

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

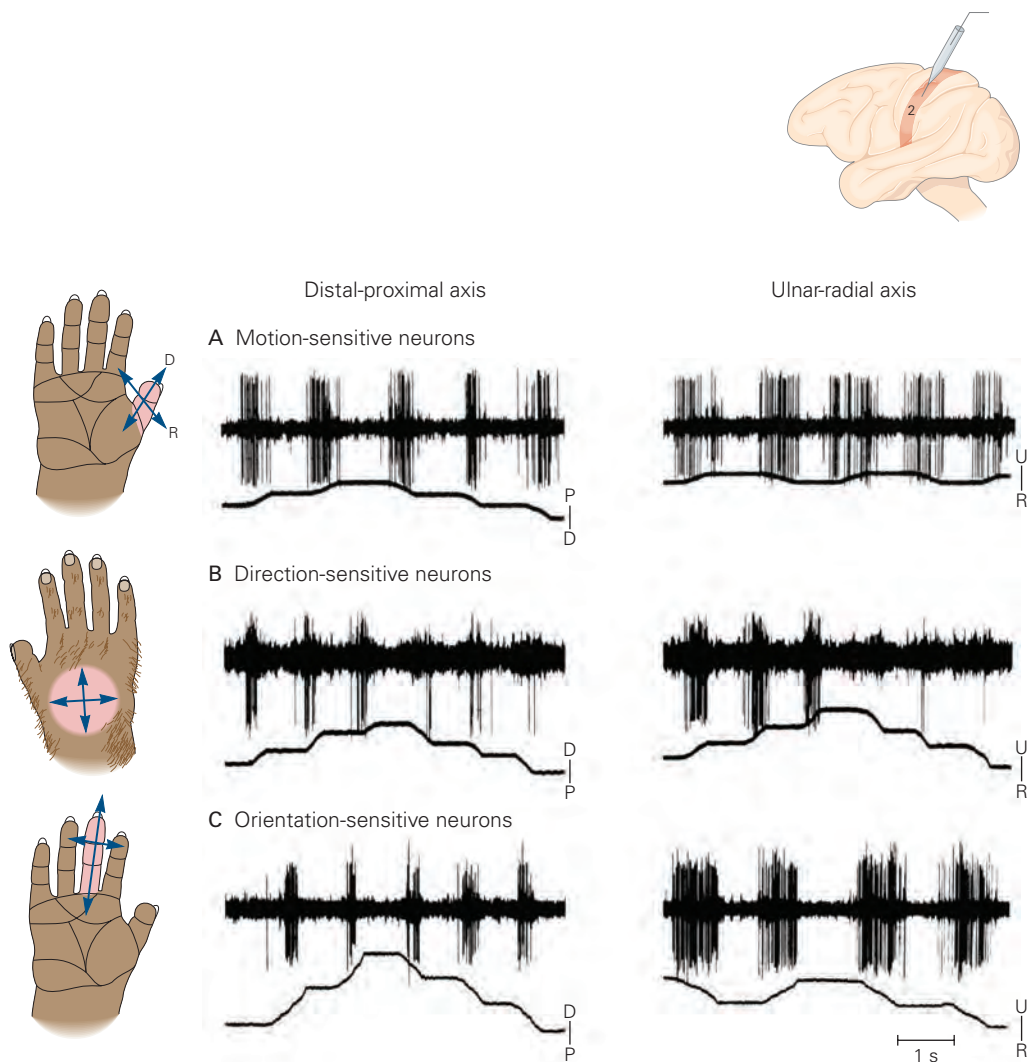


Figure 19-19 Neurons in area 2 encode complex tactile information. These neurons respond to motion of a probe across the receptive field but not to touch at a single point. The lower trace indicates the direction of motion by upward and downward deflections. (Adapted, with permission, from Warren, Hämmäläinen, and Gardner 1986.)

A. A motion-sensitive neuron responds to stroking the skin in all directions.

B. A direction-sensitive neuron responds strongly to motion toward the ulnar side of the palm but fails to respond to motion in the opposite direction. Responses to distal or proximal movements are weaker.

