

cortex (S-I), whereas the VPS nucleus conveys proprioceptive information principally to area 3a.

The Somatosensory Cortex Is Organized Into Functionally Specialized Columns

Conscious awareness of touch is believed to originate in the cerebral cortex. Tactile information enters the cerebral cortex through the primary somatosensory cortex (S-I) in the postcentral gyrus of the parietal lobe. The primary somatic sensory cortex comprises four cytoarchitectural areas: Brodmann's areas 3a, 3b, 1, and 2 (Figure 19–12). These areas are interconnected such that processing of sensory information in S-I involves both serial and parallel processing.

In a series of pioneering studies of the cerebral cortex, Vernon Mountcastle discovered that S-I cortex is organized into vertical columns or slabs. Each column is 300 to 600 μm wide and spans all six cortical layers from the pial surface to the white matter (Figure 19–13). Neurons within a column receive inputs from the same local area of skin and respond to the same class or classes of touch receptors. A column therefore comprises an elementary functional module of

the neocortex; it provides an anatomical structure that organizes sensory inputs to convey related information about location and modality.

The columnar organization of the cortex is a direct consequence of intrinsic cortical circuitry, the projection patterns of thalamocortical axons, and migration pathways of neuroblasts during cortical development. The pattern of connections within a column is oriented vertically, perpendicular to the cortical surface. Thalamocortical axons terminate primarily on clusters of stellate cells in layer IV, whose axons project vertically toward the surface of the cortex, as well as on star pyramid cells. Thus, thalamocortical inputs are relayed to a narrow column of pyramidal cells that are contacted by the layer IV cell axons. The apical dendrites and axons of cortical pyramidal cells in other cortical layers are also largely oriented vertically, parallel to the thalamocortical axons and stellate cell axons (Figure 19–14). This allows the same information to be processed by a column of neurons throughout the thickness of the cortex.

Pyramidal neurons form the principal excitatory class of somatosensory cortex; they compose approximately 80% of S-I neurons. Pyramidal neurons in

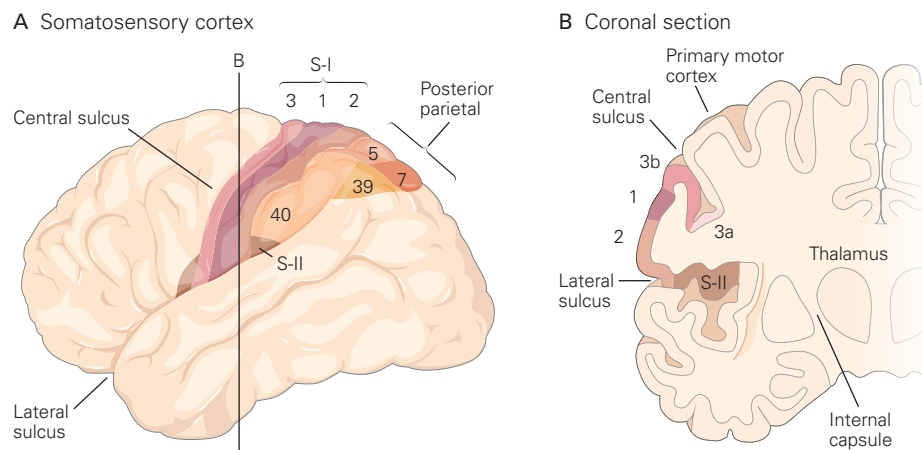


Figure 19–12 The somatosensory areas of the cerebral cortex in the human brain.

A. The somatosensory areas of cortex lie in the parietal lobe and consist of three major divisions. The *primary somatosensory cortex (S-I)* forms the anterior part of the parietal lobe. It extends throughout the postcentral gyrus beginning at the bottom of the central sulcus, extending posteriorly to the postcentral sulcus, and into the medial wall of the hemisphere to the cingulate gyrus (not shown). The S-I cortex comprises four distinct cytoarchitectonic regions: Brodmann's areas 3a, 3b, 1, and 2. The *secondary somatosensory cortex (S-II)* is located on the upper bank of the lateral sulcus (Sylvian fissure) and on the parietal operculum; it covers Brodmann's

area 43. The *posterior parietal cortex* surrounds the intraparietal sulcus on the lateral surface of the hemisphere, extending from the postcentral sulcus to the parietal-occipital sulcus and medially to the precuneus. The superior parietal lobule (Brodmann's areas 5 and 7) is a somatosensory area; the inferior parietal lobule (areas 39 and 40) receives both somatosensory and visual inputs.

B. A coronal section through the postcentral gyrus illustrates the anatomical relationship of S-I, S-II, and the primary motor cortex (area 4). S-II lies adjacent to area 2 in S-I and extends medially along the upper bank of the lateral sulcus to the insular cortex. The primary motor cortex lies rostral to area 3a within the anterior wall of the central sulcus.

