

Touch

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MIT Press

Published on: Feb 27, 2025

DOI: <https://doi.org/10.21428/e2759450.80318b2e>

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The sense of touch is intimately familiar to everyone. Touch refers to our sensitivity to the pressure and movement of objects in physical contact with the body. Touch is one aspect of a wider class of sensory abilities known collectively as *somatosensation* or *the bodily senses*. Indeed, despite the familiarity of touch, it is not always clear whether and how to distinguish touch from other bodily sensations, such as pain. Touch becomes especially powerful when combined with active movements of the hand, an ability known as *haptics*. Touch is also an important aspect of social interactions with others. While a substantial amount is known about touch and its neural bases, there is ongoing debate about many aspects of touch and how it links to other aspects of cognition, including motor control, vision, and social cognition.

History

Touch was one of the five senses listed by the ancient Greek philosopher [Aristotle \(1986\)](#), alongside vision, hearing, taste, and smell. The scientific study of touch, however, began more than 2,000 years later in the work of Ernst [Weber \(1996\)](#). Weber's work in the first half of the 19th century was instrumental in establishing the rigorous scientific study of touch specifically, and more generally in establishing the fields of experimental psychology and perceptual psychophysics. Numerous effects and concepts identified by Weber continue to be influential today, including the eponymous *Weber's law*, one of the few true laws in psychology, which states that the smallest difference between two stimuli that can be detected increases in proportion with the magnitude of the stimuli.

Insight into the brain mechanisms underlying touch came from the seminal studies of Wilder Penfield ([Penfield & Boldrey, 1937](#)), who used electrical currents to stimulate the primary somatosensory cortex (S1) in patients undergoing brain surgery for intractable epilepsy. Stimulation of specific locations in S1 produced sensations at specific locations on the opposite side of the patient's body, indicating a perceptual map of the body underlying touch known as the *somatosensory homunculus*.

Behavioral investigations by [Katz \(1989\)](#) and [Gibson \(1962\)](#) showed that the perceptual power of touch is dramatically amplified when combined with active exploratory movements of the hands, an ability known as *haptics*. An elegant series of studies by [Susan Lederman and Roberta Klatzky \(1987\)](#) showed that humans are exceptionally accurate at haptic recognition of objects, an ability which is mediated by a relatively small set of stereotyped hand actions known as *exploratory procedures*.

Core concepts

The bodily senses

It is not always easy to specify the boundary between touch and other aspects of what are sometimes called the *bodily senses*. These include things like sensations of temperature, pain, and itch; *proprioceptive* sensations of limb position and movement; and *interoceptive* sensations such as thirst or nausea. Each of these sensations arises from signals reaching the brain through the spinal cord, raising difficult issues of

classification if we start to count how many distinct senses are involved. Considering the core features of touch in terms of sensations of pressure and movement against the skin, physiological studies have identified four main classes of sensory nerve fiber, each of which is linked to a specific type of mechanosensory end organ in the skin ([Handler & Ginty, 2021](#)).

Affective touch

Recently, there has been substantial interest in another class of nerve fiber known as *C-tactile afferents*, which respond to gentle stroking of the skin ([McGlone et al., 2014](#)). This discovery has led to an explosion of interest in the proposal that in addition to the well-studied system for discriminative touch, there is a second system underlying *affective touch* ([McGlone et al., 2014](#)) [see [Affective Neuroscience](#)]. C-tactile afferents are absent from hairless skin regions like the fingertips, which are particularly important for discriminative touch. They respond maximally to stimuli moving at speeds ([Morrison et al., 2011](#)) and with temperatures ([Ackerley et al., 2014](#)) mirroring those of being gently stroked by another person. Moreover, they project not to S1 but to a different brain region known as the insula ([Olausson et al., 2002](#)). These features suggest that this system may have important roles in social bonding and attachment.

