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Boundaries of tactile acuity when exploring surfaces

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Abstract

Our sense of touch enables us to perform dexterous manipulation and to extract features of objects and textures along a large number of sensory dimensions. Tactile discrimination abilities vary greatly according to the body site, and is maximal in the hand; due to its significant role in our daily interactions and communication. A large number of studies have focused on the boundaries of tactile perception with the fingers, which are heavily involved in discriminative touch to distinguish both gross and fine features. In this review, we will explore interactions in which touch is extremely accurate and interactions that induce unprecise, illusory tactile perceptions, focusing mainly on the glabrous, non-hairy skin of the hand and fingers, due to its importance in interacting with the world. We compare the perception of tactile dimensions over various processes, including different dimensions in touch like roughness, stickiness, and texture, as well as the impact of exploring surfaces with more than one finger. We also cover the potential to include temperature in haptics and its importance in shaping tactile interactions. The research from perceptual studies in humans is compared in terms of neurophysiological studies and computational models of touch, where it is important to understand both peripheral and central coding of touch to apply the findings in haptic devices. Finally, we highlight where future work can add to knowledge and lead to tactile and haptic applications, such as in the clinical domain for better diagnostics, in industries like the cosmetic and car manufacturing sectors to improve consumer usage, and the extension into bio-inspired sensors for robotic sensing and e-skins.

1. Introduction

The sense of touch exhibits exquisite sensitivity to small displacements of the skin, where specialized mechanoreceptors capture a large variety of tactile inputs to elicit percepts such as roughness, softness, stickiness. The biomechanical properties of the skin and underlying tissues shape and attenuate mechanical contact, which is transformed into neural signals. Several types of mechanoreceptors exist, each with specific properties and sensitivities, which encode and transmit tactile information that is further processed through various central nervous system areas, like the cuneate nucleus, thalamus, somatosensory cortex, and other parietal and frontal cortical areas (figure 1). A puzzling aspect of this haptic touch system, possibly due to specialization, is that it excels in extracting some features of touch such as differentiating surfaces based on micrometer differences while it can struggle to notice very large differences in other features of tactile cues. For example, the diameter of manipulated strings needs to be more than doubled to distinguish it from a [1]. These discrepancies in the sensory resolution that touch can achieve are best shown by the numerous illusions that can trick the sense of touch and provide valuable insights on how the afferent input conveyed by tactile receptors at different body parts shapes tactile perception.

This review explores and compares the boundaries of tactile acuity across sensory dimensions, from those that are very grossly conveyed by touch to those that exhibit astonishing sensitivity. We believe that a more systematic and complete understanding of these boundaries will make it easier for future research to

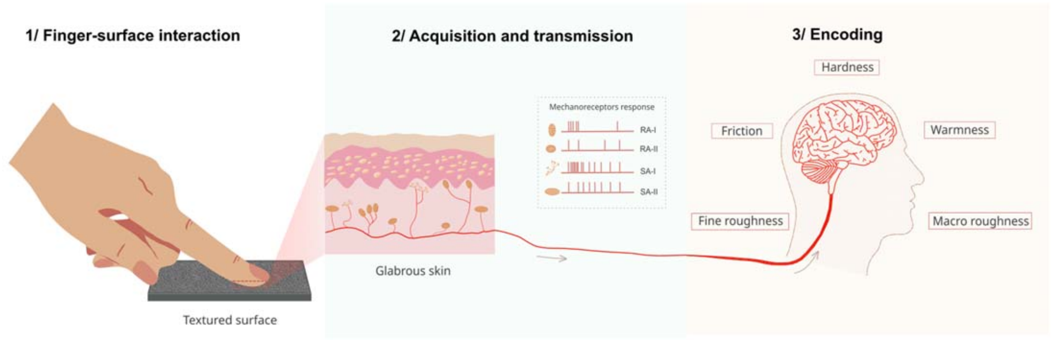

Figure 1. Simplified representation of the tactile pathway from the fingertip to the central nervous system.

identify the core computational mechanisms underlying the tactile sense. It is likely that evidence of these different percepts elicited on one hand by only tiny differences, and on the other, by the insensitivity to large variations in tactile input, will sum up to provide insights about which theories on the mechanisms of touch are still robust when evaluated against very specific perceptual phenomena. The present focus will be on the glabrous skin of the hand, an area densely innervated by mechanoreceptors, making it a key region for tactile perception that enables humans to discern subtle variations in texture, pressure, and vibration.

2. Perception of fine details through touch

Touch sensitivity is highly variable, both over the body and between individuals; however, naïve participants are remarkably efficient at finding an optimal exploration strategy to extract tactile cues that enables them to distinguish surface properties [2]. In this section, we explore specific cases in which tactile perception excels in discriminating differences, as well as perceptual tasks and tactile dimensions for which it displays a surprising lack of sensitivity.

2.1. Surface feature discrimination

A fundamental aspect of tactile perception is the ability to perceive and distinguish small surface features, including topographic details like ridges, bumps, and edges. This skill is essential in everyday life, such as to distinguish between different fabrics or material types, or for the successful exploration and manipulation of objects, and it relies largely on an almost immediate estimation of the properties of the object's surface.

