucleus. Like nucleus X, the external cuneate nucleus relays to the contralateral ventroposterior complex of the thalamus, and to the cerebellum.

Clarke's Column A long column of cells called Clarke's column is located just dorsolateral to the central canal in the medial part of the spinal cord of T1–L4 levels. Inputs are largely from muscle spindles. Clarke's column projects to nucleus Z and, via the dorsal spinocerebellar tract, to the cerebellum (for reviews, see Mann, 1973, and Willis and Coggeshall, 1978).

III. Somatosensory Regions of the Midbrain

Studies in nonhuman mammals implicate several midbrain structures in somatosensory functions, but evidence for similar roles in humans is presently lacking. (1) Neurons in the external nucleus of the inferior colliculus respond to somatosensory stimuli and receive inputs from the dorsal column nuclei. The pericentral nucleus may have spinal cord inputs as well. Schroeder and Jane (1976) speculate that auditory and somatosensory systems interrelate in these structures in the detection of low-frequency vibratory stimuli. (2) The deeper layers of the superior colliculus contain neurons activated by somatosensory stimuli via inputs from the spinal trigeminal nucleus, the spinal cord, the lateral cervical nucleus, and the dorsal column nuclei (see Huerta and Harting, 1984, for a review). The somatosensory inputs form a representation that is matched in some sense with visual and auditory maps, and the presumed role of the matched maps is to function together in directing eye and head movements toward objects (sounds, touches, and images) of interest (see Meredith and Stein, 1985).

IV. Somatosensory Thalamus

Various proposals have been made for how to subdivide the human thalamus (see Ohye, Chapter 17, for a review), but the thalamic structures related to somatosensory abilities have not been identified with complete certainty. In monkeys, where considerable experimental evidence is available (see Kaas and Pons, 1988), we subdivided the somatic thalamus into a large ventroposterior nucleus (VP), a ventroposterior superior nucleus (VPS), and a ventroposterior inferior nucleus, (VPI) (Figure 24.1). The VP is the principal relay of information from rapidly adapting and slowly adapting cutaneous receptors to anterior parietal cortex, the VPS relays information from deep receptors in muscles and joints, while the significance of the VPI is less certain. In addition, nuclei of the posterior complex (Po) appear to have somatosensory functions. Other nuclei, notably the medial and anterior divisions of the pulvinar complex and the lateral posterior nucleus, are known to have connections with parietal cortex and thereby are implicated in somatosensory functions. However, these nuclei do not appear to have a role in relaying sensory information. The somatosensory nuclei are discussed and related to proposed subdivisions of the human thalamus below. Parts of the medial thalamus with spinothalamic inputs and apparently nociceptive functions are reviewed by Craig (1987).

A. Ventroposterior Nucleus

The VP is a basic subdivision of the mammalian thalamus (Jones, 1985; Welker, 1974) that is characterized by (1) densely packed and darkly stained neurons, (2) a systematic representation of cutaneous receptors, (3) inputs from the dorsal column nuclei, the spinothalamic tract, and the trigeminal system, and (4) projections to "primary" somatosensory cortex. The nucleus has subnuclei of dense aggregates of neurons partially separated by cell-poor fiber bands, the most conspicuous of which is the arcuate lamina which separates the part of VP representing the face, the ventroposterior medial "nucleus" (VPM), from the portion representing the rest of the body, the ventroposterior lateral "nucleus" (VPL). Another notable fiber band separates the representations of the hand and foot in VPL.

In macaque monkeys, the dorsal boundaries of VP are not very distinct from the region we now identify as VPS. The "VP" of some investigators includes VPS, although this region has also been distinguished

as the VP "shell." Another problem is that Olszewski's (1952) popular atlas of the thalamus of macaque monkeys includes additional parts of the thalamus related to motor cortex within an oral division of VPL ("VPL_o"). This use of terminology is not consistent with that used in other mammals.

In the human thalamus, the region identified by Ohye (Chapter 17) as the "ventrocaudalis group" or Vc corresponds closely to our VP in monkeys. Using the terminology of Hassler (1982), Ohye refers to VPL as Vce (the external segment) and VPM as Vci (the internal segment). As described by Ohye, VP is composed of a range of neuron sizes that generally stain densely for Nissl substance. The dorsal border of the nucleus is described as indistinct, but medial borders with the anterior pulvinar and ventral borders with the VPI are distinct.

The VP contains a single systematic representation of cutaneous receptors. Each location on the body surface activates a small volume of tissue or cluster of neurons in VP, and these clusters of neurons are arranged according to body part. The general form of the somatotopic organization in mammals has been reviewed by Welker (1974), and described in detail for squirrel monkeys by Kaas *et al.* (1984; see Figure 24.6). In all primates, including humans, we can expect the tongue and oral cavity to be represented medial to the lips and upper face in VPM. For a detailed description of the gustatory part of VPM, the so-called VPM parvocellular part (VPMPC), see Norgren, Chapter 25, and Ohye, Chapter 17. The medial portion of VPL contains a mediolateral sequential representation of the digits of the hand from thumb to little finger. The lateral portion of VPL is devoted to the foot, while dorsal portions of the nucleus relate to the proximal leg, the trunk, and the proximal arm in a lateromedial sequence. This arrangement, found in monkeys and in other mammals, is basically the order described for the human VP. Recordings and electrical stimulation with microelectrodes in VP of the human thalamus (Emmers and Tasker, 1975; Lenz *et al.*, 1988) indicate that the mouth and tongue relate to ventromedial portions of VPM, that the hand and foot are in ventrorostral VPL, and the back and neck are in dorsocaudal VPL. Furthermore, the fingers activate a large portion of medial VPL and the lips and tongue relate to a large part of VPM. Figure 17.10 displays the response of neurons in the human ventroposterior nucleus (probably VPL) following tactile stimulation of the tip of the contralateral thumb (a restricted receptive field). Finally, often groups of neurons extending the parasagittal plane are activated by the same restricted

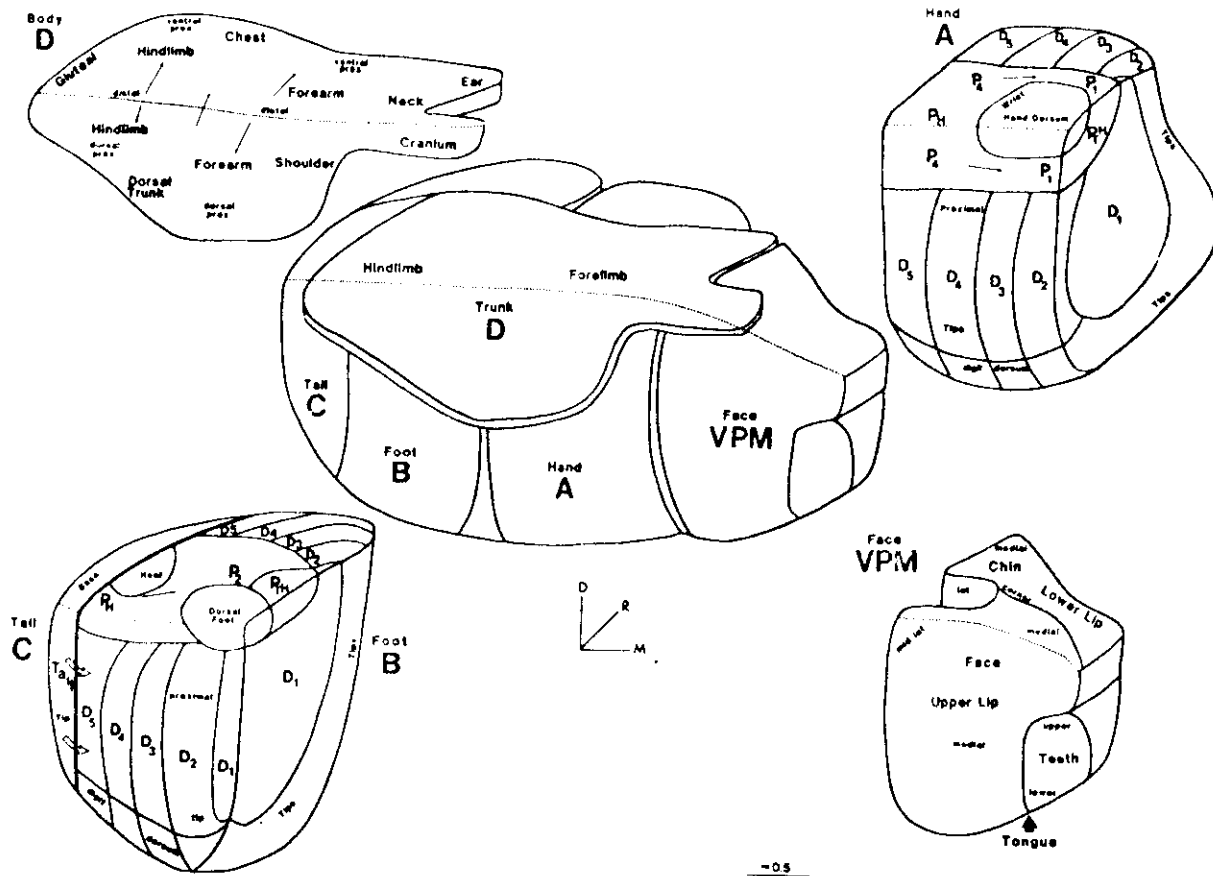


Figure 24.6. The somatotopic organization of the ventroposterior nucleus of squirrel monkeys. Except for the lack of a lateral region devoted to the tail, a similar organization appears to exist in VP of humans (Lenz *et al.*, 1988). Traditionally, VP is divided into two divisions, ventroposterior medial (VPM) for the face and

ventroposterior lateral (VPL) for the rest of the body. VPL is further divided here into subnuclei for the hand (A), foot (B), tail (C), and trunk and proximal limbs (D). The figure shows where body parts are represented in the subnuclei and how the subnuclei fit together. From Kaas *et al.* (1984).

skin surface, indicating that lines of isorepresentation are largely in the parasagittal direction.

