12

Touch

HAVING STUDIED THE PERCEPTUAL SYSTEMS for vision and hearing, you should recognize a number of questions that curious minds want asked and answered about any sense. In this chapter we will consider the following questions in light of the sense of touch:

- What are the physical stimuli for touch? More precisely, what forms of energy lead to the sensation of being touched?
- What is the sensory apparatus for touch, and how do these structures change touch stimuli into electrical signals (neural firing rates)?
- What are the neurophysiological pathways that connect touch receptors to higher-order perception and cognition in the brain?
- How do we use touch input to determine the identity (*what* tasks) and location (*where* tasks) of objects in the world?
- How does the sense of touch compare with and interact with other sensory modalities?
- What is touch good for? What might be the evolutionary "niche" of this sensory modality?

Let's start with the first and last of these questions. By its most narrow definition, the term *touch* refers to the sensations caused by mechanical displacements of the skin. These displacements occur when you are poked by your 4-year-old nephew, licked by your dog, or kissed by your significant other, or anytime you grasp, wield, or otherwise make contact with an object. We will expand this basic definition to include the perception of temperature changes, the sensation of pain, which occurs when our body tissues are damaged in some way, and the internal sensations that inform us of the positions and movements, respectively, of our limbs. These internal sensations are known as "kinesthesis" when they arise from muscles, tendons and joints and "**proprioception**" when they also arise from the vestibular system. The technical term for all these senses put together is **somatosensation**.

Touch

It is difficult to conceive of our species surviving without a sense of touch. Pain serves as a sophisticated warning system that tells us when something might be internally wrong or when an external stimulus may be dangerous, allowing us to defend our bodies as quickly as possible (e.g., by rapidly moving away from the noxious stimulus). Temperature sensations allow us to seek or create a thermally appropriate environment. Mechanical sensations play an important role in our intimate sexual and reproductive activities, and they provide a powerful means of communicating our thoughts and emotions nonverbally.

On a more fundamental level, touch is important because we can use it to identify and manipulate objects that cannot be seen or heard. Blindfold yourself for at least 10 minutes and try doing some routine tasks, like making a sandwich, getting dressed, or taking a shower. The first thing you will notice while doing this exercise is just how much our species relies on vision to inform us about the world around us. But you should also find that touch can substitute for vision to a surprising degree: You probably won't have as much trouble as you think you might distinguishing the peanut butter jar from the jelly jar. And if you pay attention, you will find that you don't actually use vision, or any sense other than touch, very much at all for some tasks (e.g., buttoning your shirt, brushing your teeth, opening that jar of peanut butter).

There is one more thing you may become acutely aware of during your experiment with the blindfold. Your eyes and ears can perceive signals from objects that are far from your body, but you must almost always be in direct contact with an object to perceive it by touch (some exceptions to this rule are a jackhammer, whose vibrations on the street outside you can feel; and the sun, from which you feel warmth, even though it is millions of miles away). Therefore, to use touch to learn about the world, you must act. If you want to know the weight of that beautiful soapstone sculpture (Figure 12.1), you pick it up. You might also stroke it to feel its exquisite smoothness or press it to your forehead to feel its coolness. In sum, touch involves action, arguably to a greater degree than any of your other senses do.

FIGURE 12.1 Soapstone sculpture from Zimbabwe.

Touch Physiology

The Sense Organ and Receptors for Touch

The sites of our sensory equipment for vision, audition, olfaction, and gustation are all localized in organs (the eyes, ears, nose, and mouth, respectively) that are more or less dedicated to sensory processing. Some other animals have analogous appendages: antennae. You might think that, for touch, humans do not have a readily apparent sense organ. In fact, the human sense of touch is housed in the largest and heaviest of the sense organs: the skin, which covers an area of 1.8 m^2 and weighs 4 kg. Touch receptors are embedded in the skin all over our body, as well as in our mouths and within our muscles, tendons, and joints.

Although the external quality of the skin varies across different parts of our bodies (it is thicker in some parts and thinner in others, smoother in some parts and coarser in others, and so on), most skin includes the basic substructures shown in Figure 12.2. Touch receptors are embedded in both the outer layer, called the **epidermis**, and the underlying layer, known as the **dermis**. As you can see, just as the eye has its rods and three types of cones, there are multiple types of touch receptors. These receptors form the basis for multiple "channels," specialized information-processing subsystems that each contribute to the overall sense of touch. For example, if you wrap your fingers around a cube of ice, different channels convey information about its coldness, its shape, and its smoothness.

We will discuss the receptors that provide the underlying support for these various channels in detail in the sections that follow (see Web Activity 12.1 Somatosensory Receptors). In general, however, each touch receptor can be characterized by three attributes:

1. *Type of stimulation the receptor responds to* (e.g., pressure, vibration, or temperature changes).
2. *Size of the receptive field*: the extent of the body area to which the receptor will respond.
3. *Rate of adaptation*.

proprioception Perception mediated by kinesthetic and vestibular receptors.

somatosensation A collective term for sensory signals from the body.

epidermis The outermost of two major layers of skin.

dermis The innermost of two major layers of skin, consisting of nutritive and connective tissues, within which lie the mechanoreceptors.

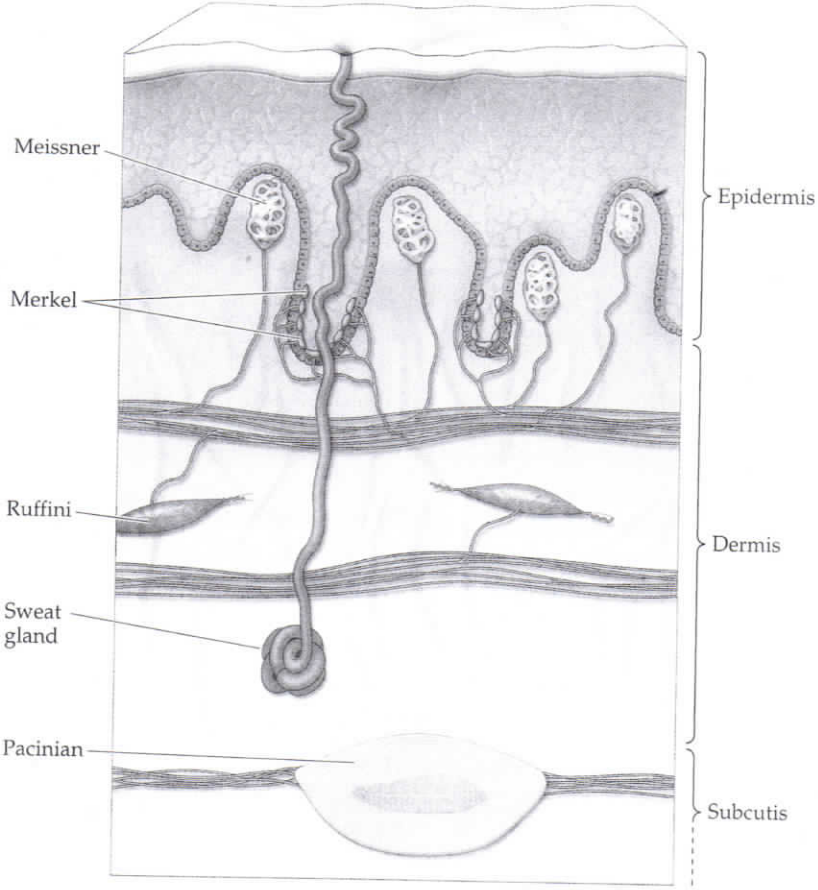


FIGURE 12.2 Cross section of hairless skin of the human hand, schematically demonstrating the locations of the four types of mechanoreceptors; the major layers of human skin are also shown. (After R. S. Johansson and Vallbo, 1983.)

mechanoreceptors Sensory receptors responsive to mechanical stimulation (pressure and vibration).

Meissner corpuscle Specialized nerve ending associated with fast-adapting fibers with small receptive fields (FA I).

Merkel cell neurite complex Specialized nerve ending associated with slow-adapting fibers with small receptive fields (SA I).

Pacinian corpuscle Specialized nerve ending associated with fast-adapting fibers with large receptive fields (FA II).

Ruffini ending Specialized nerve ending associated with slow-adapting fibers with large receptive fields (SA II).

A fast-adapting (FA) receptor responds with bursts of action potentials when its preferred stimulus is first applied and when it is removed, but it does not respond during the steady state between stimulus onset and offset. In contrast, a slow-adapting (SA) receptor remains active throughout the period during which the stimulus is in contact with its receptive field.

TACTILE RECEPTORS Four receptor types known as "tactile receptors" are shown in Figure 12.2. These are all called **mechanoreceptors** because they respond to mechanical stimulation or pressure. The endings of the receptor types are named, after the anatomists who first described them, **Meissner corpuscles**, **Merkel cell neurite complexes**, **Pacinian corpuscles**, and **Ruffini endings**. The Meissner and Merkel receptors, which are located at the junction of the epidermis and dermis, are the enlarged endings of nerve fibers that tend to have smaller receptive fields than those of the Pacinian corpuscles and Ruffini endings, which are embedded more deeply in the dermis and underlying subcutaneous tissue. The four types can be independently classified according to their adaptation rates and the sizes of their receptive fields: nerve fibers that end in Meissner and Pacinian corpuscles are fast-adapting, while those that end in Merkel cell complexes and Ruffini endings are slow-adapting. These two dimensions lead to a second set of labels for the mechanoreceptor types (Table 12.1).

TABLE 12.1 Response characteristics of the four mechanoreceptor populations

	SIZE OF RECEPTIVE FIELD	
ADAPTATION RATE	SMALL	LARGE
Fast	FA I (Meissner)	FA II (Pacinian)
Slow	SA I (Merkel)	SA II (Ruffini)

FA I = fast-adapting type I, FA II = fast-adapting type II, SA I = slow-adapting type I, and SA II = slow-adapting type II. The receptor ending associated with each type is shown in parentheses.

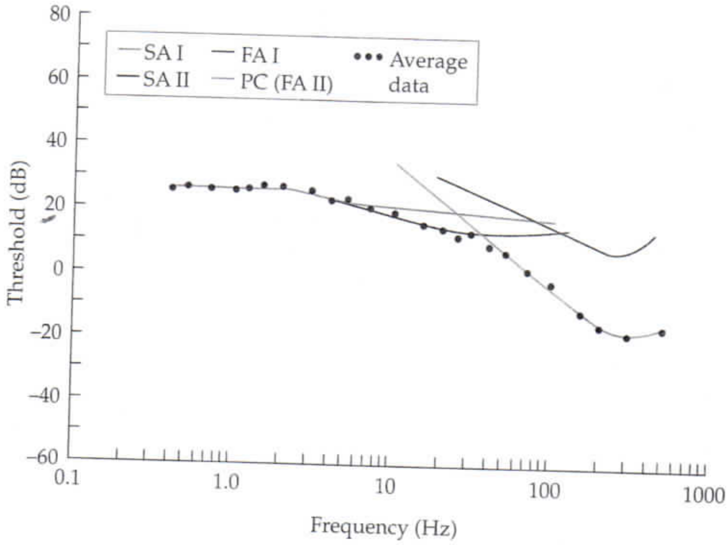


FIGURE 12.3 Proposed sensitivity ranges of the mechanoreceptors. The graph shows the minimally detectable (threshold) displacement of the skin produced by a vibrating stimulator, as a function of vibration frequency. A separate function is proposed for each mechanoreceptor population. The y-axis measures decibels relative to 1 µm. (After Bolanowski et al., 1988.)

