The roles and functions of cutaneous mechanoreceptors

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Combined psychophysical and neurophysiological research has resulted in a relatively complete picture of the neural mechanisms of tactile perception. The results support the idea that each of the four mechanoreceptive afferent systems innervating the hand serves a distinctly different perceptual function, and that tactile perception can be understood as the sum of these functions. Furthermore, the receptors in each of those systems seem to be specialized for their assigned perceptual function.

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Current Opinion in Neurobiology 2001, **11**:455–461

0959-4388/01/$ —see front matter

Abbreviations

PC	Pacinian
RA	rapidly adapting
SA1	slowly adapting type 1
SA2	slowly adapting type 2

Introduction

The four cutaneous mechanoreceptive afferent neuron types that innervate the glabrous skin comprise slowly adapting type 1 (SA1) afferents that end in Merkel cells, rapidly adapting (RA) afferents that end in Meissner corpuscles, Pacinian (PC) afferents that end in PC corpuscles, and slowly adapting type 2 (SA2) afferents that are thought to terminate in Ruffini corpuscles. Each of these neuron types responds to cutaneous motion and deformation in a different way. The mechanosensitive transducers reside in the unmyelinated endings of the afferent fibers. The receptors' selectivity seems to be due as much to the receptor structure that surrounds each of these endings as to the transducer itself.

The Merkel cell has the simplest structure; it is a special cell type in the basal layer of the epidermis that enfolds the unmyelinated ending of the SA1 afferent fiber. The SA1 receptor is selectively sensitive to a particular component of the local stress-strain field, which makes it sensitive to edges, corners, and curvature; it is not known whether this selectivity is due to the Merkel cell or to the transducer mechanism within the afferent terminal. Meissner corpuscles are relatively large cell assemblies in the dermal ridges that lie just beneath the epidermis. They comprise cell layers that cushion and enfold the large leaf-like endings of two to six RA afferent fibers. This pillow-like arrangement appears to act as a filter that protects the velocity-sensitive endings from static skin deformation. PC corpuscles reside in the dermis and deeper tissues. The PC corpuscle is a large, layered onion-like structure with as many as 70 layers, enclosing a single nerve ending that is sensitive to deformation in the nanometer range. The layers function as a series of mechanical filters to protect the extremely sensitive receptor from the very large, low-frequency stresses and strains of ordinary manual labor. The Ruffini corpuscle, which is located in the connective tissue of the dermis, is a relatively large spindle shaped structure tied into the local collagen matrix. It is, in this way, similar to the Golgi tendon organ in muscle. Its association with connective tissue makes it selectively sensitive to skin stretch. Each of these receptor types and its role in perception is discussed below.

During three decades of neurophysiological and combined psychophysical and neurophysiological studies, evidence has accumulated that links each of these afferent types to a distinctly different perceptual function and, furthermore, that shows that the receptors innervated by these afferents are specialized for their assigned functions.

As the combined psychophysical and neurophysiological evidence that supports this view is too extensive to discuss here and has been reviewed recently [1], I will focus on the apparent specialization of each of the mechanoreceptors for its assigned function. Where important references supporting a statement are pre-1990 and have been discussed previously, the reader is referred to the earlier review [1].

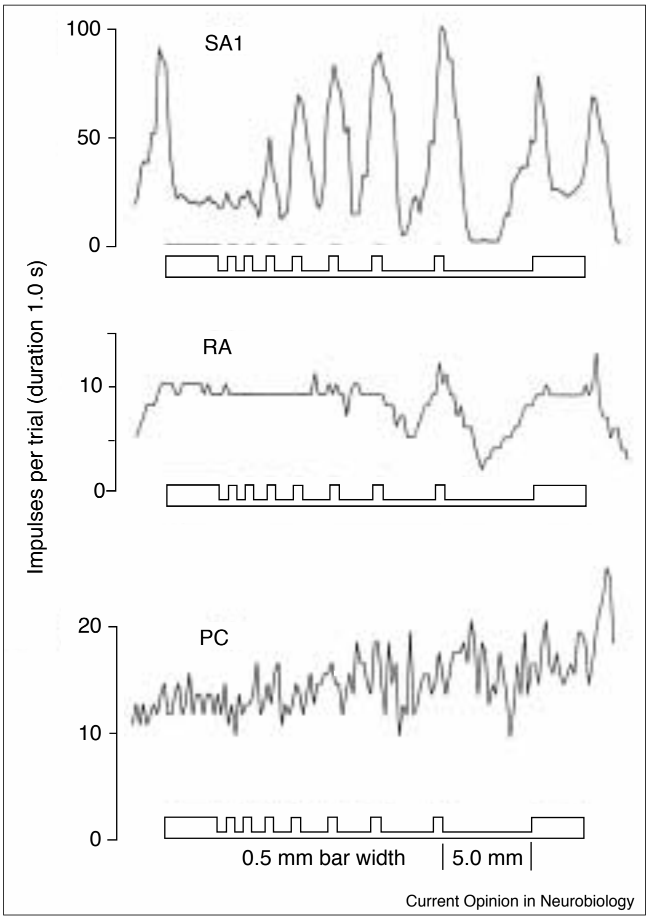
Merkel–SA1 afferents

SA1 afferents innervate the skin densely (about 100 per cm^2 at the fingertip in man and monkey [1]), and they respond to sustained indentation with a sustained, slowly adapting discharge that is linearly related to indentation depth. They have two remarkable response properties. One is their sensitivity to points, edges and curvature, which is a consequence of their selective sensitivity to strain energy density or a closely related strain component (the square of the maximum local compressive strain regardless of its orientation). The other is their spatial resolution: individual SA1 afferents resolve spatial detail of 0.5 mm, although their receptive field diameters are 2–3 mm. Because of these two properties, the SA1 population transmits an acute spatial neural image of a tactile stimulus.

Goodwin and Wheat [2,3•] have analyzed the effects of variation in population parameters such as innervation nonuniformity, and have shown that these parameters have little effect on the acuity of the SA1 neural image and the information conveyed by the population. Combined psychophysical and neurophysiological studies show that the SA1 afferents are, in fact, responsible for form and texture perception [1].

The SA1 receptors are Merkel–neurite complexes involving specialized (Merkel) epidermal cells that enfold the

Figure 1



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SA1, RA and PC responses to an aperiodic grating pressed into the skin. The grating is shown in cross-section beneath each response profile. The end bars are 3.0 mm wide; the internal bars are 0.5 mm wide. The grooves are deeper than illustrated (2.0 mm deep) and are 0.5, 0.5, 0.75, 1.0, 1.5, 2.0, 3.0 and 5.0 mm wide. The grating indented the skin by 1 mm for 1 s, was raised and moved laterally 0.2 mm for the next indentation. The ordinate represents the number of action potentials evoked during each 1-s period. RA and PC afferents responded during the indentation phase only, which accounts for their smaller impulse counts. The abscissa for each plot represents the position of the receptive field center relative to the grating; for example, the left peak in the SA1 response profile (95 impulses per s) occurred when the center of the SA1 RF was directly beneath the left edge of the grating. The RA illustrated here was the most sensitive to spatial detail out of all RAs studied. Most RA responses dipped only during the 5 mm gap and some barely registered the presence of the 5 mm gap even though they responded vigorously at all grating positions. Testing progressed from right to left. The progressive decline in PC responses results from adaptation to the repeated indentations. Adapted with permission from [7].

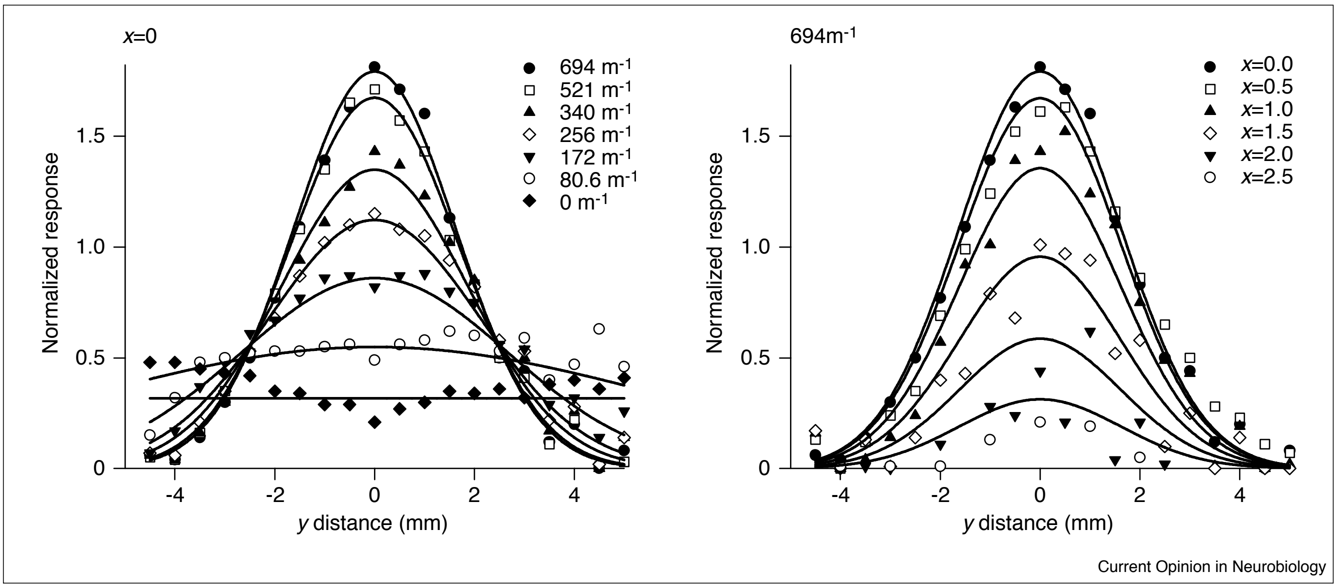
unmyelinated ends of SA1 axons [1]. Although there are synapse-like junctions between the Merkel cells and the axon terminals, action potentials appear to arise as the result of mechanosensitive ion channels in the bare nerve endings [4,5]. As individual SA1 afferent axons approach the epidermis, they branch over an area of about 5 mm^2 [6] and innervate a large but unknown number of Merkel receptors (100 is an estimate of the order of magnitude). The receptive field of an SA1 afferent has hot spots that undoubtedly correspond to individual branches of the afferent axon [7,8]. When the spatial detail becomes finer than the receptive field diameter, a single skin spot (i.e., a single terminal branch) becomes dominant, which accounts for the fact that SA1 afferents resolve spatial detail smaller than their receptive field diameters [7].

Figure 1 illustrates the SA1 afferent's two principal response properties: high spatial resolution, and responsiveness to stimulus features such as edges and bars rather than to indentation *per se.* The modulation of SA1 firing rates beginning at 0.5 mm wide gaps parallels closely the human psychometric function for discriminating grating orientation. Human discrimination begins to rise above chance behavior when gaps and bars are 0.5 mm wide and reaches threshold when they are about 1.0 mm wide [9,10]. The selective sensitivity for edges and bars illustrated in Figure 1 arises from the Merkel receptor's selective sensitivity to strain energy density or a closely related component of tissue strain [11–13].

An additional quality that makes SA1 afferents particularly suited to the representation of surface or object form is its linear response to skin deformation over a very wide range of deformations. SA1 afferents respond to skin indentation to depths of at least 1500 μm with a linear discharge rate [1,6,14]; in contrast, the RA afferent response begins to saturate at about 100 μm [6] and is insensitive to the height of surface features above 300–400 μm [14,15]. Because of the linearity and the SA1 responsiveness to strain energy density, the SA1 afferents represent object curvature very accurately as shown by a number of studies [2,16–19,20•]. For example, Goodwin *et al.* [16] showed that only SA1 afferents provide the brain with a veridical neural image of a curved surface — an image that could be used for the perception of curvature. LaMotte and Srinivasan [17] scanned a series of cylindrical waves with varying curvature across the receptive fields of SA1 and RA afferents. They found that the discharge rates of both afferent types were related to surface curvature, but SA1 firing rates represented the shapes of the cylindrical wave more effectively than did the RA firing rates [17]. Finally, Dodson *et al.* [19] showed that the human threshold for object orientation is 4 to 5 degrees at the fingertip. Only the SA1 population provides a neural image of the stimulus and its orientation that can account for the psychophysical behavior.

Goodwin and colleagues have shown also that humans can discriminate curvature independent of contact force [21] and contact area [22], which implies that subjects rely on the spatial profile of the neural activity evoked by a curved surface rather than some intensive cue like total impulse rate. Figure 2 illustrates the SA1 neural activity evoked by a series of curved surfaces. No other afferent type provides a representation on which curvature discrimination might be based [16,23,24].

Figure 2



Population response of peripheral SA1 afferents to indentation with spheres of varying curvature. The left plot shows the mean responses of SA1 afferents as a function of proximal–distal distance from the center of indentation. Data are shown for seven curved surfaces with radii ranging from 1.4 mm (curvature = 694 m^{-1}) to a flat surface (curvature = 0 m^{-1}). The right plot shows population response profiles in proximal–distal slices at varying distances from the center of indentation. Adapted with permission from [16].

There is other evidence of SA1 specialization for the representation of spatial information:

1. SA1 responses to stimulus elements on a surface are independent of the force of application [25].
2. SA1-receptive fields grow minimally (relative to RA receptive fields) with increasing indentation depth [6].
3. SA1 afferents possess a response property, surround suppression, which confers response properties similar to those produced by surround inhibition in the central nervous system [25]. This response property is a consequence of sensitivity to strain energy density, not a synaptic mechanism.
4. SA1 spatial resolution is affected minimally by changes in scanning velocity at velocities up to at least 80 mm s^{-1} [26,27].
5. SA1 afferents are at least ten times more sensitive to dynamic than to static stimuli [1].
6. SA1 responses to repeated skin indentation are practically invariant: the variability is about one impulse per trial regardless of the number of action potentials evoked [6].

The psychophysical correlate of points 1 and 2 is that tactile pattern recognition is independent of contact force [1]. The psychophysical correlate of point 3 is much greater sensitivity to curvature and surface features than to indentation *per se* [1,7,21,22]. The psychophysical correlate of point 4 is tactile spatial pattern recognition at scanning velocity up to at least 80 mm s^{-1} [28]. The psychophysical correlate of point 5 is much greater sensitivity to form and texture when fingers scan a surface than when they are stationary. David Katz [29] has said that “movement [is] as indispensable for touch as light is for color sensations”. The SA1 sensitivity to motion is the basis of this observation. The psychophysical correlate of point 6 is the human ability to discriminate surface form. For example, humans can reliably discriminate surfaces with dots or ridges, even when their spacings differ by as little as 2% [30,31].

Meissner–RA afferents

Meissner afferents innervate the skin even more densely (about 150 per cm^2 at the fingertip in man and monkey [1]) than do the SA1 afferents, they are insensitive to static skin deformation, and they are four time more sensitive to dynamic skin deformation than are SA1 afferents. Unlike SA1 afferents, they respond to stimuli over their entire receptive fields (3–5 mm in diameter) with relative uniformity and therefore resolve spatial detail poorly. A mechanistic interpretation is that, unlike the SA1 afferents, all the terminal branches of an RA afferent contribute equally when multiple endings are stimulated simultaneously by dense spatial detail.

Because of this wide, uniform sensitivity, RA afferents transmit a robust neural image of skin motion. For many years, they have been known to be responsible for the detection and discrimination of low frequency vibration [1]. A more recent observation is that they are responsible for detecting slip between the skin and an object held in the hand [1,32] and that, of the four afferent types, they are the most effective at signaling sudden forces that act on objects held in the hand [33]. Considering the importance of prehension, the RA's most important function would seem to be the provision of feedback signals for grip control [33,34].

Individual RA afferent nerve fibers end as unmyelinated, disk-like endings within Meissner's corpuscles, which occur in dermal pockets between the sweat ducts and adhesive ridges [1,35]. This position places the RA afferents as close to the surface of the epidermis as is possible within the dermis. This may account, in part, for the greater sensitivity of RA afferents to minute skin deformation relative to SA1 afferents, whose receptors are on the tips of the deepest epidermal ridges.

It is difficult to think of a more important role for the RA afferents than as the essential feedback sensors for grip control. Johansson and colleagues [1,33,34] have shown that as we lift and manipulate an object there are frequent microscopic slips between the object and the skin, and that the skin motion associated with these slips evokes reflexive increases in grip force.

