Review Article

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Neuroimaging of Tactile Information Processing

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Neural processing of tactile information in the brain has been relatively less unveiled compared to other senses, such as visual and auditory information. This is partly due to difficulties in creating tactile stimuli, a wide distribution of tactile receptors over the whole body, the lack of rich understanding of tactile perception, and tight coupling of tactile sensation with action. Nonetheless, it is important to understand how the central nervous system processes tactile information in order to develop clinical solutions for impairment of somatosensory systems, create artificial tactile systems for robots, and advance the assistive technology based on perception-action coupling for the elderly. In this review, we revisit recent investigations of neural processing of tactile information in the human brain using neuroimaging. In particular, this review focuses on cutaneous innocuous tactile information.

Keywords: Touch; Neuroimaging; Touch of perception; Information processing

INTRODUCTION

Although neural mechanisms of touch have been relatively less explored compared to those of vision and hearing [1], touch sensation is equally crucial to human lives as accurate touch sensation and perception allow us to interact with objects [2], make delicate movements [3] and even support social ability [4]. Among the various aspects of neural mechanisms of touch, neural processing of tactile information in the human brain remains largely unexplored, partly due to the complexity of involvement of tactile processing in neurological disorders, difficulty in generating various mechanical stimuli, and wide distributions of tactile receptors over the whole body concentrating towards the brain through diverse and parallel pathways. However, a recent surge of technical interests in haptics, mainly owing to touch-based user interfaces in smart devices has given rise to the need to understand how humans feel touch and related neural underpinnings. Moreover, advances in artificial intelligence (AI) have progressively extended from conventional vision (e.g., image processing) and hearing (e.g., natural language processing) to other senses, particularly touch [5]. In addition, haptics has become increasingly important for implementing artificial touch in robots [6] as well as artificial touch in virtual environments [7]. Therefore, changes in technical environments naturally drive neuroimaging research to explore human brain processing of tactile information.

To describe fundamental elements of human tactile perception, previous research has

suggested the following two to five dimensions: e.g., 'rough/ smooth' and 'slippery/adherent' [8]; 'rough/smooth', 'sticky/ slippery', and 'soft/hard' [9]; 'rough/smooth', 'sticky/slippery', 'soft/hard' and 'warm/cold' [10]; or 'uneven/relief (macro roughness), 'rough/smooth' (fine roughness), 'sticky/slippery', 'soft/hard', and 'warm/cold' [11]. These neural correlates of tactile perception can also be described from the perspective of tactile receptors and afferents. Especially, cutaneous innocuous sensations are categorized into the following four types: slowly adapting types I and II (SA-I and SA-II) and rapidly adaptive types I and II (RA-I and RA-II). SA-I senses constant pressing stimuli via the mechanoreceptor in Merkel's discs, SA-II generally senses skin stretching stimuli via Ruffini corpuscular intelligence, RA-I senses slowly oscillating stimuli, often called flutter, via Meissner corpuscles, and RA-II senses high-frequency vibration via Pacinian corpuscles. Previous findings have indicated that sensory afferents from cutaneous receptors through the spinal cord to the brain are virtually separated, akin to the labelled line theory [12]. Thus, investigations of neural responses to tactile stimulations associated with different types of mechanical sensations may assume that tactile afferent inputs from each type of mechanoreceptors would be collectively received by the primary somatosensory cortex (S1). However, other findings suggest a more complex and integrated processing of touch sensations by different types of afferents to evoke tactile perception [13,14]. Thus, neuroimaging investigations of tactile information processing in the brain may need to study a wide range of cortical and subcortical areas as well as their interconnections [15,16].

Tactile object recognition involves not only the perception of tactile stimulus properties as described above but also the perception of macro-scale properties, such as shape, location, and orientation [17]. The latter focuses on the spatial information of tactile stimuli and builds on a spatial reference system, whereas the former generally requires the discrimination of intensity [18]. As such, neuroimaging studies have also explored related brain regions and networks in the framework of macro-scale spatial properties of tactile stimuli. For instance, studies have revealed that the brain network processing the macro-scale properties is distinct from that processing the material properties of tactile stimuli [19].

