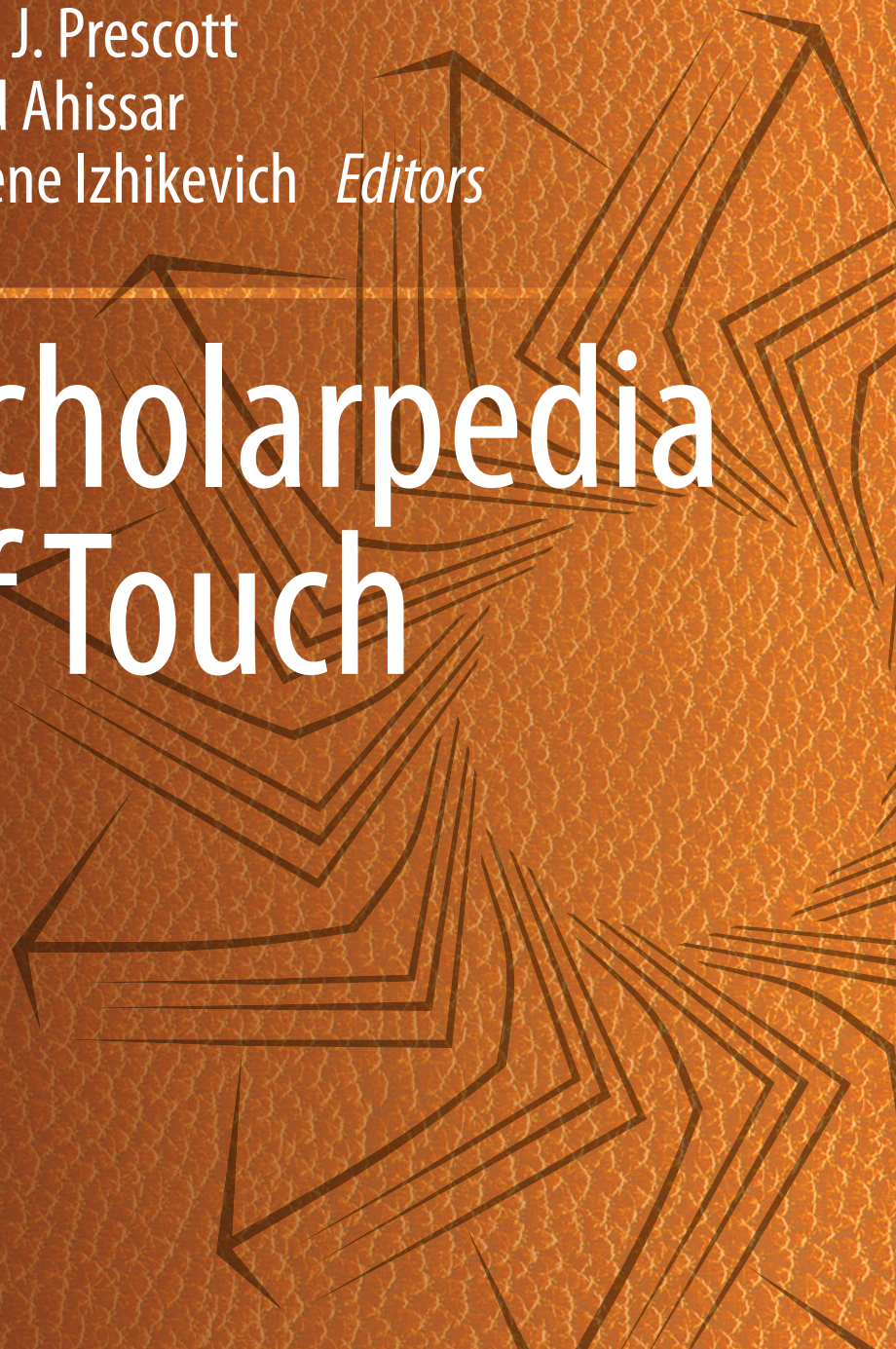Scholarpedia
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Scholarpedia of Touch

Scholarpedia

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Scholarpedia of Touch

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Preface

Touch is the ability to understand the world through physical contact. The noun "touch" and the verb "to touch" derive from the Old French verb "tochier". Touch perception is also described by the adjectives *tactile*, from the Latin "tactilis", and *haptic*, from the Greek "haptós". Academic research concerned with touch is also often described as *haptics*.

