

Haptic Perception and Its Relation to Action

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Keywords

sensory, skin, computational model, prosthetics

Abstract

Haptic perception uses signals from touch receptors to detect, locate, and mentally represent objects and surfaces. Research from behavioral science, neuroscience, and computational modeling advances understanding of these essential functions. Haptic perception is grounded in neural circuitry that transmits external contact to the brain via increasingly abstracted representations. Computational models of mechanical interactions at the skin predict peripheral neural firing rates that initiate the processing chain. Behavioral phenomena and associated neural processes illustrate the reciprocal relationship by which perception supports action and action gates experience. The interaction of sensation and action is evident in how features of surfaces and objects such as softness and curvature are encoded. By incorporating touch sensations in conjunction with motor control, biologically embedded prosthetics enhance user capabilities and may elicit feelings of ownership. Efforts to create virtual haptic experience with advanced technologies underscore the complexity of this fundamental perceptual channel and its relation to action.

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1. INTRODUCTION

Haptic perception refers to the mental phenomena that stem from physical contact and enable direct interactions with objects and surfaces. It derives from the sensory receptors of touch found in skin, muscles, tendons, and joints. “Haptic” denotes something beyond mere touch, namely, engagement of action; the label is related to the Greek words for touch, fasten onto, or hand. This article emphasizes that haptic perception inherently involves the motor system in interaction with sensory inputs. Although the touch receptors *per se* function under passive contact, without motor intentionality, it is generally action that sets the system under way. Active touch leads to a temporal unfolding of mechanical consequences on the skin and within muscles, tendons, and joints, which in turn activate associated receptors. Action further moderates the ongoing progression of neural and behavioral events.

The present article focuses on the discriminative functions of haptic perception, such as detecting, locating, analyzing, and recognizing objects and surfaces in near space. Other important perceptual functions that rely on touch receptors are not considered here. Specifically, the article does not consider the perception of noxious stimulation in the form of pain or itch (nociception and pruriception, respectively; Peirs & Seal 2016). Also excluded is the significant role touch plays in social/emotional communication and regulation, as when a person is hugged or stroked (Elias et al. 2023, McIntyre et al. 2022). Other engaging research areas not treated here are interoception, based on touch receptors found in some hollow organs like the small intestine,

and the representation of one's own body and its susceptibility to distortion by the experience of touch (Tamè & Longo 2023).

As has been noted, a theme of the present article is that haptic perception must be considered in relation to active movement. Another emphasis here is on the intrinsic connectivity of the haptic system, from physical and neural events at the sensory periphery to the higher-level functions of discriminative touch. Research from the fields of neuroscience and computational modeling increasingly informs how this continuity unfolds. Accordingly, Section 2 describes the neural underpinnings of haptic perception and computational models of transduction via the skin. Sections 3 and 4 consider the mirrored relationship by which perceptual processing supports action and action gates the course of perception. Section 5 provides a closer look at how elementary features of material and shape are acquired by means of active exploration. In Section 6, plasticity of touch is considered in relation to haptically based prostheses. Finally, Section 7 describes efforts to create virtual haptic experience and underscores the complexity of this fundamental perceptual channel.

2. PERIPHERAL PATHWAYS IN HAPTIC PERCEPTION

An account of haptic perception must be anchored by an understanding of the underlying sensory receptors, arguably more so than in other perceptual domains. Scientists may investigate speech recognition without dwelling on place coding in the cochlea, and research on visual scene recognition can be conducted without formally acknowledging molecular transduction by rods and cones. Perception through touch, however, is directly and intimately linked to the inputs stemming from the periphery. As noted above, touch receptors are found not only in skin (cutaneous sensing) but also in muscles, tendons, and joints (collectively termed kinesthetic sensing). Further analysis of the receptor signals proceeds through neural circuitry in the spinal cord and continues in nuclei of the medulla, then it ascends to the cortex. Central expectancies and local neural interactions are critical to function at all levels.

2.1. Structure of the Skin

As shown in **Figure 1**, the skin comprises a multilayered structure with coarse demarcations between the epidermis, dermis, and subcutaneous tissue. The epidermis itself has a complex layered structure with a thickness of approximately 0.1–1 mm. It is the stiffest portion of the skin, while the underlying dermis is on the order of 1–5 mm thick and is more easily deformed (Li et al. 2012). Any applied force that stretches and strains the skin impacts the structure of elastin fibers and collagen within the dermis and, ultimately, the neural pathways it contains (Zöllner et al. 2013).

Housed within the dermis are several types of neural fibers with distinct structural and functional properties. One population, low-threshold mechanoreceptors or LTMRs, consists of myelinated fibers of type A β that are sensitive to mechanical stimulation and that terminate in specialized endings (see Zimmerman et al. 2014). Fibers with lesser or no myelination, types A δ and C, have free (nonspecialized) endings and respond to thermal cues, particularly warming or cooling of the skin. The mechanoreceptors, and to some extent the thermoreceptors, are the cutaneous underpinnings of haptic perception in terms of discriminative functions. Other sensory fibers found within the skin mediate sensations of pain and itch and (in hairy skin) respond to pleasant sensations when the skin is stroked at an optimal rate.

2.2. Properties of Skin Receptors

Early anatomical studies identified the endings of A β LTMRs and gave rise to their names (Pacinian corpuscles, Ruffini endings, Merkel cell complexes, and Meissner corpuscles). However,

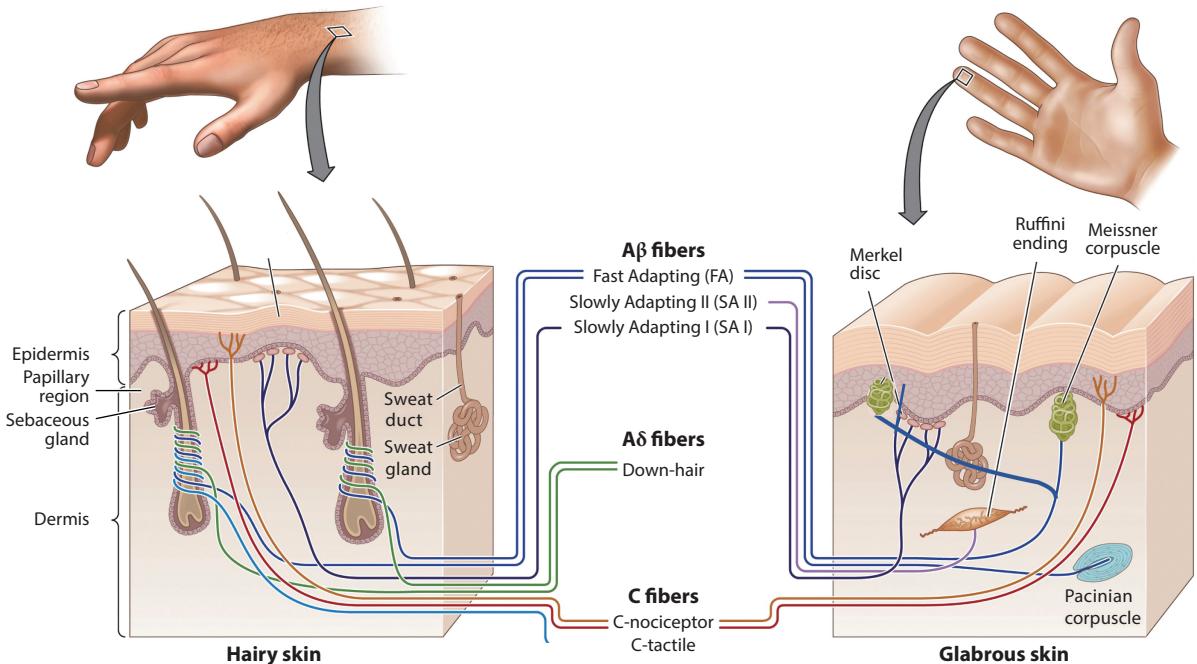


Figure 1

Structure of hairy and glabrous skin illustrating the receptor populations and fiber types. Figure adapted with permission from Wolfe et al. (2020) as adapted from McGlone et al. (2014); copyright 2014 Oxford University Press.