In this review, we have summarized neuroimaging studies of cutaneous tactile information processing in the human brain via the following two frameworks: neural correlates of the tactile perceptual dimensions and those of the macro-scale spatial information of tactile stimuli. There are various neuroimaging techniques (such as positron emission tomography [PET] and computed tomography [CT]), but in this review, we have mainly focused on functional magnetic resonance imaging (fMRI), which is widely used as a non-invasive method to investigate the whole brain. We have adopted four tactile perceptual dimensions from previous studies, including 'rough/ smooth', 'sticky/slippery', 'soft/hard', and 'warm/cool', and summarized the neuroimaging findings of individual dimensions. We have also revisited the neuroimaging findings of macro-scale tactile spatial information, such as shape and location. Finally, we have suggested future directions of further neuroimaging studies. It should be noted that the scope of this review does not include in-depth investigations of psychophysical understanding of tactile perception, tactile perception-and-action coupling, brain processing of nociceptive afferents, and animal studies of somatosensations, excluding some cases that are necessary for discussion regarding better interpretations of human neuroimaging results.

NEUROIMAGING FINDINGS OF TACTILE PERCEPTUAL DIMENSIONS

Roughness/Smoothness

Neuroimaging investigations on the roughness/smoothness have been the most widely performed amid the perceptual dimensions [20]. The perception of the roughness/smoothness for tactile stimuli is based on peripheral inputs originating from multiple mechanoreceptors, including Merkel's discs, Meissner corpuscles, and Pacinian corpuscles [21]. As the perception of the surface roughness of an object basically depends on movement between the surface and skin, studies have indicated the importance of temporal cue for accurate roughness perception [22,23]. The rate of the tangential force also contributes to the subjective estimation of the surface roughness magnitude [24].

Neuroimaging studies have reported the brain regions involved in the perception of roughness/smoothness, such as the S1, supplementary motor area (SMA), and bilateral temporal poles (Fig. 1A) [25]. As a result of using T2*-weighted gradient echo planar imaging (EPI), SMA activity is correlated with individual variations of the perception of roughness [25]. Secondary somatosensory cortex (S2) also plays an important role in the perceptual discrimination of vibrotactile frequency [26]. Other regions, including bilateral parietal operculum (PO), insula, and right lateral prefrontal cortex, are reportedly engaged in the perceptual estimation of the magnitude of surface roughness [27]. Related to the other sensory modalities, the tactile perception of roughness and visual observation of tactile roughness share neural activity in the areas of bilateral insula, supramarginal gyrus (SMG), and anterior cingulate cortex (ACC) [28].

Stickiness/Slipperiness

Neuroimaging investigations of tactile stickiness perception have been relatively sparse, and they have been conducted more recently compared to the other dimensions. In general, stickiness is sensed when the skin is stretched by adhesive materials. Thus, it is expected that Ruffini corpuscles and SA-Il afferents would be prominently involved in stickiness sensation. Studies have shown that SA-II afferents exhibit more sensitive responses to skin stretching than other afferents [29,30]. In contrast, other studies have shown that RA and SA-I afferents respond to skin stretching to a greater extent than the other afferents do [31,32]. An important issue arises here regarding how to evoke sticky senses with physical contacts. Most studies have used the tangential movement of fingers on the surface of adhesive materials to generate a frictional force between the finger skin and the surface. However, this also entails other kinematic changes in direction and vibration, which is distant from skin stretching. To avoid such issues related to the tangential force, one can generate sticky senses using adhesive materials with perpendicular forces without any tangential movement.

So far, only a few studies have reported the neuroimaging results correlated with the perception of stickiness [33,34]. By using the T2*-weighted gradient EPI, these studies found the brain regions activated in response to the perception of tactile stickiness, and they included the contralateral S1 and ipsilateral dorsolateral prefrontal cortex (DLPFC) [33] (Fig. 1B). Especially, DLPFC activity may reflect emotional responses to touch on sticky substances. Moreover, a multivariate pattern analysis study showed that posterior parietal cortex (PPC) activity discriminates the perceptual intensities of stickiness [34]. Other studies further revealed the cortical representations of stickiness shared between direct skin contact and sticky wearable gloves in bilateral angular gyri and the inferior frontal gyrus (IFG) [35].

Hardness/Softness

In connection between hardness perception and tactile sensory afferents, SA-I afferents are deemed to play a key role [36]. Considering that a physical factor for tactile hardness is a ratio between the relative force on the object surface and the consequent displacement of the surface, the perception of tactile hardness can draw upon proprioception [11]. This supposition is controversial as other studies have demonstrated greater contribution of tactile cues to cutaneous hardness perception than proprioception [10].

