Chapter title: THE BRAIN NETWORK FOR HAPTIC OBJECT RECOGNITION

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Abstract Humans can haptically identify common three-dimensional objects surprisingly well. What are the neural mechanisms underlying this ability? Previous neuroimaging studies have shown that haptic object recognition involves a distributed network of brain regions beyond the conventional somatosensory cortices. However, the relative contributions of these regions to haptic object recognition are not well understood. In this chapter, I discuss three key hypotheses concerning the brain network underlying haptic object processing and its interaction with visual object processing. The first is that the occipito-temporal cortex, which has been considered to be part of the conventional visual cortex, plays a critical role in the haptic identification of common objects. The second is that distinct brain regions are involved in the haptic processing of two types of feature used for object identification: macro-geometric (e.g., shape) and material (e.g., roughness) properties. The third is that different brain regions are also involved in the visuo-haptic interaction of macro-geometric and material properties. Finally, I discuss some issues that remain to be addressed in future studies.

1. Introduction

In daily life, we frequently touch and manipulate objects such as keyboards, cups, and coins. When we put our hands inside a bag to find a wallet, it is relatively simple to identify, even in the absence of vision. Klatzky et al. (1985) demonstrated that humans can identify around 100 common inanimate objects in the absence of vision at well over 90% accuracy [1]. Moreover, most objects were identified within five seconds. This indicates that touch is an effective sensory channel for recognizing common three-dimensional (3D) objects. More recent studies have shown that humans are also capable of haptically recognizing animate objects, such as facial identity [2, 3], facial expressions of basic emotions [3-6], body part identity [7, 8] and body expressions [9, 10]. These findings indicate that haptic recognition allows humans to identify both animate and inanimate objects to such an extent that it could be used for interpersonal communication. This raises fundamental questions concerning the nervous systems that underlie the haptic recognition of common objects. Recent advances in neuroimaging techniques have led to an accumulation of evidence regarding these brain networks. In this chapter, I discuss the findings to date in relation to the three key hypotheses introduced above.

2. A distributed brain network underlies haptic object recognition

When we touch a familiar object (e.g., an orange), we initially discern properties such as its shape, roughness, softness, and temperature (in this case, the object might be spherical, smooth, slightly soft, and cold). We then use this information to identify the object. Thus, the brain network underlying haptic recognition realizes both the extraction of object properties and the identification of the object based on them (**Fig. 1B**).

Neuroscience textbooks often highlight the function of the somatosensory cortices in tactile processing [11]. These are the primary regions that receive haptic inputs from peripheral receptors. They consist of the postcentral gyrus (PostCG), which contains the primary somatosensory cortex (SI), and the parietal operculum (PO), which contains the secondary somatosensory cortex (SII) (**Fig. 1A left**). Electrophysiological studies on non-human primates indicate that neurons in the SI can encode several properties of stimuli such as roughness [12, 13], orientation [14, 15], and curvature [16]. These findings indicate that the SI is involved in the extraction of object properties. However, it is not only the somatosensory cortices that are involved in such processing. It is now widely accepted that a distributed network of brain regions beyond the conventional somatosensory cortices is involved in haptic object recognition [17-20] (**Fig 1A**). My review focuses mainly on the posterior parts of this brain network, which contain several important nodes for haptic object recognition (**Fig 1A left**).

(Insert Fig. 1 around here)

2.1. Involvement of the “visual cortex” in haptic object recognition

The occipital cortex was once thought to be involved exclusively in the processing of visual information. In the late 1990s, the primary visual cortex was found to be active during the tactile recognition of Braille by early blind individuals [21, 22]. This activation of the primary visual cortex in the early blind is now regarded as a consequence of plastic change of its functional organization due to early visual deprivation. However, subsequent studies showed that the occipital cortex in the sighted individuals was more active when paying attention to the orientation of gratings than to the spacing of gratings [23], and when haptically identifying objects relative to the judgment of perceived roughness [24]. These findings indicate that the occipital cortex, which was once considered as the “visual cortex”, is also involved in haptic object processing.

