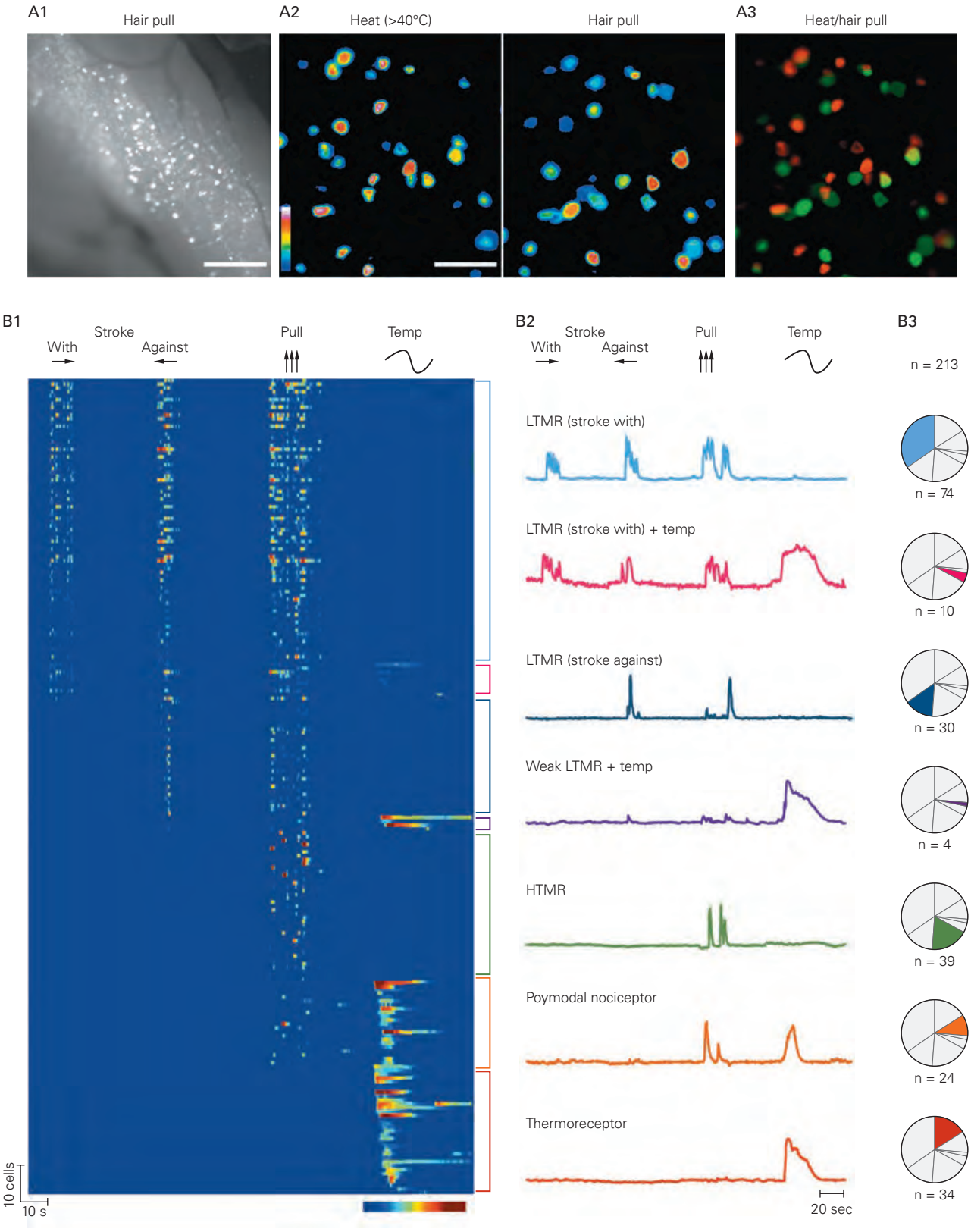
A1
Hair pull
A2
Heat (>40°C)
Hair pull
A3
Heat/hair pull
B1
Stroke
With
Against
Pull
Temp
10 cells
10 s
B2
Stroke
With
Against
Pull
Temp
LTMR (stroke with)
LTMR (stroke with) + temp
LTMR (stroke against)
Weak LTMR + temp
HTMR
Poymodal nociceptor
Thermoreceptor
20 sec
B3
n = 213
n = 74
n = 10
n = 30
n = 4
n = 39
n = 24
n = 34

information from the same region of the body, as well as some tactile information.