C. An orientation-sensitive neuron responds better to motion across a finger (ulnar-radial) than to motion along the finger (distal-proximal), but does not distinguish ulnar from radial or proximal from distal directions.

periodic spike trains linked to the oscillatory frequency, as do the sensory fibers from the skin or S-I neurons (Figure 19-9). Instead, S-II neurons abstract temporal or intensive properties of the vibratory stimulus, firing at different mean rates for different frequencies. A similar frequency-dependent transition from temporal- to rate-coding neurons underlies sound processing in primary auditory cortex (Chapter 28), a brain region juxtaposed to S-II cortex in the parietal operculum.

Importantly, the firing rates of S-II neurons depend on the behavioral context or motivational

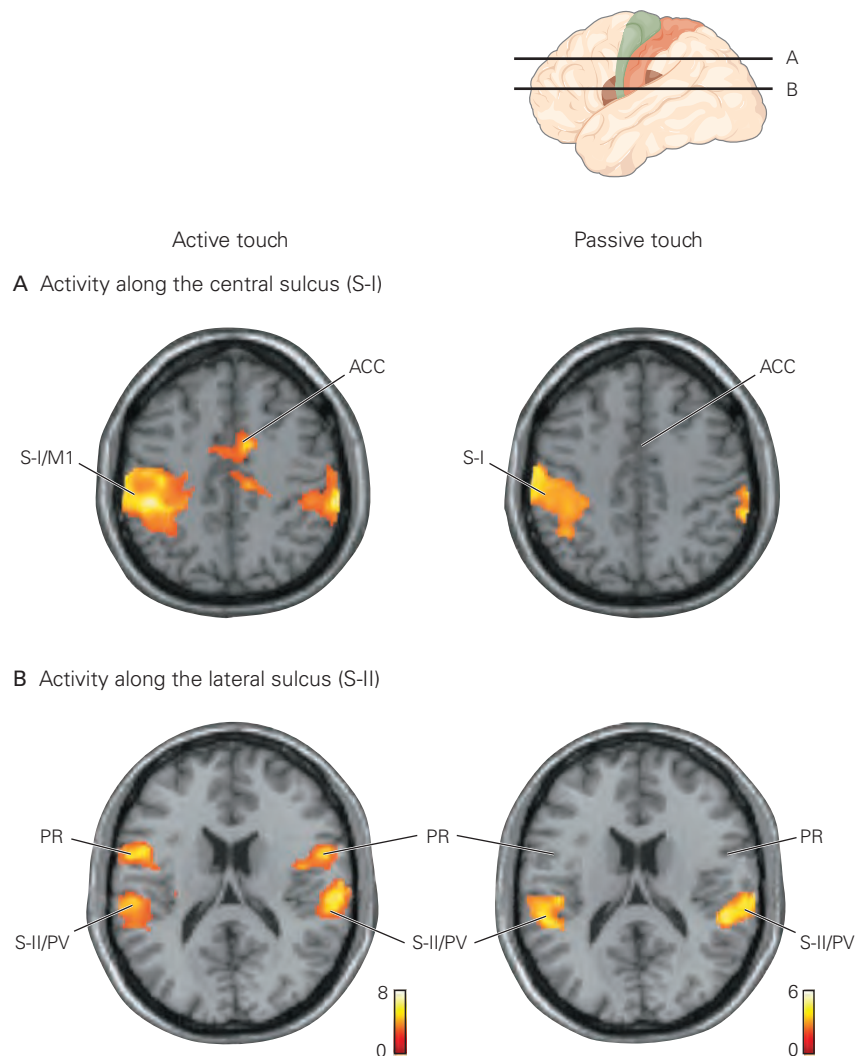
state of the subject. In elegant recent studies, Ranulfo Romo and his colleagues compared responses to vibratory stimuli of neurons in S-I, S-II, and various regions of the frontal lobe of monkeys while the animals performed a two-alternative forced-choice task. The animals were rewarded if they correctly recognized which of two vibratory stimuli was higher in frequency.

