Touch

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Touch is defined as direct contact between two physical bodies. In neuroscience, touch describes the special sense by which contact with the body is perceived in the conscious mind. Touch allows us to recognise objects held in the hand, and use them as tools. Because the skin is elastic, it forms a mirror image of object contours, allowing us to perceive their size, shape and texture. Four classes of mechanoreceptors inform the brain about the form, weight, motion, vibration and hand posture that define each object. Parallel messages from ∼20 000 nerve fibres are integrated by neurons in the cerebral cortex that detect specific object classes. Some touch involves active movement – stroking, tapping or pressing – whereby a limb is moved against another surface. The sensory and motor components of touch are connected anatomically in the brain, and are important functionally in guiding skilled behaviours.

Tactile Experience: Vibration, Touch, Pressure and Pain

Our human sense of touch is most highly developed in the hand where it serves a cognitive function when experiencing objects in the world, and guides the skilled movements of the surgeon, the sculptor and the musician. Tactile information teaches us the physical properties of objects, allowing us to identify them even in the dark (Klatzky *et al.*,

1985). Sensory receptors in the skin provide information to the brain about the size and shape of objects held in the hand. These receptors allow us to perceive whether objects appear hard or soft, smooth or rough in texture, heavy or light in weight, hot, cold or neutral in temperature and whether the overall sensation produces pain or pleasure (Johnson and Hsiao, 1992). **See also**: Proprioceptive Sensory Feedback; Sensory Systems in Vertebrates: General Overview

The tactile sense is one of the several submodalities of the somatic sensory system – the sense of one's own body. When the body is contacted by an external stimulus, its surface is indented or stretched because the skin is flexible rather than rigid. The mechanical deformation is detected by receptors that signal where contact is made, the amount of force that is exerted and the speed of motion against the surface. Contact is experienced as light touch or pressure, or even pain, depending on how much force is exerted. When the stimulus moves on the skin, touch is perceived as stroking, tapping or vibration.

Sensations of touch are often accompanied by temperature sensations of warmth or cold, or by painful or itching sensations, because the receptors for touch are intermixed in the skin with other sense organs that detect thermal energy or chemicals released by tissue damage or applied to the skin. We experience these as distinct sensory modalities because the information is processed by different sets of neurons in the central nervous system, and conveyed to the cerebral cortex in separate anatomical pathways. **See also**: Pain and Analgesia; Somatosensory Systems
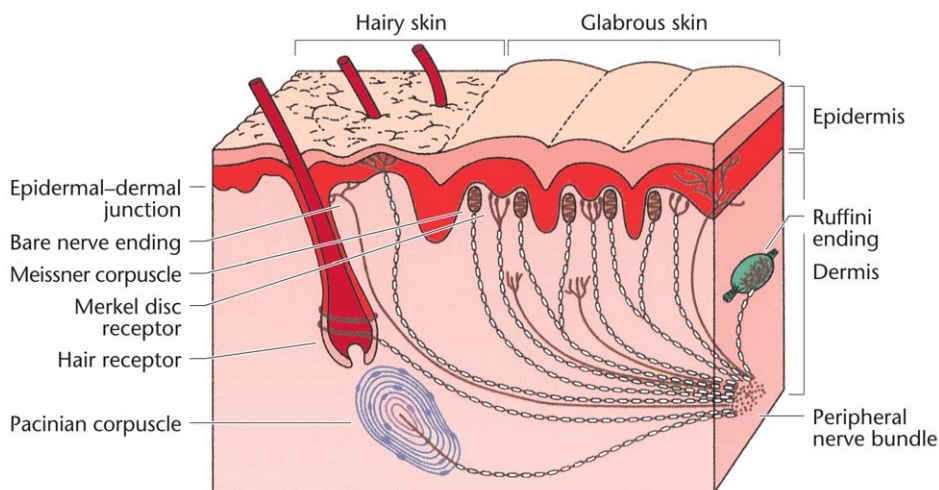
Primary Afferent Terminals Specialised for the Transduction of Tactile Information

The neurobiological processes that underlie sensations of touch begin with the sensory transduction mechanisms by

Figure 1 Cross-section of the skin showing the major classes of cutaneous mechanoreceptors. Modified from Gardner *et al.* (2000). Used with the permission of the McGraw-Hill Companies.

which physical deformation of the skin is transformed into electrical signals. The intensity of contact force and speed of motion are detected by special sense organs in the skin called mechanoreceptors, so called because they detect mechanical energy applied to the skin. The elasticity of the skin enables these receptors to detect the shape, texture and pressure exerted by the object because the skin can conform to the contours of the object, forming a mirror image of its shape. This information is translated into a pulse (action potential) code that is conveyed to the central nervous system by the peripheral nerves. **See also**: Action Potentials: Generation and Propagation; Sensory Transduction Mechanisms