Somatosensory information from the limbs and trunk reaches the central nervous system through the 31 spinal nerves, which enter the spinal cord through openings between the vertebrae of the spine. Individual spinal nerves are named for the vertebrae below the foramen through which they pass in cervical nerves or for the foramen above their entry point in thoracic, lumbar, and sacral nerves.

Somatosensory information from the head and neck is transmitted through the trigeminal, facial, glossopharyngeal, and vagus nerves, which enter through openings in the cranium. The trigeminal nerve conveys somatosensory information from the lips, mouth, cornea, and skin on the anterior half of the head, as well as the muscles of mastication. The facial and glossopharyngeal nerves innervate the taste buds of the tongue, the skin of the ear, and some of the skin of the tongue and pharynx. The glossopharyngeal and vagus nerves provide some cutaneous information, but their main sensory role is visceral. Vagal afferents regulating respiration and those regulating gastric motility project to distinct regions of the nucleus of the solitary tract.

Each spinal or cranial nerve receives sensory inputs from a particular region of the body called a *dermatome* (Figure 18–13); the muscles innervated by motor fibers in the corresponding peripheral nerve constitute a *myotome*. These are the skin and muscle regions affected by damage to peripheral nerves. Because the dermatomes overlap, three adjacent spinal nerves often have to be blocked to anesthetize a particular area of skin. The distribution of spinal nerves in the body forms the anatomical basis of the topographic maps of sensory receptors in the brain that underlie our ability to localize specific sensations.

Individual spinal or cranial nerve fibers terminate on neurons in specific zones of the spinal cord gray matter or the medullary dorsal horn (Figure 18–14). The spinal neurons that receive sensory input are either interneurons, which terminate upon other spinal neurons within the same or neighboring segments, or projection neurons, which serve as the cells of origin of major ascending pathways to higher centers in the brain.

The spinal gray matter is subdivided anatomically into 10 laminae (or layers), numbered I to X from dorsal to ventral, based on differences in cell and fiber composition. As a general rule, the largest fibers (Aα) terminate in or near the ventral horn, the medium-size fibers (Aβ) from the skin and muscle terminate in intermediate layers of the dorsal horn, and the smallest fibers (Aδ and C) terminate in the most dorsal portion of the spinal gray matter.

Lamina I consists of a thin layer of neurons capping the dorsal horn of the spinal cord and pars caudalis of the spinal trigeminal nucleus. Individual neurons of lamina I receive monosynaptic inputs from small myelinated fibers (Aδ) or unmyelinated C fibers of a

Figure 18–12 (Opposite) **The distribution of somatosensory modalities among trigeminal ganglion neurons that innervate the hairy skin of the face.** (Adapted, with permission, from Ghitani et al. 2017.)

A. In vivo epifluorescent imaging of a trigeminal ganglion in a TRPV1-GCaMP6f–expressing mouse. Calcium-sensitive dyes (GCaMP6f) fluoresce in response to Ca^{2+} entry through voltage-gated channels in individual trigeminal ganglion neurons. **A1.** Anatomical positions of 213 GCaMP6f-expressing neurons in the trigeminal ganglion of a mouse. Scale bar = 500 µm. These neurons are widely distributed within the trigeminal ganglion. **A2.** Higher magnification images of calcium signals in a subset of neurons that respond to heat pulses >40°C or to hair pull; the color bar in the left image indicates the strength of the calcium signal in each neuron. The strongest activity is shown in **white** or **red**; the weakest response in **blue**. Scale bar = 100 µm. **A3.** An overlay of the two population maps labeled in pseudocolor (**red** for heat, **green** for hair pulling) shows which neurons responded to each stimulus. These neurons were usually selective for heat or hair pull, but two responded to both modalities (**yellow**).