relatively recent technology has been needed to confirm the specialization of these different receptors for signal processing and to understand their function at a more mechanistic and neurological level. In pioneering studies, Johansson (1978) placed electrodes within the skin of the arm and recorded neural responses under different types of stimulation. This technique identified four classes of neural fiber, differentiated by the temporal stimulation that proved to excite them and the size of the receptive field. Slowly Adapting (SA) fibers responded to sustained stimulation and were of two subtypes: SA I, with small receptive fields (5–10 papillary ridges), and SA II, with larger fields. Fast Adapting (FA) fibers responded to vibration, with FA I and FA II having small and larger receptive fields, respectively. Johansson (1978), however, could only correlate fiber properties with what was known about the location and structure of the specialized endings. He proposed, and further research has confirmed, the associations of SA I with Merkel, SA II with Ruffini (although there is a question as to whether these endings are found in human skin), FA I with Meissner, and FA II with Pacinian endings.

Newer neurophysiological studies aided by genetic methods, electron microscopy, and electrophysiological recordings have provided deeper understanding of how specialized endings function in interaction with A β LTMRs. A detailed review is beyond the scope of this article, but a brief overview is provided here (excluding the Ruffini endings, given their questionable status in human skin), because the physiology and anatomy are critical to understanding certain effects such as localization, acuity, and alerting potential. (For further reviews and models of the receptors, see Fleming & Luo 2013, Quindlen et al. 2016, Woo et al. 2015, Zimmerman et al. 2014.)

Small receptive fields, which are essential for both localization and spatial acuity, are characteristic of the fibers located near the skin surface, i.e., the Merkel discs and Meissner corpuscles

(associated with fibers labeled SA I and FA I, respectively). A single neural fiber can branch into multiple Merkel or Meissner end-organs. Both types of endings are found in the papillary dermis, where the epidermal layer projects into the dermal layer, forming a rippling intersection. The ripples projecting into the dermal layer are the inner counterparts of the papillary ridges—the undulations in the observable skin surface that form fingerprints. Merkel discs are found at the tips of these projections, and Meissner corpuscles lie between them, in positions that would enhance the responsiveness to mechanical interactions between the skin and contacted surfaces. The mechanisms of these specialized endings are quite different. The SA I fiber responds to initial touch and activates the Merkel endings through a synaptic connection, leading to a more sustained response to pressure (Woo et al. 2015). Meissner corpuscles are formed by axon endings within a stacked structure wrapped by layers, which is perturbed by the mechanical deformation of the skin (Neubarth et al. 2020, Takahashi-Iwanaga & Shimoda 2003). In the more deeply situated Pacinian corpuscles, a myelinated neural fiber projects into the center of concentric layers, which it infiltrates with smaller branches (Cauna & Mannan 1958, Spencer & Schaumburg 1973). The resulting structure is sensitive to high-frequency vibration on the skin (20–1,000 Hz, with peak sensitivity around 250 Hz), triggered over a relatively large receptive field with diffuse boundaries.

The receptive fields of SA I and FA I receptors are not uniform but rather show high-sensitivity regions called subfields (Johansson 1978, Phillips et al. 1992, Pruszynski & Johansson 2014, Suresh et al. 2016). Whereas the entire receptive field of the single neural fiber covers several papillary ridges, the width of a subfield is about that of a single fingertip ridge. As noted, the fibers of receptors close to the skin surface may branch near the skin and terminate in multiple end-organs. The heightened sensitivity of a subfield area on the skin results from its proximity to one or more of the branches from a single fiber. Contact with the papillary ridge above one of these branches excites the end-organ and enhances the neural response (Jarocka et al. 2021). Additionally enhancing the neural signal, multiple fibers are activated by a single region of skin, resulting in a complex population response (Pruszynski et al. 2018). Implications of these subfield regions of heightened sensitivity will be considered further in discussions of haptic acuity.

2.3. Spinal Cord to Cortex

The spinal cord has been compared to the retina of the eye, in that it is the initial locus where signals originating in the peripheral fibers can interact. Abraira & Ginty (2013) pointed out that the dorsal horn has more interconnections than ascending pathways to higher cortical centers and suggested that many of the phenomenological subtleties of touch arise from local interactions. Inputs from different mechanoreceptor types converge within the spinal cord of the mouse and form networks with interneurons, resulting in neural populations within the dorsal horn that can be distinguished by their responses to force-time profiles (Chirila et al. 2022). Thus, functional specialization is evidenced even at this very early stage in the neural chain.

Mechanoreceptive information, directly from peripheral receptors or from synapses within the spinal cord, proceeds along the dorsal column-medial lemniscus (DCML) pathway to nuclei in the brainstem. In monkeys, one of these subcortical nuclei, the cuneate, is sufficiently advanced in the processing stream for neurons to show selectivity to edges and dot patterns (Suresh et al. 2021), rolling versus slipping interactions with the skin (Jörntell et al. 2014), and actively controlled versus passive movement (Versteeg et al. 2021). Thus, by the time sensory signals arrive at primary somatosensory cortex (S1), the neurophysiological input pathway has extracted featural information from touch interactions. It should be noted, however, that neurons in the brainstem and thalamus still show dominant response patterns to sustained versus vibratory inputs that are characteristic of a single (i.e., unmixed) class of peripheral fibers (Douglas et al. 1978,

Kaas et al. 1984). Somatosensory cortex shows further mixing of signals, in that some neurons respond during sustained pressure on the skin and at the transient signal from its offset, and their response can be modeled as a linear mixture of slowly and rapidly adapting inputs (Pei et al. 2009).

2.4. Modeling Skin Stimulation and Its Neural Outcomes

Explicit computational models have been developed to predict the responses of neural populations when force is applied to the skin (Deflorio et al. 2022). In general, such models require consideration of two broad components: the mechanical effects produced as a physical event stretches the skin (Zöllner et al. 2013), and the neural firing that ensues as the receptor populations are activated. As shown in Figure 2a, Saal et al. (2017) developed a model that followed this chain to make predictions about the millisecond-level timing of outputs from the mechanoreceptor populations in the palm of the hand. The model incorporates a map of slowly and rapidly adapting