The mechanoreceptors of the skin, like other somatic sense organs, comprise the distal terminals of the dorsal root ganglion neurons or trigeminal sensory neurons. Trigeminal sensory neurons innervate the face and head; the dorsal root ganglion neurons innervate the other parts of the body. These sensory neurons, called primary afferents, have three major components: (1) a cell body that lies in a ganglion on the dorsal root of a spinal or trigeminal nerve, (2) a peripheral branch that terminates in a specialised receptor ending and (3) a central branch that projects to the central nervous system. Primary afferent fibres originating in specific regions of the body are gathered in small bundles or fascicles that join to form the peripheral nerves. They enter the central nervous system through the dorsal roots or the sensory branches of the fifth cranial nerve. **See also**: Vertebrate Peripheral Nervous System
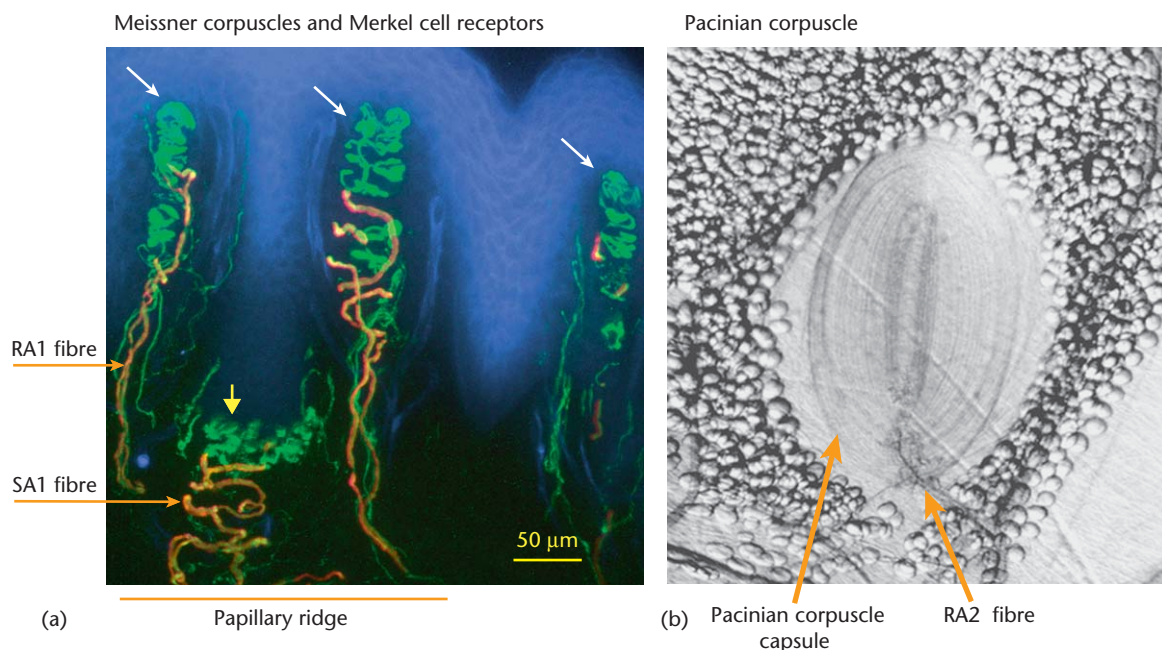
Types of mechanoreceptors in the skin

Individual primary afferent fibres respond selectively to specific types of stimuli because of morphological and molecular specialisation of their peripheral terminals. Unlike other sensory afferents in the skin, mechanoreceptors have a non-neural capsule that surrounds the distal endings. Some of the primary afferent fibres branch and have separate capsular receptors on each ending; others have a single large capsule that surrounds the entire nerve terminal. The capsular structures link the nerve terminal to the surface of the body, and therefore play a crucial role in transducing the tissue deformation that occurs when something contacts the skin. Although the sensitivity of the receptors to mechanical displacement is a property of ionic channels in the nerve terminal membrane, their response to touch is also shaped by the capsule.

Several major classes of mechanoreceptors have been identified in the human body (**Figure 1**). The principal touch receptors in the glabrous (hairless) skin of the lips, palm, fingers and sole of the foot are the Meissner corpuscle and the Merkel cell–neurite complex (Johansson and Flanagan, 2009; Johansson and Vallbo, 1983). These receptors are located close to the surface of the skin, at precise locations in the papillary ridges that form the fingerprint patterns. The anatomical arrangement of these receptors in the fingertip skin provides a precise grid for detection of spatial features such as Braille dots. The hairy skin of the hand dorsum and the other parts of the body senses touch with hair follicle afferents, field receptors and Merkel cells. Touch is also detected in both the skin types by Pacinian corpuscles and Ruffini endings in the subcutaneous tissue. **See also**: Skin: Immunological Defence Mechanisms

The human hand is richly endowed with these sensors (Johansson and Vallbo, 1983). Each hand has approximately 150 000 mechanoreceptors which are connected to the central nervous system by 30 000 primary afferent fibres. The density of these receptors is highest on the fingertips (2 500 per cm^2). Each fingertip is innervated by 250–300 mechanoreceptive fibres. This large number of nerves confers fine tactual acuity to the fingertips, enabling them to read Braille and to discriminate surface texture. **See also**: Sensors of External Conditions in Vertebrates

Meissner corpuscles and Merkel cell receptors   Pacinian corpuscle

RA1 fibre

SA1 fibre

50 µm

(a)   Papillary ridge

(b)   Pacinian corpuscle   RA2 fibre
      capsule

Figure 2 Images of the principal touch receptors in the skin. (a) Meissner corpuscles and Merkel cells are revealed in immunostained confocal images of a papillary (fingerprint) ridge from the human fingertip. Meissner corpuscles (white arrows) are located below the epidermis (blue) along the lateral borders of each ridge; each corpuscle is innervated by at least two RA1 fibres. SA1 fibres innervate clusters of neighbouring Merkel cells (yellow arrow) in the centre of the ridge, providing localised signals of pressure applied to the finger. The fibres lose their myelin sheaths (red) when entering the receptor capsule exposing broad terminal bulbs (green) where sensory transduction occurs. Photograph courtesy of M Nolano; reproduced with permission from Nolano *et al.* (2003). (b) Photograph of a Pacinian corpuscle (∼1.6 mm in length) located in the mesentery of the abdominal wall. Each Pacinian corpuscle is innervated by a single RA2 fibre. Reproduced courtesy of S Bolanowski from Bell *et al.* (1994).

Mechanoreceptors are specialised for pressure and motion

Morphological specialisation of touch receptors allows them to discriminate the amount of force applied to their receptive field, the speed of motion during stroking or pressing on an object, the fine details of the surface texture, the local curvature in the region of contact and the posture and shape of the hand when an object is grasped. These intensive and temporal properties are reflected in the physiological responses to pressure (Goodwin and Wheat, 2004; Johansson and Flanagan, 2009; Johnson, 2001; Khalsa *et al.*, 1998).

The Meissner corpuscle (**Figure 2a**) is the principal rapidly adapting receptor (RA) in the hand. These receptors respond to initial contact and to motion, but not to steady pressure (Talbot *et al.*, 1968). The capsule is linked by collagen filaments to the lateral edge of the fingerprint ridge, positioning it to sense the tangential shearing forces induced when the hand is moved across a textured surface or over edges (Bolanowski and Pawson, 2003; Iggo and Andres, 1982; Nolano *et al.*, 2003). The surface irregularities are signalled by bursts of action potentials in the sensory nerve innervating the Meissner corpuscle (RA1 fibre) (Connor *et al.*, 1990; Sathian *et al.*, 1989). The Meissner corpuscle also senses motion of an object grasped by the hand when it slips unexpectedly, signalling us to tighten the grip to prevent the object from falling

(Johansson, 1996). Hair follicle afferents and field receptors serve a similar physiological role in hairy skin.