The aim of *Scholarpedia of Touch*, first published by Scholarpedia (www.scholarpedia.org), is to provide a comprehensive set of articles, written by leading researchers and peer reviewed by fellow scientists, detailing the current scientific understanding of the sense of touch and of its neural substrates in animals including humans. It is hoped that the encyclopedia will encourage sharing of ideas and insights between researchers working on different aspects of touch in different species, including research in synthetic touch systems. In addition, it is hoped that the encyclopedia will raise awareness about research in tactile sensing and promote increased scientific and public interest in the field.

Our encyclopedia assembles a state-of-the-art understanding of the sense of touch across a broad range of species from invertebrates such as stick insects and spiders, terrestrial and marine mammals, through to humans. The different contributions show not only the varieties of touch—antennae, whiskers, fingertips—but also their commonalities. They explore how touch sensing has evolved in different animal lineages, how it serves to provide rapid and reliable cues for controlling ongoing behaviour, how it develops, and how it can disintegrate when our brains begin to fail. In addition to analysing natural touch, we also consider how engineering is beginning to exploit physical analogues of these biological systems so as to endow robots, and other engineered artefacts, with rich tactile sensing capabilities.

Scope and Structure

Following an introductory chapter—The World of Touch—our encyclopedia is structured into four parts:

- **Comparative Touch** There are a large number of specialist tactile sensory organs in the animal kingdom. This part contains articles on animal species that exhibit interesting or exceptional tactile sensing abilities. We particularly focus on antennal systems in insects, and on vibrissal systems in both terrestrial and marine mammals.
- **The Psychology of Touch** The study of human cutaneous touch has a rich and long history in psychology and psychophysics. The pioneering studies of Ernst Weber (1795–1878) distinguished different forms of touch—pressure, temperature, and pain—all of which are separately considered in our encyclopedia along with dynamical (effortful) touch, tactile perception of force, and relevant forms of interoception (internal sensing) and proprioception (sense of body position). A particular focus of recent research has been towards the combination of tactile sensing with manipulation and grasp in the human hand. Alongside the study of healthy touch, this part also considers research on touch disorders, loss of tactile acuity with ageing, and the phenomenon of phantom touch.
- **The Neuroscience of Touch** A scientific understanding of the biological substrates for tactile sensing is beginning to emerge at all levels from the sensory periphery through to the somatosensory and multimodal areas of cortex. Perhaps more than any other sensory modality, tactile sensing is critically dependent on the movement of the sensing apparatus, therefore touch is increasingly studied from an active perception perspective—understanding active touch (in contrast to passive touch) as an intentional, information-seeking activity that combines sensing with actuation. The investigation of the sensorimotor control loops involved in mammalian active touch has been significantly advanced by the availability of the rodent vibrissal sensory system as an animal model. This part therefore combines studies in both primates (including humans) and rodents to show how neurobiological research is beginning to demonstrate an in-depth understanding of tactile sensing systems in mammals.
- **Synthetic Touch** Touch sensing is giving rise to a range of exciting new technologies. This part highlights some of the most promising tactile sensors for robots and haptic displays for the visually-impaired, through to virtual touch systems that can allow the extension of touch, through telecommunication technologies, as a modality for communication.

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Acknowledgments

All articles of this volume first appeared in Scholarpedia—the peer-reviewed open-access encyclopedia. They all are freely available at http://www.scholarpedia. org, and the readers are encouraged to revise and edit these articles to keep them up-to-date, similarly to how it is done in Wikipedia—the free encyclopedia. However, such revisions and edits are not published until they are approved by the articles' curators.

The following Scholarpedia Assistants provided substantial assistance to the specified chapters:

Swetamber Das (Tactile Temporal Order, Imaging Human Touch, Whisking Control by Motor Cortex), Javier Elkin (Touch in Aging), Serguei A. Mokhov (Models of Tactile Perception and Development, Systems Neuroscience of Touch), Shruti Muralidhar (S1 Microcircuits, Tactile Object Perception), Abdellatif Nemri (Dynamic Touch), B. Lungsi Sharma (A Spider's Tactile Hairs), and Juzar Thingna (Tactile Substitution for Vision, Whisking Pattern Generation).

Additionally, Nick Orbeck provided copy-editing for most of the articles, and Michelle Jones collated and edited the proof corrections.