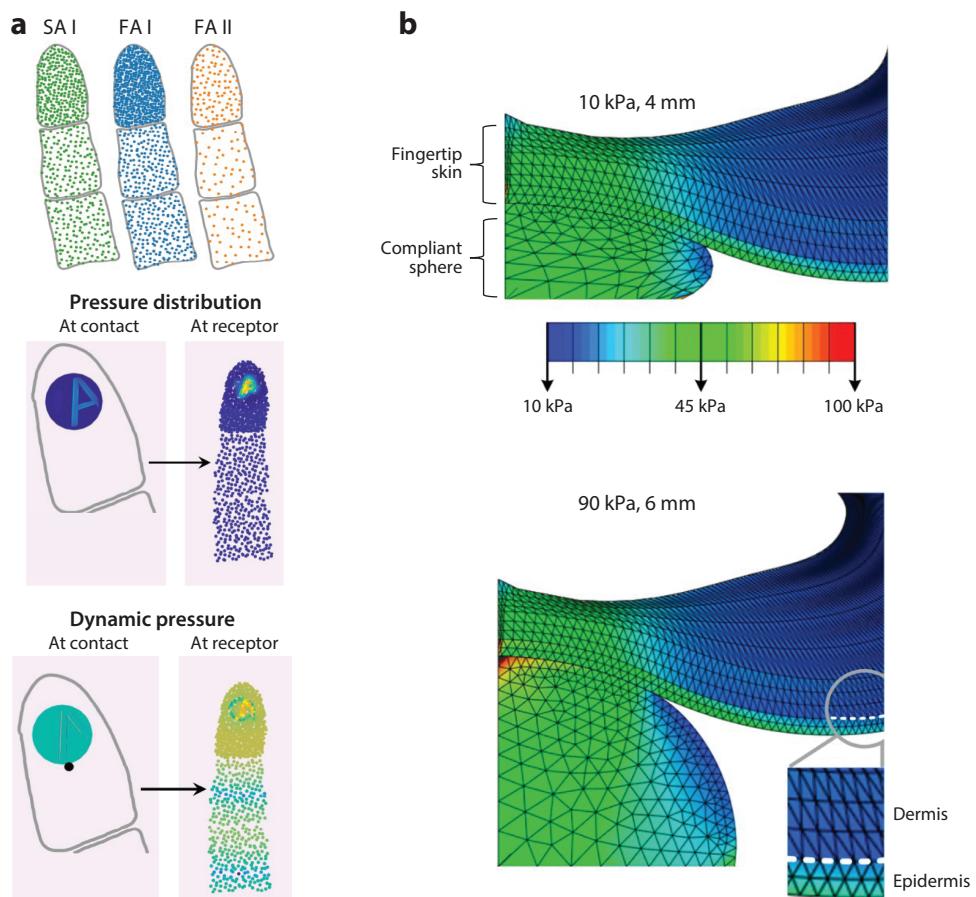


Figure 2

Two approaches to modeling skin stimulation and its effects. (a, top) Receptor density based on published reports. (Middle, bottom) Skin contact from a vibrating letter is transmitted to the receptors as a pressure array and a traveling wave over time. Panel adapted with permission from Saal et al. (2017). (b) Finite-element modeling of the skin of the fingertip (top) as it contacts a compliant sphere (bottom). Shown are two spheres differing in elasticity and radius that produce equivalent skin stress. Panel adapted from Xu et al. (2021) (CC BY 4.0). Abbreviations: FA, Fast Adapting; SA, Slowly Adapting.

afferents on the palmar surface, in numbers proportional to previously measured densities. It then predicts how the skin would mechanically respond to an indenting stimulus (for example, an embossed letter) at each skin location, with two components: a response to the stress from sustained contact that primarily affects the slowly adapting receptors, and a time-varying propagation of the pressure wave across the skin over time that stimulates receptors with large receptive fields further from the contacted region. The derived mechanical components are transmitted to a “leaky integrate-and-fire” model that converts input levels of stress into neural spike rates (e.g., Lansky et al. 2006). In Saal et al.’s (2017) model, the parameters of the neural component are adjusted for each of the mechanoreceptive populations.

The model accounts well for observed patterns of neural firing in response to sustained contact and patterns passed across the skin, among other phenomena. However, it has difficulty in predicting the effects of stimulating the skin with a dense array of small elements that can be individually activated to create time-varying spatial patterns within the fingertip (Grigorii et al. 2022). The problem with the model in this context appears to arise from its incorporating a pressure wave that propagates the response to local stimulation (as from a single pin) across regions of surrounding skin. Although this component simulates activation of the large receptive fields of the FA II receptors, it appears to produce noise in the more localized responses of the FA I receptors that are the primary target of the pin stimulation.

Saal et al. (2017) explicitly noted that a limitation of their model was to treat the skin as a plane, whereas in reality, it deforms in shape according to the stimulus in contact. For this purpose, another approach has been used, namely, finite-element analysis, which approximates a portion of the skin as a mesh with a large number of elements, as shown in **Figure 2b**. Wang et al. (2016) developed such a model with more than 14,000 elements for the SA I receptors in the mouse hind limb. The model has phases similar to those described previously: predicting how indenting the skin produces an effective stimulus as modulated by skin mechanics, and converting the effective stimulus into input to a leaky integrate-and-fire model, from which neural firing rates are derived. A distinguishing feature of this research was the use of precise measurement of the thickness and elastic parameters of specimens from the hind limbs of several mice to develop the finite-element model of skin.

The research presented so far, describing the initiation of discriminative functions of haptic perception at the periphery, largely relies on passive stimulation using controlled stimulus presentations. At this point, we turn to the contributions of voluntary action.

3. ROLE OF HAPTIC RECEPTORS IN STABLE GRASP

Anyone who has tried to manipulate with cold hands knows that touch is essential to manipulation, even to stably grasping an object in order to lift it. This fundamental capability was studied by Johansson & Westling (1984) using sensors that recorded the fingertip force applied to an object and its position as it was pinch-grasped and lifted. They found that after the initial lift, participants maintained a stable grasp on the object with just sufficient force to prevent it from slipping (the so-called safety margin). The experiments tested the effects of anesthetizing the fingers, adding extra load, and instructing the subjects to release the object gradually until it dropped. Collectively, the studies implicated the role of afferents within the skin in enabling the balance between the grip force and the load force and in quickly adjusting to changes, as with extra load or incipient slip. The timing of adjustments, on the order of 60–80 ms for slip, ruled out conscious feedback control.

Since this seminal study and follow-ups, new techniques have been applied to provide deep insights into the role of perception in grasp control. Delhaye et al. (2021) investigated the role of

tangential forces between the skin and a surface that arise when an object just begins to slip. They video-imaged a fingertip as it pressed on a transparent surface while a tangential force was applied. At the same time, responses of A β LTMRs with small receptive fields (SA I and FA I) within the contact area of the finger were recorded. Using the image data, strains in three directions (across the finger, along the finger, and diagonally) were measured. FA I firing was found to be correlated with the strain changes in the neuron's receptive fields during partial slip, which could provide a corrective signal to the motor system. The point of firing was further affected by the friction of the transparent surface, starting earlier when the moving surface was low in friction, which would correspond to greater risk of slip.

In subsequent work, camera imaging of the finger was implemented during active planar movement of an object held with pinch grasp (Schiltz et al. 2022). The results provided further evidence for a control process whereby partial slip increases the strain on the fingertip, which, presumably by afferent mediation, induces an adjustment of grip force. This control loop allows the rate of movement of the arm/hand to remain relatively constant across changes in surface friction.

4. ACTION-SUPPORTED PERCEPTION

The previous section emphasized the role of perception, albeit likely at an unconscious level, on the success of action. Here we consider the reverse: action affecting perception. Action plays multiple roles in haptic perception that appear to some extent to be in opposition. The following scenarios have been demonstrated: (a) When a primary task is directed toward action, concurrent signals from haptic sensory pathways tend to be diminished. A distinction has been made between two situations in which this process arises: down-gating, which occurs when a sensory signal stemming from an external, ad hoc source is attenuated during movement; and predictive attenuation, where the intended action is to touch oneself, and the affected percept is one's subjective experience of that touch (Kilteni & Ehrsson 2022). (b) In contrast to the previous case, action and perception may show reciprocal facilitation. Motor activity that is directed toward delivering haptic sensory information tends to accentuate, or even be necessary for, processing of the corresponding features. Moreover, when perception of a haptic feature is essential for performance of a motor act, sensory processing may be enhanced to support that act.