A Sagittal section of monkey S-I cortex

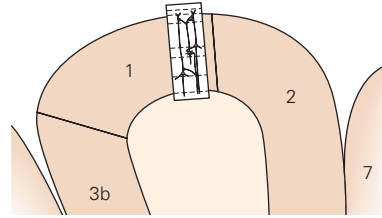
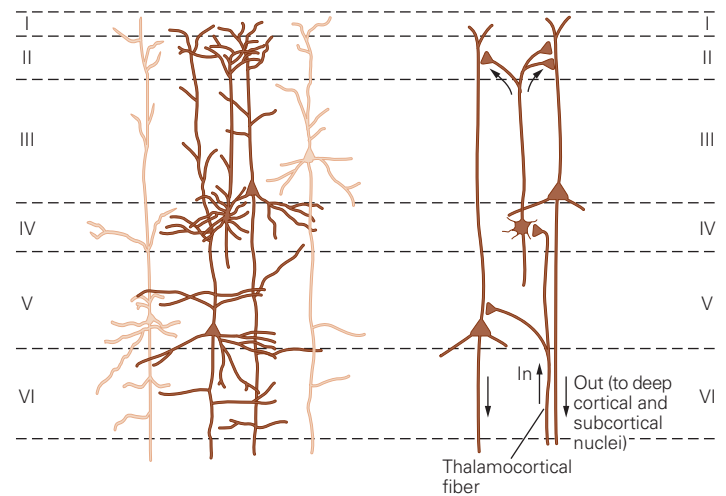


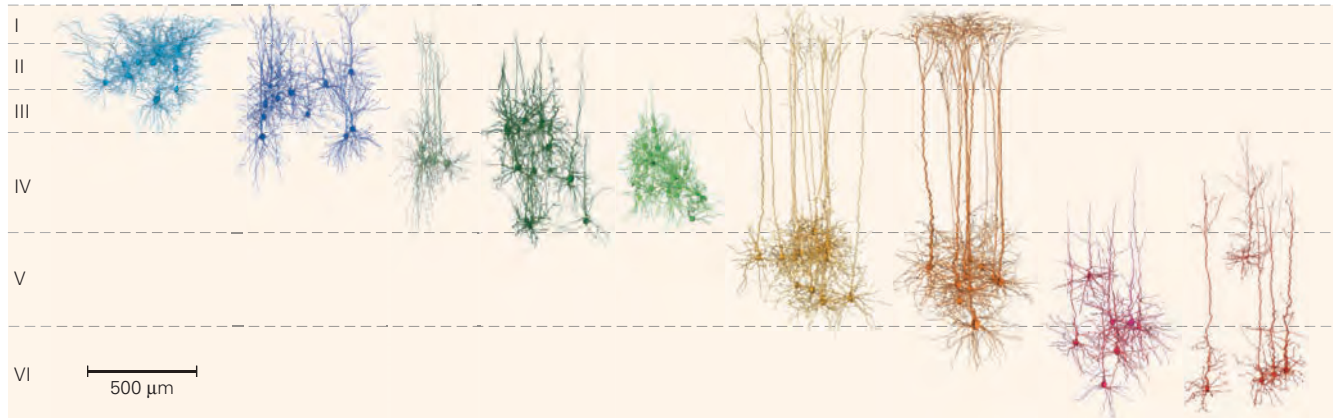
Figure 19-13 Organization of neuronal circuits within a column of somatosensory cortex. Sensory inputs from the skin or deep tissue are organized in columns of neurons that run from the surface of the brain to the white matter. Each column receives thalamic input primarily in layer IV from one part of the body. Excitatory neurons in layer IV send their axons vertically toward the surface of the cortex, contacting the dendrites of pyramidal neurons in layers II and III (supragranular layers) as well as the apical dendrites of pyramidal cells in the infragranular layers (layers V and VI). In this manner, tactile information from a body part such as a finger is distributed vertically within a column of neurons.

B Expanded view of cortical histology

C Schematic cortical circuits



Pial surface



White matter

Layer II
pyramidLayer III
pyramidLayer IV
pyramidLayer IV
star
pyramidLayer IV
spiny
stellateLayer V-A
slender tufted
pyramidLayer V-B
thick tufted
pyramidLayer VI-A
corticocortical
pyramidLayer VI-B
corticothalamic
pyramid

Figure 19-14 Columnar organization of the somatosensory cortex. Cortical excitatory neurons in the six layers have distinctive pyramidal-type shapes with large cell bodies, a single apical dendrite that projects vertically toward the cortical surface and arborizes in more superficial layers, and multiple basal dendrites that arborize close to the cell body. Pyramidal neurons differ in size, gene expression patterns, the length and thickness of their apical dendrite, and the projection targets of their axons.

All of these neurons synapse on targets within the cerebral cortex. Additionally, the pyramidal neurons in layer V project subcortically to the spinal cord, brain stem, midbrain, and basal ganglia. Corticothalamic neurons in layer VI project back to the afferent thalamic nucleus providing sensory input to that column. Spiny stellate neurons in layer IV are the only excitatory cells shown that are not pyramidal neurons. (Adapted, with permission, from Oberlaender et al. 2012.)

each of the six cortical layers project to specific targets (Figure 19–14). Recurrent horizontal connections link pyramidal neurons in the same or neighboring columns, allowing them to share information when activated simultaneously by the same stimulus. Neurons in layers II and III also project to layer V in the same column, to higher cortical areas in the same hemisphere, and to mirror-image locations in the opposite hemisphere. These feedforward connections to higher cortical areas allow complex signal integration, as described later in this chapter.

