Touch

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An Overall View

The somatic sensory system is concerned with four major modalities: discriminative touch (required to recognize the size, shape and texture of objects and their movement across the skin), proprioception (the sense of static position and movement of limbs and body), nociception (the signaling of tissue damage, often perceived as pain), and temperature sense (warmth and cold). These modalities reach the brain through two major pathways. Most aspects of touch, as well as proprioception, are carried by the dorsal column–medial lemniscal system, with which we shall here be concerned. Sensations of pain and temperature are carried by the anterolateral system, which is discussed in the next chapter.

In this chapter we shall examine how neuronal activity within the dorsal column–medial lemniscal system gives rise to perception, using discriminative touch as an illustrative example. The sense of touch is most discriminating in the finger tips. Information transmitted to the brain from mechanoreceptors in the fingers enables us to feel the shape and texture of objects so we can read braille or play a musical instrument. Here we shall learn how we perceive the surface features of objects and why fingertips are better suited to the task than our toes or the skin of the back. Next we examine the degree to which the various somatic modalities are segregated functionally in the central nervous system and how they are combined for coherent perception. Since this chapter is the first in which we discuss the central projections of a sensory system, we also introduce the question: How does the cerebral cortex transform sensory information coming from the periphery?

Sensory Information About Touch Is Processed by a Series of Relay Nuclei

We have already considered the anatomical plan of touch sensation in Chapters 24 and 25 (see for example, Figure 25–8). The skin and underlying tissue contain four types
The somatic sensory cortex, located in the parietal lobe, has three major divisions: the primary (S-I) and secondary (S-II) somatosensory cortices and the posterior parietal cortex.

A. The relationship of S-I to S-II and to the posterior parietal cortex (Brodman's areas 5 and 7) is seen best from a lateral perspective of the surface of the cerebral cortex.

B. The primary somatic cortex (S-I) is subdivided into four distinct cytoarchitectonic regions. This sagittal section shows these four regions (Brodman's areas 3a, 3b, 1, and 2)

and illustrates their spatial relationship to area 4 of the motor cortex and area 5 and 7 of the posterior parietal cortex.

C. Fibers in the medial lemniscus project to the ventral posterior lateral nucleus of the thalamus. Neurons in this nucleus project to all areas in the primary somatic sensory cortex (S-I), primarily Brodman's areas 3a and 3b but also to areas 1 and 2. In turn, neurons in areas 3a and 3b project to areas 1 and 2, and all of these project to the secondary somatic sensory cortex (S-II). (Adapted from Jones and Friedman, 1982.)

of receptors. The superficial skin has rapidly adapting Meissner's corpuscles and slowly adapting Merkel's cells, both of which respond to touch. Deeper tissue contains the rapidly adapting pacinian corpuscles, which respond to vibration, and the slowly adapting Ruffini's corpuscles, which respond to rapid indentation of the skin. These four types of receptors are innervated by peripheral axons of nerve cells in the dorsal root ganglia, their central branches ascend in the dorsal columns and synapse with second-order neurons in the dorsal column nuclei. Axons of neurons in the dorsal column nuclei cross the midline in the medulla and ascend through the brain stem on the contralateral side as the medial lemniscus. In the thalamus they synapse on third-order cells in the ventral posterior medial and ventral posterior lateral nuclei.

The third-order neurons in the thalamus send axons to the primary somatic sensory cortex (S-I), located in the postcentral gyrus of the parietal lobe. This area is subdivi-
The anatomical plan of the somatic sensory system reflects an organizational principle common to all sensory systems: sensory information is processed in a series of relay regions within the brain. To understand the serial processing characteristic of sensory systems it is necessary to examine how incoming information is transformed within each relay nucleus.

Relay nuclei are composed of projection (or relay) neurons that send their axons to the next relay nucleus in the ascending pathway of sensory information. Each projection neuron receives synaptic input from many afferent axons. Nevertheless, in the dorsal column nuclei, for example, the synaptic actions of some afferent fibers are so effective that activity in a single afferent fiber can discharge a relay cell. When such a limited number of afferent fibers can activate a cell, information can be transmitted with high fidelity. As a result, in some nuclei (as in the lateral geniculate nucleus, the major relay nucleus for afferent signals from the retina) the afferent message is relayed to the next level without modification.

More commonly, however, sensory input to relay cells follows a pattern of extensive convergence and divergence, as shown in Figure 26–2. In addition to activating relay cells, afferent fibers also activate interneurons, both excitatory and inhibitory. These interneurons can contribute to the processing of incoming sensory information by modulating the firing of the projection neurons. As a result, the firing pattern of the projection neurons leaving the relay nucleus differs from that of the afferent fibers coming into the nucleus reflecting transformation of the signal by the cells of the nucleus.

The processing of neural information at a sensory relay nucleus follows the same principles found in the motor relay nuclei that we examined in general in Chapter 2. In addition to the convergence and divergence of excitatory synaptic input, there are three types of inhibitory pathways: feed-forward, feedback, and distal inhibition (Figure 26–2).