Neurons in S-I faithfully represent the vibratory cycles of each stimulus using a temporal code: they fire brief spike bursts in phase with each cycle (Figure 19-9B).

Figure 19–20 Responses in S-I and S-II to active touch are more complex than those evoked by passive touch. Cortical regions in the human brain stimulated by passive and active touch are localized using functional magnetic resonance imaging (fMRI). (Adapted, with permission, from Hinkley et al. 2007.)

A. Axial views of activity along the central sulcus during passive stroking of the right hand with a sponge (*right panel*) and during active touching of the sponge (*left panel*). Areas 3b and 1 are activated in the left hemisphere in both conditions. Active touch also engages the primary motor cortex (**M1**) in the left hemisphere, the anterior cingulate cortex (**ACC**), and evokes weak activity in the ipsilateral S-I (right hemisphere). These sites were confirmed independently using magnetoencephalography in the same subjects.

B. Axial views of activity along the Sylvian fissure in the same experiment. Bilateral activity occurs in S-II and the parietal ventral (**PV**) area during passive stroking and is stronger when the subject actively moves the hand. The parietal rostroventral area (**PR**) is active only during active touch. Magnetoencephalographic responses in S-II/PV and PR occur later than in S-I, reflecting serial processing of touch from S-I to S-II/PV and from S-II/PV to PR.



In contrast, S-II neurons respond to the first stimulus with nonperiodic spike trains in which their mean firing rates are directly or inversely correlated with the vibratory frequency (Figure 19–21A). Their responses to the second stimulus are even more abstract. S-II spike trains combine the frequencies of both stimuli (Figure 19–21B). In other words, S-II responses to vibration depend on the stimulus context: the same vibratory stimulus can evoke different firing rates depending on whether the preceding stimulus is higher or lower in frequency.

Even more interesting, Romo's group found that neurons in S-II send copies of the spike trains evoked by the first stimulus to the prefrontal and premotor cortex in order to preserve a memory of that response. Neurons in these frontal cortical areas continue to fire during the delay period after the first stimulus ends. Romo and colleagues proposed that these regions in

the frontal lobe send the memory signal back to S-II when the second stimulus occurs, thereby modifying the response of S-II neurons to the direct tactile signals from the hand. In this manner, sensorimotor memories of previous stimuli influence sensory processing in the brain, allowing subjects to make cognitive judgments about newly arriving tactile stimuli.

S-II is the gateway to the temporal lobe via the insular cortex. Regions of the medial temporal lobe, particularly the hippocampus, are vital to the storage of explicit memory (Chapter 53). We do not store in memory every scintilla of tactile information that enters the nervous system, only that which has some behavioral significance. In light of the demonstration that the firing patterns of S-II neurons are modified by selective attention, S-II could make the decision whether a particular bit of tactile information is remembered.