B. Quantification of the responses of all TRPV1-expressing neurons visualized in this trigeminal ganglion to various modes of tactile, noxious, and thermal stimuli. **B1.** Heatmap of the simultaneously recorded responses of all 213 labeled neurons to stroking the cheek, noxious mechanical (hair pull), and thermal stimuli. Each row illustrates the response of an individual neuron to these stimuli; the pixel color indicates the strength of each neuron's response (Δf/F). (Color range = 10%–60% Δf/F.) Neuronal responses are ordered vertically by the temporal onset of increased firing rates. The symbols above the heat map indicate the type and sequence of stimulation: stroking the cheek **with** or **against** the direction of hair growth, hair pull, and thermal stimuli ranging from 25°C to 47°C to 12°C. Although more than half of these neurons responded to gentle touch (stroking), they generally responded more vigorously to noxious mechanical stimuli (hair pull) than to stroking the skin. The strongest responses were observed to noxious heat, but such neurons composed only 30% of the population studied. At the end of the experiment, records from each neuron were sorted into one of the seven response categories identified in B2. **B2.** Averaged response amplitude and time course of Ca^{2+} signals for the seven categories of trigeminal sensory responses. Note the polymodal nature of responses using this objective mode of neuronal classification. (Abbreviations: **LTMR**, low-threshold mechanoreceptor; **HTMR**, high-threshold nociceptor-mechanoreceptor.) **B3.** Pie charts illustrate the number and fraction of neurons in each category.