Feed-forward (or reciprocal) inhibition allows activity in one group of neurons to inhibit a different group of neurons. Feed-forward inhibition permits what Sherrington called a singleness of action, a winner-take-all strategy, which ensures that only one of two or more competing responses is expressed. In contrast, feedback (or recurrent) inhibition allows the most active neurons to limit the activity of all adjacent elements that are less active, irrespective of their function, thereby enhancing the contrast in firing pattern between the actively firing cells and the surrounding less active neurons. Both types of inhibition create zones of contrasting activity within the central nervous system: a central zone of active neurons surrounded by a ring of less active neurons. As we shall see in Chapter 30, by enhancing or amplifying the contrast between highly active cells and their neighbors these cellular interactions contribute to selective perception, by which we attend to one stimulus and not another.

Inhibitory interactions are quite general in sensory systems. Although there is no inhibition of the peripheral receptor in the somatic sensory system, inhibitory actions are common in all subsequent relay nuclei. For example,

![Figure 26–2](image-url)

Cells in a sensory relay nucleus have complex inputs from both primary afferent fibers and local interneurons. This illustration is based on a dorsal column nucleus. The relay (or projection) cells of this nucleus receive convergent and divergent excitatory input from afferent fibers traveling in the dorsal columns. The afferent fibers also end on inhibitory interneurons that make feed-forward inhibitory connections onto adjacent relay cells. In addition, the activity in the relay cells inhibits the surrounding cells by means of feedback inhibition. Finally, neurons in the cerebral cortex modulate by distal inhibition the firing of relay cells, acting both pre- and postsynaptically. The relay cells in this nucleus project their axons to the thalamus. [In this, as in subsequent figures, excitatory synapses are indicated by open triangles, inhibitory synapses by filled triangles.]

Both feed-forward and feedback inhibition are present in the dorsal column nuclei, the first relay point in the somatic sensory system. The afferent fibers inhibit the activity of cells in the dorsal column nuclei that surround the cells they excite (feed-forward inhibition). In addition, the active cells in a nucleus inhibit the less active cells nearby by means of recurrent collateral fibers (feedback inhibition), thereby sharpening further the contrast between the active cells and their neighbors.

Feed-forward and feedback are local inhibitory mechanisms that operate within a relay nucleus. But neurons from more distant sites, such as the motor cortex and the brain stem, can also inhibit and thereby control the flow.
of information into relay nuclei. This mechanism is called distal inhibition. In the dorsal column nuclei distal inhibition operates mostly on presynaptic terminals. Distal inhibition illustrates still another principle of organization in the sensory system: Higher areas of the brain are able to control the sensory inflow from the peripheral receptors into relay nuclei.

The Body Surface Is Represented in the Brain in an Orderly Fashion

Our knowledge of how tactile information is represented in the central nervous system comes from two types of studies—clinical observations of humans and physiological studies in experimental animals.

Somatic Sensations Are Localized to Specific Regions of Cortex

The earliest information about the function of the somatic sensory system came from the analysis of disease states and traumatic injuries of the spinal cord. For example, one of the late consequences of syphilitic infection in the nervous system is a syndrome called tabes dorsalis, which destroys the large-diameter neurons in the dorsal root ganglia, causing the degeneration of myelinated afferent fibers in the dorsal columns. Patients with tabes dorsalis have severe deficits in touch and position sense but often little loss of temperature perception and of nociception. Additional information about the somatic afferent system comes from transection of the dorsal columns in experimental animals or as a result of trauma in humans. This type of injury results in a chronic deficit in certain tactile discriminations, such as detecting the direction of movement across the skin, the relative position of two cutaneous stimuli, and two-point discrimination. The deficit is ipsilateral to the lesion and occurs at levels below the lesion.

Experimental studies of the various somatic areas of the cortex have also provided valuable information about the function of different Brodmann’s areas concerned with somatic sensibility. Total removal of S-I (areas 3b, 3a, 1, and 2) produces deficits in position sense and the ability to discriminate size, texture, and shape. Thermal and pain sensibilities usually are not abolished, but are altered. Small lesions in the cortical representation of the hand in Brodmann’s area 3b produce deficits in the discrimination of the texture of objects as well as their size and shape. Lesions in area 1 produce a defect in the assessment of the texture of objects, whereas lesions in area 2 alter only the ability to differentiate the size and shape of objects. This is consistent with the idea that area 3b, which (together with 3a) is the principal target for the afferent projections from the ventral posterior lateral nucleus of the thalamus, receives information about texture as well as size and shape. Area 3b projects to both areas 1 and 2. The projection to area 1 is concerned primarily with texture, whereas the projection to area 2 is concerned with size and shape.

Because S-II receives inputs from all areas of S-I, removal of S-II causes severe impairment in the discrimination of both shape and texture and prevents monkeys from learning new tactile discriminations based on the shape of an object. Finally, damage to the posterior parietal cortex (the higher-order sensory cortex concerned with tactile perceptions) produces complex abnormalities in attending to the sensations from the contralateral half of the body.