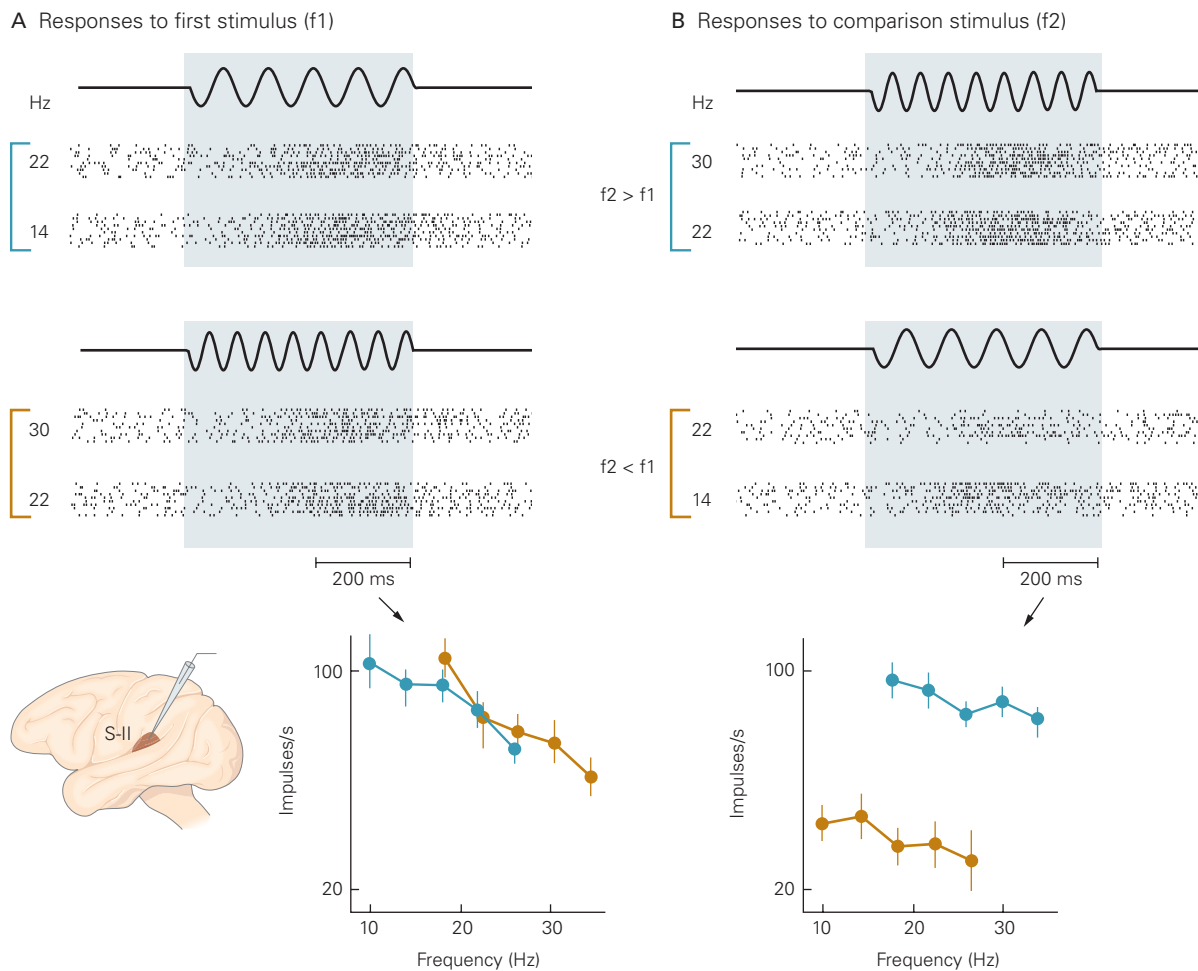


Figure 19-21 The sensitivity of an S-II neuron to vibratory stimuli is modulated by attention and behavioral conditions. A monkey was trained to compare two vibratory stimuli applied at a 3-second interval to the fingertips (f_1 and f_2) and to indicate which had the higher frequency. The plots show the mean firing rates of the neuron during each of the two stimuli. The animal's decision about which frequency is higher can be predicted from the neural data during each type of trial. The mean firing rates of this neuron are significantly higher at each stimulation frequency when f_2 is greater than f_1 than when f_2 is less than f_1 . (Adapted, with permission, from Romo et al. 2002. Copyright © 2002 Springer Nature.)

A. Raster plots show the responses of an S-II neuron to various sample stimuli (f_1). The vertical tick marks in each row denote action potentials, and individual rows are separate trials of the

stimulus pairs. Trials are grouped according to the frequencies tested. The firing rate of the neuron encodes the vibratory frequency of the sample stimulus; it is higher for low-frequency vibration regardless of the subsequent events. Note that the firing patterns recorded in S-II are not phase-locked to the vibratory cycle as in S-I (see Figure 19-9B).

B. Each row in the raster plots illustrates responses to the comparison stimulus (f_2) during the same trials shown in A. The neuron's response to f_2 reflects the frequency of both f_2 and f_1 . When $f_2 > f_1$, the neuron fires at high rates during f_2 and the animal reports that f_2 is the higher frequency. When $f_2 < f_1$, the neuron fires at low rates during f_2 and the animal reports that f_1 is the higher frequency. In this manner, the responses of S-II neurons reflect the animal's memory of an earlier event.

