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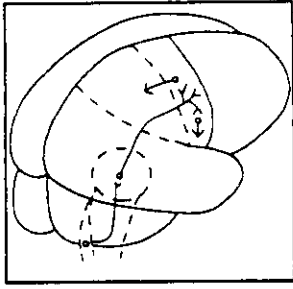
**"Somatosensory System"**

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**These are preliminary lecture notes, intended only for distribution to participants.**





# Somatosensory System

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## Glossary

**Area** Subdivision of cortex that is the equivalent of a nucleus

**Dorsal (posterior) columns** Bundles of axons of peripheral nerve afferents that ascend in the dorsal spinal cord to terminate in nuclei in the lower brain stem

**Dorsal root ganglion** Group of cell bodies of neurons for afferents that enter the spinal cord for one dorsal root

**Nociceptor** Afferent neuron that is activated by painful stimuli

**Nucleus** Group of neurons in the central nervous system that is functionally and morphologically distinct

**Pulvinar** Large region of the thalamus that is related to visual and somatosensory functions and contains a number of separate nuclei

**Slowly adapting afferent** Neuron in a peripheral nerve that slowly decreases its activity during a maintained stimulus state

**Spinothalamic path** Group of axons that cross from neurons in the dorsal grey matter of one side of the spinal cord to ascend in the ventrolateral white matter of the other side to reach the ventroposterior thalamus

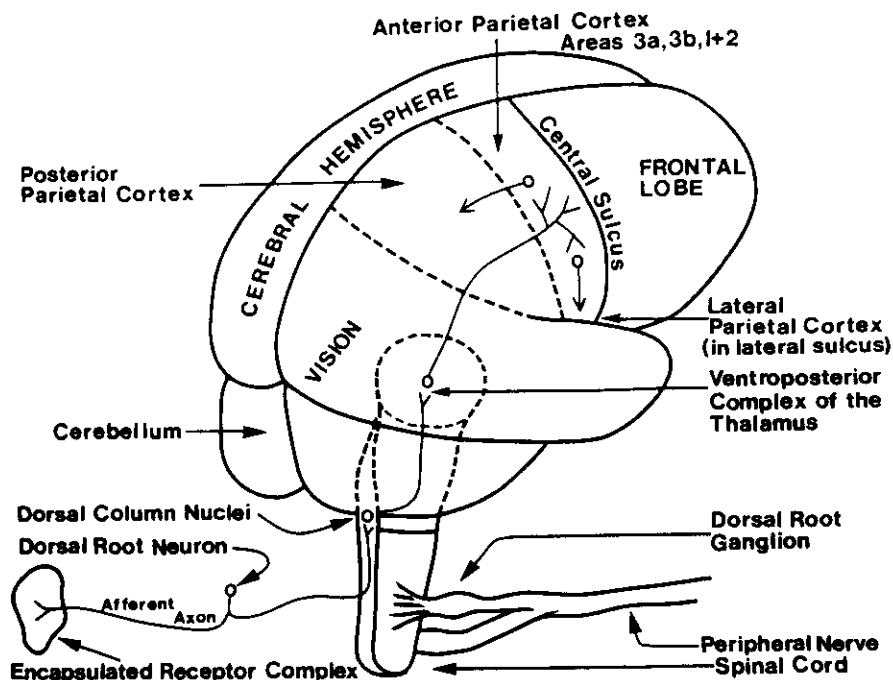
**Trigeminal nuclei** Groups of neurons in the medulla with inputs from somatosensory afferents in the trigeminal nerve innervating the face

**Ventroposterior superior nucleus** Recent term for a functional division of the thalamus that is activated by muscle spindle receptor afferents

THE SOMATOSENSORY SYSTEM allows us to make accurate inferences about the outside world by using information from receptors that respond to touch and vibration, our own movements, temperature, and noxious stimuli. The ability to recognize objects and surfaces by touch depends on this system. While shapes can be perceived passively when objects are pressed to the skin, touch is usually an active process where objects are explored with the fingers or lips. Thus, object recognition can depend on information obtained over periods of time on the relative positions of skin receptors, while those receptors are being stimulated. Much of the somatosensory system consists of brain centers that process information from sensitive mechanoreceptors in the skin that signal surface contact and from deeper receptors in muscles and joints that signal limb movements and positions.