Neuroimaging studies on tactile hardness perception have mostly revealed neural activations of S1 and PO. The perception of the stiffness of an object evokes activation of area 3b of S1 in humans, which is in accordance with the other animal in-

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vestigation results, as well as of the contralateral motor area and cerebellum, presumably related to active movements [37]. Moreover, the softness level of objects can be predicted by neural activations of the PO. A central node within the brain network engaged in the tactile perception of different material properties appears to be the PO, along with the insula. In particular, PO, insula, and medial frontal cortex show activity correlated with varying softness level of an object [16]. Performing a hardness discrimination task leads to activations of bilateral PO [38]. In conjunction with visual perception, visual modulation of tactile hardness perception induces biases and involves bilateral PO as well as the other regions of the sensory motor cortex, anterior intraparietal sulcus (aIPS), and occipito-temporal cortex (OTC) [39]. During active exploration of tactile hardness, a recent study has demonstrated that the neural activity correlated with the hardness intensity in the posterior insula and posterior lobe of the cerebellum by using T2*-weighted gradient EPI (Fig. 1C) [40].

Warmth/Coolness

The thermal information is transmitted from the surface of an object to the skin through the transient receptor potential (TRP) ion channels [41]. Numerous studies have indicated that the insular cortex is a key region for processing the innocuous thermal information. Different from other perceptual dimensions, the perception of warmth/coolness recruits the insular cortex as the primary center along with the somatosensory cortex [42]. Specifically, it has been demonstrated that activity in the anterior insular cortex (alns) correlates with subjective ratings of warm feelings [43]. In contrast, the posterior insular cortex (plns) reportedly processes sensory specific information, such as sensory discrimination [44]. Functional connectivity studies have shown that the insular cortex plays a central role in innocuous thermal information processing and both alns and plns form functional networks with many other areas, including S1, S2, cingulate gyrus, prefrontal cortex, and parietal association cortices with different degrees: alns appears to be more likely connected to areas for affective processing, whereas plns is more likely connected to areas for sensory-discriminative processing [45]. Moreover, the ambient thermal perception involves the left dorsal plns, putamen, amygdala, and bilateral retrosplenial cortices [46].

The perception of thermal stimuli also entails hedonic responses. Neural correlates of the subjective ratings of pleasantness in response to warm and cool stimuli are found in the mid-orbitofrontal and pregenual cingulate cortex and the ventral striatum [47]. In relation to the subjective feelings of pleasantness and unpleasantness induced by thermal stimuli, the following brain regions are activated: the caudate nucleus and frontal regions for pleasantness, and the medial frontal and



Fig. 1. Examples of neuroimaging findings of tactile perception. A: Primary somatosensory cortex (S1), supplementary motor area (SMA), and bilateral temporal pole showed multivoxel patterns of roughness inferred by decoding analysis (adapted from Kim et al. [25], PLoS One 2015;10:e0129777). B: S1 and dorsolateral prefrontal cortex (DLPFC) showed significant activations when sticky stimuli were served to the participants compared to baseline. Also, subcortical regions showed significant activation when subjects received sticky stimulation than when they received less sticky stimulation (adapted from Yeon et al. [33], Front Hum Neurosci 2017;11:8). C: During the object grasping task, rpcerebellum and rpINS tracked the intensity of hardness (adapted from Kim et al. [40], PeerJ 2021;9:e11760). All the results shown in Figure 1 were obtained using T2*-weighted gradient echo planar imaging (EPI). STP, superior temporal pole; Mid, middle; Sup, superior.

ACC for unpleasantness [48]. A study has reported that the reduction of sensitivity to warmth predicts increases in the assessment score of alexithymia – personality trait of deficits in emotional processing [49].

Texture

The perception of tactile texture results from a mixture of aforementioned individual fundamental perceptual dimensions. Studies have often suggested three dimensions constructing a perceptual space of texture, including 'roughness/smoothness, hardness/softness, and warmness/coolness [11]' or 'roughness/ smoothness, hardness/softness, and compressional elasticity [9,50]'. Tactile texture identification activates the contralateral posterior postcentral gyrus (PCG) [38]. S2 plays a pivotal role in encoding and maintaining working memory of the tactile surface texture information [51].