As in monkeys (e.g., Dykes *et al.*, 1981), most neurons in VP of humans are activated by RA-I or SA inputs, with local clusters of cells related to one or the other class of inputs (Lenz *et al.*, 1988). Thus, there is a double mosaic representation of the skin in VP, one for RA-I afferents and one for SA afferents. The SA inputs could be SA-I or both SA-I and II. There is little evidence for Pacinian (RA-II) inputs. A few neurons respond with an increasing frequency as light tactile stimuli become more intense and extend into the painful range (the wide-dynamic-range neurons); these neurons may have a role in pain perception (see Kenshalo *et al.*, 1980). In humans, electrical stimulation of peripheral nerves results in evoked potentials in the contralateral VP with a latency of 14–17 msec (Celesia, 1979; Fukushima *et al.*, 1976). Electrical stimulation of sites in the nucleus or

of input fibers in the medial lemniscus generally results in sharply localized sensations of numbness or tingling rather than light touch (Emmers and Tasker, 1975; Ervin and Mark, 1964; Tasker *et al.*, 1972). Localized lesions of VP are followed by a persistent numbness in a restricted skin region corresponding to the body surface map in VP (Domino *et al.*, 1965; Garcin and LaPresle, 1960; Van Buren *et al.*, 1976).

The sources of ascending inputs to VP (Figure 24.1) have been studied in many mammals including macaque monkeys. The dense inputs are from the dorsal column nuclei via the medial lemniscus and the main sensory trigeminal nucleus via the trigeminal lemniscus (quintothalamic tract). In humans, evoked potentials have been recorded in VP after electrical stimulation of the dorsal columns (Gildenberg and Murthy, 1980). Less dense, unevenly distributed inputs are from the spinothalamic tract and the lateral cervical nucleus (see Berkley, 1980, for de-

tails). In humans, degenerating spinothalamic terminations have been reported in VP after spinal cord damage (Mehler, 1966; see Bowers, 1957, for a review of classical reports).

The outputs of the ventroposterior nucleus have been studied extensively in primates and other mammals (see Kaas, 1983; Kaas and Pons, 1988, for a review). In all mammals studied, VP projects to area 3B or its nonprimate homologue, S-I. In most mammals, other projections are to the second somatosensory area (S-II) and possibly other fields, but in monkeys, and probably humans, projections to S-II are a trivial component of the output. In monkeys, VP also projects over thinner axons and in a less dense manner to area 1, and, in macaque monkeys, a sparse input exists to part of area 2 related to the hand and even a specialized part of area 5 (Pons and Kaas, 1986). In humans, lesions of anterior parietal cortex including areas 3b and 1 cause retrograde degeneration and cell loss in VP (Van Buren and Borke, 1972), supporting the conclusion that the output patterns in humans and monkeys are similar. Furthermore, recordings from the surface of somatosensory cortex indicate that potentials evoked by median nerve stimulation are reduced or abolished by lesions of VP (Domino *et al.*, 1965).

B. Ventroposterior Superior Nucleus

There has been long-standing recognition that inputs from receptors in deep tissues are at least partially segregated from inputs from cutaneous receptors in the ventroposterior thalamus of primates (see Poggio and Mountcastle, 1963) and perhaps other mammals. The zone of activation by deep receptors is dorsal to that related to cutaneous receptors in monkeys, and the deep receptor zone is further distinguished by its unique connections and architecture. We have termed the deep receptor zone the ventroposterior superior nucleus (VPS; see Kaas and Pons, 1988). Early investigators included the zone of activation by deep receptors in VP, and several recent researchers simply designate the deep receptor zone as the VP "shell." Others conclude that the deep receptor zone includes two nuclei, a VPS and a "ventroposterior oral" nucleus (see Dykes, 1983), but the evidence for such a subdivision in primates is inconclusive. Finally, the medial posterior nucleus of some investigators (see Krubitzer and Kaas, 1987, for a review) may be a nonprimate homolog of VPS.

In monkeys, VPS contains a representation of deep receptors, principally muscle spindle receptors (see Kaas and Pons, 1988; Wiesendanger and Miles,

1982). The representation parallels that in VP so that the face activates the medial portion, the hand the middle portion, and the foot the lateral portion of VPS (Kaas *et al.*, 1984). The major input appears to be from the external cuneate nucleus (Boivie and Boman, 1981), and the output is largely or exclusively to area 3a and area 2. Many of the same neurons in VPS appear to project to both area 3a and area 2 via collaterals (Cusick *et al.*, 1985).

Evidence is less complete for VPS of humans. Deep receptors are represented in an orderly manner in part of the thalamus just rostradorsal to the cutaneous representation in VP (Lenz *et al.*, 1988). The mediolateral progression in the representation corresponds to that in VPS with the jaw medial to fingers, followed by wrist, elbow, shoulder, and leg. VPS is probably within VP of most descriptions of the human thalamus. However, Hassler (1959) recognized a ventrointermedius (Vim) nucleus that may include the present VPS nucleus.

An extensive description of Vim is given by Ohye (Chapter 17). Hassler (1959) concluded that Vim (like VPS) projects to area 3a, although the autopsy material used as evidence (also see Van Buren and Borke, 1972) is limited to cases with large lesions that include area 3a and result in retrograde degeneration in Vim, and cases with more caudal lesions without notable change in Vim. In the clinical setting, recordings have been obtained from the Vim region in humans and Ohye reviews these data in detail (also see Albé-Fessard *et al.*, 1966). In summary, neurons respond during active and passive movements and to compression of muscles and joints, and never to tactile stimulation. Thus, muscle and joint receptors provide the principal or sole activation of Vim neurons. Overall, the recordings demonstrate a somatotopic organization that is consistent with that observed in VPS of monkeys. Thus, the hindlimb, hand, and face are represented in a lateromedial sequence in Vim (see Figure 17.9) as in VPS. Furthermore, electrical stimulation of peripheral nerves activates neurons with a latency (11–12 msec) that is consistent with a direct input from second-order neurons in the external cuneate nucleus (and possible spinothalamic tract neurons). Small restricted coagulations in the Vim region reduce tremor and produce an impression of "weakness" or uncertainty for the affected limb, without altering tactile sensation (Chapter 17). However, most investigators (e.g., Van Buren *et al.*, 1976) include most or all of Vim within the ventrolateral nucleus (VL, or VPL_o, of Olszewski, 1952, for monkeys) as identified by cerebellar inputs. Thus, VPS as a separate nucleus relaying muscle spindle informa-

tion to area 3a and area 2 has not been clearly identified in humans. VPS may be part of VP or Vim of some descriptions.

C. Ventroposterior Inferior Nucleus

In all primates, VPI is easily recognized as a narrow region just ventral to VP that is composed of small, pale-staining neurons. VPI is densely myelinated and reacts lightly for cytochrome oxidase. VPI extends dorsally into the cell-poor regions that separate face, hand, and foot subnuclei of VP. Inputs are uncertain, but include the possibility of spinothalamic terminations. Evidence has been presented for Pacinian receptor activation (see Dykes, 1983), but the evidence is equivocal and the nature of the input projections has not been determined. The outputs have been shown to be largely or completely to the second somatosensory area of cortex (see Friedman and Murray, 1986). Using Hassler's term, ventrocaudalis parvocellularis, Ohye (Chapter 17) describes VPI of humans. The general appearance of the human VPI closely resembles that of monkeys. Inputs are unknown, but autopsy material indicates a projection to the cortex of the lateral fissure in the general region of S-II (Van Buren and Borke, 1972). In monkeys, VPI projects to S-II (Friedman and Murray, 1986; Krubitzer and Kaas, 1986).

D. Posterior Complex of Nuclei

A poorly defined group of nuclei with somatosensory, auditory, and multimodal functions, located just caudal to the ventroposterior complex, has been referred to as the posterior group or complex (Jones, 1985). The complex is commonly divided into separate limitans, suprageniculate, and posterior nuclei. The posterior "nucleus" is often subdivided into medial, lateral, and even intermediate nuclei. The medial posterior nucleus (Pom) is composed of small cells that seem to merge with caudal VPI. There is some evidence that neurons with large cutaneous receptive fields and multinodal responses in the lateral cervical nucleus relay to Pom (see Metherate *et al.*, 1987, for a review). Cortical projections of the posterior complex appear to be to cortex of the lateral fissure near S-II.

E. Anterior Pulvinar, Medial Pulvinar, and Lateral Posterior Nucleus

Other thalamic structures without direct inputs from second-order somatic afferents can be considered

part of the somatosensory system on the basis of connections with somatosensory cortex. These include the anterior (oral) pulvinar with widespread projections to anterior parietal cortex, posterior parietal cortex, and somatosensory cortex of the lateral fissure; the medial pulvinar with connections with posterior parietal cortex and the temporal lobe (see Mesulam, 1981); and the lateral posterior nucleus with projections to posterior parietal cortex (see Kaas and Pons, 1988). In humans, degeneration has been noted in the anterior pulvinar after damage to parietal cortex of the lateral fissure, while LP degenerates after lesions of posterior parietal cortex (Van Buren and Borke, 1972). The roles of these nuclei in the processing of somatosensory information are unknown, but the lack of direct sensory input and the widespread cortical connections suggest modulatory and integrative functions.