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Introduction: The World of Touch

Tony J. Prescott and Volker Dürr

Despite its behavioural significance and omnipresence throughout the animal kingdom, the **sense of touch** is still one of the least studied and understood modalities. There are multiple forms of touch, and the mechanosensory basis underlying touch perception must be divided into several distinct sub-modalities (such as vibration or pressure), as will be made clear by the contributions elsewhere in this encyclopaedia. The commonality of all touch sensing systems is that touch experience is mediated by specialised receptors embedded in the integument—the outer protective layers of the animal such as the mammalian skin or the arthropod cuticle. Comparative research on touch, and its neuroethology, is only just beginning to provide a larger picture of the different forms of touch sensing within the animal kingdom. We begin our volume by reviewing works on several different invertebrate and vertebrate species, focusing on mechanosensation, each one with a specific requirement for tactile information. The aim of this introductory overview is to give selected examples of research on important model organisms from various classes of the animal kingdom, ranging from the skin of worms to the feelers of insects, and from the whiskers of a rat to the human hand. We conclude by discussing forms of human touch and the possibility of its future extension via synthetic systems.

Touch in Invertebrates

The Evolutionary Origins of Touch

Mechanical perturbation of the outer membrane of a ciliate such as *Paramecium* (Figure 1), will cause it to respond by moving away from the stimulus source (Naitoh and Eckert 1969). Thus, single-celled organisms already have a capacity for

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directional detection of tactile stimuli. The most primitive multicellular animals, the sponges, lack neurons, yet still show some capacity to respond to changes in water flow and pressure triggered by the deflection of non-motile cilia (Ludeman et al. 2014). Non-neural forms of sensitivity to tactile stimuli are also seen in many plants (Monshausen and Gilroy 2009; Coutand 2010). However, the evolution of neural conduction brings about a step-change in the capacity to respond rapidly and flexibly to tactile stimuli. Cnidarians, such as jellyfish and *Hydra*, despite having relatively simple nervous systems, can exhibit coordinated patterns of motor response to sensory stimuli and many have a rich capacity to respond to touch. For example, the nematocytes of *Hydra* are hair-like structures that respond to selective deflection and are thought to provide a good model for understanding the mechanoreceptors of more complex invertebrates (Thurm et al. 2004). In jellyfish such as *Aglantha digitale*, groups of hair cells, known as tactile combs, regulate complex behaviors including escape, feeding and locomotion (Arkett et al. 1988). The benefits of sensitivity to mechanical stimuli provided by hair-like structures may have encouraged their convergent evolution in multiple animal lineages. For instance, the hair cells of jellyfish appear to be sufficiently different from those in vertebrates that a common origin for both is unlikely (Arkett et al. 1988). Studies of the molecular basis of mechanosensation across different animal classes also suggest that cellular mechanisms to support tactile sensing may have evolved multiple times (Garcia-Anoveros and Corey 1997).

Lower Invertebrate Model Systems

All animals with a Central Nervous System (CNS) respond to touch. Even the tiny, un-segmented worm *Caenorhabditis elegans* (Figure 2), a nematode, shows touch-induced locomotion away from the stimulus. As in all higher animals, the corresponding mechanosensory cells are located in the integument, in this case beneath the cuticle. This worm's relevance to neuroscience stems from the fact that all of its 302 (somatic) neurons have been labelled and mapped. As a result, it has become the first animal system in which the entire network involved in touch-mediated behaviour—six sensory neurons, ten interneurons and 69 motoneurons—has been identified (Chalfie et al. 1985). Thirty years after the identification of all cellular components, many more details, including the biophysics of mechanosensory transduction (O'Hagan et al. 2005) and the molecular identity of several modulating signalling cascades (Chen and Chalfie 2014), have been unravelled.

