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REVIEW

Sensory Processing

AQ:1-4

The interaction between motion and texture in the sense of touch

AQ: au **Colleen P. Ryan**,[1,2*] **Gemma C. Bettelani**,[3,4*] **Simone Ciotti**,[1,2,4] **Cesare Parise**,[5] **Alessandro Moscatelli**,[1,2]
and **Matteo Bianchi**[3,4]
AQGRid1 [1]*Department of Systems Medicine and Centre of Space Bio-Medicine, University of Rome "Tor Vergata," Rome, Italy;*
[2]*Department of Neuromotor Physiology, Istituto di Ricovero e Cura a Carattere Scientifico Santa Lucia Foundation, Rome,*
AQ: 5 *Italy;* [3]*Research Center E. Piaggio, University of Pisa, Pisa, Italy;* [4]*Department of Information Engineering, University of*
AQ: 6 *PisaPisa, Italy; and* [5]*Independent Researcher*

Abstract

Besides providing information on elementary properties of objects, like texture, roughness, and softness, the sense of touch is also important in building a representation of object movement and the movement of our hands. Neural and behavioral studies shed light on the mechanisms and limits of our sense of touch in the perception of texture and motion, and of its role in the control of movement of our hands. The interplay between the geometrical and mechanical properties of the touched objects, such as shape and texture, the movement of the hand exploring the object, and the motion felt by touch, will be discussed in this article. Interestingly, the interaction between motion and textures can generate perceptual illusions in touch. For example, the orientation and the spacing of the texture elements on a static surface induces the illusion of surface motion when we move our hand on it or can elicit the perception of a curved trajectory during sliding, straight hand movements. In this work we present a multiperspective view that encompasses both the perceptual and the motor aspects, as well as the response of peripheral and central nerve structures, to analyze and better understand the complex mechanisms underpinning the tactile representation of texture and motion. Such a better understanding of the spatiotemporal features of the tactile stimulus can reveal novel transdisciplinary applications in neuroscience and haptics.

AQ: 8 *coarse texture; fine texture; grating; illusions and models for motion encoding; imaging studies; physiology; tactile motion; touch*

INTRODUCTION

In our daily lives, we often perform actions requiring fast and precise sequences of swiping and tapping movements, for example, to operate with our phone. To perform this efficiently, our nervous system combines the sliding movement between the skin and the screen of the phone, the short pulse of vibrations when we click on a virtual button or swipe over a rendered texture, kinesthetic information from muscles and tendons, and efference copy of our motor command. Studies from different disciplines in neuroscience, such as systems neuroscience, electrophysiology, and neuroimaging, shed light on the possible mechanisms of our brain for combining the different somatosensory and motor cues when we interact with an object by touch. In this article, we review the role of touch for the perception of texture and motion and for the control of movement of our own body. The interplay between the geometrical and mechanical properties of the touched objects, the movement of the hand exploring the object, and the motion felt by touch will be discussed.

The sense of touch is hence strongly associated with our motor system. Classic examples are the exploratory procedures, which are purposive movements of our hands maximizing the uptake of information on relevant properties of the touched object (1, 2). Touch has also a central role as an auxiliary proprioceptive cue for the control of hand movement and for motion perception (3–5). Understanding the representation of the spatiotemporal features of the stimuli in touch can increase our knowledge on the reciprocal influence between the somatosensory and the motor system. At the same time, it can also provide insight about the elaborate

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[*] C. P. Ryan and G. C. Bettelani contributed equally to this work.

AQ: 7 Correspondence: C. P. Ryan (c.ryan@hsantalucia.it); M. Bianchi (matteobianchi23@gmail.com); G. C. Bettelani (gemma.bettelani@gmail.com).

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interplay between static (e.g., texture, softness, roughness) and dynamic (e.g., direction, speed, vibrations) tactile cues. On one hand, tactile motion improves the discrimination of fine texture elements (6); on the other hand, the orientation and the spacing of coarse texture elements affect the perceived direction of motion (7, 8) and speed (9, 10). As we will discuss in this review, this interplay is central for the perceptual representation of objects' properties, like their texture and their motion status and plays an important role in the control of hand movements in tasks like grasping, manipulation, and reaching. Characterizing the response of the primary afferent fibers is of fundamental importance to understand the representation of texture and motion in touch.

The first step in the encoding of tactile stimulus is the transduction of the mechanical stimuli into neural signals by the different mechanoreceptors in the human skin. A deformation of the cutaneous tissue, either from its contact with external surfaces or from the flexo-extension of the joints nearby, produces an initial change in the mechanoreceptor that eventually triggers the action potential in the axon of the associated sensory neuron (11–13). Our hand is densely innervated by tactile afferents: about 2,000 tactile afferents innervate each fingertip and 10,000 afferent neurons innervate the remaining glabrous skin on the surface of the digits and the palm (14). Four tactile mechanoreceptors, the Merkel cells, the Ruffini endings, and the Meissner and Pacinian corpuscles, contribute to the somatosensory perception of the physical properties of external objects and provide information on the position and movement of our own body (Fig. 1). These mechanoreceptors are associated with sensory neurons of type $A\beta$ that convey the tactile information from the skin to the central nervous system (16). Based on their response during microneurography examination, sensory neurons are classified as slow- or fast-adapting fibers (17). Slow-adapting afferent fibers of type I (SA-I), associated with the Merkel cells, play an important role in the discrimination of gross texture elements, such as raised dots and ridges from static touch. Slow-adapting afferent fibers of type II (SA-II), associated with the Ruffini-like endings, have been described in the hairy skin and in the nailbed in both monkeys and humans (18). These provide information about the gross shape of objects from static hand posture and object motion from skin stretch (19). Fast-adapting (FA) fibers play an important role in encoding dynamic properties of the physical stimuli. Meissner corpuscles and their associated FA-I fibers [corresponding to rapidly adapting (RA) fibers, in Rhesus macaque] are crucial for the encoding of motion. They also respond to vibrations at a low range of frequency, typically between 8 and 64 Hz (20). FA-II fibers, corresponding to Pacinian corpuscle (PC) fibers in Rhesus macaque, are associated with Pacinian corpuscles and are extremely sensitive to vibrations in the higher frequency range, with peak sensitivity at 200–300 Hz (20, 21). The sensitivity of FA-II fibers to high-frequency vibration is an important component to explain human dexterity in tool use (22).

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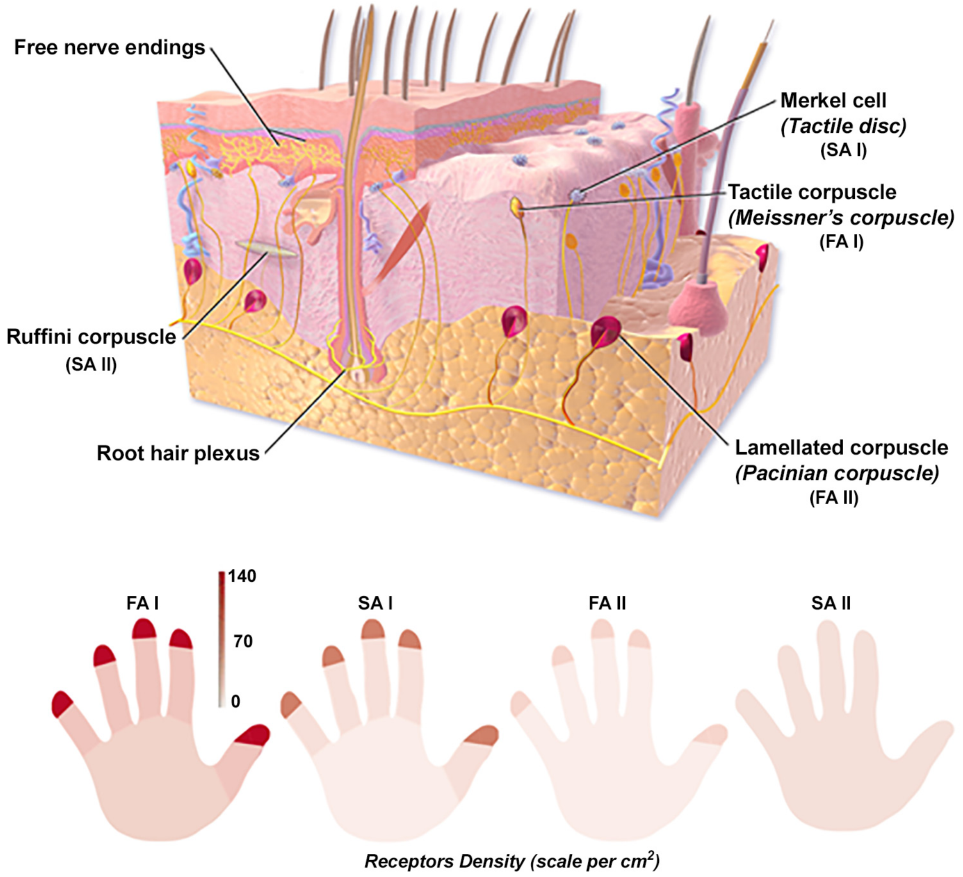

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Figure 1. *Top*: tactile receptors in the skin. *Bottom*: tactile receptors density (scale per cm^2). SA, slow-adapting fibers; FA, fast-adapting fibers. [From Blausen.com (15).]