V. Anterior Parietal Cortex

The anterior parietal cortex was first considered as several separate fields in early architectonic studies, then as a single primary somatosensory field or S-I on the basis of electrophysiological studies in monkeys (see Marshall *et al.*, 1937), and more recently as several fields again, as the validity of early subdivisions has been experimentally supported (see Kaas, 1983). These subdivisions are diagrammatically depicted in Figure 24.8 and can be compared directly with the photomicrograph (Figure 22.13) of Zilles in Chapter 22.

Early attempts to subdivide anterior parietal cortex (see Figure 24.7) included efforts by Campbell (1905), Smith (1907), Brodmann (1909), Vogt and Vogt (1919), and von Economo and Koskinas (1925). The subdivisions made by Campbell and Smith fell into disuse, but the proposals of Brodmann, Vogt and Vogt, and von Economo are in use today. In brief, Brodmann distinguished a mediolateral strip of cortex in the caudal bank of the central (Rolandic) fissure as area 3, an immediately superficial and caudal strip on the caudal lip of the sulcus as area 1, and a more caudal strip on the surface of the postcentral gyrus as area 2. Area 3 was described as a field with densely packed small granule cells in layer IV, as is characteristic of sensory fields, while area 1 and 2 had less dominant sensory features. Brodmann further described a "transitional" field in anterior (deep) area 3 with both prominent sensory (layer IV granule cells) and motor (layer V pyramidal cells) features. Vogt and Vogt (1919) added to this proposal by stress-

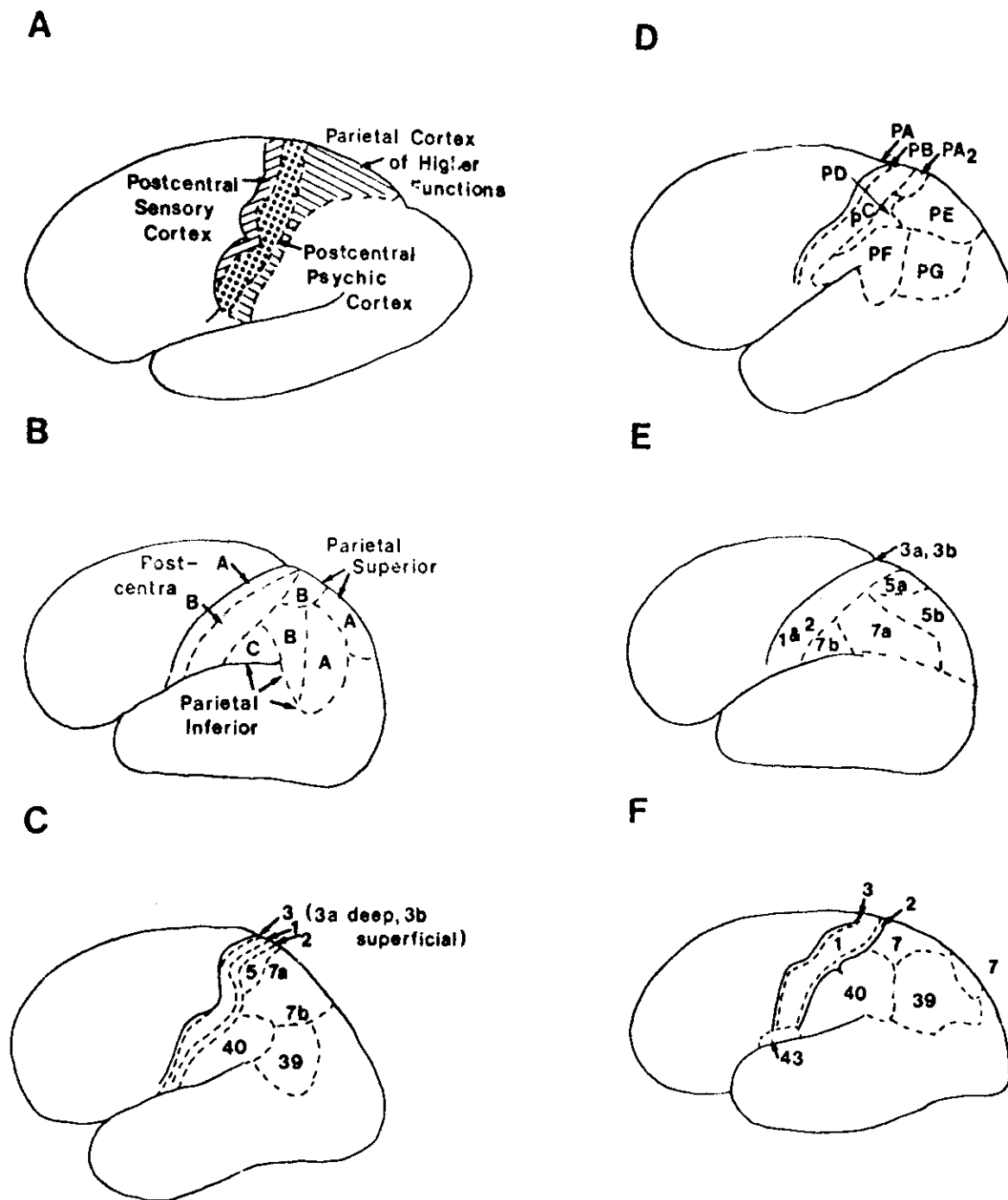


Figure 24.7. Early concepts of how parietal cortex of humans is subdivided into architectonically distinct and functionally significant areas. Only the parietal areas are reproduced here. (A) The first complete map of the human cortex was by Campbell (1905). His postcentral sensory area includes both area 3b and area 1, while his postcentral psychic cortex includes area 2 and parts of posterior parietal cortex. (B) A later architectonic map, based on the staining of myelinated fibers, produced by Smith (1907). His area postcentralis A roughly corresponds with areas 3b and 1 combined, while area postcentralis B approximates area 2. (C) The most influential cortical map was that of Brodmann (1909), which included the currently used subdivisions of area 3 (areas 3a and 3b), area 1, and area 2. However, area 3b on the caudal bank of

the postcentral sulcus does not quite extend up to the surface of brain and onto the lip of the postcentral sulcus, and area 1 probably does not extend as far caudally as shown. (D) The cortical map of von Economo and Koskinas (1925) introduced the only other terminology besides Brodmann's that is in wide use today. Area PA (area 3a) is in the depths of the central sulcus, and area PB (area 3b) is on the caudal bank of the central sulcus. Area PC includes both area 1, which extends slightly onto the upper part of the central sulcus, and area 2 of the present report. (E) Vogt and Vogt (1919, 1926) described the boundaries of 3a and 3b, and delimited other fields in parietal cortex after the scheme of Brodmann. Illustration modified from summary in Penfield and Jasper (1954). (F) A more recent map by Sarkissov *et al.* (1955).

ing the distinctiveness of anterior area 3, and subdivided area 3 into two fields, area 3a and area 3b (see Jones and Porter, 1980, for a review). These four architectonically defined subdivisions of postcentral somatosensory cortex are in common use today. However, some investigators use the terms of von Economo (1929) for these subdivisions.

Rather than number cortical fields, von Economo used two letters to denote fields, with the first letter indicating the lobe of the brain for the field, and the second letter indicating the order in which fields were described in the lobe, typically starting with fields of obvious sensory nature. In general, Brodmann (1909) and von Economo (1929) divided the human brain in different ways, but the proposed subdivisions of anterior parietal cortex are quite similar, the agreement suggesting the validity of the divisions. von Economo's most anterior field, deep in the central sulcus, is area PA, equivalent to area 3a. The adjacent field, area PB, was denoted as sensory "koniocortex" due to the powderlike appearance of the small granule cells in layer IV of what clearly corresponds to area 3b. Area PC, characterized by a less distinct laminar structure, is equivalent to area 1. A more caudal strip of cortex, with a more distinct layer IV and layer VI, is area PD, closely corresponding to area 2. Figure 23.7 of this chapter as well as Figures 22.11 and 22.12 show the most influential of the parietal lobe maps.

A. Anterior Parietal Cortex in Monkeys

Over the last few years, research on monkeys has greatly clarified the significance of the four architectonic strips. Conclusions based on an extensive number of anatomical and electrophysiological studies are briefly summarized below (see Kaas and Pons, 1988, for a more extensive review).

Area 3b We have termed area 3b "S-I proper" because it appears to be the homolog of the primary somatosensory area, S-I, in nonprimates (Kaas, 1983). Area 3b contains a separate, complete map of the cutaneous receptors of the body. The representation proceeds from the foot in medial cortex to the face and tongue in lateral cortex, with the digits of the foot and hand pointing "rostrally" (or more precisely, deep in the central sulcus), and the pads of the palm and sole of the foot caudal in 3b near the area 1 border. The activation of area 3b neurons is from RA-I and SA (I and II?) afferents relayed from the ventroposterior nucleus. RA-I and SA inputs appear to be segregated into bands (columns) in layer IV (Sur *et al.*, 1984). At least 70% of the neurons in VP proj-

ect to area 3b via thick rapidly conducting afferents. Major outputs of area 3b are to area 1, area 2, and S-II, and these fields provide feedback inputs. Area 3b is callosally interconnected with areas 3b, 1, and 2, and S-II of the opposite hemisphere. The callosal connections are unevenly distributed, with the large representation of the glabrous hand and foot having less dense connections. The excitatory receptive fields do not reflect the callosal connections, which may contribute to surround suppression or enhancement, but instead are confined to locations on the contralateral body surface. In monkeys, inactivation or lesions of area 3b result in impairments in all but the crudest of tactile discriminations involving texture and shape (Hikosaka *et al.*, 1985; Randolph and Semmes, 1974). Small objects are unrecognized by touch and are ignored.