The Merkel cell receptor is the principal slowly adapting (SA) receptor in the hand. It resides at the centre of the fingerprint ridge where skin elasticity is greatest (**Figure 2a**). This small epithelial cell transmits compressive strain to the sensory nerve ending, evoking sustained responses that are proportional to the pressure applied to the skin (Goodwin and Wheat, 2004; Johnson, 2001). Thus, when an object is placed in the hand, the frequency of firing conveys information about its weight; the heavier the object, the higher the firing rate of the Merkel cell afferents (SA1 fibres). Similarly, these receptors sense the grip forces applied by the fingers as an object is enclosed and held by the hand (Johansson, 1996). Because individual Merkel cells are the smallest touch receptors, they also provide high-fidelity information about the spatial structure of objects that is the basis of form and texture perception (Connor *et al.*, 1990; Johnson and Hsiao, 1992; Khalsa *et al.*, 1998; Phillips *et al.*, 1992).

Biophysics of sensory transduction by mechanoreceptors

Indentation or lateral stretch of the skin is believed to excite mechanoreceptors by direct gating of cation channels in the sensory nerve ending. Mechanical stimulation deforms the receptor protein, thus opening stretch-sensitive ion

channels, and increasing Na^+ and Ca^{2+} conductance. The resulting inward current through these channels produces a local depolarisation of the nerve or receptor cell called the *receptor potential*. The amplitude of the receptor potential is proportional to the amount of pressure exerted by the object and how fast it is applied. Removal of the pressure stimulus relieves mechanical stretch on the receptor and allows stretch-sensitive channels to close. Direct activation of mechanoreceptive ion channels permits rapid activation and inactivation as forces are applied to the skin. **See also**: Cell Biophysics; Sodium Channels

The molecular biology of mechanoreception in the mammalian skin is not well understood, primarily because it is difficult to isolate the receptors from other cell types in this tissue. Various mechanisms for mechanotransduction have been proposed in other sensory systems (Christensen and Corey, 2007; Lumpkin and Caterina, 2007). The most widely accepted hypothesis for mechanically gated channels involves structural proteins that link the channel to the surrounding tissue of the skin and to the cytoskeleton. The channel subunits are tied to extracellular matrix elements such as collagen or other filamentous proteins that are stretched by mechanical deformation; these links are often represented as a spring. The intracellular portion of the channel is anchored to the cytoskeleton most likely by actin filaments. Other models propose indirect activation of the ion channel through second-messenger pathways. In the indirect model, the force sensor is a protein in the receptor cell's membrane distinct from the ion channel. Stimulation of these receptors by a mechanical stimulus is conveyed to the ion channel by a variety of intracellular messengers that cause the channel to open or close. **See also**: Cytoskeleton; Extracellular Matrix; Ion Channels

Studies of touch receptors in *Caenorhabditis elegans* suggest that the transduction proteins in mammals may belong to the degenerin/epithelial Na^+ channel (DEG/ENaC) superfamily. Other studies have implicated various transient receptor potential (TRP) cation channels in mechanotransduction (Christensen and Corey, 2007). Mechanosensory channels in individual receptors differ somewhat in their structural linkage to the matrix elements, and these molecular properties modify the channel open times. Thus some mechanoreceptors yield slowly adapting, sustained depolarisation to pressure, whereas others inactivate rapidly. The molecular diversity of gating and adaptation mechanisms is also expressed in the morphology of the capsules surrounding the sensory nerve terminal. **See also**: Receptor Adaptation Mechanisms

Pacinian corpuscle is designed to detect vibration

The role of the non-neural capsule in sensory transduction has been studied extensively in the Pacinian corpuscle, a mechanoreceptor located in subcutaneous tissue and in the mesentery of the abdominal wall (Bell *et al.*, 1994). The Pacinian corpuscle (**Figure 2b**) consists of a 1-mm long, multilamellar, fluid-filled capsule that encloses the sensory ending of a primary afferent fibre. The nerve loses its myelin sheath inside the capsule; its naked endings contain mechanosensory channels sensitive to compression.

When the skin is touched, or a probe is applied experimentally to the capsule, the lamellar structure filters the stimulus so that only rapid displacements are transmitted to the nerve terminal. If the probe is vibrated at frequencies of 200 Hz, the capsule is sufficiently stiff that it cannot change shape as fast as the probe moves. Therefore, all of the lamellae move up and down together in phase with the probe, compressing and decompressing the nerve. Each vibratory cycle evokes a brief depolarising response in the sensory nerve that is sufficiently intense to generate an action potential. However, if the vibratory frequency is slowed to 20 Hz, the displacement is so slow that the upper layers of the capsule are squeezed together, displacing the fluid laterally within the capsule, whereas the bottom layers close to the nerve remain rigid. The nerve is unresponsive to the low-frequency stimulus because the energy is not transmitted by the capsule to the mechanosensory channels.

This physical structure endows the Pacinian corpuscle with exquisite sensitivity to vibration in the range 100–400 Hz (Talbot *et al.*, 1968). It is the most sensitive mechanoreceptor in the body, and can capture signals from a wide area of skin because of its large size. Humans are able to detect vibrations as weak as 1 μm in amplitude when tested at 250 Hz. The hum of motors on a computer disc drive that one perceives with the hand, or the vibrations felt in the concert hall during *forte* passages played by a symphony orchestra, are detected by the Pacinian corpuscles. These receptors can also sense the weak shock waves transmitted to a grasped object when it is placed on a rigid surface and released (Johansson, 1996). This type of sensory feedback is particularly useful in controlling the actions of the hand during skilled movements and when using tools. **See also**: Motor Neurons and Spinal Control of Movement

Receptive fields of mechanoreceptors

Individual Meissner corpuscle and Merkel disc receptors are smaller than a fingerprint ridge. Their morphology enables them to detect displacements localised to the ridge in which they reside. However, the primary afferent fibre that transmits this information to the brain detects touch over a larger region of skin, called its *receptive field*, because it has 10–25 terminals, each enclosed by a Meissner corpuscle or Merkel cell (Johansson and Vallbo, 1983). This arrangement allows the nerve to sample the activity of multiple receptors of the same class, while also resolving fine details.