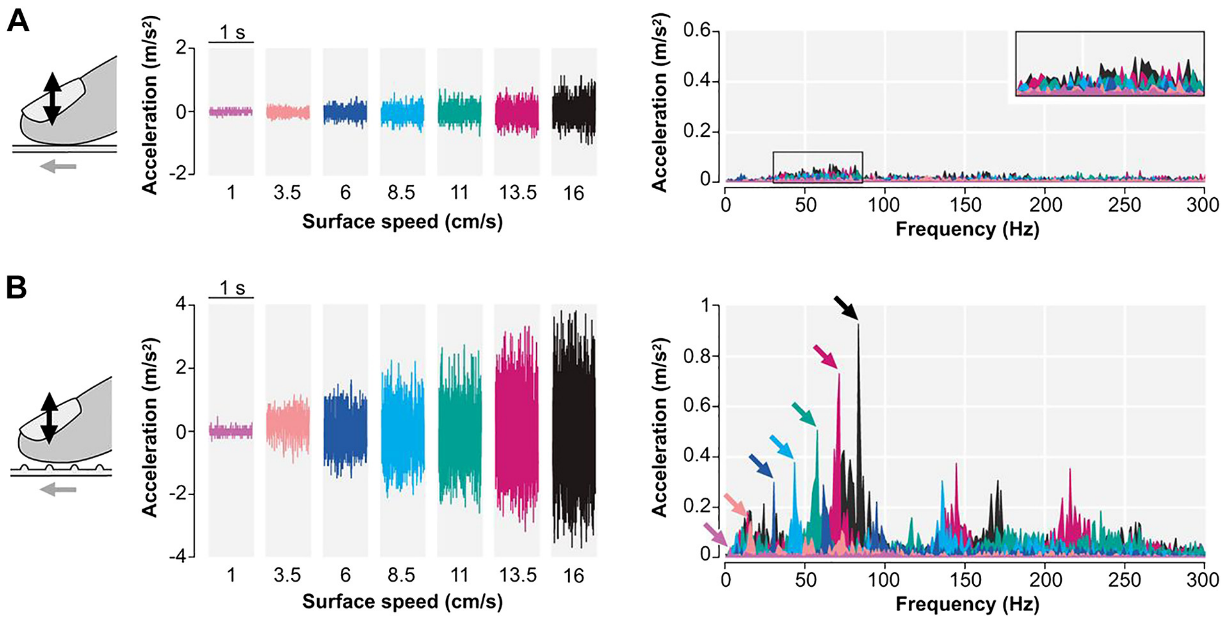

Figure 2. Movement of both the fine-textured surface (*A*) and the ridged surface (*B*) induced vibrations in the right index fingertip that increased with increasing surface speed. Adapted with permission from Dallmann et al. (42).

The spatial resolution is different between type I and type II fibers. Responses of rapidly and slow-adapting type I (FA-I and SA-I) afferents can resolve surface element down to a spacing of ∼1.5 mm, while responses of type II (FA-II and SA-II) afferents can resolve elements down to a spacing of ∼3.5 mm (23). According to a recent study, SA-I and FA-I afferents can resolve elements with spatial periods of ∼0.4 mm (where the spatial period is the distance between consecutive corresponding points of the texture). Often, multiple mechanoreceptor types respond to a given physical stimulus (24). For example, SA afferents also respond to vibrations in the lower frequency range (25) and FA-I afferents also encode spatial features (e.g., edges) (26). The coordinated feedback from all afferent fibers is important to timely adjust grip force during grasping and preventing the full slippage of handheld objects (27). In addition to the four myelinated fibers described above, the slow and gentle movement of a probe on the hairy skin recruits also slow-conducting, tiny unmyelinated fibers, known as CT afferents. These play an important role in the encoding of stimuli with an affective or social valence (28–30). As we will highlight in the next sections, response properties of afferent fibers can explain important aspects in tactile perception in humans and in nonhuman primates.

TACTILE PERCEPTION OF OBJECT MOTION

Touch is an intrinsically dynamic sense, and our brain relies on the relative motion between our skin and external surfaces to jointly extract information about the object being touched and about movement of our body. Four fundamental types of motion are relevant for the sense of touch (31, 32): a contact between the skin and the surface of an external object can be initiated or cease to exist, producing a characteristic change in the area of contact (*contact on* and *contact off motion*). When a contact exists, movement can be in a sliding state (*slip motion*) or a nonsliding state (*roll motion*). Different cues contribute to the perception of these different types of motion in touch. These can be broadly classified as spatiotemporal cues (like the minute deformation of the skin produced by a moving probe), cues from the gross deformation of the skin (like skin stretch generated by a shear force), and vibrations (such as the stick-and-slip patterns arising in slip motion) (33–35). In humans, the ability to detect slip motion depends on the presence of fine and coarse texture (33). The detection of slip of surfaces with barely detectable raised elements is mediated by the activation of fast-adapting fibers of either type I or type II. The slip of a smooth glass plate is indistinguishable from simple skin stretch for a normal force equal to 0.2 N (33). Instead, humans can reliably detect fingertip slip on a glass surface at higher values of normal force, ranging from 2 to 5 N, possibly based on deformation cues (35). Unlike slip detection, the direction of skin stretch can be perceived also at low force based on the information conveyed by the slow-adapting afferents (33). In addition to the stimuli discussed above, it is also possible to elicit a sensation of motion by means of computer-controlled tactile stimulators. Gardner and Palmer (36, 37) proposed the Optacon device (New York University Medical Center) where a computer-controlled grid of sequentially activated probes was used to simulate bars moving across the fingers. The moving bar patterns rendered with the Optacon strongly excited the two fast-adapting fiber types in rhesus monkeys. Another example is the Latero device (Tactile Labs, Montreal) that renders the sensation of a moving object by producing a minute deformation across adjacent areas of the skin (32, 38, 39).

To the best of our knowledge, relatively few studies focused on speed discrimination by touch. Essick et al. (40) investigated tactile perception of speed across a wide range of motion stimuli. The stimuli were generated by a brush controlled by a servo motor moving across the forearm of the participant with different speeds, from 1.5 to 140 cm/s. The Weber Fraction was grossly constant within the tested range of speed, around 0.2–0.25. Other studies focused on the role of high-frequency vibration in tactile representation of F2 object motion (34, 41). As illustrated in Fig. 2, vibrations generated by slip motion change in frequency and in amplitude with the motion speed (42). Therefore, skin vibrations could provide heuristics for the perception of speed. Accordingly, masking vibrations in the range between 64 Hz and 128 Hz, which is the working range of the fast-adapting mechanoreceptive afferents, impairs the ability of discriminating the speed of tangential motion stimuli with either fine or coarse textured surfaces (42).