In larger, arguably more advanced, animals such as the leech (*Hirudo medicinalis*, Figure 3), touch-induced behaviour becomes more versatile and complex. However, increased complexity generally means less complete understanding. In terms of complete mapping and understanding of touch-induced behaviour, the leech comes second to the champion nematode. Owing to the larger size of its neurons, the neurobiology of touch has been investigated primarily by means of electrophysiological recordings, which are almost impossible in tiny *Caenorhabditis*. As a
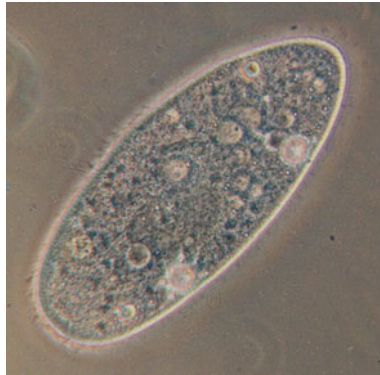
Figure 1 The ciliate *Paramecium* is a unicellular organism that responds to touch on either end of its oval-shaped cell body by active movement away from the stimulus. The corresponding change in the beat of the cilia is triggered by ion currents that are activated through touch (Photograph by Barfooz, CC BY-SA 3.0)
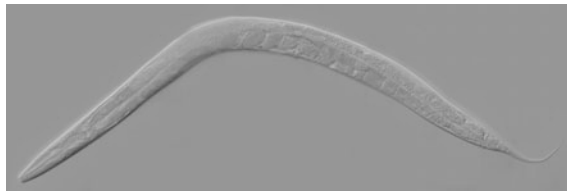
Figure 2 The nematode *Caenorhabditis elegans* is an important model organism in neuroscience. It has 16 sensory and interneurons involved in touch-mediated behaviour (CC BY-SA 2.5)

Figure 3 An important model organism for the electrophysiological study of touch-mediated movements is the medicinal leech (*Hirudo medicinalis*). The neurons of its ganglia have been mapped and many of them have been characterised individually (Photograph by Karl Ragnar Gjertsen, CC BY 2.5)

result, behaviourally relevant processing of touch-related information is perhaps best-studied in the leech (Muller et al. 1981). Because of its segmented body structure, the CNS of the leech has a chain of ganglia (one per segment), all of which contain the same, or at least very similar, sets of cellular elements. With regard to touch, three groups of mechanosensory neurons can be found in each ganglion, all of which respond to mechanical stimulation of the body, but with varying response thresholds: Touch cells (T-cells) are the most sensitive and respond to gentle touch of the body wall; Pressure cells (P cells) respond to stronger touch stimuli, and Nociceptive cells (N-cells) respond to very strong, potentially harmful, stimuli (Nicholls and Baylor 1968). After the original description of what has meanwhile become a textbook example of range fractionation of stimulus intensity, a number of general aspects of sensorimotor systems have been studied in leech: Notable examples are the recruitment of T-, P- and N- cells in crawling (Carlton and McVean 1995), the "mapping" of sensory input to distinct motor output by means of a population code (Lewis and Kristan 1998a), the encoding and decoding of touch (Thomson and Kristan 2006), and the modelling of the entire sensorimotor pathway underlying touch-induced directed movements (Lewis and Kristan 1998b).

Tactile Learning in Molluscs

Among the molluscs, a sister group of the segmented invertebrates, several species have become important model organisms in neuroscience, particularly with regard to research on learning and memory (see e.g. Brembs 2014). Most famous of these is probably the sea hare *Aplysia californica*, in which a number very fundamental cellular mechanisms underlying learning have been described for the first time. Although the historical paradigm of sensitisation and habituation of the siphon/gill withdrawal response can be induced by mechanical stimuli, the modality of touch has not been in the focus of these studies. Another fascinating mollusc model system is the **octopus**, that has long been known for its cognitive abilities. A number of behavioural studies on tactile discrimination and tactile shape recognition have been conducted, largely following an animal psychology approach, in combination with ablation studies (e.g., Young 1983). As a result, touch-related behaviour in octopus has been analysed at a different level of description than in other invertebrate groups. A review of the touch-related behavioural repertoire in octopus is given by Grasso and Wells (2013) in this volume.

The Arthropod Tactile Hair

Compared to the soft-bodied animals mentioned above, animals with a skeleton no longer work as hydrostats in which body deformation is best monitored by

deformation of the surface, i.e., the integument. In contrast to a hydrostat, skeletons require the formation of joints, thus "focussing" any change in posture on a limited set of locations. As a consequence, skeletons impose a physical limit to the number of degrees of freedom of movement. With regard to touch, this is important because mechanoreceptors may be dedicated to "strategically relevant locations" across the body, i.e., locations where displacement is most likely to occur. In proprioception, such strategically relevant locations are the joints themselves (and/or the muscles and tendons actuating them). In touch, strategically relevant locations are surface areas where contact with external objects is most likely to occur. Arthropods (that is the group comprising spiders, Crustaceans, insects and their relatives) appear to exploit such strategically relevant locations in two ways: In proprioception, they often use patches of hairs, so-called *hair fields* or *hair plates*, to sense displacement of two adjoining body segments. In touch, they use very much the same kind of hairs, too, but at various locations on the body, with particularly high "hair density" at places where contacts are most likely to occur and/or most relevant to detect.