2.1.1. Vision and touch share category-sensitivity in the ventral visual pathway

The visual cortex is characterized by its unique functional organization. It consists of anatomically different structures and functionally distinct regions. For instance, neuroimaging studies have consistently shown that the occipito-temporal cortex (OTC), known as the high-order visual cortex, contains regions that are distinctively responsive to different categories of objects: face-sensitive regions, such as the occipital face area (OFA) and the fusiform face area (FFA) [25-27]; body-sensitive regions, such as the extrastriate body area (EBA) and the fusiform body area (FBA) [28, 29]; a scene-sensitive region known as the parahippocampal place area (PPA) [30]; and a word-sensitive region known as the visual word-form area (VWFA) [31]. These category-sensitive regions appear to play critical roles in the identification of objects within the corresponding groupings. Previous neuroimaging studies on sighted individuals have found that haptics and vision share the same category-sensitivity in some of these regions, such as the FFA [5, 7], EBA [7, 10, 32], PPA [33], and VWFA [34]. For instance, Kitada et al. (2009) showed that the FFA in the sighted individuals had a greater response to faces identified haptically than to other categories of objects (hands, feet, and bottles) [7]. These findings indicate that the category-sensitive regions in the OTC are critical nodes of the brain network underlying the haptic, as well as the visual, recognition of common objects **(Fig. 1C)**.

2.1.2. Development of functional organization in the OTC of early blind and sighted individuals

A common criticism of these findings is that the involvement of this region is not essential for haptic object recognition. For instance, this region might be activated due to visual imagery, which could help, but not be indispensable for, haptic object recognition. To what extent is this area critical for haptic object recognition? One approach to addressing this question is to investigate the effect of visual deprivation on the development of the functional organization of the OTC. If this region is essential for the haptic recognition of common objects, its unique functional organization should develop regardless of visual experience. Alternatively, if it is not essential for haptic object recognition, its functional organization might be subject to plastic change like the primary visual cortex [21].

Previous neuroimaging studies have investigated the brain activation during haptic object recognition in early-blind individuals, who cannot recall seeing familiar objects [6, 10, 33-35]. These studies have revealed that some category-sensitive regions, such as the VWFA, PPA, and part of the EBA, develop object sensitivity in both early-blind and sighted individuals. Although it is necessary to examine the effect of visual deprivation on other category-sensitive regions (e.g., the FFA), these findings support the view that the functional organization of the OTC develops even without visual experience. Thus, the OTC, which has been considered as the high-order visual cortex, might play an essential role in haptic object recognition.

2.2. Are object properties processed separately in the brain?

In order to identify the category of an object, we need to determine properties such as its shape, roughness, and softness (**Fig. 1C**). Recognizing additional properties can improve the accuracy of haptic object identification [2]. Thus, one possible mechanism underlying haptic object identification involves the OTC receiving information on the extracted object properties from other brain regions (**Fig. 1C**). Submodalities of visual information (e.g., motion, disparity, contrast, color, and orientation) are thought to be processed in a parallel-distributed manner in the brain [36]. Is the same principle applicable to touch?

Object properties can be broadly categorized as macro-geometric or material. Macro-geometric properties, such as shape and orientation, can be characterized by spatial coding that involves reference frames beyond somatotopic representation (e.g., allocentric reference frame) (spatial coding) [37]. By contrast, material properties indicate physical object information that is characterized by intensity data (intensity coding) [37]. So, are macro-geometric and material properties processed in a parallel-distributed manner in the brain?

2.2.1. Involvement of the posterior parietal cortex in processing macro-geometric properties

Previous neuroimaging studies have indicated that the the posterior parietal cortex (PPC) is critical for the haptic recognition of macro-geometric properties [38-42]. Roland et al. (1998) found that the PPC was more active during discrimination of the shape of ellipsoids than the roughness of cylinders [38]. This finding was supported by subsequent studies [39, 42].

However, the difference in activation between macro-geometric and material properties in these studies can be explained by confounding factors such as variations in the stimuli (e.g., ellipsoids vs. cylinders) and in the hand movements used to extract each object property (the exploratory procedures) [43]. In order to eliminate these potentially confounding factors, Kitada et al. (2006) conducted a functional magnetic resonance imaging (fMRI) study in which the subject's finger was passively stimulated by a surface of linear gratings [40]. Roughly speaking, these comprised a series of bars that were aligned in parallel on a plate (**Fig. 2**). The advantage of using linear gratings is that we can control the amount of stimulation between macro-geometric and material properties. More specifically, linear gratings can be used for orientation perception by changing the orientation of the bars, and can also be used for roughness perception by changing the distance between bars (i.e., the groove width). The authors found that the intraparietal sulcus, which is a part of the PPC, and the caudal part of the PostCG were more strongly activated by the condition of orientation than by the roughness classification. This result indicates that the intraparietal sulcus is involved in haptic orientation classification. The PPC might have a role in employing spatial reference frames to represent macro-geometric properties [44].