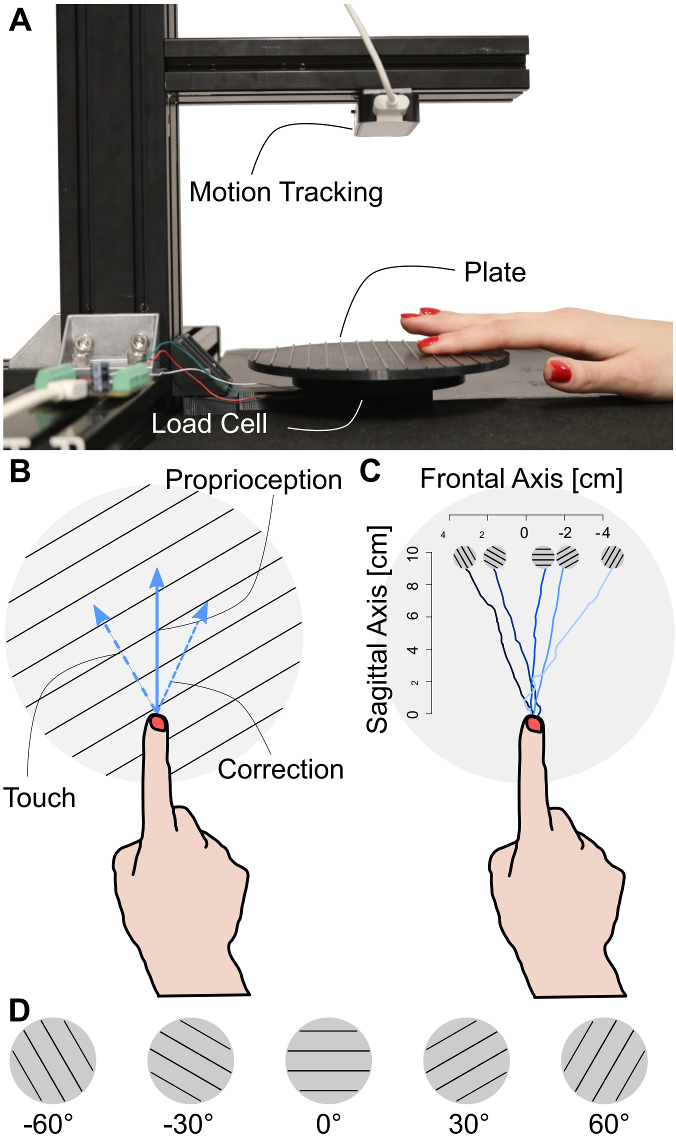

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Figure 3. *A*: the experimental setup used in Moscatelli et al. (5, 9) included a textured circular plate, a load cell, and a motion tracking system. In each trial, a servo-motor placed under the plate (not visible in the picture) set the orientation of the plate. *B*: blindfolded participants were asked to slide their finger over the ridged plate, along a straight direction away from the midline of their body. We assumed that extra-cutaneous proprioceptive cues provided an accurate measurement of motion direction (solid arrow). Instead, the cutaneous feedback produced an illusory sensation of bending toward a direction perpendicular to the ridges, in accordance with previous literature (dashed arrow). This eventually led to an adjustment of the motion trajectory toward the direction indicated by the dotted arrow. *C*: AQ: 19 example of trajectories with different ridges. *D*: plate orientations ranged AQ: 20 from −60° to 60°. Adapted with permission from Moscatelli at al. (5, 9).

Electrophysiological and behavioral studies investigated the ability of humans and other primates to encode the shape and the orientation of the moving stimuli. Humans are able to integrate tactile velocity over time to estimate two-dimensional (2-D) shapes and linear displacement (43, 44). Yao and Hayward (44) studied multisensory integration in a sensorimotor task where participants estimated the length of a tube by the haptic and auditory feedback of a (virtual) ball rolling inside it. The participants tilted the tube twice, first downward and then upward and reported which of three cavities of different lengths the ball fell into. To inform the participants about the displacement of the rolling ball inside the tube, the experimenter provided congruent or incongruent auditory and/or haptic cues. Participants were able to incorporate prior knowledge of gravity, and multisensory information, to perceive the length of the tube. This was true even when auditory noise and tactile cues were incongruent. This finding is in accordance with other studies showing that participants integrate prior knowledge of Earth's gravity and multisensory information from vision, touch, and the vestibular sense for the interception of a ball rolling on an incline (45, 46).

Another study evaluated the ability of human participants to integrate velocity of slip motion over time to perceive 2-D motion paths (43). A tactile device delivered a motion stimulus on the fingertip and the participants were asked to estimate the length of the motion path, to reproduce its shape, and to estimate the angle between two-line segments generated by the moving stimulus. Participants were able to accurately indicate the length of the path, whereas the perceived direction was affected by a direction bias. This bias faded when the interstimulus interval increased, possibly due to the emergence of tactile motion aftereffects. This finding that humans integrate slip motion velocity over time to perceive a motion path has important implications for the control of hand movement in reaching tasks, as we will discuss more in detail in TOUCH PROVIDES FEEDBACK FOR THE CONTROL OF HAND MOVEMENTS.

TACTILE PERCEPTION OF TEXTURE

Textures are fundamental properties of surfaces defined by the three characteristics of arrangement, roughness, and waviness (47). We can broadly distinguish between fine textures, which are characterized by features of lateral dimensions less than ~200 μm, and coarse textures that are equal or greater than 200 μm (48). Natural textures display a huge variability in spatial frequency, roughness, and isotropy. However, for the sake of simplicity, experimental settings usually focus on textures with raised dots or gratings made from raised ridges, whose spatial frequency can be parametrically manipulated by varying the separation between the elements. With the use of such stimuli, the ability of human observers to perceive textures can be examined by varying the distance between ridges and determining the minimum difference in separation across the ridges that is sufficient for detecting a gap or discriminating among two samples at a set criterion level, which determines the detection or the discrimination threshold, respectively (49).

The discrimination thresholds of texture elements were investigated in passive and in active exploration (1, 50). In a study using passive touch, participants were required to discriminate between stimuli with and without gaps, by keeping the hand stationary on the surface (49). The discrimination threshold was equal to 0.87 mm, whereas the separation index (d') was about constant and equal to 0.86 for a gap size 0.7 mm and increased as a linear function of the gap size for larger values of the gap. Similar thresholds for gap size were reported in two studies on grating orientation (51, 52). In the study by Grant and Hayward (51), the experimenter applied the gratings to the index finger pad for ~1 s, with the ridges oriented either perpendicular or parallel to it. The mean threshold for the discrimination of grating orientation was 1.29 ± 0.11 mm for the dominant hand and 1.19 ± 0.10 mm for the nondominant one. This suggests a mild effect of hand dominance on texture perception. The variation in the results between the three studies reported above is consistent with the variability among participants within the same study (51).

Exploring a texture while moving requires our brain to discriminate the spatial properties of surface texture from the spatiotemporal pattern of tactile input. Overall, discrimination thresholds improve during lateral motion, and during active as compared to passive exploration. During active exploration tasks of sinusoidal gratings, the average discrimination thresholds ranged from 0.278 mm for the 0.25-cm spatial periods to 0.64 mm for the 1.0-cm spatial periods (53). In another study, participants were requested to discriminate between grating surfaces either by sliding the finger laterally, or by moving it up and down without lateral motion (two sets with standard spatial periods equal to 0.77 and 1.0 mm) (54). Discrimination thresholds were ~5% of the standard stimulus during lateral motion, whereas it was degraded, and it increased to 10% when tangential movement between the surface and the finger was eliminated. This role of lateral motion for the discrimination of textures is in accordance with the exploratory procedures (1).

The studies discussed up to now show that the threshold for discrimination of texture is lower when the stimulus is moving across the skin as compared to static exploration. This may be explained by the recruitment of both fast- and slow-adapting fibers during tactile movement, as we will further discuss below. Additionally, passive versus active movement might affect the discriminability of the stimulus, possibly due to the efference copy of the motor command during active tactile exploration (see TOUCH PROVIDES FEEDBACK FOR THE CONTROL OF HAND MOVEMENTS). Interestingly, the discrimination of textures at different scales requires distinct exploratory procedures (1, 50). For example, when we are exploring a larger object, we follow its contour whereas we use back and forth movement to detect smaller elements. The ability to discriminate between different textures depends also on the scale of the texture elements. Bernard Katz (55) first suggested that tactile perception of textures in humans is based on two channels for the perception of fine and coarse textures: a hypothesis later confirmed by other studies (49, 56–58). Under a physiological point of view, elements of coarse textures, like the raised dots of Braille characters, gratings, and ridges, produce a local indentation in the skin, recruiting type I fibers in the glabrous skin (SA-I and FA-I) (33). Tactile texture perception is hence mediated by spatial cues in the case of coarse textures, and by vibrational cues in the case of fine textures (6). For the latter case, temporal cues such as the vibrations elicited on the skin during exploration are crucial for the perception of fine texture (59). In another study, participants were not able to discriminate fine textures (texture elements size of 100 μm) from static touch (6). Lateral motion improved the discrimination of fine and to a lesser extent of coarse textures.