Active Touch Engages Sensorimotor Circuits in the Posterior Parietal Cortex

Studies in the mid-1970s by Vernon Mountcastle, Juhani Hyvärinen, and others demonstrated that regions of the posterior parietal cortex surrounding the intra-parietal sulcus play an important role in the sensory guidance of movement rather than in discriminative

touch. These regions include areas 5 and 7 in monkeys and the superior parietal lobule (Brodmann's areas 5 and 7) and inferior parietal cortex (areas 39 and 40) in humans. These and subsequent studies demonstrated that neural activity in the posterior parietal cortex during reaching and grasping coincides with activation of neurons in motor and premotor areas of the frontal cortex and precedes activity in S-I. Areas 5 and 7

are postulated to be engaged in the planning of hand actions, because the posterior parietal cortex receives convergent central and peripheral signals that allow it to compare central motor commands with somatosensory feedback during reaching and grasping behaviors. Sensory feedback from S-I to the posterior parietal cortex is used to confirm the goal of the planned action, thereby reinforcing previously learned skills or correcting those plans when errors occur.

Predicting the sensory consequences of hand actions is an important component of active touch. For example, when we view an object and reach for it, we predict how heavy it should be and how it should feel in the hand; we use such predictions to initiate grasping. Daniel Wolpert and Randy Flanagan have proposed that during active touch the motor system controls the afferent flow of somatosensory information to the brain so that subjects can predict when tactile information should arrive in S-I and reach consciousness. Convergence of central and peripheral signals allows neurons to compare planned and actual movements. Corollary discharge from motor areas to somatosensory regions of the cortex may play a key role in active touch. It provides posterior parietal cortex neurons with information on intended actions, allowing them to learn new skills and perform them smoothly.

Lesions in Somatosensory Areas of the Brain Produce Specific Tactile Deficits

Patients with lesions in S-I cortex have difficulty responding to simple tactile tests: touch thresholds, vibration and joint position sense, and two-point discrimination (Figure 19–22A). These patients also perform poorly on more complex tasks, such as texture discrimination, stereognosis, and visual–tactile matching tests.

Loss of tactile sensation in the hand produces significant motor as well as sensory deficits. Motor deficits are less pronounced than sensory losses, particularly during tests of force and position control. Exploratory movements and skilled tasks such as catching a ball or pinching small objects between the fingertips are also abnormal.

Local anesthesia of sensory nerve fibers in the hand provides a direct way to appreciate the sensorimotor role of touch. Under local anesthesia of the median and ulnar nerves, hand movements are clumsy and poorly coordinated, and force generation during grasping is abnormally slow. With the loss of tactile sensibility, one is completely reliant on vision for directing the hand. Loss of touch does not cause paralysis or weakness because much of skilled movement is predictive,

relying on sensory feedback for adjustment if necessary. The motor system in these subjects compensates for the absence of tactile information by generating more force than necessary.

These motor problems are exacerbated by long-term, chronic loss of tactile function because of injury to peripheral nerves or dorsal column lesions. Deafferentation produces major changes in the afferent connections in the brain, as do certain diseases. Myelinated afferent fibers in the dorsal columns degenerate in patients with demyelinating diseases, such as multiple sclerosis. In late-stage syphilis, the large-diameter neurons in the dorsal root ganglia are destroyed (tabes dorsalis). These patients have severe chronic deficits in touch and proprioception but often little loss of temperature perception and nociception. The somatosensory losses are accompanied by motor deficits: clumsy and poorly coordinated movements and dystonia. Similar impairments occur in patients with damage to S-I caused by stroke or head trauma, or following surgical excision of the postcentral gyrus.

Patients with lesions in the posterior parietal cortex usually have only mild difficulty with simple tactile tests. However, they have profound difficulty with complex tactile recognition tasks and use few exploratory and skilled movements (Figure 19–22B). They display kinematic deficits when interacting with objects, failing to shape and orient the hand properly to grasp them and misdirecting the arm during reaching. They typically use too much grip force when an object is placed in their hand and are unable to direct the fingers properly when asked to evaluate its size and shape. These deficits are described clinically as the “useless hand” syndrome (tactile apraxia).