Area 1 Like area 3b, area 1 contains a systematic representation of the body surface. The representation parallels and also roughly mirrors that in area 3b. Thus, the foot, leg, trunk, forelimb, and face are represented in a mediolateral cortical sequence (as in area 3b), but the digit tips are represented caudally near the area 2 border rather than rostrally near the area 3b border. Most neurons in area 1 are rapidly adapting and respond as if they were related to RA-I cutaneous receptors. A small proportion of neurons, perhaps 5%, respond as if activated by RA-II (Pacinian) afferents. Neurons in area 1 tend to have larger and more complex receptive fields, including strong suppressive or inhibitory surrounds, than area 3b neurons (Sur, 1980; Sur *et al.*, 1985). Some neurons code for the direction of movement on the skin (Hyvärinen and Poranen, 1978). The activity patterns of most area 1 neurons, but not area 3b neurons, are modified according to what motor behavior will follow the stimulus (Nelson, 1984). Area 1 receives strong activating inputs from both area 3b and the ventroposterior nucleus. The VP inputs are partly from collaterals of neurons projecting to area 3b, and the terminations are largely of thinner axons than those to area 3b. Feedforward cortical outputs are predominantly to area 2 and S-II, and feedback inputs are from these fields. Callosal connections are more evenly distributed than for area 3b, but connections in the hand, foot, and parts of the face regions remain sparse. In monkeys, lesions impair discriminations of texture rather than shape (Carlson, 1981; Randolph and Semmes, 1974).

Area 2 This field contains a complex representation of both cutaneous and noncutaneous receptors. Neu-

rons appear to be influenced by cutaneous receptors, deep receptors, or both. The portions of area 2 related to the hand and face are most responsive to cutaneous stimulation. The representation is in parallel with those in areas 3b and 1 so that the foot, trunk, hand, and face form a mediolateral cortical sequence. A mirror reversal organization of that in area 1 is apparent for parts of area 2 near the area 1 border. However, the overall organization is more complex than in areas 3b and 1, and some body parts are represented more than once in area 2 (Pons *et al.*, 1985b). Receptive fields for neurons in area 2 are typically, but not always, larger than those for neurons in areas 3b and 1, and receptive field properties appear to be complex. Many neurons are best activated by stimuli of certain shapes or directions of movement. The inputs from deep receptors are largely those related to muscle spindles, suggesting that area 2 combines information about limb and digit position with tactile information during active touch. The major thalamic input to area 2 is from VPS (Figure 24.8), but a sparse input to the hand region of area 2 originates in VP. Major cortical inputs are from areas 1, 3b, and 3a. There also appear to be sparse inputs from motor cortex and the supplementary motor area. Major outputs are to subdivisions of posterior parietal cortex, and to S-II. Callosal connections are fairly evenly distributed and include the hand representation. Neurons, however, have excitatory receptive fields only on the contralateral body. Lesions of area 2 in monkeys impair finger coordination (Hikosaka *et al.*, 1985) and discriminations of shape and size (Carlson, 1981).

Area 3a This field in the depth of the central sulcus forms the fourth systematic representation of the body in anterior parietal cortex. Area 3a is largely activated by muscle spindle and other deep receptors, but some cutaneous activation is apparent also, especially in the portion devoted to the hand. The representation parallels that in area 3b, but few details are known. Neurons in area 3a are responsive during movements and are influenced by behavioral intentions ("motor-set," see Nelson, 1984). The major input is from VPS (or the ventroposterior oral nucleus of some investigators), and roughly half of the VPS neurons project to both area 3a and area 2, thus providing the same information. Area 3a projects to area 2, motor cortex, S-II, and other fields. Callosal connections are uneven, but the hand region is more densely connected than in area 3b.

Subcortical Projections of Anterior Parietal Cortex All four fields project to a number of sub-

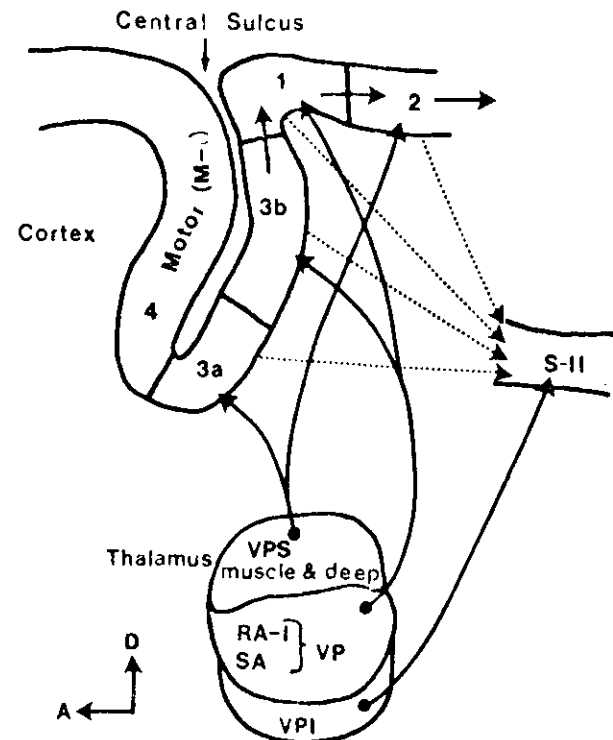


Figure 24.8. The relationship of areas 3a, 3b, 1, and 2 relative to the central sulcus in humans. Compare with the photomicrograph in Figure 22.13. Major inputs from the thalamus and some of the cortical connections are indicated. VP, Ventroposterior nucleus; VPS, ventroposterior superior nucleus; VPI, ventroposterior inferior nucleus; RA-I, class I rapidly adapting cutaneous afferents; SA, slowly adapting cutaneous afferents; S-II, the second somatosensory field in the lateral sulcus; A, anterior; D, dorsal.

cortical fields including feedback to the thalamic relay nuclei, the basal ganglia, the anterior pulvinar, the pons, the dorsal column nuclei, and the spinal cord (see Kaas and Pons, 1988). These projections presumably function in modifying motor behavior and sensory afferent flow.

B. Anterior Parietal Cortex in Humans

Evidence from clinical cases with lesions or where parts of cortex were electrically stimulated or recordings were obtained, as well as information based on recording through the skull, support the conclusion that the organization and functions of anterior parietal cortex in humans are similar to those in monkeys.

Architectonic Fields As in monkeys, four architectonic fields can be identified in the anterior parietal cortex of humans, areas 3a, 3b, 1, and 2 (see Figure 22.13). Somewhat surprisingly, these fields have never been adequately delimited in humans. However, even in monkeys, various investigators differed

considerably on how they placed some of the boundaries of the fields. Therefore, electrophysiological and connective evidence proved to be of great benefit in evaluating the significance of architectonic change. Some of the variability in early brain maps of humans is apparent in Figure 24.7. Braak (1980) provides an excellent review of architectonic studies of the human brain, discusses and illustrates previous architectonic maps, and includes a map of his own. There is considerable disagreement and no map seems adequate even for subdivisions of anterior parietal cortex, which are more obvious than most fields.

Figure 24.8 provides a rough approximation of the location of the four fields at about the middle of the postcentral gyrus. *Area 3a* can be seen at the depths of the cortical sulcus, where it extends somewhat from the posterior to the anterior bank. This field was described as part of area 3 by Brodmann (1909) and distinguished as area 3a by Vogt and Vogt (1919). In area 3a, layers IV and VI are less pronounced than in area 3b, and layer V pyramidal cells are more obvious. *Area 3b* occupies roughly the middle half or more of the posterior bank of the central sulcus. The field appears on the surface as the central sulcus ends near the medial wall, and the field extends into the medial wall. Area 3b is easily distinguished over most of its extent by the dense packing of small cells in layer IV, and the relatively dense packing of cells in layer VI. The small cells have led to the terms "konocellular cortex" and "parvicellular core." Most investigators show area 3b as ending with the lateral extent of the central sulcus (Figure 24.7; also see Braak, 1980, for a review), but area 3b extends anteriorly past the end of the sulcus in monkey, where it represents the mouth and tongue. However, these body parts may be represented more medially in humans (see below). *Area 1* occupies the anterior lip of the postcentral gyrus where it borders area 3b on the posterior bank of the central sulcus and extends over the anterior third of the postcentral gyrus. Layers IV and VI are less densely packed with cells than is area 3b, so the overall appearance is of less conspicuous lamination. Area 1 would roughly correspond to the posterior half of the postcentral area of Campbell (1905), and the full extent (allowing for a protrusion onto the upper bank of the central sulcus that is not shown) of area 1 of Brodmann (see Figure 24.7). Area 1 is unlikely to be as wide as area PC of von Economo and Koskinas (1925) (Figure 24.8), area 1 of Sarkossov and co-workers (see Braak, 1980), or the medial half of the paragrannular belt of Braak (1980). *Area 2* is characterized by a denser layer IV than is found in area 1. The caudal border is difficult to delimit in monkeys even with the aid of electro-

physiological data, and the location of this border remains uncertain in humans. However, the expected width of area 2 would approximate that of area 1.