Pyramidal neurons in layer V provide the principal output from each column. They receive excitatory inputs from neurons in layers II and III in the same and adjacent columns as well as sparse thalamocortical inputs. Neurons in the superficial portion of layer V (layer V-A) send feedforward outputs bilaterally to layer IV of higher-order cortical areas (see Figure 19–17C) as well as to the striatum. Neurons deeper in layer V (layer V-B) project to subcortical structures, including the basal ganglia, superior colliculus, pontine and other brain stem nuclei, the spinal cord, and dorsal column nuclei. Layer VI neurons project to local cortical neurons, and back to the thalamus, particularly to regions of the ventral posterior nuclei providing inputs to that column.

In addition to feedforward signals of information from touch receptors, feedback signals from layers II and III of higher somatosensory cortical areas are provided to layer I in lower cortical areas, regulating their excitability. Such feedback signals originate not only in somatosensory cortical areas but also in sensorimotor areas of the posterior parietal cortex, frontal motor areas, limbic areas, and regions of the medial temporal lobe involved in memory formation and storage. These feedback signals are thought to play a role in the selection of sensory information for cognitive processing

(by the mechanisms of attention) and in short-term memory tasks. Feedback pathways may also gate sensory signals during motor activity. Various local inhibitory interneurons within each column serve to focus columnar output.

Cortical Columns Are Organized Somatotopically

The columns within the primary somatic sensory cortex are arranged topographically such that there is a complete somatotopic representation of the body in each of the four areas of S-I (Figure 19–15). The cortical map of the body corresponds roughly to the spinal dermatomes (see Figure 18–13). Sacral segments are represented medially, lumbar and thoracic segments centrally, cervical segments more laterally, and the trigeminal representation of the face at the most lateral portion of S-I cortex. Knowledge of the neural map of the body in the brain is important for localizing damage to the cortex from stroke or head trauma.

The body surface is represented in at least 10 distinct neural maps in the parietal lobe: four in S-I, four in S-II, and at least two in the posterior parietal cortex. As a result, these regions mediate different aspects of tactile sensation. Neurons in areas 3b and 1 of S-I process details of surface texture, whereas those in area 2 represent the size and shape of objects. These attributes of somatic sensation are further elaborated in S-II and the posterior parietal cortex, where neurons are engaged in object discrimination and manipulation, respectively.

Another important feature of somatotopic maps is the amount of cerebral cortex devoted to each body part. The neural map of the body in the human brain, termed the *homunculus*, does not duplicate exactly the spatial topography of the skin. Rather, each part of the body is represented in proportion to its importance to the sense of touch. Disproportionately large areas are

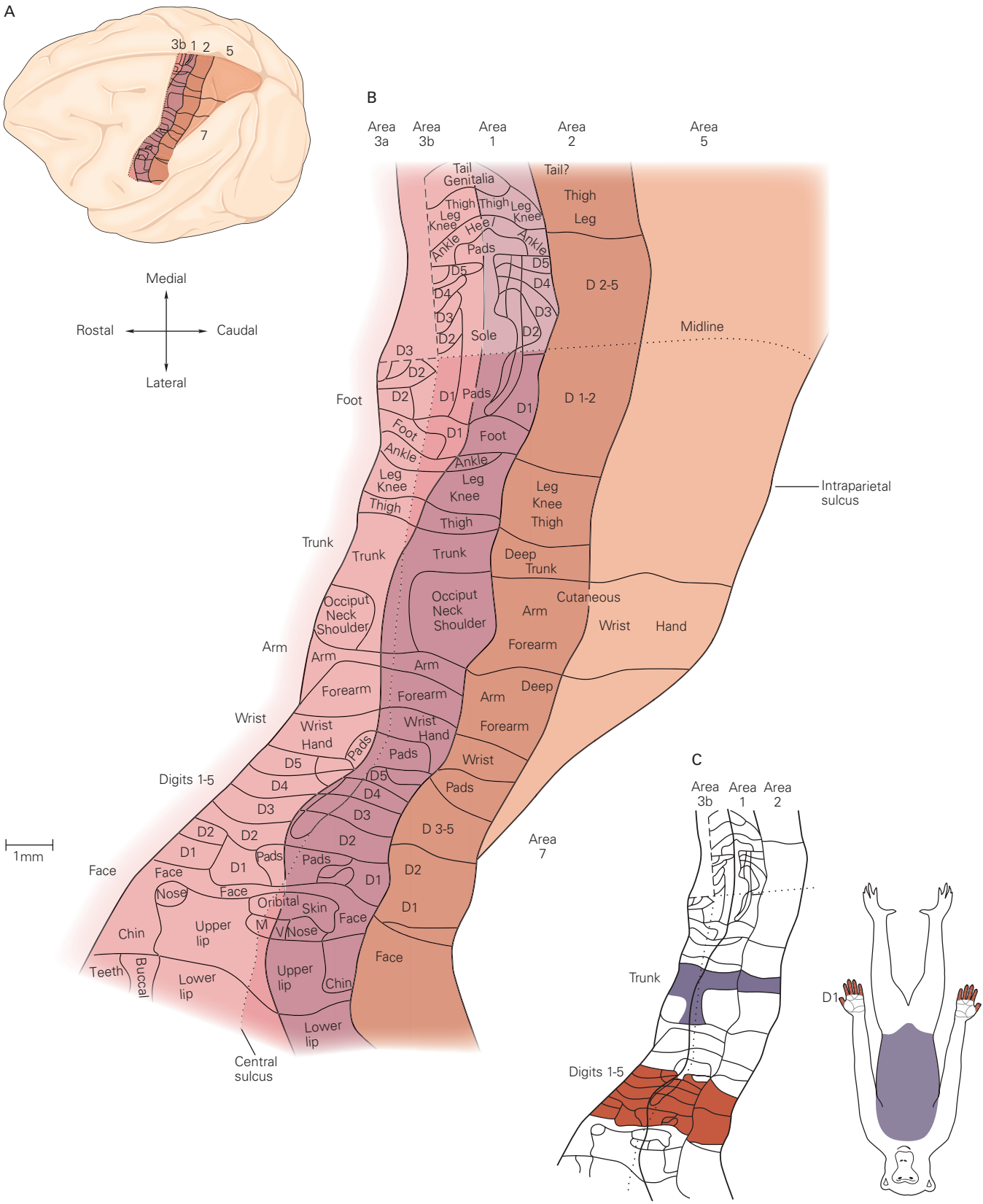
Figure 19–15 (Opposite) Each region of the primary somatosensory cortex contains a topographic neural map of the entire body surface. (Adapted, with permission, from Nelson et al. 1980. Copyright © 1980 Alan R. Liss, Inc.)