This constant adjustment allows us to manipulate objects with delicacy — with grip forces not far above the forces that result in overt slip. A complication is that the required grip forces depend on factors like surface coefficient of friction as well as the object's weight. The evidence from microneurographic recordings in humans as they lift and manipulate objects and in controlled psychophysical and neurophysiological experiments is that RA afferents provide the signals that are critical for grip control [1,32–34].

The RA afferent responses possess several qualities that appear to be specialized for this function. First, studies using indentation, vibration and scanned raised elements have shown that RA afferents are four times more sensitive to skin motion than SA1 afferents [1]. Second, as illustrated in Figure 1, they are more uniformly sensitive to stimuli within their receptive fields than are SA1 afferents [6,7,36,37]. RAs fail to represent the gaps in a grating until they are 3–5 mm wide because of their uniform responsiveness over receptive fields that are 3–5 mm wide. The result is poor spatial acuity but a robust response to local events such as slip. On the basis of their innervation density at the fingertip (150 per cm^2) and their receptive field sizes (10–30 mm^2) it can be estimated that 15–50 RA afferents signal transient local skin motion. Third, they are insensitive to static force and very low-frequency vibration. If they were not, the response to forces required to grip an object would mask the small signals produced by local microslip. The basis of this insensitivity is probably the fluid-filled corpuscle within which the very sensitive receptors reside (see section on PC corpuscles below).

The RA and SA1 systems are, in some ways like the scotopic and photopic systems in vision. The RA system, like the scotopic system, has greater sensitivity but poorer spatial resolution and limited dynamic range. The SA1 system, like the photopic system, is less sensitive but has higher spatial resolution and operates over a wider dynamic range.

Pacinian afferents

PC afferents terminate in single corpuscles [38] that are distributed throughout the palm and fingers (about 350 per finger and 800 in the palm) [1]. These afferents have three remarkable response properties.

The first is their extreme sensitivity: the most sensitive PC afferents respond to 10 nm of skin motion or less at 200 Hz [39]. Because of their extreme sensitivity and the deep locations of PC receptors, PC afferents have almost no spatial resolution, as can be seen in Figure 1. The receptive field of a PC receptor may include an entire hand. The second is their intense filtering (at nearly 60 dB per decade) of low-frequency stimuli that would otherwise overwhelm the sensitive PC receptors. Third, they respond to stimuli less than 100–150 Hz with a phase-locked, Poisson discharge [40]. The theoretical importance of a Poisson discharge (auditory primary afferents also respond to a sinusoidal stimulus with a phase-locked Poisson discharge) is that no single afferent can accurately represent the waveform of a complex stimulus in the 30–150 Hz range with its instantaneous firing rate. However, a whole population firing randomly but at a rate proportional to the instantaneous stimulus amplitude can represent the stimulus waveform accurately.

Because of these response properties, the PC population produces a high-fidelity neural image of transient and vibratory stimuli transmitted to the hand by objects held in the hand. For many years, they have been known to be responsible for the perception of high frequency stimuli [1]. Combined psychophysical and neurophysiological experiments show that an important consequence of this function is the perception of distant events through transmitted vibrations when we grasp an object in the hand [39]. When we become skilled in the use of a probe or a tool, we perceive events at the working surface of the tool or probe as though our fingers were present. The PC afferents are responsible for this critical perceptual capacity.

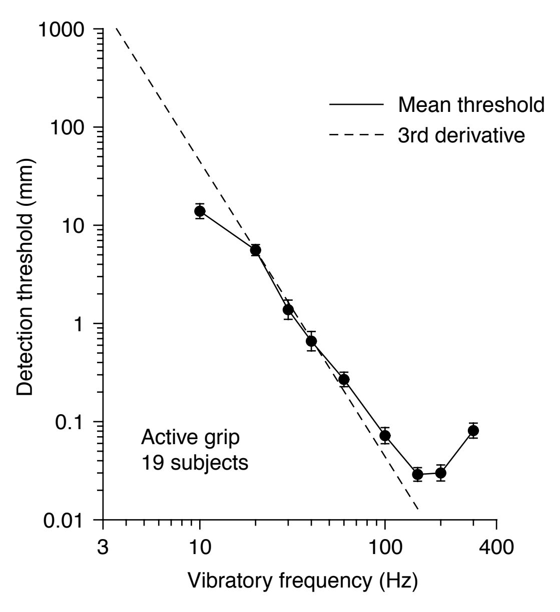
Hunt first showed that PC afferents are sensitive to distant events through transmitted vibrations [1]. He discovered that the spontaneous discharge that he was recording was, in fact, a response to ambient vibrations in the laboratory. The most sensitive PC corpuscles respond to vibratory amplitudes as small as 3 nm applied directly to the corpuscle [41] and 10 nm applied to the skin [39]. Sensitivity thresholds have been shown to be much lower when grasping a large object vibrating parallel to the skin surface as opposed to vibrating normal to the skin surface [39]. When a human subject grasps a rod conveying vibrations from a shaker embedded within the rod, thresholds for individual subjects are as low as 10 nm [39].

In contrast, RA afferents are about two orders of magnitude less sensitive than PC afferents. These observations show that the PC afferents play a principal, if not the exclusive role in the perception of distant events through an object held in the hand.

The most obvious specialization for this function is the extreme sensitivity of the PC receptor, but that sensitivity would be of little use if the receptor were not protected from the intense, low-frequency forces that accompany many manual tasks. Even though we grip a tool, such as a shovel, vigorously, we perceive events at the working surface of the tool, such as the texture of sand at the end of the shovel, as though our fingers were present.

The layered lamellae of the PC corpuscle function as an extremely selective cascade of high-pass filters [42]. Between 20 and 150 Hz, the human threshold for detecting transmitted vibration falls from 5.6 to 0.03 μm, which amounts to a drop of 52 dB per decade (Figure 3). This is close to the filtering characteristic of a mechanism sensitive to the third temporal derivative of tissue displacement (–60 dB per decade, dashed line in Figure 12), which is called 'jerk' because it corresponds to the rate of change of acceleration. Our hands are used constantly in manual tasks that subject the cutaneous and subcutaneous tissues to large, dynamic stresses and strains. If it were not for the steep filtering provided by the multilayered, fluid-filled corpuscles, the sensitive receptor within would be overwhelmed by the deformations produced by these forces. If the extrapolation to low frequencies illustrated in Figure 3 is accurate, a peak-to-peak motion of 1 cm at 2 Hz would not activate the PC system.

Figure 3



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Threshold for the detection of transmitted vibration when subjects grasp a 32-mm diameter cylindrical rod. Vibrations were produced by a linear motor mounted at one end of the rod. Vibratory amplitudes were measured with a three-dimensional accelerometer mounted on the rod. The ordinate represents the mean threshold amplitude measured as half the vibratory peak-to-peak excursion. Filled circles and solid lines represent the psychophysical thresholds. The dashed line has the slope of an ideal detector sensitive to the third derivative of stimulus motion (i.e. –60 dB/decade). The human vibratory threshold at 10 Hz is less than the dashed line because the RA afferents are more sensitive at 10 Hz than are the PC afferents. Adapted with permission from [39].

SA2 afferents

SA2 afferents innervate the skin less densely than either SA1 or RA afferents. SA2 receptive fields are about five times larger, they are about six times less sensitive to skin indentation, but they are 2–4 times more sensitive to skin stretch than SA1 afferents [1,43]. They signal skin stretch more effectively than SA1 afferents and with much less interference by stimulus features within their receptive fields. Consequently, the SA2 population transmits a neural image of skin stretch to the central nervous system with relatively little interference from objects held in the hand.

SA2 afferents present a puzzle. They are reported regularly in microneurographic studies of mechanoreceptors in the human hand but have never been observed in neurophysiological studies of mechanoreceptors in the monkey hand. For this reason, they have been studied less extensively than the other afferent types.

Even so, combined psychophysical and neurophysiological studies in the human have identified two important roles for SA2 afferents. The first is perception of the direction of object motion or force when the motion or direction of force produces skin stretch [44•]. SA2 afferents are not, however, exclusively responsible for the perception of motion because motion is clearly perceived when only RA afferents can provide the relevant information [45]. Gardner and Sklar [45] used a device comprising an array of vibrating pins that activate only RA and PC afferents and found that motion and motion direction are discriminated effectively. This demonstrates that motion perception is possible on the basis of RA responses alone (because the PC afferent population response has too little spatial resolution to signal motion detection).

The second is a substantial role, along with muscle spindles and possibly joint afferents, in the perception of hand shape and finger position through the pattern of skin stretch produced by each hand and finger conformation [1,46,47,48•]. Two studies have shown that simply stretching this skin, which activates SA2 afferents strongly (and SA1 afferents more weakly), produces the illusion of finger flexion [46,47], as does tendon vibration [47].

The much greater sensitivity to stretch than to indentation suggests that the SA2 receptor is sensitive to horizontal tensile strain, which is less sensitive to local indentation than other strain components [11,13]. This and the SA2 receptor's deep location seem to shield SA2 afferents from the confounding effects of the indentation produced by an object, leaving it free to signal the object's direction of motion and hand conformation.

Conclusions

The accumulated evidence suggests that there is a sharp division of function among the four cutaneous afferent systems that innervate the human hand. First, the SA1 system provides a high-quality neural image of the spatial structure of objects and surfaces that is the basis of form and texture perception. Second, the RA system provides a neural image of motion signals from the whole hand. From this, the brain extracts information that is critical for grip control and information about the motion of objects contacting the skin. Third, the PC system provides a neural image of vibrations transmitted to the hand from objects contacting the hand or, more frequently, objects grasped in the hand. This provides the basis for the perception of distant events through probes and tools held in the hand. Fourth, the SA2 system provides a neural image of skin stretch over the whole hand. The evidence for this is less secure but the most likely hypothesis is that the brain extracts information about hand conformation from the dorsal SA2 image (and the ventral image when the hand is empty). When the hand is occupied, the ventral SA2 image signals information about the direction of motion of objects moving across the skin surface and about the direction of forces exerted on the hand.

The distinctively different functions identified for the four cutaneous mechanoreceptive afferent systems suggest the existence of distinct and separate central systems for processing the information provided by each of the primary afferent groups. For example, the computational problems inherent in processing information for form and texture perception (the SA1 system) have little in common with the problems inherent in processing information about motion and motion direction (RA and SA2 functions). A recent study of neurons in area 3b of primary somatosensory cortex shows, for example, that neurons in this region are highly selective for spatial form and have mechanisms that seem designed to preserve spatial information at high scanning velocities [49•]; on the other hand, neurons in area 3b are no more sensitive to motion or motion direction than are primary afferents. This suggests that the very important processes underlying motion perception lie elsewhere.

A major challenge is to map and understand the central pathways processing the information provided by each of the four primary afferent systems. A feature of the four afferent systems that has made the inferences laid out in this paper difficult to come by, is that all four of the afferent systems are very sensitive and almost all suprathreshold stimuli activate all four systems. An important goal for peripheral neurophysiologists is to learn how to selectively stimulate each of the afferent systems with meaningful stimuli so that the central pathways for each of the systems can be identified and studied. The challenge for central neurophysiologists is to understand the operations that underlie the perceptual functions of each of the four systems.

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An object moving over the surface of the skin produces local skin deformation related to the shape of the object and a large region of skin stretch in the wake of the object. Because of their sensitivity to skin stretch at a distance, the SA2 afferents send a neural image of skin stretch that defines movement direction. SA1 afferents signal the pattern of local deformation much more effectively than do SA2 afferents.

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Neuroscience and Biobehavioral Reviews 34 (2010) 148–159

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

The cutaneous sensory system

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ARTICLE INFO

Keywords:
Somatosensory
Cutaneous
C-fibres
CT-afferents
Touch
Temperature
Itch
Pain
Pleasure

ABSTRACT

The cutaneous senses are traditionally thought to comprise four recognized submodalities that relay tactile, thermal, painful and pruritic (itch) information to the central nervous system, but there is growing evidence for the presence of a fifth modality that conveys positive affective (pleasant) properties of touch. Cutaneous sensory channels can be further classified as serving predominantly either *discriminative* or *affective* functions. The former provides information about the spatial and temporal localisation of events on the body surface, e.g., the presence of an insect or the temperature of a cold wind; and the latter, although widely recognised as providing the afferent neural input driving the negative emotional experience of pain, is here posited to provide the afferent neural input driving the positive emotional experience of affiliative touch as well. A distinction is made between the properties of fast conducting myelinated afferents and those of slowly conducting unmyelinated afferents, with the former subserving a sensory-discriminative role, and the latter an affective-motivational one. Here we review the basic elements of the somatosensory system and outline evidence for the inclusion of the 'fifth' sub-modality, conveyed by low-threshold C-fiber mechanoreceptors as the counterpart of high-threshold C-fiber nociceptors with both C-fiber systems serving opposing aspects of affective touch, yet underpining a common mechanism for the preservation of self and species.

Contents

1. Introduction to the somatosensory system

The primary sensory modality subserving the body senses is collectively described as the somatosensory system. It comprises all those peripheral afferent nerve fibers, and specialised receptors, subserving proprioceptive (joint, muscle) and cutaneous sensitivity. The former processes information about limb position and

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0149-7634/$ – see front matter © 2009 Published by Elsevier Ltd.
doi:10.1016/j.neubiorev.2009.08.004

muscle forces which the central nervous system uses to monitor and control limb movements and to ensure that a planned action or movement is executed fluently via elegant feedback and feedforward mechanisms. This review paper will focus on sensory inputs arising from the skin, namely cutaneous sensibility.

Sensory modalities operate within interconnecting, intermodal and crossmodal networks, ensuring that interactions with the environment are generally multisensory (see Calvert et al., 2004, for review). Vision and hearing are classified as exteroceptive senses and provide information that can be used to guide approach or avoidance behaviours; olfaction is also able to provide such information: think only of the smell of burning, or the aroma of coffee. For many behaviours, a physical and/or chemical contact sense is required in order to extract more information about stimuli in the immediate environment, and the senses of touch and taste provide this information. The cutaneous senses are classically defined as including tactile, thermal, pain and itch sensing submodalities, and there is growing evidence for an additional cutaneous sensory channel that subserves positively affective aspects of touch, such as those generated during grooming and nurturing behaviours. 'Touch' in this context is seen as interoceptive, providing information about the homeostatic state of the body, and even the sense of self (Craig, 2009). The skin is a highly complex organ, innervated by a wide array of specialised sensory neurones sensitive to heat, cold, pressure, irritation, itch and pain. Touch is the first sense to develop *in utero*, Montagu (1978, p. 195) reporting tactile responses to a hair stroking the cheek of a foetus at around 8 weeks gestational age. Cutaneous sensitivity of the embryonic body extends to the genital area by week 10, the palms by week 11, the soles by week 12, the abdomen and buttocks by week 17, and by week 32 every part of the body is responsive to the gentle stroke of a single hair. This developmental hierarchy of tactile sensitivity is reflected anatomically: the sites developing cutaneous sensitivity first possessing the greatest number and variety of sensory receptors in adults. Consequently, they are also represented cortically with larger areas of primary somatosensory cortex. In addition to demonstrating sensitivity to light touch, prenates also respond to tissue harming stimuli. Giannakoulopoulos et al. (1994) have reported that within 10 min of inserting a hypodermic needle into a fetus's intrahepatic vein, for a transfusion, there is a 590% rise in beta-endorphin and a 183% rise in cortisol. This biochemical evidence of a physiological response to nociception, and evidence that cutaneous C-fiber systems are functional at a discriminative level at an early developmental stage, raises the possibility that C-fiber systems are also functional at an affectively positive level. The component of the cutaneous senses that is relayed to the somatosensory cortex includes the entire body from the neck down; sensations from the face are relayed via cranial nerves, with both parts sharing a common central organization. As with other sensory modalities, information is relayed from entry level cortex to higher order neural systems controlling perception, attention and emotion, as well as systems that integrate this information with other sensory modalities. This pattern of connectivity enables neural processing systems to maximize information received from the senses about the conditions in the external world.