## I. Introduction

The processing of information in the somatosensory system starts with the activation of receptors and afferents by objects indenting or vibrating skin and deeper tissue and by movements stretching receptors in muscles, joints, and tendons. The afferents conduct information to other neurons in the spinal cord and brain stem. Further steps in processing



involve centers in the lower brain stem and thalamus (Fig. 1). In turn, somatosensory neurons in the thalamus activate somatosensory fields in the anterior parietal cortex, which then relay to fields in the posterior parietal cortex related to attention, motivation, and motor somatosensory functions, fields in the cortex of the lateral (Sylvian) sulcus related to object identification and memory, and motor fields of the frontal lobe. These cortical fields also have connections with subcortical centers including the basal ganglia, sensory nuclei of the thalamus and brain stem, and motor components of the brain stem and spinal cord for the control of movements and the modulation of information flow.

## II. Receptors and Peripheral Pathways

In humans, the hand is the most important structure for identifying objects by touch. Receptors in the hand convey information about texture and shape, and this largely depends on activation patterns from the fingerpads during exploration. Much of the coding depends on four types of afferents related to highly sensitive cutaneous receptors in the skin. The four types of low-threshold mechanoreceptors found in the skin have been studied, in part, by stimulating and recording from single afferents in the nerves for the hand in humans. Two classes of

**FIGURE 1** The basic components of the somatosensory system on a posterolateral view of the human brain. Somatosensory afferent neurons enter the dorsal spinal cord to course to the lower brain stem. Second-order neurons cross and ascend to the thalamus where third-order neurons project to the somatosensory fields of the anterior parietal cortex.

afferents continue to respond during a maintained skin indentation and are called slowly adapting, and two classes respond to the beginning and end of such stimuli and are called rapidly adapting.

The slowly adapting type I (SA-I) afferent responds to light pressure on the skin and continues to respond during maintained pressure. This receptor is thought to signal static pressure and the locations of edges of objects pressed on the skin. In humans, electrical stimulation of a single afferent produces a sensation of light, uniform pressure that is located in a small region of skin, the receptive field, where light touch activates the same afferent. Single electrical impulses are typically not felt, but bursts of electrical stimulation produce feelings of pressure that become more intense with increases in stimulation rate. SA-I afferents originate from a number of disklike nerve terminals (Merkel disks) associated with specialized skin cells (Merkel cells) that are thought to have a role in the transduction process. SA-I receptors are densely distributed on the glabrous fingertips, and they constitute about  $\frac{1}{4}$  of the 17,000 tactile afferents of the human hand.

SA-II slowly adapting afferents make up about  $\frac{1}{3}$  of the tactile afferents from the human hand. These afferents originate from endings encapsulated by specialized cells, Ruffini corpuscles, that are also found in ligaments and tendons. The Ruffini corpuscle is attached to surrounding tissue in such a way that stretching of the skin or tendon deforms the corpuscle and activates the afferent. Thus, SA-II afferents are extremely sensitive to skin stretch, and they are often sensitive to directions of stretch. Because Ruffini corpuscles can be activated from a distance, the afferents have large, poorly defined receptive fields. SA-II afferents, by providing information about skin stretch, may combine with sensory inputs from muscles and joints to provide information about digit and limb position and movements. They may also contribute to sensations of the weight of objects by being active during skin shearing.