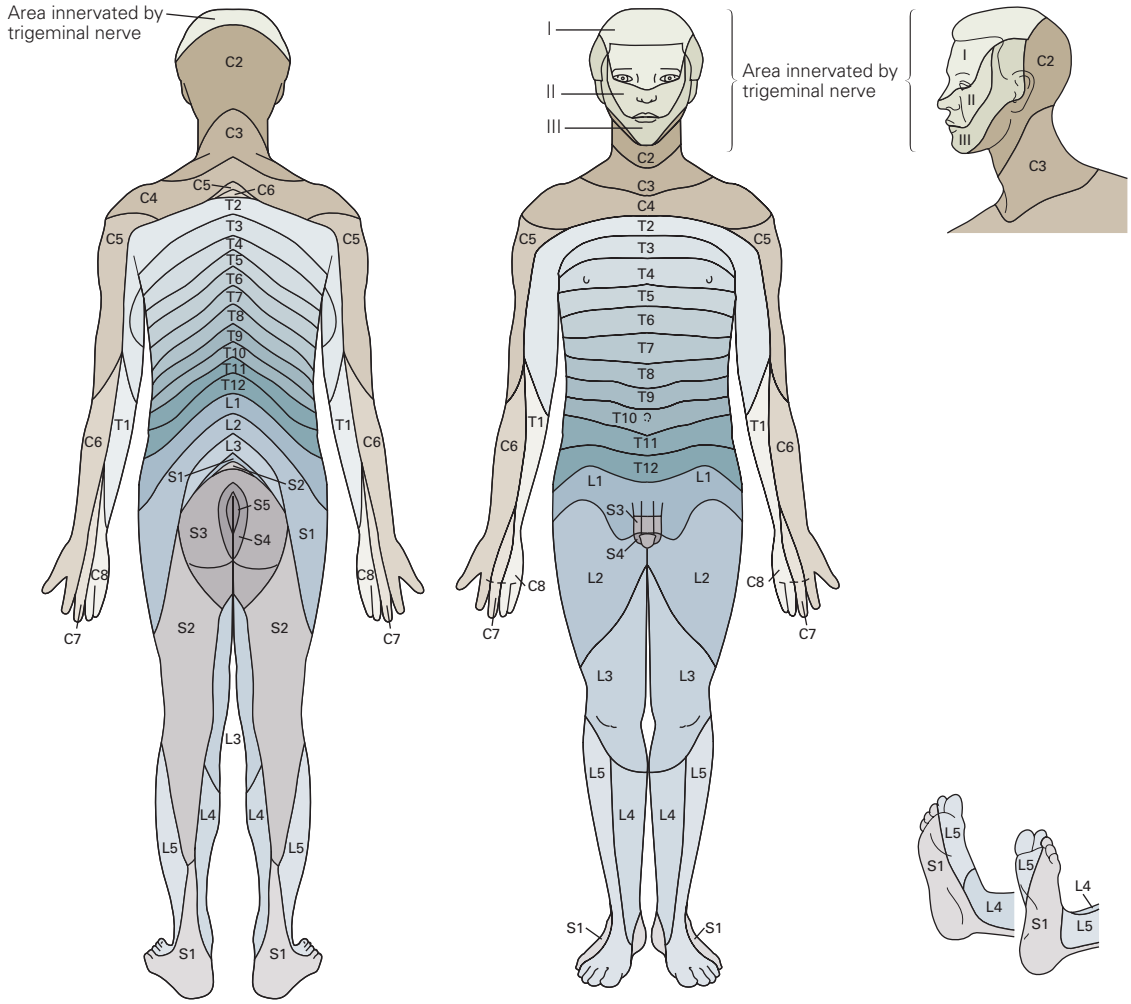

Figure 18–13 The distribution of dermatomes in the spinal cord and brain stem. A dermatome is the area of skin and deeper tissues innervated by a single dorsal root or branch of the trigeminal nerve. The dermatomes of the 31 pairs of dorsal root nerves are projected onto the surface of the body and labeled by the foramen through which each nerve enters the spinal cord. The 8 cervical (C), 12 thoracic (T), 5 lumbar (L), 5 sacral (S), and single coccygeal roots are numbered rostrocaudally for each division of the vertebral column. The facial skin, cornea, scalp, dura, and intraoral regions are innervated by the ophthalmic (I), maxillary (II), and mandibular (III) divisions of the trigeminal nerve (cranial nerve V). Level C1 has no dorsal root, only a ventral (or motor) root. Dermatome maps provide an important diagnostic tool for localizing the site of injury to the spinal cord and dorsal roots. However, the boundaries of the dermatomes are less distinct than shown here because the axons comprising a dorsal root originate from several different peripheral nerves, and each peripheral nerve contributes fibers to several adjacent dorsal roots.

single type (Figure 18–14) and therefore transmit information about noxious, thermal, or visceral stimuli. Inputs from warm, cold, itch, and pain receptors have been identified in lamina I, and some neurons have unique cellular morphologies that correlate with sensory modalities. Lamina I neurons generally have small receptive fields localized to one dermatome.

Neurons in lamina II are interneurons that receive inputs from Aδ and C fibers and make excitatory or inhibitory connections to neurons in laminae I, IV, and V that project to higher brain centers. The more superficial portion of lamina II receives input from peptidergic nociceptors that release substance P or CGRP together with glutamate at their central synapses. Fibers terminating in the deeper part of lamina II are purinergic; they release ATP at their central synapses and express the lectin IB4. Co-transmitters such as ATP provide useful immunostaining markers for identifying specific classes of sensory nerve fibers (Figure 18–2C,D).