2. The peripheral nervous system

The skin is the most extensive and versatile of the body's organs and in a fully grown adult covers a surface area approaching 2 m^2. Apart from its role as a sensory organ the skin contains in excess of 2 million sweat glands and 5 million hairs, that may be either fine vellous types covering all surfaces apart from the soles of the feet and the palms of the hands (glabrous skin). Skin consists of an outer stratified squamous epithelium of ectodermal origin – the epidermis – and an inner, thicker, supporting layer of connective tissue of mesodermal origin—the dermis. The thickness of this densely innervated layer varies from 0.5 mm over the eyelid to >5.0 mm in glabrous skin. Afferent nerve impulses are conveyed by fibers of primary sensory neurons located in trigeminal and dorsal root ganglia, which are comprised of a heterogeneous population comprising of cell bodies of all the peripheral afferents innervating the skin. Efferent axons of dorsal root ganglia neurons terminate in the skin where they innervate a variety of cutaneous structures such sweat glands, hair follicles, Merkel cells, Meissner's corpuscles and blood vessels. The nerve bundles course through the dermis vertically, forming a horizontal sub-epidermal neural plexuses before losing their Schwann cell covering at the dermo-epidermal junction and penetrating the epidermal basement membrane, ascending between the keratinocytes and terminating as free nerve endings. Cutaneous innervation consists mainly of unmyelinated fibers, accounting for around 90% of all dermal nerve fibers (Ebenezer et al., 2007).

2.1. Touch

Most primate research into skin sensory processing has focused on the glabrous surface of the hand, in particular the digits, and a description of this somatic site will provide for a general understanding of somatosensation (Johansson, 1976; Vallbo et al., 1979; Darian-Smith, 1984a,b; Willis and Coggeshall, 1991; Gescheider et al., 1992; Greenspan and Lamotte, 1993). Of the four 'classical' submodalities of the somatosensory system the tactile one subserves the perception of pressure, vibration, and texture, and relies upon four different receptors in the digit skin: (1) Pacinian corpuscles, (2) Meissner's corpuscles, (3) Merkel's disks, and (4) Ruffini endings, collectively known as low-threshold mechanoreceptors (LTMs), a class of cutaneous receptors that are specialised to transduce mechanical forces impinging the skin into nerve impulses (Fig. 1). The first two are classified as fast adapting (FA) as they respond to the initial and final contact of a mechanical stimulus on the skin, and the second two are classified as slowly adapting (SA), continuing to fire during a constant mechanical stimulus. A further classification relates to the LTM's receptive field (RF), i.e., the surface area of skin to which they are sensitive which is determined by the LTM's anatomical location within the skin. Those near the surface, at the dermal/epidermal boundary (Meissner's corpuscles and Merkel's disks) possessing small RFs, and those lying deeper within the dermis, (Pacinian corpuscles and Ruffini endings), having large RFs.

Psychophysical procedures have traditionally been used to study the sense of touch and, as in hearing research where the sensory receptor is another type of specialised mechanoreceptor, differing frequencies of vibration are used to quantify the response properties of this sensory system. George von Bekesy (1939) was the first to use vibratory stimuli as an extension of his research interests in audition. In a typical experiment participants would be asked to respond with a simple button-press when they were just able to detect the presence of a vibration presented to a digit within one of two time periods. This two alternative forced choice paradigm (2-AFC) generates a threshold-tuning curve, the slopes of which provide information about a particular class of LTM's response properties. As can be seen from Fig. 2, a 'U'-shaped function is generated, with detection thresholds increasing in sensitivity as vibrotactile frequency increases to a 'peak' at around 300 Hz, at which point the curve begins to increase again as sensitivity decreases (Table 1).

By carefully controlling the stimulus parameters of the vibrating probe (spatial configuration, frequency, amplitude, duration and skin surface temperature) as well as the use of various masking techniques, Bolanowski et al. (1988) proposed

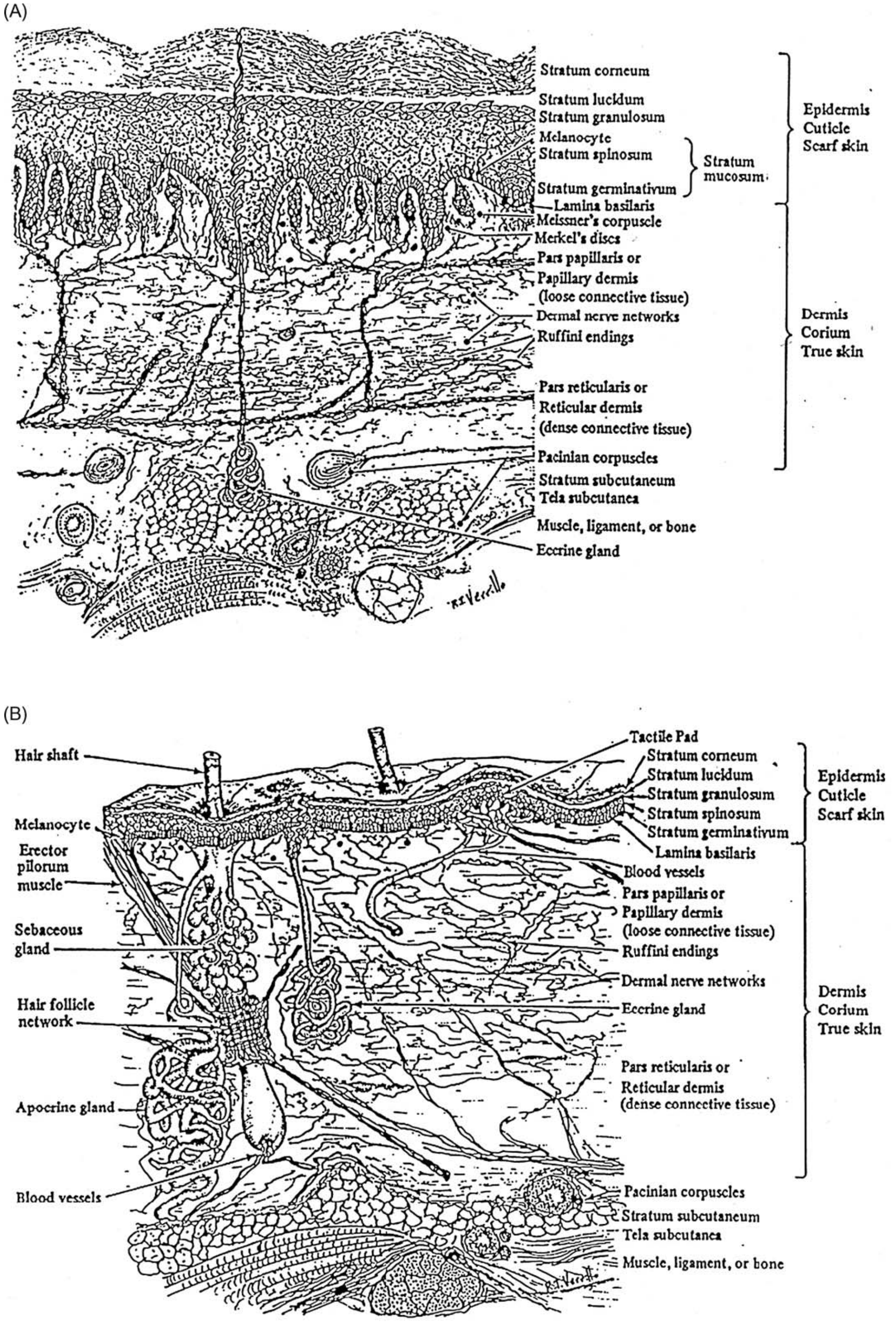

Fig. 1. A cross-sectional perspective of glabrous (A) and hairy (B) skin (with permission of the artist R.T. Verrillo).

that there are four distinct psychophysical channels mediating tactile perception in the glabrous skin of the hand. This model proposes that each psychophysically determined channel is represented by one of the four anatomical end organs and nerve fiber subtypes. Frequencies in the 40–500 Hz range provide a sense of 'vibration', transmitted by Pacinian corpuscles (PC channel or FAII), Meissner corpuscles transmit a sense of 'flutter' in the 2–40 Hz range (NPI channel or FAI), while 'pressure' is mediated by Merkel's disks in the 0.4–2.0 Hz range (NPIII or SAI) and Ruffini end organs produce a 'buzzing' sensation in the 100–500 Hz range (NPII or SAII). Neurophysiological studies have by and large supported this model. See Table 2 for a summary of the properties of these LTMs.

There have been relatively few studies of tactile sensitivity on the hairy skin, the cat being the animal of choice for most of these studies. Mechanoreceptive afferents (Aβ fibers) have been

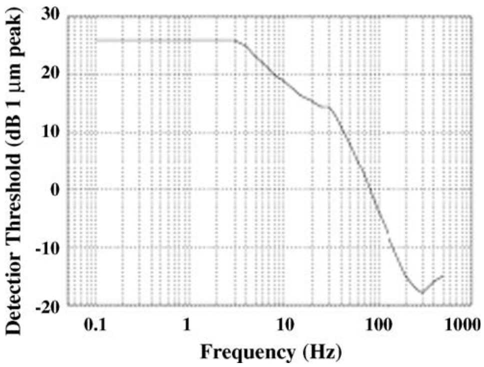

Fig. 2. Absolute detection thresholds for sinusoidal stimuli (from Bolanowski et al., 1988) where it can be seen that as vibration frequency increases detection thresholds decrease (note–log axis).

Table 2
Summarizes the main characteristics of primary sensory afferents innervating human skin.

Sensory afferent nerves			
Class	Modality	Axonal diameter (um)	Conduction velocity (m/s)
Myelinated			
Aα	Proprioceptors from muscles and tendons	20	120
Aβ	Low-threshold mechanoreceptors	10	80
Aδ	Cold, noxious, thermal	2.5	12
Unmyelinated			
C-pain	Noxious, heat, thermal	1	<1
C-tactile	Light stroking, gentle touch	1	<1
C-autonomic	Autonomic, sweat glands, vasculature	1	<1

described that are analogous to those found in human glabrous skin (FAI, FAII, SAI, SAII). Essick and Edin (1995) have described sensory fibers with these properties in human facial skin, however, the relationship between these sensory fibers and tactile perception is still uncertain, and this is exemplified by the response properties of SAI afferents. Harrington and Merzenich (1970) reported that these afferents are responsive to levels of stimulation that are below perceptual thresholds. Meanwhile, Jarvilehto et al. (1976) describe high levels of activity in human hairy skin SAIs that are not perceivable, in contrast to the responses of this class of afferent in glabrous skin where SAI nerve activity is directly correlated with a sense of pressure.

Sensory axons are classified according to their degree of myelination, the fatty sheath that surrounds the nerve fiber. The degree of myelination determines the speed with which the axon can conduct nerve impulses, and hence the nerve's conduction velocity. The largest and fastest axons are called Aα, and include some of the proprioceptive neurons, such as the muscle stretch receptors. The second largest group, called Aβ, includes all of the discriminative touch receptors being described here. Pain and temperature include the third and fourth groups, A-δ and C-fibers, and will be discussed in Section 2.2 (see Table 2).

Vallbo and Johansson (1978) developed an electrophysiological technique called microneurography to study the function of single peripheral nerve fibers innervating the human hand, which has provided a generally accepted model of touch that relates the four anatomically defined types of cutaneous or subcutaneous sense organs to their neural response patterns. Microneurography involves inserting a fine tungsten microelectrode, tip diameter $<5\ \mu m$, through the skin of the wrist and into the underlying median nerve, which innervates the thumb and first two digits. A sensitive biological amplifier records and amplifies the spike discharges conveyed by the axons and feeds these to a loudspeaker to enable the experimenter to hear the spike activity and 'hone-in' on a single unit. Skilled manual micromanipulation of the electrode, coupled with stroking across the hand to stimulate LTMs, results first in a population response being recorded, i.e., neural activity in a nerve fascicle containing hundreds of peripheral axons until finally, sometimes after many hours, a single axon is isolated. At this stage the threshold force for activation and receptive field (RF) of the single unit are mapped with thin nylon filaments (Von-Frey hairs') and the unit subtype (i.e. FA or SA) is identified. Once this stage is completed, a small pulsed current of a few microamps (typically $<7\ \mu A$) is delivered to the nerve to provides additional perceptual confirmation of the unit subtype. If, for example, a FA unit has been isolated, microstimulation is perceived as a 'flutter' or 'vibration', depending on the frequency of the electrical pulses, and is perceptually localised to the previously mapped RF. Fig. 3 depicts the relationships between RF, adaptation rate and unit type from studies carried out on the human hand (Westling, 1986).

2.2. Temperature

The cutaneous somatosensory system detects changes in ambient temperature over an impressively wide range, initiated when thermal stimuli that differ from a homeostatic set-point excite temperature specific sensory nerves in the skin (see Ringkamp, in this issue). Within the innocuous thermal sensing range there are two populations of thermosensory fibers, one responding to warmth and the other to cold, and include fibers from the Aδ and C range. Specific cutaneous cold and warm receptors have been defined as slowly conducting units that exhibit a steady-state discharge at constant skin temperature and a dynamic response to temperature changes (Hensel and Boman, 1960; Hensel, 1973). Cold-specific and warm-specific receptors can be distinguished from nociceptors that respond to noxious low and high temperatures ($<20\ ^\circ C$ and $>45\ ^\circ C$) (Torebjörk and Hallin, 1976; Campero et al., 1996), and also from thermo-sensitive mechanoreceptors (Hensel and Boman, 1960; Konietzny, 1984). Konietzny recorded from 13 cold-specific units in humans using microneurography, and measured conduction velocities (CVs) in the C-fiber range (0.43–2.04 m s^{-1}). Serra et al. (1999) uncovered a number of spontaneously active fibers with microneurography,

Table 1
Summarizes the major findings in Bolanowski et al. (1988) and previous work done by these researchers at the Institute for Sensory Research, Syracuse University (Verrillo, 1963; Gescheider et al., 1982, 1983, 1985).

Channel	Pacinian	NPI	NPII	NPIII
Frequency response	40–80 Hz	3–100 Hz	15–400 Hz	<0.3–>100 Hz
Threshold (re 1 μm)	<−20 dB @ 300 Hz	28 dB @ 3 Hz	10 dB @ 300 Hz	28 dB @ 3 Hz
Sensation	Vibration	Flutter	Not known	Pressure
Temporal summation	Yes	No	Yes	No
Spatial summation	Yes	No	Not known	No
Receptor type	FAI Pacinian corpuscle	FAII Meissner's corpuscle	SAII Ruffini end organ	SAI Merkel's disk

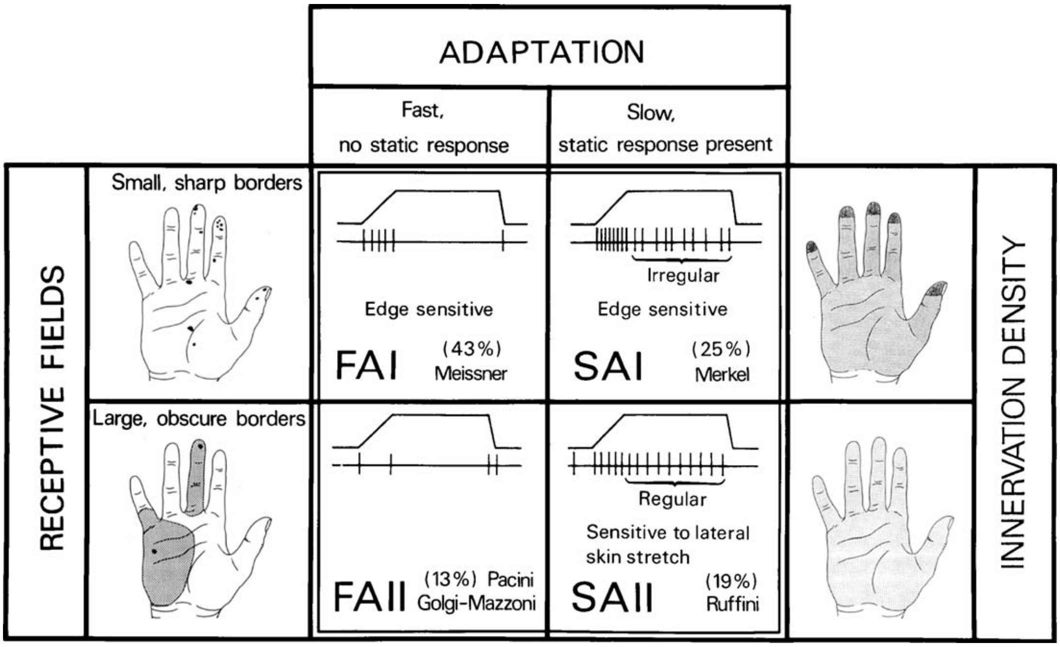

Fig. 3. The four types of low-threshold mechanoreceptors in human glabrous skin are depicted. The four panels in the centre show the nerve firing responses to a ramp and hold indentation and in % the frequency of occurrence and putative morphological correlate. The black dots in the left panel show the RFs of Type I (top) and Type II (bottom) afferents. The right panel shows the average density of Type I (top) and Type II (bottom) afferents with darker areas depicting higher densities (after Westling, 1986).

which were sensitive to small temperature changes and that were described as cold-specific units, but all had CVs in the C-fiber range (0.43–1.27 m s^{-1}). Textbooks describe the cutaneous cold sense in man as being mediated by myelinated A-fibers with CVs in the range 12–30 m s^{-1} (Darian-Smith, 1984a,b). However, Campero et al. (2001) have found that either human cold-specific afferent fibers are incompletely myelinated 'BC' fibers, or are C as well as A-cold fibers, with the C-fiber group contributing little to sensation. Duclaux et al. (1976) described 'BC' fibers as having electrophysiological and morphological properties of C-fibers in their distal part of the axon process, and B fibers at their proximal end. An example of a feature of these units can be seen in Fig. 4 where the resting activity at room temperature (21 °C), which is characterized by a low frequency discharge ($\sim$1 Hz), is suppressed by the sudden warming of the RF and is increased by cooling.