NEUROIMAGING FINDINGS OF TACTILE PROCESSING OF SPATIAL PROPERTIES

Shape

Many human fMRI studies have reported the postcentral sulcus (PCS) and parietal regions as the main centers for the perception of haptic shape. Lesions in the parietal opercular area cause tactile agnosia, which refers to the inability to recognize objects by touch [52]. Neural activity in the PCS has been reportedly found in relation to haptic shape recognition. Specifically, discrimination of haptic shapes activates the area 2 in S1 [53]. Also, the PCG is commonly activated during the recognition of haptic shape and texture [38]. Effective connectivity analysis has revealed information pathways from the PCS to intraparietal sulcus (IPS) and from the lateral occipital complex (LOC) to PCS during haptic shape recognition [54]. Parts of the IPS are also involved in haptic shape recognition, including the anterior IPS [54,55] and posterior IPS [56,57].

Recognition of object shape often involves multisensory information processing. Most studies have investigated the neural substrates of tactile and visual representations of shape. Shape-selective areas for both tactile and visual perception include posterior parietal parts over superior parietal gyrus and IPS as well as the LOC [54,55,58,59]. However, a lesion study on the LOC has demonstrated that although the LOC is central to visual and haptic shape recognition, it is not essential for haptic shape recognition per se [60]. Identification of haptic shape representation in the visual cortex demonstrates topdown involvement of visual imagery in haptic shape recognition [61]. Effective connectivity studies have shown both bottom-up and top-down networks for multisensory shape perception [62]. A further study has revealed that object familiarity enhances visual imagery-driven effective connectivity from the frontal areas to the LOC during haptic shape perception [63]. In contrast, spatial imagery-driven effective connectivity is more modulated for unfamiliar objects [64].

Location

Tactile information processing, initiated from S1, is deemed to be separated into the following two pathways: the ventral pathway for surface texture information processing and the dorsal pathway for tactile location information processing [65]. The latter includes the IPS and frontal eye fields (FEFs). Locating a tactile stimulus over different fingers activates the inferior and superior parietal lobules [66]. Selective attention to grating location activates the right temporoparietal junction independent of hands [67]. Haptic location-selective activations are found in both FEFs and IPS, and they converge with the visual location-selective pathways in the dorsal frontoparietal cortical areas [68]. Multivoxel pattern analysis (MVPA) studies have found neural activity in the SMG by decoding stimulation locations over different fingers [69] or in S1, primary motor cortex (M1), IPS, paracentral gyrus, and superior frontal gyrus by decoding stimulation locations over the upper limbs [70]. On obtaining a neuroimage from the T2*-weighted gradient EPI, discrimination of finger stimulation locations using MVPA involves activities of the secondary somatosensory cortices, such as PPC and SMG (Fig. 2A) [71]. Moreover, maintaining spatial layout of tactile stimuli in working memory involves neural activities over the PPC and premotor cortex [72].

Orientation

A neuroimaging study using T2*-weighted gradient EPI has shown that tactile orientation discrimination reportedly activates the right PCS and IPS, regardless of the hand used (Fig. 2B) [73]. On the other hand, discrimination of grating orientation contrasted to discrimination of grating spacing activates the left anterior IPS, right PCS and PCG, left parieto-occipital cortex, bilateral FEFs, and bilateral ventral premotor cortices [74]. Some of these regions are also known to be related to visual orientation discrimination [73]. In fact, tactile discrimination of grating orientations activates the parieto-occipital areas, suggesting a key role of visual imagery in the processing of tactile orientation information [75]. Interference by transcranial magnetic stimulation (TMS) over the occipital cortex disrupts tactile discrimination of grating orientation, but not tactile discrimination of grating texture [76]. This implies a top-down influence of visual imagery on tactile information processing [77].



Fig. 2. Examples of neuroimaging findings of tactile perception of spatial properties. A: Location of stimuli on fingers can be distinguished by the multivoxel patterns of contralateral posterior parietal cortex (PPC) and supramarginal gyrus (SMG) (adapted from Kim et al. [71], Front Hum Neurosci 2015;8:1070). B: The right postcentral sulcus and intraparietal sulcus (IPS) are activated during tactile orientation perception (adapted from Kitada et al. [73], J Neurosci 2006;26:7491-7501). All results shown in Figure 2 were obtained using an T2*-weighted gradient echo planar imaging (EPI) sequence. Min, minimum; Max, maximum; n.s., not significant; MOG, middle occipital gyrus; CS, central sulcus.