4.1. Reach-and-Grasp Action Down-Gates Concomitant Sensory Input

It has been known for some time that the anticipation and execution of voluntary action have inhibitory effects on perception (Coquery 1978). Chapman et al. (1987) stimulated the arm of a participant with weak electrical shock during no movement, passive movement, or active movement. Detection thresholds were elevated under movement, and particularly so when the active arm was stimulated. Other contact-suppression effects at near-threshold levels of stimulation have been found, including detection rates (Chapman & Beauchamp 2006) and the just-noticeable difference (Voudouris & Fiehler 2017), and the effect has been extended to perceived intensity of low-level but supra-threshold stimulation (Williams & Chapman 2000).

Down-gating effects can be observed even prior to movement. Williams et al. (1998) found decreased detection of electrical stimulation approximately 100 ms before movement initiation, prior to the time when preliminary muscle activity was detected by myelography. Seki & Fetz (2012) measured monkeys' evoked-potential response to electrical stimulation of the radial nerve in the wrist during active flexion and extension as well as during a preparatory still period. Measures were taken at the spinal cord and multiple cortical sites. All areas showed suppression of evoked potentials during active movement, but preparatory suppression was restricted to motor cortex. A negative correlation between the magnitude of cortical suppression and subsequent reaction time

(i.e., greater inhibition produced faster movement initiation) suggested that the down-gating of extraneous sensory input was initiated top-down to facilitate the wrist movement. Afferent signals from voluntary movement could not play a part in this effect, as the animal was motionless during preparation.

If voluntary action reduces bottom-up signals from sensory channels, there is presumably some adaptive advantage for this mechanism. The thermal component of haptic perception provides one adaptive scenario. Green & Schoen (2005) pointed out that thermal perception has two quite different roles: to induce regulation of the body (e.g., through sweat or shiver) and to convey the heat conduction of surfaces, an important cue to material substance. Active touch may be a signal to the thermoreceptive system that the ensuing perceived temperature should be attributed to an external object, and on that basis, thermoregulation of the body should be inhibited. Green (2009) compared the perception of thermal sensations on the hand and forearm during static holding and active grasping. In addition to exploring nociceptive thermal sensations, he considered levels of intensity that were unpleasant despite the thermal level being below the nociceptor threshold, a phenomenon called low-threshold thermal nociception (LTN), and during perception of benign thermal sensations of heat and cold. All types of sensation exhibited contact suppression, that is, attenuation of the percept during active grasping of the thermal contact area, as compared to heating or cooling the skin during continuous contact. Contact suppression was greater in magnitude for nociceptive stimulation, but the fact that it is found with benign thermal sensations indicates that thermal perceptual signals are generally reduced during active touch.

Other adaptive scenarios for down-gating arise in tasks involving manipulation. As noted above, top-down signals from motor cortex appear to facilitate rapid wrist movements by a mechanism of sensory inhibition (Seki & Fetz 2012). Another purpose for suppression is to reduce noise in neural transmission (Voudouris & Fiehler 2017). In mice, this may be associated with complex inhibitory circuits within the cuneate nucleus in the brainstem, which can suppress or enhance signals from the periphery as they are sent to the cortex (Conner et al. 2021).

4.2. Action Predictively Suppresses Sensory Signals

Another manifestation of contact suppression occurs when a person initiates action on another part of their body, that is, self-touch. Tickling is a well known but not unique example; self-contact such as tapping is also perceived as less intense than the same contact initiated externally (Bays et al. 2006, Kilteni & Ehrsson 2017). Multiple brain areas show differentiated activity during self-initiated versus external contact, including cerebellum and primary somatosensory cortices (Blakemore et al. 1999) as well as higher areas associated with body representation such as insular cortex (Limanowski et al. 2020). Self-contact suppression is not just reactive, but predictive. In a clever setup, Bays et al. (2006) showed that equivalent attenuation of sensation from a self-tap occurred when the fingers made contact (in this case, through a rigid intermediary surface) as when the contact was surreptitiously imitated by an external force while the fingers physically passed by one another. What was critical was the attribution of the distal event as a self-tap, as further indicated by the fact that temporal asynchrony between action and force feedback eliminated the attenuation.

These effects have been attributed to the use of forward models, i.e., motor predictions about the expected consequences of action (Shadmehr et al. 2010, Wolpert & Ghahramani 2000). Comparison of predicted to actual afference is essential to determining whether a peripheral event is self-caused or externally initiated (e.g., when voluntary eye movements produce movement across the retina that simulates the effects of a moving object). It has further been suggested that the

forward model particularly attenuates predictable sensory signals during movement, because they carry reduced information relative to externally initiated signals from contact (Kilteni & Ehrsson 2017, Shergill et al. 2013).

Predictive attenuation may seem reminiscent of the down-gating described above, whereby central, top-down mechanisms initiate the suppression of sensory information even prior to movement. However, whereas down-gating functions to avoid distraction from irrelevant signals, predictive attenuation reduces the processing load of relevant signals that can be anticipated. This distinction was made clear by Kilteni & Ehrsson (2022), who combined both externally produced touch (a moving limb was touched by an external agent) and self-touch manipulations within a single experiment. Comparisons of effect sizes (greater attenuation for self-touch) and statistical independence of the effects supported the argument that the phenomena of sensory down-gating and predictive attenuation are distinct.

4.3. Purposive Exploratory Movements Facilitate Haptic Perception

In contrast to the inhibitory effects of down-gating and predictive attenuation, certain movements positively impact perceptual outcomes. Of note are what Lederman & Klatzky (1987) called haptic exploratory procedures, that is, stereotyped interactions that are linked to particular perceptual goals. People rub to determine the roughness of a surface, while they poke or pinch to determine its compliance. Klatzky et al. (1989) noted that the actions associated with perceptual exploration tend to be quite distinct from the hand movements associated with manipulation, even when there are superficial similarities (e.g., objects may be grasped to perceive their size and shape as well as for wielding and functional usage).

More than 30 years have passed since the original paper by Lederman & Klatzky (1987) on exploratory procedures, and there has been considerable subsequent work on related topics: the development of systematic exploration in children (Kalagher & Jones 2011), the neural consequences of exploratory movement (Weber et al. 2013), and extension to animals with dexterous limbs and/or whiskers (Milne et al. 2021). Exploration associated with specific haptically extracted properties will be discussed further below.

4.4. Surface Features That Guide Action Are Preferentially Processed

Edges (i.e., spatially continuous protrusions from a surface) are rapidly detected by touch in parallel across the fingertips (Lederman & Klatzky 1997). Processing of edges extends to spatial localization and orienting with respect to a frame of reference, either egocentric (e.g., on fingertip skin) or exocentric (on an object or external coordinates). The value of the just-noticeable difference (JND) for linear edge orientation on the fingertip suggests coarse coding of angle (20° in Bensmaia et al. (2008) and 12.5° in Peters et al. (2015) for the longest 10-mm bars, which yielded best discrimination).