Electrophysiological Studies Have Correlated Body Areas and Cortical Areas

Electrophysiological techniques were first used to study the cortical representation of the somatic sensory system in the late 1930s. This important series of experiments began with a chance observation made by Wade Marshall while studying the electrical activity of the cerebral cortex in the cat and monkey. Marshall found that by touching a specific part of the animal’s body surface he could produce an evoked potential in the cortex over an area of several

![Figure 26-3](image_url)

A map of evoked potentials can be obtained in a monkey from the surface of the left postcentral gyrus of the cerebral cortex by applying stimuli to the body surface on the opposite side. This figure shows the responses of one large group of cells in the left postcentral gyrus to a light tactile stimulus applied to different points on the right palm. These cells respond much more effectively to tactile stimuli applied to the thumb and forefinger (points 15, 16, 17, 20, 21, and 23) than to those applied to the middle or the small finger (points 1, 2, 3, 12, and 13). (Adapted from Marshall, Woolsey, and Bard, 1941.)
FIGURE 26–4
An early map of cortical responses to tactile stimulation in monkeys. [Adapted from Marshall, Woolsey, and Bard, 1941.]

A. Recordings were made in the primary somatic sensory cortex (S-I). The lateral view of the brain (left) shows the recording site. A sagittal view of S-I (right) shows Brodmann’s subdivisions.

B. The maps reflect the responses evoked in different points of Brodmann’s areas 3b and 1 by stimulation of the palmar and dorsal surfaces of the right hand. Black dots indicate sites in S-I that respond to stimulation of dorsal or palmar areas of the right hand. The sites on the left side of the figure are in the anterior wall of the postcentral gyrus, corresponding roughly to areas 3b and 3a in S-I. The sites on the right side of the figure are on the dorsal surface of the postcentral gyrus, corresponding roughly to area 1 in S-I.

millimeters. Evoked potentials are recorded electrical signals that represent the summed activity of thousands of cells and are obtained by using large, tipped metal electrodes or electrolyte-filled glass capillaries (Figure 26–3).

This evoked response method was later used by Marshall, Clinton Woolsey, and Philip Bard to map the representation of the body surface in Brodmann’s area 1 of the postcentral gyrus in monkeys. The map was constructed by relating a point on the body surface to a point of maximal electrical activity in the cortex (Figures 26–4). Because each area in the map is involved in both convergent and divergent relationships, a coherent map of the body surface emerges only if one considers the points of maximal response. In later experiments the body surface and deep tissue were found to be represented in the thalamus and dorsal column nuclei as well.
A Sensory homunculus

B Motor homunculus

FIGURE 26–5
Somatic sensory and motor projections from and to the body surface and muscle are arranged in the cortex in somatotopic order.

A. Sensory information from the body surface is received by the postcentral gyrus of the parietal cortex (areas 3a and 3b, and 1 and 2). Here the map for area 1 is illustrated. Areas of the body that are important for tactile discrimination, such as the tip of the tongue, the fingers, and the hand, have a disproportionately larger representation, reflecting their more extensive innervation. (Adapted from Penfield and Rasmussen, 1950.)

B. The analogous motor map exists for the motor cortex.

A similar organization was found in the human cortex by the neurosurgeon Wilder Penfield during operations for epilepsy and other brain disorders. Working with locally anesthetized patients, Penfield stimulated the surface of the postcentral gyrus at various points in the area of S-1 and asked the patients what they felt. [This procedure was necessary to ascertain the focus of the epilepsy and therefore to avoid unnecessary damage during surgery.] Penfield found that stimulation of points in the postcentral gyrus produced tactile sensations—paresthesias [numbness, tingling] and pressure—in discrete parts of the opposite side of the body. From these studies Penfield was able to construct a map of the neural representation of the body in the somatic sensory cortex.

As shown in Figure 26–5A, the leg is represented most medially, followed by the trunk, arms, face, and finally, most laterally, the teeth, tongue, and esophagus. Note that in Figure 26–5A, each part of the body is represented in the brain in proportion to its relative importance in sensory perception. The face is large compared with the back of the head; the index finger is gigantic compared with the big toe. As we shall see later, this distortion reflects differences in innervation density in different areas of the body. Similar distortion is seen in other species. In rabbits, for example, the face and snout have the largest representation because they are the animal’s primary means of exploring its environment [Figure 26–6].

These cortical maps of the body surface and the parallel motor maps [Figure 26–5B] are important and explain why neurology has always been a precise diagnostic discipline, even though for many decades its practice relied on only the simplest tools—a wad of cotton, a safety pin, a tuning fork, and a reflex hammer. Disturbances within the somatic sensory system can be localized clinically because there is a direct relationship between the anatomical organization of the brain and specific perceptual and motor functions.

A particularly dramatic example of this relationship is the Jacksonian seizure, a characteristic sensory epileptic attack described by the neurologist John Hughlings Jackson. An early feature of the Jacksonian seizure is progression of numbness and paresthesia that begins in one place and spreads throughout the body. For example, numbness might begin at the fingertips, spread to the hand, up the arm, across the shoulder, into the back, and down the ipsilateral leg. The progress of this kind of sensory seizure is explained by the arrangement of the sensory projections in the brain [Figure 26–5A]. In this example the seizure is initiated laterally, in the hand area, and propagates medially.