Each receptor type has a different range of responsiveness (Figure 12.3) and is responsible for perceiving a different feature of mechanical stimulation (Table 12.2):

- SA I units (Merkel cell neurite complexes) respond best to fine spatial details and are especially important in texture and pattern perception. Some activities that are particularly dependent on this touch channel include reading Braille and determining the location and orientation of the slot on the head of a screw that you can feel but not see.
- SA II units (Ruffini endings) respond to sustained downward pressure, and particularly to lateral skin stretch, which occurs, for example, when you grasp an object. When you reach out for your coffee cup, your SA II receptors help determine when your fingers are shaped properly for picking up the cup.
- FA I units (Meissner corpuscles) respond to low-frequency vibrations (3–40 Hz). If your coffee cup is heavier than you expected and begins to slip across your fingers, this motion across your skin will cause just such vibrations, and your FA I receptors will help you correct your grip before your coffee spills all over you.
- FA II units (Pacinian corpuscles) detect high-frequency vibrations (40–500 Hz), which occur whenever an object first makes contact with your skin—for example when a mosquito lands on your arm. Such vibrations are also

ABLE 12.2 Mechanoreceptors: Feature sensitivity and associated function

IECHANORECEPTOR OPULATION	MAXIMUM FEATURE SENSITIVITY	PRIMARY FUNCTIONS
SA I	Sustained pressure, very low frequency (0.4–3 Hz) Spatial deformation	Texture perception Pattern/form detection
FA I	Temporal changes in skin deformation (3–40 Hz)	Low-frequency vibration detection
FA II	Temporal changes in skin deformation (40 to >500 Hz)	High-frequency vibration detection
SA II	Sustained downward pressure, lateral skin stretch, skin slip (low sensitivity to vibration across frequencies) (100 to >500 Hz)	Finger position, stable grasp

generated when an object that you're holding contacts another object, so FA II receptors help you determine how hard you are tapping your pencil on your desk as you try to cram all this information into your brain.

Just as both rods and cones contribute to your perception of every individual visual stimulus, the four types of mechanoreceptors are always working together to inform you about every individual object you touch. Johnson (2002) gives the example of opening a door with a key. Feeling the shape of your key in your pocket requires the SA I channel. Shaping your fingers to grasp the key involves the SA II channel. As you insert the key into the lock, your grip force increases so that the key does not slip, thanks to your FA I channel. Finally, your FA II channel tells you when the key has hit the end of the keyhole.

KINESTHETIC RECEPTORS In addition to the tactile mechanoreceptors in the skin, yet other types of mechanoreceptors lie within muscles, tendons, and joints. These are collectively referred to as **kinesthetic** receptors, and they play an important role in our sense of where our limbs are and what kinds of movements we are making (Clark and Horch, 1986; Jones, 1999). The angle formed by a limb at a joint is perceived primarily through muscle receptors called **spindles** (Figure 12.4), which convey the rate at which the muscle fibers are changing in length. Receptors in the tendons provide signals about the tension in muscles attached to the tendons, and receptors directly in the joints themselves come into play particularly when a joint is bent to an extreme angle.

The importance of kinesthetic receptors is graphically illustrated by the strange case of a neurological patient named Ian Waterman (read *Pride and a Daily Marathon* [1991] by Johnathan Cole for more about this interesting case). The cutaneous nerves that connected Waterman's kinesthetic and other mechanoreceptors to his brain were destroyed by a viral infection when he was 19 years old. Lacking kinesthetic senses, Waterman is now completely dependent on vision to tell him the positions of his limbs. If the lights are turned off, Waterman cannot tie his shoes, walk up or down stairs, or even clap his hands, because he has no idea where his hands and feet are! Caught in an elevator when the lights went out, he was found on the floor, unable to stand until the illumination returned. (Additional details about Waterman's troubles, and the amazing degree to which he has compensated for his lack of kinesthetic receptors, can be found in **Web Essay 12.1 Living without Kinesthesis**.)

kinesthetic Referring to perception involving sensory mechanoreceptors in muscles, tendons, and joints.

muscle spindle A sensory receptor located in a muscle that senses its tension.

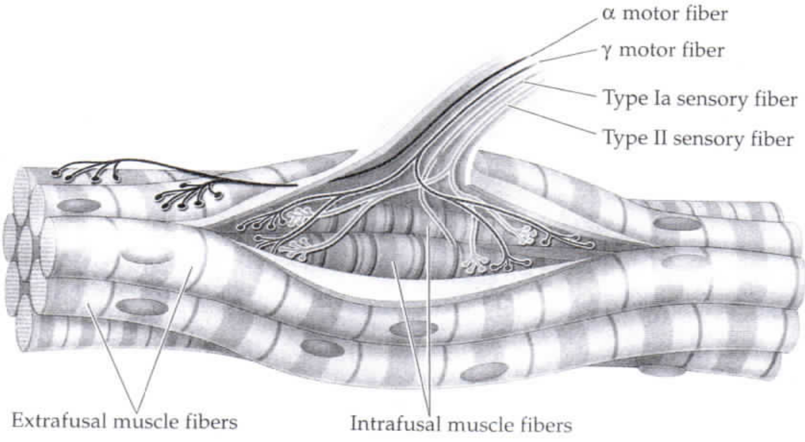
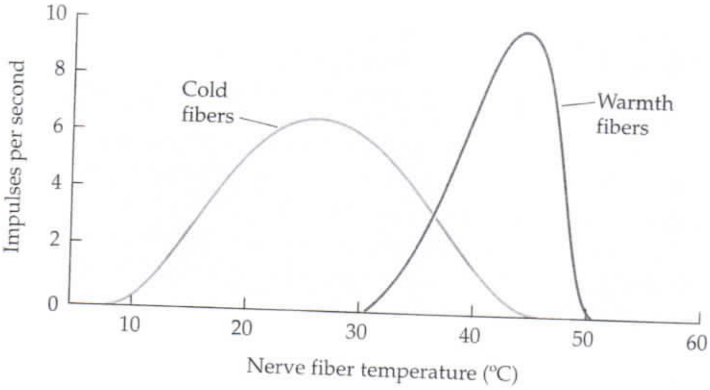


FIGURE 12.4 A muscle spindle embedded in main (extrafusal) muscle fibers contains inner (intrafusal) fibers. When the inner fibers contract, a sensory response from the spindle is sent back to the central nervous system, conveying information about muscle length and thus regulating muscle tension.

FIGURE 12.5 Thermal receptivity functions, showing the response of warmth and cold fibers to different temperatures. (After Guyton, 1991.)



THERMORECEPTORS **Thermoreceptors**, located in both the epidermal and dermal layers of the skin (see Figure 12.2), inform us about changes in skin temperature. There are two distinct populations of thermoreceptors (Figure 12.5): **warmth fibers** fire when the temperature of the skin surrounding the fibers rises; **cold fibers** (which outnumber warmth fibers by a ratio of about 30:1) fire in response to decreases in skin temperature.

Your body is constantly working to regulate its internal temperature, so under normal conditions your skin is kept between 30°C and 36°C (86°F and 96°F), and neither cold nor warmth fibers respond much while skin temperature remains within this range. If you bundle up in your long underwear and snowsuit but then sit inside in front of the fire, your skin temperature will probably rise above 36°C, and your warmth fibers will begin to fire. If you then take the snowsuit off and walk out into the snow, your skin temperature will rapidly begin to fall, and as soon as it goes below 30°C, your cold receptors will start firing.

Your thermoreceptors also kick into gear when you make contact with an object that is warmer or colder than your skin. Objects in the environment are typically cooler than 30°C, so it is usually the cold fibers that tell you about the object. For example, steel conducts heat more efficiently than stone. Your cold fibers will thus fire less rapidly and for a shorter period of time when you touch a steel object than when you touch a stone object (because the steel object will warm more quickly to match your skin temperature). If you've had prior experience with steel and stone, you can interpret the thermoreceptor responses to make this distinction.

NOCICEPTORS Pain is the realm of touch that has the dubious honor of being home to the sensations we like the least. We may find some visual stimuli revolting and some olfactory or gustatory stimuli disgusting, but of all the sensations, it is pain that we take the most drastic actions to avoid.

Pain begins with signals from **nociceptors**, touch receptors that have bare nerve endings and that respond to various forms of tissue damage or to stimuli that have the potential to damage tissue (including extreme skin temperatures lower than 15°C or higher than 45°C). Nociceptors can be divided into two types based on the nerve fibers rather than the endings. **A-delta fibers** respond primarily to strong pressure or heat and are myelinated, which allows them to conduct signals very rapidly. **C fibers** are unmyelinated and respond to intense stimulation of various sorts: pressure, heat or cold, or noxious chemicals. Both types of pain fibers are smaller in diameter than those coming from non-nociceptive mechanoreceptors in the skin—the wider-diameter fibers known as type "A-beta." Many painful events seem to occur in two

thermoreceptors Sensory receptors that signal information about changes in skin temperature.

warmth fiber Sensory nerve fiber that fires when skin temperature increases.

cold fiber Sensory nerve fiber that fires when skin temperature decreases.

nociceptors Sensory receptors that transmit information about noxious (painful) stimulation that causes damage or potential damage to the skin.

A-delta fiber Intermediate-sized, myelinated sensory nerve fiber that transmits pain and temperature signals.

C fiber Narrow-diameter, unmyelinated sensory nerve fiber that transmits pain and temperature signals.

stages: a quick sharp burst of pain followed by a throbbing sensation. These two stages may reflect the onset of signals first from the A-delta fibers and then from the C fibers (Price et al., 1977).

You might think that pain perception has no upside, but consider what would happen if you had no nociceptors. You wouldn't be able to sense dangerously sharp or hot objects. Lacking alarms, you might soon lack fingers! Some diseases, such as Hansen's disease (leprosy) and diabetes, are characterized by the loss of pain sensation and provide real-life examples of the consequences. The case of "Miss C," reported by Melzack and Wall (1973), shows what can happen to people born with insensitivity to pain. Not only did Miss C lack pain sensation, but she did not sneeze, cough, gag, or protect her eyes reflexively. She suffered childhood injuries from burning herself on a radiator and biting her tongue while chewing food. As an adult, she developed problems in her joints that were attributed to lack of discomfort, for example, from standing too long in the same position. She died at age 29 from infections that could probably have been prevented in someone who was alerted to injury by painful sensations.

From Skin to Brain

Because the receptors for sights, sounds, tastes, and smells are all located in your skull, the pathways that deliver information from these receptors to the brain are fairly short. Touch sensations, on the other hand, must travel as far as 2 meters to get from the skin and muscles of your feet to your brain. To cross this distance, the information must pass up through your spinal cord.

Initially the axons of various tactile receptors are combined into single nerve trunks, in much the same way that retinal ganglion axons converge in the optic nerve and cochlear hair cells converge in the auditory nerve. But right from the start, we see two major differences between the visual and auditory pathways and the touch pathways. First, whereas there are only two optic nerves and two auditory nerves, there are a number of somatosensory nerve trunks, arising in the hands, arms, feet, legs, and other areas of the skin. Second, axons in the optic and auditory nerves go directly to the brain, whereas axons in the older nerve trunks, which we discuss next, synapse first in the spinal cord.

Once in the spinal cord, touch information proceeds upward toward the brain via two major pathways, as shown in Figure 12.6. The evolutionarily older **spinothalamic pathway** (Figure 12.6*a*) is the slower of the two and carries most of the information from thermoreceptors and nociceptors. This pathway includes a number of synapses within the spinal cord, thus slowing conduction while providing a mechanism for inhibiting pain perception when necessary, as will be discussed shortly. The **dorsal-column-medial-lemniscal (DCML) pathway** (Figure 12.6*b*) includes wider-diameter axons and fewer synapses and therefore conveys information more quickly to the brain. Tactile and proprioceptive information carried along this pathway is used for planning and executing rapid movements, where quick feedback is a must.

Neurons in the DCML pathway make their first synapse in the medulla, near the base of the brain (see Figure 12.6*b*). Activity is then passed on to neurons that synapse in the ventral posterior nucleus of the thalamus. You may recall from Chapters 3 and 9 that the auditory and visual pathways also pass through the thalamus, each synapsing in its own modality-specific nucleus. Because this portion of the brain is largely shut down when you are asleep, your brain does not register (and therefore does not attempt to respond to) the relatively gentle touch sensations that occur, for example, when you roll over in your sleep.

spinothalamic pathway Route from the spinal cord to the brain that carries most of the information about skin temperature and pain.

dorsal-column-medial-lemniscal (DCML) pathway Route from the spinal cord to the brain that carries signals from skin, muscles, tendons and joints.