The receptive field of a mechanosensory neuron labels the tactile information conveyed to the brain with a specific topographic location (**Figure 3**). Thus the brain knows where touch occurs by determining which receptors are activated. The regions of the body that are used most extensively to touch other persons or things – the fingertips
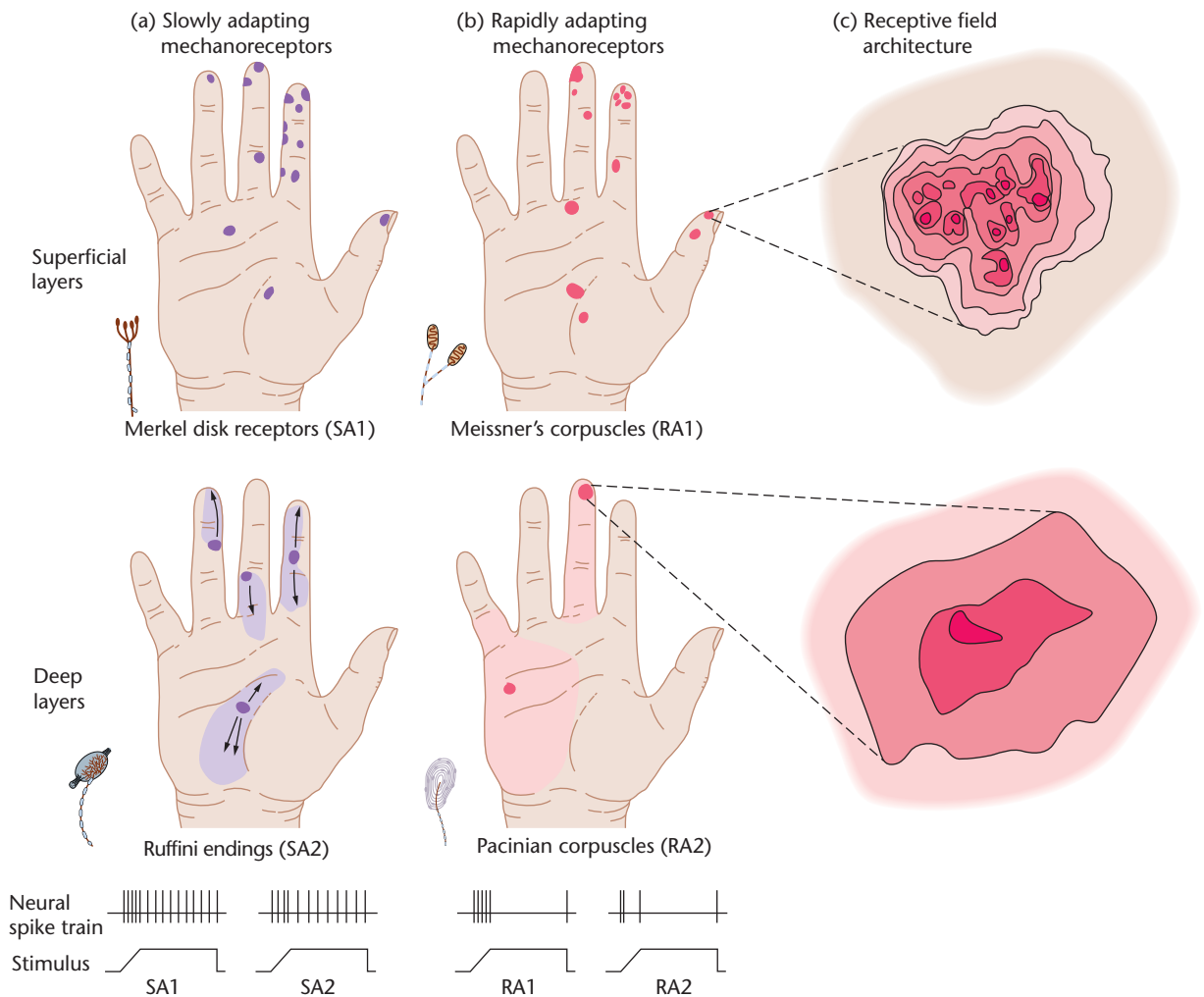
Figure 3 Receptive fields in the human hand mapped with single fibre recordings from the median nerve. Each coloured area on the hands indicates the receptive field of an individual sensory nerve fibre. Receptive fields of Merkel disk receptors and Meissner corpuscles cover spot-like patches of skin on the hand, and are smaller than those of Ruffini endings and Pacinian corpuscles because of differences in receptor cell size. SA1 and RA1 fibres innervate clusters of mechanoreceptors; SA2 and RA2 fibres innervate only one large receptor cell. The neural responses in the lower panels illustrate responses of the four fibre types to steady pressure on the skin. Adapted from Johansson and Vallbo (1983) and reproduced from Gardner and Johnson (In press). Used with the permission of the McGraw-Hill Companies.

and lips – have the largest number of receptor organs in the skin and the smallest receptive fields; the ability to localise touch is highest here. The more proximal regions of the body – the arm, leg and trunk – are less densely innervated and have fewer receptors. These areas have large receptive fields and do not resolve fine spatial details.

The specificity of the spatial information transmitted from each receptor is also essential for perceiving the size, shape and texture of the object. Mechanoreceptors subdivide the object that is touched into small regions and analyse the local curvature profile. The collective activity in the population of stimulated receptors indicates the total area of skin that is touched, and the profile of skin indentation defines the object's shape. The brain must reassemble the individual parts to construct a unified percept of the object.

Organisation of Somatosensory Pathways that Transmit Tactile Information to the Brain

An important principle of sensory information processing is illustrated by touch receptors. The brain analyses sensory information by deconstructing the stimulus into component parts, and sensing local features such as surface curvature or edges. For example, each of the dots that comprise a letter of the Braille alphabet is read by a different set of touch receptors in the fingertip (Phillips *et al.*, 1992). The shape of the entire letter is thus distributed across the population of receptors – bursts of impulses are transmitted in parallel by primary afferent fibres touching each dot, while the other are silent. The signals are brought

together by central processing networks in the brain to reconstruct the complete pattern of dots and perceive it as a single character. This mechanism requires an orderly arrangement of somatosensory neurons such that neighbourhood relations on the body are preserved in the brain. In addition, since sensory information is transmitted to the brain as sequences of nerve impulses, the different submodalities and receptor types must remain segregated so that responses to pressure are not confounded with those signalling motion or temperature.