(Insert Fig. 2 around here)

In addition to the PPC, previous neuroimaging studies have also shown that the haptic perception of an object's shape activates a part of the OTC called the lateral occipital complex (LOC) [45-48]. More specifically, this region is functionally defined by showing a greater response to visually recognized shapes (relative to textures). In previous studies, the LOC was not activated during the haptic perception of object orientation [40, 41, 49] or the perception of object location [50]. Thus, it is possible that the contributions of the PPC and LOC to haptic object processing differ, with the former being involved in spatial coding and the latter in the processing of shape among the macro-geometric properties.

2.2.2. Involvement of the PO and insula in processing material properties

Is any brain region more involved in processing material properties than macro-geometric properties? Previous studies showed that, compared to the discrimination of the shape of objects, roughness discrimination of different types of object produced stronger activation in the PO [38, 42]. Kitada et al. (2005) revealed that the PO and insula showed activation that was inversely related to the magnitude estimate of roughness: the rougher the linear gratings felt, the smaller the activation in this region became [51]. Other than roughness perception, Craig et al. (2000) showed that the insula and possibly the PO showed activation dependent on thermal perception [52]. Servos et al. (2001) showed evidence that the haptic classification of hardness activated the PO as compared to motor control (i.e., gripping movement without an object) [53]. These studies indicate that the PO and insula play critical roles in the processing of material properties.

However, these findings do not provide conclusive evidence that the PO and insula are more important for processing material properties than macro-geometric properties. Again, the activation of the PO and insula in previous studies [38, 42] can be explained by confounding factors such as differences in stimuli and patterns of hand movements. In fMRI studies that controlled for these factors, the PO and insula showed relatively little difference between roughness and orientation classification [40, 41]. In electrophysiological studies in non-human primates, the PO contained neurons that are sensitive to macro-geometric properties such as object orientation [54]. Accordingly, future studies are needed to determine the relative contributions of the PO and the insula to the processing of material properties and macro-geometric properties.

Collectively, the previous findings of neuroimaging experiments provide partial support for the perspective that haptically-perceived object properties are processed in a distributed manner in the brain.

3. Brain networks involved in visuo-haptic interactions of object properties

In daily life, we frequently recognize common objects using both vision and touch. According to the two stages of object identification (i.e., the extraction of object properties and object identification), information that originates from touch and vision can interact both at the level of the processing of object properties and at the level of object identification (**Fig. 3A**). In this section, I review the brain network in which visuo-haptic object interaction occurs in relation to these two levels.

(Insert Fig. 3 around here)

3.1. Supramodal representation of common objects in the brain

In the previous section, I explained that the OTC is involved in visual and haptic object recognition. In other words, this region plays a critical role in supramodally representing common objects in the brain. However, it is not the sole region contributing to supramodal object representation. For instance, we can recognize others' facial and bodily expressions by touch [3, 4, 9, 10]. It is well known that the brain contains a distributed network called the "action observation network" (AON). This network involves not only the OTC, including the EBA [28], but also the inferior parietal lobule and the inferior frontal gyrus. Some of these regions are considered to constitute the human homologue of the mirror-neuron system, in which neurons discharge both when individuals perform a particular action and when they observe the same action of others [55]. The AON is activated during the visual recognition of others' body actions and facial expressions [56, 57]. However, a part of the AON is also activated by the haptic recognition of other's facial expressions [5] and hand gestures [10]. Moreover, the presence of such activity is independent of visual experience [6, 10]. These findings indicate that the AON is related to the recognition of others' actions supramodally.

A limitation of the previous findings on supramodal object representation should be noted. Previous studies have demonstrated a convergence of activation between touch and vision in the OTC and AON. If there is supramodal representation, there should be mechanisms that integrate haptic and visual information in these structures. Neuroimaging studies are needed to examine this integration process by investigating the interaction effects between visual and tactile information: supra-additive effects ([58, 59] but see [18]) and cross-modal repetitive suppression [60] or enhancement [61]. Moreover, it would be useful to employ a cross-modal multi-voxel pattern (MVPA) approach, in which the differences of activation patterns between recognized objects in one modality can explain those that are recognized by the other modality [35, 62]. Such an approach could provide support for the hypothesis that the visuo-haptic interaction of common objects occurs at the level of object identification in these regions.