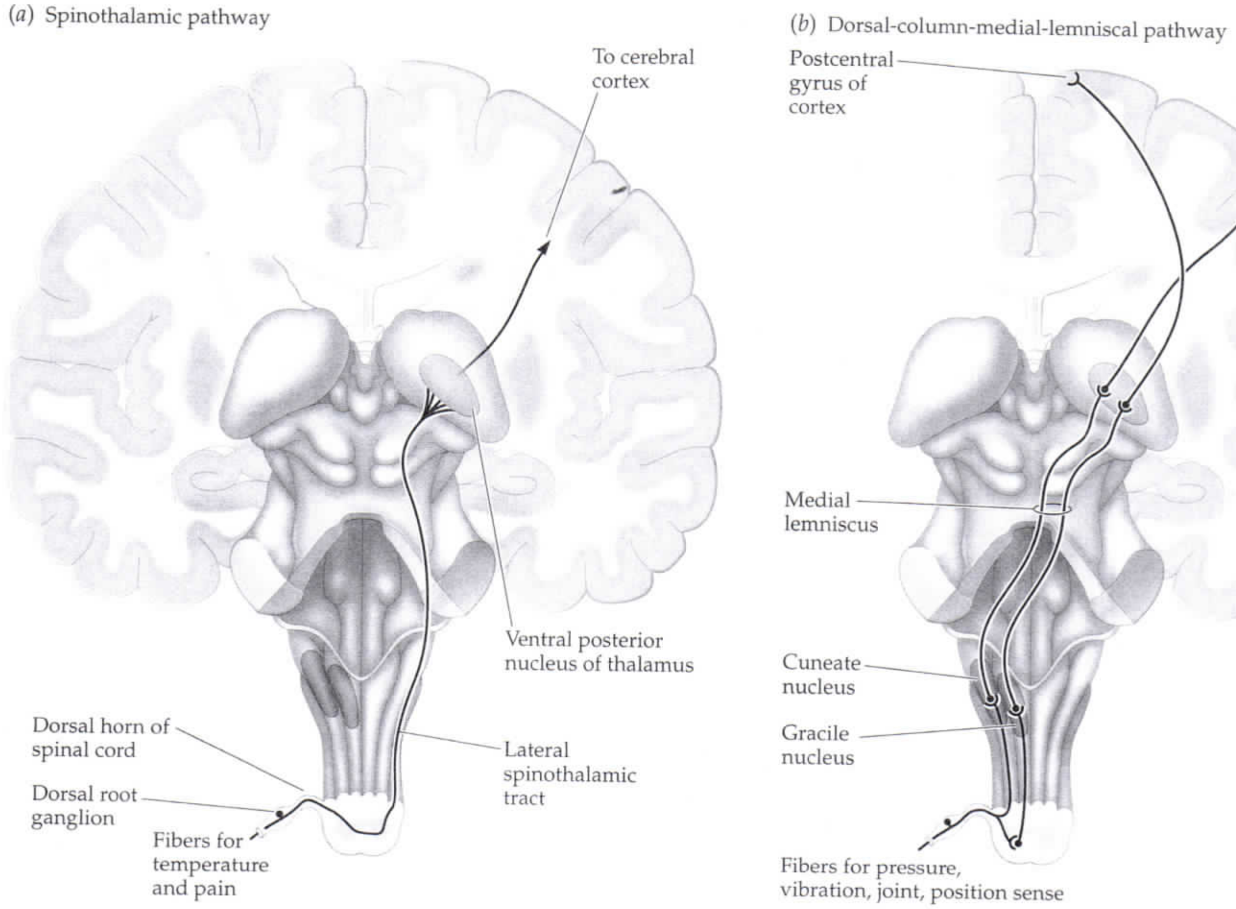


FIGURE 12.6 Pathways from skin to cortex. (After Levine 2000.)

From the thalamus, much of the touch information is carried up to the cortex (Figure 12.7) into **somatosensory area 1 (S1)**, located in the parietal lobe just behind the postcentral gyrus. S1 is analogous to V1 in vision. Neurons in S1 communicate with **somatosensory area 2 (S2)**, which lies in the upper bank of the lateral sulcus, and with other cortical areas. The motor areas of the cortex, which control movements of body parts, are located in front of the central sulcus, facilitating communication between the somatosensory and motor control systems.

Touch sensations are represented in area S1, and to some extent beyond, **somatotopically**. Somatotopy is analogous to the retinotopy found in vision (see Chapter 6); adjacent areas on the skin are ultimately connected to adjacent areas in the brain. As a result, the somatosensory cortex is organized into a spatial map of the layout of the skin, often called the sensory **homunculus** (plural *homunculi*) (Figure 12.8). We all have twin homunculi, one in each hemisphere of the brain. The left-hemisphere S1 receives information from the right side of the body and vice versa.

The sensory homunculus is largely derived from the work of Canadian neurosurgeon Wilder Penfield, who charted the somatotopic map with the aid of patients undergoing brain surgery to alleviate epilepsy. Because there are no pain receptors in the brain, patients do not need to be anesthetized during this surgery. During these surgeries, Dr. Penfield systematically stimulated different parts of a patient's somatosensory cortex with an electrode. As the probe moved from one location in S1 to another, the patient reported feeling

somatosensory area 1 (S1) Primary receiving area for touch in the cortex.

somatosensory area 2 (S2) Secondary receiving area for touch in the cortex.

somatotopic Mapped in correspondence to the skin.

homunculus (pl. homunculi) Maplike representation of regions of the body in the brain.

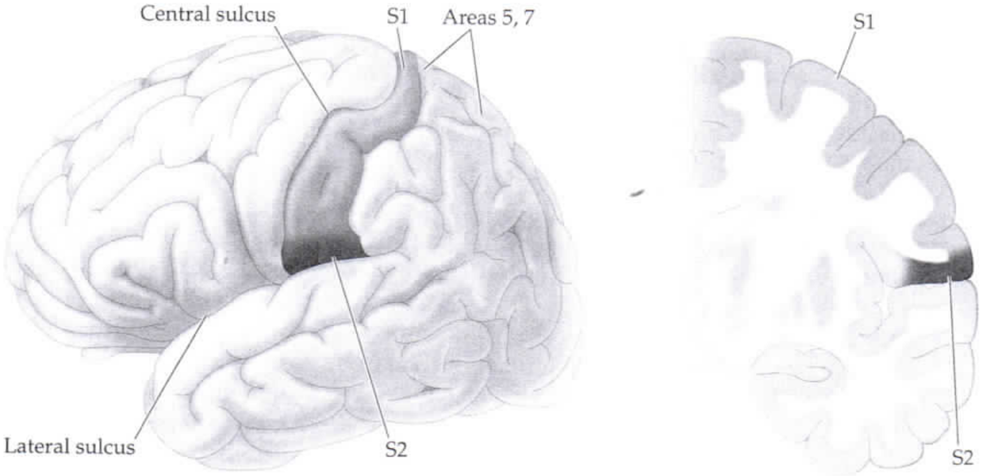


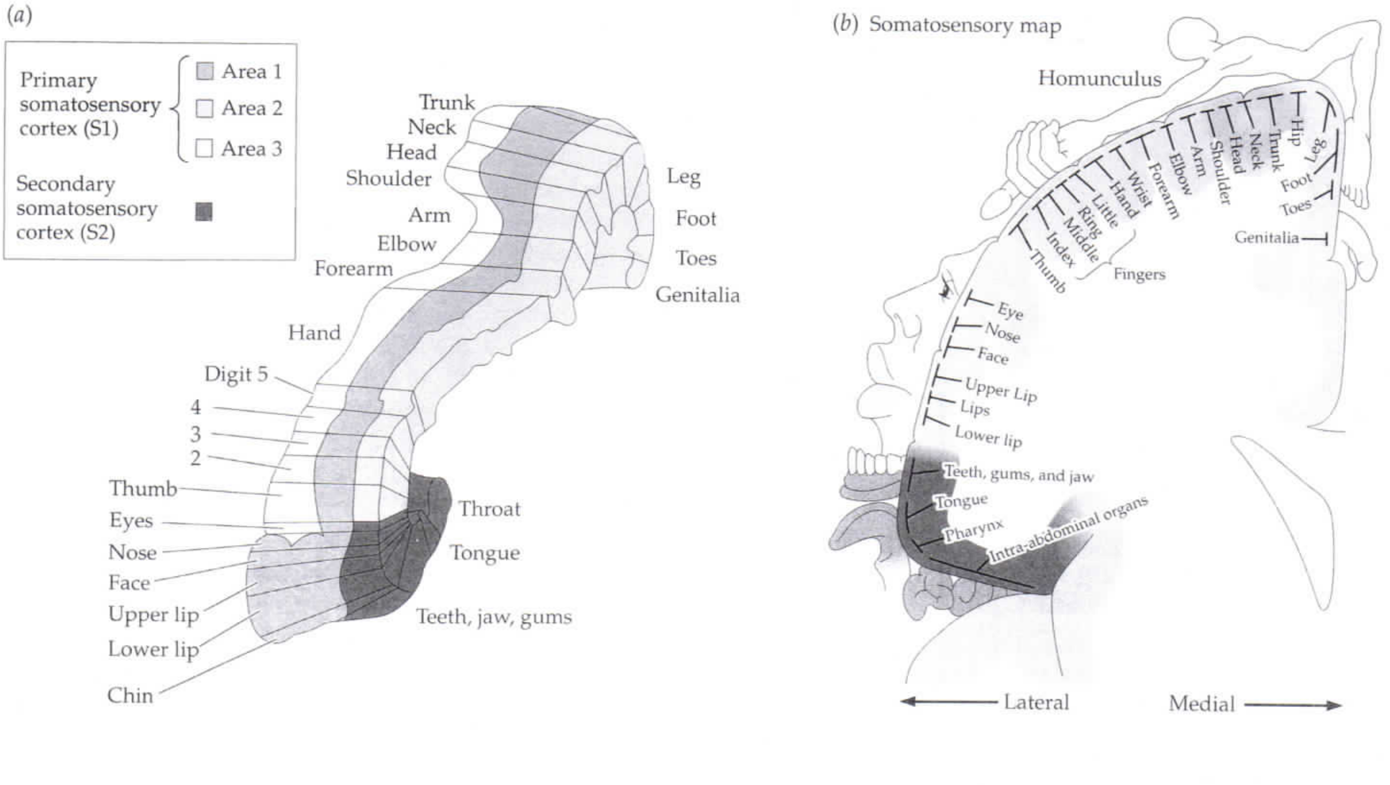
FIGURE 12.7 Primary somatosensory receiving areas in the brain. S1 includes Brodmann areas 1, 2, 3a, and 3b. Areas 5 and 7 are immediately posterior to S1. S2 lies within the lateral sulcus.

sensations in the arms, legs, face, and so on. The correspondence between the stimulation and the sensation gave rise to a map of the body in the brain (see **Web Activity 12.2 The Sensory Homunculus**).

In fact, the brain contains multiple sensory maps of the body. Separate maps are now known to exist in the different subareas of S1, and additional maps exist in secondary areas, as shown in Figure 12.8.

Note that, like the retinotopic map in area V1, Penfield's somatotopic map found in S1 is distorted. The thumb, for example, grabs a big piece of real estate relative to its size. In contrast, sensations from the leg are processed in a relatively small portion of S1. In the visual system, the foveal area is overrepresented in V1 (cortical magnification) because there are many more photoreceptors in the fovea than in peripheral parts of the retina. Similarly, a larger chunk of S1 is dedicated to processing information from the lips and the

FIGURE 12.8 The sensory homunculus, showing brain regions that respond to stimulation of different parts of the body. (*a*) Multiple maps exist in primary and secondary somatosensory areas, four of them within S1. (*b*) A schematic of the relative distribution of body parts in S1, as originally derived by Penfield and Rasmussen (1950).