The sensory information detected by touch receptors is conveyed to the central nervous system along the peripheral nerves together with nerve fibres subserving other somatosensory modalities in the same body segment such as pain, temperature and proprioception (Gardner and Johnson, 2010). Touch fibres enter the spinal cord through the dorsal roots, and ascend through the dorsal columns together with fibres for proprioception to the medulla where they terminate in the dorsal column nuclei (the cuneate and gracile nuclei). The second-order neurons in the dorsal column nuclei send their axons across the midline in the medulla where they ascend in the medial lemniscus to the ventral posterior lateral (VPL) and medial (VPM) nuclei of the thalamus. **See also**: Somatosensory Systems

The ascending somatosensory pathways and processing centres are organised along two orthogonal axes: one topographic and the other functional. One axis displays the topography of the body in what are called somatotopic maps. The somatotopic map of the body is preserved in all the somatosensory areas of the brain, although the details of the body orientation and receptive field topography differ in each representation. The other axis segregates the various somatosensory modalities into functional groups of neurons. Thus receptors for touch and proprioception are grouped into distinct anatomical fascicles and columns of cells. Eventually the modalities converge on to common neurons. This convergence occurs at the highest levels of cortical processing involved in cognition and motor planning, at spinal interneurons involved in reflex pathways and at the motor neurons whose firing patterns govern all behaviour. **See also**: Motor System Organization; Spinal Reflexes; Topographic Maps in the Brain

The somatosensory nuclei of the brainstem and thalamus use convergence of sensory afferents to bring together sensory information from neighbouring skin regions. These inputs mutually reinforce each other, providing the first step in object representation. For example, inputs from groups of receptors aligned along an edge that are stimulated simultaneously will be enhanced by convergence, whereas those aligned across the edge will be less effective because only a few receptors are activated. In addition, inhibitory interneurons in these nuclei suppress weakly stimulated neurons, thereby sharpening the outputs from the most active groups of mechanoreceptors so that the strongest signals are relayed forward. The inhibitory networks also filter noise from random neural activity. Thus the signal transmitted to the cerebral cortex preserves the accurate spatial and intensive information encoded by mechanoreceptors, while integrating these signals to enhance feature recognition. Finally, higher centres in the brain, such as the cerebral cortex, use the inhibitory networks in the brainstem and thalamic nuclei to modulate the sensory information transmitted from the skin. These descending inhibitory connections provide contextual information about the immediate behavioural significance of input from touch receptors needed to enhance or suppress it. **See also**: Modulatory and Command Interneurons for Behaviour

Primary somatosensory cortex

Tactile information reaches the conscious mind when it enters the cerebral cortex. Thalamic information is conveyed initially to the primary somatosensory cortex (S-I) located in the postcentral gyrus of the parietal lobe (Jones and Friedman, 1982). S-I cortex spans four cytoarchitectural areas (Brodmann areas 3a, 3b, 1 and 2) that are arrayed as parallel strips along the rostral–caudal axis of the parietal lobe (**Figure 4**). The four areas of the S-I cortex are extensively interconnected, such that both serial and parallel processing networks are engaged in higher-order elaboration of information from the sense of touch (Jones and Powell, 1969; Pons *et al.*, 1992). The four areas differ in anatomical connectivity and function. Thalamic fibres from VPL and VPM terminate in areas 3a and 3b, and the cells in areas 3a and 3b project their axons to areas 1 and 2, respectively. Areas 3b and 1 receive information from receptors in the skin, whereas areas 3a and 2 receive proprioceptive information from receptors in muscles, joints and the skin. This information is conveyed in parallel from the four areas of S-I cortex to higher centres in the cortex, including the second somatosensory (S-II) cortex, the posterior parietal cortex and the primary motor (M-I) cortex. **See also**: Cerebral Cortex; Sensory System Organization

Each cortical neuron receives inputs arising from receptors in a specific area of the skin, and these inputs together are its receptive field (Gardner and Johnson, In press). We perceive that a particular location on the skin is touched because a specific population of neurons in the brain is activated. Conversely, when a point in the cortex is stimulated electrically we experience tactile sensations on a specific part of the skin.

The receptive fields of cortical neurons are much larger than the receptive fields of touch fibres in peripheral nerves. For example, the receptive fields of SA1 and RA1 fibres innervating the fingertip are tiny spots on the skin, whereas those of the cortical neurons receiving these inputs are large areas covering the entire fingertip (DiCarlo *et al.*, 1998; Sripati *et al.*, 2006). The receptive field of a neuron in area 3b represents a composite of inputs from 300 to 400 touch fibres innervating neighbouring areas of the skin on the opposite (contralateral) side of the body. An individual neuron in area 3b resolves fine details of spatial patterns, such as an array of Braille dots, by faithfully reproducing

The somatosensory cortex

Coronal section

(a)

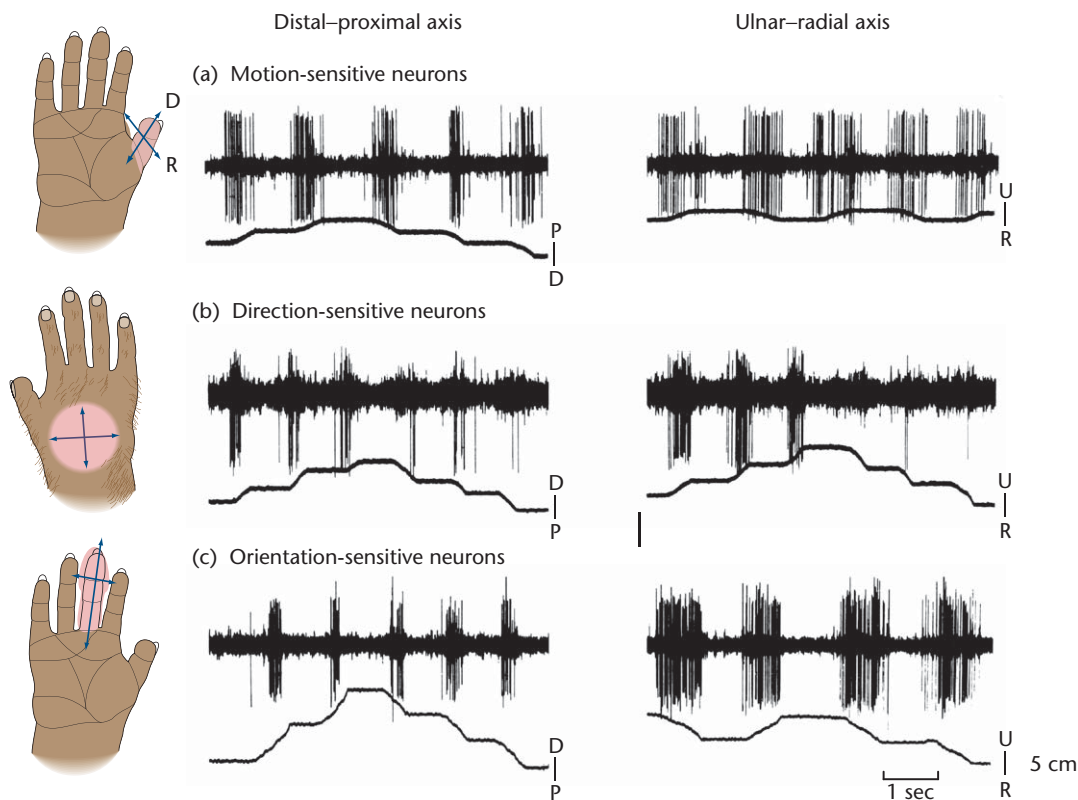(b)