Research has demonstrated the impressive precision of human tactile perception in detecting microscale features. Johansson and Vallbo [3] related the sensitivity of human hand mechanoreceptors with perceptual thresholds, finding that thresholds for tactile detection could be as low as 1 micrometer. Johansson and LaMotte [4] also observed that humans can detect edges as small as 0.85 micrometers, allowing for precise identification of surface relief. Miyaoka *et al* [5] showed that humans can perceive surface variations as subtle as 2.4 to 3.3 micrometers, with tactile thresholds for detecting ridge height differences as low as 0.95 micrometers. Other studies have shown that the extent of tactile sensitivity reaches the nanometric scale. For instance, Skedung *et al* [6] demonstrated that humans can detect nanometer-scale geometric features on microscopic sinusoidal patterned surfaces and Loomis *et al* [7] showed that the motion direction of a 0.1 mm probe on the skin can be detected. Without motion that elicits vibratory of frictional phenomena, perception of surface features by an immobile finger is reduced, but remains sharp with a minimum detectable feature size of around 0.2 millimeters [8, 9].

In addition to detecting and discriminating fine surface features, humans excel at material discrimination, relying on their ability to perceive subtle surface variations. In everyday activities, such as distinguishing between different fabrics in clothing, individuals rely on tactile exploration to identify these materials quickly and accurately [8, 10, 11]. Hollins and Risner [12] and Miyaoka *et al* [5] demonstrated that individuals can perceive fine gradations in roughness across abrasive surfaces. Sahli *et al* [13] extended these findings by creating artificial surfaces with controlled roughness and observed that participants could discern differences in the Hurst roughness exponent as small as 0.2. The microgeometry of surfaces can also play an indirect role by enabling the perception of a slipping surface [14]. When it comes to intricate macroscopic tactile features, people can easily recognize hundreds of everyday objects by touch only [2].

Beyond surface topography, humans can distinguish other characteristics of the surfaces that they touch. Remarkably, smooth materials with very similar properties, such as plastic and glass [15], or plain paper [16], can be distinguished despite the absence of topographical differences. Recent studies have advanced this understanding by showing that humans can differentiate smooth surfaces based solely on variations of the surface chemistry [17, 18] by exploiting subtle differences in skin-surface adhesion.

On the contrary, humans exhibit rather poor performance at distinguishing certain tactile features. Surface features can be completely overshadowed by other tactile cues, such as the experienced lateral force [19]. It has also been shown that humans are incapable of distinguishing differences in the second order statistics of a 3D printed tactile pattern [20], which means that they can sense the average size of topographical features, but not their associated variance. Participants further show a rather poor performance at detecting differences in the randomness of embossed dots on a surface, especially when comparing more organized patterns [21]. In contrast with daily objects, humans also struggle to discriminate nonsense shapes printed on a flat surface [22], showing how expectation and recognition can influence touch perception.

2.2. Perception of tactile cues related to contact forces and elicited vibrations

The ability to perceive and finely adjust forces plays a critical role in tasks that require interactions with various surfaces, where slight changes in force can directly impact the tactile sensation of grip accuracy. Force regulation is dependent on tactile feedback and, for some tasks, the force applied has to be specific to enable subtle variations in surface characteristics to be detected [23, 24]. As a consequence, humans can sense small differences in applied force, down to the millinewton scale [25]. Similarly, Panarese and Edin [26] demonstrated that individuals could accurately detect and adapt to small directional changes in force, ranging from 7 to 10 degrees, when sliding a finger across a surface. This continuous force regulation is heavily dependent on tactile feedback, allowing for dynamic and responsive interactions with the environment. For instance, Westling and Johansson [27] showed that grip adjustments occur almost instantly in response to shifts in surface texture during object manipulation. Perception of softness also involves the processing of the applied force by comparing it to the resulting displacement of the surface [28–30]. When touching a soft material, like rubber, people gauge softness by estimating how much the material deforms under a given force, allowing them to detect the differences. Studies estimate the minimum detectable difference in stiffness at around 0.1–0.2 N mm^{-1} [31, 32].

Roughness perception entails the integration of both vibrational and pressure-based feedback. Judging a surface's roughness typically involves either sliding or pressing the fingertips into the surface. A rough surface generates uneven distribution of the applied force on the skin when touched and vibrations are elicited during movement. Vibrational sensing is particularly important in discerning fine textures with spatial periods below 200 μm [12, 33]. Through these vibrational and force signals, individuals can detect small features like fine ridges and minuscule bumps on a surface, even when these features are on a near-microscopic scale. On the other hand, a recent study has shown that human tactile acuity for detecting missing tones from complex tactile vibrations that include several frequencies is generally quite low, especially for tones that are towards the high end of the waveform frequency spectrum [34]. This finding suggests that touch cannot rely on vibrations alone to distinguish complex tactile sceneries.

Increasing evidence suggests that surface friction, and its perceptual counterpart stickiness [23, 35, 36] , also plays an important role in surface perception [15, 37]. Frictional cues are the mechanical cues generated when sliding a finger over a surface to explore it, with the skin stretching and sticking against the surface before initiating finger movement [15, 38]. Frictional cues inform us about the degree of lateral resistance of the surface against the skin, as quantified by the friction coefficient [23, 37] and which is widely used in physics to characterize basic features of surface properties. Research by Sahli *et al* [13] has shown that humans are very sensitive to small variations in surface friction, where participants can distinguish between surfaces whose coefficient of friction varies by only 0.035 during active touch. Gueorguiev *et al* [15] identified frictional forces experienced during the initial contact as a crucial factor in distinguishing flat surfaces, such as glass and plexiglass (figure 2). In the same vein, Skedung *et al* [39] reported that it is possible to successfully distinguish between flat materials that differ in several properties (i.e. the water contact angle or free energy), due to the molecular composition of their surface coating. Other studies have focused on the clingy aspect of stickiness perception with exploring it as skin detachment, to reveal how the former pressure required to provoke detachment as well as the pull-off itself impacted experienced sensations [40].