Peters et al. (2015) proposed a computational model of edge orientation perception, derived from the firing rates of multiple cortical receptive fields recorded from monkeys. The model assumes the following steps. (a) A bar stimulus on the skin initially activates SA I mechanoreceptors, which have relatively high spatial resolution. (b) Responses from multiple SA I afferents converge in the cortex, producing an emerging elongated receptive field oriented along the axis of the peripheral population (similar to proposals for edges formed in visual cortex by convergence from dot-like receptive fields in the retina) and/or an inhibitory response field (a “sideband”) around the corresponding axis. (c) The human perceiver acts as an ideal observer, reading the firing rates of a collection of cortical neurons with a small range of orientation preferences and using Bayesian inference to form a posterior probability of angular orientation between horizontal and

vertical. Probability distributions are compared to arrive at a psychophysical judgment of relative orientation.

Perceiving edge orientation is an important part of many manipulation tasks, particularly of the peg-in-hole type (e.g., inserting a button into a buttonhole). With this in mind, Pruszynski et al. (2018) tested the acuity of edge orientation in a manipulatory context, namely, grasping a dial with an oriented edge on its surface and rotating it to a target orientation. Short edges (2 mm) produced errors in angular position that fell within the 1-JND value observed for the longest bars in Peters et al.'s (2015) study, but longer edges (8 mm) produced average accuracy within 3°, well below the JND value. Moreover, responses were fast (average of medians = 0.2 sec). The authors suggested a neural coding model capitalizing on the sensitive subfields found within the entire receptive fields of skin afferent fibers. An afferent signaled a response if the edge activated any one of its subfields. Given the density and overlap in the active neural populations, an edge is indicated by the coincident responding of a subgroup of neurons present. Edge orientations could be discriminated by differences in as few as 5% of the actively signaling afferents. The subfield model achieved discrimination at a human level or better, demonstrating that information supporting precise differentiation is neurally available.

While the model of Pruszynski et al. (2018) does not specifically account for action-based facilitation of edge discrimination, the authors note that action could play multiple roles. At the periphery, grasping may produce signals on the skin that passive contact does not, due to its effects on the mechanical interaction. Considering cognitive levels, psychophysical comparison tasks with sequential presentations, as used in the passive discrimination paradigm, have a memory component that may reduce precision. It is further possible that neural pathways are process dependent, such that passive tactile reception is gated differently from skin contact during grasping.

5. HAPTICALLY ACCESSIBLE PROPERTIES AND ASSOCIATED ACTIONS

Of necessity, given the technology of the time, Lederman & Klatzky (1987) described haptic exploratory procedures in terms of visible gestural features. Improved technology and classification methods from machine learning have enabled detailed analysis of hand movement kinematics and dynamics, leading to a more fine-grained partitioning of the basic procedural categories. An emerging theme is that exploration is highly adaptive to top-down influences—goals, expectancies, past experience—and bottom-up stimulus characteristics. This section selectively reviews haptic properties, emphasizing the adaptive nature of exploration during perception.

5.1. Texture

Texture is the property of surfaces produced by variations in fine-grained geometry. Within this general category, there are variations such as roughness/smoothness, slipperiness/stickiness, etc. Textural variations are generally associated with the exploratory procedure that Lederman & Klatzky (1987) called lateral motion between the skin and the surface. The detailed interactions have been measured in terms of movement kinematics (speed and derivatives; Callier et al. 2015), force (Roberts et al. 2020), direction within body or surface coordinates (Lezkan & Drewing 2016), and the temporal window of interaction (at contact versus across sustained motion; Richardson et al. 2022, Roberts et al. 2020).

An important consideration in evaluating these data is that the underlying information for judgments of texture varies with the intrinsic scale of the surface: According to the duplex model of texture perception (Hollins & Risner 2000), surfaces with elements spaced at or below approximately 0.2 mm (this estimate sometimes reaches 1 mm or above) are primarily sensed by vibration

and then by rapidly adapting mechanoreceptors, whereas coarser textures are processed through spatial coding via SA I receptors. Exploration by means of lateral motion is needed regardless of scale: It produces the vibratory code used for fine textures (Bensmaia & Hollins 2005), and it enhances the spatial signaling associated with coarse surfaces (Johnson & Lamb 1981).

Callier et al. (2015) described the kinematics of texture exploration derived from video taken during a magnitude estimation task (i.e., assigning a number to represent the perceptual intensity of a stimulus along a designated dimension). Samples of 14 commonplace surface materials were included, each large enough to allow free movement (30×30 cm). Participants moved faster and for greater distances when judging slipperiness as compared to roughness, even when presented with identical physical samples. The authors attributed these kinematic variations to reliance on different neural populations: slowly adapting receptors responding to skin stretch when judging slipperiness, and fast adapting receptors responding to temporal frequency information when judging roughness. The difference in speed increased over the course of the experiment, demonstrating that the kinematics of exploration are further modulated as people become more experienced with the particular perceptual judgments.

It is well established that the perceptual response to texture variations varies little with exploratory speed, as, for example, when participants provide ratings of roughness magnitude (Lederman 1974). Under conditions of active exploration, speed-invariant texture perception might be attributed to knowledge of motor intention and feedback from movement, both of which could be used to calibrate movement speed and normalize texture responses accordingly. This explanation is invalidated, however, by the further finding that speed invariance is maintained even under conditions of passive exploration, that is, when speed is externally controlled. Without direct coding of movement parameters, how is speed adjusted for in texture perception? A study by Lieber & Bensmaia (2020) indicates that the peripheral signals provide sufficient information for speed normalization to occur at more central levels. They observed that, although the responses of peripheral fibers are strongly affected by exploration speed, neurons at the cortex are much less affected, and speed sensitivity varies within the cortical population. They presented a computational model showing that speed and texture could be separately decoded at cortical levels on the basis of variations in the temporal and spatial signals from subcortical neurons.

Although computation at the cortex appears capable of extracting texture independent from exploratory movement, the reverse problem of decoding speed independently from texture proves less successful. The perceived speed of stroking is to some extent texture-dependent—exploring vinyl tends to feel slow and denim fast, for example (Delhaye et al. 2019).

5.2. Softness

When people apply force to a surface during the course of haptic exploration, they receive cutaneous and kinesthetic signals of deformation and resisting force; another component of feedback is the internal representation of the motor command. Several words refer to the ensuing perceptual experience, reflecting differences in corresponding physical properties, but softness (inverse to resistance) is an encompassing and conventional term. Stiffness (and its inverse, compliance), elasticity, deformability, and viscosity are all variants. The dimension of softness is not applicable to all surfaces; it lies between the extremes where the force is simply absorbed by a change in the shape of the surface (like pressing into a foamy substance) and where the surface does not adapt and returns the force to the user (like a stone). Lederman & Klatzky (1987) labeled the exploratory procedure associated with softness “pressure.”

A narrow conception of softness, or rather an inversely related variable, is stiffness. In a spring, stiffness is k , the spring constant, which is measured as $k = -F/d$, where F denotes force and d is the

distance of spring compression. People exploring a spring by touch alone can extract its stiffness from kinesthetic (muscle/tendon/joint) cues to the distance their effector moves and force cues from skin deformation and (for higher force levels) kinesthesia (Srinivasan & LaMotte 1995). Wu & Klatzky (2018) modeled stiffness perception as a recursive Bayesian process, where the estimate of k was updated iteratively over small steps over the course of spring compression. At each new step, the previous estimate of stiffness was linearly combined with the estimate derived from the recent change in position and concomitant change in force, thus providing a new value that acted as a prior. Critically, the weight given to the prior estimate was greater when (a) the variability in previous estimates was smaller and (b) there was a larger difference between the new estimate and the prior. In other words, the system was designed to trust (give more weight to) reliable (low-variability) prior data and to distrust sudden changes in the ongoing estimate. The model was tested with a haptic force-feedback device that was capable of simulating linear springs over a range of k values as well as nonlinear springs with a k value that progressively changed over the course of compression. On each trial, participants compressed a standard virtual spring, with stiffness designated as 100, and a novel spring (linear or nonlinear) with stiffness varying from trial to trial. They then numerically reported the perceived stiffness of the novel spring relative to the standard. For simulations of both linear and nonlinear springs, model predictions of participants' stiffness estimates closely conformed to the observed data.