Somatotopy

The features of the somatosensory homunculus have provided rich insight into the neural mechanisms underlying touch. One feature, known as *somatotopy*, reflects the fact that adjacent bits of the skin are represented by adjacent regions of S1. This is true not only at the coarse scale of entire body parts (as seen in Penfield's studies) but also at a much finer scale, for instance, within a single fingertip ([Sur et al., 1980](#)).

Cortical magnification

Another feature, known as *cortical magnification*, reflects the fact that the size of each body part's representation in S1 corresponds not to the physical size of the body part but to its sensitivity. Comparative studies have shown the pattern of magnification across body parts is closely linked to each animal's mode of life ([Krubitzer, 2007](#)). For humans, it is the fingertips and lips that show highest magnification, reflecting the centrality of manual dexterity and spoken language to our everyday behaviors. In striking contrast, the star-nosed mole is a small North American mammal with an extraordinary nose with 22 appendages that it uses to find and capture prey. Reflecting the centrality of its nose to its ecological niche, more than half of S1 is devoted to representing the nose ([Catania, 2011](#)).

Questions, controversies, and new developments

Sensory attenuation

For centuries, people have noticed that we are unable to tickle ourselves. This deceptively simple observation suggests that tactile sensations produced by our own actions are importantly different from those produced by other people. Indeed, studies have found that self-produced tactile sensations are felt as both less ticklish ([Weiskrantz et al., 1971](#)) and less intense ([Shergill et al., 2003](#)). Such results have been

interpreted as reflecting attenuation of predictable sensory signals generated by self-produced action, consistent with internal models of online control of action ([Wolpert et al., 1995](#)). In other cases, however, self-produced touches are perceived more intensely ([Thomas et al., 2022](#)), consistent with Bayesian models that emphasize expected, rather than surprising, stimuli [see [Bayesian Models of Cognition](#)]. Understanding how these seemingly contradictory principles affect perception of self-touch is an ongoing area of research and debate.

Relation to action

A longstanding issue concerns the relation between touch and motor control. The somatosensory homunculus in S1 is mirrored by an analogous motor homunculus in the primary motor cortex (M1; [Penfield & Boldrey, 1937](#)). The similar structure of these maps and parallel organization on either side of the central sulcus in the brain suggest that these regions work closely together. Indeed, recent research has highlighted ways in which M1 appears to be involved in somatosensory function ([Hatsopoulos & Suminski, 2011](#)) and S1 is involved in motor function ([Matyas et al., 2010](#)).

Visuo-tactile interactions

Another important issue concerns the connections between touch and other sensory modalities, notably vision. While vision has commonly been thought of as dominant over touch in cases of multisensory conflict ([Rock & Victor, 1964](#)), more recent research has shown that information is combined near optimally based on the precision of each modality in a given context ([Ernst & Banks, 2002](#)). Other research has shown that regions of the ventral visual pathway underlying visual object recognition are also recruited in haptic object recognition as well ([Amedi et al., 2001](#)), indicating deep levels of shared processing across modalities.

Broader connections

Referred touch in tools

One longstanding topic of interest is the way in which touch can be extended by the use of tools. Consider a blind person using a cane, who despite not having tactile receptors in the cane is nevertheless able to obtain rich information about the external world from the tip of the cane. Recent research has investigated this ability and the specific neural processes involved ([Miller et al., 2018](#)).

Tactile feedback in prosthetics

Another emerging area of research concerns the integration of tactile feedback from prosthetic limbs. Historically, the development of prostheses has focused on action, what amputees can do with their prosthetic limbs. Providing rich tactile feedback from prostheses, however, may enhance their utility and the quality of life of people who use them. For example, amputees commonly complain that their prostheses are too heavy, even when they weigh substantially less than an actual limb does. A recent study found that when a prosthetic leg was given tactile feedback from pressure sensors connected to

electrical nerve stimulation, the perceived weight of the prosthetic leg was dramatically reduced ([Preatoni et al., 2021](#)).

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