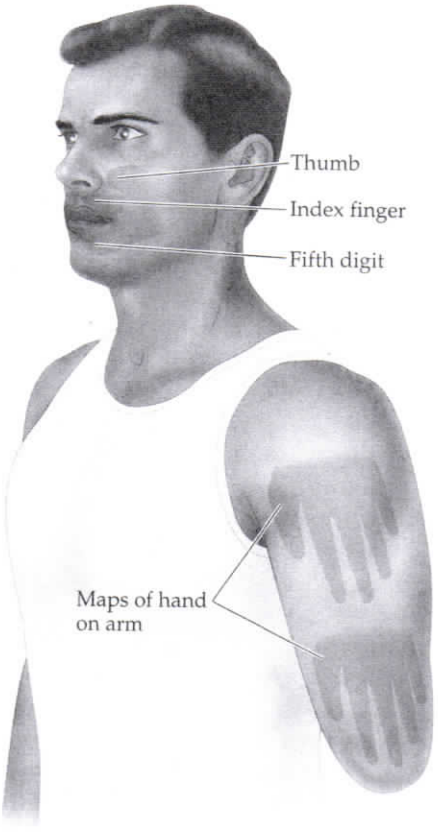


FIGURE 12.9 Phantom limbs may appear on the face and stump subsequent to amputation. Amputees report feeling the amputated hand when their face or remaining limbs are stimulated. (After Ramachandran, 1993.)

fingers than from the neck because tactile receptors are much more heavily concentrated in the lips than they are in the neck.

The relatively tight correspondence between body parts and areas of S1 can have unfortunate side effects when people have limbs amputated. If an amputee's left arm is missing, obviously no mechanoreceptors are sending touch signals from that arm. However, sporadic activity can continue in the area of the amputee's right S1 corresponding to the arm, leading to the perception of a **phantom limb**. At times, patients may perceive their phantom limbs to be in uncomfortable positions, leading to persistent (and very real) pain.

The psychologist Vilayanur Ramachandran recently made the astonishing observation that amputees often report feeling sensations in their phantom arms and hands when their faces or remaining limbs are touched (Figure 12.9). The source of this somatosensory confusion can be traced to an idiosyncrasy in the homunculus. Note in Figure 12.8 that the area responding to the face is located (somewhat arbitrarily) adjacent to the area responding to the hand and arm. Apparently the hand and arm areas of S1 are, to some extent, "invaded" by neurons carrying information from touch receptors in the face. However, other parts of the brain listening to the hand and arm areas are not fully aware of these altered connections, and therefore they attribute activity in these areas to stimulation from the missing limb. (You can read more about Ramachandran's fascinating studies on phantom limbs in **Web Essay 12.2 Phantom Limbs**.)

Projections from S1 form the basis for further analysis of objects and surfaces by the cortex of the brain. Analogous to vision, the sense of touch appears to show a division between *what* and *where* systems in higher cortical centers. A patient studied by Reed, Caselli, and Farah (1996) showed an impairment in recognizing objects by touch (*what*), but she showed no deficit in spatial ability (*where*). Another patient could locate and manipulate objects by touch without recognizing them (Rossetti, Rode, and Boisson, 1995). Activation of the brain, observed with fMRI imaging, has been found in different areas, depending on whether the task is to locate an object or to recognize it tactually, and, as in vision, there is relatively more dorsal activation for locating objects and more ventral activation for recognizing objects (Reed, Klatzky, and Halgren, 2005; Reed, Shoham, and Halgren, 2004).

The pathways from the skin to the brain tell just one part of the story of the transmission of signals in touch. Downward pathways from the brain can alter the sensations produced by stimulating the periphery. Some of the most surprising effects of these downward pathways relate to the feeling of pain, which we discuss next.

Pain

ANALGESIA AND GATE CONTROL THEORY Pain sensations are triggered by the nociceptors, which were described earlier in this chapter. Pain experiences, however, are the complex result of sensory signals interacting with many other factors. Responses to noxious stimulation can be moderated by anticipation, religious belief, prior experience, watching others respond, or excitement. For example, there are many stories of soldiers in battle who did not feel painful wounds until the stress was over. Such damping of pain sensations (without

phantom limb Perceived sensation from a physically amputated limb of the body.

analgesia Decreasing pain sensation during conscious experience.

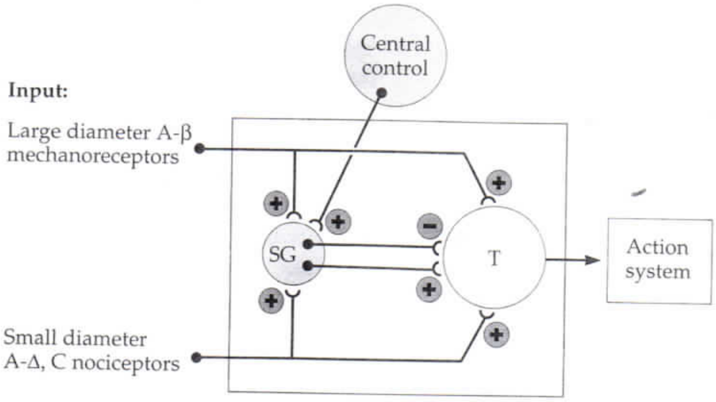


FIGURE 12.10 Gate control theory of Melzack and Wall (1988). Pain signals transmitted to the brain are moderated by activity in the substantia gelatinosa (SG) located in the dorsal horn of the spinal cord. The orange and green circles represent SG signals that decrease and increase pain, respectively, by their inhibitory and excitatory connections with transmission (T) cells. The T cells combine pain signals from the small-diameter fibers with signals inhibiting pain produced by stimulation of the large-diameter fibers. Direct excitatory pathways from both types of fibers are also found outside of the SG. Like the large diameter fibers, the central control excites mechanisms in the SG that inhibit activation of T cells, thus decreasing the pain response.

losing consciousness) is called **analgesia**. In the case of the soldiers, the analgesic effect was probably caused by **endogenous opiates**, chemicals released by the body that block the release or uptake of neurotransmitters necessary to transmit pain sensations to the brain. Differences between individuals with respect to pain responsiveness (that is, pain "thresholds") may reflect differences in their baseline levels of these substances. Externally produced substances such as morphine, heroin, and codeine are similar in chemical structure to these endogenous opiates, and thus they have similar analgesic effects. Other drugs, such as acetominophen and ibuprofen, alleviate pain at its source, by counteracting chemicals that would otherwise start the nociceptors firing.

According to the very influential **gate control theory** (Figure 12.10), pain sensations can also be blocked via a feedback circuit located in an area called the **substantia gelatinosa** of the **dorsal horn** of the spinal cord. Neurons in this area receive information *from* the brain and synapse with the neurons that are conveying sensory information from nociceptors *to* the brain (see Figure 12.6). When these gate neurons send excitatory signals, the sensory information is allowed to go through, but inhibitory signals from the gate neurons cancel transmission to the brain.

The gate neurons that block pain transmission can also be activated by "counterirritation" or "diffuse noxious inhibitory control"—extreme pressure, cold, or other noxious stimulation applied to another site distant from the source of the pain. For example, pain from electrically stimulating a tooth can be reduced by noxious stimulation of the hand (Motohashi and Umino, 2001). It appears that ascending signals from the counterirritation reach the brain stem and initiate a new set of signals that are sent back down to the pain-blocking gate in the spinal cord (Rollman, 1991).

A different, and certainly more pleasant, way of modulating pain is to use relatively benign counterstimulation. Thus, although your mother may have told you not to scratch a mosquito bite, gate control theory says that rubbing the skin near the bite can in fact provide some relief. This effect involves stimulating fibers other than the nociceptors and can be produced by interactions between neurons within the spinal cord.

PAIN SENSITIZATION Nociceptors provide a signal when there is impending or ongoing damage to the body's tissue. This is called "nociceptive" pain. Once damage has occurred, the site can become more sensitive, triggering the feeling of pain more readily than before. This experience is hyperalgesia and reflects an increased or heightened response to a normally painful stimulus. The resulting pain is called "inflammatory," and the heightened pain sensi-

endogenous opiates Chemicals released by the body that block the release or uptake of neurotransmitters necessary to transmit pain sensations to the brain.

gate control theory Description of the system that transmits pain that incorporates modulating signals from the brain.

substantia gelatinosa A jellylike region of interconnecting neurons in the dorsal horn of the spinal cord.

dorsal horn Region at the rear of the spinal cord that receives inputs from receptors in the skin.

tivity usually goes away once the tissue heals. Pain can also arise in the absence of immediate trauma, because of damage to or dysfunction of the nervous system. The resulting pain is called "neuropathic." Some neuropathic pain reflects changes in the sensory fibers at the skin that do not normally produce pain, but now become pain inducers (a phenomenon known as "allodynia"); other neuropathic pain arises from changes in the dorsal horn of the spinal cord. The changes at the level of the skin are called "peripheral," and those at the level of the spinal cord are called "central." The mechanisms by which neuropathic pain arises are increasingly understood at the cellular and molecular levels (Scholz and Woolf, 2002).

An important implication of sensitization research is that no single medication will alleviate all types of pain. Different underlying mechanisms for nociceptive, inflammatory, and neuropathic pain (peripheral or central) call for different analgesics.

COGNITIVE ASPECTS OF PAIN Pain is actually a subjective state with two distinguishable components: the sensation of the painful source, and the emotion that accompanies it (Melzack and Casey, 1968). The latter aspect of pain can be affected by social and cultural contexts and higher-level cognition. For example, reports of painful strains of the arm from tasks requiring repetitive motion spread rapidly in Australia during the 1980s—like a contagious disease—but they were communicated by workers who did nothing more than talk to one another about their experiences.

We have known for some time that areas S1 and S2 are responsible for the sensory aspects of pain, but researchers have recently been able to use new methods to identify the areas of the brain that correspond to the more cognitive aspects of painful experiences. In one study (Rainville et al., 1997) (Figure 12.11),

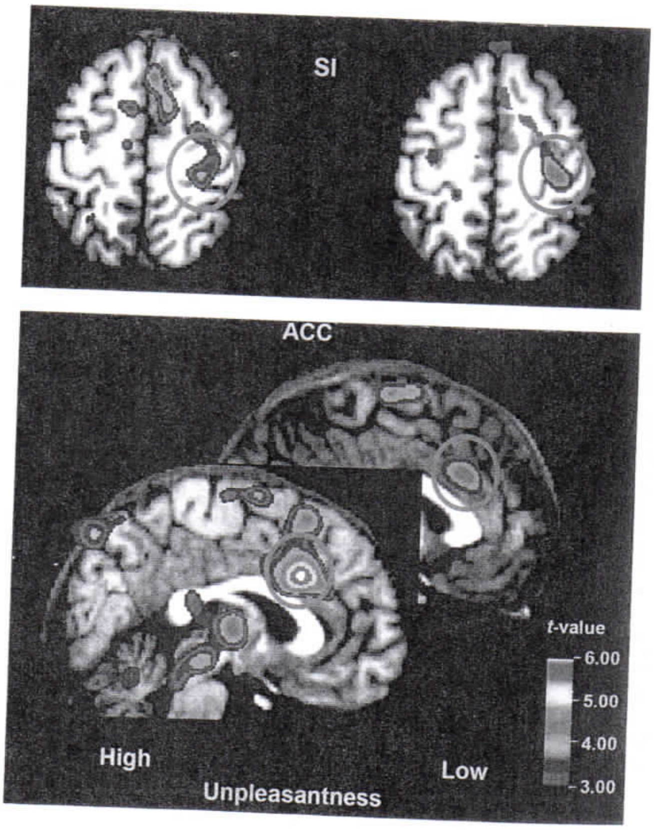


FIGURE 12.11 PET signals showing the effect of hypnosis on the brain, as observed by Rainville et al. (1997). Primary somatosensory cortex (S1, top) was not affected by the suggested unpleasantness of pain (high on the left, low on the right). The anterior cingulate cortex (circled at bottom), however, showed significantly different activation, depending on suggested unpleasantness.

participants were hypnotized and their hands were placed in lukewarm or very hot water (which activated thermal nociceptors). The participants were sometimes told that the unpleasantness from the water was increasing or decreasing, and their brains were imaged during these periods by positron emission tomography (PET). The primary sensory areas of the cortex, S1 and S2, were activated by the hot water, but the suggestion of greater unpleasantness did not increase their response relative to the suggestion of decreased unpleasantness. In contrast, another area, the **anterior cingulate cortex** (**ACC**), did respond differentially to the two hypnotic suggestions, by increasing or decreasing its activity according to the suggestion of increased or decreased unpleasantness. The researchers concluded that the ACC processes the raw sensory data from S1 and S2 in such a way as to produce an emotional response.