The role of high-frequency vibrations was also investigated in adaptation paradigms, where a few seconds of vibration stimulus reduced participants' tactile sensitivity even after the stimulus had ceased. Adapting high-frequency vibrations in the range of PC fibers, for example, generated by a vibration motor, produces a significant impairment of fine texture perception (60). Conversely, this adaptation produces only a small effect with coarse textures (60). Interestingly, as reported in TEXTILE PERCEPTION OF TEXTURE, the presence of masking vibrations also impaired the discrimination of motion speed, and this effect is more evident in the case of fine textures (42). Another study investigated the effect of vibrations on the discrimination of grating orientation from static touch (57). Participants were presented with gratings (spatial period between 2 and 8 mm), which were either static or vibrated at a frequency in the range of 5–80 Hz, and they were requested to discriminate the orientation of the gratings (either parallel or perpendicular to the long axis of the finger). The discrimination threshold was not affected by the amplitude of vibration. Instead, this changed nonlinearly with vibration frequency.

The propagation of skin vibration far from the contact site is another noteworthy concept to understand the functional basis of texture encoding in the sense of touch (61, 62). During natural interactions with ordinary objects, mechanical energy originating at finger contact propagates through the whole hand as vibration signals that contain sufficient information to discriminate between the touched objects (34, 62, 63). Similarly, using coarse and fine textures of commonly used objects, Manfredi et al. (64) found that the frequency composition of texture-elicited vibrations is highly informative about texture identity. Vibrations propagating to a remote part of the limb can partially compensate for a loss of tactile sensitivity on the hand (61). Patients with loss of tactile sensitivity in the hand, as well as anesthetized controls, can discriminate textures from vibrations propagating to the wrist and to the forearm. Likewise, vibrations mediate the discrimination of textures sensed with a probe (65) and the position on the probe where it impacts an object (66).

The role of skin vibration and spatial-temporal coding in texture perception was investigated through the afferent recordings in rhesus monkeys and by means of psychophysical studies in humans (67). A custom-built rotating drum stimulator was used to deliver textured surfaces to the fingertips. The texture ranged from very coarse, such as embossed dot patterns, like the one used for the Braille code, and corrugated paper (element sizes in the order of millimeters), to very fine textures, such as satin and nylon (elements sized in the tens of micrometers). The tactile processing of coarse textures can be usually accounted for by only spatial coding in SA1 and RA fibers (23). Instead, primary afferent fibers use both spatial and temporal coding for the representation of fine textures. The responses of RA and PC fibers are likely conveying most of the time-varying signals. As we will discuss in CORTICAL REPRESENTATION OF TEXTURE AND MOTION, spatial and temporal cues are integrated in the primary somatosensory cortex to provide a coherent representation of texture (68).

Roughness is another important dimension in tactile perception, which has been defined as the sensation that occurs when a nonuniform, 2-D pattern is scanned across the skin (69). As for fine textures, skin vibrations generated by the lateral movement between the finger and a surface influence the perception of surface roughness. In rhesus macaques, the encoding of roughness is mediated by SA-I, PC, and RA nerve fibers (70). The perceived roughness is also determined by the variation in the population response: a surface will feel rough depending on the variability of the firing rate across nerve fibers and across time within nerve fibers (70). Humans are also highly sensitive to roughness, and the movement between a surface and the skin improves the capability of roughness discrimination (71). The perception of roughness increases with the logarithm of vibratory power (59, 72). In a roughness discrimination task, vibrating surfaces were perceived as rougher than stationary ones (73). These results further highlight the role of lateral motion and vibrations for perception of surface microgeometry by touch.

Both the spacing between texture elements (e.g., dots, ridges) and their size affect roughness perception (74). Large spatial periods (range: 0.6 –1.4 mm) produce a stronger sensation of roughness and small texture elements (range of diameters used: 0.1–0.5 mm) are perceived as rougher than large texture elements of the same wavelength. Accordingly, previous studies showed that the roughness of gratings increases linearly with spatial period (75) and that the roughness of embossed dots increases monotonically with interelement spacing up to a spatial period ~2 mm, then decreases with further increases in spatial period (54). Roughness perception of unfamiliar dot pattern textures is well described by a biexponential function of the interdot spacing (76). The perceived roughness of sandpapers increases as a power function of particle size (77).

All the studies reported above demonstrate that lateral motion between the surface and the skin improves the ability to discriminate between surface features (spatial period, roughness, and fine textures). On the other hand, the perception of both coarse and fine textures is independent from the scanning speed (78, 79). Indeed, it was found that tactile perception of textures is invariant from the speed of the touched object (78). The authors performed experiments using naturally occurring textured surfaces (fabrics, fur and sandpaper) as well as gratings and a dotted texture. The textures were presented passively to the participant's fingertip at four different scanning speeds and participants were asked about the properties of the texture such as roughness, hardness, and stickiness. Texture perception was minimally affected by the scanning speeds; hence, it was concluded that our brain creates a robust representation of the object, regardless of how the object is explored. Differently from the speed, the scanning modality, direct versus indirect, can change the perception of the elements of a texture (80). The authors analyzed the perception of texture by direct tactile scanning with bare fingers and indirect tactile scanning via a probe. Participants performed a dissimilarity judgement task between textures and an adjective rating task (i.e., rating the roughness, hardness, and stickiness). Interestingly, they found that while roughness perception remained constant between the two modes of scanning, the other qualities of the texture such as hardness or stickiness were perceived differently. The authors suggested that the neural correlates for the perception of texture may be different depending on the scanning methods.

INTERPLAY BETWEEN TEXTURE AND MOTION IN THE TACTILE SYSTEM

Behavioral studies on motor control and perception showed that tactile representation of surface texture and motion are strictly intertwined. As we reported above (see TACTILE PERCEPTION OF OBJECT MOTION), the ability of humans to detect the slip motion of a plate that moved under the finger-pad improves dramatically with the presence of coarse or fine textures. In a classical study, participants were not able to detect slip motion between the finger-pad and a smooth glass plate that was moved under the finger-pad (33). Instead, the presence of either a single raised dot or of fine texture improved the performance with a percentage of correct responses between 90% and 100%. In a more recent study, Delhaye and colleagues (81) measured the ability of humans to report the motion speed of natural textures (e.g., thick corduroy, stretch denim, microsuede, wool blend, city lights, nylon, huck towel, metallic silk, vinyl, and chiffon). Participants were passively presented with one pair of textures, a reference and a comparison, and reported which of the two moved faster. The reference texture was scanned at 80 mm/s, and the comparison texture at one of the following speeds: 20, 40, 60, 80, 100, 120, and 140 mm/s. The results showed that textures that elicit stronger skin vibrations tend to be perceived as moving faster: for, e.g., vinyl always felt slower than metallic silk. The authors concluded that speed perception is intertwined with the type of the natural texture, which is surprising if we look at independence of texture perception to the scanning speed (see TACTILE PERCEPTION OF TEXTURE). As discussed in TACTILE PERCEPTION OF OBJECT MOTION, the discrimination of motion speed is significantly impaired by the presence of external masking vibrations, and this effect was much stronger on a fine-textured than on a coarse-textured surface (42). These findings support the hypothesis that skin vibrations are an important cue to the discrimination of motion speed especially in the presence of fine textured surfaces.

Periodic textures like raised dots and gratings also produce a bias in the perceived tactile motion. For instance, the orientation of raised ridges affects the perceived direction of surface and hand motion (5, 7), and the spatial frequency influences the perceived velocity of slip motion (9, 10). Dépeault and colleagues (10) first studied the relationship between coarse texture and its perceived tactile speed. Participants kept their fingertips stationary and touched moving surfaces with embossed raised dots, with a scanning speed ranging from 33 to 110 mm/s. Across different blocks, surface textures varied in dot spacing (2, 3, 8 mm), dot density (25, 16.7, 6.3 dots/cm^2), and in dot placement that was either periodic or random. The spatial distance of the dots influenced speed perception, where surfaces with 8-mm spatial period were perceived as moving 15% slower than surfaces with spatial distance of 2–3 mm. Neither dot disposition (periodic or random) nor dot density contributed to the results, suggesting that the critical factor for the determination of surface speed was dot spacing in the direction of the scanning speed. This biasing effect of texture on the perceived speed was confirmed by our recent study, where we compared the perceived speed of a surface with parallel raised ridges versus a smooth surface lacking any detectable textural elements (9). We found that the former was perceived as moving faster than the smooth surface moving at the same physical speed.