3.2. Visuo-tactile interaction of macro-geometric properties

Touch and vision share spatial information regarding macro-geometric properties. By employing common frames of reference, spatial information can be directly compared between the two sensory modalities (**Fig. 3B left**). I have discussed the involvement of the PPC in the haptic processing of macro-geometric properties and of the LO in the haptic processing of shape in Section 2.2.1. Previous neuroimaging studies have shown that these regions are activated by the visual recognition of macro-geometric properties, and show evidence of interactions between vision and touch [40, 63-66]. For instance, Kitada et al. (2006) showed that the intraparietal sulcus is activated by both tactile and visual classification of object orientation [40]. Saito et al. (2003) compared brain activity during the visuo-tactile comparison of two-dimensional (2D) spatial patterns (Mahjong tiles) with that during the uni-sensory (i.e., either visual or tactile) comparison of the same stimuli. They found that a posterior part of the IPS showed greater activation in a cross-sensory condition than in uni-sensory conditions [65].

In the LOC, the haptic and visual perception of object shapes relative to textures showed overlapping activation [45-47]. Moreover, other studies showed evidence of the visuo-haptic interaction of shape in this region [46, 48, 66]. For instance, viewing visually and haptically primed objects produced more activation than viewing non-primed objects in this region [46]. These findings indicate that both the LO and the IPS play a critical role in the visuo-haptic integration of object shape.

An additional region that has been implicated in the visuo-tactile interaction of object shape is the claustrum/insula [67, 68]. However, it is unclear whether this region is involved in the visuo-tactile interaction of macro-geometric properties rather than material properties or is involved with all object properties.

3.3. Visuo-tactile interaction of material properties

Unlike macro-geometric properties, relatively little is known about the brain network involved in the visuo-tactile interaction of material properties. There is limited information on material properties that can be directly integrated between touch and vision. More specifically, the physical properties of the object material itself (e.g., roughness, softness, and temperature) are perceived by touch, whereas the properties of surface reflectance (e.g., color and gloss) are accessible only by vision. As the physical object information that is extracted by vision and touch differs substantially, it has been argued that they might contribute to the perception of material properties in an independent, rather than an integrated, manner [69]. How then can different types of physical information (from touch and vision) be compared in the brain?

One possible heuristic is to compare the physical object information extracted by touch and vision in the same “format”, after translating it from one sensory modality to the corresponding other. This comparison might be implemented by interactions between visual and tactile physical object information in the brain. For instance, we can retrieve tactile information that was previously associated with the visual appearance of an object (e.g., the high thermal conductivity of gold) and compare it with incoming tactile information (e.g., the low thermal conductivity of plastic). In order for this heuristic to be implemented, previously learned physical associations between vision and touch must be retrieved [70], otherwise there is no link for this translation between the two modalities. Accordingly, comparing visuo-tactile information about material properties involves neural mechanisms that can retrieve and then utilize previously learned vision-touch associations.

Several neuroimaging studies have reported that parts of the occipital cortex are active during the tactile, as well as visual, perception of material properties [42, 50, 71]. Thus, like the category-sensitive regions, these visual regions might be involved in the interaction of visual and tactile material information. However, if the retrieval of information that is shared between touch and vision is critical, additional cortical regions, such as memory-related areas, should be involved. Previous studies have identified the neural substrates underlying the retrieval of stimulus pairs during paired-association tasks such as the medial temporal lobe [72-76], lateral prefrontal cortex [72, 74, 77, 78], and precuneus [72, 74, 79, 80].

Given this background, Kitada et al. (2014) investigated whether these regions are involved in the visuo-tactile comparison of material properties rather than macro-geometric properties [41]. The stimuli consisted of surfaces on which an oriented plastic bar was placed on a background texture (**Fig. 4**). The subjects determined whether the orientations of visually- and tactually-presented bar stimuli were congruent in the orientation conditions, and whether the visually- and tactually-presented background textures were congruent in the texture conditions. The texture conditions revealed greater activation of not only the occipital cortex, but also the medial temporal lobe and lateral prefrontal cortex compared with the orientation conditions. In the texture conditions, the precuneus showed a greater response to incongruent stimuli than to congruent stimuli. This incongruency effect was greater for the texture conditions than for the orientation conditions. These results suggest that the precuneus is involved in detecting incongruency between tactile and visual texture information in concert with the medial temporal lobe, which is tightly linked with long-term memory.

(Insert Fig. 4 around here)

A limitation of this finding is that it is unclear to what extent it can be generalized to the dissociation of the neural substrates involved in the visuo-tactile interaction of macro-geometric and material properties. For instance, the visuo-tactile comparison of familiar shape might involve not only common spatial frames of reference, but also cross-modal association [81]. Thus, it remains critical to examine the dissociation by employing different types of material and macro-geometric stimuli.