At a higher level still, pain can produce what Price (2000) has called "secondary pain affect." This is the emotional response associated with long-term suffering that occurs when painful events are imagined or remembered. For example, cancer patients who face a second round of chemotherapy may remember the first and dread what is forthcoming. This component of pain is associated with the **prefrontal cortex**, an area concerned with cognition and executive control.

It may seem odd to associate pain with laughter, but at least some of the response people have to tickling seems to depend on nociceptors (Zotterman, 1939). And, just as signals from the brain can control pain perception, they appear to come into play when we try to tickle ourselves. Self-induced tickling not only produces less laughter, it produces less activity in the somatosensory cortex, because of canceling signals (probably mediated by endogenous opiates) from other brain areas that know where the tickling stimulation came from (S.-J. Blakemore, Wolpert, and Frith, 1998).

anterior cingulate cortex (ACC) Region of the brain associated with the perceived unpleasantness of a pain sensation.

prefrontal cortex Region of the brain concerned with cognition and executive control.

Tactile Sensitivity and Acuity

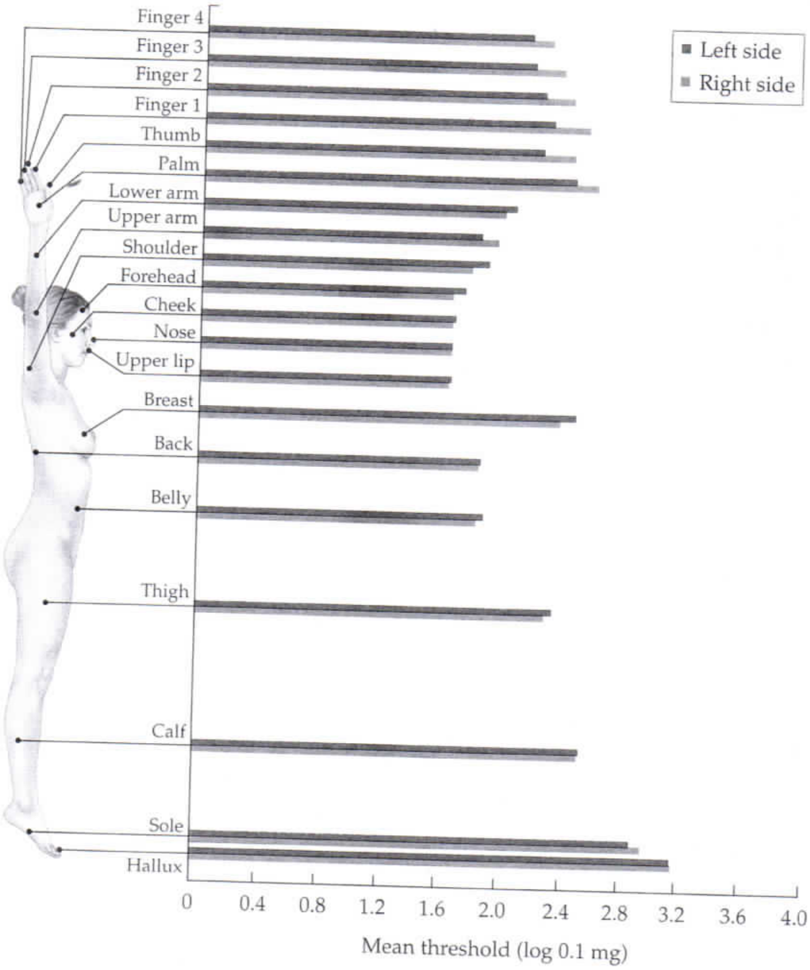
Now that we've covered the physiological substrate of the touch system, we can turn to psychological and psychophysical aspects. How sensitive are we to mechanical stimulation? What are the limits on tactile acuity in time and space? Put a bit differently, what are the smallest details that we can feel?

How Sensitive Are We to Mechanical Pressure?

If you want to measure the minimum pressure that can be reliably sensed on a piece of skin, you need a way to present well-defined amounts of pressure over and over again. In the nineteenth century, Max von Frey developed an elegant and simple way to do this using carefully calibrated stimuli, including horse and human hairs. Modern researchers typically use nylon monofilaments (e.g., fishing lines) of varying diameters. The smaller the diameter, the less force the line applies to the skin before it buckles.

To replicate von Frey's method yourself, you can touch different parts of your skin with a hair from your head and a bristle from a hairbrush, revealing the relative skin sensitivity to these two different forces. With the thinner hair, you will probably find that you can feel it on your more sensitive areas, such as your lips and perhaps on some parts of your hand. You probably will not feel it pushing into your thigh or upper arm. With the bristle, however, you should discover that your skin is sensitive to mechanical pressure all over, but not uniformly so. For example, if you explore the skin on the back of your hand, you should be able to convince yourself that there are spots of greater and lesser sensitivity (Geldard, 1972).

FIGURE 12.12 Sensitivity to pressure at different sites on the body. (After Weinstein, 1968.)



Data from a more controlled pressure sensitivity study are presented in Figure 12.12. This graph shows pressure thresholds for women as a function of body site (a high threshold means that that part of the body is less sensitive). In general, tactile pressure sensitivity is highest on the face, followed by the trunk and upper extremities (arms and fingers) and then the lower extremities (thigh, calf, and foot) (Weinstein, 1968). The pattern for males and females is very similar, except that women tend to be more sensitive to pressure than men. Sensitivity to temperature, as well as to pain, also varies markedly as a function of body site.

How Finely Can We Resolve Spatial Details?

two-point touch threshold The minimum distance at which two stimuli (e.g., two simultaneous touches) are just perceptible as separate.

Pressure detection is the tactile equivalent of detecting a spot of light, where the basic question is, "Can you see or feel anything at all?" For the tactile equivalent of visual acuity ("Can you make out the pattern of what you see or feel?"), you can try measuring your **two-point touch threshold**. As the name suggests, this is the smallest separation at which you can tell that you are being touched by two points and not just one. This experiment is best done with a partner, although it will work to some degree if you test yourself. A compass (the kind that draws circles) is a useful stimulator, but you can use anything that allows you to vary the separation between two points, such as a bent paper clip. Pick one of your or your partner's body parts and see if you

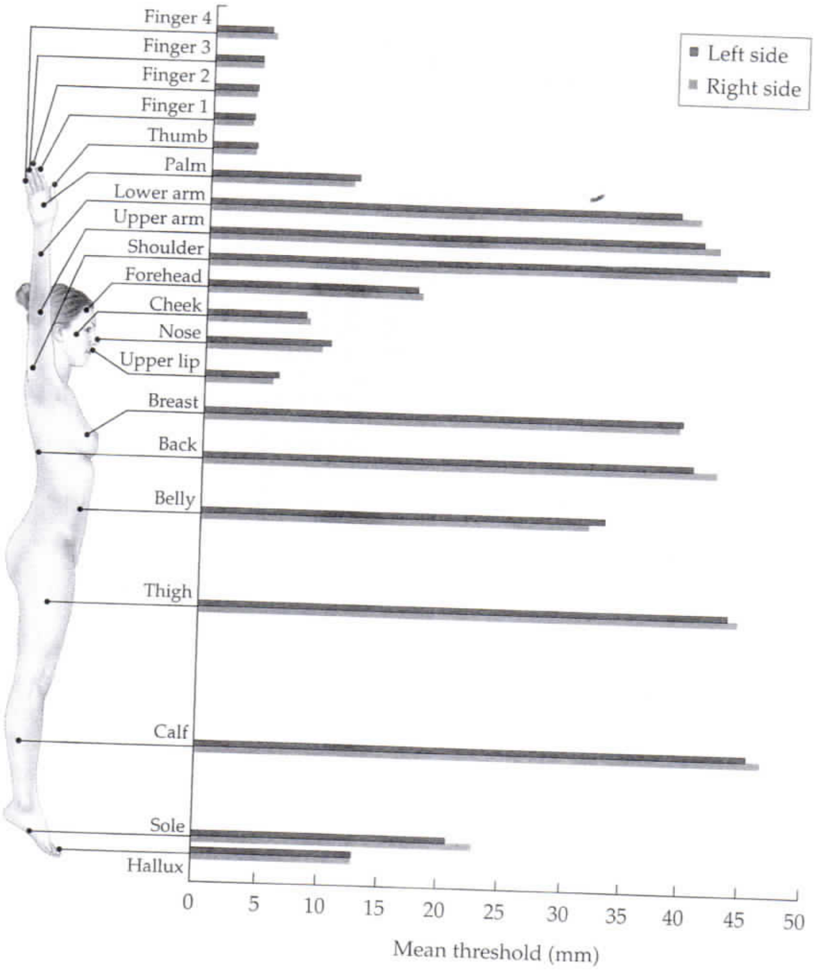


FIGURE 12.13 The minimal separation between two points needed to perceive them as separate (two-point threshold), when the points are applied at different sites of the body. (After Weinstein, 1968.)

can distinguish between a single point and both points. Then repeat the procedure with different separations of the two points (e.g., 0.5, 2, and 4 cm) and at different places on the skin.

Results from a systematic study of two-point thresholds are shown for females in Figure 12.13 as a function of body site (again, the pattern for males is very similar). Like sensitivity to pressure, spatial acuity varies across the body, but the extremities (fingertips, face, and toes) show the highest acuity. More sensitive psychophysical methods show that, on the fingertips, we are capable of resolving a separation of only about 1 mm (Loomis, 1981). These results place tactile acuity somewhere between vision and audition: it is worse than visual acuity, but better than auditory spatial resolution.

Note the correspondence between the pattern of two-point thresholds across the body in Figure 12.13 and the relative distortion of different body parts in the sensory homunculus of Figure 12.8. This is not coincidental. The determination that two closely spaced points instead of just one are touching your skin—that is, a low two-point threshold—requires that your brain receive two separate signals. This means that at the skin (Figure 12.14), there must be a sufficient concentration of receptors, each with a small enough receptive field, that the two contact points will elicit different responses. An additional constraint is that, as the signals are sent to the cortex, they must not converge. A large enough chunk of cortical real estate is necessary to receive them separately. In short, the two-point threshold is low only when the density of recep-

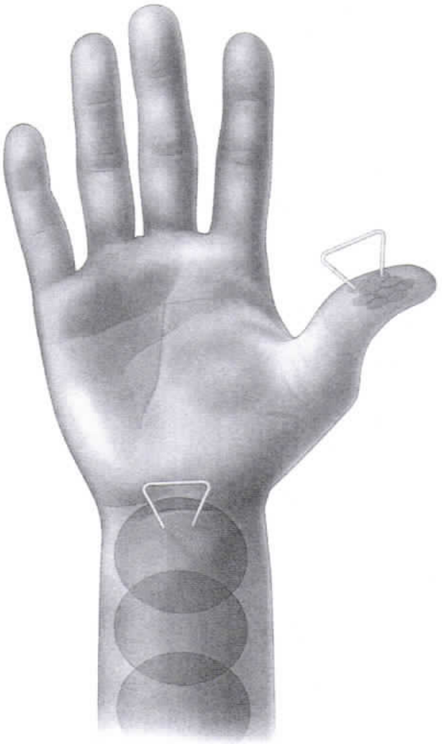
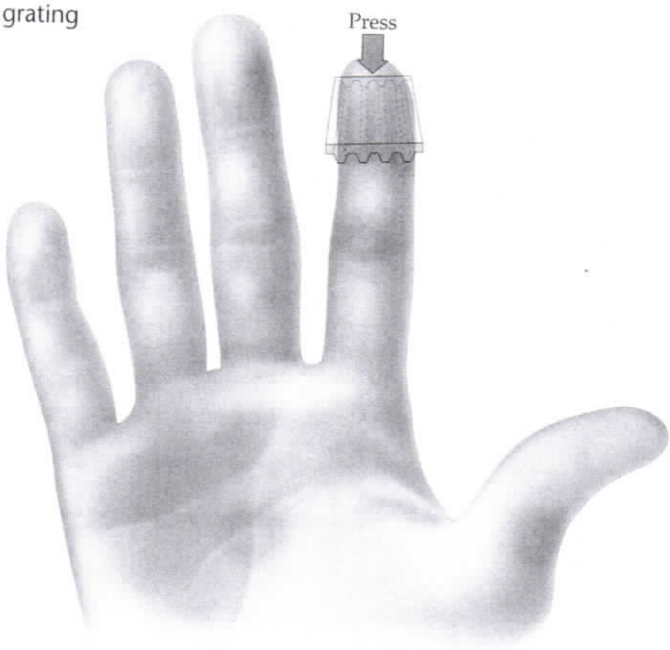


FIGURE 12.14 Two-point thresholds are determined primarily by the concentration and receptive-field sizes of touch receptors in an area of the skin. The triangles represent point stimulators, and the circles represent the areas of skin that would respond to a single stimulation.