Cortical connections

(c)
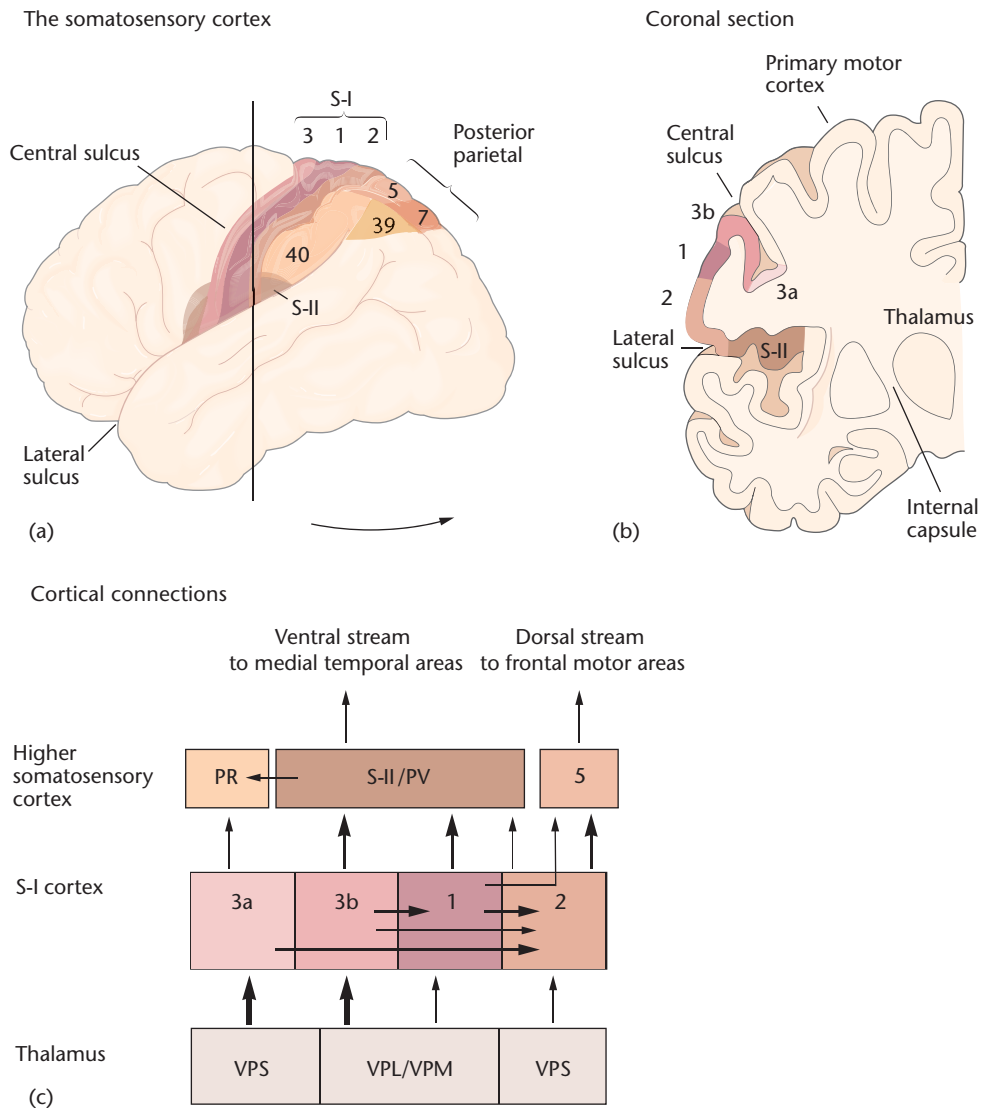
Figure 4 Somatosensory areas of the cerebral cortex. (a) Lateral view of the brain showing primary (S-I), secondary (S-II) and posterior parietal areas. (b) Coronal section through the postcentral gyrus indicating the cytoarchitectural subdivisions of S-I cortex, and their relation to S-II cortex. (c) Schematic outline of the hierarchical connections to and from the S-I cortex. Neurons projecting from the thalamus send their axons to areas 3a and 3b, but some also project to areas 1 and 2. Neurons in areas 3a and 3b project to areas 1 and 2. Information from the four areas of S-I cortex is conveyed to neurons in the posterior parietal cortex (area 5) and S-II cortex. Reproduced from Gardner and Johnson (In press). Used with the permission of the McGraw-Hill Companies.

the activity of the receptors that provide the strongest input. As in the periphery, complex spatial patterns are encoded in area 3b by bursts and silences distributed across a population of topographically arranged neurons.