These arthropod hairs are not like mammalian hairs at all: The Arthropod tactile hair is a cone-shaped cuticular structure, filled with fluid and equipped with a number of cells as the base. At least one of these cells is a ciliated mechanoreceptor that encodes the deflection of the cuticular structure (Thurm 1964). Arthropods have a large variety of such sensory hairs (called *seta* or, more generally, *sensillum*; plural: *setae* and *sensilla*). Their information encoding properties have been described in different ways (e.g., see French 2009). Apart from various mechanoreceptors (the basic type being the *Sensillum trichoideum*), there are also variants with chemoreceptors, subserving gustation and olfaction.

Both spiders and insects use hair sensilla also in proprioception and, as a consequence, in active touch sensing, where the active movement of a limb needs to be monitored. To date, a number of such proprioceptive hair fields have been characterised functionally (e.g., French and Wong 1976). As part of this encyclopedia, tactile hairs are the key sensory elements in three chapters, one dealing with the functional properties and behavioural relevance of tactile hairs in **spiders** (Barth 2015), and two more dealing with tactile hairs on dedicated sensory organs in insects—the **antennae** (Okada 2009; Dürr 2014).

The Arthropod Antenna: Elaborate Touch in Invertebrates

Among the living Arthropods, only the Myriapods (millipedes, etc.), Crustaceans and insects carry antennae (singular: antenna). Antennae are commonly called feelers, which is appropriate given the fact that they are dedicated sensory limbs (Staudacher et al. 2005). As such, they are equipped with a particularly large number of sensilla, and the density of sensilla per unit surface area is much higher than on most other parts of the body. With regard to touch this means that the antennae are the major sensory organ of touch, although all other body parts that carry tactile hairs may contribute tactile information as well.

During evolution of the Arthropoda, several body segments have fused to form the head. For example, in insects, the common view is that the head has developed from six body segments, three of which carry the mouthparts, and another three that carry the main sensory organs of the head: the eyes and the antennae (or feelers). In Crustaceans, there are two pairs of antennae: the smaller, anterior pair—the *Antennules* (or 1st antennae)—are known to have important functions in chemoreception (as in an underwater sense of smell). The larger, posterior pair (the 2nd antennae) is known to serve the sense of touch.

Tactually mediated behaviour in Crustaceans has mostly been studied in lobsters, crayfish and other large, decapod Crustaceans (Staudacher et al. 2005). Given the fact that the *Decapoda* represent only a small fraction of the morphological, behavioural, and ecological diversity of Crustaceans, it is very likely that antennal touch works differently in different taxa. An example for a reasonably well-studied Crustacean with regard to touch is the Australian crayfish *Cherax destructor* in which both biomechanical and behavioural aspects have been studied (Sandeman 1985, 1989). *Cherax* actively explores the environment ahead with its 2nd antennae and shows directed attacks towards objects that it has localised tactually (e.g., Zeil et al. 1985).

Insects carry only one pair of antennae. The common view is that, during evolution, insects lost one pair of antennae. According to this view, insects must have lost the second pair of antennae, such that the insect antenna is homologous to the Crustacean antennule, i.e., both organs have a common evolutionary origin. Like the Crustacean antennule, the insect antenna is the most important sensory organ for olfaction. Other than the Crustacean antennule, the insect antenna is also the most important sensory organ for touch (Figure 4).