A. The primary somatosensory cortex in the macaque monkey lies caudal to the central sulcus as in the human brain. The colored areas on the macaque cortex correspond to the homologous Brodmann's areas of the human brain in Figure 19–12. Area 5 in the macaque monkey is homologous to areas 5 and 7 in humans. Area 7 in macaques is homologous to areas 39 and 40 in humans.

B. The flat map diagram on the right shows the somatosensory cortex of the macaque monkey unfolded along the central sulcus (dotted line that parallels the border between areas 3b and 1). The upper part of the diagram includes cortex unfolded from

the medial wall of the hemisphere. Body maps were obtained from microelectrode recordings in the postcentral gyrus. The body surface is mapped to columns within rostrocaudal bands arranged in the order of the spinal dermatomes. The body maps in areas 3b and 1 form mirror images of the distal-proximal or dorsal-ventral axes of each dermatome. Each finger (D5–D1) has its own representation along the medial-lateral axis of the cortex in areas 3b and 1, but inputs from several adjacent fingers converge in the receptive fields of neurons in areas 2 and 5.

C. Cortical magnification of highly innervated skin areas. Although the trunk (violet) is covered by a greater area of skin than the fingers (red), the number of cortical columns responding to touch on the fingers is nearly three times the number activated by touching the trunk because of the higher innervation density of the fingers.



devoted to certain body regions, particularly the hand, foot, and mouth, and relatively smaller areas to more proximal body parts. In humans and monkeys, more cortical columns are devoted to the fingers than to the entire trunk (Figure 19–15C).

The amount of cortical area devoted to a unit area of skin—called the *cortical magnification*—varies by more than a hundredfold across different body surfaces. It is closely correlated with the innervation density and thus the spatial acuity of the touch receptors in an area

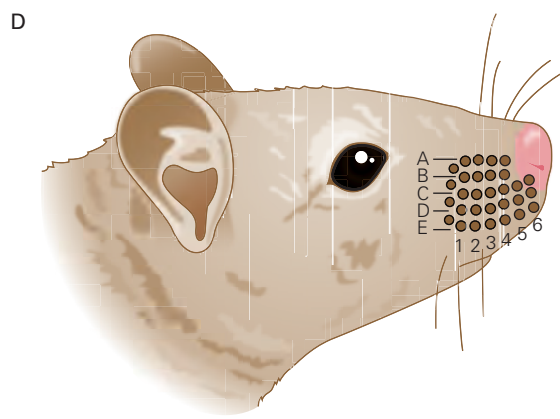
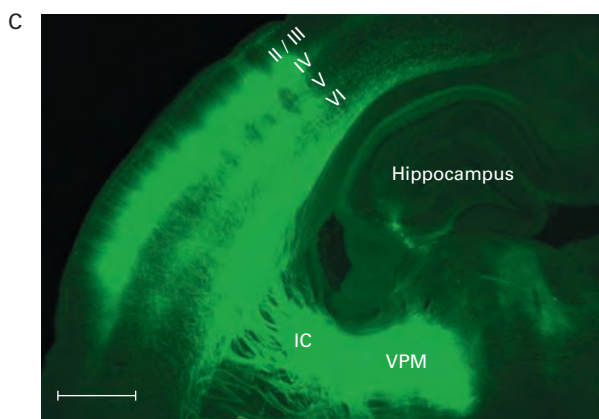
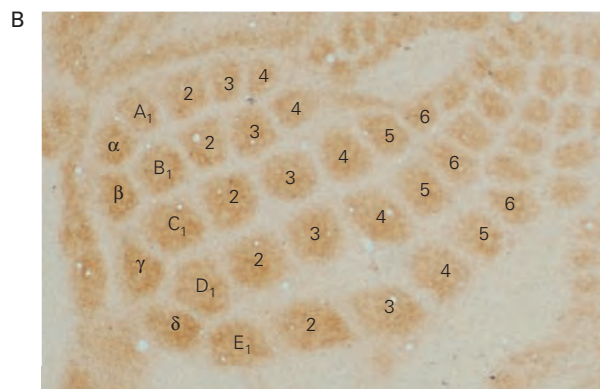
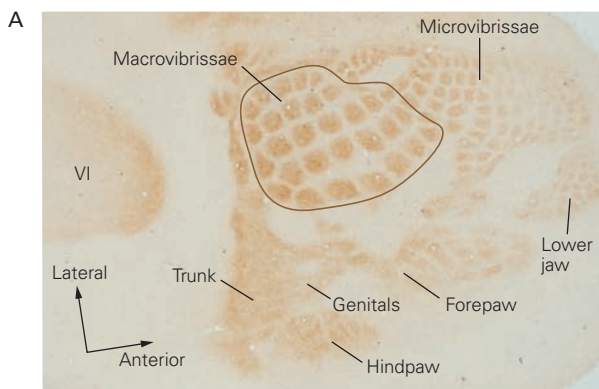
of skin. The areas with greatest magnification in the human brain—the lips, tongue, fingers, and toes—have tactile acuity thresholds of 0.5, 0.6, 1.0, and 4.5 mm, respectively.