Studies of sensory deficits in human patients are complicated by the fact that disease states or trauma rarely produce damage confined to one localized brain area. For this reason, analyses of experimentally controlled lesions in animals have been useful for understanding the etiology of the sensory deficits observed in human patients. For example, macaque monkeys with a lesion of the cuneate fascicle show chronic losses in tactile discrimination, such as higher touch thresholds, impaired vibration sense, and poor two-point discrimination. They also display major deficits in the control of fine finger movements during grooming, scratching, and object manipulation. A similar deficit in skilled movements can be produced experimentally in monkeys by inhibiting the neurons in the hand-representation region of area 2.

Experimental ablation of somatosensory areas of the cortex in monkeys has provided valuable information about the function of these areas. Small lesions

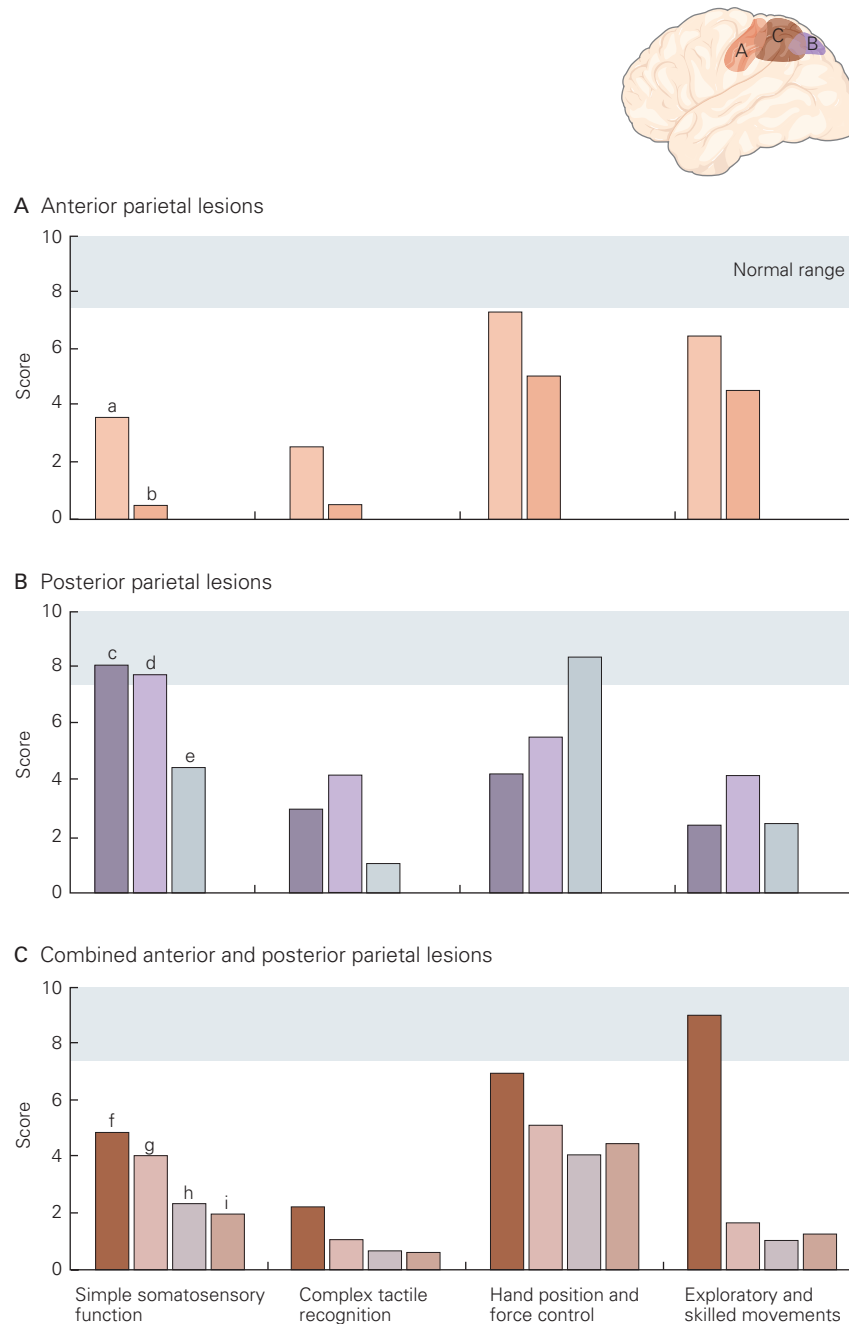


Figure 19-22 Lesions of anterior and posterior regions of the parietal lobe produce characteristic sensory and motor deficits of the hand. Bar graphs rank the performance of nine patients (a–i) with unilateral parietal cortex brain lesions on four sets of standardized tests of sensory and motor function of the contralateral hand. The behavioral scores are ranked from normal (10) to maximal deficit (0). The normal range shown is the performance score of these patients for the ipsilateral hand. Tests of *simple somatosensory function* include light touch from a 1-g force-calibrated probe, two-point discrimination on the finger and palm, vibration sense, and position sense of the index finger metacarpophalangeal joint. Tests of *complex tactile recognition* assess texture discrimination, form recognition, and size discrimination. Tests of *hand position and force control* measure grip force, tapping, and reaching to a target. Tests of *exploratory and skilled movements* evaluate insertion of pegs in slots, pincer grip of small objects, and exploratory movements

when palpating objects. (Adapted, with permission, from Pause et al. 1989. Copyright © 1989, Oxford University Press.)

A. Two patients with lesions to the anterior parietal lobe show severe impairment in both sets of tactile tests but only moderate impairment in the motor tasks.

B. Three patients with posterior parietal lesions show only minor deficits in simple somatosensory tests but severe impairment in complex tests of stereognosis and form. Motor deficits are greater in skilled tasks.

C. Four patients with combined lesions to anterior and posterior parietal cortex show severe impairment in all tests. Interestingly, the patient who showed the least impairment in this group (patient f) suffered brain damage at birth; the developing brain was able to compensate for the loss of major somatosensory areas. Lesions in the other patients resulted from strokes later in life.