FIGURE 12.15 Discriminating the orientation of a grating. Is a grating pressed into the hand oriented along the finger or across it?



tors is relatively high, the receptive fields are small, and cortical convergence does not occur. (See **Web Activity 12.3 Two-Point Touch Thresholds**.)

The two-point threshold, although useful, has some drawbacks, as you may see when you try your own experiment. Even when the two stimulated points feel like one, it is not quite the same as stimulating the skin with a single continuous contact. Therefore, asking people whether they are really being touched by one point or two will yield quite a different answer than asking them if it *feels like* one point or two, especially in sensitive areas like the fingertip. Alternatives that are more objective have been suggested, including judging whether an edge has a gap or indicating how a grating (grooves and ridges) applied to the skin is oriented (Craig and Johnson, 2000) (Figure 12.15).

How Finely Can We Resolve Temporal Details?

It is a bit more difficult to do your own measures of temporal sensitivity. However, if you have ever found yourself in the presence of very loud music, you may have felt the low notes as a tactile stimulus; the sound pressure changes of these low-frequency notes actually translate into vibratory skin pressure changes that your mechanoreceptors pick up. Higher-frequency notes can be heard, but not felt, regardless of how loudly they are being played.

Figure 12.16 shows absolute vibrotactile thresholds as a function of the frequency of a vibratory stimulus presented to a finger and the contact area (Verillo, 1963). People are capable of detecting the presence of a vibration up to about 700 Hz (700 cycles in 1 second). This means that they can detect a single temporal cycle of about 1.4 milliseconds (ms). Compare this to vision (an upper limit of only 50 Hz for a flickering light) and audition (20,000 Hz) and you will see that touch again lies between vision and audition, but this time audition is the best and vision the worst. Vibratory sensitivity is greatest at frequencies of 250–300 Hz, reflecting the responses of the FA II mechanoreceptors.

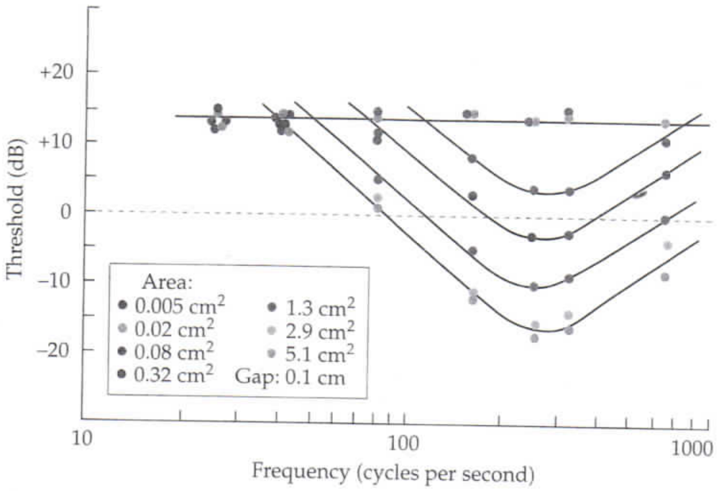


FIGURE 12.16 Minimally detectable displacement (threshold) of a vibrating stimulus pressed into the palm, as a function of frequency and area. The y-axis measures decibels relative to 1 μm. Note the similarity to the function associated with the FA II mechanoreceptors in Figure 12.3. (From Verrillo, 1963.)

Haptic Perception

Now that we've covered the physiology and basic psychophysics of the touch system, we can turn to questions about how we use the information gathered by our thermoreceptors, muscle spindle fibers, Pacinian corpuscles, and so on. The term **haptic perception** refers to perceptual processing of inputs from multiple subsystems, including those in skin, muscles, tendons, and joints. Haptic perception is usually active and information-seeking: the perceiver explores the world rather than passively receiving it.

Perception for Action

As we mentioned earlier, touch relies on action to get information from the world. Expanding on this point a bit more, we can say that touch is active in two complementary ways. When we use our hands to actively explore the world of surfaces and objects outside our bodies, that is *action for perception*. When we use somatosensation to control our impressive ability to grasp and manipulate objects in a stable and highly coordinated manner and to maintain proper posture and balance, that is *perception for action*.

In the section on kinesthetic receptors, we discussed how the loss of these internal touch receptors leads to a devastating inability to know (without looking) where our limbs are positioned. Westling and Johansson (1984) showed that mechanoreceptors in the skin also play critical roles when we are interacting with objects (Figure 12.17). These investigators anesthetized the skin on volunteers' hands so that activity in the mechanoreceptors was no longer available for processing. Even though their kinesthetic receptors were still active and they could still see what they were doing, the experiment participants could no longer maintain a stable grasp of the objects they were required to lift, hold, and then replace on a supporting surface. Feedback from the mechanoreceptor populations in the skin appears to provide crucial information about when an object is about to slip on the skin.

Action for Perception

Let's now consider the "action for perception" side of haptic processing. Lederman and Klatzky (1987) coined the term **exploratory procedure** for a par-

haptic perception Knowledge of the world that is derived from sensory receptors in skin, muscles, tendons, and joints, usually involving active exploration.

exploratory procedure Stereotyped hand movement pattern used to contact objects in order to perceive their properties; each exploratory procedure is best for extracting one (or more) object properties.

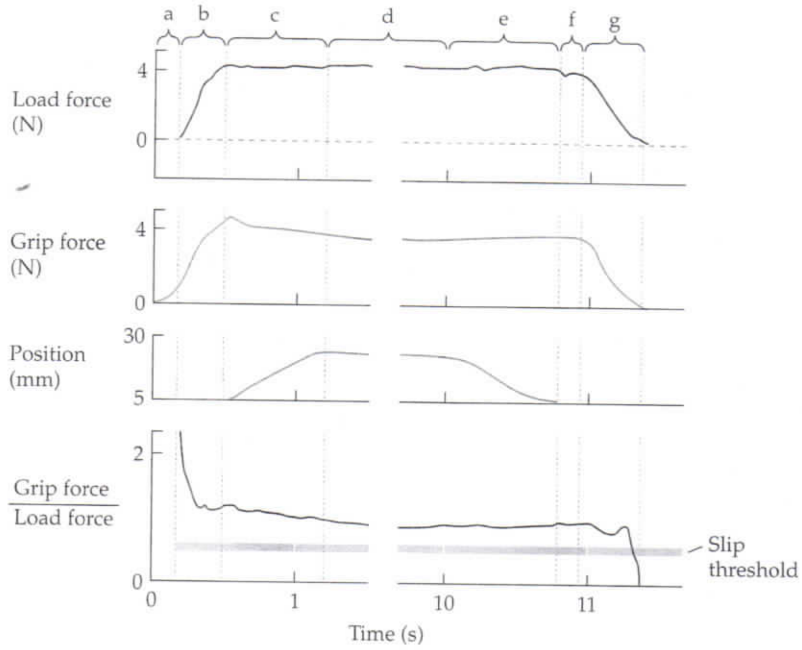
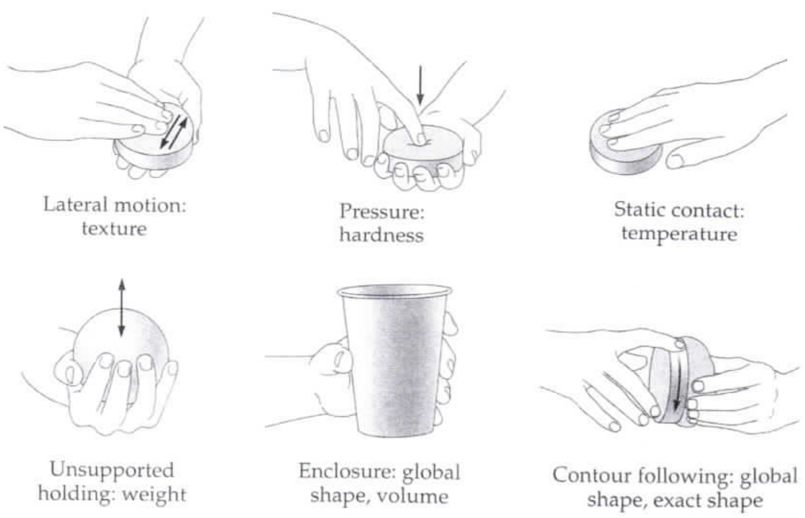


FIGURE 12.17 Force and position during lifting, grasping, and replacing a cube. Region a = grasp; b and c = lift; d = hold; e = lower; f and g = release. The load force (in newtons) is in the gravitational direction, the grip force is imposed by the fingers pinching the cube, and the position is the height relative to the table. The ratio of grip force to load force is set so as to just prevent the cube from slipping. (From Westling and Johansson, 1984.)

ticular way of feeling an object in order to extract one or more of its properties (Figure 12.18). Each exploratory procedure is optimal for obtaining precise details about one or two specific properties. For example, to find out how rough an object is, the best exploratory procedure is *lateral motion*—moving the fingers back and forth across the surface. This is the exploratory procedure that people freely choose when they wish to learn about roughness, and research indicates that it is also the one that works best.

To explain why each exploratory procedure is linked to a specific object property, we must consider both the neural structures that transduce information and the processes that operate on that information. For example, Johnson and his colleagues (Johnson, 2002) have shown that the activity of slow-adapting mechanoreceptors (SA I) is a principal basis for the perception of roughness (unless surface variations are minute). These units are ten times as


Lateral motion: texture

Pressure: hardness

Static contact: temperature

Unsupported holding: weight

Enclosure: global shape, volume

Contour following: global shape, exact shape

FIGURE 12.18 Exploratory procedures described by Lederman and Klatzky, and the object properties with which each is associated. (After Lederman and Klatzky, 1987.)

responsive when there is relative motion between the skin and the surface as when the fingers statically rest against the surface without motion. As your finger sweeps across a surface, the pattern of force across the receptors varies with the hills and troughs on the object's surface, providing a kind of spatial map of the variations in skin deformation. This map is passed on to higher-level neural structures, which integrate the lower-level information into an overall measure of the amount of variation. The brain then uses this neural measure to generate an estimate of the surface's roughness. When surfaces become very fine, the mechanoreceptors responsive to vibration (FA II) appear to govern roughness, but again, stroking with the fingers is needed to set up the vibration (see Hollins, 2002).

The What *System of Touch: Perceiving Objects and Their Properties*

Chapter 4 described the processes that underlie visual object recognition. We need somatosensation to control simple actions such as standing or grasping and to warn of danger through pain, but how much value does somatosensation have as an object recognition system? You know the answer if you have ever gotten up in the dark to use the bathroom. The designers of coins know that it is imperative to be able to identify change while it is still in your pocket—hence the failure of the Susan B. Anthony dollar, which felt too similar to the quarter. And the next time you get dressed, try to keep your gaze constantly focused on your hands as you button your shirt and zip your zipper. This simple exercise should convince you that even when you can use vision, you sometimes rely on touch to recognize objects and their parts.

PERCEIVING MATERIAL VERSUS GEOMETRIC PROPERTIES People can perform haptic object recognition very well. Klatzky, Lederman, and Metzger (1985) asked people to identify each of 100 common objects (e.g., a fork, a brush, and a paper clip) that were placed in their hands. Not only did people perform almost perfectly, but they also generally responded in less than 2 seconds. However, the information used when recognizing objects haptically and visually is quite different. Consider the difference between material properties—those that do not depend on the structure of a particular object, like its surface roughness—and geometric properties like size and shape. In haptic perception, the observer is in contact with the object being observed, so material properties of the object (Is it soft? cold? fuzzy?) are easy to perceive and play a crucial role in the recognition process. In vision there is no physical contact, so thermal and textural properties of objects are much more difficult to perceive.