As we shall see in Chapter 50, potentials from the somatic sensory cortex can be recorded in humans in a completely noninvasive manner. Computers are used to obtain an average of many evoked signals so that the response can be distinguished from background electrical activity. Computer-averaged potentials provide clinical information that may not be detected in a routine neurological examination, about the somatic sensory cortex, and the ascending pathways in the spinal cord, brain stem, and thalamus. For example, the evoked potentials in the cortex can reveal a slowing of conduction in the spinal cord and brain stem due to demyelinating disease. This is useful in diagnosing multiple sclerosis, a common cause of demyelination in the central nervous system, since con-
FIGURE 26–6
The relative importance of body regions in the somatic sensibilities of different species are shown in these drawings, which were based on studies of evoked potentials in the thalamus and cortex.

duction can be slowed at an early stage of the disease when sensation is still normal.

The first neural maps of the body surface—those developed by Marshall, Woolsey and Bard, and by Penfield—used gross recording electrodes that sampled more than 1 mm of cortex and probed primarily the convex region of the post central gyrus (Brodmann’s area 1). Fine-resolution maps obtained more recently by Jon Kaas, Michael Merzenich, and their colleagues, using microelectrodes instead of gross recording electrodes, have revealed that there are actually four independent and fairly complete maps in each Brodmann’s area of the primary somatic sensory cortex [S-I]: areas 3a, 3b, 1, and 2. The secondary somatic sensory cortex [S-II] has still another map. Each of the four areas in S-I has its own somatosensory input and most areas are interconnected. As illustrated in Figure 26–7, the somatosensory maps in Brodmann’s areas 3b and 1 lie parallel to one another and correspond in their medial-to-lateral representation of the body surface. This explains why earlier studies, which probed a limited area of

FIGURE 26–7
Each of the four subregions of the primary somatic sensory cortex (Brodmann’s areas 3a, 3b, 1, and 2) has its own complete representation of the body surface. This figure illustrates the representation for the hand and the foot in areas 3b and 1. (Adapted from Kaas et al., 1983.)

A. Somatosensory maps in areas 3b and 1 are shown in this dorso-lateral view of the brain of an owl monkey. The two maps are roughly mirror images. The digits of the hand and foot are numbered D1 to D5.

B. 1. A more detailed illustration of the representation of the glabrous pads of the palm in areas 3b and 1. These include the palmar pads (numbered in order, P4 to P1), two insular pads (P1), two hypothenar pads (H), and two thenar pads (T). An idealized map of the hands based on studies of a large number of monkeys. The distorted representations of the palm and digits reflect the extent of innervation of each palmar area in the cortex. The five digital pads (D1 to D5) include distal, middle, and proximal segments (d, m, p).
the postcentral gyrus and used techniques with poorer resolution, led to the inference that there was only a single large representation of the body surface in the cortex.

Each Central Neuron Has a Specific Receptive Field

When the first cortical maps of the body surface appeared in the 1930s they presented two puzzles. The contours of the map of each region of the body, like the hand area illustrated in Figure 26–4, are not sharply defined, and there is much overlap in the representation of parts of the body. This apparently inexact representation seemed inconsistent with the precise tactile sensibilities of humans. In addition, the various submodalities appeared to project to roughly the same area of cortex. Since superficial sensations can be discriminated from deep ones, and touch and position sense are distinct, the fact that there appeared to be only one map was puzzling.

To solve these problems, Vernon Mountcastle, Jerzy Rose, and their colleagues began in the late 1940s to examine the somatic sensory system at the cellular level. Using extracellular microelectrodes (which had just become available), they recorded the electrical responses of individual neurons. Extracellular recordings reveal only the action potentials of the cell; thus, they do not show synaptic activity except under certain circumstances. It is more difficult to record intracellularly than extracellularly in the intact brain because the neurons are small and the brain pulsates, making it difficult to maintain intracellular penetrations.) Nevertheless, through extracellular recording a great deal has been learned about how sensory stimuli modulate the firing patterns of single cells.

Mountcastle and his colleagues found that cortical neurons in the somatic sensory system are mostly silent, with little or no spontaneous activity. Moreover, each cell responds only to stimulation of a specific area of the skin; that is, like the sensory receptors, central neurons have receptive fields. Any point on the skin is represented in the cortex by a population of cells connected to the afferent fibers that innervate that point on the skin. All of these cells will have similar receptive fields. When a point on the skin is touched the population of cortical neurons connected to that point on the skin will be excited. Stimulation of another point on the skin activates another population of cortical neurons. Thus, we perceive that a particular point on the skin is being stimulated because a specific population of neurons in the brain is activated. Conversely, as Penfield illustrated, when a point on the cortex is stimulated electrically, we experience tactile sensations on a specific part of the skin.

There are four other important features of receptive fields: their size and distribution on the body surface, modifiability, and fine structure.

Sizes of Receptive Fields Vary in Different Areas of the Skin

In the areas of the skin that are most sensitive to touch—the tongue and the tips of the fingers—the number of receptors per unit area of skin is large and the receptive field of each receptor is proportionally small. The finger tips of humans have the highest density of receptors: about 2500 per square centimeter! Of these, 1500 are Meissner’s corpuscles, 750 are Merkel’s cells, and about 75 are pacinian and Ruffini’s corpuscles. These receptors are innervated by 300 myelinated axons per square centimeter. For example, each afferent fiber connects to about 20 Meissner’s corpuscles and each corpuscle receives about two to five afferent fibers. The receptive fields for most of these receptors (the Meissner’s corpuscles and Merkel’s cells) are about 3 to 4 mm in diameter.