In the studies discussed above, the participant kept the hand stationary and the surface moved underneath (passive touch). In other studies, we investigated the effect of texture on the perceived surface motion when the participants actively moved their hand on the movable surface. These studies were inspired by well-established illusions in vision showing that eye pursuit and texture produce a bias on the perceived motion of a visual background: refer to Ref. 82 for a review of these visual illusions. We found that during guided hand motion, a static surface sensed from touch was erroneously perceived as moving in the opposite direction of the hand (39). This is a putative analogue in touch of the Filehne illusion in vision. In a second study, we asked participants to estimate the speed of a moving stimulus either from tactile motion only, while keeping the hand world stationary, or from kinesthesia by tracking the stimulus with a guided hand movement (9). Participants overestimated the velocity of the stimulus determined from tactile motion compared with kinesthesia, in analogy with the visual Aubert-Fleischl phenomenon. Like in vision, the overestimation of tactile motion was modulated by surface texture, with the effect being larger when the spatial frequency of the texture was higher. Together, these experiments demonstrate similarities between vision and touch during active motion perception involving eye or hand pursuit. We further assessed the interplay between these two sensory channels, vision and touch, by investigating a dual task that combines eye pursuit of a visual target and slip motion over the skin of the fingertip (83). We showed that smooth pursuit eye movements can bias the perceived direction of motion in touch. Similarly, to the classical report from the Filehne illusion in vision, a static tactile surface was perceived as moving rightward with a leftward eye pursuit movement, and vice versa. However, this time the direction of surface motion was perceived from touch. The biasing effects of eye pursuit on tactile motion were modulated by the texture of the tactile and visual stimuli.

The orientation of raised ridges also produces a bias in the perceived direction of surface motion (7, 8). Particularly, the motion direction of a ridged surface (1-mm high, 1-mm wide ridges separated by 1-cm wide grooves) moved under the fingertip is perceived as significantly biased toward the direction perpendicular to the grating orientation (7). A similar result was observed with pin based tactile display (8). Bicchi and colleagues (7) proposed a mathematical model to explain this phenomenon, the *tactile flow model*. This model was first proposed in Ref. 7 and further confirmed in Ref. 84 with numerical simulations. The tactile flow represents the tactile counterpart for motion encoding of the optical flow (85). It suggests that, in dynamic conditions, a large part of contact sensing in the finger pad can be described by the flow of strain energy density (SED) $\varepsilon\,(\xi P)$, at a point ξ within the volume V, under a given resultant load condition P. Let be Σ_i the iso-strain surface whose points have the same SED, which is equal to ε_i. When the loading condition changes to $P + \Delta P$, we can consider the surface Σ_i as if it moves to points that are farther away with respect to the center of the contact zone. The apparent motion of the iso-SED surface across the volume V can be formalized with the following equation, by imposing the conservation of the (SED): $\frac{d\varepsilon(\xi,P)}{dp} = 0$: that is equivalent to $\nabla\varepsilon \cdot \varphi = -\frac{\vartheta\varepsilon}{\vartheta P}$, where φ represents the infinitesimal motion of a surface element in Σ_i (i.e., the 3-dimensional tactile flow) and $\nabla\varepsilon$ the spatial gradient. As for the optical flow, there is an intrinsic ambiguity in the determination of the flow vector, which cannot be defined for the components that are tangent to the iso Σ_i. The dependency of the perceived direction of surface motion on the orientation of parallel ridges (7) can be explained by the lack of availability of all the signals needed to solve this ambiguity of solution, also referred to as the aperture problem (in analogy with the visual counterpart).

In a recent study, we used this phenomenon, where parallel ridges produce a bias on the perceived motion direction, to evaluate the role of touch for the control of reaching movement (5). Participants were requested to move along a straight path toward a target, by sliding their fingertips on a lubricated plate with parallel raised ridges. In different experiments, visual feedback on hand position was prevented either by a blindfold or by showing a virtual reality environment. Tactile slip motion, which was biased by the orientation of the parallel ridges, induced the illusory sensation that the hand was bending away from straight (according to the *tactile flow model*). In turn, this produced a correction movement eliciting the systematic motor error illustrated in Fig. 3, *B* and *C*. The authors accounted for this F3 effect with an optimal observer model implying a Bayesian integration of the musculoskeletal and cutaneous cues (86). In a second experiment, we reduced tactile sensitivity by asking participants to wear a rubber thimble, and we found that this reduced the systematic motor error produced by the parallel ridges, in accordance with the assumptions of the model (Fig. 4) (5, 87). We found a similar effect when F4 participants were required to slide over a rotating surface with ridges, i.e., when the contribution of touch changed over time (88). This demonstrates that this tactile bias can override the contribution of the rotating plate, which instead induces the illusion of the hand rotating in the opposite direction with respect to the plate rotation, as reported in Ref. 89. In a recent study, we investigated to which extent these observations also depend on the lateral component of the reaction force that arises during the dynamic interaction between the finger-pad and the surface of the ridges (90, 91). If not properly addressed, this point could raise an alternative explanation that the systematic bias in hand trajectories was determined by the insufficient compensation of the

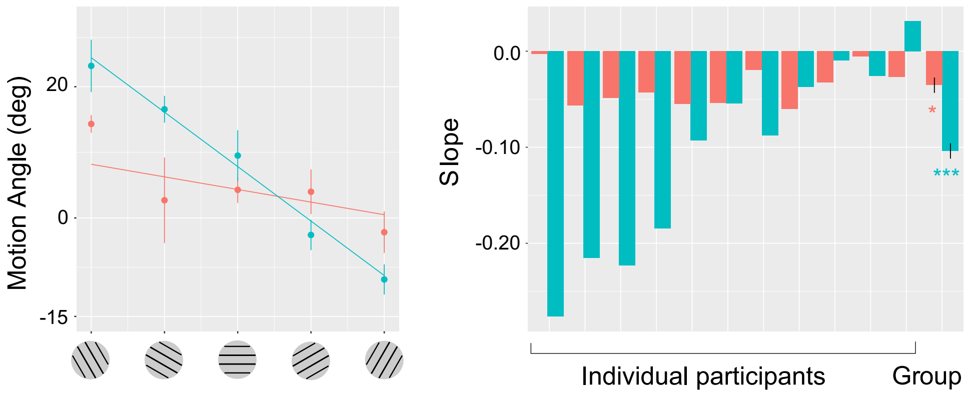

Figure 4. *Left*: angular error of the hand trajectory with respect to the midline of the plate regressed against the orientation of the ridges. Positive values of the motion angle are for a leftward deviation from the midline and negative values of the motion angle are for a rightward deviation. In accordance with Moscatelli et al. (5, 9), when the participant did not wear the glove, there is a negative relationship (negative slope) between the angular deviation and the ridges orientation (green line), and this relationship is significantly less negative when participants wore the glove (i.e., the bias induced by tactile flow is reduced) than without it (red line). Data are fit linearly for a representative participant. *Right*: slope of the linear relationship for all the tested participants with group estimate and standard deviation (linear mixed model estimates). Adapted with permission from Moscatelli et al. (5, 9).

reaction force by participants. Participants performed a reaching task like the one described above (Fig. 4), however this time participants were required to exert two different levels of contact force (less than 0.7 N and 2 N, respectively). In the low normal force condition, the lateral reaction force was found to be negligible. The effect of ridge orientation was larger for the high compared to the low force level. However, in the latter case, the same biased trajectories reported in Ref. 5 were still observed. Overall, the experimental results supported the hypothesis that the motor bias arises from the integration of the tactile motion estimate, biased by the texture orientation, and proprioceptive cues from the muscle spindles.

TOUCH PROVIDES FEEDBACK FOR THE CONTROL OF HAND MOVEMENTS

The sense of touch is intrinsically connected with our motor system. Cutaneous feedback is indeed important for the representation of hand position and motion (proprioception), in perceptual and motor tasks. For example, the findings of multimodal neurons in the early (92) and higher (93–95) areas of the primary somatosensory cortex of nonhuman primates highlights the interplay between touch and proprioception and supports the hypothesis of the role of touch in motor control. At the same time, cutaneous sensory signals are acquired through purposive movements of our hands and our limbs that maximize the information gathered about the world around us (1, 2). There is indeed a tight relationship between the specific hand movements performed by a human agent and the information available to the tactile channel, given the physical properties of the environment (2). For example, Lederman and Klatzky (1) described the existence of exploratory procedures, which are characteristic hand movements that are optimized to collect the maximum amount of information about object properties.