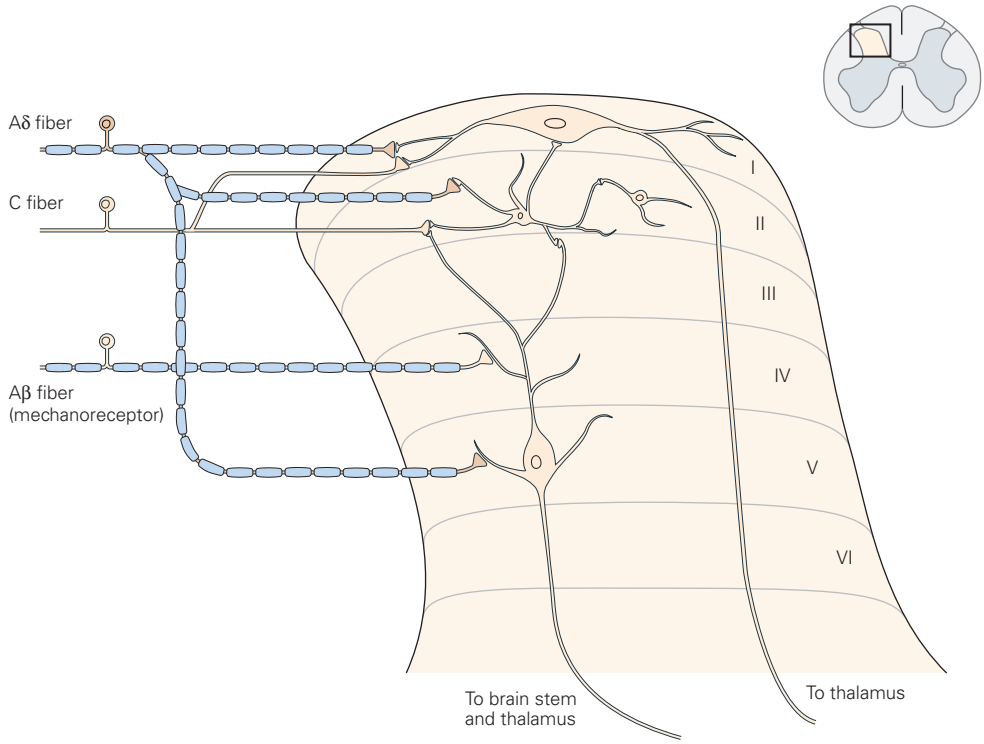

Figure 18–14 Touch and pain fiber projections to the spinal cord dorsal horn. The spinal gray matter in the dorsal horn and intermediate zone of the spinal cord is divided into six layers of cells (laminae I–VI), each with functionally distinct populations of neurons. Neurons in the marginal zone (lamina I) and in lamina II receive nociceptive or thermal inputs from receptors innervated by Aδ or C fibers. The zone for inputs from low-threshold mechanoreceptors (LTMR) is located below lamina II and spans laminae III to V, with the smallest fibers (C-LTMRs) located dorsally, and the largest fibers (Aβ LTMRs) terminating ventrally. LTMRs innervating a particular patch of skin are aligned to form a narrow cell column in the spinal dorsal horn, terminating on spinal interneurons or on projection neurons that send their axons to the brain stem. The medial-lateral arrangement of spinal nerves in the dorsal horn provides a somatotopic representation of adjacent skin areas in the body. The spinal nerve projections of Aβ LTMRs extend to multiple spinal segments along the rostrocaudal axis, whereas those of Aδ or C fibers are more localized to the immediate entry segment (not shown). Aβ LTMRs also send branches to the dorsal column nuclei in the brain stem (Chapters 19 and 20).

Neurons in laminae III to V are the main targets of LTMRs, particularly the large myelinated sensory (Aβ) fibers from cutaneous mechanoreceptors (Figure 18–14). Spinal cord circuits of the dorsal horn have been characterized anatomically and functionally by Victoria Abraira and David Ginty. These local spinal networks enable sensory integration of multiple modalities within a local zone of the body, enabling motoneuron pools to react rapidly to local sensory feedback. Large-diameter fibers mediating touch (Aβ) or proprioception (Aα) also send ascending branches to the medulla through the dorsal columns or dorsolateral funiculi.

Additionally, neurons of the cerebral cortex project to the dorsal horn, permitting direct cortical regulation of local sensorimotor circuits and thus coordinating purposeful behaviors. These higher-order, top-down pathways are supplemented by intraspinal circuits between dermatomes that enable coordinated movements of different fingers or distal and proximal joints.

Neurons in lamina V typically respond to more than one modality—low-threshold mechanical stimuli, visceral stimuli, or noxious stimuli—and are therefore named *wide-dynamic-range neurons*.

Many of the dorsal horn circuits also transmit somatosensory information directly to higher structures in the brain stem, such as the dorsal column, parabrachial, and raphe nuclei, and to the cerebellum or various thalamic nuclei.

Afferent C fibers from the viscera have widespread projections in the spinal cord that terminate ipsilaterally in laminae I, II, V, and X; some also cross the midline and terminate in lamina V and X of the contralateral gray matter. The extensive spinal distribution of visceral C fibers appears to be responsible for the poor localization of visceral pain sensations.

Afferent fibers from the pelvic viscera make important connections to cells in the central gray matter (lamina X) of spinal segments L5 and S1. Lamina X neurons in turn project their axons along the midline of the dorsal columns to the nucleus gracilis in a postsynaptic dorsal column pathway for visceral pain.

Primary afferent fibers that terminate in the deepest laminae in the ventral horn provide sensory information from proprioceptors (muscle spindles and Golgi tendon organs) that is required for somatic motor control, such as spinal reflexes (Chapter 32).

Somatosensory information is conveyed by several ascending pathways to higher centers in the brain, particularly the thalamus and cerebral cortex. The dorsal column–medial lemniscal system transmits tactile and proprioceptive information to the thalamus (Chapter 19), and the spinothalamic (anterolateral) tract conveys pain and thermal information to the midbrain parabrachial nucleus or to the thalamus (Chapter 20). A third pathway, the dorsolateral tract, conveys somatosensory information from the lower half of the body to the cerebellum. The anatomical and functional roles of these networks are described in detail in later chapters.