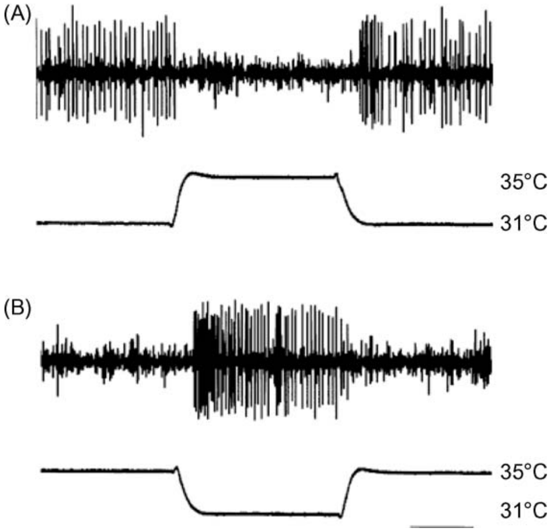

Fig. 4. Resting discharge of a C cold fiber at room temperature. (A) The resting discharge is suppressed by warming of the receptive field (RF) from 31 °C to 35 °C. (B) From a holding temperature of 35 °C, at which the unit is silent, activity is initiated by cooling the RF to 31 °C. (Time bar: 5 s) (see Campero et al., 2001 for single unit responses to a range of temperatures).

Free nerve endings for cold-sensitive or warm-sensitive nerve fibers are located just beneath the skin surface, and the terminals of an individual temperature-sensitive fiber do not branch profusely or widely. Rather, the endings of each fiber form a small, discretely sensitive point, separated from the sensitive points of neighboring fibers. The total area of skin occupied by the receptor endings of a single temperature-sensitive nerve fiber is relatively small ($\sim$1 mm in diameter) with the density of these thermo-sensitive points varying in different body regions. For example, there are approximately 20 cold points per square centimeter in the lips, 4 in the finger, and less than 1 cold point per square centimeter in trunk areas. There is also a differential innervation of cold and warm neurons with at least 5 times as many cold-sensitive points as warm-sensitive points. It is well established from physiological and psychophysical testing that warm- and cold-sensitive nerve fibers differ in both structure and function.

2.3. Pain

Here we consider a system of peripheral sensory nerves that innervate all cutaneous structures and whose sole purpose is to protect the skin against potential or actual damage. These primary afferents comprise $A\delta$ and C-fibers that respond selectively and linearly to levels of thermal, mechanical and chemical intensity/strength that are tissue threatening or damaging. This encoding mechanism is termed nociception and describes the sensory process detecting any overt, or impending, tissue damage (see Auvray et al., in this issue). Pain is described in terms of an 'experience' rather than just a simple sensation. Within the nociceptive system there are submodalities which are evident at the peripheral anatomical level are evident with respect to the degree of nerve fiber myelination (see Table 1). $A\delta$ fibers are thin (1–5 um), myelinated axons of mechanical and thermal nociceptors, with average CVs of 12 m/s. C-fibers are thin ($<$1 um), unmyelinated, slowly conducting axons ($<$1 m/s). Mechanical nociceptors in the Aδ range and possess RFs distributed as 5–20 small sensitive spots over an area approximately 2–3 mm in diameter. In many cases activation of these spots depends upon stimuli intense enough to produce tissue damage, such as a pinprick. Aδ units with a short latency response to intense thermal stimulation in the range 40–50 °C have been described as well as other units excited by heat after a long latency—usually with thresholds in excess of 50 °C.

Over 50% of the unmyelinated axons of a peripheral nerve respond not only to intense mechanical stimulation, but also to heat and noxious chemicals, and are therefore classified as polymodal nociceptors (Bessou and Perl, 1969) or C-mechano-heat (CMH) nociceptors (Campbell et al., 1989). A subgroup of polymodal nociceptors have been reported to respond to extreme cold, however, many of these units develop an excitatory response to cooling after prior exposure to noxious heat. A small number of C-fibers have mechanical thresholds in the nociceptor range with no response to heat while others have been found that respond preferentially to noxious heating. RFs of these C-fiber units consist of single zones with distinct borders and in this respect they differ from Aδ nociceptors that have multipoint fields. Innervation densities are high and responses have been reported to a number of irritant chemicals such as dilute acids, histamine, bradykinin and capsaicin. Schmidt et al. (1995) described not only CMH responsive units, but a novel class of C-fiber nociceptors responding only to mechanical stimuli (CM), units responding only to heating (CH), and units that were insensitive to mechanical and heating stimuli and also to sympathetic provocation tests (CMiCHi). Some CM, CH, and CMiCHi units can be sensitised to thermal and/or mechanical stimuli after topical application of skin irritants such as mustard oil or capsaicin—these units then acquire responsiveness to stimuli to which they were previously unresponsive. Recruitment of these 'silent' nociceptors implies spatial summation to the nociceptive afferent barrage at central levels, and may therefore contribute to primary hyperalgesia after chemical irritation and to secondary hyperalgesia as a consequence of central sensitisation (see below).

The axon terminals of nociceptive axons do not possess specialised end organ structures and for that reason are referred to as free nerve endings. This absence of any encapsulation renders them sensitive to chemical agents, both intrinsic and extrinsic. Inflammatory mediators released at a site of injury can initiate or modulate activity in surrounding nociceptors over an area of several millimetres leading to two types of hyperalgesia responses—the phenomenon of increased sensitivity of damaged areas to painful stimuli. Primary hyperalgesia occurs within the damaged area while secondary hyperalgesia occurs in undamaged tissues surrounding this area.

2.4. *Itch*

The sensation of itch has, in the past, been thought to be generated by the weak activation of pain nerves, but with the recent finding of primary afferent neurons in humans (Schmelz et al., 1997; Schmelz, in this issue), and spinal projection neurons in cats (Andrew and Craig, 2001), that have response properties matching those subjectively experienced after histamine application to the skin, it is now recognised that separate sets of neurons mediate itch and pain, and that the afferent neurons responsible for histamine-induced itch in humans are unmyelinated C-fibers. Until relatively recently is was though that histamine was the final common mediator of itch, but clinical observations in which itch can be induced mechanically or is observed without an accompanying flare reaction, cannot be explained as being mediated by histamine sensitive pruriceptors. These observations support the existence of histamine-independent types of itch nerves (Ikoma et al., 2005) in which itch is generated, without a flare reaction, by cowhage spicules. As with the existence of multiple types of pain afferents, different classes of itch nerves are also likely to account for the various experiences of itch reported by patients (Yosipovitch et al., 2002).

2.5. *Pleasure*

It is generally accepted that human tactile sensibility is solely mediated by LTMs with fast conducting large myelinated afferents (as described above). However, in recent years a growing body of evidence has been accumulating, from anatomical, psychophysical, electrophysiological and neuroimaging studies, for the presence of a population of C-fibers, found only hairy skin, that are neither nociceptive nor pruritic, but that respond preferentially to low force, slowly moving mechanical stimuli traversing their RFs. These nerve fibers have been classified as C-tactile afferents (CT-afferents), and were first described by Johansson et al. (1988) using microneurography. Evidence of a more general distribution of CT-afferents has subsequently been found in the arm and the leg, but they have never been found in glabrous skin sites (Vallbo et al., 1979). It is well-known that mechanoreceptive innervation of the skin of many mammals is subserved by A-fiber and C-fiber afferents (Zottermann, 1939; Bessou and Perl, 1969; Iggo and Korhuber, 1977), but until the observations made by Nordin (1990), C-fiber mechanoreceptive afferents in human skin appeared to be lacking entirely.

The functional role of CT-afferents is not fully understood (Mackenzie et al., 1975), but their neurophysiological response properties, fiber class, and slow conduction velocities preclude their role in any form of rapid mechanical discriminative or cognitive tasks, and point to a more limbic function, particularly the emotional aspects of tactile perception (Vallbo et al., 1993; Essick et al., 1999). However, the classification of a population of afferent low-threshold C-fiber mechanoreceptors responding preferentially to low velocity and low force mechanical stimulation, and the assignment of a functional role in human skin, has only recently been achieved as described by Olausson et al., in this special issue, and in Loken et al. (2009).

The recognition that cutaneous sensitivity can serve both discriminative and affective functions is best exemplified in the case of pain, in which two independent systems of cutaneous nerves serve two very different qualitative perceptual and emotional states, known as 1st and 2nd pain (Cross, 1994). The former is experienced as sharp or pricking sensation and is conveyed to the central nervous system by fast conducting myelinated Aδ afferents. 1st pain is responsible for controlling withdrawal reflexes such as when a potentially tissue threatening stimulus contacts the body surface. The sensations evoked by transitory stimulation are experienced immediately and are qualitatively devoid of any lasting emotional distress, serving a primary discriminative function—something is damaging the skin. The latter, 2nd pain, is conveyed to the central nervous system by C-fibers and generates far more qualitatively complex and, importantly, temporally delayed sensations and emotions, comprising qualities such as dull, throbbing, radiating and burning (Melzack, 1975). Stimulation of fast conducting A-fibers provides information for discriminative purposes, whereas stimulation of the C-fibers evokes emotional responses. Pain is defined as 'an unpleasant *sensory* and *emotional* experience associated with actual or potential tissue damage, or described in terms of such damage'. Use of the terms 'sensory' and 'emotional' refers to the dual nature of pain, with descriptions like "throbbing, prickly, hot, dull" referring to the sensory component of pain, and descriptions like "torturing, annoying, frightful, sickening" referring to the emotional qualities of pain. Pain is always a subjective psychological state – see Auvray et al., this issue – and it is an accepted fact that cutaneous ‘pain’ has both sensory/discriminative and affective/motivational properties – qualities that are critically dependent upon two classes of peripheral afferents – myelinated A-fibers and unmyelinated C-fibers. We propose that ‘touch’ is also characterised by sensory/discriminative and affective/motivational components, and that there are two touch systems parallel to the two pain systems. 1st touch is subserved by fast conducting Aβ afferents responsible for rapid identification of the physical properties of a tactile stimulus. The sensory information is primarily discriminative and non-emotional, conveying qualitative states such as “wet, hard, rough, etc.” and is essentially ‘immediate’ in terms of conscious awareness. By contrast, 2nd touch, mediated by slowly conducting mechanosensitive C-fibers (CTs), conveys information related to tactile inputs associated with affiliative and affective touch, such as those gentle and slow stroking touches experienced during grooming or nurturing behaviours. Importantly, as these inputs are conveyed via C-fibers, they do not reach immediate conscious awareness, generating the temporally delayed positive emotional attributes of touch in a similar manner to the delayed onset and qualitative properties of 2nd pain.

Work is in progress to identify this class of C-fibers histologically, with a study using the pan-neuronal marker PGP9.5 and confocal laser microscopy to identify a population of free nerve endings located solely within the epidermis that may represent the putative anatomical substrate for this sub-modality (Reilly et al., 1997). Recent evidence from Anderson’s group has shown, in a mouse model, a molecular genetic visualization of a rare subset of unmyelinated sensory neurons that they suggested may detect gentle touch (Liu et al., 2007). Using a genetically encoded tracer, they found that Mas-related G protein-coupled receptor B4 (MrgprB4) marks a subpopulation of unmyelinated, non-peptidergic sensory fibers that exclusively, and importantly in terms of the human microneurographic data, only innervate hairy skin. These fibers terminate in large arborisations similar in size and distribution to human C-fiber tactile afferent’s RFs, suggesting that MrgprB4 may provide genetic access to these elusive neurons in mice and enable the elucidation of their receptor molecular neurobiology.

2.6. *Sensory transduction*

Signalling of stimuli such as touch, temperature, pain and pleasure requires molecular recognition of stimulus and mobilization of a response in the form of an electrical signal. However, the relationship between stimulus and transduction pathway is anything but simple, and it is clear that perception of a single stimulus often requires several transduction mechanisms. Conversely, a given protein can contribute to several senses, e.g., heat and touch (Lumpkin and Caterina, 2007). The sensitivity of sensory circuits is further influenced and tonally regulated by extrinsic (e.g. UV radiation) and intrinsic (e.g. nerve growth factor) mediators.

Touch and tactile sensitivity require rapid and direct signalling that is provided by ion channels via interaction with both intracellular cytoskeletal and extracellular matrix proteins (Gillespie and Walker, 2001). The key mammalian ion channel candidates studied to date are the epithelial sodium channels and the acid-sensing ion channels (ASICs), both of which belong to the Degenerin/epithelial amiloride sensitive Na+ channel (DEG/ENaC) superfamily of ion channels, reviewed recently by Bonsch and Lewin (2006).

Although the fundamental role of ion channels as the molecular basis of mechanotransduction was first established in the nematode worm *Caenorhabditis Elegans*, and the fruitfly *Drosophila melanogaster*, a related vertebrate channel from mammalian tissue was later identified by Canessa et al. (1993). The first neural channel identified was the brain sodium channel (BNC1, also known as ASIC2), and it is one of several mammalian DEG/ENaC channels known to form homo- and hetero-multimers and is the basis of voltage-insensitive sodium channels which are expressed in both small and large dorsal root ganglia sensory neurons (Price et al., 2000). These amiloride sensitive sodium channels also respond to protons, although when expressed in low-threshold mechanoreceptors, the ASIC2 channels are not gated by low pH, possibly due to the requirement for activation of intact cytoskeletal support structures to allow gating. Likewise, in ASIC2 knockout mice, phenotypic testing shows that only LTMs are affected (Price et al., 2000; Driscoll and Tavernarakis, 2000; McIlwrath et al., 2005).

Protons can activate members of the ASIC family, generating a perception of sting and pain. However, other candidates have also been identified in recent years. Stimuli such as temperature, pain or chemical challenges acting on nociceptors are controlled peripherally via a complex regulation of activity in another series of ion channels, the thermoTRPs (Transient Receptor Potentials). One of the earliest proteins associated with heat pain was the vanilloid receptor subtype-1 (VR1, also referred to as TRPV1), identified as the molecular target for the pungent irritant, capsaicin (Caterina et al., 1997). TRPV1 is a classical cation channel and is expressed in cutaneous sensory nerve fibers, mast cells and epithelial cells of appendage structures (Stander et al., 2004). Interestingly, activity for temperature (hot and cold), pain and chemesthetic activity can all be explained in terms of the plasticity of a family of thermoTRP cation channels (Montell et al., 2002) which consist of 6-transmembrane polypeptide units that assemble as tetramers to form cation-permeable pores (Clapham, 2003). The presence of multiple TRP channels, with distinct localisation on sub-sets of C- and Aδ-sensory neurons allows for a wide spectrum of physiological activities to be regulated by these channels and accounts, at least in part, for the complexity of these transducer systems (Minke and Cooke, 2002). The gating mechanism for stimuli such as radiant heat remains to be elucidated, but again cytoskeletal components are believed to be crucial for activation of these cation channels.