Additionally, signals from cutaneous mechanoreceptors provide proprioceptive information (3). The stretch of the skin above the finger, knee, and elbow joints provides information about joint position and movement (3, 96, 97). Edin and Johansson (3) investigated the role of skin stretch in the index finger in movement perception and execution. The authors manipulated the dorsal and the palmar skin of the middle phalanx and the proximal interphalangeal (PIP) joint of five participants to generate specific strain patterns in the proximal part of the index finger. To mask sensations directly related to contact with the experimenter, the skin and deeper tissues were blocked distal to the midportion of the proximal phalanx of the index finger using local anesthesia (Fig. 5). Participants were asked to move their unanesthetized right index finger to mimic the perceived movement of the anesthetized finger. When the experimenter produced skin strain patterns that were compatible with those observed during PIP joint flexion, participants reproduced a flexion movement. In the same way, they indicated extension movement at the PIP joint when strain patterns corresponding to PIP joint extension movements were induced. This supports the hypothesis that dorsal skin receptors supply the central nervous system with accurate information about joint movements and potentially contribute to

F5

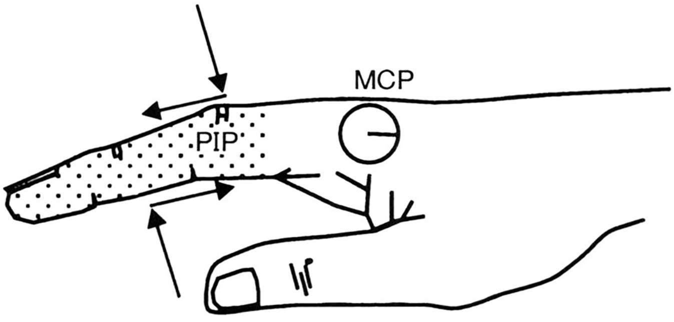

Figure 5. The dashed area is the anesthetized region of the index finger. The 2 arrows parallel to the finger indicate the direction of forces applied to induce the strain pattern observed during flexion of the proximal interphalangeal phalanx (PIP) joint. To counteract the torque at the metacarpophalangeal (MCP) joint resulting from the application of these forces, additional forces had to be applied as indicated by the 2 arrows perpendicular to the skin. Adapted with permission from Edin and Johansson (3).

adjustments of evolving finger motions, such as grasping or pinching (98). Cutaneous receptors contribute also to the sensation of position and movements at elbow and knee joints (99).

The contribution of skin receptors and muscle spindle to kinesthesia was examined at the index finger, the elbow, and the knee in Ref. 100. Skin receptors were activated by skin stretch using adhesive tape, and muscle receptors were activated by vibration. The combination of skin stretch and muscle vibration significantly increased perceived movement sensation above that from each stimulus alone. The contribution of cutaneous receptors is of crucial importance for the control of finger movements. Here, signals from muscle spindles are potentially ambiguous because the muscles that move the fingers lie in the forearm and their tendons must cross multiple joints.

Not only the skin next to the joints contributes to proprioception but also the finger pad during contact with objects. For example, a change in contact area at the finger pad provides an auxiliary proprioceptive cue to finger displacement (4). When we push our finger pad against an external surface, this induces a growth of the contact area. We demonstrated that this change provides a cue to finger displacement. This phenomenon can be regarded as the tactile counterpart of the looming in vision (101); therefore, we describe this phenomenon as *tactile looming*. This growth is also related to object compliance, as reported in Ref. 7. Since the compliance of a given object is assumed not to change over time, an artificial change of it and hence, ultimately, of the contact area, could be interpreted in terms of variations of the finger displacement. In psychophysical experiments, participants were required to compare the perceived displacement of the finger, while the compliance of the contacting surface was varied in a pseudorandom manner. A perceptual bias was found that was elicited by the compliance changes, confirming the hypothesis that the contact area is a cue for finger proprioception.

Another pivotal role of the sense of touch is the delivery of direct information about surface friction, compliance, and microslip, which are important for dexterous manipulation of objects and grasp control (102, 103). Indeed, the tactile channel plays an important role in the control of digit force (104, 105) and in the perception, execution, and planning of fine hand movements (3). Several studies demonstrated the crucial role of cutaneous information in other motor tasks, such as in the control of grasp and finger posture (106) and guiding hand reaching (5).

Multiple sensory channels provide information for the execution of the different subtasks in hand grasping. For example, internal models based on visual cues are important to preadapt digit load force in a feed-forward fashion (107). However, vision can only provide indirect information on contact mechanics based on experience, and it is of limited utility when objects are out of sight or partially occluded. On the contrary, cutaneous mechanoreceptors convey direct information about the mechanical interactions between the skin and the object surface. Tactile cues include the magnitude, direction, and spatial distribution of fingertip forces, the local shape of the contact site, and the friction between the skin and the grasped object (106). The four afferent fibers described in the introduction provide various types of contact information for the control of hand grasping. For example, cutaneous inputs are of pivotal importance for the adjustment of the grip force to different levels of surface friction (27, 98). Tactile signals can compensate for incorrect predictions about the mass and the friction coefficient of the object (84, 108, 109). For example, if an object is heavier than expected, microslips between the object and the skin produce vibrations that excite the cutaneous afferents and trigger a fast reaction for increasing the grip force, with delays around 80 ms (27). Similar compensatory actions can also be triggered by cutaneous mechanoreceptors when task perturbations occur, within the framework of "sensory discrete-event driven control" (110). The Pacinian receptors are particularly useful in grasping tasks because they can detect transient mechanical events that occur when making and breaking contact between a held object such as a tool and another object. The fundamental role that touch plays in grasping and manipulation can be clearly seen in people with pathologically impaired digital sensitivity or when local anesthesia is applied to the fingertip. In these conditions, people tend to drop the objects more often and crush fragile items more easily, experiencing severe difficulties performing simple everyday life activities such as lighting a match (111). Furthermore, the transitions between the phases of a simple manipulation task (grasp, lift, hold, and replace) that requires a precision grip between the index finger and the thumb are delayed (41).

The role of touch for the control of hand movements is evident in studies on tool use. The ability to respond quickly and effectively when objects in the world suddenly change position is essential for skilled action (e.g., reaching toward a dog collar while holding the dog leash). Touch provides an important contribution to this and similar tasks. In Ref. 112, the authors showed that the spatial information about a change in target location provided by tactile inputs to one hand elicits a rapid correction of the other hand trajectory. Participants moved their left thumb along a smooth rod that changed direction (uni-planar of either 10 or 20°, when the finger was 5 cm from the starting position). Using the right finger, participants were able to compensate for the directional changes felt by the left thumb and corrections were made in 90–110 ms. The authors concluded that the tactile motor reflex compensates for moving target position during object reaching across a rod, triggering motor corrections as rapid as visuo-motor correction.

CORTICAL REPRESENTATION OF TEXTURE AND MOTION

Over the decades, neural representation of texture and motion in the central nervous system have been investigated with different imaging and neurophysiological techniques (113–117). In their pioneer studies, Vernon Mountcastle (118) and other scientists provided a characterization of somatosensory cortices by using electrical recording techniques, which have since been used by several generations of neuroscientists. Functional brain imaging is the second area in which remarkable technical advances have been made (116). Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have excellent spatial resolution, and since the 1990s the second has become one of the primary tools in studying the central neural correlates of touch in humans. Albeit having a lower spatial resolution, electroencephalography (EEG) and magnetoencephalography (MEG) allow a subsecond temporal resolution (119). Recent studies combine EEG or MEG with machine learning techniques for an efficient analysis of the neural signals in tactile processing (120).

The cortical representation of tactile motion has been evaluated for different types of moving textures, in both nonhuman primates and humans. In an early study, neurons in the primary somatosensory cortex in monkeys (S1) were classified as motion sensitive, direction sensitive, and orientation sensitive neurons, based on their firing patterns (121). A specific population of direction sensitive neurons were found to be activated during passive tactile stimulation in area 1 of S1 (122). The authors stimulated the monkey with different types of motion stimuli (scanned bars, dot patterns, and random dot displays). A population of neurons was found, which encoded the direction of motion of the stimuli, regardless of the texture, the speed, or the force with which they contact the skin. Neurons in area 1 of S1 are also sensitive to shear force direction (123). The neural representation of slip motion speed in S1 was studied in Ref. 124, which characterized the activation of motion sensitive neurons in S1 in monkeys, during passive tactile stimulation. The stimulus consisted of a moving cylindrical drum (speed = 40–105 mm/s) composed of a coarse surface of raised dots (longitudinal spatial period, 2– 8 mm; periodic or nonperiodic). A population of cells in area 1 and area 2 of S1 showed an increase in discharge with increasing speed, consistent with a role of these neurons in tactile speed scaling. However, in all the speed-sensitive cells the pattern of discharge did not change with the spatial frequency of the texture. These results seem to contrast the biasing effect of texture at a behavioral level, whereby coarse textures affect perceived tactile speed (10), as discussed in TACTILE PERCEPTION OF TEXTURE.