Evidence for Functional Distinctions and Somatotopy from Surface and Scalp Recordings As part of efforts to localize abnormal tissue and for other clinical reasons, recordings have been made from the scalp, the surface of anterior parietal cortex, and depth probes in the cortex of area 3b of a number of patients. In addition, neuromagnetic recordings and scalp-evoked potentials have been recorded from healthy volunteers. Such recordings support the viewpoint that separate representations exist in areas 3a, 3b, 1, and 2.

1. Electrical stimulation of cutaneous afferents in the median nerve of the hand results in a focus of evoked potentials after 20–30 msec in area 3b of the caudal bank of the central sulcus and a second focus after 25–30 msec in area 1 of the dorsolateral surface of postcentral cortex (see Allison *et al.*, 1988). The two foci support the view that area 3b and area 1 have separate maps of the body surface. The area 1 potentials are caudal to the area 3b potentials, indicating parallel maps, although a slight medial shift of the area 1 focus suggests a small displacement of one map relative to the other. As in monkeys, activity was generated only from stimulating contralaterally.

2. Stimulation of muscle afferents from the human hand results in a focus of activity that is caudal to that for cutaneous afferents (Gandevia *et al.*, 1984). A reasonable interpretation of this result is that the muscle afferents activate area 2, which is caudal to the activity produced in areas 1 and 3b by cutaneous afferents.

3. Another focus of activity produced by deep receptor or muscle spindle afferents is deep to foci related to cutaneous stimulation. Using neuromagnetic recordings, Kaukoranta *et al.* (1986) found that mixed nerve stimulation resulted in a deeper focus of activity in the central sulcus than cutaneous nerve stimulation. The results were interpreted as evidence for muscle spindle receptor input to area 3a and cutaneous receptor input to area 3b.

Recordings of evoked activity also support the conclusion that the maps of receptor surfaces in anterior parietal cortex are organized much as they are in monkeys. Thus, electrical stimulation of the little finger activates cortex 1–2 cm medial to that activated by stimulating the thumb (see Hari and Kaukoranta,

1985), and activity evoked in cortex by tapping the tongue is lateral to that produced by tapping the finger (Ishiko *et al.*, 1980). Measurements of magnetic fields, thought to be generated in the depths of the central sulcus in area 3b, indicated that the thumb, index finger, and ankle are represented at successively more medial positions (Okada *et al.*, 1984).

The most extensive observations on the organization of postcentral cortex in humans obtained from direct surface recordings of evoked potentials are those reported by Woolsey *et al.* (1979). In a sequence of recording sites along the posterior lip of the central sulcus, from near the medial wall to over two-thirds of the distance to the lateral (Sylvian) sulcus, potentials were evoked from foot, leg, thigh, trunk, and hand. In individual patients, there was some notable variability in organization, so that the leg representation extended from the medial wall onto the dorsolateral surface in some but not other cases.

Sensations and Movements Produced by Electrical Stimulation More details about the sequence of representation of body parts in postcentral cortex have been obtained by electrically stimulating the brain in patients. Using higher levels of stimulating current than used for motor cortex, Foerster (1931, 1936a) was able to produce a postcentral motor map that roughly matched the precentral motor map in a mediolateral cortical order of leg, hand, and face. Penfield and Rasmussen (1950) also reported evoked movements for postcentral stimulation sites, with the postcentral motor map roughly paralleling the precentral motor map in mediolateral organization. In addition, sensations could sometimes be elicited from sites in motor and premotor cortex.

The most precise information about the somatotopic organization of postcentral cortex has been obtained by noting where sensations are located during electrical stimulation of cortical sites. As one might expect, sensations evoked from stimulating cortex match in somatotopic location the source of afferents related to the stimulation sites. Thus, stimulating cortex where evoked responses were obtained to ulnar nerve stimulation resulted in sensations largely confined to the ulnar hand (Jasper *et al.*, 1960).

The extensive report of Penfield and Boldrey (1937) summarizes the results from stimulating precentral and postcentral cortex in 163 patients. Stimulation sites resulting in sensations were scattered over the precentral and postcentral gyri, and even a few more posterior or more anterior sites were effective. However, the vast majority of sites were along the

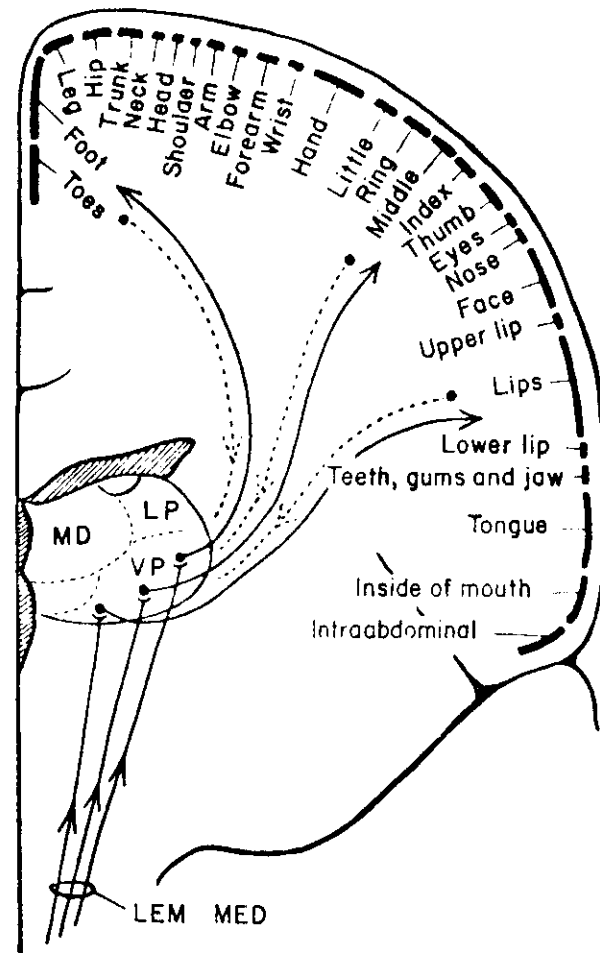


Figure 24.9. The sensory sequence revealed by electrical stimulation of the surface of postcentral somatosensory cortex (largely area 1) in humans. LP, lateral posterior complex; VP, ventroposterior nucleus. From Penfield and Jasper (1954).

posterior lip of the central sulcus and were probably evoking sensations by activating neurons in area 1 and perhaps even deeper to the electrode site in the superficial segment of area 3b. Surprisingly, the evoked sensations were not of light touch, but were described as a localized numbness, tingling, or, infrequently, the feeling of movement. Figures 24.9 and 24.10 summarize the conclusions based on these cases. Sensations were evoked from cortex extending from the medial wall, where the foot is represented, to the lateral fissure, where the mouth is represented. In general, the sensory order corresponds to the detailed maps compiled for monkeys (e.g., Nelson *et al.*, 1980). As in monkeys, cortex devoted to the region of the genitals was most ventral on the medial wall, but a split representation of the leg, with the posterior leg ventral to the foot, followed by the anterior leg, was not evident in humans. In both mon-

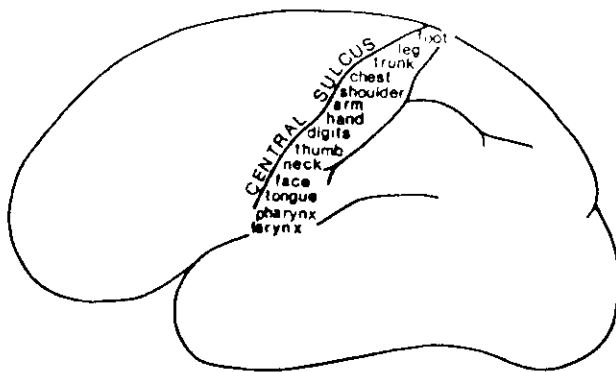


Figure 24.10. The order of representation in postcentral cortex based on motor and sensory effects with electrical stimulation in humans. Modified from a summary illustration of Foerster (1931).

keys and humans, the back of the head and neck are in medial cortex with the trunk representation, while the face is in lateral cortex separated from the head by cortex devoted to the arm and hand. As in monkeys, the digits are represented from little finger to thumb in a mediolateral sequence. As for the area 1 representation in macaque monkeys, the orbital skin and the nose are represented just lateral to the thumb in humans. In monkeys and humans, the tongue and mouth are most lateral in the responsive cortex. Thus, the mediolateral sequences of representation in the region of anterior area 1 appear to be quite similar in humans and monkeys. Little can be said about sequences of change in the rostrocaudal direction, however, since only microelectrode maps provide much detail about this direction in monkeys, and the surface stimulation and recordings in humans may involve amounts of tissue that are large relative to the narrow widths of the representations in areas 3b, 1, and 2.

Somatotopic Order Revealed by Epileptic Seizures

Some aspects of somatosensory organization have long been known from the order of progressions of sensations or movements ("the Jacksonian march") during epileptic seizures. Since the seizure starts from a focus and spreads to more distant tissue, the order of sensations reflects the order of representation. Typical cases are described by Foerster (1936b) and by Penfield and Jasper (1954). The orders of three sensory marches correspond to the evoked sensation map (Figure 24.9). For example, a sensation of tingling or numbness in the thumb may be followed by tingling in the face, or a tingling that passes from thumb to fingers, to arm. Sensations are contralateral to the postcentral focus, and they seldom spread over many body parts (Mauguiere and Courjon, 1978).