Nearly half of the tactile afferents of the human hand are of the rapidly adapting type I (RA-I) afferents, which innervate Meissner corpuscles. These corpuscles consist of a nerve terminal disk surrounded by layers of Schwann cells and connective tissue. Outer collagen fibers link the corpuscles to adjacent skin cells so that skin deformations stretch the corpuscles. Each afferent innervates a small, tight group of corpuscles, producing a small receptive field with sharp boundaries. RA-I afferents are most dense in the glabrous fingertips. In the hairy skin, Meissner type endings are largely replaced by RA afferents around hair shafts. RA-I afferents respond to changes in skin indentation and not during maintained pressure. Electrical stimulation of these afferents produces a sensation of light taps, with one tap for each pulse. RA-I units are thought to be important in discrimination of textures moved across the skin and in the sensation of flutter.

The rapidly adapting type II (RA-II) afferents originate in large Pacinian corpuscles and, hence, are also known as Pacinian afferents. The receptor unit consists of a central nerve terminal surrounded by a capsule of many layers of cell processes that attenuate low-frequency components of skin compression. RA-II afferents are extremely sensitive but respond only to transient indentations and not to maintained pressure. Because of sensitivity to vibrations transmitted in the skin and deeper tissue to the receptor, receptive fields are large and have poorly defined boundaries. Pacinian corpuscles are not common, and they are located in deeper skin as well as in subcutaneous tissue. The afferents can be

activated by such weak stimuli as gently blowing on the skin and light taps on a surface in which a skin surface rests. The RA-II afferents have the lowest thresholds for high-frequency vibrations and appear to be the only receptors capable of subserving the sensations of high-frequency vibration. Electrical stimulation of single RA-II afferents produces a sensation only at high pulse rates, and then vibration is felt. The afferents appear to have little or no role in object identification, but they are important in detecting sudden skin deformations produced by ground and air vibrations and by skin contacts.

Other receptors that are important in active touch are the muscle spindle receptors, which were once thought to participate in only spinal cord reflexes and other motor control. Muscle spindle afferents also appear to contribute to sensations of posture and movement, and they may provide all or nearly all of the input used by the nervous system to compute limb position. Such information is critically important in judgments of shapes from multiple contacts during active touch. Other afferents from the skin and deeper tissues signal temperature, pain, itch, and poorly localized aspects of touch. Separate classes of afferents are excited by warming or cooling the skin, whereas pain is signaled by several afferent classes. [See PAIN.]

All afferents course from the skin and other receptor locations to combine and form nerve fascicles. These fascicles join and combine with outgoing motor axons to muscles to form peripheral nerves. Near the spinal cord, the motor and sensory components of nerves separate into ventral motor "roots," consisting of axons from motor neurons in the ventral spinal cord, and sensory dorsal roots, with cell bodies in the dorsal root ganglion and axons continuing into the dorsal spinal cord. Afferents from a given skin area may enter over several adjacent sensory roots, and the skin areas subserved by each root is typically an elongated strip of skin referred to as a dermatome. Sensory axons entering the spinal cord terminate at various depths of the dorsal grey (dorsal horn), depending on afferent class. Axons entering the dorsal horn produce complex arbors of fine branches with synaptic endings. These arbors are in the form of short, narrow tubes that are elongated along the length of the spinal cord. Afferents from different skin regions activate separate populations of neurons in the spinal cord, thereby creating a somatotopic map. Low-threshold mechanoreceptor afferents with terminations in the spinal cord divide to send branches in the dorsal

columns that terminate in the dorsal column–trigeminal complex of the lower medulla. Afferents from muscle spindles may branch and join the other ascending axons, or they may terminate on dorsal horn neurons that in turn send their axons to the medulla.