The studies described above evaluated the response of cortical neurons to simple moving textures. In another study, the authors evaluated the spatial integration of the different components of a moving plaid texture in the somatosensory cortex (125). The authors recorded the evoked responses of somatosensory neurons in macaque monkeys and related these with psychophysical experiments in humans. The moving textures were generated by means of a tactile display, which consisted of 400 independently controlled probes spaced 0.5 mm apart. Tactile motion stimuli were generated by adjacent probes indenting the skin in succession, at a rate that was determined by the nominal speed of the stimulus. The stimuli consisted of three types of plaid textures generated by superimposing two square-wave grating whose direction of motion was separated by 120°. The authors recorded the neural responses in areas 3b, 1, and 2 of the S1 cortex. It was possible to classify the neurons in area 1 in three types, based on the response to motion stimuli. A first type responded to the two components of the textures, yielding a bimodal distribution of responses separated by 120°. The second neuron yielded a unimodal distribution of responses to the stimuli, and it produced its highest response when either a plaid or a pure grating moved in its preferred direction. The response of these neurons was like the response to visual stimuli of component and pattern neurons in visual cortex MT. A third neuron exhibited intermediate integration properties. In contrast, neurons in areas 3b and 2 exhibited only very weak pattern tuning, in part because relatively few neurons in these areas were tuned for direction when stimulated with plaids.

In addition to these electrophysiological investigations, functional imaging techniques provided important insights about the role of higher cortical areas in processing tactile motion (Fig. 6). Using PET and MRI, Hagen et al. (127) studied the contribution of hMT + /V5 in tactile motion processing in humans. The authors found a bilateral activation of hMT + /V5 in response to tactile motion delivered with a brush stroking the volar side of the forearm (127). This finding was confirmed in a second study using 7T fMRI (128). The authors stimulated the fingertip of the participant by using different types of stimuli including a static plate, a moving bar, and a moving random pattern. Different patterns of activation in S1 and S2 were found depending on motion direction and texture orientation. Motion and pattern processing activated hMT + /V5 and the inferior parietal cortex (IPC). The role of hMt + /V5 in tactile motion processing was confirmed by transcranial magnetic stimulation (TMS) studies (129, 130). In a TMS study by Basso and colleagues (129), blindfolded participants were asked to detect the speed change of a moving grid with their fingertip. The inactivation of hMt + /V5 by TMS significantly impaired tactile speed detection. Similarly, the TMS inactivation of either S1 or hMT + /V5 impaired the discrimination of tactile motion direction (130). A later fMRI study evaluated the

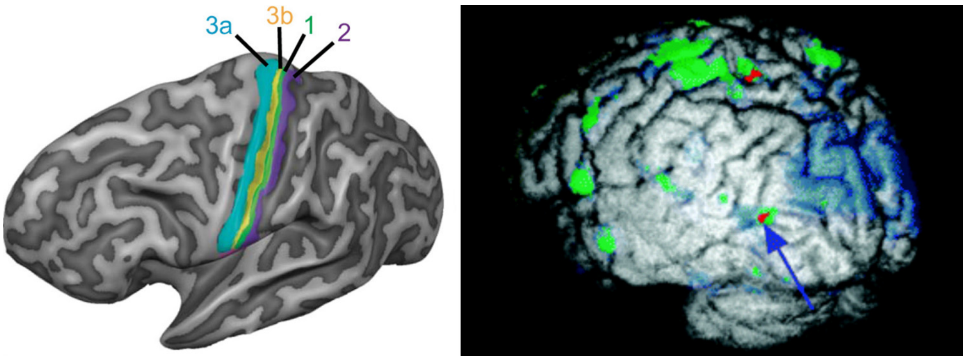

Figure 6. *Left*: Locations of areas 3a, 3b, 1, and 2 in the primary somatosensory cortex. Adapted from Sathian (126). *Right*: the activation of hMT + /V5 while participants attended to tactile motion stimuli, consisting of a brush stroking proximal-to-distal along the volar forearm and palm. Adapted with permission from Hagen et al. (127).

activation of this area to tactile motion delivered with or without a visual task (131). They unexpectedly found a weak response in hMT+/V5 when the visual task was not present. While the region was activated by the combination of tactile and visual stimuli, the lack of related visual tasks strongly reduced activation in hMT+/V5. Therefore, although there is significant evidence in favor of hMT+/V5 in tactile motion processing, its role should be further investigated.

As for motion perception, electrophysiological and imaging studies have played an important role also in the understanding of central neural correlates of the representation of texture. The neural encoding of texture in both S1 and S2 of monkeys was characterized during a passive texture discrimination task (132). Rhesus monkeys were instructed to discriminate a standard surface (raised dots with a spatial period of 2 mm) from three surfaces with spatial periods of 3, 4, and 5 mm. The texture was presented using a rotating drum with the different textured stripes attached. The animals rested the tips of digits 3 and 4 on the textured surface. Neurons were divided based on their response pattern to the stimulus into *graded* and *nongraded potential*. Neurons with graded potential had a linear relationship between mean discharge frequency and the spatial frequency of the stimulus. Instead, neurons with nongraded potential showed a significant change in discharge over the test surfaces, but the discharge did not distinguish between 3-, 4-, and 5-mm surfaces. The distribution of these texture responses was significantly different in S1 and S2. Most of the texture-related neurons in S1 (86%) had graded potential while the majority of those in S2 (63%) had nongraded potentials. As stated in TACTILE PERCEPTION OF TEXTURE, the variability in primary afferent fibers may provide information about surface roughness (70). It needs to be further evaluated, whether the within-neuron variability of nongraded potential neurons may convey similar information at a cortical level.

As we discussed before, tactile speed representation is independent from texture. This raises the question whether the opposite is true. The extent to which the scanning speed affects the representation of texture is different between the central and peripheral neurons (133). Everyday textures were scanned across the fingertips of rhesus macaques at various speeds and then recorded the responses evoked in tactile nerve fibers and somatosensory cortical neurons of S1 (Brodmann areas 3b, 1, and 2). The response of peripheral neurons was characterized by a wide variability depending on scanning speed. Instead, consistently with previous findings, the representation of texture in the somatosensory cortex was largely speed invariant (79, 133, 134). This result is in accordance with some behavioral findings (78, 79) reported in TACTILE PERCEPTION OF TEXTURE. Unlike speed and texture, the orientation of a bar or an edge is not explicitly represented in the responses of single afferents, but orientation detectors can be found in areas 3b and 1 of S1 (114). The response tuning of these cortical neurons is preserved across different modalities of stimulus presentation, either scanned or indented.

According to the studies discussed above and other recent studies, texture signals are processed first in S1 and then in S2 (115, 135). In addition to this, some features of coarse textures are encoded by the motor cortex (M1) (136). The authors recorded neurons in M1 during texture scanning while the animals were either performing a texture discrimination task or simply attending to the stimulus (no-task condition). It was found that most of M1 cells (88%) were modulated during surface scanning, but only 24% of these were texture related. In contrast, 44% of M1 neurons were texture related in the condition where no response was required. The recordings from the primary somatosensory cortex found that S1 neurons were significantly more texture related during the task (54%) than M1. No difference was observed in the no-task condition (52% for M1 and 44% for S1). This interplay between somatosensory and motor cortices further supports the hypothesis of a tight interaction between touch and motor control discussed in TOUCH PROVIDES FEEDBACK FOR THE CONTROL OF HAND MOVEMENTS at a behavioral level.

EEG studies confirmed the sequential activation of S1 and S2 in response to tactile stimulation (119). Blindfolded participants were presented with a tactile stimulus consisting of a three-dot array with the middle dot placed 1.94 mm to the left or right of the line joining the two outer dots spaced 4 mm apart (dot height was 0.64 mm above the plate surface). They had to report whether the central dot was offset to the left or right. After the initial response in S1, the activation of S2 follows at 100 ms, confirming the neurophysiological findings (132). S1 was activated 45 ms after the initial cutaneous stimulation, followed by other areas including the lateral occipital complex at 130 ms, intraparietal sulcus at 160 ms and the dorsolateral prefrontal cortex at 175 ms.