In contrast, frictional cues give only limited information in conveying more complex tactile features, such as two-dimensional shapes on a surface [41]. Mayet *et al* [1] showed that kinesthetic force in a close to real life scenario involving plucking strings differing in tension is more challenging than predicted by sensitivity in highly controlled experiments. Participants displayed a Weber fraction of 1.53 for string diameter discrimination and 0.4 for string tension discrimination. Moreover, perception of the pressure felt on the finger seems to be unidimensional, following the amplitude of the total force vector, rather than depending on its orientation [42].

2.3. Temperature perception

The ability to perceive temperature is an important aspect of touch. When a surface contacts the skin, there is often a thermal transfer that entails the heating or cooling of the skin. This interaction provides key information about the composition and characteristics

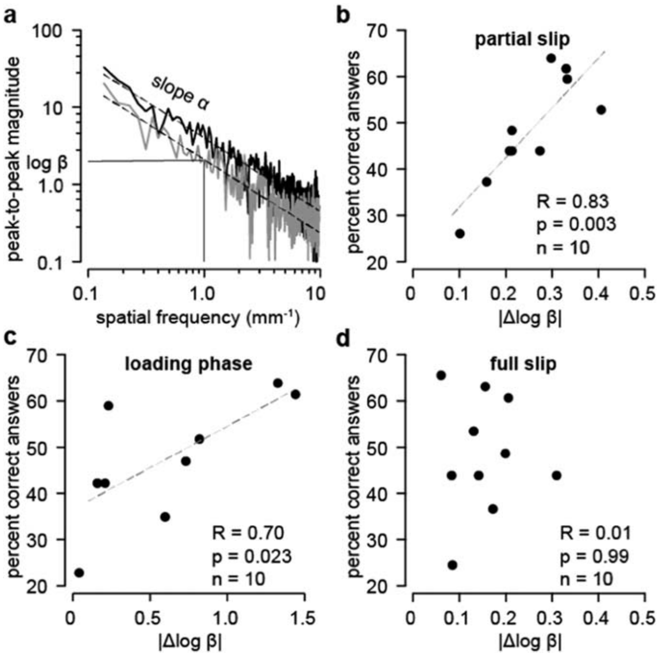

Figure 2. Analysis of the differences in contact mechanics between glass and PMMA. (**a**) Comparison of the amplitude spectra of the tangential force component in the spatial domain. Linear regression gave parameters α and $\log\beta$. The differences $\Delta\alpha$ and $\Delta\log\beta$ between the mean spectra of the two materials were computed for all participants. (**b–d**) The differences in the frictional noise $|\Delta\log\beta|$ plotted for each phase against performance: (**b**) Partial slip. (**c**) Loading phase. (**d**) Full slip. The correlation between individual performance and transient frictional dynamics observed during early stages of a swipe suggests that during these stages, frictional dynamics of the interactions between the fingertip and the two materials differed. Reproduced from [15]. CC BY 3.0.

of surface materials. Thermal changes are detected by skin thermoreceptors, which encode variations in skin temperature and transmit the signals to the central nervous system, although some mechanoreceptors can be thermally-sensitive and nociceptors encode painful thermal sensations [43].

Humans are sensitive to changes in skin temperature, and are generally better at detecting transient cooling compared to warming of the skin surface [44], likely due to having more thermoreceptors for cold. Many factors influence temperature perception, including the initial temperature of the skin, thickness of the skin layers and their respective thermal properties, the density, sensitivity and conduction velocity of thermosensitive afferents, the temperature of the touched object, as well as its conductance/capacitance properties, and the area contacted. This can make concluding about temperature perception challenging and limit the generalizability of findings.

Temperature perception can vary by magnitudes over the body, with the upper half of the body being generally more sensitive to thermal changes than the lower half [44]. Temperature perception even varies over the hand, showing a proximal-distal increase in temperature sensitivity, where the region nearing the wrist being most sensitive [45]. Temperature sensitivity can be very precise, where rates above 0.1°C per second can be readily detected and a difference of 0.05°C from skin temperature can be perceived; however, very slow rates of change (e.g. <0.5°C per minute) can remain undetected until around a 5°C deviation from skin temperature [46].

Humans can distinguish between materials using thermal cues [47–49]. The interaction between the hand and the material also affects discrimination performance [50, 51]. For effective material discrimination and identification, noticeable differences in thermal properties are required [52], but this ability diminishes when the material's temperature closely matches the skin's temperature, due to minimal heat transfer between the skin and the object [53].

Recognizing materials through thermal cues involves linking temperature changes felt during a contact to a mental representation of the material's properties [47]. Studies have explored material recognition using thermal displays that simulate materials through thermal cues [49, 54]. Recognition performance is influenced by various factors, such as the materials used and the temperature transient of the objects [55, 56]. Additionally, performance can vary with the number of fingers used in exploration, where recognition improves significantly when transitioning from single-digit to multi-digit exploration [50].

Table 1 provides an overview of human tactile acuity to surfaces features, tactile dimensions and temperature. Tactile acuity is commonly assessed using several psychophysical methods, including discrimination tasks (e.g. forced-choice task, odd-one-out), detection thresholds, recognition, similarity judgments and magnitude estimation. In the listed studies, tactile acuity is based on behavioral responses,

Table 1. Characteristics of studies on tactile acuity: stimuli type, performed task, and tactile threshold measurement.