Moving up the arm, the receptive fields become larger, reflecting the decreased density of innervation and thus the reduced fineness of the tactile discrimination [Figure 26–8]. In the trunk the receptive fields of sensory receptors are about 100 times larger than those in the finger tips. Conversely, the cortical magnification unit area of cortex per unit area of body surface is about 100 times greater for the fingers than for the trunk. Thus, receptive field size and cortical magnification are inversely related.

A remarkable feature of receptive fields in the somatic sensory system, and especially in the cerebral cortex, is that the size of the receptive field is not fixed. Although size stays approximately the same under normal conditions, it can be modified greatly by experience or injury. We shall consider this feature in Chapter 65 when we examine the neural mechanisms of learning.

Receptive Fields of Central Neurons Have Inhibitory and Excitatory Components

The discharge of a receptor cell is greatest when a stimulus is applied to the center of the receptive field, and weakest at the perimeter. This gradient of excitatory activity within the receptive field is maintained in the central nervous system at each relay point, including the cortex. In addition, there is a gradient of inhibition, which is largely masked by the more powerful excitation. The inhibition is also greatest at the center of the field and decreases with distance from the center. Since the inhibition is delayed, it gives rise to a sequence of synaptic actions—excitation followed by inhibition—at the center of the receptive field. Inhibition sometimes extends beyond the perimeter of the excitatory zone of the receptive field, giving rise to an inhibitory surround. Thus, at each relay point in the somatic afferent system a stimulus in the excitatory center of the receptive field produces a peak of excitation among the responding population of cells, which is surrounded by a population of inactive (inhibited) cells, and this spatial distribution of activity serves to sharpen the peak of activity within the brain [Figure 26–9].

Lateral Inhibition Can Aid in Two-Point Discrimination

Fine tactile discrimination, such as reading braille, involves perceiving textures. We can understand how this is accomplished by considering the simplest example of spatial discrimination: the ability to distinguish two closely placed point stimuli as two rather than as one. Mountcastle pro-
posed a model for two-point discrimination by reconstructing the neural events in the postcentral gyrus of the cortex produced by a light tactile stimulus on the skin. The model was derived from studies using a method called reciprocal interpretation. In this method a stimulus is moved systematically across the receptive field of a single nerve cell and the response of the cell is used to obtain an idea about how activity is distributed across a population of neurons. Reciprocal interpretation is based on the following argument. At each relay the stimulus activates a population of neurons with similar properties, whose responses are assumed to be uniformly distributed on the surface of the skin. Thus, moving the stimulus across the skin and examining the firing pattern of a single cell is equivalent to keeping the position of the stimulus constant and moving the recording electrode from one cell to the next in the relay nucleus receiving input from that piece of skin.

Consider first a single-point stimulus. This stimulus activates several touch receptors within a circumscribed area around the stimulus, producing short trains of impulses in each receptor. These impulses then discharge a group of cells in a dorsal column nucleus, and those cells activate another group of cells in the ventral posterior nucleus of the thalamus, which in turn discharge a group of cells in the primary somatic sensory cortex. At each relay in the central nervous system the population of cells that discharges is limited by two factors: [1] the afferent pathway activated by the stimulus connects anatomically only to a limited number of central cells, the responding population, and [2] the population of neurons directly excited by the afferent signals at each relay also engages inhibitory interneurons that restrict, by means of recurrent inhibition, the firing of the responding population (Figure 26–9). This inhibition is not present at the level of the receptor but comes in at the dorsal column nuclei and is found at each subsequent relay step.

The location of a single stimulus on the body surface is thus signaled in the nervous system by the firing of specific populations of neurons activated by the stim-
FIGURE 26–9
Effect of feedback inhibition. [Adapted from Dudel, 1983.]

A. 1. Diagram of the excitatory synaptic connections among three receptors and the interneurons at the next two relays in the absence and presence of inhibitory interneurons. The inset over each axon shows its relative rate of discharge during stimulation. 2. In the absence of inhibitory interneurons, there is a large discharge zone (the excitatory region or discharge zone) at each of the relays in response to a stimulus in the excitatory region of the receptive field.

B. The addition of inhibitory interneurons (black) narrows the discharge zone. On either side of the excitatory region the discharge rate is driven below the resting level by feedback inhibition.

ulus. Those populations are located at specific points in each relay nucleus as well as in the cerebral cortex. The intensity of the stimulus is signaled by the frequency of firing of the specific populations and by the size of the active populations, because a strong stimulus to the skin produces a higher frequency of firing and activates a larger population of cells than does a weak stimulus. Not all cells in this population respond in an identical manner. Cells at the center, which have the most powerful connections to the area being stimulated, discharge most effectively and with the shortest latency. Cells just off the center have a lower probability of firing and discharge fewer impulses with longer latency.