Development of transgenic mouse models lacking expression of the VR1 gene shows that phenotypic characteristics in VR1 null (−/−) mice support a functional role for VR1 in sensory transduction of nociceptive stimuli, although it was apparent that other receptors could partially compensate for the loss of VR1 function (Caterina et al., 2000; Davis et al., 2000). As an understanding of the process involved in sensing temperature and chemical stimulation of nociceptors has evolved, it has become apparent that there are additional non-TRP proteins and receptors which also play a role in nociception, e.g., ASICs and the P2-X3 ATP receptor (Askwith et al., 2001; Souslova et al., 2000).

A key question in recent years has been whether the sensory neurons are the primary transduction element, or whether non-neuronal cells can act as the key signalling pathway, with subsequent activation of adjacent nerve terminals or neuronal structures resulting in a perception of touch, temperature, pain, or pleasure. Specialised epithelia structures such as hair cells, Merkel cells, and receptors on taste buds are known to play a role in sensory transduction, but recent evidence suggests that other candidates such as keratinocytes may also be primary transducers of mechanical stimuli (Lumpkin and Caterina, 2007). This emerging hypothesis stems from the observation, typically by immunohistochemical visualization, of mechano-, thermo- and chemo-sensitive receptors such as TRPV1 on epidermal keratinocytes (Inoue et al., 2002; Chung et al., 2004) and other non-neuronal cell types. The presence of sensory receptors on epidermal keratinocytes suggested a functional role in terms of permeability barrier homeostasis and it has been shown that TRPV1 agonists delay barrier recovery, whereas TRPV4 accelerates barrier recovery (Denda et al., 2007a). However, Denda et al. (2007b) further suggested that keratinocytes could be the primary transduction pathway, using signal transduction cascade mechanisms such as intracellular Ca^{2+} fluxes to evoke a response in adjacent C-fibers. Putative keratinocyte–neuron interactions, intermediate molecules and 2nd messenger cascades have been proposed and await validation (Lumpkin and Caterina, 2007).

A tonal balance in terms of mechanotransduction is achieved via several interconnected mechanisms, e.g., modulation of growth factors and receptors; 2nd messenger signalling pathways; interaction with cytoskeletal elements; alteration of nerve firing thresholds following presentation of the stimulus and consequent perceptual processing (e.g. the increase in touch sensitivity and hyperalgesia following inflammation reactions such as sunburn). Without this intricate level of control the sensory system would be swamped with redundant signals, or worse, would fail to recognise noxious and threatening stimuli and would thus fail to act to remove, neutralise or repair the threat. This ensures that at all times an appropriate response is mounted by the organism, whether it be in response to touch, temperature, pain or pleasure.

3. The central projections

The submodalties of skin sensory receptors and nerves that convey information to the brain about mechanical, thermal, and painful/pruritic stimulation of the skin are grouped into three different pathways in the spinal cord and project to different target areas in the brain. They differ in their receptors, pathways, and targets, and also in the level of decussation (crossing over) within the CNS. Most sensory systems *en route* to the cerebral cortex decussate at some point, as projections are mapped contralaterally, e.g., the discriminative touch system crosses in the medulla, where the spinal cord joins the brain, while the affective pain system crosses at the point of entry into the spinal cord.

3.1. *Spinal cord*

All the primary sensory neurons described above have their cell bodies situated outside the spinal cord in the dorsal root ganglion, with there being one ganglion for every spinal nerve. Unlike most neurons the nerve signal does not pass through the cell body of a sensory neuron: with the cell body sitting off to one side the signal passes directly from the distal axon process to the proximal process, which enters the dorsal half of the spinal cord.

Tactile primary afferents, or first order neurons, immediately turn up the spinal cord towards the brain, ascending in the dorsal white matter and forming the dorsal columns. In a cross-section of the spinal cord, at cervical levels, two separate tracts can be seen: the midline tracts comprise the gracile fasciculus conveying information from the lower half of the body (legs and trunk), and the outer tracts comprise the cuneate fasciculus conveying information from the upper half of the body (arms and trunk). Primary tactile afferents make their first synapse with second order neurons at the medulla where fibers from each tract synapse in a nucleus of the same name: the gracile fasciculus axons synapse in the gracile nucleus, and the cuneate axons synapse in the cuneate nucleus. The neurons receiving the synapse provide the secondary afferents and cross the midline immediately to form a tract on the contralateral side of the brainstem – the medial lemniscus – which ascends through the brainstem to the next relay station in the midbrain, specifically, in the thalamus.

As with the tactile system, pain and thermal primary afferents synapse ipsilaterally and the secondary afferents cross, but the crossings occur at different levels. Pain and temperature afferents enter the dorsal horn of the spine and synapse within one or two segments, forming Lissauer's tract. The dorsal horn is a radially laminar structure, the thin outermost layer is the posterior marginalis layer, the second layer the substantia gelatinosa, and the layer medial to that, the nucleus proprius. The two types of pain fibers, C and Aδ, enter different layers of the dorsal horn. Aδ fibers enter the posterior marginalis and the nucleus proprius, and synapse on a second set of neurons which are the secondary afferents which relay the signal to the thalamus. The secondary afferents from both layers cross to the opposite side of the spinal cord and ascend in the spinothalamic tract. C-fibers enter the substantia gelatinosa and synapse on interneurons—neurons which do not project out of the immediate area, but relay to secondary afferents in either the posterior marginalis, or the nucleus proprius. The spinothalamic tract ascends the entire length of the spinal cord and the entire brainstem, and on reaching the midbrain is continuous with the medial lemniscus. These tracts enter the thalamus together.

It is important to note that although the bulk of afferent input adheres to the plan outlined above a degree of mixing occurs between the tracts, for example, with some light touch information traveling in the spinothalamic tract, with the result that damage to the dorsal columns does not completely remove touch and pressure sensation. Some proprioceptive information also travels in the dorsal columns, and follows the medial lemniscus to the cortex providing conscious awareness of body position and movement. The pain and temperature system also has multiple targets in the brainstem and other areas.

Having now covered the basic anatomy of the part of the somatosensory system that serves the trunk and limbs, the peripheral and central anatomy/neurophysiology of facial skin will be briefly summarised here, as there are gross similarities in its innervation. The trigeminal (Vth) nerve innervates all facial skin structures (including the oral mucosa) and, as with the spinal afferents, these neurones have their cell bodies outside of the CNS in the trigeminal ganglion, with their proximal processes entering the brainstem. As in the spinal cord, the four modalities of touch, temperature, pain and itch have different receptors in the facial skin, travel along different tracts, and have different targets in the brainstem—the trigeminal nuclei extending from the midbrain to the medulla. The large diameter (Aβ) fibers enter directly into the main sensory nucleus of the trigeminal nuclei and as with the somatosensory neurons of the body, synapse and then decussate, with the secondary afferents joining the medial lemniscus as it projects to the thalamus. The small diameter fibers conveying pain and temperature enter the midbrain with the main Vth cranial nerve, but then descend through the brainstem to the caudal medulla where they synapse and cross the midline. These descending axons form a tract, the spinal tract of V, and synapse in the spinal nucleus of V, so-called because it reaches as far down as the upper cervical spinal cord, comprising three regions along its length: the subnucleus oralis, the subnucleus interpolaris, and the subnucleus caudalis. The secondary afferents from the subnucleus caudalis cross to the opposite side and join the spinothalamic tract where somatosensory information from the face joins that from the body, entering the thalamus in a separate nucleus, the ventroposterior medial nucleus (VPM).

In summary of this section, somatosensory paths are located in the dorsal columns and spinothalamic tracts, with axons in the former transmitting tactile, pressure, vibration and proprioception impulses, and in the latter pain and temperature. Which pathway CT-afferents travel in is not yet known, but low-threshold tactile inputs to spinothalamic projection cells have been documented (Applebaum et al., 1975), lending credence to reports of subtle, contralateral deficits of touch detection in human patients following destruction of these pathways after chordotomy procedures (White and Sweet, 1969). As will be seen in the next section, we have better knowledge of the cortical projections of CT-afferents.

3.2. Brain

Although we are only considering the peripheral to central pathways of the somatosensory system, the thalamus, often called the 'gateway' to the cerebral cortex, also acts as a relay structure for all other senses—even those from the archaic sense of smell pass through this structure (Herrrero et al., 2002). It should be noted, however, that the thalamus is not simply a 'relay' structure: it plays a major integrative role prior to projecting to the overlying primary sensory cortices. Its sensory inputs are both discriminative and affective, and, the thalamus is critical in adjusting affective scale, as is evidenced by lesions of this structure causing chronic pain for example (Jones, 2002).

The third order thalamocortical afferents (from thalamus to cortex) travel up through the internal capsule to reach the primary somatosensory cortex, located in the post-central gyrus, a fold of cortex just posterior to the central sulcus (Fig. 5A).

The thalamocortical afferents convey all of the signals, whether from VPL or VPM, to primary somatosensory cortex where sensory information from all contralateral body surfaces is mapped in a somatotopic (body-mapped) manner (Penfield and Rasmussen, 1952; Maldjian et al., 1999), with the legs represented medially, at the top of the head, and the face represented laterally (Fig. 5B). Within the cortex there are up to eight separate areas primarily subserving somatosensation. Primary somatosensory cortex. SI, comprising four sub-regions (2, 1, 3a and 3b), secondary somatosensory cortex, SII, located along the superior bank of the lateral sulcus (Woolsey, 1946; Maeda et al., 1999; Coghill et al., 1994; Francis et al., 2000; McGlone et al., 2002), the insular cortex (Schneider et al., 1993), and the posterior parietal cortex, areas 5 and 7b (Fig. 6). The secondary somatosensory cortex receives input primarily from SI and in turn projects to the somatic sensory fields in the insular region. Olausson et al. (2002) have also shown that CT-afferents project to the dorsal posterior part of the insular, presumably bypassing SI, since patients with no Aβ afferents demonstrate a lack of activation to brush stroking of hairy skin in this region (see Olausson et al., in this special issue). In addition to the primary and secondary somatosensory cortices, the posterior parietal lobe also receives somatic inputs. This region is a higher order sensory cortex, similar in function to an association cortex, it relates sensory and motor processing and is concerned with integrating the different somatic sensory modalities necessary for perception.

As with studies of the peripheral nervous system, outlined above, the technique of microneurography has again been used in somatosensory research, in this case to study the relationship between skin sensory nerves and their central projections, as evidenced by the use of concurrent functional magnetic resonance imaging (fMRI). Microstimulation of individual LTM afferents, projecting to RFs on the digit, produces robust, focal and orderly (somatotopic) haemodynamic (BOLD) responses in both primary and secondary somatosensory cortices (Trulsson et al., 2000)—in accordance with the findings of Penfield and Boldrey (1937). It is expected that this technique will permit the study of many different topics in somatosensory neurophysiology, such as sampling from FA and SA mechanoreceptors and C-fibers with neighboring or overlapping RFs on the skin, and quantifying their spatial and temporal profiles in response to electrical chemical and/or mechanical stimulation of the skin areas they innervate, as well as perceptual responses to microstimulation.

Finally, the forward projections from these primary somatosensory areas to limbic and prefrontal structures have been studied with fMRI and PET in order to understand the affective representations of skin stimulation for both pain and pleasure. Evidence for the representation of pleasant touch in the brain has been provided by Francis et al. (1999). They showed that the

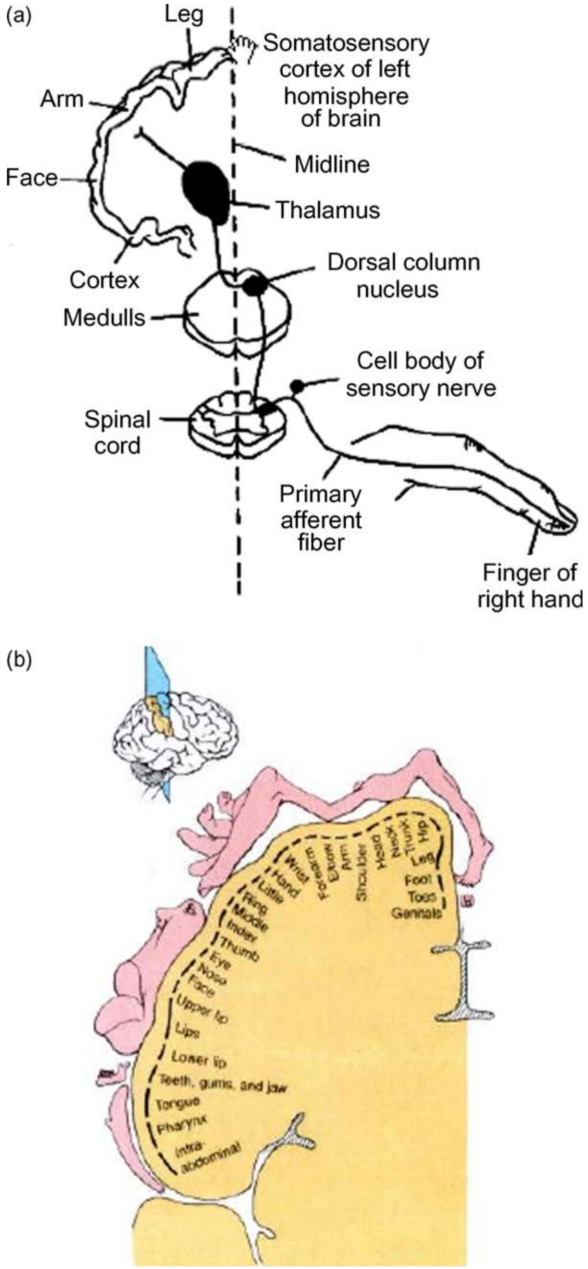

Fig. 5. (A) Outline of the somatosensory pathways from the digit tip to primary somatosensory cortex, via the dorsal column nuclei and the thalamus. (B) Penfield's (Jasper and Penfield, 1954) somatosensory homunculus. Note the relative overrepresentation of the hands and lips, and the relative under-representation of the trunk and arms.

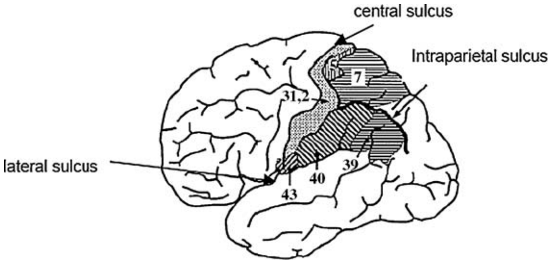

Fig. 6. Cortical areas subserving somatosensation. Primary somatosensory cortex (SI) is located in the posterior bank of the central sulcus and the posterior gyrus and comprises Brodmann Areas 2, 1, 3a and 3b. Secondary somatosensory cortex (SII) is located in the upper bank of the lateral sulcus and comprises Brodmann Areas 43 with two further somatosensory regions in the posterior parietal cortex, Brodmann Areas 5 and 7b.

discriminative and affective aspects of touch are processed in different brain areas, by stroking the body with either a wooden dowel or a piece of velvet. Activation of primary somatosensory cortex was found to be greater to the wood stimulus, whereas the orbitofrontal cortex (an area of the frontal lobes involved in emotion) was activated more by the velvet stimulus. This area has also been shown to represent painful as well as pleasant touch, demonstrating the relevance of this brain region for representing the emotional dimensions of skin sensitivity—the positive and the negative (Rolls et al., 2003).

4. Conclusion

This overview of the cutaneous senses provides a landscape view of the system's structure and function, with the following review papers in this Special Issue highlighting specific aspects and properties of the skin senses and their roles in sensation, affect and cognition. Cutaneous sensitivity is central to human functional, emotional and social life, as is evidenced by it being the most developed sensory modality at birth, contributing to brain and cognitive development throughout infancy and childhood (Stack, 2001; Hertenstein, 2002), and continuing to play a vital role into old age. That the skin senses can serve both a discriminative as well as affective role is well known from our understanding of pain. The different conduction speeds with which tissue-damaging cutaneous sensations are conveyed to the CNS, by myelinated (Aδ) and unmyleninated (C) fibers, leads to the distinction of 1st and 2nd pain, with the former having a discriminative quality and the latter an emotional one. Here we have suggested a similar dualism for touch with discriminative touch being conveyed by myelinated Aβ afferents, and emotional touch by CT-afferents leading to the description of 1st and 2nd touch.