Rodents and other mammals that probe the environment with their whiskers have a large number of columns in S-I, named *barrels*, that receive inputs from individual vibrissae on the face (Box 19–2). Barrel cortex provides a widely used experimental preparation for studying cortical circuitry.

Box 19–2 The Rodent Whisker-Barrel System

The rodent whisker-barrel system is a widely used animal model in modern neuroscience. Most mammals and all primates except man possess specialized tactile hairs on their face called *vibrissae*. Distinct from other hairs on

the skin, vibrissae grow from a follicle that is densely innervated by the trigeminal cranial nerve and surrounded by a blood-filled sinus.



The Receptive Fields of Cortical Neurons Integrate Information From Neighboring Receptors

The neurons in S-I are at least three synapses beyond touch receptors in the skin. Their inputs represent information processed in the dorsal column nuclei, the thalamus, and the cortex itself. Each cortical neuron receives inputs arising from receptors in a specific area of the skin, and these inputs together are its receptive field. We perceive that a particular location on the skin is touched because specific populations of neurons in

the cortex are activated. This experience can be induced experimentally by electrical or optogenetic stimulation of the same cortical neurons.

The receptive fields of cortical neurons are much larger than those of somatosensory fibers in peripheral nerves. For example, the receptive fields of SA1 and RA1 fibers innervating the fingertip are tiny spots on the skin (Figure 19–5), whereas those of the cortical neurons receiving these inputs cover an entire fingertip or several adjacent fingers (Figure 19–17B). The receptive field of a neuron in area 3b represents a

Many mammalian species actively move these large facial whiskers using specialized muscles that wrap like slings around each individual follicle. Mice and rats, two of the most commonly used vertebrate model organisms, rely more heavily on their sense of whisker-mediated touch than on their other senses during exploration.

Rodents rhythmically sweep their whiskers across objects in much the same way that humans palpate objects with their fingertips. Despite their structural differences, vibrissae and fingertips afford similar psychophysical thresholds and discriminative sensitivities. Whiskers mediate diverse abilities, including localizing objects in space, discriminating textures and shapes, navigating the environment, interacting socially, and capturing prey.

The rodent somatosensory cortex has evolved proportional to this system's high ethological relevance. For

instance, the rat somatosensory cortex is thicker than the primary visual cortex of the cat, a highly visual animal.

The representation of the largest whiskers (macrovibrissae) in rodent S-I is enlarged relative to that of other parts of the body (Figure 19–16). In contrast to the continuous representations of the skin or retina, the cortical networks dedicated to processing information from individual whiskers are discrete and anatomically identifiable. Each whisker maps one-to-one onto a distinct cluster of excitatory neurons visible in cortical layer IV called a *barrel*.

Barrels are densely interconnected networks that are established during development by the interaction of thalamocortical axons with cortical neurons. This unique correspondence facilitates diverse studies of cortical microcircuits, development, experience-dependent plasticity, sensorimotor integration, tactile behavior, and disease.

Randy M. Bruno

Figure 19–16 (Opposite) The “barrel cortex” of rodents represents the vibrissae in topographic patterns. The barrel cortex, a subregion of the rodent primary somatosensory (S-I) cortex that represents the facial vibrissae, is a widely studied structure used to decipher cortical circuits. (Adapted from Bennett-Clarke et al. 1997 and Wimmer et al. 2010.)

A. Tangential histological section through layer IV of the somatosensory cortex of a juvenile rat stained for serotonin. The darker immunoreactive patches correspond to cortical representations of specific body parts. The largest part of the rodent somatosensory cortical map is devoted to the vibrissae.

B. Enlarged view of the macrovibrissae representation in S-I. The spatial pattern of the whiskers on the face is stereotyped from animal to animal, allowing each cortical “barrel”

to be identified by row with the letter, and by arc (column) with the number of the corresponding whisker. Neurons in each barrel are most responsive to motion of this principal whisker.