The haptic exploration assumed in Wu & Klatzky's (2018) model follows along a smooth linear trajectory, which was guided during their experiments by a visual cue. More generally, of course, haptic exploration for softness is quite variable; we do not test a melon in the same way as we do a mattress. Kaim & Drewing (2011) found that softness-directed haptic exploration is affected by both expectations about the stimulus and the judgment to be made. In a two-choice softness discrimination task, participants optimized performance by applying greater force when an expected stimulus was stiffer and also when the anticipated difference between the stimuli was smaller.

Softness can be considered a feature not only of bounded objects but also of granular substances like sand, substances with countable elements like beans, surfaces with nap like fur, or viscous substances like paint (Cavdan et al. 2021, Dövencioğlu et al. 2022). When the stimulus population is opened to such diverse objects and materials, related exploration is quite varied and clearly affected by the stimulus itself. Even if we restrict consideration to objects and surfaces that retain coherence under force (e.g., excluding granular materials), the concept of softness is considerably broader than the formal definition of stiffness. In Cavdan et al.'s (2021) study, participants rated a collection of objects on multiple softness-related German adjectives. Of greatest current relevance is how they explored when using rating adjectives denoting hard, inflexible, or elastic materials, which collectively emerged as a construct of deformability. Along with pressing, rubbing emerged as a frequent mode of exploration for these ratings, particularly when the objects had surfaces with underlying structural elements (cotton balls and fur).

5.3. Curvature

Formally, an edge is curved when it deviates from a straight line, as does the circumference of a circle, and a surface is curved when it deviates from a plane, as does that of a sphere. The extent of curvature can be quantified by the radius of the circle or sphere. Curvature is a parameter of shape, which Lederman & Klatzky (1987) associated with two forms of exploration: To a coarse extent, curvature can be detected by grasping and enclosing an object, but for more precision, following its contour with the fingers is necessary. Contour following provides two types of cues: local cutaneous cues to slant deriving from relative skin stretch across the fingerpad, and kinesthetic cues from the change in joint angle as the contour is traversed. Wijntjes et al. (2009) separated these

cues with an apparatus where the traveling fingertip rested on a small platform that could rotate and/or be raised and lowered during transit. Rotating the platform as the finger traveled simulated changes in local surface slant, while accompanying changes in platform height simulated the joint angle changes imposed by a real curve. Experiments showed that the cutaneous slant cue dominated in curvature judgments.

Other findings confirm the importance of cutaneous cues to curvature and add further to our understanding of the underlying process. Cheeseman et al. (2016) found that the threshold to detect curvature (relative to a flat surface) was higher (i.e., less sensitivity) during active exploration than during passive presentation, where the edge was moved under the stationary finger. They attributed the greater sensitivity with passive presentation to the neural down-gating of perception under movement, as discussed above. Since down-gating tends to occur when a perceptual cue is treated as extrinsic to the ongoing action, like an ad hoc tap on the arm when it reaches to grasp, this would suggest that local cutaneous information about fingertip slant and moving the finger along the edge (which changes local slant) act as competing neural channels.

An intriguing illusion connects curvature and softness perception through cutaneous cues (Xu et al. 2021). As illustrated in **Figure 2b**, when pressed into a single finger at a controlled rate, a small and compliant sphere can be confused with a large, stiff one. The key here is that the fingertip interacts with the surface of the sphere in the same way in both conditions. In contrast to the passively induced illusion, the same discrimination is readily made under active exploration. In Xu et al.'s (2021) study, the specific combinations of sphere radius (i.e., curvature) and compliance that would be confusable under passive stimulation were predicted from a finite-element model (Wang et al. 2016) of the skin's mechanical response, taking into account the mechanically induced activity in the type I mechanoreceptive fibers (Lesniak et al. 2014). The illusions occurred in just those situations in which the extent of skin deformation and stress on the fingertip, as profiled by the model and confirmed by direct measurement of contact area, were similar for the two stimulus spheres, even though the spheres changed shape quite differently. Those same shape differences affected the displacement of the finger during active touch and hence allowed discrimination that was not possible under passive presentation.

Collectively, the studies reviewed here indicate a dominant role for local cutaneous cues during the exploration of an edge to decode its curvature. Indeed, active exploration and the kinesthetic cues it provides may impede curvature perception. If an edge is nonrigid, however, the situation changes, and kinesthetic cues deriving from changing finger posture during edge exploration may play a critical role.

6. HAPTIC NEURAL PLASTICITY AND SENSORY SUBSTITUTION TO SUPPORT ACTION

Neural plasticity refers to the capability of neurons and networks to alter function in response to experience. Sensory substitution refers to interventions that use intact perceptual channels as a source of information when otherwise dominant systems are impacted congenitally or adventitiously. Although effective sensory substitution does not intrinsically rely on neural plasticity, successful long-term use of alternate channels has been found to be coupled to changes in neural systems. For example, skilled blind readers of Braille and echo-locators (people who detect objects by producing sounds and interpreting the reflected sound waves) show involvement of visual areas that, in sighted people, function for spatial vision (Sadato 2005, Thaler & Goodale 2016). Neural plasticity of cortical areas associated with the sense of touch was demonstrated decades ago in research by Merzenich and colleagues (as reviewed in this journal by Kaas et al. 1983). In brief, mammals and other species evidenced profound reorganization of primary somatosensory brain areas after surgical alteration at the periphery such as amputation of a finger.

Touch can be utilized for sensory substitution in two distinct ways: one is to serve as the substituting channel when other senses are impaired, and the other is for touch to constitute the target for substitution by another sense. The first of these roles, where touch serves as a substitute channel, is exemplified by Braille reading. In this example, however, the active nature of haptic perception is minimally employed, as movement is used primarily to position tangible input for pickup by the tactile receptor. Increasingly, signals from wearable technology like the smartphone are being used to help blind travelers locomote. Navigation aids for the blind are varied in purpose: alerting to impending obstacles, guiding users along a predetermined path by signaling turns and correcting for drift, and assisting with developing a cognitive map of surrounding space. These applications may invoke active touch, as when the user explores a tangible map on a spatial display, but passive vibratory or tapping signals are more common. The pace at which aids for the blind are being developed is indicated by recent reviews (Kappers et al. 2022, Messaoudi et al. 2022).

Given the emphasis of the present review on the active nature of haptic perception, the second role for touch in sensory substitution, namely, to serve as the target of neural malleability, is of greater relevance. Recent advances in prosthetic limbs have provided remarkable demonstrations of how the plasticity of haptic neural systems can be exploited to the advantage of otherwise compromised sensory-motor capabilities (for review, see Bensmaia et al. 2023). Although a prosthetic appendage is intended to implement motor commands in some way, interventions that rely exclusively on this feed-forward function have limited use. Greater utility requires feedback about the consequences of motor commands, in order to “close the loop.” Visual feedback, though certainly useful for this purpose, has proven to have limited functionality in complex motor tasks like grasping (Saunders & Vijayakumar 2011). Technological advances have led to alternatives in the form of neuroprosthetics, which recruit intact sensorimotor pathways both to drive the apparatus and to feed back data from its sensors.