The results of anatomical, psychophysical, behavioural, neurophysiological and neuroimaging studies have shown that separate information processing channels, each with its own neurobiological mechanism exist for the perception of tactile, thermal, pruritic and painful stimuli. Evidence is also presented here (and elsewhere in this Special Issue) for a specific 'fifth' channel, coding for the perception of the rewarding aspects of touch. However, fundamental questions remain concerning the nature of how these channels, with their individual properties, operate together in the perception of the various stimuli naturally encountered by the skin. Co-activation of channels is the norm: mechanical stimuli also activate thermal channels, scratching reduces itch while rubbing reduces pain, and with all forms of affective and affiliative touch there is co-activation of mechanosensitive A-fibers as well as, in hairy skin, mechanosensitive CT fibers. An adequate test of the hypothesis that the perception of any complex cutaneous stimulus involves the interaction of individual channels requires that we fully understand the characteristics of each channel, and determine the mechanisms by which they interact. Evidence for such interactions driving the perception of complex skin sensations comes from the early work of Bentley (1900), who showed that the "touch blend" of pressure and coldness leads to an emergent perceptual experience of wetness. The more recent discovery of linear summation of perceived magnitudes from different mechanosenstive channels provides further partial confirmation of the hypothesis (Gescheider et al., 2003), but there are many other possible ways in which these and the other channels outlined in this paper could interact that must be investigated before the hypothesis becomes a general principle of cutaneous sensory information processing.

The musical analogy of a piano keyboard can best describe the distinctions between activation of single channels, and co-activation of a number of channels. Stimulation of a single SAI channel (note on the keyboard) for example, such as occurs with intra-neural microstimulation, leads to a distinct sensation of pressure emanating from the RF of the unit. We know from the work of Bentley (1900) that if a cold sensing unit were also able to be co-activated (playing a second note on the keyboard), then a 'chord' is struck, perceptually, that relates to neither of the specific channel's coding properties (pressure and temperature), but generates the percept of wetness. The richness of perceived bodily sensations (far more than a channel specific view would serve) is dependent upon the diversity of the many channels of cutaneous sensory input to the CNS, as well as to the integrative properties of the various stages at which these inputs are processed, from the dorsal horn to the sensory awareness stages in SI/SII, to the affective representation in insula and orbitofrontal cortices. It has been recognised for some time that the mind can affect the skin (O'Donovan, 1927; Stokes and Beerman, 1940; Arck et al., 2006), we are now recognising that the skin can affect the mind . . ..

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Sensors and Actuators A 179 (2012) 17–31

Contents lists available at SciVerse ScienceDirect

Sensors and Actuators A: Physical

journal homepage: www.elsevier.com/locate/sna

Review

A review of tactile sensing technologies with applications in biomedical engineering

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ARTICLE INFO

Article history:
Received 27 September 2011
Received in revised form 28 February 2012
Accepted 28 February 2012
Available online 7 March 2012

Keywords:
Tactile sensing
Tactile devices
Shear-stress sensors
Review of technology
Advancements and challenges

ABSTRACT

Any device which senses information such as shape, texture, softness, temperature, vibration or shear and normal forces, by physical contact or touch, can be termed a tactile sensor. The importance of tactile sensor technology was recognized in the 1980s, along with a realization of the importance of computers and robotics. Despite this awareness, tactile sensors failed to be strongly adopted in industrial or consumer markets. In this paper, previous expectations of tactile sensors have been reviewed and the reasons for their failure to meet these expectations are discussed. The evolution of different tactile transduction principles, state of art designs and fabrication methods, and their pros and cons, are analyzed. From current development trends, new application areas for tactile sensors have been proposed. Literature from the last few decades has been revisited, and areas which are not appropriate for the use of tactile sensors have been identified. Similarly, the challenges that this technology needs to overcome in order to find its place in the market have been highlighted.

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0924-4247/$ – see front matter © 2012 Published by Elsevier B.V.
doi:10.1016/j.sna.2012.02.051

1. Introduction

As humans, we utilize our vision, touch, taste, smell and sound sensory receptors as a means to experience and interact with the surrounding environment. Exploiting one or a combination of these senses, humans discover new and unstructured environments. For example, as humans, the ease with which we perform dexterous tasks, such as manipulating an egg, is taken for granted. When manipulating an egg, the shape, size, temperature, color and texture are transmitted to the brain from the sensory receptors. If the applied force is too little, the egg slips. Contrarily, if the force applied is too great, the egg will break. A precise force is applied and constant feedback of the measured applied forces keeps the egg intact. In addition, *a priori* knowledge of the egg's physical attributes, such as its weight and fragility are also integrated into the cortical processing used for the manipulation task. If the same task is to be achieved using a robotic manipulator, sensory inputs similar to those possessed by humans are essential to provide the necessary feedback to explore and interact with objects. Given that a robotic manipulator is unlikely to possess contextual *a priori* information about the object being manipulated, accurate sensory feedback is even more critical.

1.1. What is tactile sensing?

This paper reviews artificial research in the field of tactile sensor design. Tactile sensors are a category of sensors that acquire tactile information through physical touch. The measured characteristics can be properties such as temperature, vibration, softness, texture, shape, composition and shear and normal forces. A tactile sensor may measure one or more of these properties. Although pressure and torque sensing is often not included in the definition of tactile sensing, pressure and torque are important properties, typically acquired by physical touch, and can be included as tactile parameters.

1.2. Scope of tactile sensing technology

The maturation of tactile sensing technology has been anticipated for over 30 years. Early researchers such as Harmon, saw huge potential and application of tactile sensing in areas of robotics [1–3]. It is interesting to mention that Harmon considered tactile sensing unfit for areas such as medicine and agriculture because of technical difficulties and low return on investment [4]. In the same time, other researchers such as Nevins and Whitney argued that passive monitoring will eliminate the need of tactile sensing [5]. Around the start of the 21st century, it was envisioned that this technology would have the potential to support the development of more intelligent products and systems and hence improve the quality of human life [6,4]. At the top of this list of applications were medical robotics and industrial automation [6]. It is the belief of the authors that the scope of this technology is much wider and spans across many other disciplines, as discussed later in Section 4.5 of this review and summarized in Table 6. This survey will show, however, that this technology failed to gain significant entry into many of its target markets, either industrial or commercial, until the 1990s. The importance of tactile systems becomes apparent in applications where other sensing modalities, such as vision for example, may not be the best sensing modality; especially in unstructured or space-limited scenarios, as discussed later. Although particular importance and effort has been put into the development of tactile sensors over the past three decades, a satisfactory artificial tactile sensor that can provide feedback matching the human sense of touch has not yet been realized and in turn limits progress in fields such as robotics and minimally invasive surgery [7–12].

1.3. Earlier technological reviews

Force and tactile feedback research is currently a multidisciplinary enterprise [13]. Comprehensive surveys of tactile sensor technologies have been performed in the past and are available in the literature. Some of the earliest surveys were carried out by Harmon in 1980 [3], 1982 [1] and 1984 [2]. Tactile sensing for robotics and mechatronics applications have also been reviewed and reported in the literature [6,14–19]. In 2000, Lee published a short, yet comprehensive, review on tactile sensing technology and analyzed the causes of delayed acceptance of this technology among industrial and consumer markets [4]. In 2003, Eltaib and Hewit examined tactile sensing systems for minimally invasive surgery and reasserted the importance of the technology for this particular field [20].

Although a number of books written on robotics and sensors cover tactile sensors, not many books have been written on tactile sensors alone [21–25]. A few noteworthy books have also been published on tactile sensing. Wettels in his book [26], demonstrated how sensor can mimic human skin. One of the most comprehensive book on tactile sensing for biomedical applications was published in 2009 by Najarian and Dargahi [27]. The book encompasses the basics of human tactile sensing, intrinsic sensing technologies and applications in areas of biomedical engineering.

In comparison to previous reviews of tactile sensing technology, this paper extends previous reviews by focusing on the current state-of-the-art in the discipline, trends in tactile sensor research, outstanding challenges which must be overcome, principles of operation and advantages and deficits of different tactile sensor designs are also discussed. We also propose additional applications of this technology, in the fields of recreational sport, aerospace engineering, automotive manufacture and rehabilitation medicine, in addition to the previously explored fields.

We start with a overview of some common tactile sensing transduction techniques.

2. Tactile transduction techniques

Some commonly researched tactile transduction techniques are based on capacitive, piezoresistive, thermoresistive, inductive, piezoelectric, magnetic and optical methods. The intrinsic principles associated with these techniques have their own advantages and disadvantages, which are well established [27,28]. In general, capacitive, piezoresistive, piezoelectric, inductive and optical methods show a potentially superior performance and usefulness and are often the preferred choice of sensor designers. In this section, we give a brief review of these methods and their relative advantages and disadvantages; these are also summarized in Table 1.

2.1. Capacitive tactile sensors

A capacitive sensor consists of two conductive plates with a dielectric material sandwiched between them. For parallel plate capacitors, capacitance can be expressed as, $C = (A\varepsilon_0\varepsilon_r)/d$. Where C is the capacitance, A is the overlapping area of the two plates, ε_0 is the permittivity of free space, ε_r is the relative permittivity of the dielectric material and d is distance between the plates. Capacitive tactile sensors generally exhibit a good frequency response, high spatial resolution, and have a large dynamic range. These sensors are more susceptible to noise, especially in a mesh configurations because of crosstalk noise, field interactions and fringing capacitance and require relatively complex electronics to filter out this noise.

2.2. Piezoresistive tactile sensors

These sensors typically consist of a pressure sensitive element which changes its resistance upon application of force. The voltage–current characteristic of a simple resistive element can be expressed as, $V = IR$; where V is the voltage, I is the current and R is the electric resistance of the material. Usually some property of the voltage (or current) is fixed and a change in resistance is observed by a change in the current (or voltage). This resistive element generally takes the form of a conductive rubber, elastomer, or conductive ink which is pressure sensitive. They generally require less electronics as change in resistance can easily be quantified and are therefore easy to manufacture and integrate. They are less susceptible to noise and therefore work well in mesh configurations as there is no cross talk or field interactions. Resistive tactile sensors suffer from hysteresis and therefore have a lower frequency response when compared to capacitive tactile sensors.

2.3. Piezoelectric tactile sensors

Various materials, especially certain crystals and some ceramics, generate a voltage potential when the crystal lattice is deformed [10,11]. The sensitivity of the crystal depends on its cut/structure, allowing it to distinguish between transverse, longitudinal and shear forces. The voltage, V, generated is directly proportional to the applied force, pressure or strain. These sensors exhibit a very good high-frequency response, which makes them an ideal choice for measuring vibrations; however, they are limited to measuring dynamic forces and are unable to measure static forces due to their large internal resistance. The charge developed decays with a time constant which is determined by the internal impedance and dielectric constant of the piezoelectric film. During sensor design, the input impedance of the interface electronics must be considered as it significantly effects the response of the device.

2.4. Inductive tactile sensors

A primary coil induces a magnetic field which is sensed in a secondary sense coil. Modulating the mutual inductance between the coils, for example by changing the length of an iron core in the case of a linear variable differential transformers, in turn modulates the amplitude and phase of the voltage measured in the sense coil. These sensors have a very high dynamic range and an often rugged construction, but are bulky in size, which leads to a very low spatial resolution when arrayed. Due to their mechanical nature, they have lower repeatability as coils do not always return to the same position between readings. Since these sensors use an alternating current in the primary coil, hence producing an output voltage at the same frequency, they require more complex electronics than normal resistive tactile sensors as the alternating signal amplitude must be demodulated.

2.5. Optoelectric tactile sensors

Optoelectric sensors employ a light source and a transduction medium and a photodetector, the latter often in the form of a camera or a photodiode. Usually transduction occurs when changes in the tactile medium modulate the transmission or reflectance intensity, or the spectrum of the source light, as the applied force varies. They have high spatial resolution, and are immune to common lower frequency electromagnetic interference generated by electrical systems, which is their major advantage. Although they have many benefits, their size and rigidness are major disadvantages. Camera-based tactile sensors require considerable processing power but give a wide ranging frequency response.

2.6. Strain gauges

Strain gauges are widely used, low cost sensors that measure mechanical strain, typically by a change in resistance [29]. Strain gauges are often attached to the substrate using special glues,

Table 1
Transduction techniques and their relative advantages and disadvantages. For in depth discussion on these techniques, refer to [27,28].

Transduction technique	Modulated parameter	Advantages	Disadvantages	Typical design examples
Capacitive	Change in capacitance	Excellent sensitivity Good spatial resolution Large dynamic range	Stray capacitance Noise susceptible Complexity of measurement electronics	[41–47]
Piezoresistive	Changed in resistance	High spatial resolution High scanning rate in mesh Structured sensors	Lower repeatability Hysteresis Higher power consumption	[48–53]
Piezoelectric	Strain (stress) polarization	High frequency response High sensitivity High dynamic range	Poor spatial resolution Dynamic sensing only	[54–60]
Inductive LVDT	Change in magnetic coupling	Linear output Uni-directional measurement High dynamic range	Moving parts Low spatial resolution Bulky Poor reliability More suitable for force/torque measurement applications	[61–67]
Optoelectric	Light intensity/spectrum change	Good sensing range Good reliability High repeatability High spatial resolution Immunity from EMI	Bulky in size Non-conformable	[68–74]
Strain gauges	Change in resistance	Sensing range Sensitivity Low cost Established product	Calibration Susceptible to temperature changes Susceptible to humidity Design complexity EMI induced errors Non-linearity Hysteresis	[38,75–77]
Multi-component sensors	Coupling of multiple intrinsic parameters	Ability to overcome certain limitations via combination of intrinsic parameters	Discrete assembly Higher assembly costs	[31,32,36,37]

depending on their required lifetime. Strain gauges are very sensitive and highly susceptible to humidity and temperature changes. To overcome these problems, strain gauges are often used in Wheatstone bridge configurations [30]. If overloaded, strain gauges cannot be recovered. Due to their mechanical nature, they have high hysteresis and often are non-linear in response. One major advantage of strain gauges is that they have been widely used for a long time and therefore best practices for their use are well established.

2.7. Multi-component tactile sensors

Combining multiple different transducers in one sensor to overcome the shortcomings of each different devices has also been investigated by several researchers [31,32]. For example, a PVDF (polyvinylidene fluoride) film can only detect dynamic forces and has a well established ability to detect slip [33–35], but cannot measure static forces. This limitation can be overcome through the addition of a resistive or capacitive element, and thus making a slip and static force detecting sensor [31,32,36,37]. For applications where flexibility or large area coverage is a requirement, fluid based tactile sensors are commonly used, combining various intrinsic methods to achieve the task [38–40].

3. Past trends and advancements

In this section, research and development trends and advancements are presented, from emerging applications to commercialization of tactile sensors. A steadily increasing trend in research and demand can be seen in both academic (Table 2) and commercial sectors (Table 3).

3.1. Inception in the 1970s

A detailed survey of related research in the 1970s was performed by Harmon [3,1,2]. Although these surveys covered 160 papers, a careful review of the references reveal that most of the papers addressed other sub-areas of robotics rather than directly contributing to tactile sensor technology [4]. For example, it was realized that if robotic grippers could handle soft, fragile and hard objects, robots could be used in a broader range of fields, such as manufacturing industry, military weapon systems, medical treatments and agriculture [78]. Hence to develop better grippers, some researchers developed tactile sensors or tactile sensing mechanisms [78–82].

3.1.1. Major contributions

As stated above, although tactile sensing was not a mainstream research area, the use of tactile sensors in products to improve quality of human life, especially in the field of biomedical engineering, resulted in some cutting edge outcomes.

For example, Pfeiffer et al. took the challenge of developing a prosthetic device intended to overcome neuropathy of the hand that can result from injury or disease [83]. Neuropathy of the hand is a very severe, untreatable condition, as the patient is always

Table 2
Count of papers per decade, starting in the 1970s, using the search terms “tactile AND sensor” grouped by decade.

Year	Scopus	IEEE	Compendex	SPIE Digital Library	Springerlink
1970–1979	47	4	42	–	0
1980–1989	536	97	480	–	8
1990–1999	647	342	607	40	117
2000–2009	1341	675	1132	70	1709

Table 3
Count of patents filed, grouped by decade, using the search terms “tactile AND sensor”.