Therefore, it is the geometric properties of objects that are most important for visual recognition. Indeed, sparse line drawings are quite easy to recognize visually when portrayed as raised contours (Figure 12.19). To determine the overall shape of an object haptically, we are usually required to explore the object by tracing its contours with our fingers. Integrating tactile information over time is possible but not very efficient, which is why the instantly recognizable material properties tend to be much more important in haptic recognition (See **Web Activity 12.4 Haptic Object Recognition**.)

HAPTIC SEARCH As we saw in Chapter 6, a number of so-called preattentive features in the visual domain are presumed to be critical in the visual object recognition process. These features can be identified by the extent to which they "pop out" in a visual search task. For example, if you are search-

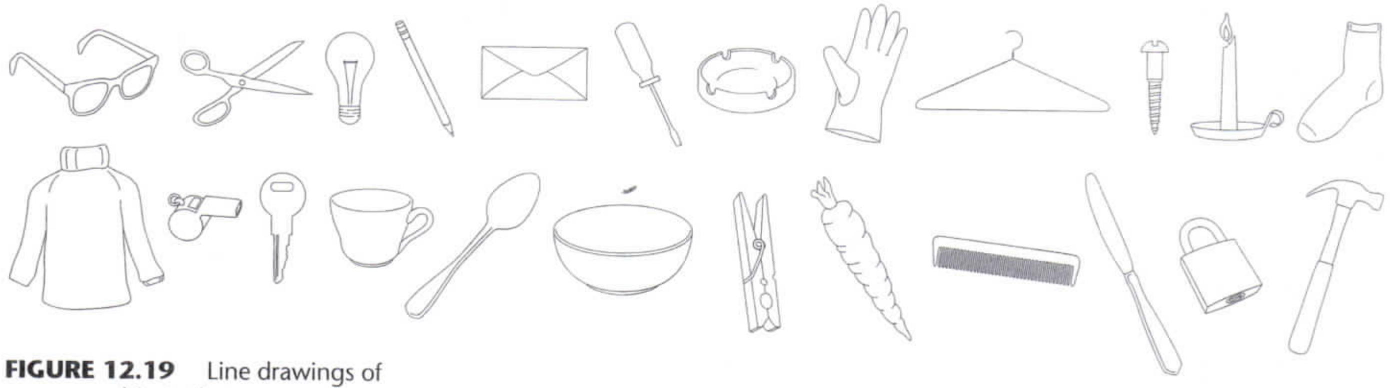


FIGURE 12.19 Line drawings of common objects that are easy to recognize by vision but not by touch. (After Klatzky et al., 1993.)

ing for a red object, you will be equally fast at finding it, regardless of how many green objects are presented along with it. This result implies that the "redness" of an object is available to recognition processes before attentional mechanisms examine the objects in the display and integrate the various features of each one.

Does the sense of touch also support preattentive feature detection? To find out, Lederman and Klatzky (1997) constructed a set of surfaces somewhat like a tactile slot machine with one key for each finger (Figure 12.20*a*). Stimulus patches were mounted around the planar edges of each of six stimulus wheels. On each trial, the wheels were rotated until the desired stimulus patches were facing upward to form the haptic display. The entire display was then moved up to contact different combinations of the middle three fingertips of each hand. Using this apparatus, Lederman and Klatzky found that a number of haptic features do indeed pop out. As Figure 12.20*b* shows, participants in these experiments were just as fast at detecting a rough surface when there was no smooth surface in the tactile "display" as when there were as many as five smooth surfaces. Similarly, a hard surface popped out of a group of soft surfaces, a cool surface popped out of warm surfaces, and a surface with an edge popped out of perfectly flat surfaces.

However, not every haptic difference supports efficient search. For example, response times increased with the number of distractors when the task was to find a target with a horizontally oriented edge among distractors hav-

FIGURE 12.20 (*a*) Apparatus used to display targets to the fingertips by Lederman and colleagues. The rotating drums bring either a stimulus patch or a cutout (no stimulus) to the upper surface, then rise as a whole to contact the fingers. (*b*) The amount of time required to detect a rough target among smooth distractors as a function of the number of fingers stimulated. (After Lederman and Klatzky, 1997.)

ing vertical edges. Note that horizontal targets do pop out of vertical distractors in visual search tasks. This distinction fits nicely with the previous observation that haptic recognition relies extensively on material properties, but that the tactile system does not appear to be set up to efficiently process object contours.

PERCEIVING PATTERNS WITH THE SKIN Even if pattern perception by touch is not terribly efficient, it can be done, especially if the patterns are small enough to be perceived by a single fingertip. Loomis (1990) has suggested that, to some extent, touch acts like blurred vision when the fingertip explores a raised pattern. He tested people's ability to identify a set of patterns including Braille symbols, English and Japanese letters, and geometric forms (Figure 12.21). Sometimes the patterns were presented to the fingertips as raised elements. Other times they were presented visually behind a blurring screen that matched the resolution of the eye with the more limited acuity of fingertip skin. Interestingly, Loomis found very similar patterns of visual and tactile confusion errors—responses in which one pattern was taken to be another. This finding suggests that a common, amodal decision process operates on both haptically and visually perceived patterns.

Figure 12.21 shows the Braille alphabet in various sizes. Note that each letter is formed by raising some of the dots in a 2 × 3 array. For the letter *A*, for example, a single dot is raised in the top left position; and for the letter *Q*, all dots except for the one in the lower right position are raised. This design

FIGURE 12.21 The character recognition sets used by Loomis. (After Loomis, 1990.)

reflects a compromise between the skin's acuity and its "field of view." It would be nice to include more than six dots in the array, but because of the spatial blurring imposed by the skin, denser patterns would be difficult to resolve and discriminate (remember that two-point thresholds on the fingertips are about 1 mm). Spreading a greater number of dots across a larger contact area would not work either, because then the pattern would extend beyond the fingertip.

TACTILE AGNOSIA Just as lesions in the temporal lobe can produce visual agnosia (see Chapter 5), lesions of the parietal lobe can produce **tactile agnosia**, an inability to identify objects by touch. In making a diagnosis of tactile agnosia, the neurologist needs to be able to eliminate other possibilities. Is this impaired motor control, which would prevent the exploratory procedures needed to effectively learn about an object's properties? Or might the problem be a higher-level cognitive dysfunction, such as a loss of access to object names?

We've already described a patient who could not recognize objects by touch but could locate them. She had tactile agnosia with her right hand, due to a lesion in the left inferior parietal region of her brain, but the deficit did not extend to the left. Reed and Caselli (1994) documented that, although the patient could not recognize objects such as a key chain or a combination lock with her right hand, she could easily recognize these objects visually or with the left hand, ruling out a general loss of knowledge about objects. Other capabilities were normal in both hands, including sensory threshold levels and the movements with which objects were explored. The patient could also discriminate between objects with different levels of weight and roughness using either hand. And she could answer questions about the haptic properties of named objects, such as whether an orange was harder than an apple, indicating that she had the ability to remember and imagine how objects felt.

Thus the patient could acquire information with her impaired hand about an object's properties (e.g., its weight and roughness), and she had intact haptic knowledge about objects she had encountered in the past. What she lacked was a connection between these two components of object identification. That is, she was either unable to integrate the perceived properties into a coherent object representation, or she was unable to match perceived representations to stored representations in memory.

The Where *System of Touch: Locating Objects*

As in other sensory modalities, knowing *what* a haptic stimulus might be is only part of the perceptual problem. We also need to know *where* that stimulus is located. If you are already touching an object, you obviously know where it is (a tree limb that you bump your head on is in the air; one that you stumble over has fallen to the ground). If you are not yet touching the object but can see it, your sense of vision can work out where the object is and guide your reaching behavior. But what about groping for the snooze button on your alarm clock when your eyes have not yet opened for the day? As we have mentioned, there is evidence that touch, like vision, has a specialized neural pathway for dealing with questions of where objects are located, as compared to knowing what they are like.

Haptic object localization, like visual and auditory localization, first requires that you establish a **frame of reference**. For vision, the center of your reference frame—your **egocenter**—is located near the bridge of your nose, between your two eyes; your auditory egocenter is a point smack in the mid-

tactile agnosia The inability to identify objects by touch.

frame of reference The coordinate system used to define locations in space.

egocenter The center of a reference frame used to represent locations relative to the body.

(*a*) Top view

(*b*) Front view

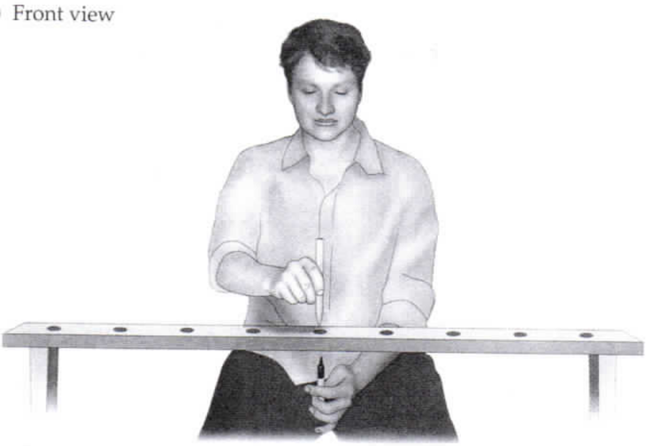


FIGURE 12.22 Locating the haptic egocenter. One hand places a stylus on the target on the upper table surface, and the other hand attempts to match up underneath the table in the corresponding location. (After Haggard et al., 2000.)

dle of your head (between your two ears). One way to get at your haptic egocenter is to place your left index finger on top of the edge of a desk or table, close your eyes, and try to match this location by placing your right index finger on the bottom of the desk (Figure 12.22). If you do this many times, you may find that you consistently err to the left. Conversely, if you try to match the location of your right index finger with your left, you will be more likely to err to the right.

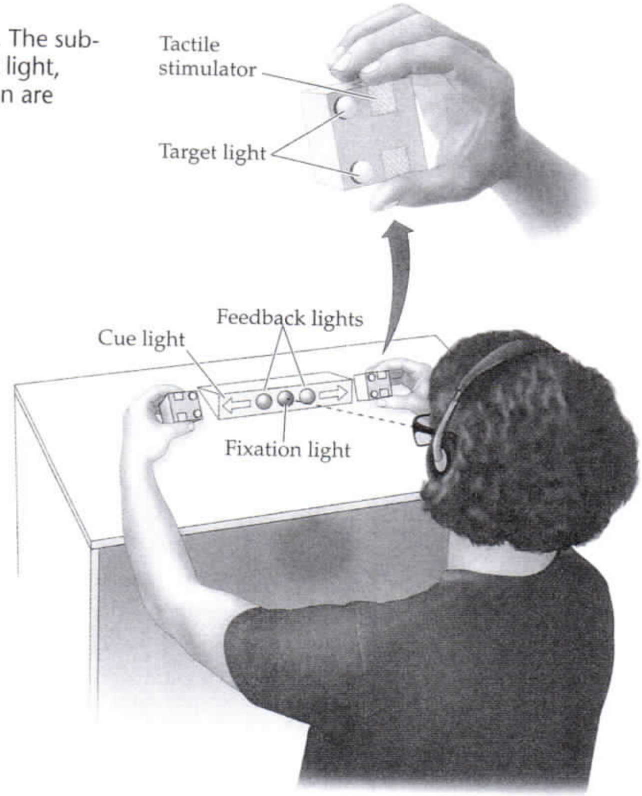
A careful analysis of errors in a task of this type led Haggard et al. (2000) to conclude that there is, in fact, no single fixed frame of reference for the haptic perception of locations. In the case of the index finger reaching task, your egocenter appears to be located at the shoulder of the arm doing the reaching. In other tasks, the egocenter may move to other positions on your body.

Interactions between Touch and Other Modalities

Touch does not occur only in the absence of other sensory input, of course. We commonly touch objects that we see, and we hear the consequences of contact. How does the perceptual system as a whole deal with signals from multiple modalities? Sometimes they compete, and sometimes the whole is an integrated combination of the different inputs.

Competition can arise when resources are limited—that is, when attention comes into play in a particular task. When people anticipate being touched in a particular location, they can direct attention to that location. In one study (Spence, Pavani, and Driver, 2000), participants were asked to indicate whether a sustained force or a series of pulses was delivered to a fingertip (Figure 12.23).