Regional Changes in Blood Flow in Postcentral Somatosensory Cortex Related to Sensory Stimulation Because regional cortical blood flow is coupled to regional cortical metabolism, and since regional blood flow can be measured with detectors of radioactive isotopes in the blood, sites of high cortical activity can be distinguished from background activity. This basic method, though presently crude in the ability to localize, has proved to be useful in revealing the functional organization of cortex. During discrimination of forms of objects by touch and active manipulations in human subjects, this method revealed that activity increased in both motor fields and in postcentral cortex (Roland and Larsen, 1976). Furthermore, discrimination made with the foot activated the most medial portion of postcentral cortex, using the hand activated a middle cortical region, while discriminations of objects placed in the mouth activated cortex near the lateral end of the central sulcus. Thus, the somatotopic pattern of evoked activity corresponded to the maps produced by other methods. Furthermore, while sensory stimulation and sensory tasks activate anterior parietal cortex, focal attention changes metabolic activity in this region also. When subjects directed their attention to the tip of one finger in a sensory detection task, activity in the hand region of postcentral cortex increased, even though no stimulus was delivered (Roland, 1981).

Sensory and Perceptual Impairments following Lesions

Damage to postcentral cortex, if extensive, causes severe and lasting impairments in pressure sensitivity, two-point discrimination, point localization, and discrimination of object shape, size, and texture (Corkin *et al.*, 1970; Head and Holmes, 1911; Roland, 1987a; Semmes *et al.*, 1960). Roland (1987a) reported that lesions of the deep and anterior part of the hand region of postcentral cortex, presumably including much but not all of the area 3b representation and probably the area 1 representation, abolished the ability to discriminate edges from rounded surfaces, while lesions of the surface, apparently involving areas 1 and 2, left the ability to distinguish edges from round, but removed the ability to discriminate shapes and curvatures. This difference is similar to that reported for monkeys (Carlson, 1981; Randolph and Semmes, 1974), where lesions of area 1 impaired texture discriminations, while area 2 lesions altered discrimination of shape. Remarkably, small lesions of part of the hand representation result in no obvious impairment (Evans, 1935; Roland, 1987a,b). Roland (1987a) estimated that a notable impairment

resulted only after lesions involving three-fourths or more of the hand region of anterior parietal cortex. Furthermore, the larger the lesion of the region, the greater the impairment (Roland, 1987b). The preservation of abilities after lesions to parts of somatotopically organized representations could be the result of cortical reorganizations that result in the recovery of lost parts of representations. Removing part of a representation or deactivating part of a representation in monkeys can be followed by reorganization, even in adults, so that remaining cortex is activated by skin formerly related to the damaged area, and deactivated cortex becomes responsive to alternative inputs (see Kaas *et al.*, 1983, for a review).

VI. Posterior Parietal Cortex

The posterior parietal region is an arbitrary subdivision of the brain that includes most of the parietal lobe caudal to area 2, but excludes the cortex of the lateral (Sylvian) fissure and the supplementary sensory area of the medial wall. Current investigators commonly refer to the architectonic subdivisions of Brodmann (1909) or von Economo (1929) (Figure 24.8), and both systems are in use. However, research on monkeys suggests that the proposed fields (areas 5a, 5b, 7a, and 7b or areas PD, PE, PF, and PG) have little validity other than denoting general regions of the lobe. Other subdivisions have been suggested by patterns of connections and the response characteristics of neuronal populations, but the organization of posterior parietal cortex is not well understood. Electrical stimulation in humans seldom produces any sensations or motor responses (Penfield and Rasmussen, 1950), although Foerster (1931, 1936a) was able to produce hand movements and leg movements on occasion with high levels of stimulating current. Posterior parietal cortex has been implicated in both somatosensory and visual functions, but lesions do not produce simple sensory impairments. Rather, large lesions produce a variety of complex symptoms, many included within the general category of contralateral sensory neglect or inattention. In monkeys, impairments are basically the same regardless of the hemisphere of the lesion, but in humans, lesions of the right or "minor" hemisphere produce a much more profound defect. Major reviews of posterior parietal cortex organization and function in monkeys and humans include those of Mountcastle (1975), Lynch (1980), Hyvärinen (1982), and Yin and Medjbeur (1988).

A. Posterior Parietal Cortex in Monkeys

Since posterior parietal cortex in macaque monkeys may have many features of functional organization in common with posterior parietal cortex in humans, a brief review of current views of connections, neuron properties, and functional subdivisions in monkeys serves as a guide. As a point of caution, data in monkeys are still limited, and a consensus of opinions has not yet occurred.

One currently acceptable scheme for subdividing posterior parietal cortex in macaque monkeys is shown in Figure 24.11 (for an alternative proposal, see Pandya and Seltzer, 1982; Seltzer and Pandya, 1980). The proposal follows the traditional subdivision into "areas" 5a, 5b, 7a, and 7b introduced by Brodmann and the Vogts (Figure 24.7), with the addition of the ventral intraparietal area (VIP) of Maunsell and Van Essen (1983) and the lateral intraparietal area (LIP) of Andersen *et al.* (1985). Both VIP and LIP overlap a region distinguished by Seltzer and Pandya as POa. The most obvious flaw with the scheme summarized in Figure 24.11 is that considerable evidence suggests that anterior 7b is similar to area 5a in having predominantly somatosensory connections and functions, and that the distinction between 7b and 5a is poorly justified.

Area 5a Area 5a is not uniform in histological structure, connections, and neuron types, but clear subdivisions have not yet been established. Subdivisions of anterior parietal cortex, especially area 2, provide indirect somatosensory inputs from both deep and cutaneous receptors (Pons and Kaas, 1986). Major thalamic inputs are from the anterior pulvinar and the lateral posterior nucleus (see Yeterian and Pandya, 1985), nuclei without significant sensory inputs from the brainstem or spinal cord. However, a specialized portion of area 5 (Pons *et al.*, 1985a) receives some input from the ventroposterior nucleus (Pons and Kaas, 1986). Feedforward cortical projections are to area 7, S-II, premotor cortex, limbic cortex, and parts of the superior temporal gyrus; callosal connections are largely limited to subdivisions of posterior parietal cortex (see Hyvärinen, 1982). Subcortical projections include thalamic nuclei, the basal ganglia, and pontine nuclei and the spinal cord through the pyramidal tract. Neuron properties include those related to passive and active limb movement, and, to a lesser extent, cutaneous stimuli. Specific combinations of positions in several joints may be the most effective stimulus for many neurons (Hy-

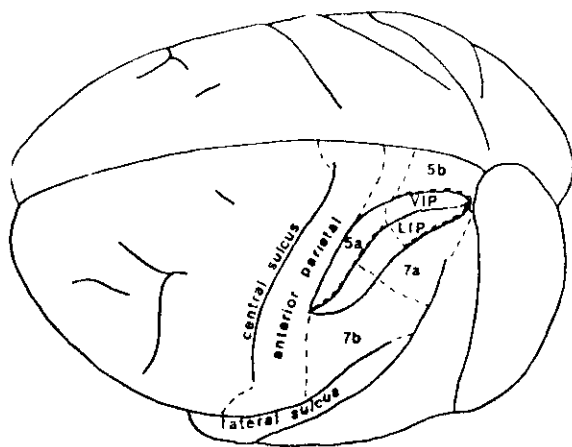


Figure 24.11. A dorsolateral view of the brain showing proposed subdivisions of posterior parietal cortex in macaque monkeys. Areas 5a, 5b, 7a, and 7b are traditional subdivisions from Brodmann (1909) and Vogt and Vogt (1919). The ventral intraparietal region (VIP) and the lateral intraparietal region (LIP) are subdivisions that have been distinguished by visual and visuomotor connections (Anderson *et al.*, 1985; Maunsell and Van Essen, 1983).

värinen, 1982). Very few neurons are activated by visual stimuli.

Area 7b Area 7b also appears to be involved in the higher-order processing of somatosensory information. Inputs to the anterior part include those from anterior parietal cortex (Pons and Kaas, 1986). Thalamic connections include the ventral lateral nucleus and the anterior pulvinar. Cortical projections include premotor areas of the frontal lobe, more caudal regions in posterior parietal cortex, and the superior temporal sulcus. Neurons are predominantly somatosensory in function, particularly relating to the head and face in anterior 7b and the hand and arm in posterior 7b (Leinonen, 1984).

Area 5b Area 5b appears to be largely somatosensory in function, despite its posterior position near the visual cortex. Major cortical inputs are from area 5a, while outputs include adjoining parietal cortex of the medial wall and parts of 7b as well as cortex caudal to S-II in the lateral fissure (Pandya and Seltzer, 1982).

Area 7a Area 7a is related to visual and visuomotor activities. The visual functions are reflected in both connection patterns and neuron properties. Visual inputs include those from superior temporal cortex involved in processing visual motion information (see Maunsell and Van Essen, 1983). Other visual inputs

are from adjacent dorsal portions of the prelunate gyrus (May and Andersen, 1986). Outputs include the cortex of the intraparietal sulcus, cortex of the medial wall, prefrontal cortex, multimodal and visual areas of the superior temporal sulcus, and cortex of the ventral temporal lobe (see Kaas and Pons, 1988). Other connections are with the medial pulvinar. Several classes of visual and visuomotor neurons have been described (see Hyvärinen, 1982). Visual tracking neurons respond during the visual pursuit of targets. Another class of neurons is activated during fixation on a moving or stationary visual target. Some neurons seem to be important to the visual guidance of reaching movements with the hand. Almost all neurons respond to visual stimuli.