Year	US Patents		European Patents		Japanese Patents	World Intellectual Property Organization (WIPO)
	Scopus	Compendex	Scopus	Compendex	Scopus	Scopus
1970–1979	84	4	–	–	3	2
1980–1989	377	45	102	29	69	36
1990–1999	1281	91	411	77	107	570
2000–2009	11772	447	969	229	107	2291

in danger of accidental self-inflicted injury due to the absence of sensation, including pain. The prosthetic device was intended to provide haptic feedback to such patients using tactile sensors worn on fingers. The flexible pressure sensors used a mercury strain gauge. An signal generator emitted an audible sound whose frequency was modulated as a function of pressure. Although the device had several limitations, such as signal distortion, it gave patients the ability to differentiate between no force and modest forces. Pfeiffer et al. concluded that tactile sensors held the potential to ease the disability of neuropathy, but much work was needed before such devices could become standard prosthetic aides, as it only gave an indication of the presence of force, rather than its magnitude.

In a similar effort, Shaw et al. used tactile sensors in myoelectric upper limb prostheses to provide electrocutaneous feedback to the wearer [84]. Stojiljkovic and Clot took their efforts one step further and tried to detect slip in upper limb prostheses [85]. They covered a hand prostheses with planary distributed transducers and called it “artificial skin”. This artificial skin consisted of deformable elastomer electrodes, covered with a superior conductive layer, to which a voltage was applied. Upon application of force, the resistance of the elastomer electrodes changed. Experimentation showed that tactile sensors could be used to provide slip perception of the grasped objects in prosthetic grippers. But at that time it was not possible to measure the elasticity of materials using these tactile sensors [86].

One impressive development was reported by Kinoshita et al. [87]. In an attempt to develop pattern classification methods for systems utilizing visual and tactile sensors, a tactile sensor array using piezoelectric sensing elements was developed and integrated in a robotic hand. With the aid of a pattern classification model, the device was able to discriminate between cylindrical and square pillars. Kinoshita et al. concluded that for stereometric pattern recognition, a visual-tactile symbiotic system was more practical and efficient than conventional methods [87].

3.1.2. Advancements and achievements

The work in the 1970s laid the cornerstone of tactile sensing research. The research outcomes in this period were understandably primitive, but by the end of this decade tactile sensing was recognized as a field of study that had the potential to address many engineering problems associated with robotic manipulation.

3.1.3. Hurdles and challenges

By end of the 1970s a number of challenges remained. Although the need for tactile sensing technology was accepted by many, and some success was achieved in demonstrating its feasibility to solve real life problems, as discussed previously in Section 3.1.1, tactile sensing was often reported as a minor area of research within a major project. The main reason was that robotics and computers were starting to gain the interest of research and funding organizations, as research in these fields was still in its embryonic stages but obviously offered great returns on investment [4]. It is therefore fair to state that tactile sensing was a minor interest, secondary to what would become a feverish interest in developing sophisticated, reliable and faster robotic and computer systems. A second but inevitable impediment to progress was immaturity of the field, as many tactile transduction materials were yet to be discovered. Lastly, research was lacking direction and focus, as no design criteria had ever been specified, taking into consideration the industrial or biomedical engineering needs at the time.

Ultimately, researchers did demonstrate that this field of tactile sensing had the potential to investigate a number of unsolved problems and therefore deserved attention as a mainstream research area.

3.2. Evolution in the 1980s

A major step in highlighting the significance of tactile sensing technology and its possible applications was taken by Harmon in 1980 with his review [3]. The potential of this technology was further emphasized by two more papers which followed shortly afterwards [1,2]. The unavailability of any design criteria was still a major obstacle to progress. Harmon also attempted to specify design criteria for tactile sensors. He surveyed the industry with a set of questionnaires and interviews and based his design criteria on the desired sensor parameters required by the respondents at that time. Harmon proposed that a spatial resolution of 1–2 mm, frequency response of up to 100 Hz, a minimum sensitivity of 1 g and a preferably monotonic relationship between the sensor output and the force applied, were preferred characteristics of most tactile sensors. Later, Lee summarized this criteria, shown in Table 4 [4].

3.2.1. Motivation and research direction

The primary research objective in the 1980s was to develop reliable tactile sensors for robotics. Harmon’s proposed design criteria were often used by researchers to justify their research direction [4]. Development of tactile sensors for medical devices, as described in Section 3.2.2, was the second major area of interest.

Due to the coupling of biomedical and tactile sensing technologies, an important outcome was the inspiration to develop sensors and materials which could mimic the response of mechanoreceptors in the human skin [88,89]. Rossi felt that the tendency of researchers to develop sensors which mimic the human tactile system was placing unnecessary restrictions on sensor requirements, as the human tactile system may not be the universal solution to tactile sensing [28]. Rossi believed that every design problem has its own set of challenges and constraints, and advocated the need for different specifications and design requirements.

Table 4
Design criteria proposed by Harmon [3] and later summarized by Lee [4].

Sensing surface	Complaint and durable
Spatial resolution between sensing points	1–2 mm
Number of sensing points in an array	Between 50 and 200
Minimum pressure sensitivity	1 g
Dynamic range	About 1000:1
Output response	Monotonic, not necessarily
Frequency response	At least 100 Hz
Stability and repeatability	Good
Hysteresis	Low

3.2.2. Advancements and noteworthy contributions

Research trends to this date had been device-driven rather than task or application-driven [4]. It was hoped that these devices would find application in the market upon development; although very few, if any, reached the market or became part of other systems. This survey indicates that work in this decade did move towards application driven designs. Attempts were made to solve real problems such as overcoming birth injuries [90,91], orthoses for the disabled [92,93], development of a portable terminal for the blind [94], and as an aid for neuromuscular control [95]. The research outcomes were often not deployed in real world medical applications due to the regulatory constraints required before new devices could be used in clinical settings.

Another novel research area was the development of an audio-tactile device for the blind, with the aim to improve the accessibility of stored information for blind people [93]. The device enabled the vision impaired to read data stored in computer memory. The system consisted of a multi-touch tactile sensor, data memory unit and a voice synthesizer. By touching a point on the tactile sensor, the corresponding data in memory was synthesized. Although it was a very promising design with an actual need in real life, the design was limited by the lack of technological advancements in data storage and data acquisition devices.

One state-of-the-art tactile sensor array, based on a very large scale integration (VLSI) computing array, was developed in the 1980s [96]. The force transduction was performed using conductive rubber and metal electrodes assembled on the surface of the purposely built integrated circuit. The use of VLSI technology led to an integrated, low wire count, serial output and high resolution sensor array which could operate at very high speeds. The most important contribution of this research was the introduction of arrayed, high speed and high spatial resolution concepts in tactile sensing technology. The high cost of VLSI-based designs kept this approach within the confines of the laboratory, with little adoption by industry.

3.2.3. Limitations and challenges

Although some researchers tried to test tactile sensors in real world environments, both in the disciplines of robotics and biomedical engineering, these efforts were limited. The main advancement in this decade was the exploration of different transduction techniques and the collation of the relative advantages and disadvantages between these techniques. The high cost of manufacturing small-scale designs (both electrical and mechanical) and high computational costs were major technological constraints preventing advancement.

By the end of the 1980s, major advancements in low cost manufacturing and computational capabilities were occurring, which would lay the foundations for progress in subsequent years. For a detailed review of transduction techniques explored in this time, and pros and cons established, refer to [97,28]. For a detailed review of this decade, refer to the review by Nicholls and Lee [16].

3.3. Developments in the 1990s

By the end of the 1980s, with advancements in computational processing power, realization of complex and real time algorithms became possible. Characterization and discrimination algorithms became a new area of interest.

As shown in Tables 2 and 3, an increased interest in this technology is evident. But a shift in the interests of researchers was also evident. Lee reported a shift towards softer, natural systems, away from constrained, solid-materials of the industrial arena [4].

3.3.1. Demand and motivation

During this period, Nicholas and Lee reported on sensor design and construction, haptic and active perception, and analysis and experience, as the three major areas of research in tactile sensing [6]. Lee reported better engineering and new materials, the increased importance of the understanding of sensors, improved dexterous robotic hands and new medical applications as the notable areas of development in the 1990s [4]. However, due to lack of penetration of this technology into industrial applications, the focus of research changed from industrial to unstructured domains [6].

3.3.2. Emergence of new problems, challenges and application areas

A major highlight of this era is the application of tactile sensing in minimally invasive surgery (MIS). The term MIS was first coined by Wickham in 1984, and later published in 1987 [98]. MIS, also known as endoscopic surgery, is considered to be one of the biggest success stories in medical history [99]. But this technology is somewhat limited by restricted mobility, lack of perception of depth and minimal tactile feedback [100]. Some notable attempts to apply tactile sensing in endoscopic surgery have been reported [101–107].

A sophisticated optical tactile array of 64 measurement points on a 0.64 cm^2 surface area was presented by Fischer et al. [108]. The sensor was conceived to be integrated in the laparoscopic grasping forceps, while the measured values activated a vibrotactile display unit for tactile feedback to the surgeon's fingertip. Another important development was that of a tactile sensor for thoracoscopic detection of small and invisible pulmonary nodules [109]. This sensor was first tested on pigs, followed by clinical testing on humans, showing that tactile sensing is not just a laboratory technology but can be used to solve real life challenges.

Rehabilitation and service robotics concept designs also began to emerge, motivated by concerns for aging populations and to improve quality of life for the disabled. For service robots, especially those which are intended to assist elderly or disabled people, the robot's ability to interact with a changing environment is of critical importance. This calls for dexterous robots with intelligent sensors.

This need for tactile sensing to overcome the challenges associated with useful functioning of service robots in uncontrolled environments was realized in the early 1990s. Keane and Greg highlighted that although further research in tactile sensors is required in order to develop robust, economic and general purpose sensors, there are a number of applications where information is best acquired by tactile means [110].

For such robots, Hohm et al. suggested rule-based behavior to autonomously plan navigation, using mainly tactile sensor information [111]. Seitz integrated vision and tactile sensing to overcome the limitations of using vision systems in unstructured environments [112]. Their research showed that vision and tactile sensors can be integrated into the hands/manipulators of service robots to assist humans in industrial or service environments. A significant attempt was made by Ueno and Haruki to develop an autonomous anthroposophic service robot (HARIS) [113]. The five fingered robot had 178 tactile sensors.

Although, industrial service robots have been a success, service robots capable of working in unstructured environments have not yet been realized. Research in this area not only explored the benefits of research to develop service robots, but also provided motivation for further research.

3.3.3. Advancement and limitations

Research in this period led to an increased demand for the application of tactile sensing in the fields of food processing, automation and biomedical engineering. Increased spatial resolution was achieved, which lead to surface texture profiling and hardness characterization. Piezoelectric elements and arrays of capacitive and resistive elements evolved as the preferred choice of transduction. Integrated circuit devices were also fabricated which helped to miniaturize the sensor systems. Analysis of effects of elastomer skins on tactile sensor responses, the dynamics of slip and a deeper understanding of human tactile sensing were also reported. For a detailed survey of this period, refer to reviews by Nicholas and Lee and Lee [6,4].

3.4. *Recent advancements in the 21st century*

Both research and commercial sector have recently begun to direct their attention towards tactile sensing technologies, as evidenced by Tables 2 and 3. Tactile sensing is finding its place as a feasible technology and is enhanced by advancements in computation, fabrication methods and materials. The limitations of vision systems have also been established and calls have been made for the development of novel sensing systems, especially for space confined and/or unstructured environments [114,112].

In contrast to the 1970s and 1980s, when the motivation for research in tactile sensing technology was primarily to develop intelligent robotics, the main motivation today is to develop systems for biomedical applications and tactile sensing systems for unstructured environments. Some of these applications of tactile sensing in biomedical engineering and robotics are discussed below.

3.4.1. *Minimally invasive surgery*

The state-of-the-art in force and tactile sensing for MIS has recently been reviewed [115]. Although the benefits of MIS technology have been proven, the limitations of two-dimensional visualization, lack of haptic feedback and long learning times are their limiting factors [116–118].

Haptic feedback refers to restoring sense of both tactile and force information [119]. The need for restoration of haptic touch has increased; especially due to the expectations of tele-robotic systems in general, and MIS in particular. Although force feedback is provided in the da Vinci surgical system (Intuitive Surgical Inc., USA) to compensate for lack of a tactile sense, having tactile feedback would enable analysis of tissue characteristics and pathological conditions. Similarly, force feedback allows detection of collisions with rigid structures but does not prevent damage to soft tissues or tearing of sutures [120]. These limitations can be overcome with a haptic feedback system. Furthermore, haptic feedback using visual and auditory cues may prove distracting during surgeries, hence haptic feedback is preferable [121].

A number of attempts aiming to provide haptic feedback for MIS have been reported. Force feedback systems have been developed [122–127] and are useful as a partial replacement for complete tactile feedback. Studies have indicated a reduced application of force by a factor of 2% to 6%, a 30% to 60% reduction in RMS force, 60% less errors, and a faster surgery completion time by 30% [128–130]. Although visual systems do provide limited feedback, providing both vision and force feedback leads to better tissue characterization [131].

Attempts have also been made to develop systems which provide comprehensive tactile feedback for MIS. Cultaj et al. developed a pressure stimuli system for the da Vinci surgical system. Mechanoreceptors were stimulated using a pneumatic array of 3 mm inflatable balloons [132–134]. Human psychophysics tests performed with this actuator demonstrate the effectiveness of the 3 mm diameter balloon in providing effective haptic input to the human sensory system, by stimulating the finger mechanoreceptors.

During classical surgeries, surgeons often use their hands to estimate how much force should be applied so that the surrounding tissues are not damaged [27]. Similarly, to detect arteries, surgeons use their hand to sense a time varying pressure [135–137]. Another important tactile assessment is to differentiate between a normal artery and a stenotic artery, which is often done by palpation or rolling between the fingers [135,136]. Although artery detection is not possible in MIS at this time, progress has been made to over come this limitation [138–140].

Besides tumor and artery detection, due to lack of tactile feedback in MIS, detection of kidney stones and determining their exact location is not possible [141]. In order to remove stones, methods such as extracorporeal shock wave lithotripsy (ESWL), percutaneous nephrolithotomy (PNC), open surgery and in some cases MIS are employed, based on size of kidney stone [142]. Some recent conceptual simulation studies have shown that detection and localization of kidney stone is possible [143–145].

Despite increasing interest from researchers in developing tactile sensors for MIS, the employment of these sensors in developed systems has been minimal. However, it is important to consider that the da Vinci surgical system, shown in Fig. 1, is the only master–slave MIS system, approved by US Food and Drug Administration (FDA). The system has been successfully used for general, urological, gynecological, thoracoscopic, and thoracoscopically assisted cardiotomy procedures. The system provides force feedback and a 3D vision, but lacks feedback of tactile sensation.

Designing tactile sensors for MIS tool ends still remains an unsolved problem. Commercial robotic surgery systems currently use a tactile feedback system and the alternative visual and force feedback systems have many limitations. Although many sensors that are able to detect shear and tissue characteristics have been developed, not all are biocompatible, robust, miniature and do not hinder tool movement. Easy assembly/disassembly and cost are also major challenges due to the disposable nature of these sensors.

3.4.2. *Tissue elasticity and palpation characterization*

Tissue elasticity and palpation are important parameters used by surgeons to assess the quality of soft tissues and to find tumors and arteries in the human body. In clinical practice, doctors often use the hand and palm to assess the condition of organs and tissues. Although this is a useful method of diagnosis, doctors often miss nodules and small lumps [146]. The issue of improving the qualitative nature of palpation characterization has received considerable attention in recent times, as indicated by Hall et al. [147], and recently reported devices [148–152].

Since palpation characterization and detection of tumors and arteries share many goals with MIS and haptic feedback, advancements related to these fields are not discussed here, as they have already been discussed in previous sections.

Palpation is often used to detect breast cancer at an early stage. Methods such as clinical breast examination (CBE), ultrasound, mammography, magnetic resonance imaging, and biopsy are already in use. Tactile sensing devices are currently being developed and tested. Almost 70% of cancer deaths occur in low or medium earning countries, because of lack of healthcare resources [153,154]. Therefore, efficient yet low-cost diagnosis systems for breast cancer are required [155]. A comparison of all the available methods, shown in Table 5, indicates that tactile based diagnosis systems have the potential to provide an effective, low-cost solution [156].