FIGURE 12.23 Studying competition between sensory modalities. The subject holds a cube in each hand that has a vibrotactile stimulator and a light, either of which can signal the required response. The arrows at fixation are used to direct attention. (After Spence, Pavani, and Driver, 2000.)



The stimulated fingertip could be on the left or the right hand. A visual precue, in the form of an arrow, predicted which hand would receive the stimulation. If people could make use of this precue to direct attention to the predicted hand, it was expected that they would be faster at deciding whether the stimulus was sustained or pulsed. And indeed, this was the case: the precue sped up responses relative to a no-cue control. Occasionally, however, the precue directed the participant's attention to the wrong hand, and on such trials, people responded more slowly than in the no-cue condition. This is exactly analogous to attentional cueing effects in vision and audition.

Thus we see that haptic attention, like visual and auditory attention, is a limited resource that must be allocated in one way or another. Do the different modalities compete with each other for attentional resources as well? Consider the fact that the pressure stimulus of your posterior on your seat seems to have lost out to this visual text in the current competition for your attention (until just now, that is). In the lab, Spence, Nicholls, and Driver (2001) did a cross-modal version of the same sort of cueing experiment that was described in the previous paragraph: They led participants to expect a stimulus to be presented via one modality and then sometimes presented it in a different modality. The participants were instructed to indicate with a foot pedal whether a target stimulus appeared on their left or right side. The stimulus could be noise from a loudspeaker (audition), a red circle at the location of the loudspeaker (vision), or a rod pressing the finger while it touched the loudspeaker (touch), and a cue could direct attention toward any of the three modalities. Again, responses were faster when the cue was valid and slower when it was invalid.

Interestingly, the greatest cost for an invalid cue occurred when observers expected a tactile stimulus but a visual or auditory stimulus was presented instead. This result may imply that the sense of touch has a particularly restricted attentional channel—that once attention is focused on the touch modality, it is relatively difficult to reallocate it. Or it may be that visual and auditory attention could be shared to some extent because expectancies in those modalities could be directed to a common location in external space, whereas the expectancy for touch was directed to a location on the body.

In contrast to attentional competition, intersensory integration can occur when different modalities receive information about the same object. Suppose, for example, you are touching sandpaper. The roughness you feel also depends on the roughness you see. Lederman, Thorne, and Jones (1986) found that when people saw and felt different sandpaper surfaces and they were asked about how closely packed the elements in the surface were, they were more strongly influenced by vision. When they were asked about the roughness of the surface, however, touch became more important and vision less important.

In some circumstances, one modality may appear to dominate. In a classic study pitting vision against touch, Rock and Victor (1964) had people grasp a square while looking at it through a distorting lens. What these participants felt was pretty much what they saw: a rectangle. But dominance by one modality over the other is not the rule. A more general model is that people integrate the signals from two modalities, producing a weighted average. That is, they use x percent of the information from one modality and $(100 - x)$ percent from the other. The relative weighting reflects the quality of the signal from each modality. Ernst and Banks (2002) demonstrated such integration with an apparatus that created virtual touch and sight of the same surface simultaneously. The surface consisted of two planes connected by a step (Figure 12.24). The

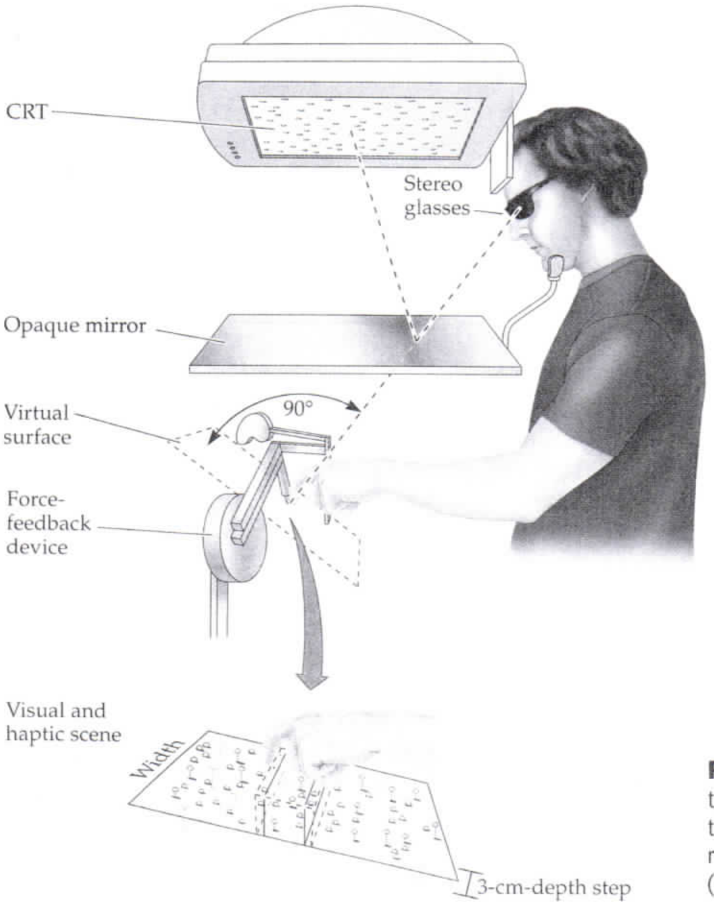


FIGURE 12.24 Testing the integration of sensory modalities. The observer could see a virtual surface of raised dots through stereo goggles and could touch the virtual surface and receive resisting forces consistent with the surface height. (After Ernst and Banks, 2002.)

Tadoma Method by which people who are both deaf and blind can perceive speech using their hands.

visual step was created with stereo glasses, and the touched step was created with a device that generated forces on the hand, pushing back whenever contact was made with the simulated surface. When discrepant step sizes were presented to the two modalities, the perceived depth of the step was a weighted compromise between them. When the investigators made the information from vision less reliable by randomly changing the apparent depth of some of the surface elements, the weight assigned to touch increased, and it had a greater role in determining the perceived depth.

Virtual Haptic Environments

The experiment by Ernst and Banks just described uses a virtual haptic environment. Anyone who has played a video game has been in a virtual environment. The actions of the player (e.g., button presses or joystick movements) are sensed by the machine and filtered through a program that creates a simulated world, causing new events and outcomes that are fed back to the user through vision and audition. Although some joysticks employ crude vibration, what is missing from most of these environments at present is haptic feedback. However, interfaces have recently been developed that provide such feedback in the form of vibration or sustained forces to the hand.

Imagine yourself, for example, exploring the inside of a box in a virtual haptic environment. The environment has been programmed so that some locations within it are assigned to walls of the box. These locations simulate rigid surfaces with material properties such as coefficients of friction. You grasp a handle and move your hand, which causes motion of a probe in the simulated environment. When the probe reaches the location that has been assigned to a wall, you encounter resisting forces on the handle, which depend on variables such as your angle and speed of approach to the wall. This example is very simple; devices in use today are also capable of creating diverse objects varying in shape, size, surface texture, and softness.

There are many applications other than video games for which haptic virtual environments would be useful. One such application is training physicians for minimally invasive surgery, where the surgeon manipulates an implement inserted into the body through a small incision while viewing the surgical site on a video display. In a virtual haptic training environment, the patient's body is replaced by a dummy, and the surgical tool connects to a computer that tracks the trainee's movements. The computer contains a simulation of the patient that describes body structures and their properties such as slipperiness and softness. As the computer tracks the surgeon's actions with the tool, it determines the effect they would have on the simulated patient, and it generates high-precision graphics and forces to feed back to the surgeon. Such systems are currently under development. Commerce on the Internet is another potential domain for force-feedback devices, which could allow products to be felt as well as seen.

One form of low-tech haptic interface that has been around for some time is the **Tadoma** method of speech perception for deaf and blind people (named after its first known American practitioners, Tad Chapman and Oma Simpson). In this method, the haptic listener spreads the fingers of one hand across the speaker's lips, jaw, and throat (Figure 12.25). Movements and vibrations of the speaker's speech apparatus provide inputs to the cutaneous and kinesthetic components of the recipient's haptic system, and these signals can be translated by a skilled recipient into spoken words. The existence of Tadoma has inspired researchers to develop a virtual display that could transmit information analogous to that from the speaker's vibrating bone and moving jaw

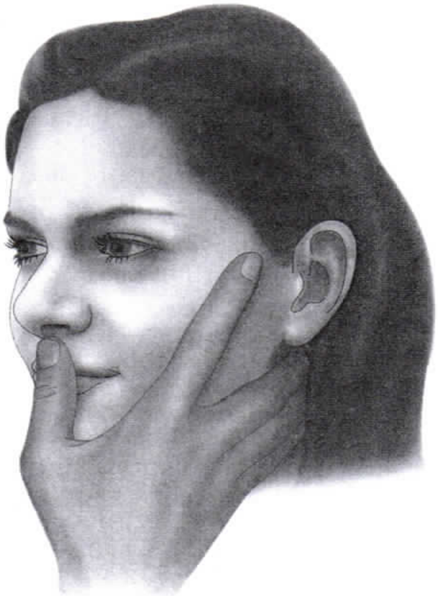


FIGURE 12.25 The Tadoma method for conveying speech to the blind and deaf. (After Goldstein, 2002.)

delivered to the perceiver's hand. This device is called the Tactuator (Tan et al., 1999). Eventually such devices might translate recorded speech to the hand of a deaf-blind user, an outcome made possible by understanding the capabilities and limitations of touch.

Summary

1. The sense of touch produces a number of distinct sensory experiences, each mediated by its own sensory receptor system(s). Touch sensors are responsive not only to pressure, but also to vibration, temperature, and noxious stimulation. The kinesthetic system, which also contributes to our sense of touch, is further involved in sensing limb position and the movement of our limbs in space.
2. The skin is the largest sensory organ, covering the entire exterior surface of the body. Four classes of pressure-sensitive (mechano-) receptors have been found within the skin. The organs used to sense limb position and movement (namely, our muscles, tendons, and joints) are more deeply situated within the body. Thermoreceptors respond to changes in skin temperature that occur, for example, when we contact objects that are warmer or cooler than our bodies. Nociceptors signal tissue damage (or its potential) and give rise to sensations of pain.
3. The pathways from touch receptors to the brain are complex. Two major pathways have been identified: a fast pathway that carries information from mechanoreceptors, and a slower one that carries thermal and nociceptive information. Only the second pathway synapses when it first enters the spinal cord. These pathways project to the thalamus and from there to the primary somatosensory area, located in the parietal lobe just behind the central sulcus. This area contains several somatotopically organized subregions, in which adjacent areas of the body project to adjacent areas of the brain.
4. Downward pathways from the brain play an important role in the perception of pain. According to the gate control theory, signals along these pathways interact at the spinal cord with those from the periphery of the body. Such interactions can block the pain signals that would otherwise be sent forward to the brain. The sensation of pain is further moderated by areas in the cortex.
5. Investigators have measured sensitivity to mechanical pressure by applying nylon hairs of different diameters to the skin. They determine spatial acuity of the skin by measuring the two-point touch threshold, and more precisely by discriminating the orientation of gratings applied to the skin. Tactile pressure sensitivity and spatial acuity vary with body site, because of varying concentrations of different types of mechanoreceptors. The minimum depression of the skin needed to feel a stimulus vibrating at a particular rate (frequency) provides a measure of vibration sensitivity.
6. The sense of touch is intimately related to our ability to perform actions. Signals from the mechanoreceptors are necessary for simple actions such as grasping and lifting an object. Conversely, our own movements determine how touch receptors respond and, hence, what properties of the concrete world we can feel. Touch is better adapted to feeling the material properties of objects than it is to feeling their shapes, particularly when an object is large enough to extend beyond the fingertip.
7. Like other sensory modalities, touch gives rise to internal representations of the world, which convey the positions of objects using the body as a spatial reference system. Touch-derived representations are inputs to higher-level functions like allocation of attention and integration with information from other modalities.
8. The psychological study of touch is useful for a number of applications. Virtual environments that transmit forces to the touch receptors can provide a basis for training people to perform remote operations like surgery and perhaps, in the future, will convey the illusion of touched objects over the Internet.

Refer to the ***Sensation and Perception*** website (www.sinauer.com/wolfe) for activities, essays, study questions, and other study aids.