Authors	Year	Stimulus	Modality	Task	Acuity
			Surface features		
Loomis and Collins [7]	1978	Water-jet stimulation	Only tactile	Discrimination	Up to 75% correct shift discrimination with 0.1 mm probe
Johansson and LaMotte [4]	1983	Micro-textured surfaces	Only tactile	Detection	0.85 μm edge, 10 μm diameter
Lederman and Klatzky [2]	1985	Everyday objects	Only tactile	Recognition	Almost Perfect
Miyaoka *et al* [5]	1999	Abrasive papers	Only tactile	Discrimination	2.4 μm texture discrimination, 0.95 μm ridge height discrimination
Hollins and Risner [12]	2000	Abrasive papers	Only tactile	Discrimination/ Magnitude estimation	9 μm with motion, 100 μm without motion
Summers *et al* [16]	2008	Plain white paper	Only tactile	Odd-one-out	Up to 67% accuracy at distinguishing plain paper
Skedung *et al* [6]	2013	Nano-texture surfaces	Only tactile	Similarity of pairs	14 nm edge versus flat
Gueorguiev *et al* [15]	2016	Hydrophobic versus hydrophilic surfaces	Only tactile	Odd-one-out	Molecular bounds
Carpenter *et al* [17]	2018	Hydrophobic versus hydrophilic surfaces	Only tactile	Odd-one-out	Surface chemistry
Sahli *et al.* [13]	2020	Micro-textured surfaces	Visual / Tactile	Similarity	Hurst roughness exponent of 0.2 for a difference in surface curvature of 0.8 mm^{-1}
Mayet *et al* [1]	2024	Strings	Only tactile	Odd-one-out	JND of 1 .53 for string diameter
			Tactile dimensions		
Cholewiak *et al* [31]	2008	Virtual surfaces	Only tactile	Magnitude estimation	0.1 N force magnitude, 0.2 N/mm stiffness magnitude
Karadogan *et al* [32]	2010	Virtual surfaces	Visual / Tactile	Discrimination	Average Weber fraction between 0.2–0.3 for stiffness discrimination
Panarese and Edin [26]	2011	3D force stimuli	Only tactile	Direction discrimination	Threshold at 7.1°
Gueorguiev *et al* [15]	2016	Hydrophobic versus hydrophilic surfaces	Only tactile	Odd-one-out	Up to 60% accuracy at distinguishing glass and PMMA
Skedung *et al* [39]	2018	Coated float glass	Only tactile	Similarity of pairs	Surface chemistry
Sahli *et al* [13]	2020	Micro-textured surfaces	Visual / Tactile	Similarity	0.035 in difference of friction coefficient
Mayet *et al* [1]	2024	Strings	Only tactile	Odd-one-out	JND of 0.4 for string tension discrimination
Le *et al* [34]	2024	Vibrotactile signals	Only tactile	Odd-one-out	Low acuity for discriminating missing tones in complex tactile vibrations
			TEMPERATURE		
Erickson and Poulos [54]	1973	Thermal stimuli	Only tactile	Discrimination	Threshold of about 0.4°C–0.5°C
Dyck *et al* [52]	1974	Materials of varying thermal conductivity	Only tactile	Discrimination	Above chance discrimination of copper and steel
Darian-Smith and Johnson [46]	1977	Pulses	Only tactile	Discrimination	Smallest differentiated increment is 0.05°C
Steven and Cho [44]	1998	Simulated surfaces	Only tactile	Detection	Highest sensitivity in upper body
Jones and Berris [49]	2003	Material of varying thermal conductivity	Only tactile	Discrimination	Average thermal responses of 0.5°C
Yang *et al* [51]	2008	Real and simulated materials	Only tactile	Discrimination / identification	Comparable performance with real and simulated materials

participant verbally or manually report their answers. Physiological measurements is not the primary method in the research summarized here. The stimuli used ranged from highly controlled textures (nano or micro-patterned surfaces, abrasive papers) to everyday materials (e.g. paper, glass) as well as simulated or virtual stimuli that modulate force feedback or thermal properties. To reduce variability, most studies control tactile exploration using passive or guided active movement. Overall, table 1 illustrates the diversity of experimental designs and metric used to study human tactile acuity.

2.4. Multi-digit perception

Humans most often explore the surfaces and objects of their surrounding using several fingers. Compared to single-digit touch, multi-digit touch increases the quantity of incoming tactile information. Consequently, one could predict that multi-digit touch should improve tactile performance. This intuitive prediction is supported by several experimental measures of acuity. For example an improvement in tactile discrimination of about 15% was found in a review summarizing the results from 33 studies using the same type of stimulation [57]. However, the effect of multi-digit touch remains quite complex, with both positive and negative effects observed. This complexity is well illustrated in Braille reading, where some of the readers use multi-digit scanning to read Braille dots with positive effects [58–60]. On the negative side, a tendency to confuse the fingers is often reported in multi-digit readers. This effect is referred to as a ‘mislocalization’, which is an error in locating a tactile stimulus applied to the skin. For example, the participant responds finger B when asked to locate a tactile stimulation applied to finger A. Errors are typically restricted to the fingers that are routinely used to read, without affecting the other fingers [58]. It is unclear if this negative effect influences the reading itself through a confusion in the perceived letters. This phenomenon help to better understand the fundamental neurophysiological mechanisms at play, such as experience-driven cortical plasticity in the finger representations [61] whose effects are complex and multidetermined [62].