limited to area 3b produce major deficits in touch sensation from a particular part of the body. Lesions in area 1 produce a defect in the assessment of the texture of objects, whereas lesions in area 2 alter the ability to differentiate the size and shape of objects. The damage to tactile function is less severe when such lesions are made in infant animals, apparently because in the developing brain S-II cortex may take over functions normally assumed by S-I.

Removal of S-II cortex in monkeys causes severe impairment in the discrimination of both shape and texture and prevents the animals from learning new tactile discriminations. Ablation or inhibition of areas 2 or 5 produces deficits in roughness discrimination but few other alterations in passive touch. However, motor performance is impaired as these animals misdirect reaching toward objects, fail to preshape the hand

to grasp objects skillfully, and have difficulty coordinating finger movements because tactile feedback is absent (Figure 19–23).

The similarity between impairments observed in humans and monkeys is an important basis for understanding clinical losses of somatosensory function. We shall learn in later chapters that lesioning studies of other cortical areas in monkeys have also provided insight into higher-order sensory and motor functions of the brain.

Highlights

1. When we explore an object with our hands, a large part of the brain may become engaged by the sensory experience, by the thoughts and emotions it evokes, and by motor responses to it. These sensations result from the parallel actions of multiple cortical areas engaged in feedforward and feedback networks.
2. At the first touch, the peripheral sensory apparatus deconstructs the object into tiny segments, distributed over a large population of approximately 20,000 sensory nerve fibers. The SA1 system provides high-fidelity information about the object's spatial structure that is the basis of form and texture perception. The SA2 system provides information about the hand conformation and posture during grasping and other hand movements. The RA1 system conveys information about motion of the object in the hand, which enables us to manipulate it skillfully. Together with RA2 receptors, they sense vibration of objects that allows us to use them as tools.
3. The information from touch receptors is conveyed to consciousness by the dorsal column fiber tracts of the spinal cord, relay nuclei in the brain stem and thalamus, and a hierarchy of intracortical pathways. By analyzing patterns of activity across the entire population, the brain constructs a neural representation of objects and actions of the hand.
4. Computations in central pathways are complex and accomplished serially, beginning in the dorsal column nuclei, progressing through the thalamus and several cortical stages, and terminating in regions of the medial temporal cortex concerned with memory and perception and in motor areas of the frontal lobe that mediate voluntary movements.
5. The brain's processing of touch is aided by the topographic, somatotopic organization of the neurons involved at each relay. Adjacent skin areas that