According to Mountcastle’s model for two-point discrimination, two stimuli applied to different positions on the skin set up excitatory gradients of activity in two cell populations at every relay point in the somatic sensory system. The activity in each population of cells has its own maximal region of activity, or peak, and the perception of two points rather than one occurs because two distinct populations are active. Neurons in each population have a receptive field with a central excitatory zone surrounded by a weaker excitatory zone, which is further depressed by the inhibitory surround. The inhibitory surround sharpens each peak and further enhances the distinction between the two peaks. When two stimuli are brought close together, the activity in the two populations tends to overlap so that the distinction between the two peaks could become blurred. However, as the stimuli are brought together, the inhibition produced by each sum-
mates. As a result of this more effective inhibition, the peaks of activity in the two responding populations become sharpened and the two active populations become more effectively separated spatially. This sculpturing role of the inhibition allows two distinct peaks of activity to continue to be registered at the cortical level, thus preserving the spatial separation of the two stimulus sites (Figure 26–10). At each level of the nervous system recurrent inhibition enhances contrast between stimuli. It is easy to see how this feature of neural organization can lead to the ability to recognize patterns and contours.

When two stimuli occur within a single large receptive field, as in the forearm, the separation of the two stimuli is encoded in the signals of a single population of receptors. Ian Darian-Smith, Esther Gardner, and their colleagues found that in such cases the spacing between two stimuli is encoded by the firing frequency of the individual afferent fibers. When the stimuli are widely separated they elicit high frequencies from the afferents responding to each stimulus. As the separation narrows, the frequencies decrease and the duration of their firing decreases so markedly that rapidly adapting receptors can distinguish spacing between stimulus probes as small as about 1 mm.

Inputs to the Somatic Sensory Cortex Are Organized into Columns by Submodality

Most nerve cells in the somatic sensory system are responsive to only one modality: touch, pressure, temperature, or pain. Neurons mediating touch are responsive to superficial tactile stimuli and not to deep pressure.

FIGURE 26–10
Two-point discrimination depends on separation of signals.
(Adapted from Mountcastle and Darian-Smith, 1968.)
A. Stimulation of a single point of the skin activates one population of cells in the cortex with maximal activity in the center of the population.
B. Stimulation of two adjacent points activates two populations of cells, each with a peak of activity. In one population lateral (recurrent) inhibition is shown. Here the active neurons excite inhibitory interneurons that in turn inhibit neighboring less active cells. In the other population there is no lateral inhibition. Therefore, each active population has a broader representation in the cortex so that the two active peaks of activity readily merge into one another.
In addition to being organized by modality, S-1 is further subdivided into submodalities. For example, in Brodmann’s area 3b, the neural map of cutaneous receptors for each finger is divided into two columns, one each for inputs from rapidly adapting and slowly adapting receptors (Figure 26–11). Thus, within each of the four areas of S-1 there are several interrelated modality-specific maps of the body surface.

How does the layering of the cortex participate in the modality-specific organization of the cortex? As described in Chapter 20, each layer of cells has connections with different parts of the brain: layer 6 projects back to the thalamus, layer 5 to subcortical structures, layer 4 receives input from the thalamus, and layers 2 and 3 project to other cortical regions. As a result, the modality-specific output from each column is conveyed to different regions of the brain. As we shall see in a later chapter, the visual cortex is also organized by submodalities.

**FIGURE 26–11**

Inputs of individual modalities to the somatic sensory cortex are organized in columns. (Adapted from Kaas et al., 1979.)

A. Inputs to each region of the somatic sensory cortex—Brodmann’s areas 3a, 3b, 1, and 2—are primarily from one type of receptor in the skin (indicated in the figure). Inputs from specific parts of the body are organized in columns of neurons that run from the surface to the white matter. This schematic drawing shows the columnar arrangement of inputs from digits 2, 3, 4, and 5.

B. This detail of columns for digits 2, 3, 4, and 5 in part A shows the arrangement of inputs in a portion of Brodmann’s area 3b that receives inputs from rapidly adapting (RA) and slowly adapting (SA) cutaneous receptors of tactile stimuli.

**Detailed Features of a Stimulus Are Communicated to the Brain**

*In Early Stages of Cortical Processing the Dynamic Properties of Central Neurons and Receptors Are Similar*

Throughout the nervous system the various somatosensory submodalities are conveyed by anatomically separate pathways. Sensory receptors and primary sensory neurons responsive to one submodality are connected to clusters of cells in the dorsal column nuclei and thalamus that receive inputs only for that submodality. These relay neurons in turn project to modality-specific cells in the cortex. The cells that make up these anatomically distinct mechanoreceptor pathways have distinctive response properties. For example, as we saw in Chapters 23 and 24, some receptor cells in both the skin and deep tissue adapt rapidly to a stimulus and others adapt slowly. Psycho-
FIGURE 26–12
The spatial characteristics of embossed letters are represented in the discharge of cutaneous mechanoreceptors and neurons in primary somatosensory cortex. (Adapted from Phillips et al., 1988.)