A device called SureTouch (Medical Tactile Inc., CA, USA) has demonstrated up to four times more sensitivity than the human hand in finding breast tumors during clinical examination [157]. Currently the device consists of 192 high resolution pressure sensors that mimic the human sense of touch. The device detects changes in elasticity caused by developing lesions. This change in

Fig. 1. The da Vinci surgical system. The surgeon operates while seated at the master console. Tools are controlled by translating the surgeon's hand, wrist and finger. Reproduced with permission © 2010 Intuitive Surgical Inc.

elasticity is then used to indicate masses or lumps in the breast, which are displayed as 2D and 3D images. Due to high sensitivity, SureTouch claims to detect lumps or masses as small as 5 mm, which cannot be felt by human touch. It is worth noting that this claim does not agree with other studies where sensitivity of CBE was shown to be 56.5%. A similar device called palpation imaging has shown a positive predictive value of 94%, compared to 78% for physical examination [158]. There is scope and need for further research in this area.

3.4.3. *Tactile pattern recognition*

Almost all biological creatures, including human beings, explore and interact with their environment using biological sensing systems including touch. While physiologists report a better understanding of human tactile physiology, microelectronics attempts to mimic the physiological structure. The area has also attracted an increased interest from researchers in computer sciences. This interest has led to research in areas of tactile pattern classification.

Gait analysis is a primary means of identifying walking disorders in people, and for monitoring results of rehabilitation treatment. Generally, these tests are performed with the help of a camera and force–plate systems. Besides the small area of the force plates being a limitation, some patients have been observed to target and strike the plate abnormally hard, creating false readings [165]. The acquired data is large and is often analyzed manually by experts [166]. Recently, a replacement of force plates with tactile based sensors has been proposed [167]. The tactile sensing plate acquires data only from the area of contact and hence greatly reduces the amount of data that must be processed, allowing automation of the data analysis.

An important parameter in service and exploratory robots is to distinguish between different textures and materials. Mazid and Ali used optical tactile sensors to acquire data from different objects such as a carpet, stone, rough sheet metal, a paper carton and a table surface [168]. Similar studies have also shown that texture classification can be performed using inexpensive tactile sensors [169–173].

3.4.4. *Tactile sensors for prostheses*

Measurement of how prostheses fit during motion can also be estimated using tactile sensors. For prostheses, the fit at the stump-socket interface is critical. Unconformable fitting leads to over-stressing, pistoning, shear induced ulcers and ultimately future amputations [174,175]. Furthermore, the problem becomes

Table 5
Comparative data for breast cancer detection and cost effectiveness [156].

Screening/diagnostic technique	Sensitivity/specificity, %	Procedure cost of bilateral exam, USD	Cost-effectiveness, USD per life year gained
Clinical breast examination	56.5/93.7	–	522, India [159] 31,900, Japan [160]
Mammography	73.7/94.3	112[*]	1846, India [159] 26,500–331,000 [161]
Ultrasound	Limited, see [156]	70[*]	–
MRI	87.7/92.8	1037[*]	55,420–130,695 [162]
Biopsy	96.6/100.0	2061[***]	2250–77,500 [163,164]
Elasticity imaging	95.1[#]/100.0	–	–
Tactile imaging	91.9[##]/88.9	5–50[***]	162[***]

[*] The US average Medicare reimbursements in 2005.
[***] Projections based on a physician's assistant performing the exam.
[#] Averaged for nine clinical studies.
[##] Averaged for two clinical studies.

more severe in patients with diabetes because of slow or limited healing of wounds and ulcers [176–178], which might be caused due to unconformable fitting. Generally, custom-made limb fittings rely on static measurement of residual tissue mechanics and topology; however, static measurement of the fit will not adequately predict the severity of the aforementioned conditions. Efforts are being made to overcome this problem using tactile sensing technology [179–182].

Another important utility of tactile sensing technology is to provide feedback in prostheses. Managing aspects of object manipulation, such as the amount of force or torque applied during object manipulation, or the force and position information acquired by mechanoreceptors of the foot during walking, are trivial for able-bodied people. Acquiring such information from prosthetic limbs is challenging. Attempts have been made to overcome this challenge using visual, auditory, electrical, tactile and vibrotactile stimulation [183–189]. Although each of these modalities have their advantages and disadvantages, but electrical and tactile sensing have proven to be most effective [185].

3.4.5. Recent advancements

Advancements in data processing and computational technologies have given researchers the opportunity to seriously pursue the work of researchers of the 1970s and 1980s. For example, Burger et al. have worked to develop a compact electronic module for non-visual display of alphanumeric data, that was previously hindered by limitations in data storage and data acquisition devices [93]. Efforts to develop wearable, tactile-based Braille reading devices have since been reported [190–194].

A major success of this technology is seen in smart phones. Tactile sensors have enabled the users to quickly browse through content on a small screen accepting high resolution tactile input commands. However this area is beyond the scope of this review.

3.4.6. Obstacles and challenges

With the demographics of many societies increasing in age, the need for automated production lines, improvement of human lives with prosthetic devices, acceptance of robotic surgery systems in hospitals, increased popularity of touch-based commercial and home products, a tremendous amount of responsibility has shifted to the shoulders of researchers working in the area of tactile sensing. With the need for reliable and smarter tactile sensing solutions, the amount of research in the area does not seem to be enough. Since the technology failed to gain prominence in either commercial or industrial markets for almost two decades, it needs to undergo a re-evaluation. This review is one such effort reflecting on the possible application and value of such technologies.

4. Reasons for delayed acceptance of tactile technology

4.1. Overoptimistic prediction

Although Harmon's work was significant in terms of realizing the importance of design criteria for tactile sensing technologies, his predictions for the success of this technology was seen as overoptimistic until 2000 [4]. By the end of the 20th century very few, if any, tactile sensors or devices could be found in the robotics and medical industries, or consumer markets.

Around the start of the 1990s, Nicholls and Lee identified that a large market existed for low-cost, robust, accurate and reliable sensors, but saw no significant contribution of tactile sensing technology to real applications in factory systems [16]. Lee even goes so far as to concluded that the technology had been "neglected or even rejected" by industry [4].

Since many advances in computing and robotics technologies were so successful over the previous three decades, this led to very high expectations for tactile sensing technologies. The authors believe that Harmon's predictions were not overly optimistic or unrealistic, especially today, when a wide use of this technology can be seen in smart phones. However, when other technologies were a success and are at a very advanced stage of research today, why has tactile sensor technology failed, at least until the year 2000. There are bitter realities underlying the answer.

4.2. Characterization parameters

Most reported efforts to develop tactile sensors were not supported by rigorous testing; even during laboratory testing, sensor parameters, such as hysteresis, sensitivity, standard deviation and repeatability, which are critical for assessing usefulness of a sensor, are not reported. This has left the technology at a juncture where there are no definitive standards or benchmarks available to guide further development. One attempt to alleviate this situation has been made by Eltaib and Hewit, investigating design considerations for MIS and minimum access surgery [20].

4.3. Cost

The cost of tactile sensors is one of the primary reasons for the failure of the technology to enter industrial and consumer products, especially in the field of health care and service robotics [4]. Lee wrote [4]:

> . . . the overriding factor is cost – if large numbers of personal manipulation aids are to be sold, as will be needed to satisfy demand, then costs must be brought down. This is perhaps the most pressing challenge, especially for our engineering and design expertise.

In nearly all reviews of tactile sensor technology, the call for cost effectiveness, repeatability and reliability has been made [16,3,4,2,6,19], yet these issues remain largely ignored. This has led to hesitation in the adoption of the technology, especially in the fields of biomedical engineering and healthcare.

4.4. Poor design criteria

Although Harmon's design criteria are useful and serve as a benchmark by which researchers guide their research, they are too generic. Design requirements for tactile sensing need to be redefined according to the field of application. For example, a biocompatible sensor is not needed for the manufacturing industry and a sensor with wide dynamic range may not be needed in biomedical applications. Likewise, a sensor designed for the biomedical industry with non-biocompatible materials can never get regulatory approval. In short, it seems that task-centered design is necessary.

4.5. Target applications

It is necessary to realize that tactile sensing technology is definitely not the best solution for all robotics applications. Tactile sensors have shown promising results in unstructured environments, but optical, infrared, laser or vision based systems are far superior in structured environments. It is important to realize that tactile-based approaches are an ideal choice in scenarios where vision is partially or totally occluded, or in similar scenarios as those mentioned in Table 6.

Table 6
Proposed application industries with key areas and challenges.

Application industry	Key utility and application areas	Design challenges
Robotics	Dexterous manipulation Tele-robotics Service robots Exploration robots Rescue robots	Arrayed sensors Discrimination and classification algorithms Repeatability, wear resistance and wide dynamic range Customization Characterized response over wide temperature range High frequency response
Biomedical	MIS tools Tele-robotic operations Diagnostics tools Rehabilitation medicine Dentistry Patient care Gait analysis systems	Biocompatibility Rugged to withstand sterilization process Cost due to their disposable nature Characterization and classification algorithms Wireless interfaces Power consumption High frequency response Electrocutaneous feedback mechanisms Safety and reliability Ergonomics
Sports	Posture analysis Sports training	Conformable and customizable sensors Durability Wiring and power constraints Wireless interfaces
Agriculture and food processing	Service robots, such as for fruit picking	Adaptability to unstructured environments Toxin and allergin free construction Hygiene and cleanliness Safe for food handling Dexterous movement Soft grippers Unexplored application area
Aerospace and automobiles industry	Safety studies Safety devices Diagnostic tools Acceleration optimization systems Navigation interfaces for mobile devices	Device centered sensor design Safety and reliability Rugged to withstand high shear, tensile and normal forces Unexplored application area
Consumers products	Healthcare products such as intelligent toothbrushes Service Robots for elderly Textile and clothing	User acceptance Wear resistance and reliability Cost, so that it can target wider application market Rugged to bear abuse

5. Future directions and challenges

5.1. Task centered design criteria

Robotics and biomedical technologies have been attracting increasing levels of attention in recent years. This calls for much sophisticated solutions than before. This can be achieved if task specific design criteria are specified. Task-based design criteria's can help optimize and therefore lower sensor cost.

5.2. Arrayed sensor design and algorithms

In general, single point sensing sensors have reached maturity and their pros and cons are well understood and many promising devices have been reported in literature. Capacitive, resistive, piezoelectric, optical and piezoresistive transduction techniques are well established, but customizable interfaces and characterization/discrimination algorithms are required.

From a hardware design viewpoint, mesh-based, multiple sensing point sensors are required. The distance between the sensing elements is another important criteria. Human glabrous skin can be set as the standard as a starting point, but the desired resolution mainly depends on the requirement of the task to be achieved.

5.3. Gold standard

As emphasized previously, any sensor design parameters should be centered around its application, but in cases where researchers want to explore the area of tactile sensing in general, anatomical structure and characteristics of glabrous skin can be set as the gold standard. Human glabrous skin consists of four types of tactile sensors, also called cutaneous mechanoreceptors. These four types are Pacinian corpuscles, Meissner corpuscles, Merkel discs, and Ruffini corpuscles. The nature and physiology of these receptors has been well established and reported [195–198]. Tactile perception can be understood as the sum of these four receptor functions [195]. A characteristic summary of mechanoreceptors is given in Table 7.

5.4. Frequency response

Previous work has shown that slip has a major frequency component between 10 Hz and 30 Hz [199,34]. Another study has indicated that humans are sensitive to spatial differences at the frequency bands of 1–3 Hz and 18–32 Hz [200]. Pacinian corpuscles, which are sensitive to vibrations, have a bandwidth of approximately 250 Hz and have a lower spatial resolution [201,202]. Hence any sensor with a minimum frequency response of 32 Hz is deemed sufficient to detect incipient slips, which is a desirable endpoint in many robotic and prosthetic applications. Similarly a sensor with a minimum frequency response of 250 Hz is required for the detection of vibration, but can have a lower spatial resolution. A number of PVDF-based sensors have been reported, as discussed earlier in Section 2, but the ability to detect static forces has yet not been achieved, as discussed in Section 2.3.

5.5. Spatial resolution

Early studies to find innervation density of mechanoreceptors in glabrous skin indicated a discrimination threshold of 2–3 mm in

Table 7
Characteristic summary of mechanoreceptors in human glabrous skin.

Type	Merkel	Ruffini	Meissner	Pacini
Number	25%	19%	43%	13%
Adaptivity	Slow	Slow	Fast	Fast
Receptor type	SAI	SAII	FAI	FAII
Field diameter	3–4 mm	>10 mm	3–4 mm	>20 mm
Frequency range	0–30 Hz	0–15 Hz	10–60 Hz	50–1000 Hz
Response to indentation $S(t)$	$S,\ \frac{ds}{dt}$	S	$\frac{ds}{dt}$	$\frac{d^2s}{dt^2}$
Response to constant indentation	Yes	Yes	No	No
Location	Superficial	Deep	Superficial	Deep
Receptive field	Small	Large	Small	Large
Innervation density	High, variable	Low, constant	High, variable	Low constant
Sensed parameter	Local skin curvature	Directional skin stretch	Skin stretch	Non localized vibration

Table 8
A proposed generic design criteria based on physiological characteristics of mechanoreceptors in the glabrous human skin.

Transduction technique	Capacitive, resistive, piezoelectric, piezoresistive or a combination
Structural design	Arrayed/mesh type. Ease of assembly and disassembly
Spatial resolution	1.25 mm
Frequency response	At least 32 Hz for normal and shear force estimation and 250 Hz for vibration detection
Cost	Low, especially where their use is disposable in nature such as medical devices
Conformability	Not a necessary attribute
Dynamic range	Application specific
Repeatability and stability	High

fingers [203]. Later studies reported a higher spatial resolution of about 1.25 mm [204]. Although some promising mesh type designs are reported [205–209], designs with greater scanning frequency of individual sensing points/elements and greater spatial resolution are required.

5.6. *Assembly and maintenance*

Ease of assembly and disassembly is also an important area that needs to be addressed. This design criterion is necessary for sensors designed for applications where disposable equipment or parts are required, such as in medical surgery and diagnostic tools. Eltaib and Hewit have attributed it as an important design consideration when designing systems for use in MIS [20].

5.7. *Conformity*

Conformity is a desirable attribute for specific applications, but not a generic specification for every sensor.

5.8. *Cost*

Considering MIS where most equipment is disposable, only a suitable sensor with a reasonably low cost would be able to successfully enter the market. Low-cost tactile sensors are required which can sustain wear, have high repeatability and low hysteresis. A proposed design criteria is summarized in Table 8.

6. Conclusion

Developments in tactile sensing and trends over the last four decades have been analyzed. New areas for future applications of tactile sensing technology have been proposed and current challenges have been identified, while emphasizing the importance of application centric design criteria.

6.1. *Recent trends*

An increase in the demand and uptake of tactile sensing technologies by industry has been observed. This is clearly indicated by the numbers of papers being published and patents being filed. As an indicator, the number of products being patented since 2010 with the US Patent Office, compared to the 1990s, has increased by a factor of ten, as seen in Table 3. Similarly, research activity in this area has also doubled, which is apparent from a comparison with the number of publications in the 1990s, as shown in Table 3.

6.2. *Success and maturity*

Unlike the previous three decades, where all reviewers have indicated either the rejection or failure of this technology, industrial and commercial enterprises now appear to be on the cusp of accepting this tactile sensing technology. The major uptake has been in mobile devices in the form of tactile touch screens and navigation interfaces. Design engineers seem to take advantage of tactile sensors in order to cope with the requirement for smarter touch interfaces and the ability to navigate through voluminous content with ease. Some of the most successful uses of this technology have been in products like iPods (Apple Inc., USA) and personal digital assistants (PDAs).

6.3. *Future of tactile technology*

This technology has the potential to aid future advancements in many of the areas discussed earlier. Successful commercial products have provided motivation and possibilities of funding for further research in this technology. Tactile sensing is no longer a laboratory technology. The success of companies such as Pressure Profile Systems Inc. (Los Angeles, USA), Tekscan Inc. (Boston, USA) and X-sensors (Alberta, CANADA) has proven the existence of a market for these products. With more and more gadgets being developed, the need for automation, the acceptance of intelligent robots and biomedical products, the demand for tactile sensing solutions can only be expected to increase.

Acknowledgement

This research was supported in part by an Australian Research Council Thinking Systems grant.

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