### III. Pathways in the Spinal Cord

The dorsal or posterior column afferent pathway is largely composed of branches of afferents entering the spinal cord, but it also includes axons of spinal cord neurons and descending axons of neurons higher in the nervous system. The more medial gracile tract has axons from receptors in the trunk and lower limb, and the more lateral cuneate tract subserves the upper limb and adjacent trunk and neck. Afferents from the face and head enter the brain stem and descend via an analogous tract to the lower medulla. Lesions of the dorsal columns produce major defects in the abilities to detect the speed and direction of moving stimuli and the ability to identify figures drawn on the skin. These changes probably reflect the loss of RA-I afferents. Other defects in the control of forelimb movements may relate to the disruption of muscle spinal afferents that course in the cuneate tract. Lesions that involve both the dorsal columns and other fibers of the dorsolateral spinal cord related to muscle spindle afferents result in severe defects in the sense of limb position.

Many of the neurons in the spinal cord with inputs from peripheral afferents have axons that cross in the spinal cord to ascend in the ventrolateral white matter. These axons terminate in the lower brain stem, the midbrain, and several nuclei of the ventroposterior region of the thalamus. Neurons in this crossed spinothalamic tract convey information about painful stimuli and temperature as well as touch. Although some touch sensibility remains after large lesions of other ascending pathways, electrical stimulation of the spinothalamic tract in humans produces sensations of temperature and pain. [See SPINAL CORD.]

### IV. The Dorsal Column–Trigeminal Complex

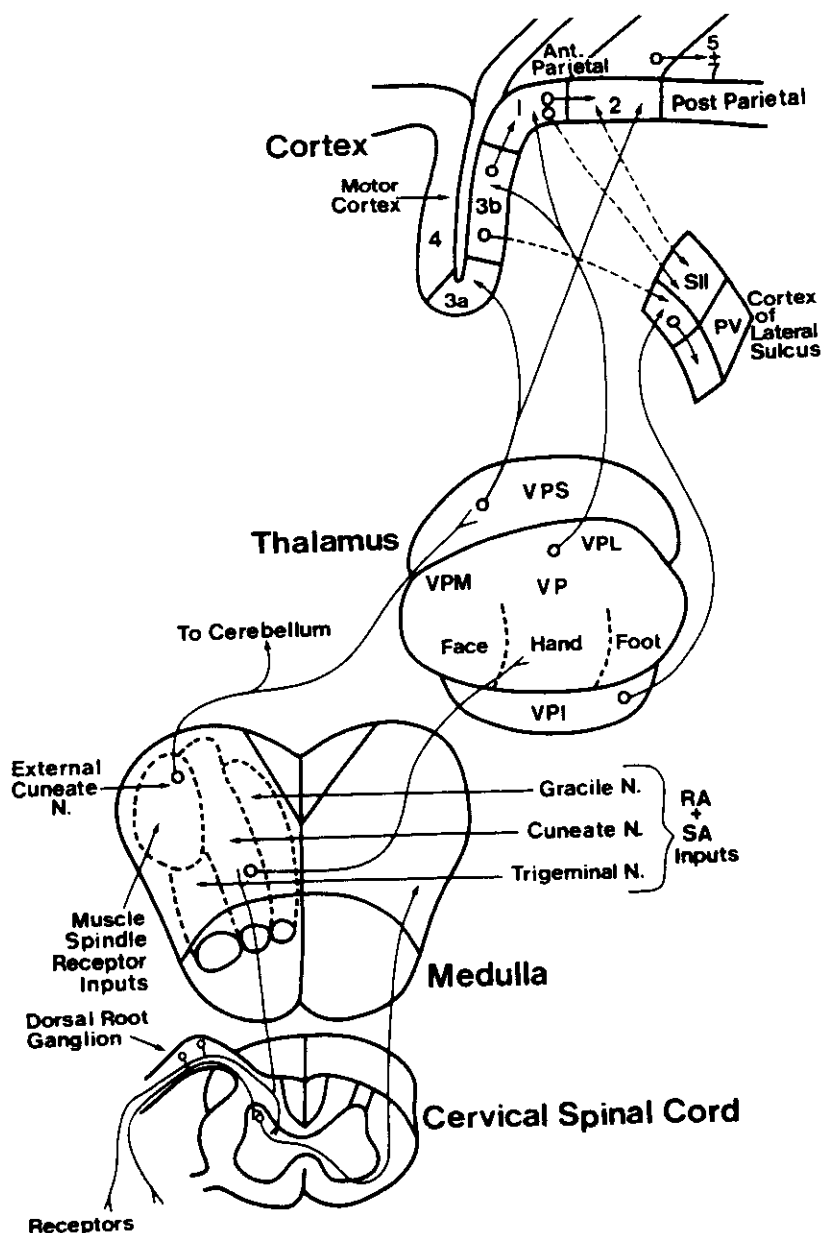
Inputs from tactile RA and SA receptors terminate in nuclei of the dorsal column–trigeminal complex