3. Neural coding of fine tactile features

The exquisite sensitivity of touch to specific features raises the question of the mechanisms that code them, which ranges from the induced effects on the skin to the computational principles underlying the processing in higher-level brain areas, through the activation of the vast and diverse populations of afferents. In the skin, there exist many different types of receptors that are sensitive to mechanical deformation. In the glabrous skin of the hands and feet, there are four main types of fast-conducting, myelinated mechanoreceptors, namely fast-adapting types I (FA1, Meissner corpuscles) and II (FA2, Pacinian corpuscles) and slowly-adapting types I (SA1, Merkel cells) and II (SA2, Ruffini corpuscles), as comprehensively covered in the classic review by Vallbo and Johansson [63]. In the hairy skin that covers the majority of the body, Meissner corpuscles are not found, but we have the other types and, additionally, hair follicle afferents and field afferents that are all fast-conducting, myelinated mechanoreceptors [64]. There also exist low-threshold C-tactile fiber afferents that are unmyelinated and send their signals at a much slower speed to the brain. These are found densely in the hairy skin, especially on the upper body, and are thought to contribute more to positive affective touch signaling, rather than adding to the encoding of conscious, discriminative aspects of touch [65]. Recent literature [66] has shown that most stimuli, especially largely above threshold ones, activate all receptors. Nevertheless, it remains true that SAI and SA2 are most sensitive to dynamic stimuli with variations around a few Hz, FAI primarily respond to frequencies around 30–50 Hz, and Pacinian reach their peaks sensitivity around 250 Hz but also display an impressive sensitivity range (40–400 Hz) [67]. These properties probably influence the choice to model stimuli that rely on rather slow indentations through the SA activity while textures and vibratory signals, which exhibit rather high-frequency signals, are usually addressed by models mainly relying on Pacinian properties. We will not cover the exact properties of all these mechanoreceptors here, but they are well-documented in the above papers and for further information, Corniani and Saal [68] provide a detailed and comprehensive review of tactile afferents all over the body.

3.1. Spatial and temporal acuity of the tactile afferents

Our ability to distinguish feature differences between surfaces is not uniform across the body. The highest ability to discriminate small tactile features is observed on the glabrous skin of the hand, where the density of tactile afferents is the largest [68]. This ability varies across the hand, with the highest spatial resolution at the fingertips and a steady decrease towards the wrist [3]. Sensory threshold differences are even observed at different locations over the finger pad, which is most sensitive at its center [69]. High spatial information input enables precise exploration and discrimination of surface characteristics that coincides with the use of fingertips by primates to explore small features [70]. The spatial representation of tactile afferents’ activity efficiently encodes topographical elements at the millimeter scale [71]. Specific properties such as the anisotropy of the receptive field can encode higher-order features like edge orientation [72]. Transient cues such as the direction of a suddenly applied force can be extracted by the first spikes produced within a population of mechanoreceptors [73] and the precise temporal encoding of dynamic stimuli, especially from the Pacinian corpuscles and Meissner corpuscles, complements the spatial encoding, more from Merkel cells, to allow the enhanced perception of complex surfaces, such as textures [74]. It is pertinent to further explore the role of these mechanoreceptors in encoding texture perception for perceptual dimensions other than roughness, e.g. stickiness, hardness [36]. Further to this, the role of Ruffini corpuscles is underexplored in tactile perception [75] , where they likely play a relevant part in encoding surface friction, due to their sensitivity to skin stretch and pressure, especially concerning tangentially applied forces [36, 76] .

3.2. Representation and acuity in the somatosensory cortex

Neural codes in the cortex are typically dedicated to higher-level features such as decoding tactile motion and shape that are mediated by cortical processes that integrate afferent activity over time and over receptor populations [66]. Interestingly, enlargement or shrinking of the size of the cortical areas representing limbs that are either overstimulated or deprived from sensory feedback have been observed in the human primary somatosensory cortex (S1) using neuroimaging methods, in the neurotypical population with overstimulation of the skin [77, 78], individuals to whom routine manual activities overstimulate their fingers such as Braille readers [59, 60], musicians [79], and individuals with sensory feedback deprivation, such as amputees [80, 81].

This plasticity phenomena were tested in studies with rats; enriching the tactile environment enlarges the size of the cortical areas coding tactile inputs [82], whilst increasing proprioceptive inputs reduces it, even though it enlarges the cortical areas coding proprioceptive inputs. Recently, active touch (i.e. through self-generated movements) has been proposed as a potential factor as well [83], based on the observation that cortical receptive fields were larger from active touch, compared to passive tactile stimulation. However, these findings remain difficult to interpret as the surfaces and numbers of fingers used to touch were different between the active and passive conditions [62].

Multiple factors can alter the size of a body area representation in S1 and it is challenging to disentangle these processes based only on the interpretation of the size of cortical representations. Furthermore, maladaptive effects have been described in populations demonstrating such plastic changes in the brain, which can be predictive of dystonia in musicians [84] or phantom pain in amputees [85]. Thus, it is still unclear which processes enhance tactile abilities and those that reduce or alter sensitivity. For example, blind people's tactile acuity clearly benefits from cortical plasticity, which increases neuronal resources dedicated to the specific tactile tasks [86, 87].

Multi-digit stimulation can induce important cortical changes. Primary somatosensory regions of the brain normally represent the individual fingers in a somewhat segregated fashion, with respect to the somatotopy [88] and size of the representations at cortical level, as well as the size of their respective receptive fields on the skin. However, these can change after repeated intensive synchronous multi-digit stimulation, causing enlarging and fusing of the cortical representations of the fingers stimulated into either large cortical representations or enlarged and often multi-digit receptive fields [89, 90]. The effect is referred to as 'experience-driven' as it is restricted to the area of tactile stimulation [89]. It is also reversible, with passing time [90] or asynchronous stimulation [89].