Highlights

1. The bodily senses mediate a wide range of experiences that are important for normal bodily function and for survival. Although diverse, they share common pathways and common principles of organization. The most important of those principles is *specificity*: Each of the bodily senses arises from specific types of receptors distributed throughout the body.
2. Dorsal root ganglion (DRG) neurons are the sensory receptor cells of the somatosensory system. The functional role of an individual DRG neuron is determined by the sensory receptor molecules expressed in its distal terminals in the body. Mechanoreceptors are sensitive to specific aspects of local tissue distortion, thermoreceptors to particular temperature ranges and shifts in temperature, and chemoreceptors to particular molecular structures. Recordings of physiological responses from these neurons reveal the cellular and molecular mechanisms underlying the senses of touch, pain, temperature, and proprioception, as well as visceral senses.
3. Mechanosensation is mediated by Piezo2 proteins that form ion channels in the axon terminals of DRG fibers sensitive to compression or stretch. These include touch fibers that innervate hair follicles or specialized epithelia such as Merkel cells, Meissner and Pacinian corpuscles, or Ruffini endings. Muscle stretch is signaled by intramuscular spindle receptors and contractile force by Golgi tendon organs. These receptors transmit sensory information via rapidly conducting Aα and Aβ peripheral nerve fibers.
4. Thermoreceptors are excited by transient receptor potential (TRP) ion channels in the axon terminals that are gated in response to local temperature gradients and respond selectively to particular ranges of temperature: cold, cool, warm, or hot. Chemoreceptors change their conductance when binding specific chemicals, both natural and exogenous, giving rise to sensations of pain, itch, or visceral function. Thermosensory and chemosensory information is conveyed centrally via Aδ and C fiber pathways.
5. Activation of somatosensory receptors produces local depolarization of the distal nerve terminals, called the *receptor potential*, whose amplitude is proportional to the strength of the stimulus. Receptor potentials are converted near the distal nerve terminals to trains of action potentials whose frequency is linked to the strength of the stimulus, much as synaptic potentials at synapses produce complex firing patterns in postsynaptic neurons.
6. Individual DRG neurons have multiple sensory endings in the skin, muscle, or viscera, forming complex receptive fields with overlapping territories. The combination of divergent distal terminals and innervation of sense organs by multiple axons enables redundant, parallel pathways for information transmission to the brain.
7. The information transmitted from each type of somatosensory receptor in a particular part of the body is conveyed in discrete pathways to the spinal cord or brain stem by the axons of DRG neurons with cell bodies that generally lie in ganglia close to the point of entry. The axons are gathered together in peripheral nerves. Axon diameter and myelination, both of which determine the speed of action potential conduction, vary in different sensory pathways according to the need for rapid signaling.
8. When DRG axons enter the central nervous system, they separate to terminate in distinct layers of the spinal cord gray matter and/or project directly to higher centers in the brain stem. These circuits form the foundation of five separate sensory pathways with different properties. In three of those systems (the medial lemniscal, lamina I

spinothalamic, and solitary tract systems), the pathways for submodalities appear to be segregated until they reach the cerebral cortex.

9. Future studies of the peripheral nervous system will likely engage high-resolution optical methods for identification of specific receptor classes in the DRG that are labeled with genetic markers. Functional studies of these neurons will also employ optical imaging of entire sensory ganglia labeled with voltage-sensitive or calcium-sensitive fluorescent dyes that enable quantitative temporal monitoring of ensemble responses to specific somatosensory modalities. These receptor neurons will thereby be studied as identified physiological populations rather than one at a time in isolation.

Esther P. Gardner

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19

Touch

In this chapter on the sense of touch, we focus on the hand because of its importance for this modality, in particular its role in the appreciation of object properties and in performance of skilled motor tasks. The human hand is one of evolution's great creations. The fine manipulative capacity provided by our fingers is possible because of their fine sensory capacity; if we lose tactile sensation in our fingers, we lose manual dexterity.

The softness and compliance of the glabrous skin play a major role in the sense of touch. When an object contacts the hand, the skin conforms to its contours, forming a mirror image of the object's surface. The resultant displacement and indentation of the skin stretches the tissue, thereby stimulating the sensory endings of mechanoreceptors at or near the region of contact.

These receptors are highly sensitive and are continually active as we manipulate objects and explore the world with our hands. They provide information to the brain about the object's position in the hand, its shape and surface texture, the amount of force applied at the contact points, and how these features change over time when the hand or the object moves. The fingertips are among the most densely innervated parts of the body, providing extensive and redundant somatosensory information about objects manipulated by the hand.