to form a somatotopic (topological) representation of the body surface in the lower medulla and adjoining spinal cord (Fig. 2). Inputs entering the spinal cord ascend in the dorsal columns to terminate in the gracile nucleus for the lower body and the cuneate nucleus for the upper body. The peripheral or main sensory nucleus of the trigeminal complex receives inputs from cutaneous receptors for the head and joins with the gracile and cuneate nuclei to complete the body surface representation. Axons from neurons in the complex cross to the opposite side of the brain stem, ascend in the medial lemniscus, and terminate in the ventroposterior nucleus of the thalamus. Other inputs from muscle spindle receptors terminate in the external cuneate nucleus where neurons relay to the contralateral ventroposterior superior nucleus. In addition to sensory inputs and relay neurons projecting to the thalamus, the dorsal column–trigeminal complex contains inhibitory neurons with only local connections and descending inputs from the somatosensory cortex that modulate the ascending flow of sensory information.

### V. The Somatosensory Thalamus

Ascending afferents from the spinal cord and dorsal column–trigeminal complex terminate in the ventroposterior complex of the thalamus (Fig. 2). The RA and SA tactile afferents terminate to form a systematic representation of the body surface in the ventroposterior nucleus (VP), while afferents related to muscle spindle receptors and other deep receptors in joints and tendons form a representation in the ventroposterior superior nucleus (VPS). A ventroposterior inferior nucleus (VPI) projects to somatosensory cortex, but the sources of sensory inputs to the VPI are not yet certain. Other nuclei of the thalamus are part of the somatosensory system in that they are interconnected with subdivisions of somatosensory cortex, but they do not have major sensory inputs from the lower brain stem and spinal cord. These include the medial and anterior divisions of the pulvinar complex and the lateral posterior nucleus. In addition, parts of the medial thalamus with inputs via the spinothalamic tract are related to pain and temperature. [See THALAMUS.]

The VP traditionally has been divided into a ventroposterior medial subnucleus (VPM) representing the contralateral face and a ventroposterior lateral subnucleus (VPL) representing the rest of the con-



**FIGURE 2** Somatosensory pathways from receptors to the spinal cord, medulla, thalamus, and cortex. Portions of the spinal cord and medulla are also shown. 3a, 3b, 1, 2, 5, and 7, areas of somatosensory cortex; PV, parietal ventral somatosensory area; RA, rapidly adapting neural inputs; SII, second somatosensory area; SA, slowly adapting inputs; VP, ventroposterior nucleus; VPI, ventroposterior inferior nucleus; VPL, ventroposterior lateral subnucleus; VPM, ventroposterior medial subnucleus; VPS; ventroposterior superior nucleus.

tralateral half of the body surface. The tongue and oral cavity are represented medial to the lips and face in the VPM. The medial portion of the VPL

represents the digits of the hand from thumb to little finger in a mediolateral sequence, while the lateral VPL is devoted to the foot. Dorsal parts of the VPL are devoted to the proximal limbs and trunk.