3.3. Computational models of the acuity of touch

Computational models are powerful tools for understanding the mechanisms underlying tactile acuity. Models can provide a better understanding of how tactile features are extracted and how neural activation relates to perception, as such complex processes are often difficult to fully capture through experimental approaches alone.

Computational models can simulate the mechanics of the skin and the responses of tactile neurons. A first category of model was proposed to simulate the tactile properties of the hand and the response of the skin, afferents, and first-order neurons to stimuli such as contact with a rod or an edge [91]. To simulate the activity of single unit SA1 afferent, Gerling *et al* [92] focused on precisely modelling the distal phalanx, including its different skin layers and properties during static indentation. The TouchSim model by Saal *et al* [93] simplifies the considered skin properties to simulate the activity of population of afferents, including Pacinian corpuscles, in the entire hand, which enables the simulation of vibrational contact and the dynamics of the indentation with its tactile afferents. A further model proposed by Hay and Pruszynski [94] modeled the activity of first-order neurons through their many connections to afferents that constitute complex anisotropic receptive fields. These models fairly accurately reproduce the activity recorded in experiments, but face severe limitations in the kind of stimuli they can reproduce. For example, none of them can simulate lateral tactile motion or friction. The application to psychophysics also bears limitations since they do not account for cortical processing and the maximum resolution that could be extracted by afferent responses do not necessarily translate to the actual limits of human sensory abilities. Nevertheless, these models can set the plausible range for acuity hence inform future psychophysical studies. Gerling *et al* could reproduce Goodwin's results on curvature discrimination [95] but the 3 degrees resolution for

Table 2. Overview of computational models that aim to simulate neural activity or psychophysical dissimilarity. Grey shades represent the main focus of the proposed model.

	Skin Mechanics	Tactile Afferents	Primary Somatosensory Cortex	Higher-order Cognition	Outcomes
Gerling et al., 2014 [92]	▨	▨			Neural Activity
Saal et al. 2017 [93]	▨	▨			
Hay and Pruszynski 2020 [94]		▨			
Katic et al. 2023 [101]	▨	▨			
Foffani et al. 2008 [102]		▨	▨		
Detokaris et al. 2014 [103]			▨	▨	
Horch 1991 [104]		▨			Psychophysics
Bensmaïa et al. 2005 [105]		▨			
Senkow et al. 2019 [106]		▨			
Lin and Park. 2023 [107]		▨			
Le et al. 2024 [34]				▨	

edge detection of Hay and Pruszynski outperforms the 12 degrees human accuracy for edge orientation discrimination [96].

These models have already enabled researchers to replicate the activity of tactile afferents in the glabrous skin when subjected to mechanical stimuli. The TouchSim model, for instance, has been used to simulate afferent responses to edges of different orientations [97] and to study how age-related changes in skin elasticity and afferent density impact tactile acuity [98–100]. Similar models have been developed to study tactile responses in other body parts. The FootSim model [101] simulates neural firing in the foot based on human microneurography data. It enables the reproduction of the temporal pattern of skin deformation to simulate realistic strides, even though it focuses on deformation in the normal direction only.

As discussed in section 3.2, computational modelling offers the possibility to test neurophysiological assumptions. For example, Foffani *et al* [102] used models to investigate the activity of neurons with small and large receptive fields, which correspond respectively to sharp and broad tuning curves, in the primary somatosensory cortex (S1).

Computational models can also leverage the sensory properties of tactile channels to reproduce and predict perceptual outcomes [108], such as codes that rely on the encoding of the signal's intensity [104] or on the specific activation elicited by each constitutive frequency of the signal [106, 109]. These models mainly simulate the responses of Pacinian channels to predict the psychophysical outcome. Recent work [107] has combined the four-channels theory with neural network training to predict the perceived dissimilarity of complex vibrations. Le *et al* [34] have suggested a simple empirical model that predicts whether missing tones will be noticed based on their ratio with the lowest frequency of the signal. When it comes to mechanical transmission of vibrations, Scheibert *et al* [110] designed a tactile sensor modeled on the human fingertip to investigate how epidermal ridges transmit vibrations during contact with surfaces. Models that output neural activity rather focus on non-pacinian systems while models that aim to directly predict perceived signal dissimilarity tend to focus on Pacinian responses. Le *et al* [34] proposed an empirical model whose biological mechanisms are still to be elucidated. Table 2 provides an overview of computational models and their main focus area.

However, these models only are valid for a limited range of stimuli and simulate in depth only a small part of the ascending sensory pathway. For example, no model accounts for lateral touch of surfaces. Moreover, those that focus on the peripheral mechanisms do not necessarily output the human perception but rather the maximum accuracy that could theoretically be achieved based on the elicited neural activity. Thus, beyond afferent responses, a more in depth understanding of the full chain of processes underlying sensations is needed to improve the model as well as interoperability between models that focus on different parts of the chain. Through iterative extensions, models of perception will ultimately be able to predict the boundaries of touch even for complex interactions and become an integral part of the development of devices capable of providing fine, precise tactile feedback, mimicking natural tactile sensation.