A. 1. Embossed letters on a cylindrical drum are used to study the spatial pattern of neuronal activity in mechanoreceptors innervating the finger tip and, in separate experiments, in cortical neurons in Brodmann's areas 3b and 1. Letters of the alphabet are repeatedly swept across a receptive field in the finger tip of a monkey by rotating the drum. The action potentials evoked by each letter in single afferent fibers (or cortical neurons) are plotted in spatial event plots. 2. Spatial event plots are constructed as follows. Embossed letters [about 6.0 mm high and 500 µm in relief] are swept [50 times at 50 mm/s] across a given location within the receptive field of a single neuron innervating the finger pad, thereby producing action potentials. The drum is rotated and the stimulus is moved across the receptive field from proximal to distal (vertical bar of the K entered the receptive field first on each sweep). After each sweep, the drum is then shifted vertically within the receptive field by 200 µm and swept again. The time of occurrence of each action potential relative to adjacent stimulus position markers is recorded and ordered from top to bottom so as to assign a spatial location relative to the stimulus surface. 3. In an actual spatial event plot for the letter K, each action potential in A1 is presented as a dot.

B. 1. Spatial event plots reconstructed from the afferent fibers from three types of receptors in a monkey: slowly adapting (top), rapidly adapting (middle), and pacinian corpuscle (bottom). 2. Spatial event plots reconstructed from five slowly adapting neurons in area 3b of an awake monkey.

physical studies on flutter and vibration that we considered in Chapter 24 show that several types of human tactile perceptions are determined by the response properties of the receptors. Mountcastle and his colleagues examined how these response property features are communicated to neurons in the brain and found that the dynamic properties of the receptors are matched by those of the central neurons to which they are connected. Rapidly adapting skin receptors connect to rapidly adapting neurons in the thalamus that connect to similar neurons in areas 3b and 3a in the primary somatosensory cortex (S-I). Likewise, slowly adapting receptors connect to neurons in the thalamus and 3b and 3a that also adapt slowly. Thus, the second- and third-order cells do not merely repeat the firing pattern of the primary afferent fibers but actually have adaptation properties similar to those of the receptors themselves. As a result, Mountcastle argued that the signal received by the input to the cortex faithfully reproduces the stimulus features encoded by the receptor in the skin.
How far does this fidelity extend? Kenneth Johnson and his colleagues addressed this question by examining the neural representation of the surface texture of objects. They examined the responses of single afferent fibers and cortical neurons in areas 3b and 1 when the fingers of awake monkeys were stimulated with embossed letters, the sort of stimulus used in pattern recognition experiments with humans. In separate experiments a single letter was repeatedly swept across the skin of the monkey's finger and the action potentials evoked in single receptor neurons and cortical neurons were plotted. As we have seen in considering two-point discrimination, the responses of a single neuron to a stimulus moved systematically across its receptive field can be assumed to represent the responses of a population of neurons with similar response properties. Johnson and his colleagues found that both slowly and rapidly adapting receptors in the skin (Merkel's cells and Meissner's corpuscles) transmit a faithful neural image of the letters, while the pacinian receptors in deep tissue do not [Figure 26-12].

Are these initial representations of the stimulus maintained at higher levels within the brain? In area 3b, the first stage of processing in the somatic sensory cortex, the projections from skin receptors give rise to relatively sharp images. In later stages, however, for example in area 1, the responses are more abstract. Since certain cutaneous peripheral afferents but not all cortical neurons represent letter stimuli faithfully, it should be possible to determine the steps by which the initial representation becomes abstracted.

In the Later Stages of Cortical Processing the Central Nerve Cells Have Complex Feature-Detecting Properties and Integrate Various Sensory Inputs

To sense the texture, form, and motion of an object the nervous system must integrate information from many different mechanoreceptors sensitive to superficial touch, deep pressure, and the position of the fingers and hand. How is this integration accomplished? At least four factors are involved: (1) the response properties of neurons at successive levels of sensory processing become more complex; (2) the submodalities converge on one common cell; (3) the size of the receptive field becomes larger at each level of processing; and (4) the profile of activity in the responding population changes.

The increasing complexity of response properties in somatic sensory systems was discovered by Gerhard Werner and his colleagues. They found cells in the hand region of the somatic sensory cortex that respond briskly to three-dimensional objects placed within the receptive fields, and particularly to movement of the object across the skin. These same cells, however, do not respond well to punctate stimuli, although cells located at earlier relay points are easily excited by such stimuli.

Studies by Juhani Hyvärinen and Antti Poranen, as well as by Yoshiaki Iwamura and by Gardner, revealed that neurons involved in the input to the cortex (areas 3b and 3a) respond to relatively simple punctate stimuli, whereas the neurons involved in subsequent cortical processing stations (areas 1 and 2) have complex response properties. For example, at least three types of neurons respond to movement across the skin in areas 1 and 2. Motion-sensitive neurons respond well to movement in all directions but do not respond selectively to movement in any one direction. Direction-sensitive neurons respond much better to movement in one direction than in another. Orientation-sensitive neurons respond best to movement along a specific axis of the receptive field [Figure 26-13].

Detection of movement and other features of the stimulus is a property of higher cortical neurons. These properties are not apparent in dorsal column nuclei, in the thalamus, or even in areas 3a and 3b. Feature-detecting neurons sensitive to stimulus direction and orientation are first found in area 1 and even more extensively in area 2, the areas concerned with stereognosis (the perception of the three-dimensional shape of objects) and with discriminating the direction of movement of objects on the skin. Thus, these complex stimulus properties arise not from thalamic input but from cortical processing of more elementary inputs. The convergent projections from areas 3a and 3b onto areas 1 and 2 also permit neurons in areas 1 and 2 to respond to other complex features, such as edge orientation. Whereas neurons in 3b and 1 respond only to touch, and neurons in areas 3a respond only to position sense, certain neurons in area 2 have both inputs. These neurons respond best when an object is grasped by the hand. As we shall see below, this information is thought to provide the necessary tactile clues for skilled movement of the fingers.