FUTURE DIRECTIONS

Neuroimaging research has deepened our understanding about how the human brain processes tactile information. However, many aspects of neural mechanisms regarding tactile information processing are not yet well understood. For instance, compared to cutaneous tactile sensations and pain sensations, neural processing of proprioception has been less explored. Relevant studies have focused on high-level body representations in the cortex, often called somatoperception and somatorepresentation [78]. Also, neural representations of body schema, including somatotopic representations of the skin surface, body size and shape representations, and postural representations, have been widely investigated, in which the first somatotopic representations are particularly plastic and subject to changes by peripheral alterations [79]. This will become more important when people connect themselves with a virtual avatar in the metaverse through motor and sensory communications, presumably extending the body ownership to the avatar [80]. Another interesting research area related to tactile processing is understanding how the brain deals with indirect touch via tools. This also raises questions regarding how somatosensations play a role in using tools by reorganizing the body schema, referred to as tool embodiment [81]. However, few studies have investigated neural underpinnings of tool use in humans. Finally, neural mechanisms and applications of affective touch will become more significant, as social interactions in the aging society as well as virtual environments will be increasingly crucial [82]. More extensive investigations using neuroimaging approaches are required to understand the brain networks related to affective touch.

In conclusion, neuroimaging studies of tactile information processing have revealed the basic neural mechanisms of tactile perception as well as multisensory integration. As the haptic interface will become more prevalent in the era of using touch-based smart devices and communicating in the virtual world, more in-depth neuroimaging research for tactile perception is required in the future. Consequently, it is desired that real-world applications, such as tactile intelligence in robots and virtual haptic sensations in the metaverse, will benefit from the understanding of neural tactile processing.

Conflicts of Interest

The authors have no potential conflicts of interest to disclose.

Author Contributions

Conceptualization: Sung-Phil Kim. Funding acquisition: Sung-Phil Kim. Supervision: Sung-Phil Kim. Writing—original draft: Ji-Hyun Kim, Sung-Phil Kim. Writing—review & editing: Ji-Hyun Kim.

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REFERENCES

- 1. Goldstein EB. Sensation and perception. 9th ed. Boston: Cengage Learning, 2013.
- Monzée J, Lamarre Y, Smith AM. The effects of digital anesthesia on force control using a precision grip. J Neurophysiol 2003;89: 672-683.
- Shin YK, Proctor RW, Capaldi EJ. A review of contemporary ideomotor theory. Psychol Bull 2010;136:943-974.
- Marco EJ, Hinkley LB, Hill SS, Nagarajan SS. Sensory processing in autism: a review of neurophysiologic findings. Pediatr Res 2011; 69(5 Pt 2):48R-54R.
- 5. Niu H, Li H, Gao S, et al. Perception-to-cognition tactile sensing based on artificial-intelligence-motivated human full-skin bionic electronic skin. Adv Mater 2022;34:e2202622.
- 6. James JW, Church A, Cramphorn L, Lepora NF. Tactile model O: fabrication and testing of a 3d-printed, three-fingered tactile robot hand. Soft Robot 2021;8:594-610.
- 7. Shi Y, Wang F, Tian J, et al. Self-powered electro-tactile system for virtual tactile experiences. Sci Adv 2021;7:eabe2943.
- 8. Ballesteros S, Reales JM, de Leon LP, Garcia B. The perception of ecological textures by touch: does the perceptual space change under bimodal visual and haptic exploration? Proceedings of First Joint EuroHaptics Conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems; 2005 Mar 18-20; Pisa, Italy. IEEE; 2005. pp.635-638.
- Hollins M, Bensmaïa S, Karlof K, Young F. Individual differences in perceptual space for tactile textures: evidence from multidimensional scaling. Percept Psychophys 2000;62:1534–1544.
- 10. Tiest WM. Tactual perception of material properties. Vision Res 2010;50:2775-2782.
- 11. Okamoto S, Nagano H, Yamada Y. Psychophysical dimensions of tactile perception of textures. IEEE Trans Haptics 2013;6:81-93.
- Ma Q. Population coding of somatic sensations. Neurosci Bull 2012; 28:91-99.
- 13. Johansson RS, Flanagan JR. Coding and use of tactile signals from the fingertips in object manipulation tasks. Nat Rev Neurosci 2009;10:345-359.
- Saal HP, Bensmaia SJ. Touch is a team effort: interplay of submodalities in cutaneous sensibility. Trends Neurosci 2014;37:689-697.
- Kilteni K, Ehrsson HH. Functional connectivity between the cerebellum and somatosensory areas implements the attenuation of self-generated touch. J Neurosci 2020;40:894–906.
- Kitada R, Doizaki R, Kwon J, et al. Brain networks underlying tactile softness perception: a functional magnetic resonance imaging study. Neuroimage 2019;197:156-166.
- 17. Jones LA, Lederman SJ. Human hand function. 1st ed. New York: Oxford University Press, 2006.
- Lederman SJ, Klatzky RL. Relative availability of surface and object properties during early haptic processing. J Exp Psychol Hum Percept Perform 1997;23:1680–1707.
- 19. Roland PE, O'Sullivan B, Kawashima R. Shape and roughness activate different somatosensory areas in the human brain. Proc