Neurons at the next stage of cortical processing, in areas 1 and 2, integrate information from large groups of receptors. Receptive fields in these areas are larger than in area 3b, spanning functional regions of skin that are activated simultaneously during motor activity (Iwamura *et al.*, 1993). These include the tips of several adjacent fingers, or both the fingers and the palm. Their responses are less tightly linked to the actual location of stimuli on the skin. Instead, specific combinations of sensory inputs are required for optimum activation of these cells. Their firing

patterns are tuned to features such as the orientation of edges, the spacing of repeated patterns in gratings or Braille dot arrays, the surface curvature, the direction of motion across the skin or the integrated posture of the hand and arm (**Figure 5**; Costanzo and Gardner, 1980; Hyvärinen and Poranen, 1978; Warren *et al.*, 1986). These neurons signal properties common to a variety of shapes such as vertical or horizontal edges, rather than their exact location on the body. **See also**: Neural Information Processing

Feature detection is a property of cortical processing common to a variety of sensory systems including touch (Gardner, 1988). The higher cortical areas assemble the components detected by the receptors into a coherent representation of the entire object by requiring specific

Distal–proximal axis   Ulnar–radial axis

(a) Motion-sensitive neurons

(b) Direction-sensitive neurons

(c) Orientation-sensitive neurons

Figure 5 Spike trains recorded from neurons in Brodmann area 2 of the cerebral cortex in response to motion across their receptive fields; the direction of motion is indicated by upward and downward deflections in the lower trace and by arrows on the hands. (a) A motion sensitive neuron responds to stroking the skin in all directions. (b) A direction sensitive neuron responds strongly to motion towards the ulnar side of the palm, but fails to respond to motion along the same path in the opposite direction. Responses to distal or proximal movements are weaker. (c) An orientation sensitive neuron responds better to motion across a finger (ulnar–radial) than to motion along the finger (distal–proximal), but does not distinguish ulnar from radial nor proximal from distal directions. Adapted from Warren *et al.* (1986), and reproduced from Gardner and Johnson (In press). Used with the permission of the McGraw-Hill Companies.

spatiotemporal conjunctions of sensory inputs. Convergent excitatory connections between neurons representing neighbouring skin areas and intracortical inhibitory circuits enable higher-order cortical cells to integrate global features of objects to detect their size, shape, weight and texture (Gardner and Costanzo, 1980). Although most neurons in areas 3b and 1 respond only to touch, and neurons in area 3a respond to muscle stretch, many of the neurons in area 2 receive both inputs. This convergence of modalities allows neurons in area 2 to integrate the hand posture used to grasp an object, the grip force applied by the hand and the tactile stimulation produced by the object that allows us to recognise it. In this manner, the somatosensory areas of the brain represent properties common to particular classes of objects.

However, it would be a mistake to assume that each object that is handled becomes imprinted on a single neuron at the apex of cortical processing. Although, the mechanisms underlying the binding of features that give rise to a unified percept are not fully understood, it is believed that temporal synchrony between different cortical areas plays an important role in this process. This mechanism permits integration of the detailed representation of spatial properties at the early stages with the more abstract representations further along the anatomical network. **See also**: Neural Networks and Behaviour

Higher-order somatosensory areas of the cerebral cortex

Neuronal responses to touch in S-I cortex depend almost exclusively on input from within the neuron's receptive field. This feed-forward pathway is often described as a 'bottom-up' process because the receptors in the hand are the principal source of excitation of S-I neurons. Higher-order somatosensory areas of the parietal lobe not only receive information from peripheral receptors, but are also strongly influenced by 'top-down' processes, such as behavioural goals, attentional modulation and working memory. Data obtained from single-neuron studies in monkeys, from neuroimaging studies in humans, and clinical observations of patients with lesions in higher-order somatosensory areas of the brain suggest that the ventral and dorsal regions of the parietal lobe serve complementary functions in the sense of touch similar to the

'what' and 'where' pathways of the visual system (Ungerleider and Mishkin, 1982).

The ventral pathway originates in the second somatosensory cortex (S-II cortex), located on the upper bank and adjacent to parietal operculum of the lateral fissure (Robinson and Burton, 1980). It plays an important sensory role in tactile object recognition, as selective attention increases neuronal responses to specific shapes. Although neurons in S-II respond to textures such as Braille dots, embossed letters or periodic gratings, they do not replicate the spatial or temporal patterns of these stimuli in their spike trains. Instead, they fire at different rates for each pattern. Moreover, the context in which tactile stimuli are presented influences the responses of neurons in S-II cortex (Hsiao et al., 2002; Romo et al., 2002). Firing patterns of these neurons are modified by the behavioural relevance of the tactile information, or memories of the preceding stimuli, suggesting that S-II cortex may be a decision point for tactile memory formation. This is consistent with its anatomical connections to the insular cortex, which in turn innervates regions of the temporal lobe that are important for tactile memory (Friedman et al., 1986). This somatosensory pathway for tactual form has a parallel function to the visual pathway for form recognition through the inferotemporal cortex.

The dorsal pathway in the parietal lobe plays a sensorimotor role in the guidance of movement (Brochier and Umiltà, 2007; Culham and Valyear, 2006; Fogassi and Luppino, 2005; Jeannerod et al., 1995; Milner and Goodale, 1995). The sense of touch is extremely important for skilled use of the hand. When tactile sensations are lost, due to nerve injury or to local anesthesia, hand movements are clumsy, poorly coordinated and utilise abnormally high forces when grasping objects (Jenmalm and Johansson, 1997; Monzée et al., 2003). Without touch one is completely reliant on vision for directing the hand.

Tactile information from the skin is transmitted to the motor areas of the frontal lobe through direct pathways from S-I to motor cortex. Touch is also communicated to the frontal lobe through a higher-order pathway that involves somatosensory connections to regions of the posterior parietal cortex surrounding the intraparietal sulcus: areas 5 and 7 in monkeys and the superior (SPL, Brodmann areas 5 and 7) and inferior parietal lobules (IPL, areas 39 and 40) in humans. Tactile information from the skin is integrated in area 5 with postural inputs from the underlying muscles and joints to define the position and action of the hand. Neurons in the SPL respond vigorously when a monkey reaches out and shapes the hand in anticipation of grasping an object (Mountcastle et al., 1975; Buneo and Andersen, 2006). These responses peak when the object is acquired in the hand thereby integrating tactile and postural information from the hand (Gardner et al., 2007). IPL neurons integrate tactile and visual stimuli conjoining the feel of objects with their appearance and location in space. Their firing patterns are correlated with the hand posture used to grasp an object rather than its geometric shape (Murata et al., 2000). The multimodal

information encoded in the posterior parietal cortex is transmitted to the premotor areas of the frontal lobe that formulate complex movement sequences such as specific grasp styles (Fogassi and Luppino, 2005). These networks thus provide feedback from the senses of touch, proprioception and vision that can modify the behaviours used to handle objects. **See also**: Nervous Control of Movement

Predicting the sensory consequences of hand actions is an important component of active touch. For example, when we view an object and reach for it, we predict how heavy it should be and how it should feel in the hand; we use such predictions to initiate grasping (Johansson, 1996). During active touch the motor system may control the afferent flow of somatosensory information so that subjects can predict when tactile information should arrive in S-I cortex and be perceived in the conscious mind (Flanagan et al., 2003; Johansson and Flanagan, 2009). Convergence of central and peripheral signals allows neurons to compare prediction and reality. Corollary discharge from the motor areas of the cortex to somatosensory regions may play a key role in active touch. It provides a neural signal of intended actions to posterior parietal areas allowing these neurons to compare predicted and actual neural responses to tactile stimuli. Such mechanisms may explain why it is so difficult to tickle oneself.