C. A rat brain section cut obliquely along the path axons travel from the ventroposterior medial (VPM) thalamic nucleus to S-I. Green fluorescent protein–labeled VPM axons project through the internal capsule (IC) to the subcortical white matter and travel parallel to the pial surface before entering the cortex. The axons densely innervate layer IV where they form discrete barrels and more sparsely and diffusely innervate the border of layers V and VI. Scale bar = 1 mm.

D. The topographic arrangement of the barrels in the cortex matches the spatial arrangement of vibrissae on the face in rows (letters) and arcs (numbers).

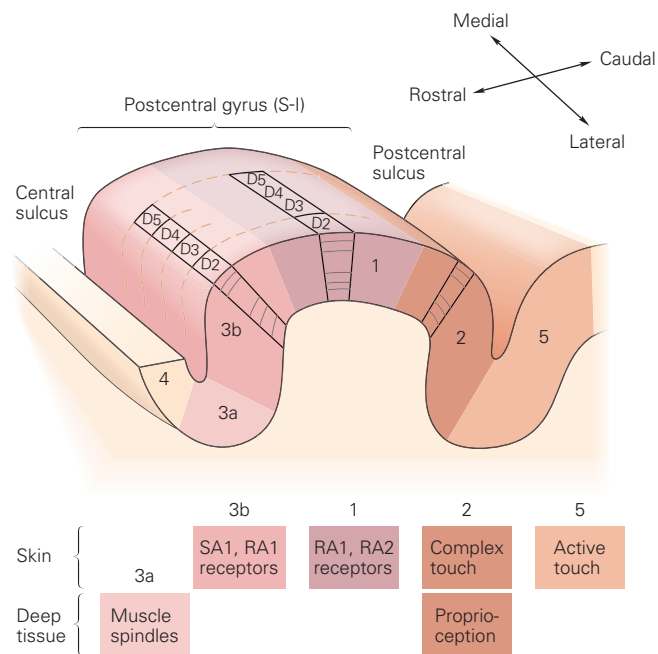
Figure 19–17 The hand area of S-I cortex.

A. This sagittal section through the hand representation illustrates the rostrocaudal anatomy of the four subregions of S-I (areas 3a, 3b, 1, and 2) in the human brain and the adjacent primary motor cortex (area 4) and posterior parietal cortex (area 5). Labels on the cortical surface indicate columns representing individual fingers (D2–D5); arrows to the right denote the section orientation in the brain. The four S-I regions process different types of somatosensory information indicated by color-matched rectangles below the cortical section. Neurons in area 5 respond mainly to goal-directed active hand movements. (Abbreviations: **RA1**, rapidly adapting type 1; **RA2**, rapidly adapting type 2; **SA1**, slowly adapting type 1.)

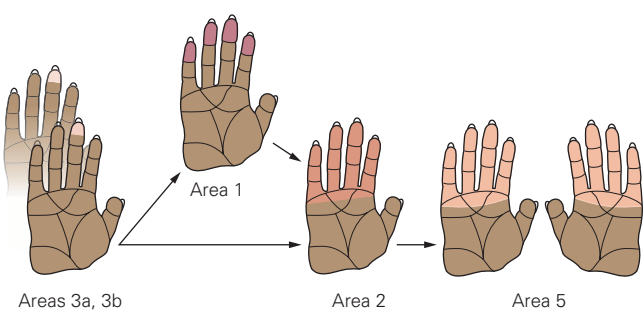
B. Typical receptive fields of neurons in each area of S-I of macaque monkeys are shown as colored patches on the hand icons. The fields are outlined by applying light touch to the skin or moving individual joints. Receptive fields are smallest in areas 3a and 3b, where tactile information first enters the cortex, and are progressively larger in areas 1, 2, and 5, reflecting convergent inputs from neurons in area 3b that are stimulated together when the hand is used. Neurons in area 5 and in S-II cortex often have bilateral receptive fields because they respond to touch at mirror-image locations on both hands. (Adapted from Gardner 1988; Iwamura et al. 1993; Iwamura, Iriki, and Tanaka 1994.)

C. Feedforward hierarchical connections between somatosensory cortical areas. The strength of thalamocortical and corticocortical connections is indicated by the thickness of arrows interconnecting these areas. Neurons in the thalamus send their axons mainly to areas 3a and 3b, but some also project to areas 1 and 2. In turn, neurons in cortical areas 3a and 3b project to areas 1 and 2. Information from the four areas of S-I is conveyed to neurons in the posterior parietal cortex (area 5) and in S-II. Many of these connections are bidirectional; neurons in higher order cortical areas project back to lower order regions, particularly to layer I. (**PR**, parietal rostroventral cortex; **PV**, parietal ventral cortex; **VPL**, ventral posterior lateral nuclei; **VPM**, ventral posterior medial nuclei; **VPS**, ventral posterior superior nuclei). (Adapted, with permission, from Felleman and Van Essen 1991. Copyright © 1991, Oxford University Press.)