Natl Acad Sci U S A 1998;95:3295-3300.

- 20. Bensmaia S. Texture from touch. In: Prescott T, Ahissar E, Izhikevich E, eds. Scholarpedia of touch. 1st ed. Paris: Atlantis Press, 2015. pp.207-215.
- 21. Blake DT, Hsiao SS, Johnson KO. Neural coding mechanisms in tactile pattern recognition: the relative contributions of slowly and rapidly adapting mechanoreceptors to perceived roughness. J Neurosci 1997;17:7480-7489.
- 22. Cascio CJ, Sathian K. Temporal cues contribute to tactile perception of roughness. J Neurosci 2001;21:5289-5296.
- 23. Gamzu E, Ahissar E. Importance of temporal cues for tactile spatial- frequency discrimination. J Neurosci 2001;21:7416-7427.
- 24. Smith AM, Chapman CE, Deslandes M, Langlais JS, Thibodeau MP. Role of friction and tangential force variation in the subjective scaling of tactile roughness. Exp Brain Res 2002;144:211-223.
- 25. Kim J, Chung YG, Park JY, et al. Decoding accuracy in supplementary motor cortex correlates with perceptual sensitivity to tactile roughness. PLoS One 2015;10:e0129777.
- 26. Chung YG, Kim J, Han SW, et al. Frequency-dependent patterns of somatosensory cortical responses to vibrotactile stimulation in humans: a fMRI study. Brain Res 2013;1504:47-57.
- 27. Kitada R, Hashimoto T, Kochiyama T, et al. Tactile estimation of the roughness of gratings yields a graded response in the human brain: an fMRI study. Neuroimage 2005;25:90-100.
- Kim J, Bülthoff I, Kim SP, Bülthoff HH. Shared neural representations of tactile roughness intensities by somatosensation and touch observation using an associative learning method. Sci Rep 2019;9:77.
- 29. Hale KS, Stanney KM. Deriving haptic design guidelines from human physiological, psychophysical, and neurological foundations. IEEE Comput Graph Appl 2004;24:33-39.
- 30. Johnson KO. The roles and functions of cutaneous mechanoreceptors. Curr Opin Neurobiol 2001;11:455-461.
- Birznieks I, Jenmalm P, Goodwin AW, Johansson RS. Encoding of direction of fingertip forces by human tactile afferents. J Neurosci 2001;21:8222–8237.
- Srinivasan MA, Whitehouse JM, LaMotte RH. Tactile detection of slip: surface microgeometry and peripheral neural codes. J Neurophysiol 1990;63:1323–1332.
- Yeon J, Kim J, Ryu J, Park JY, Chung SC, Kim SP. Human brain activity related to the tactile perception of stickiness. Front Hum Neurosci 2017;11:8.
- 34. Kim J, Yeon J, Ryu J, Park JY, Chung SC, Kim SP. Neural activity patterns in the human brain reflect tactile stickiness perception. Front Hum Neurosci 2017;11:445.
- Kim J, Bülthoff I, Bülthoff HH. Cortical representation of tactile stickiness evoked by skin contact and glove contact. Front Integr Neurosci 2020;14:19.
- Srinivasan MA, LaMotte RH. Tactual discrimination of softness. J Neurophysiol 1995;73:88-101.
- Bodegård A, Geyer S, Herath P, Grefkes C, Zilles K, Roland PE. Somatosensory areas engaged during discrimination of steady pressure, spring strength, and kinesthesia. Hum Brain Mapp 2003;20: 103-115.