The LIP has been distinguished by Andersen *et al.* (1985) as a major source of projections to the frontal eye fields, superior colliculus and pons. Shibutani *et al.* (1984) found that eye movements can be elicited from this cortex by electrical stimulation, and neurons which respond to eye movements are found within the region (see May and Andersen, 1986). VIP was distinguished by Maunsell and Van Essen (1983) as the main target region in posterior parietal cortex of afferents from the middle temporal visual area, MT. The distinctiveness of VIP from LIP is presently uncertain, and Seltzer and Pandya (1980) include both fields in their larger POa field.

B. Posterior Parietal Lobe Function in Humans

Concepts of posterior parietal lobe function in humans are largely derived from the much discussed behavioral changes that typically follow large lesions (for reviews, see Critchley, 1949; Denney-Brown and Chambers, 1958; De Renzi, 1982; Hyvärinen, 1982; Mesulam, 1981, 1983). In brief, patients with posterior parietal lobe injury tend to neglect visual and tactile information coming from visual space or the body surface opposite the lesion. The defect is most severe after lesions of the right or nondominant (non-language or minor) hemisphere. The defect may be profound, leading to bizarre symptoms, or it may be quite mild, resulting in little notable change in spontaneous behavior. Mild defects are typically revealed by bilateral stimulation. The expected result is that the ipsilateral stimulus is preferentially attended, either immediately or after a series of trials. In more dramatic cases, there is a denial of the existence of the contralateral (typically left) side of the body and of objects in the left side of visual space. Patients may fail to shave or dress the neglected side, and food on

the contralateral side of the plate may be uneaten. The defect can be characterized as a change in attention, since it is clearly not a result of a sensory impairment. More specifically, a unique aspect of the impairment seems to be a difficulty in the ability to disengage attention from a current focus and move that attention to a new focus in the contralateral world (Posner *et al.*, 1984). Right hemisphere damage produces a reluctance or inability to redirect attention from the right visual field to the left visual field, as well as a reluctance to shift attention within the left visual field (Baynes *et al.*, 1986).

Other defects also occur.

1. Errors may exist in localizing objects, so that accurate pointing does not occur. Right and left may be confused, and the patient may have difficulty in moving from place to place.
2. Eye movement patterns are altered, and a reduction in spontaneous eye movements and tracking movements may occur. Lesion experiments in monkeys show that the direct connections to the superior colliculus from posterior parietal cortex are critical in eliciting eye movements (Keating *et al.*, 1983).
3. Errors in reaching into the contralateral hemifield are common. Targets may be missed by several inches.
4. Lesions of the right or minor hemisphere may produce a defect in drawing even simple objects such as a house, and in constructing simple models. Furthermore, during constructional tasks, blood flow is increased in posterior parietal cortex (Roland *et al.*, 1980).
5. Lesions, especially those involving the anterior half of posterior parietal cortex, may produce somatic deficits. Reported changes include impairment in length discrimination, weight judgement, shape discrimination, and limb position sense (see Hyvärinen, 1982).

While posterior parietal cortex is not uniform in function, much of the region appears to relate to attention to nearby visual space and the body surface. Clearly, the anterior part of posterior parietal cortex is more related to the somatosensory system, and the posterior part is more related to the visual system. The connections of posterior parietal cortex suggest that a motivational component depends on relationships with limbic cortex of the medial wall and perhaps the ventral temporal lobe (see Mesulam, 1981). Connections with the frontal lobe, and connections with subcortical extra motor structures such as the

superior colliculus undoubtedly are important in initiating behavior. Mountcastle (1975) more specifically hypothesized that posterior parietal cortex functions as a "command" center for movements in immediate extrapersonal space. Finally, the functional asymmetry of posterior parietal cortex in humans can be explained if the right hemisphere contains the neural substrate for attending to both sides of space, though predominantly contralateral space, while the left hemisphere is almost exclusively concerned with contralateral space (Mesulam, 1981). Thus, unilateral lesions of the left hemisphere are partially compensated by the functions of the right hemisphere, but the reverse does not hold. This difference may relate to the specialization of the left hemisphere for language.

VII. Somatosensory Cortex of the Medial Wall: The Supplementary Sensory Area and Cingulate Cortex

Penfield and Jasper (1954) postulated the existence of a supplementary sensory area, as an analogy to the supplementary motor area, on the medial wall of the cerebral hemisphere where electrical stimulation evoked sensations from the contralateral leg, arm, and face. More recently, Woolsey *et al.* (1979) reported in a single patient that sensations were obtained from the arm or leg after electrical stimulation of sites on the medial wall.

There have been only a few experimental studies in monkeys that relate to the existence or organization of a supplementary sensory area (see Murray and Coulter, 1982, for a review). In macaque monkeys, neurons on the medial wall respond to somatosensory stimuli, and there is some suggestion of anterior sites relating to the lower body and posterior sites relating to the upper body. These neurons have large receptive fields, and appear to have inputs related to both skin and deep receptors. Major inputs are from dorsolateral posterior parietal cortex, especially the anterior half. Other connections of medial parietal cortex are with premotor and supplementary motor cortex and the lateral posterior nucleus of the thalamus.

Posterior parietal cortex also provides inputs to the cingulate cortex of the medial wall (see Mesulam, 1981). Thus, part of the cingulate cortex is part of, or closely associated with, the somatosensory system. Such connections could help mediate motivational or attentional aspects to perception.

VIII. Somatosensory Cortex of the Lateral (Sylvian) Sulcus

Much of the cortex of the upper bank of the lateral sulcus and probably some of the cortex of the insula are somatosensory in function. Because of the general inaccessibility of this region in humans, there have been only a few attempts to reveal aspects of functional organization by stimulation or recording. However, there is clear evidence for the existence of the second somatosensory area, S-II. Interest has been limited because lesions in the region typically do not produce major sensory or perceptual impairments. However, the lateral somatosensory cortex may be part of a critical corticolimbic pathway for touch (see Friedman *et al.*, 1986). Monkeys have severe deficits in tactual memory after combined removal of the amygdala and hippocampus (Murray and Mishkin, 1984a). The pathways for input to these limbic structures involve convergent input to S-II from areas 3a, 3b, 1, and 2 of the anterior parietal cortex, and a relay from S-II over more rostral subdivisions of the somatosensory cortex in the lateral sulcus (Figure 24.12). Because this lateral pathway is best understood in macaque monkeys, the organization of lateral somatosensory cortex in these primates is briefly reviewed below.

A. Organization of Cortex of the Lateral Sulcus in Monkeys

Cortex in the lateral sulcus contains several subdivisions (see Kaas and Pons, 1988, for a review) that are basically somatosensory in function (Figure 24.13). Architectonic subdivisions are described by Mesulam and Mufson (1982a). Most caudally, area 7b continues into the lateral sulcus. Area 7 adjoins the retroinsular area (R-I) and the second somatosensory area (S-II), named because it was the second representation discovered in cats and later in other mammals. More rostrally, a systematic representation of the body surface is found in the granular insular cortex (Ig). The dysgranular insular cortex (Id) also has somatosensory connections. A wide range of inputs converge from anterior parietal and posterior parietal cortex into S-II, and relay into Id and Ig and then into limbic cortex (see Friedman *et al.*, 1986; Pons and Kaas, 1986; Mesulam and Mufson, 1982a).

In S-II, the face representation lies rostrally, the hand is caudal to the face, and the trunk, leg, and foot are deepest in the sulcus. Neurons in S-II are activated by cutaneous stimuli, with almost all recep-

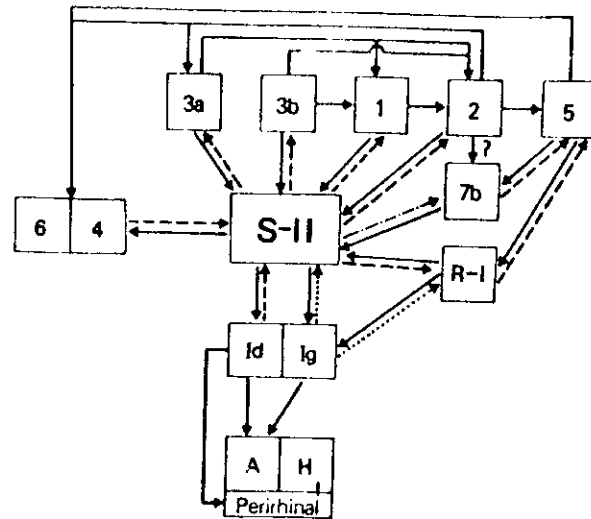


Figure 24.12. A summary of cortical somatosensory connections leading to inputs to the amygdala (A) and the hippocampus (H) of the limbic system via S-II and insular fields. Solid lines, feedforward projections; dashed and dotted lines, feedback projections. Reproduced from Friedman *et al.* (1986).

tive fields on the contralateral body surface. Most neurons rapidly adapt to touch or movement of hairs. A small proportion of neurons may relate to deep receptors, and some neurons have Pacinian-like responses. Besides cortical connections (shown in Figure 24.12), a major thalamic input is from the ventro-posterior inferior nucleus (Friedman and Murray, 1986; Krubitzer and Kaas, 1986; Figure 24.10). However, the significance of the VPI input is not yet clear, since VPI inputs alone are not sufficient to activate S-II (Pons *et al.*, 1987). The R-I has neurons that respond to light touch and to high-frequency vibrations, suggesting a Pacinian receptor input. Thalamic connections appear to be from parts of the posterior group. The Ig is activated by cutaneous stimuli; receptive fields are largely on the contralateral body surface, although bilaterally symmetrical receptive fields are found, and the region forms a systematic representation with rostral Ig devoted to the face and mouth and caudal Ig activated by stimulating the limbs and trunks. Ig may receive thalamic input from the posterior group. The Id has somatosensory connections, but little else is known about the field.