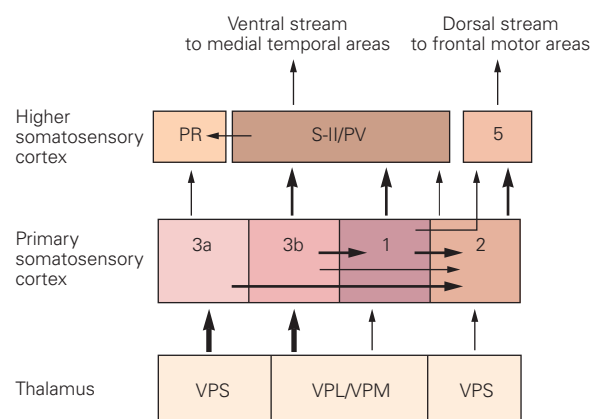
A The hand area of primary somatosensory (S-I) cortex



B Receptive fields



C Hierarchical connections to and from S-I



composite of inputs from 300 to 400 nerve fibers, and typically covers a single phalanx or palm pad. Inputs from SA1 and RA1 touch receptors in the same skin region converge on common neurons in area 3b.

Receptive fields in higher cortical areas are even larger, spanning functional regions of skin that are activated simultaneously during motor activity. These include the tips of several adjacent fingers, or an entire finger, or both the fingers and the palm. Neurons in areas 1 and 2 of S-I are concerned with information more abstract than just their innervation sites on the body. Neurons whose receptive fields include more than one finger fire at higher rates when several fingers are touched simultaneously and, in this way, signal the size and shape of objects held in the hand. These large receptive fields allow cortical neurons to integrate the fragmented information from individual touch receptors, enabling us to recognize the overall shape of an object. For example, such neurons may distinguish the handle of a screwdriver from its blade.

Convergent inputs from different sensory receptors in S-I may also allow individual neurons to detect the size and shape of objects. Whereas neurons in areas 3b and 1 respond only to touch and neurons in area

3a respond to muscle stretch, many of the neurons in area 2 receive both inputs. Thus, neurons in area 2 can integrate information about the hand shape used to grasp an object, the grip force applied by the hand, and the tactile stimulation produced by the object; this integrated information may be sufficient to recognize the object.

The receptive fields of cortical neurons usually have an excitatory zone surrounded by or superimposed upon inhibitory zones (Figure 19–18A). Stimulation of regions of skin outside the excitatory zone may reduce the neuron's responses to tactile stimulation within the receptive field. Similarly, repeated stimulation within the receptive field may also decrease neuronal responsiveness because the excitability of the pathway is diminished by longer lasting inhibition mediated by local interneurons.

Inhibitory receptive fields result from feedforward and feedback connections through interneurons in the dorsal column nuclei, the thalamus, and the cortex itself that limit the spread of excitation. Inhibition generated by strong activity in one circuit reduces the output of nearby neurons that are only weakly excited. The inhibitory networks ensure that the strongest of

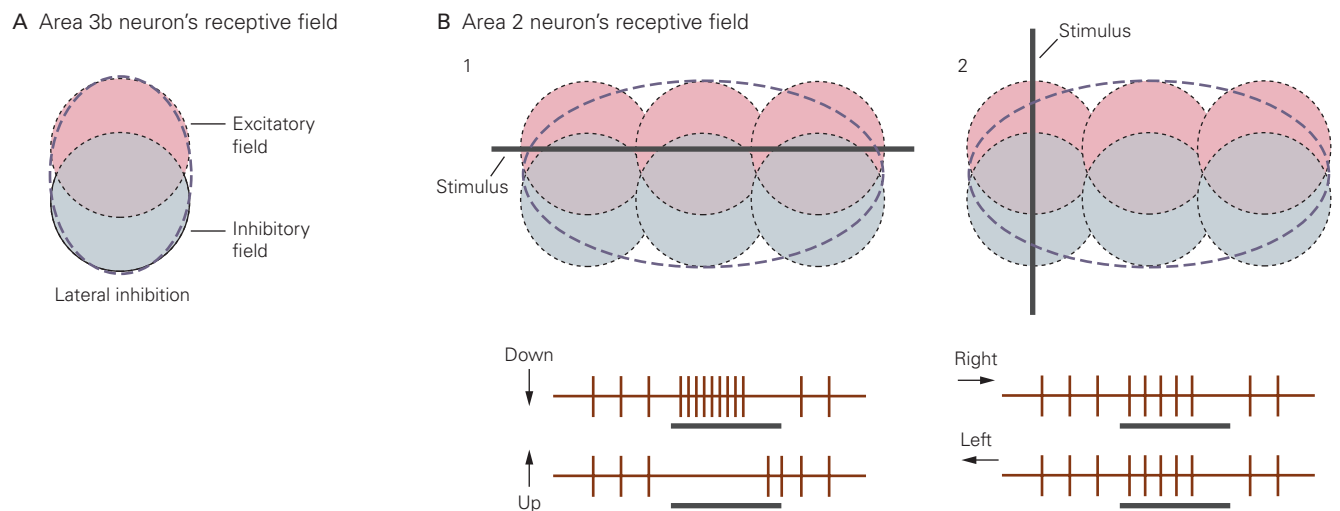


Figure 19–18 The spatial arrangement of excitatory and inhibitory inputs to a cortical neuron determines which stimulus features are encoded by the neuron.