While EEG studies are useful to understand the temporal dynamics of tactile processing, most central imaging studies were made using fMRI. Kitada and colleagues (137) investigated the neural correlates of roughness perception of a coarse texture in humans. The tactile apparatus consisted of a cylinder with four different textures (spatial periods 0.5, 1.2, and 1.8 mm and 1 smooth surface) that was rotated against the fingertip of the participants (137). When participants experienced the tactile stimulation without reporting its roughness, the areas of the bilateral parietal operculum (PO), which includes S2, and the insula were activated. These two areas play a role in higher somatosensory processing and in conscious perception of touch (137, 138). A later study supported the bilateral involvement of the PO during tactile perception, in both vibrotactile and rubbing stimuli (139). The activation of the PO and insula suggests that conscious sensory processing still takes place in conditions where participants do not report surface roughness but are stimulated passively by a texture (138). In contrast, when participants were also requested to estimate the roughness of the surface, the prefrontal cortex was also activated, suggesting its role in higher cognitive processing of the stimuli (137). The activation in the PO was not significantly affected by exploration procedure, active or passive (140).

In TOUCH PROVIDES FEEDBACK FOR THE CONTROL OF HAND MOVEMENTS, we discussed the role of touch in the framework of action-perception. Cortical differences during passive and active touch in object exploration were investigated using fMRI (141). During passive touch (tactile-only condition), tactile stimulation was applied to the right hand by moving a small-pored sponge across the surface of the fingers. The active touch condition had a movement component where the hand was initially open, the sponge was placed in the hand and were instructed to form a power grip around the sponge. They showed that the active touch conditions evoked broader activation responses in the secondary somatosensory cortex (S2) as well as the activation of the primary motor cortex (M1). Also, during active touch two additional areas, the parietal rostroventral area and anterior cingulate cortex were activated which indicates sensorimotor integration and decision making respectively. In another study, participants were required to explore surfaces of aluminum oxide sandpaper with different grades of roughness, either by moving their finger (active touch) or with their finger being passively stimulated (passive touch) (140). Active touch produced higher activation than passive touch in the contralateral primary somatosensory cortex (S1) independent of roughness of the surface. Active touch also demonstrated brain activity that was overall more diffuse than in passive touch.

FUTURE RESEARCH DIRECTIONS

In this review, we discussed important findings on tactile perception of motion including motion direction and speed, texture perception, and on the role of touch for proprioception and motor control, in tasks like reaching, object grasping, and manipulation. We highlighted the intertwined relation between the perception of coarse and fine textures and the resulting perceived motion. While tactile motion is crucial for the discrimination of fine textures, on the other hand, the orientation and frequency of textures affect the perceived motion direction and speed of the moving surface. Some of the effects of coarse texture on perceived direction and/or speed can be explained by assuming a model for motion encoding in touch that is sensitive to the strain energy density, as, for example, the tactile flow model (7) or analogous models tested in vision (142). Furthermore, skin vibrations produced by slip motion are an important cue to the discrimination of speed and fine textures. The propagation of vibrations when we interact with objects (143) could explain this phenomenon.

An open question that stems from the current literature is on the neural mechanisms to construct a robust representation of texture that is invariant to velocity (144). During active exploration, kinesthetic information from muscle spindles and from the forward model of motor command provides an independent measurement of hand motion speed that the brain can use to disentangle texture and spatiotemporal frequency of the moving stimulus. The motion stimuli from kinesthesia provides an auxiliary cue that the brain can use to calibrate the tactile stimulus to the different textures. Likewise, it is less obvious how the brain can disentangle the two during passive exploration. The brain is possibly provided with other information from tangential strain and shear force from the finger that could help in calibration the perception of texture (9).

Another important notion mentioned in this review is the role of touch for the control of hand movements. For example, in our recent study we showed that a change in contact area at the finger pad provides an auxiliary proprioceptive cue to finger displacement (4). Next, we demonstrated that changing the orientation of the parallel ridges of a surface produces a systematic bias in reaching movement (5). In our studies, the plate was stationary during the trials, therefore, tactile motion was not physically decoupled from hand motion. The next step in reaching studies could be to extend the previous results to evaluate hand reaching when tactile motion is fully decoupled from hand motion. Using a novel device described in Ref. 145, we are extending this idea and evaluating the role of slip motion in hand reaching, when the two motions cues from kinesthesia and touch are fully decoupled.

An ideal observer model based on Kalman filtering predicts the systematic deviation during reaching movement when parallel ridge orientation was manipulated (5). Different signals are integrated in such models, including somatosensory feedback from proprioception and touch, and the efference copy of the motor command (5, 7, 146). A standing question relates to the neural substrates for the ideal observer model. The posterior parietal cortex, which includes Brodmann's area 5 and 7 in humans, is a possible neural substrate for it. Brodmann's area 5 receives projections from the primary somatosensory cortex, conveying information from cutaneous mechanoreceptors, muscle spindles and joint receptors (12). Additionally, during reaching movements, neurons in the posterior parietal cortex discharge almost in synchrony with neurons from motor and premotor areas, advocating for a role of this area for the control of hand reaching (147). Brodmann's area 7 integrates tactile and visual stimuli that overlap in space and thus may play a role in tasks requiring the hand to reach for a visual target. It has been hypothesized that the convergence of motor signals and somatosensory feedback in this cortical region allows comparing planned and actual movements, as postulated in Kalman filter models (146). The weight of tactile and proprioceptive signals, and of the efference copy of the motor command may change, depending on whether the task prompts the observer to use cutaneous signals for exteroception or as auxiliary proprioceptive cues. In future studies, it will be possible to evaluate this hypothesis with behavioral and brain imaging techniques.

The investigation of the role of touch for motion and space perception represents an active, open, and exciting research field, which could also positively impact and cross-fertilize other disciplines. In our previous work, it was demonstrated that the noisier the tactile channel of information, the smaller the error of motor pursuit of the path (5, 87). This is consistent with a Bayesian framework of integration between proprioceptive and tactile cues, where the weight of each cue in the fused estimate is an inverse function of the sensory noise. This finding could open interesting perspectives for devising protocols for the assessment of dysfunction in the sense of touch, which is a common symptom in many neurological conditions.

The investigation of the computational aspects that underlie touch-mediated motion and texture representation could benefit from and capitalize on mathematical models already applied to other sensory modalities, such as vision. As also previously discussed with respect to tactile looming or tactile flow, vision and touch share many commonalities under a functional, behavioral and neuroanatomical point of view (39, 142, 148). Specifically, these two sensory channels retrieve information on object motion from the spatiotemporal patterns of activation across the two sensors, the retina and the skin, respectively (144). Accordingly, a model based on the spatiotemporal pattern of skin deformation reproduced the tactile afferent signals quite accurately (149). This notion suggests that, despite the differences in physical properties of the stimuli, vision and touch would share common mechanisms of motion processing at a higher level of representation. In this regard, the role of multimodal cortical areas such as of hMT + /V5 could represent a promising target for future investigation in visuo-tactile motion processing.

These findings in neuroscience may impact the technological development of haptic devices. Under this regard, the contribution of tactile stimulation to motion perception and the interplay with surface texture properties, including skin vibration propagation, could be used to devise suitable stimulation protocols as well as design guidelines for tactile and haptic interfaces. The goal could be to elicit illusory percepts (including proprioceptive percepts) in users to be used in virtual and augmented reality settings. For example, we showed that ridge orientation produced a systematic error in motion direction. It could be possible to use this perceptual phenomenon to develop a mechatronic system to guide the user's finger sliding on the ridged plate toward an arbitrary desired point A, while the user is instructed (and perceives) to move toward another point B (91). These outcomes could positively impact the field of virtual and mixed reality, for example, in the framework of haptic retargeting (150), thus advancing human machine interaction.

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AQ: 11 DISCLOSURES

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AQ: 12 AUTHOR CONTRIBUTIONS

C.P.R., G.C.B., and A.M. prepared figures; C.P.R., G.C.B., C.V.P., A.M., and M.B. drafted manuscript; C.P.R., G.C.B., S.C., C.V.P., A.M., and M.B. edited and revised manuscript; C.P.R., G.C.B., S.C., C.V.P., A.M., and M.B. approved final version of manuscript.

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