Tactually mediated behaviour in insects has been studied in great detail in a number of species, most notably in cockroaches, crickets, stick insects and bees (Staudacher et al. 2005). Antennal touch has been shown to be important for

Figure 4 An Indian stick insect (*Carausius morosus*) climbs a rung that it has detected by tactile contact with its antennae. Location of the rung is highlighted in the leftmost frame. From left to right, frames show instants of (i) missing the rung with the antennae, (ii) touching the rung with the left antenna during upstroke, (iii) touching the rung again during the subsequent downstroke, (iv) first foot contact with the rung and (v) climbing the rung. *Numbers* indicate the time in [s] relative to the first antennal contact with the rung

near-range sensing during locomotion, for example in tactually mediated course control (Camhi and Johnson 1999). In many cases, the relevant mechanoreceptors have been identified, for example the antennal hair fields in touch-mediated turning towards an object (Okada and Toh 2000). In the past, sensors involved in course control have mostly been viewed as passive systems that do not require active movement for acquiring information. In some behavioural paradigms, such as tactile wall following, antennae are thought to be used passively. However, active movement of antennae is a key feature of active tactile exploration during loco-motion. Antennal contact events may trigger decisions between mutually exclusive behavioural actions (e.g., Harley et al. 2009) or goal-directed motor actions such as tactually elicited reaching movements of the front legs (Schütz and Dürr 2011).

As a higher-order aspect to active tactile exploration, antennal movements are also involved in attentive behaviour such as visually guided pointing in crickets (e.g., Honegger 1981) and touch-related motor learning in the honeybee (Erber et al. 1997). In addition to non-associative motor learning, honeybees have also been demonstrated to show different associative learning behaviours (with regard to touch). For example, it is possible to condition them to different surface patterns (e.g., Erber et al. 1998) but also to condition antennal sampling movements as such in an operant conditioning paradigm (Erber et al. 2000).

The antennal mechanosensory system of insects has also been studied electro-physiologically, in particular with respect to the information transfer from the head to the ganglia of the ventral nerve cord. Owing to the fact that insect neurons can be identified and labelled individually, there is hope that some aspects of tactually mediated behaviour will be understood at the level of neuronal networks as research progresses. Today, the collection of identified antennal mechanosensitive neurons comprises descending interneurons in the brain (e.g., Gebhardt and Honegger 2001) and in the suboesophageal (or gnathal) ganglion (e.g., Ache et al. 2015).

As part of the present collection of articles, two insect model organisms are presented in more detail: the **cockroach** (Okada 2009) and the **stick insect** (Dürr 2014).

Touch in Vertebrates

The Lateral Line System of Fish and Amphibians

In fish and amphibians, vertebrate mechanoreceptor organs, known as *neuromasts*, are arranged in lines on the body, head and tail, either free-standing on the skin or inside fluid-filled canals. In many fish species, a line of neuromasts within a canal that lies on the center line of each flank forms what is known as the lateral line system (Bleckmann and Zelick 2009) (Figure 5). The number of neuromasts can vary between species from a few dozen to several thousand. The main sensory structure in each neuromast is a bundle of hair cells that respond to hydrodynamic stimuli resulting from water displacement or changes in water pressure. The lateral
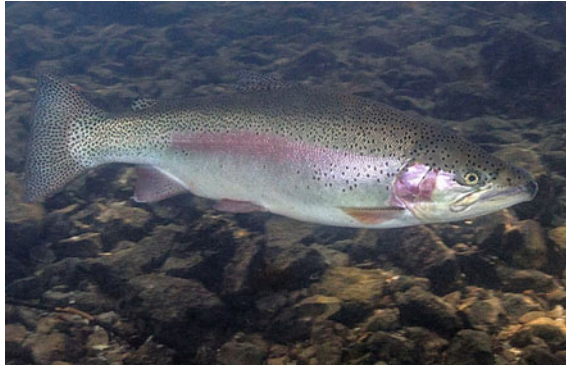
Figure 5 The fish lateral line system provides a sensitive organ for detecting hydrodynamic stimuli. In the Rainbow Trout (*Oncorhynchus mykiss*), pictured here, the position of the lateral line is marked by the distinctive pink coloring. *Photograph* by Liquid Art (CC 4.0)

line system therefore provides a refined sensory system for detecting remote causes of water movement such as the behavior of predator or prey animals, water currents, and topographical features of the underwater environment. The lateral line, in effect, provides a form of remote or distal touch. A remnant of the lateral line system in mammals (including humans) are the liquid-filled (semicircular) canals of the inner ear, a structure informing us about rotational movements of the head.