4. Haptic systems and application

4.1. Emerging technologies to study tactile acuity

Haptic technologies have the potential to push forward the limits of the types, precision and versatility of tactile features that can be generated by controlling precisely the parameters and tactile dimension of the signals or adjusting the range of stimuli, depending on the task or population evaluated (i.e. experts versus patients). Devices delivering vibrotactile stimulation [111] and force-feedback have been developed for three decades [112], but new categories of devices have recently been proposed. For example, devices relying on ultrasonic lubrication [113] can generate programmable variations in friction on a surface depending on

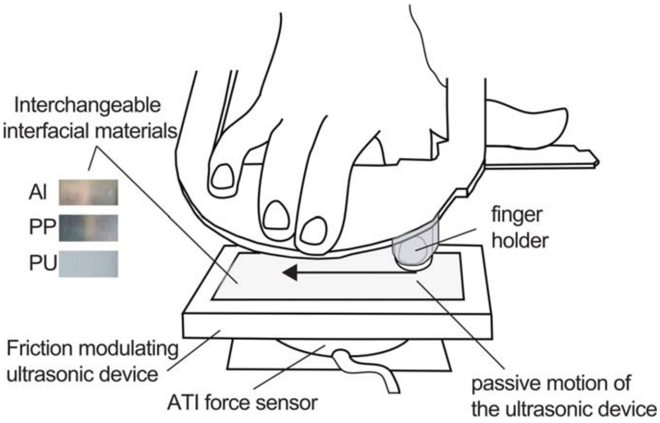

Figure 3. Structure of the Stimtac, a tactile actuator display based on ultrasonic vibrations for haptic rendering that can be coupled with visual interfaces. Reproduced from [114]. CC BY 4.0.

the contact location and can be coupled with visual feedback on the display (figure 3). One can alternate bands with and without modulated friction to simulate tactile gratings. Each abrupt change in friction can be programmed regarding its amplitude, sharpness, and duration, thus providing a wide range of possibilities for creating stimuli. The device has proven to be efficient for studying the fundamental aspects underlying the perception of friction [114, 115] and the human peripheral neural code corresponding to periodic changes in friction levels [116] (figure 4). This type of haptic stimulation has the potential to detect changes in tactile sensitivity, such as those occurring with ageing [117]. Limitations exist as well. In Dione *et al* [116], the maximal friction reduction that the device can achieve was shown to be smaller than what is measured in more ecological situations, such as when an object slips from the fingers. It was also discussed that the frequency up to which changes in friction can be induced on the skin might be limited to 60 Hz, due to skin viscoelastic properties, potentially limiting the possibility of simulating very fine gratings using this device, due to its inherent constraints. There is great interest in developing devices that can be used with several fingers, for example, to enable blind individuals to read from their phone, and, overall, to increase accessibility to content through the tactile channel. Some applications already enable multiple finger use [118], and others are being developed [119, 120]. Some devices provide an active lateral force along the direction of movement, making it possible to feel actual forces on the finger and changes in lateral forces even with a stationary finger [121].

Similar stimulations can be achieved by electroadhesion-based haptic devices, which modulate electrostatic forces between the skin and a surface to create controllable friction variations. Devices based on electro-adhesion can also be used to mimic the frictional properties of various textures or surfaces, making them valuable tools for investigating tactile discrimination threshold [122].

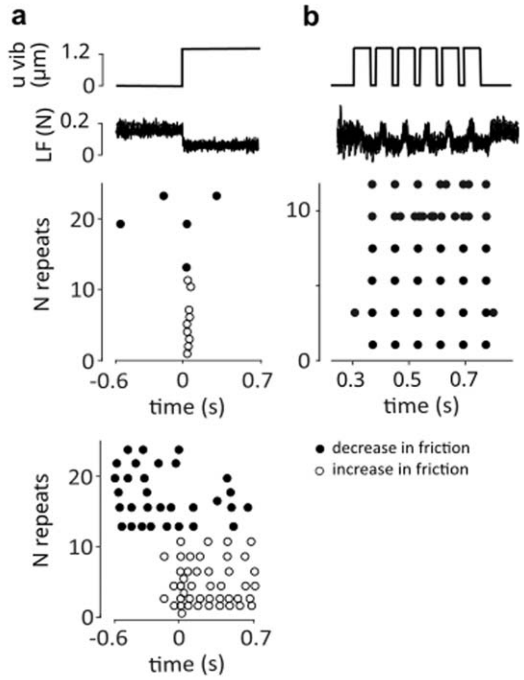

Figure 4. Neural responses of human afferent fibers to friction modulation controlled by ultrasonic vibration technology. (**a**) Response to a step modulation from two distinct SA1 fibers are shown in the two graphs for 24 stimulations (robot sliding the device over the skin). On the top graph, fiber responds distinctively to the change in friction. On the bottom, the fiber responds to the initial friction level of the surface, and then significantly reduces its responses when friction is reduced. (**b**) FAI response to a simulated grating, in which the friction is repeatedly modulated over the time of the stimulation, with longer phases of friction reduction compared to the moments with natural friction (12 Hz), hence favoring neural responses to the dynamic changes of friction. This illustrates how innovative technology can be used to deliver temporally precise and structured patterns of tactile stimulation. Adapted from [116]. CC BY 4.0.

Mid-air haptic devices have also been proposed and can be used as a novel tool for studying tactile acuity. They can stimulate tactile feedback on the skin without direct contact, by using pressurized acoustic waves [123, 124]. This technology enables specific sensations to be targeted and stimulated, as well as to dissociate the tactile and kinesthetic components of touch. For example, spatial acuity is usually assessed using a two-point discrimination test with skin indentation, but this method is often reliable. Mid-air haptics have been used to overcome problems associated with the variability in manually-applied tactile stimuli, having novel characteristics that cannot be obtained with traditional tests [125].

Despite these advancements, challenges remain since the power and resolution of mid-air haptic stimulation is still limited, making it difficult to replicate fine surface details [124]. Similarly, the perception of electro-adhesion and ultrasonic lubrication devices may suffer from variation in perception due to differences in skin moisture or impedance [122]. Still, emerging haptic technologies offer promising perspectives for investigating tactile acuity. By integrating new approaches, these technologies enable us to gain a deeper understanding of the underlying mechanisms involved in tactile processing.