Marasco et al. (2021) evaluated an integrated sensory-motor neuroprosthetic system in two individuals with amputations below the upper arm. Motor nerves originally controlling the amputated hand were routed back to innervate residual muscles of the upper arm or torso. This connectivity allowed voluntary motor commands to the absent limb to activate the muscles. The ensuing contraction signals were detected by electromyography and used to control the prosthetic hand and arm. To simulate touch feedback, sensory nerves detached from the hand were routed to the skin of the upper arm. As components of the prosthetic hand made contact, sensed data were sent to arm-mounted tactors that activated the nerves associated with corresponding parts of the missing hand. Similarly, deep muscle locations associated with hand closure were identified and stimulated in correspondence with the grip of the prosthetic hand. By these means, tactile and kinesthetic perceptual pathways above the amputation site could be activated according to feedback generated by the prosthesis. Functional tests, such as grasping blocks and sorting them by stiffness, verified the advantages of adding sensory feedback to the prosthetic controller.

Much as tools extend and transform the body representation (Martel et al. 2016, Miller et al. 2018), a neuroprosthetic appendage may come to feel part of its wearer. Marasco et al. (2021) reported that their integrated sensorimotor prosthesis induced acceptance and sense of ownership. George et al. (2019) introduced distributed electrode arrays into the residual sensory nerves of a patient whose prosthesis replaced a distal arm portion and hand. Contact with a particular part of the prosthesis, such as the index finger, activated specific electrodes, which in turn produced sensations that were subjectively perceived as originating from the corresponding location in the amputated limb. Along with variations in the perceived location of stimulation of the phantom appendage, various qualitative sensory phenomena were induced, including sustained pressure and vibration (characteristic of SA and FA mechanoreceptors, respectively) along with painful

sensations and kinesthetic experiences like joint movement. The long-term experience of living with such prostheses has been documented for a small number of individuals, who reported in interviews that in addition to enhanced functionality and diminished phantom limb pain, the integrated prosthesis led to an improved self-image (Middleton & Ortiz-Catalan 2020).

One issue for bio-interactive prosthetic systems is how to activate the nerves that remain after amputation so as to optimize functionality and embodiment. George et al. (2019) noted that during manual interaction with objects, the aggregate signal from the receptor populations in the hand takes the form of a firing burst at the onset and offset of contact, with weaker firing during steady-state grip. They attempted to recreate this signal pattern when stimulating the residual sensory nerves of an amputee. They compared four patterns of electrical stimulation to the nerves as the prosthetic finger touched an object: constant signal level, signal proportional to force, and two biomimetic algorithms that sent signals in proportion to the change in force, which would peak at initial contact and release. Biomimetic feedback produced a substantial (nearly 50%) improvement in the time to perform perceptual discriminations in the size and compliance of a contacted object.

7. HAPTIC PERCEPTION OF VIRTUAL SURFACES

Virtual haptics refers to the use of devices that mimic feedback from real interactions with objects and surfaces. Haptic interfaces have been used to enhance entertainment and games, for training surgeons and dentists, and for physics education, among other applications. These technologies can also provide insights into human haptic perception.

Paraphrasing Theodore Roosevelt, the cardinal rule of virtual reality (VR) is, if you've got the receptors, the mind will follow. The key problem is how to control the receptors. Visual VR stimulates the retina via stereo head-mounted displays with wide field of view, fine resolution, and a rich color palette. The tools of virtual haptic technology are rapidly advancing, but fooling tactile and kinesthetic receptors is an elusive goal. Interfaces that provide haptic stimulation fall into three broad categories (Kuchenbecker 2018). Grounded interfaces are mounted to a stable surface, and the user typically interacts with the device by actively moving an attachment (e.g., handle, thimble, or knob). Ungrounded or wearable interfaces are mounted on the hand or body of the user, who receives stimulation in correspondence with free movement. Given constraints on weight, power, and tracking, the effects tend to be coarse-grained vibrations or transient forces. Surface haptic devices sense the user's touch on a physical surface and react with location-specific effects. The effects may be produced by vibration (sustained or transient, the latter producing click-type effects), arrays of movable elements such as pins, or changes in friction induced by electrical or ultrasonic mechanisms. (For technological reviews, see Basdogan et al. 2020, Giri et al. 2021, Kuchenbecker 2018, Pacchierotti et al. 2017, Zhu et al. 2022.)

Two technologies are commonly used to modulate the friction of a surface, namely, ultrasonic waves and electrostatic effects. The first approach vibrates a physical surface such as glass in a transverse direction at a very high frequency, causing small elements of fingertip skin to separate from it and thereby reducing friction (Wiertlewski et al. 2016). The second approach produces forces that attract the finger toward the surface, thereby increasing friction (Strong & Troxel 1970). Whether friction is modulated upward or downward, two features of the approach have implications for haptic perception. First, friction modulation is typically applied to a region of the touched surface larger than the fingerpad. For example, friction might be triggered across the entire surface of a smartphone at the moment the finger is detected at a target location. Accordingly, it is not possible for users to experience edges running across the fingertip, as if they were pressing on a wire or thread. Second, friction by definition corresponds to resistance to movement, which means that friction can be perceived only when the finger and surface are in motion relative to one

another. Although this article has emphasized the importance of movement to haptic perception, in this case the necessity to move produces tactile blur, acting to reduce the precision with which a friction-rendered element can be located in space and time.

In principle, friction-modulating surface displays can be used to present stimuli at two scales: textures and patterns, which comprise variations in friction over relatively small and large regions, respectively. Burns et al. (2022) used stimuli constructed from “texels” to identify the boundary between the two scales. A texel is formed by varying friction magnitude as a sinusoid with fixed peak amplitude and frequency over some surface length. Aligning a series of texels that differ in the sinusoidal parameters creates a complex texture. Experimental participants explored such a sample texelized surface by swiping with the finger, and then they attempted to discriminate between an exact match to the sample versus one in which the texel segments were rearranged. The task required assigning specific texels to spatial locations, or in other words, perceiving the surface as a pattern. No participant could succeed once the texel lengths fell below 1 mm, suggesting that at finer levels of variation, the representation is no longer represented as a spatial pattern. The 1-mm point where pattern information appears to be lost is similar to the boundary between coarse and fine surfaces established by the duplex theory of texture perception described above.

Although surface-friction displays can represent patterns at a relatively coarse scale, constraints on information pickup limit the utility of the spatial information. One might imagine, for example, using friction to display graphical patterns like a linear trendline to people lacking vision. One problem is simply following the pattern information along the surface. A surface-friction device typically vibrates the fingertip as a whole. The signal is sensed when the finger enters the region assigned to the trendline, and it is lost whenever the finger moves outside its boundary. Once this happens, there is no cue as to how to find the frictional signal again. In contrast, a physical edge creates pressure variations across fingertip space, like the wire example described above, that can be followed with ease (Rosenbaum et al. 2006). A practical consequence is that judging the slope of a friction-rendered straight line can take on the order of a minute, twice the time needed for an equivalent tangible stimulus (Gershon et al. 2016).

Surface haptics has evidenced more success in creating novel textures by changing friction on the fly as the finger travels through space, producing corresponding vibrations of the fingertip. Similarity judgments between surfaces generated from texels found that they are perceptually differentiated according to the amplitude, frequency, and irregularity (added noise) of the source wave (Friesen et al. 2021). Multidimensional scaling indicated that the emergent perceptual dimensions were not simply aligned with the physical ones; for example, the first extracted dimension combined frequency with amplitude (reverse signed). Verbal labels such as “chirpy” and “breeze” indicated that parameter combinations were capable of producing highly varied virtual textural phenomena.