Evolutionary Origins of Mammalian Hair and Skin

Skin serves many functions, including to house and protect the organs and internal body parts, and to act as the body's largest sensory organ sensitive to tactile, thermal, and chemical stimuli (Chuong et al. 2002). Mammalian skin has evolved from the integument of earlier vertebrates via a complex path that is still only partially charted (Maderson 1972, 2003). What is clear, however, is that hair evolved anew in early mammals, or in their therapsid reptilian ancestors, as a specialization of the outer epidermal layers of the integument (Sarko et al. 2011). Whereas dense or pelagic hair serves an obvious thermoregulatory function, the evolution of mammalian hair cannot be explained by the need to improve maintenance of body temperature. Rather, the first hairs almost certainly had a largely tactile function, and their subsequent proliferation allowed hair to gain a secondary role as an insulator. The primary sensory role of hair is retained in the tactile hair, or **vibrissae**, found on all therian mammals (marsupials and placentals) except humans (Prescott et al. 2011). In the **naked mole rat**, an animal that has lost all of its pelage, tactile hair has been retained across the whole body surface for its value in supporting the sense of touch (Crish et al. 2015) (Figure 6).

Figure 6 The naked mole rat (*Heterocephalus glaber*) has lost all of its pelagic hair but retains tactile hair across its body surface. *Photograph* by Trisha Shears

Many mammals have also evolved areas of non-hairy, glabrous skin. In humans, these include the skin areas on the lips, hands and fingertips and the soles of the feet. These are the parts of the body that are most important when physically interacting with the world and where accurate tactile discrimination is most critical; unsurprisingly, then, glabrous skin has a high density of **mechanosensory receptors** including Meissner corpuscles, Pacinian corpuscles, Merkel-cell neurite complexes and Ruffini endings (Moayedi et al. 2015). The same mechanoreceptor types are also found in hairy skin alongside hair follicles and a system of unmyelinated low threshold C-tactile (CT) mechanoreceptors (Loken et al. 2009). The CT fibers are particularly sensitive to light 'stroking' touch and thus are thought to underlie an affective, or social, touch capacity that may be unique to mammals (McGlone et al. 2014) (Figure 7).

Figure 7 The CT fiber system in mammalian hairy skin appears to be part of an affective system that encourages social touch and promotes bonding in mammals. *Photograph* by Jim Champion (CC 3.0)

Glabrous skin forms the basis for specialized sensory organs in a variety of animals including the electroreceptive bill of the platypus and the unusual tactile snout of the star-nosed mole (see below). A notable feature of mammalian tactile sensing systems is the presence of **somatotopic maps** of the skin surface in primary somatosensory cortex (S1) (Kaas 1997) (Wilson and Moore 2015). These maps are organized to match the topographic layout of the periphery but in a distorted manner, such that skin areas that have a higher density of receptors, greater receptor innervation, or that are functionally more important to the animal, have a proportionately larger representation in cortex. The human sensory "homunculus" described by Penfield and Boldrey (1937) is probably the best known of these maps, and the "barrel" field of rat and mice somatosensory cortex, first described by Woolsey and van der Loos (1970), the best studied. However, maps whose size, shape and organisation reflect the sensory specialization of the species have also now been described for a wide range of mammals (Krubitzer et al. 1995; Catania and Henry 2006).

Mechanosensation in Monotremes

Sensing in the monotremes, or egg-laying mammals, is perhaps most remarkable for the sensitive electroreceptive capability of the platypus (Scheich et al. 1986). However, all three monotreme species (the platypus and both species of spiny anteater—*Echidna*) also possess a distinctive tactile sensing system, quite different from the vibrissae of the therian mammals. Specifically, all monotremes have mechanoreceptive structures on the snout or bill known as "pushrods" (Proske et al. 1998). These are compact, rigid columns of cells embedded in the skin that are able to move relative to the surrounding tissue. Most of the rod structure is below the skin surface with a convex tip raised slightly above it. The tissues of the pushrods are associated with four types of nerve ending including Merkel cells, and the structure has been compared to the Eimer organs of moles (see below). In platypus, up to 50,000 pushrods are scattered across surface and along the edges of the bill. The bill also contains an extensive venous system that can be engorged with blood, possibly boosting the acuity of the pushrod system. In platypus (Figure 8) the electroreceptive system provides a strongly directional sense for detecting and orienting to prey animals; the pushrods might then assist targeting of prey in the final attack phase. In echidna the pushrod system might similarly be important when the animal probes the ground with its snout looking for insect prey.

Mammalian Vibrissal Systems

Long facial whiskers, or macrovibrissae, are found in many mammalian species, projecting outwards and forwards from the snout of the animal to form a tactile