B. S-II and Other Somatosensory Fields in Humans

According to the electrical stimulation studies of Penfield and Rasmussen (1950), the second somatosensory area in humans is located just lateral and slightly anterior to the lateral end of the central fissure. Part

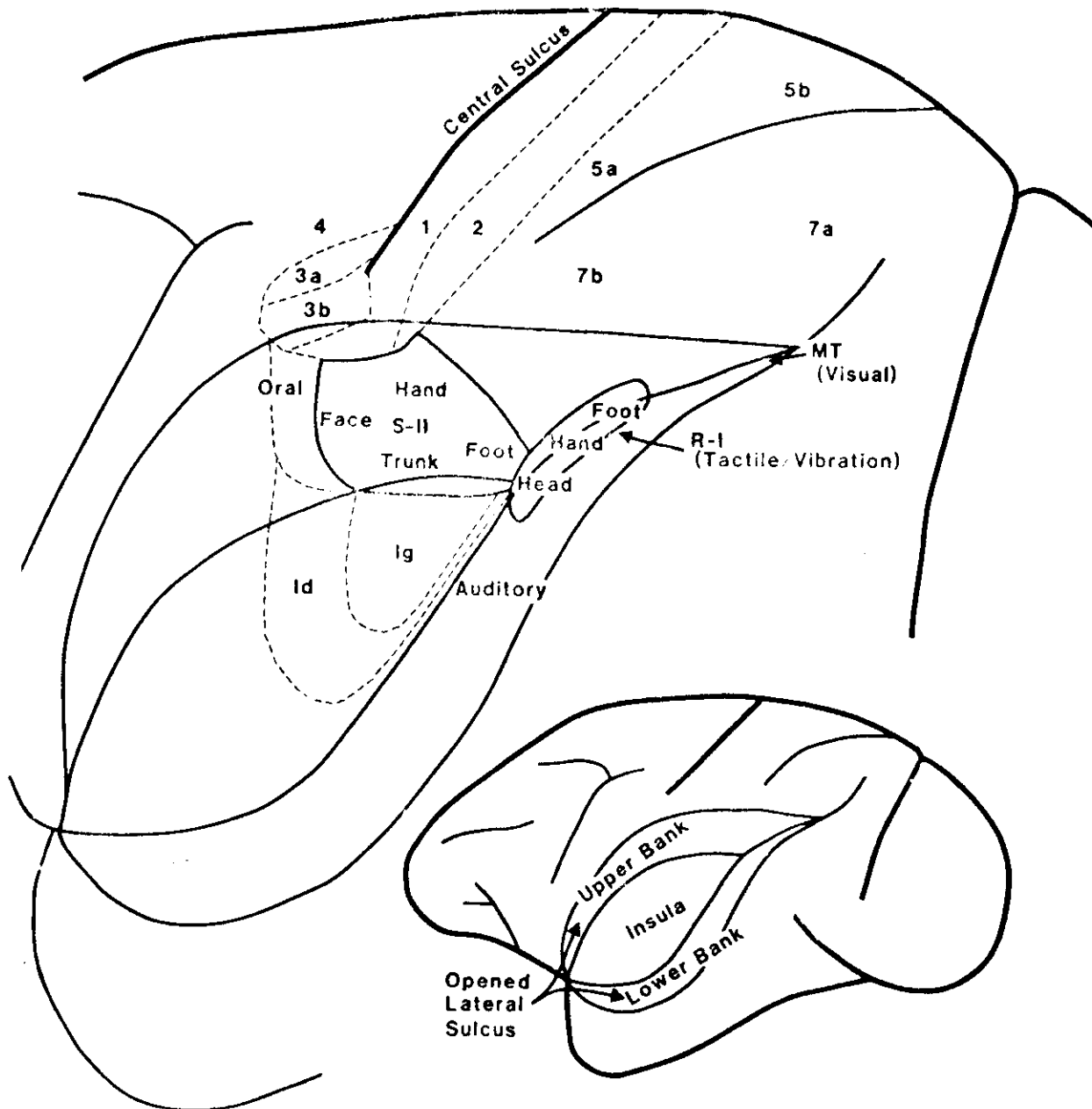


Figure 24.13. Subdivisions of cortex in the lateral fissure of macaque monkeys. A large second representation of the body (S-II) is bordered caudally by a retroinsular representation (R-I) and rostrally by a tactile representation in insular granular cortex (Ig).

The dysgranular insular region (Id) also appears to be involved in processing somatosensory information. A lateral view with the lateral fissure opened to show the insula. From Kaas and Pons (1988).

of the face representation of S-II is on the dorsolateral surface of the hemisphere, and the hand and leg are represented in successively deeper locations on the upper bank of the lateral fissure. Stimulation of sites in S-II largely produces sensations of numbness or tingling in contralateral skin locations, although ipsilateral or bilateral sensations are occasionally reported. Recordings of evoked potentials in the S-II region support the view that the leg is represented in

cortex that is deeper and caudal to that of the hand and face, and indicate that neurons are activated at a longer latency in S-II than in anterior parietal cortex (Woolsey *et al.*, 1979). Somatosensory evoked cerebral magnetic fields have been reported for the S-II region after median and peroneal nerve stimulation, further demonstrating the existence of S-II in humans (Hari *et al.*, 1984). Remarkably, removal of S-II is thought to produce "no obvious sensory or motor

defect" (Penfield and Roberts, 1959). Although recent reports are consistent with this conclusion (e.g., Roland, 1987a), Murray and Mishkin (1984) note that previous investigators have reported both severe deficits and no deficits after S-II lesions in monkeys, and concluded that the lack of impairment was the result of incomplete lesions. With complete lesions in monkeys, Murray and Mishkin (1984b) found severe impairments of texture and shape discrimination learning, and elevated size and roughness discrimination thresholds.

Other somatosensory fields undoubtedly exist in the cortex of the lateral sulcus. Architectonic studies suggest granular and dysgranular subdivisions similar to those reported for monkeys (see Brockhaus, 1940; Mesulam and Mufson, 1982b; Sanides, 1968). Electrical stimulation of the anterior insula results in sensations and motility of the digestive tract (Penfield and Faulk, 1955).

IX. Summary and Conclusion

This chapter describes the organization of the parts of the somatosensory system thought to be concerned with object identification and tactile discriminations. The relevant sensory information depends on receptors in skin, muscles, and joints, and is relayed over parallel afferent pathways to reach the ventroposterior complex of the thalamus. The ventroposterior complex includes a ventroposterior "proper" nucleus (VP) composed of ventroposterior lateral (VPL) and ventroposterior medial (VPM) subdivisions. The ventroposterior nucleus processes and relays information from rapidly and slowly adapting cutaneous receptors to area 3b of cortex, and information from rapidly adapting cutaneous receptors to area 1. Sparse projections exist to parts of area 2. The ventroposterior superior nucleus (VPS) relays largely muscle spindle receptor information to areas 3a and 2. The ventroposterior inferior nucleus (VPI) projects to the second somatosensory area (S-II), but the

significance of this projection is uncertain. The lateral posterior nucleus, the anterior pulvinar, and the medial pulvinar, without obvious sensory inputs, interconnect with subdivisions of somatosensory cortex, perhaps to modulate neural activity.

The somatosensory cortex includes anterior parietal cortex with four functional subdivisions, areas 3a, 3b, 1, and 2; posterior parietal cortex with at least 5-6 fields; the supplementary sensory area of the medial wall of the cerebral cortex; and the second somatosensory area and other fields in cortex of the upper bank and insula of the lateral fissure. Areas 3a, 3b, 1, and 2 all contain somatotopic representations of body receptors, with area 3b corresponding to the primary field, S-I, of nonprimates, though it is common and traditional to include all four fields of anterior parietal cortex in "S-I." Basic processing of tactile information occurs in area 3b, higher-order processing of tactile information occurs in area 1, and tactile information is combined with limb and digit position information in area 2 for the recognition of shapes and objects during active touch. Muscle spindle receptor information in area 3a, combined with inputs from area 2, may relate to motor control mechanisms.

Information from anterior parietal cortex is relayed laterally to S-II and adjoining fields as part of a processing sequence related to object identification and memory, and to posterior parietal cortex for computations relating to intention, attention, motor behavior, and multimodal motor control. In particular, much of the posterior parietal cortex relates to the visual control of eye, hand, and arm movements via outputs to frontal cortex and to brain stem centers. Posterior parietal cortex is asymmetrical in humans, with the right (nondominant) hemisphere having a more dramatic role in mediating attention and motor behavior for the contralateral body and visual space. The significance of the supplementary sensory area is uncertain, but a role in motivation and other limbic cortex functions seems likely.

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