Moreover, the anatomical structure of the hand, with its multiple joints and apposable digits, enables humans to shape the hand in ways that mirror an object's overall shape, providing a hand-centered proprioceptive representation of the external world. This ability to internalize the shape of objects allows us to create tools that extend the abilities of our hands alone.

When we become skilled in the use of a tool, such as a scalpel or a pair of scissors, we feel conditions at

the working surface of the tool as though our fingers were there because two groups of touch receptors monitor the vibrations and forces produced by those distant conditions. When we scan our fingers across a surface, we feel its form and texture because another group of mechanoreceptors has high spatial and temporal acuity. A blind person uses this capacity to read Braille at a hundred words per minute. When we grip and manipulate an object, we do so delicately, with only as much force as needed, because specific mechanoreceptors continually monitor slip and adjust our grip appropriately.

We are also able to recognize objects placed in the hand from touch alone. When we are handed a baseball, we recognize it instantly without having to look at it because of its shape, size, weight, density, and texture. We do not have to think about the information provided by each finger to deduce that the object must be a baseball; the information flows to memory and instantly matches previously stored representations of baseballs. Even if we have never previously handled a baseball, we perceive it as a single object, not as a collection of discrete features. The somatosensory pathways of the brain have the daunting task of integrating information from thousands of sensors in each hand and transforming it to a form suitable for cognition and action.

Sensory information is extracted for the purpose of motor control as well as cognition, and different kinds of information are extracted for those purposes. We can, for example, shift our attention from the baseball's shape to its location in the hand to readjust our grip for an effective throw or pitch. This selective attention to different aspects of the sensory information is brought about by cortical mechanisms.

Active and Passive Touch Have Distinct Goals

Touch is defined as direct contact between two physical bodies. In neuroscience, touch refers to the special sense by which contact with the body is perceived consciously. Touch can be active, as when you move your hand or some other part of the body against another surface, or passive, as when someone or something else touches you. Active touch is fundamentally a top-down process in which the subject has agency, seeks particular information, and controls what occurs. Subjects select relevant salient features of objects to determine subsequent behaviors. They choose which object to grasp and the most efficient hand shape needed to acquire it, and decide how to manipulate it to achieve particular goals. During active touch, somatosensory information depicts the physical properties of objects as well as the motor actions of the subject's hand and arm, and their relation to the task goals. Importantly, active manipulation of objects is based upon the concept of touch as a three-dimensional modality designed to capture the volumetric, topographic, and elastic properties of objects, as first proposed by Roberta Klatzky and Susan Lederman. These three-dimensional qualities are best appreciated by active manipulation including grasping, rotation, and contour tracing by the hand.

Passive touch engages a bottom-up process in which subjects react to external stimuli specified by the experimenter or clinician. The experimenter selects and controls the location, amplitude, force, timing, duration, and spatial spread of stimuli delivered to the skin. Subsequent behaviors are guided by instructions provided in the paradigm. Tactile stimuli are classified into experimenter-selected categories and/or rated along an intensive or hedonic scale. Subjects therefore need to analyze all of the transmitted somatosensory information and select specific features guided in part by the task instructions.

Active and passive modes of tactile stimulation excite the same population of receptors in the skin and evoke similar responses in afferent fibers. They differ somewhat in cognitive features that reflect attention and behavioral goals during the period of stimulation. Passive touch is tested by naming objects or describing sensations; active touch is used when the hand manipulates objects. The sensory and motor components of touch are intimately connected anatomically in the brain and are important functionally in guiding motor behavior.

During active touch, descending fibers from motor centers of the cerebral cortex terminate on interneurons in the medial dorsal horn that receive tactile information from the skin. Similar fibers from cortical motor areas terminate in the dorsal column nuclei, providing an *efference copy* (or corollary discharge) of the motor commands that generate behavior (Chapter 30). In this manner, tactile signals from the hand resulting from active hand movements may be distinguished centrally from passively applied stimuli in the neurological exam or in psychophysical tests.

The distinction between active and passive touch is important clinically when patients have deficits in hand use. Motor deficits such as weakness, stiffness, or clumsiness may result from sensory loss, which is why passive sensory testing is important in the neurological examination. Common neurological tests for touch include measurements of detection thresholds, vibration sense, two-point or texture discrimination, and