- Servos P, Lederman S, Wilson D, Gati J. fMRI-derived cortical maps for haptic shape, texture, and hardness. Brain Res Cogn Brain Res 2001;12:307–313.
- 39. Kim Y, Usui N, Miyazaki A, et al. Cortical regions encoding hardness perception modulated by visual information identified by functional magnetic resonance imaging with multivoxel pattern analysis. Front Syst Neurosci 2019;13:52.
- 40. Kim JH, Kim J, Yeon J, Park JY, Chung D, Kim SP. Neural correlates of tactile hardness intensity perception during active grasping. PeerJ 2021;9:e11760.
- 41. Schepers RJ, Ringkamp M. Thermoreceptors and thermosensitive afferents. Neurosci Biobehav Rev 2010;34:177-184.
- 42. Craig AD, Chen K, Bandy D, Reiman EM. Thermosensory activation of insular cortex. Nat Neurosci 2000;3:184-190.
- 43. Olausson H, Charron J, Marchand S, Villemure C, Strigo IA, Bushnell MC. Feelings of warmth correlate with neural activity in right anterior insular cortex. Neurosci Lett 2005;389:1-5.
- 44. Lin CS, Hsieh JC, Yeh TC, Lee SY, Niddam DM. Functional dissociation within insular cortex: the effect of pre-stimulus anxiety on pain. Brain Res 2013;1493:40-47.
- Peltz E, Seifert F, DeCol R, Dörfler A, Schwab S, Maihöfner C. Functional connectivity of the human insular cortex during noxious and innocuous thermal stimulation. Neuroimage 2011;54: 1324-1335.
- 46. Oi H, Hashimoto T, Nozawa T, et al. Neural correlates of ambient thermal sensation: an fMRI study. Sci Rep 2017;7:11279.
- 47. Rolls ET, Grabenhorst F, Parris BA. Warm pleasant feelings in the brain. Neuroimage 2008;41:1504-1513.
- 48. Aizawa Y, Harada T, Nakata H, Tsunakawa M, Sadato N, Nagashima K. Assessment of brain mechanisms involved in the processes of thermal sensation, pleasantness/unpleasantness, and evaluation. IBRO Rep 2019;6:54-63.
- 49. Borhani K, Làdavas E, Fotopoulou A, Haggard P. "Lacking warmth": alexithymia trait is related to warm-specific thermal somatosensory processing. Biol Psychol 2017;128:132–140.
- Hollins M, Faldowski R, Rao S, Young F. Perceptual dimensions of tactile surface texture: a multidimensional scaling analysis. Percept Psychophys 1993;54:697–705.
- 51. Kaas AL, van Mier H, Visser M, Goebel R. The neural substrate for working memory of tactile surface texture. Hum Brain Mapp 2013;34:1148-1162.
- 52. Caselli RJ. Ventrolateral and dorsomedial somatosensory association cortex damage produces distinct somesthetic syndromes in humans. Neurology 1993;43:762–771.
- 53. Bodegård A, Geyer S, Grefkes C, Zilles K, Roland PE. Hierarchical processing of tactile shape in the human brain. Neuron 2001;31: 317-328.
- Peltier S, Stilla R, Mariola E, LaConte S, Hu X, Sathian K. Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. Neuropsychologia 2007; 45:476-483.
- 55. Zhang M, Weisser VD, Stilla R, Prather SC, Sathian K. Multisensory cortical processing of object shape and its relation to mental imagery. Cogn Affect Behav Neurosci 2004;4:251-259.