4.2. Applications of tactile acuity mechanisms

Tactile acuity is of a great interest to the medical field and its related applications. Tactile acuity tests are performed as part of many medical procedures, such as to assess the extent of injury of a body part or in tests of functional loss, as found in the extremities with diabetes. Standard approaches included in quantitative sensory testing (QST), such as the detection of monofilaments delivering different forces and detecting vibrations [126], are useful, especially considering normative and comparative values between different groups, but these tests have little-evolved and newer technology could improve their accuracy and ease of application, as well as allowing testing at home in an automatic way. Further, QST focuses on understanding the underlying mechanisms in painful conditions, yet tactile disturbances can occur without pain (e.g. in aging, in psychiatric disorders) and require finer tactile tests, including a wide range of stimulus intensity to account for both loss of tactile function and hypersensitivity [127, 128]. Beyond the precise recognition of specific tactile features, some diseases induce intolerance to touch (tactile allodynia) that could come from an over-sensitivity to certain tactile dimensions or elements. In that respect, a better knowledge of people's sensory profile could be explored to provide solutions to these conditions [129]. It is known that tactile acuity within several tactile dimensions decreases with age [130] especially in the glabrous skin of the fingers [128, 131]. It is also well-known that there is a serious decrease in tactile acuity of the feet with age [132], which could cause falls. Consequently, preservation of tactile sensations, such as friction or vibrotactile cues, in addition to skin appearance, has become a goal of the next generation of the cosmetic and health industries [133]. The cosmetics industry may especially be able to take advantage of haptic developments in the use of tools for self-care and in massage, to give a more relaxing and positive experience.

Manufactured surfaces in cars are less and less made from natural materials, but rather feature plastic that mimics textures like wood and leather [134]. Knowledge of whether human touch can be tricked to feel an engineered material, (e.g. chrome or lacquered wood), is a key interest for many consumer products [135]. Similarly, manufacturers of haptic devices need to consider tactile acuity to avoid under-engineering devices that deliver a poor tactile experience or over-engineered devices that display a resolution that is far above that of touch.

Another application of the principles of discriminative touch are bio-inspired sensors. A recent study shows how small actuator technology can be used in a dynamic way to stimulate different mechanoreceptor classes preferentially and combine stimuli to provide more complex, realistic tactile features, including opening up the possibility to stimulate various body parts simultaneously for a more immersive experience [136]. Research has also developed in the application of biologically-inspired skins, where these could be applied to improve robotic sensing [137] and in the improvement of neuroprostheses [138]. A further example is the investigation of the computational principles behind the phenomenon of tactile hyperacuity, in which tactile resolution goes beyond the resolution stemming from afferent density [7]. The computational principles of this occurrence of super resolution have been studied and have already inspired a new generation of optical and tactile sensors [139].

5. Discussion and conclusion

Scientific literature on the human capacity to distinguish challenging tactile features shows both occurrences of exquisite sensitivity, as well as surprising limitations. This discrepancy likely stems from the fundamental structuring of the sense of touch, but the type of haptic exploration and learning mechanisms can also impact acuity. Recent studies have shown that optimal exploration strategy improves the capacity to sense subtle features [140–142]. Tactile discrimination skills can also be improved through prior experience with the stimuli [2] or practice. For example, Ragert *et al* [143] found significantly better tactile acuity in professional pianists, compared to controls, and found a relationship between tactile acuity and the extent of piano playing. Hughes *et al* [144] reported that training could enhance sensitivity to subtle changes, with participants showing improved accuracy in categorizing dotted surfaces after training. This adaptability is particularly evident in Braille readers, who, through daily practice, develop heightened tactile acuity and an enlarged somatosensory representation of the fingers used for reading [60, 145].

Although some studies leave participants free to explore as they wish and control for learning curves, most scientific experiments exhibit constraints due to the setup complexity or the reasonable duration of a study. Typically, studies test the tactile acuity resulting from a specific finger-surface interaction, sometimes in passive touch, and are often not able to implement enough different conditions to probe stronger hypotheses on the underlying computational and neurological mechanisms. To this date, experimental procedures that enable data to be easily compared between experiments have only been partly achieved only for the study of vibrotactile perception [146].

As a consequence, optimal exploration strategies and speeds that are observed in tasks specifically designed to highlight them are rarely witnessed in studies on the accuracy of touch, and some cues might be better detected in tasks that are more optimal at fostering the detection of very small differences. Moreover, data are still limited to truly understand the mechanisms underlying the perception of important tactile dimensions like friction and compliance. The physical phenomena underlying the cues related to these dimensions are multiple and even small differences in the experimental procedure make it difficult to compare the results of different studies. As a consequence, the neural processing of these phenomena has to be modeled on scarce or disparate data. For friction, an initiative has started with the STIMTAC device that was used in several studies, which made them more comparable, but the number of manufactured devices remains limited and not as widespread as vibrotactile actuators, which are industrial products. In the same vein, no standards exist to reliably modulate temperature in experiments.

In this context, the boundaries of tactile acuity are particularly informative since they highlight conditions of clear limitations or successes of the tactile system in rather compact experiments. We believe that it is essential to use and extend these findings in future studies with comparable experimental setups to better define these psychophysical limits and the computational and biological mechanisms that underlie the tactile sensations elicited in these discrimination tasks.

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Data availability statement

No new data were created or analysed in this study.

Authors contributions

JF, MD, AM, RA, and DG designed the review plan. JF, MD, and DG drafted the manuscript. JF, MD, AM, RA, and DG edited the paper.

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