Despite the potentially rich palette of effects that might be possible, friction-varying surfaces do not appear to be sufficient to emulate real textures like silk and corduroy. Grigorii et al. (2021) tested how well a friction-based simulation of real texture matched physical reality (see **Figure 3**). To create the simulation, recordings were made of the lateral force encountered by a fingertip as a real texture slid beneath it at a fixed rate, while normal force and temperature were controlled. From this trace a playback was produced for presentation by a surface haptic device, which modulated friction as surface regions passed beneath the finger at a fixed scanning rate, so that the previously recorded lateral forces from the real texture were precisely reproduced. Next, participants took part in trials where three textures were presented in succession: a physical texture (e.g., denim) straddled by two playbacks, one corresponding to the presented physical texture and the other derived from a different texture. The participant’s task was to match the presented physical texture to its friction-based playback. Performance in this task was, in a word, poor. Matching was

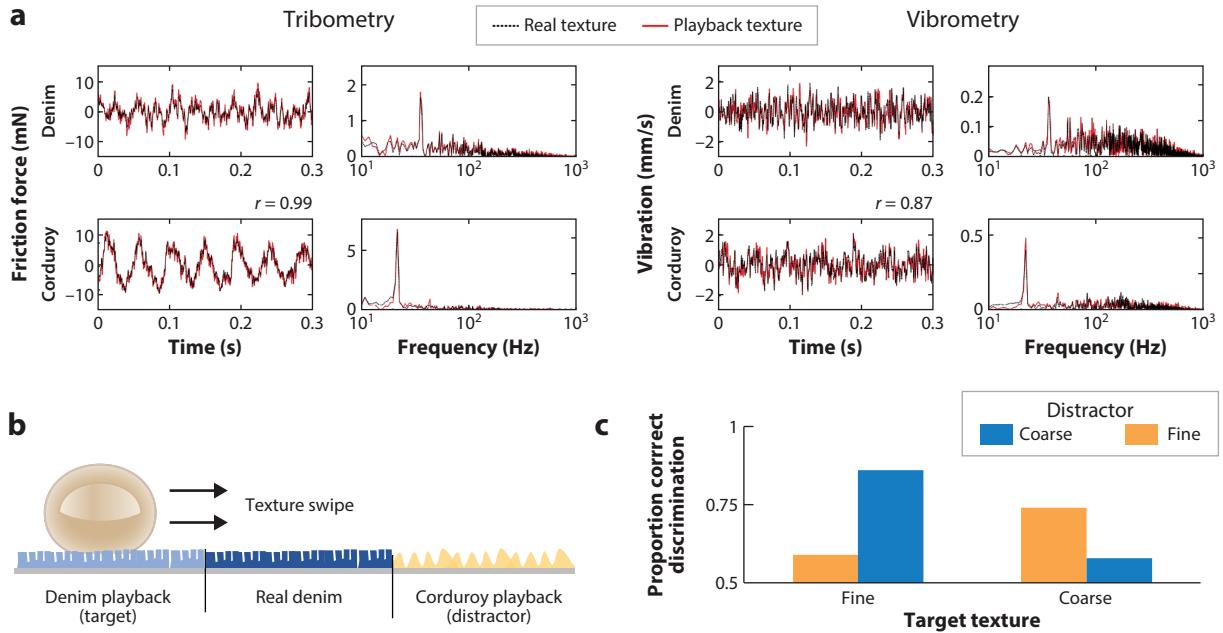


Figure 3

Rendering textures by friction modulation. (a) Measures over time (left, friction; right, vibration) during scanning of denim (above) and corduroy (below), and corresponding frequency spectra. The black and red functions show real and electrostatic-playback versions of the given texture, respectively. (b) Experimental task where a real texture (middle of swipe) must be matched to one of two adjacent playback textures, a match (target) and a distractor. (c) Discrimination accuracy in the experimental task for target and distractor textures at two levels of coarseness. Figure adapted from Grigorii et al. (2022) with permission from IEEE.

successful only when the target and distractor textures were highly discriminable (e.g., physical denim versus playback from nylon). Given the evidence that natural texture perception relies on the spatial or temporal responses of distributed receptors, it is perhaps not surprising that vibrating the fingertip as a whole is not sufficient to recreate a tangible surface, however well matched the synthetically produced vibrations may be to those induced by the real surface.

8. HAPTIC PERCEPTION RESEARCH AT THE CONFLUENCE OF PSYCHOLOGY, NEUROSCIENCE, COMPUTATION, AND ENGINEERING

This article began by emphasizing the fundamental role of action in haptic perception. The parameters of action directly affect the receptor signals that then drive the system bottom-up. Not only does action facilitate and regulate perception but also, and conversely, haptic perception is integral to actions from simple grasping to complex manipulation. Individuals whose perceptual and/or motor capabilities are not fully functional can be aided by sensorimotor interventions to the point where artificial limbs become in some respects their own. Efforts to create virtual touch with haptic interfaces must take into account how the complex skin interactions from real-world interactions affect the chain of processing from information pickup to attribution to external sources.

A further emerging theme from this review is that research on haptic perception should be approached from a multidisciplinary perspective. Along with psychological science, fundamental components of this perspective are neuroscience, computational modeling, and engineering.

Each field makes critical contributions. Among the directly psychological concerns are the phenomenological richness of touch experience, the discriminative power it affords in time and space, and the categorical structure of objects and surfaces that emerges through haptics. Neuroscience is essential to understanding how signals are transmitted, combined, and gated to support the richness of touch experience and the remarkable dexterity of which organisms are capable. Computational modeling is an increasingly powerful tool for understanding how neural signals contribute to perception and action. Neural receptors are embedded in a physical substrate that responds to mechanical forces that produce stretch and strain. Engineering and allied fields are essential to describing these interactions, providing support for modeling. Complex engineered interfaces provide test beds for research and novel possibilities for virtual touch experiences.

Future efforts that combine these disciplines will no doubt lead to advances in addressing fundamental questions about haptic perception, including how the sparse population of peripheral receptors produces the extraordinarily nuanced fabric of discriminative touch.

FUTURE ISSUES

1. This article has focused on discriminative touch. An important extension is to elucidate the connections between perception and action in the context of other modalities of touch, such as social interactions and representation of one's body.
2. Computational models of skin stimulation separately account for the effects of skin stimulation on local neural afferents and the precise deformation of skin elements over a region of contact. Integration of these approaches is needed for a fuller account of the perceptual consequences of skin contact.
3. Perception and action interact through multiple pathways, such as central down-gating, local neural inhibitory circuitry, and centrally initiated predictive suppression. How these mechanisms combine in elementary actions is an intriguing issue.
4. Perception of objects by touch encompasses a variety of features, such as roughness, curvature, and compliance. This article has described efforts to catalogue subvariations within such coarsely defined perceptual categories and to characterize their relation to purposive exploration. Refining the ontology of object features and actions promises to remain an active area of research.
5. Research on bio-interactive prostheses has revealed the potential of interventions that target residual sensory and motor neurons at the periphery and in the brain. Further developments in these efforts will rely on a multidisciplinary research effort involving neuroscience, psychological science, computation, and engineering.
6. The goal of virtual touch, the rendering of objects and surfaces that affords seemingly natural contact and haptic exploration, remains elusive. Technical advances are needed in areas like skin sensing, active stimulation, wearability, and modeling. Such developments will need to be closely coupled with studies of the consequences of simulation technologies for perception and action.

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