Neurons involved in the later stages of cortical processing also have larger receptive fields. For example, neurons in areas 3a and 3b, the sites of initial input of S-I, have quite small receptive fields that usually encompass one or two phalanges on a finger. In contrast, neurons in areas 1 and 2, which receive inputs from areas 3a and 3b, have receptive fields that include several fingers [Figure 26-14]. Thus, the receptive fields and response properties of neurons in areas 1 and 2 reflect convergent input from different regions of the hand and fingers, areas that are separately represented in areas 3a and 3b [see Figure 26-11]. Inputs for the finger areas are commonly adjacent to one another and the cells respond most effectively when adjacent fingers are stimulated, as when the hand is used to hold and manipulate an object. These complex cells in areas 1 and 2 become active during movements of the hand around an object, and seem to have a role in stereognosis, the tactile discrimination of three-dimensional shapes.

This increase in the complexity of neuronal response is important not only for perception but also for the execution of skilled movements. Indeed, area 2 sends somatosensory inputs from the entire body surface to the primary motor cortex. Moreover, reversible inhibition of neural
activity in area 2 produced pharmacologically (using a GABA agonist that inhibits cortical cells) leads to an inability to assume functional postures of the hand and to coordinate the fingers for picking up small objects (Figure 26–15). In addition to projecting to the motor cortex for movement, the somatic sensory areas project to the posterior parietal cortex (Brodman’s areas 5 and 7), the cells of which have very complex properties, receive inputs from several modalities, and are often related to movement. There the information for tactile discrimination and position sense is integrated with visual information and with the neural systems in the brain stem, thalamus, and temporal lobe concerned with attention.

A. Motion-sensitive neurons respond to wheel motion in all directions. (Distance of wheel movement, 2.4 mm.)

B. Direction-sensitive neurons respond better to movement in one direction than another. Strongest responses are to motion in the ulnar direction; weakest responses are to the radial direction. Responses to distal movement are more vigorous than to proximal movement. (Distance of wheel movement, 1.2 mm.)

C. Orientation-sensitive neurons respond more vigorously to transverse than to longitudinal motion, but responses to motion in opposite directions are about the same. (Distance of wheel movement, 1.6 mm.)

An Overall View

Examination of the receptive properties of neurons in the somatosensory cortex has revealed a precise representation of the external body surface onto the cortical surface. However, the somatosensory map or homunculus is not an exact representation of the body surface but is distorted. The finger tips, for example, are allotted a much greater cortical area than regions like the back. Receptive field sizes of cortical neurons are inversely related to the density of innervation. Somatotopy, the orderly projection of the sensory sheet in the brain, permits orderly intracortical connections.
Like all sensory and motor modalities, tactile information from the periphery reaches the cortex by several pathways, each carrying both redundant and unique information. As a result, lesions of the medial lemniscus, which carry information from the dorsal column to the thalamus, do not completely abolish tactile perception. Patients with these lesions retain sensibility of crude touch through pathways that ascend in the anterolateral column.

In addition to parallel ascending pathways, many pathways project to more than one cortical area. Thus, there are five representations of the body surface in the parietal cortex, one in S-II and four in S-I. Why are there so many representations of the body surface? Somatic sensation involves the parallel analysis of different stimulus attributes in different cortical areas. Parallel processing in the brain is a form of processing that we shall encounter again. It is designed not to achieve multiplication of identical circuitry, but to allow different neuronal pathways and brain relays to deal with the same sensory information in
slightly different ways. Because of parallel processing, simple neuronal transformations of signals based on synaptic excitation, synaptic inhibition, and action potentials are able to endow our perceptions with richness.

In the cortex sensory submodalities are arranged in columns, so that all six layers in any column represent the same modality. For example, layer 4 receives input from the thalamus, whereas other layers project out to other areas of the cortex and subcortex. Each of the four subregions in the somatosensory cortex contains its own map of the body surface, specific to a particular somatic sensory modality. Thus, area 3a primarily receives input from muscle stretch receptors, area 3b receives cutaneous receptor input, area 1 receives input from rapidly adapting receptors, and area 2 contains a map of deep pressure receptors. As a result, these different regions are involved in slightly different aspects of somatic sensation. Area 1 is involved in sensing the texture of objects, while area 2 is responsible for sensing the size and shape of objects.

Neurons in areas 2 and 1 are involved in the later stages of somatosensory processing, have more complex feature-detecting properties, receive convergent input from a number of submodalities, and have larger receptive fields than first-order cortical neurons. At least three types of higher-order somatosensory cells have been found: motion-sensitive, orientation-sensitive, and direction-sensitive neurons. Even more complicated processing seems to be carried out by neurons activated when the hand is manipulating an object; these neurons project to the motor cortex for sensory-motor integration. Finally, the somatosensory cortex also sends outputs to the posterior parietal cortex, where integration with other senses takes place, and where an overall picture of the body is formed.

**Selected Readings**


**References**