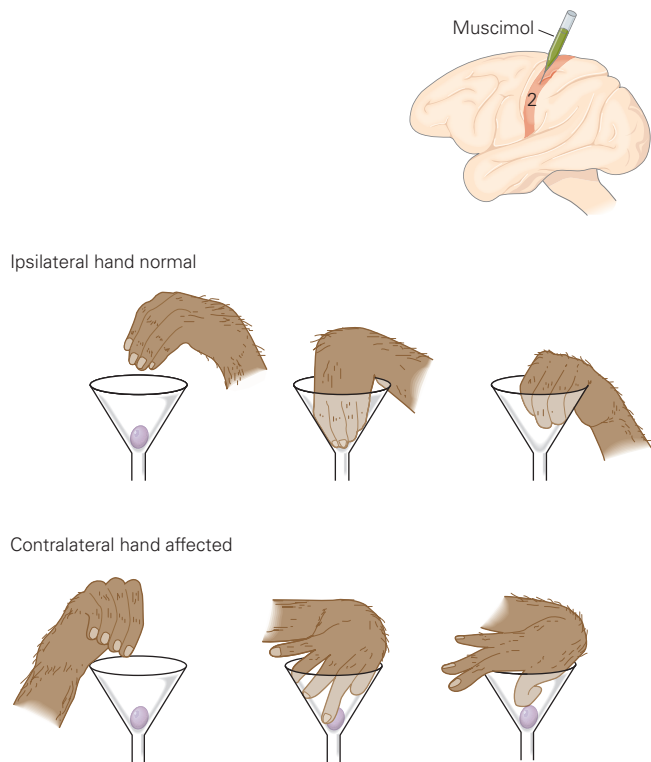


Figure 19–23 Finger coordination is disrupted when synaptic transmission in the somatic sensory cortex is inhibited in a monkey. Muscimol, a γ -aminobutyric acid (GABA) agonist that inhibits cortical cells, was injected into Brodmann's area 2 on the left side of a monkey's brain. Within minutes after injection, the finger coordination of the right hand (contralateral) was severely disrupted; the monkey was unable to pick up a grape from a funnel. The injection effects are shown to be specific to the injected hemisphere because the left hand (ipsilateral) continues to perform normally. (Adapted, with permission, from Hikosaka et al. 1985. Copyright © 1985 Elsevier B.V.)

are stimulated together are linked anatomically and functionally in central relays. Body parts that are especially sensitive to touch—the hands, feet, and mouth—are represented in large areas of the brain, reflecting the importance of tactile information conveyed from these regions.

6. Another function of the central pathways is the transformation of the disaggregated representation of object properties among thousands of neurons to an integrated representation of complex object properties in a few neurons. Convergent excitatory connections between neurons representing neighboring skin areas and intracortical inhibitory circuits enable higher-order cortical cells to integrate global features of objects. In this manner, the somatosensory areas of the brain represent properties common to particular classes of objects.
7. A third function is regulating the afferent flow of somatosensory information. The peripheral fibers deliver much more information than can be handled at any one moment; the central neural pathways compensate by selecting information for delivery to the mechanisms of perception and memory. Recurrent pathways from higher brain areas modify the ascending information provided by touch receptors, thus fitting the stream of sensory information to previous experience and task goals.
8. Finally, the touch system provides information necessary for the control and guidance of movement. Interactions between sensory and motor areas of parietal and frontal cortex provide a neural mechanism for planning desired actions, for predicting the sensory consequences of motor behaviors, and for skill learning from repeated experience.

Esther P. Gardner

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