Alteration of Different Modalities of the Tactile Experience by Lesions of Different Somatosensory Cortical Maps

Information is processed within S-I cortex in vertical arrays of neurons called columns (Mountcastle, 1997). The neurons within a cortical column receive sensory inputs from the same receptor class, and share overlapping receptive fields on the skin (Friedman et al., 2004; Sur et al., 1984). The columns are arranged topographically such that sacral segments are represented medially, lumbar and thoracic segments centrally, cervical segments more laterally and the trigeminal representation at the most lateral boundary (Nelson et al., 1980). The internal representation of the body in the human brain is essential for maintaining self-awareness and for controlling movement. This somatotopic map is referred to as a homunculus, because it provides a distorted image of the body surface. Each part of the body is represented in the brain in proportion to its relative importance to sensory perception, as measured by its innervation density rather than its surface area. Thus the homunculus exaggerates the hand, foot and mouth, and compresses more proximal body parts. There are approximately 100 times more cortical neurons per square centimetre of skin that sense touch on the tips of the fingers than sense touch on the back (Sur et al., 1980). Therefore, it is not surprising that deficits in touch sensation following injury to the cortex are more pronounced in these magnified areas of the body.

Plasticity of somatotopic maps

Although all brains in a given species share a common somatotopic arrangement of columns, the details of the map characterise each individual and are determined largely by experience. The importance of these maps for constructing one's body image is demonstrated most dramatically in human amputees. These individuals often experience phantom sensations of touch on their missing limbs, long after they know that the limb is gone forever. Although the neurons in the brain that previously represented the missing limb are deprived of their normal inputs, most of them do not die. They continue to function, but are apparently activated by receptors that innervate neighbouring portions of the body. For example, neurons representing an amputated arm eventually receive inputs from touch receptors on the face or on the limb stump, and acquire new receptive fields on these regions (Pons *et al.*, 1991; Ramachandran, 1993). However, gentle touch of these body parts evokes phantom sensations that are referred to the missing limb, because the patient has many years of experience that correlate firing in that portion of the cortex with touch on a particular region of the hand. We do not understand fully why the hand becomes permanently imprinted on these neurons, even though the patient is fully cognizant that the missing arm is no longer a part of the body. **See also**: Cortical Plasticity: Use-dependent Remodelling

Not only can the maps in the brain be altered by depriving certain areas of their normal input, but they can also be changed by increasing the sensory input (Recanzone *et al.*, 1992). We do this when we learn, and we learn by practice, repeating a task over and over. Repetitive activation of a pathway strengthens those synapses, making it easier to pass information forward. The alteration of the sensory maps by experience is highly specific to the stimulated pathway. For example, functional magnetic resonance imaging (fMRI) studies of professional violinists demonstrate an unusually large representation of the fingers placed on the strings of their instruments, and on the fingertips of the bowing hand. The long hours of practice have impressed themselves on the brain. **See also**: Repetitive Action Potential Firing

Deficits in the sense of touch caused by damage to the brain

An intact cerebral cortex deprived of its normal sensory innervation still preserves its representation of the entire body. However, when specific regions of the parietal cortex are damaged by stroke, head injury or disease, deficits in tactile sensation occur. These sensory abnormalities are localised to the regions of the body that innervate the injured cortex. The losses in the sense of touch are so specific that they are widely used by neurologists to diagnose cortical malfunction. **See also**: Traumatic Central Nervous System Injury

Lesions to S-I cortex in humans result in a loss of touch sensation on the contralateral side of the body (Freund, 2003; Pause *et al.*, 1989). The severity of the deficit depends on the extent of cortical tissue that is damaged. Although some sensations of touch are eventually restored, the ability to discriminate shape and textures is disrupted permanently. Experimental lesions in animals provide even clearer insights into the sensory functions of specific cytoarchitectonic fields (Brochier *et al.*, 1999; Carlson, 1981; Hikosaka *et al.*, 1985; LaMotte and Mountcastle, 1979). Lesions confined to area 3b produce the severest sensory deficits, as the tactile input to the cortex is almost completely severed. Ablation of area 1 results in deficits in texture discrimination, whereas lesions in area 2 impair stereognosis (the ability to discriminate the size and shape of objects). **See also**: Cerebral Cortex Diseases and Cortical Localization

Lesions to the higher somatosensory cortical areas result in deficits consistent with their sensory properties. In these higher cortical areas, the sense of touch flows seamlessly into the act of touching. Although the patient can detect and localise touch in the lesioned area, complex cognitive or sensorimotor functions of touch are abnormal (Milner and Goodale, 1995; Pause *et al.*, 1989). Lesions to S-II cortex result in deficits in both stereognosis and texture discrimination, but hand movements are relatively normal. By contrast, lesions in posterior parietal cortex disrupt normal hand motor behaviour. Reaching movements are inaccurate, the wrist cannot be oriented properly to place an object in a narrow space, and visually guided preshaping of the fingers for grasp is disrupted.

Disruption of active touch is perhaps the most striking deficit observed following lesions to the parietal cortex. Hand movements are clumsy and poorly coordinated, the fingers are difficult to control, and the patient is often unable to manipulate or explore novel objects without visual guidance. Faced with this motor deficit, patients refrain from touching objects in the environment, further depriving the remaining tissue of sensory stimulation.

Summary

The neurobiological processes that underlie sensations of touch are initiated by mechanoreceptors that transform physical deformation of the skin into electrical signals proportional to the applied forces. The information is conveyed to the central nervous system by the peripheral nerves as a pulse code of action potentials. Topographically organised ascending anatomical pathways transmit tactile information to the cerebral cortex where it is analysed by the conscious mind to perceive the specific object that is touched. Tactile sensations may be altered by experience or by lesions in somatosensory areas of the brain. **See also**: Somatosensory Systems

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