Neurons in the VP are activated by RA-I and SA (SA-I or both SA-I and -II) inputs. Probably the VP is the target of RA-II (Pacinian) inputs as well, since neurons with Pacinian-like response characteristics have been recorded in area 1 of the cortex, a target of VP neurons (Fig. 2). A few neurons in the VP respond with increased frequency as tactile stimuli become more intense and extend into the painful

range, suggesting a role in mediating judgments of the intensities of painful stimuli. Lesions of the VP produce a persistent numbness in skin regions corresponding to the location of the lesion in the body map in the VP, and electrical stimulation produces localized sensations of numbness or tingling.

The major projections of the VP are to area 3b (S-I proper) of the somatosensory cortex. Some of these same neurons project via collateral axon branches to area 1, while other neurons in the VP project only to area 1. A few neurons in the VP project to area 2. These cortical fields in turn provide feedback projections to the VP and to the adjacent part of the reticular nucleus of the thalamus, which sends inhibitory projections into the VP. In addition, about 20% of the neurons in the VP are inhibitory and have only local connections. Thus, there are neural mechanisms for modifying the responsiveness of the neurons in the VP that relay sensory information to cortex.

The ventroposterior superior nucleus (VPS) contains a systematic representation of muscle spindle and probably other deep receptors, with the face, hand, and foot represented in a mediolateral sequence. A major input appears to be from the external cuneate nucleus. Relay neurons in the VPS project to areas 3a and 2, to a large extent via neurons with axons that branch to both targets.

The VPI is a narrow region of small neurons just ventral to the VP. The source of inputs is not yet certain, but the major cortical projection is to the S-II area. This input is not effective in activating S-II neurons, because lesions of the anterior parietal cortex deactivate S-II neurons in monkeys. However, the VP provides the major thalamic input to S-II neurons in nonprimate mammals, and this input is effective in activating S-II neurons.

## VI. Anterior Parietal Cortex

The anterior parietal cortex of higher primates contains four striplike fields, areas 3a, 3b, 1, and 2, that were previously all considered to be combined to form a single representation of the body, the primary somatosensory field (S-I). However, each of the four architectonic fields of the anterior parietal cortex contains a separate representation of body receptors, with the foot, trunk, hand, and face represented in a mediolateral sequence in all four fields. Only area 3b of higher primates is the homologue of S-I in nonprimates, and therefore area 3b

has been referred to as S-I proper in these primates. Information processing is done partly in a sequence and partly in parallel across areas 3a, 3b, 1, and 2. Thus, inputs from the VP activate area 3b, and neurons in area 3b project forward to activate area 1, forming a sequence or series of processing steps (serial processing). However, both areas 3b and 1 project forward to activate area 2 (parallel processing). In addition, the VP provides some tactile information to areas 1 and 2 directly (parallel processing), and the VPS provides muscle spindle information to area 2. These connections result in area 1 having neurons with more complex receptive field properties and larger cutaneous receptive fields than neurons in area 3b, and neurons in area 2 having even more complex properties, including combined influences of deep and cutaneous receptors. Lesions of area 3b impair discriminations of texture and shape and result in small objects being unrecognized by touch. Lesions of area 2 impair finger coordination and discrimination of shape and size. Area 3a relates to motor cortex and may largely function in the sensory control of motor behavior.

All four fields of anterior parietal cortex project forward to S-II and perhaps other lateral parietal fields. These projections are part of the object identification and recognition pathway. Other projections are directed to the posterior parietal cortex to influence attention and intention and to motor fields of the frontal lobe to more directly modulate motor behavior. Subcortical projections are to the ventroposterior nuclei, the basal ganglia of the motor system, the pulvinar, and sensorimotor regions of the midbrain, pons, medulla, and spinal cord. The fields of the two sides of the brain also are interconnected via the corpus callosum so that information about receptors on one side of the body can influence processing concerned with receptors on the other side of the body. These interhemispheric connections relate not only to anterior parietal fields, but to higher-order fields including the S-II of the lateral parietal cortex. Finally, all somatosensory fields send feedback connections to the cortical areas and thalamic nuclei that provide activating inputs. [See HEMISPHERIC INTERACTIONS.]