- 56. Van de Winckel A, Sunaert S, Wenderoth N, et al. Passive somatosensory discrimination tasks in healthy volunteers: differential networks involved in familiar versus unfamiliar shape and length discrimination. Neuroimage 2005;26:441-453.
- 57. Jäncke L, Kleinschmidt A, Mirzazade S, Shah NJ, Freund HJ. The role of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. Cereb Cortex 2001;11: 114–121.
- 58. Stilla R, Sathian K. Selective visuo-haptic processing of shape and texture. Hum Brain Mapp 2008;29:1123-1138.
- 59. Lacey S, Sathian K. Multisensory object representation: insights from studies of vision and touch. Prog Brain Res 2011;191:165-176.
- 60. Snow JC, Goodale MA, Culham JC. Preserved haptic shape processing after bilateral LOC lesions. J Neurosci 2015;35:13745-13760.
- 61. Lee Masson H, Bulthé J, Op de Beeck HP, Wallraven C. Visual and haptic shape processing in the human brain: unisensory processing, multisensory convergence, and top-down influences. Cereb Cortex 2016;26:3402-3412.
- 62. Deshpande G, Hu X, Stilla R, Sathian K. Effective connectivity during haptic perception: a study using Granger causality analysis of functional magnetic resonance imaging data. Neuroimage 2008;40:1807-1814.
- 63. Deshpande G, Hu X, Lacey S, Stilla R, Sathian K. Object familiarity modulates effective connectivity during haptic shape perception. Neuroimage 2010;49:1991–2000.
- 64. Lacey S, Stilla R, Sreenivasan K, Deshpande G, Sathian K. Spatial imagery in haptic shape perception. Neuropsychologia 2014;60: 144-158.
- 65. Sathian K. Analysis of haptic information in the cerebral cortex. J Neurophysiol 2016;116:1795-1806.
- Renier LA, Anurova I, De Volder AG, Carlson S, VanMeter J, Rauschecker JP. Multisensory integration of sounds and vibrotactile stimuli in processing streams for "what" and "where". J Neurosci 2009;29:10950-10960.
- 67. Van Boven RW, Ingeholm JE, Beauchamp MS, Bikle PC, Ungerleider LG. Tactile form and location processing in the human brain. Proc Natl Acad Sci U S A 2005;102:12601-12605.
- 68. Sathian K, Lacey S, Stilla R, et al. Dual pathways for haptic and visual perception of spatial and texture information. Neuroimage 2011;57:462-475.
- 69. Kim J, Chung YG, Chung SC, Bülthoff HH, Kim SP. Decoding pressure stimulation locations on the fingers from human neural activation patterns. Neuroreport 2016;27:1232-1236.
- Lee IS, Jung WM, Park HJ, Chae Y. Spatial information of somatosensory stimuli in the brain: multivariate pattern analysis of functional magnetic resonance imaging data. Neural Plast 2020; 2020:8307580.
- Kim J, Müller KR, Chung YG, et al. Distributed functions of detection and discrimination of vibrotactile stimuli in the hierarchical human somatosensory system. Front Hum Neurosci 2015;8:1070.
- 72. Schmidt TT, Blankenburg F. Brain regions that retain the spatial layout of tactile stimuli during working memory A 'tactospatial



sketchpad'? Neuroimage 2018;178:531-539.

- Kitada R, Kito T, Saito DN, et al. Multisensory activation of the intraparietal area when classifying grating orientation: a functional magnetic resonance imaging study. J Neurosci 2006;26: 7491-7501.
- 74. Zhang M, Mariola E, Stilla R, et al. Tactile discrimination of grating orientation: fMRI activation patterns. Hum Brain Mapp 2005; 25:370-377.
- 75. Sathian K, Zangaladze A, Hoffman JM, Grafton ST. Feeling with the mind's eye. Neuroreport 1997;8:3877-3881.
- Zangaladze A, Epstein CM, Grafton ST, Sathian K. Involvement of visual cortex in tactile discrimination of orientation. Nature 1999; 401:587-590.
- 77. Sathian K, Zangaladze A. Feeling with the mind's eye: the role of vi-

sual imagery in tactile perception. Optom Vis Sci 2001;78:276-281.

- Longo MR, Azañón E, Haggard P. More than skin deep: body representation beyond primary somatosensory cortex. Neuropsychologia 2010;48:655-668.
- 79. Medina J, Coslett HB. From maps to form to space: touch and the body schema. Neuropsychologia 2010;48:645-654.
- 80. Müsseler J, von Salm-Hoogstraeten S, Böffel C. Perspective taking and avatar-self merging. Front Psychol 2022;13:714464.
- 81. Bell JD, Macuga KL. Are tools truly incorporated as an extension of the body representation?: assessing the evidence for tool embodiment. Psychon Bull Rev 2022;29:343-368.
- Cruciani G, Zanini L, Russo V, Boccardi E, Spitoni GF. Pleasantness ratings in response to affective touch across hairy and glabrous skin: a meta-analysis. Neurosci Biobehav Rev 2021;131:88-95.