A. A neuron in area 3b of the primary somatosensory cortex has overlapping excitatory and inhibitory zones within its receptive field. (Adapted, with permission, from DiCarlo et al. 1998; Sripati et al. 2006. Copyright © Society for Neuroscience.)

B. Convergence of three presynaptic neurons with the same arrangement of excitatory and inhibitory zones allows direction and orientation selectivity in a neuron in area 2. 1. Downward

motion of a horizontal bar across the receptive field of the post-synaptic cell produces a strong excitatory response because the excitatory fields of all three presynaptic neurons are contacted simultaneously. Upward motion of the bar strongly inhibits firing because it enters all three inhibitory fields first. The neuron responds poorly to upward motion through the excitatory field because the initial inhibition outlasts the stimulus. 2. Motion of a vertical bar across the receptive field evokes a weak response because it simultaneously crosses the excitatory and inhibitory receptive fields of the input neurons. Motion to the left or right cannot be distinguished in this example.

several competing responses is transmitted, permitting a winner-take-all strategy. These circuits prevent blurring of tactile details such as texture when large populations of touch neurons are stimulated. In addition, higher centers in the brain use inhibitory circuits to focus attention on relevant information from the hand when it is used in skilled tasks, by suppressing unwanted, distracting inputs.

The size and position of receptive fields on the skin are not fixed permanently but can be modified by experience or injury to sensory nerves (Chapter 53). Cortical receptive fields appear to be formed during development and maintained by simultaneous activation of the input pathways. If a peripheral nerve is injured or transected, its cortical projection targets acquire new receptive fields from less effective sensory inputs that are normally suppressed by inhibitory networks, or from newly developed connections from neighboring skin areas that retain innervation. Likewise, extensive stimulation of afferent pathways through repeated practice may strengthen synaptic inputs, improving perception and thereby performance.

Touch Information Becomes Increasingly Abstract in Successive Central Synapses

Somatosensory information is conveyed in parallel from the four areas of S-I to higher centers in the cortex, such as the secondary somatosensory cortex (S-II), the posterior parietal cortex, and the primary motor cortex (Figure 19–17C). As information flows toward higher-order cortical areas, specific combinations of stimulus patterns are needed to excite individual neurons.

Signals from neighboring neurons are combined in higher cortical areas to discern global properties of objects such as their orientation on the hand, or the direction of motion (Figure 19–19). In general, cortical neurons in higher cortical areas are concerned with sensory features that are independent of the stimulus position in their receptive field, abstracting object properties common to a particular class of stimuli.

A cortical neuron is able to detect the orientation of an edge or the direction of motion because of the spatial arrangement of the presynaptic receptive fields. The receptive fields of the excitatory presynaptic neurons are typically aligned along a common axis that generates the preferred orientation of the postsynaptic neuron. In addition, the receptive fields of inhibitory presynaptic neurons at one side of the excitatory fields reinforce the orientation and direction selectivity of postsynaptic neurons (Figure 19–18B).

Cognitive Touch Is Mediated by Neurons in the Secondary Somatosensory Cortex

An S-I neuron's response to touch depends primarily on input from within the neuron's receptive field. This feedforward pathway is often described as a *bottom-up* process because the receptors in the periphery are the principal source of excitation of S-I cortical neurons.

Higher-order somatosensory areas not only receive information from peripheral receptors but are also strongly influenced by top-down cognitive processes, such as goal-setting and attentional modulation. Data obtained from a variety of studies—single-neuron studies in monkeys, neuroimaging studies in humans, and clinical observations of patients with lesions in higher-order somatosensory areas—suggest that the ventral and dorsal regions of the parietal lobe serve complementary functions in the touch system similar to the “what” and “where” pathways of the visual system (see Figure 17–13).

S-II is located on the upper bank and adjacent parietal operculum of the lateral sulcus in both humans and monkeys (Figures 19–12B and 19–20B). Like S-I, the S-II cortex contains four distinct anatomical subregions with separate maps of the body. The central zone—consisting of S-II proper and the adjacent parietal ventral area—receives its major input from areas 3b and 1, largely tactile information from the hand and face. A more rostral region, the parietal rostroventral area, receives information from area 3a about active hand movements as well as tactile information from areas 3b and 1 (Figure 19–20). The most caudal somatosensory region of the lateral sulcus extends onto the parietal operculum (Figure 19–12A). This region abuts the posterior parietal cortex and plays a role in integrating somatosensory and visual properties of objects.

Physiological studies indicate that S-II plays key roles in tactile recognition of objects placed in the hand (stereognosis), distinguishing spatial features, such as shape and texture, and temporal properties, such as vibratory frequency. The receptive fields of neurons in S-II are larger than those in S-I, covering the entire surface of the hand, and are often bilateral, representing symmetric, mirror-image locations on the contralateral and ipsilateral hands. Such large receptive fields enable us to sense the shape of an entire large object grasped in one hand, allowing us to integrate the overall contours of a tool as it contacts the palm and different fingers. Bilateral receptive fields enable us to perceive still larger objects with two hands, such as a watermelon or basketball, sharing the load between them.

The large receptive fields of S-II neurons also influence their physiological responses to motion and vibration. S-II neurons do not represent vibration as