## VII. Posterior Parietal Cortex

The portion of the parietal lobe that is caudal to area 2 has been subdivided in various ways by different



investigators, but functional subdivisions remain uncertain. The subdivisions presently recognized (e.g., Brodmann areas 5a, 5b, 7b, and 7a, Fig. 3) indicate general regions of the posterior parietal cortex rather than functionally significant subdivisions.

The cortex that is most anterior in the posterior parietal cortex is largely somatosensory in function, whereas more posterior regions are more visual. In monkeys, more of the anterior cortex in the region of area 7b has neurons that are activated by touch and movements of the hand and face, and these responses may depend on inputs from area 2. In contrast, more of the posterior cortex in the region of area 7a has neurons that respond to visual stimuli, or during eye movements, and some of the outputs are to the frontal eye fields. The posterior cortex also has interconnections with the limbic cortex of the medial wall of the cerebral hemispheres, and these connections presumably mediate emotional and motivational factors. In addition, evidence indicates a supplementary somatosensory area of uncertain functions exists in the posterior parietal cortex on the medial wall of the cerebral hemisphere.

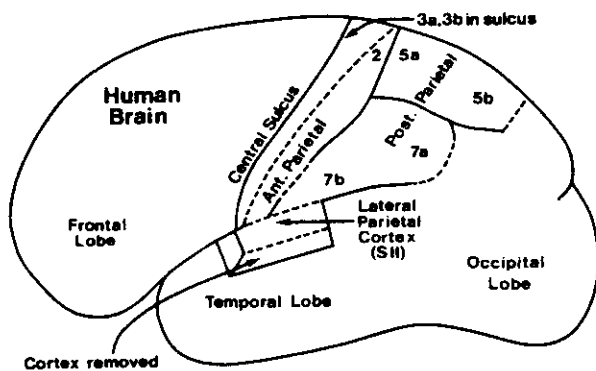
In humans, concepts of posterior parietal cortex function are largely derived from clinical reports of the behavioral changes that follow large lesions. Such patients tend to ignore visual and tactile stimulation related to the contralateral body or visual space. The changes are most severe after damage to the nondominant, usually the right, hemisphere. However, such asymmetry is not found in monkeys, where the defects produced by lesions of the right hemisphere are less profound. In humans, the impairments include difficulties in changing the fo-

cus of attention, localizing objects in space, directing eye movements, drawing, and even object identification. The functional asymmetry of the posterior parietal cortex in humans suggests that the right hemisphere contains the mechanisms for attending to both sides of the body, while the left hemisphere is largely devoted to the contralateral side of the body.

### VIII. Somatosensory Cortex of the Lateral (Sylvian) Sulcus

The fields of the anterior parietal cortex and some of the posterior parietal cortex project to the S-II and adjoining fields on the upper bank and insula of the lateral sulcus. These projections appear to be part of a critical pathway for somatosensory memory involving S-II, a parietal ventral area and other lateral fields before reaching the amygdala and hippocampus. Lesions of the S-II region in monkeys produce profound deficits in object identification by touch. The amygdala and hippocampus have long been known to be important in memory and object identification, although the memory traces are probably in the cortex, and the amygdala has been shown to have a role in the cross modal recognition of objects (visual to tactile).

In summary, the coding of information for object identification by touch largely involves four classes of afferents activated by tactile stimuli and afferents signaling muscle contractions. These afferents relay in the spinal cord and in the lower medulla, where neurons send this information to the ventroposterior complex of the contralateral thalamus. Further processing occurs in separate body representations in areas 3a, 3b, 1, and 2 of the anterior parietal cortex, and projections from these fields converge on higher processing stations including the S-II and the parietal ventral area in the cortex of the lateral sulcus. Further connections with the amygdala and hippocampus are critical in the formation of memories.



**FIGURE 3** Subdivisions of the somatosensory cortex on the surface of a lateral view of a human brain. Part of the temporal lobe has been cut away to show the somatosensory cortex of the lateral sulcus.

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