4. Future questions

Three key points should be addressed in future studies. First, I have discussed the contributions of several nodes of the brain to haptic object identification. However, it is clear that other brain regions (e.g., frontal cortex) are involved in haptic object processing and its interaction with vision (**Fig. 1 right**). It is necessary to clarify the contribution of these brain regions such that the process can be modelled. Second, I have explained the relative contributions of the brain regions to haptic object recognition (functional specialization). A critical next step is to consider how these brain regions interact with each other to achieve haptic object recognition (functional integration).

Third and finally, when we touch objects, we not only identify them (discriminative touch), but also experience associated affective sensations such as pleasantness and unpleasantness (affective touch). A fundamental question in tactile research is how affective touch and discriminative touch are related. Their relationship has been psychophysically investigated for material properties such as roughness [82-85] and temperature [86-89]. These studies showed that the perceived magnitudes between discriminative and affective touch were different in thermal perception, but not in roughness perception. For instance, Kitada et al. (2012) conducted a psychophysical experiment wherein the participants estimated the magnitude of roughness and unpleasantness when surfaces consisting of 2D raised-dot patterns moved on the subjects' skin. The patterns of perceived estimates of roughness and unpleasantness as a function of inter-element spacing were highly similar when the speed of movement was held constant (Pearson's $r > 0.98$) [84]. Previous studies have shown that regions in and around the limbic system are related to affective touch, including the insula [90-92], the orbitofrontal cortex [93, 94] and the ventral striatum [94]. Thus, the insula, which is related to the processing of roughness perception [51], could also be related to the processing of unpleasantness and pleasantness. Further studies are necessary to investigate the nature of affective touch and how it is related to discriminative touch.

5. Conclusion

A wide cortical network underlies haptic object recognition. In this chapter, I have discussed its underlying functional organization. Under the current working hypothesis, haptic object processing and its interaction with vision might be conducted differently for macro-geometric and material properties. These separately processed properties are combined in supramodal regions such as the occipito-temporal cortex. A fundamental question that remains to be addressed is how haptic object processing is related to the affective processing of touch in the brain. Answering this question might also provide clues as to how contact from others (e.g., child–parent interactions) influences and maintains homeostasis in the mind.

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7. References

[1] Klatzky RL, Lederman SJ, Metzger VA (1985) Identifying objects by touch: an "expert system". Percept Psychophys 37:299–302.

[2] Kilgour AR, Lederman SJ (2002) Face recognition by hand. Percept Psychophys 64:339–352.

[3] Lederman SJ, Kilgour A, Kitada R, Klatzky RL, Hamilton C (2007) Haptic face processing. Can J Exp Psychol 61:230–241.

[4] Lederman SJ, Klatzky RL, Abramowicz A, Salsman K, Kitada R, Hamilton C (2007) Haptic recognition of static and dynamic expressions of emotion in the live face. Psychol Sci 18:158-164.

[5] Kitada R, Johnsrude IS, Kochiyama T, Lederman SJ (2010) Brain networks involved in haptic and visual identification of facial expressions of emotion: an fMRI study. Neuroimage 49:1677–1689.

[6] Kitada R, Okamoto Y, Sasaki AT, Kochiyama T, Miyahara M, Lederman SJ, Sadato N (2013) Early visual experience and the recognition of basic facial expressions: involvement of the middle temporal and inferior frontal gyri during haptic identification by the early blind. Front Hum Neurosci 7:7.

[7] Kitada R, Johnsrude IS, Kochiyama T, Lederman SJ (2009) Functional specialization and convergence in the occipito-temporal cortex supporting haptic and visual identification of human faces and body parts: an fMRI study. J Cogn Neurosci 21:2027–2045.

[8] Kitada R, Dijkerman HC, Soo G, Lederman SJ (2010) Representing human hands haptically or visually from first-person versus third-person perspectives. Perception 39:236–254.

[9] Hertenstein MJ, Keltner D, App B, Bulleit BA, Jaskolka AR (2006) Touch communicates distinct emotions. Emotion 6:528–533.

[10] Kitada R, Yoshihara K, Sasaki AT, Hashiguchi M, Kochiyama T, Sadato N (2014) The brain network underlying the recognition of hand gestures in the blind: the supramodal role of the extrastriate body area. J Neurosci 34:10096–10108.

[11] Gardner EP, Johnson KO (2012) 23. Touch. In: Kandel ER, Schwartz JH, Jessell TM, Siegelbaum SA, Hudspeth AJ (eds) Principles of Neural Science. 5th edn. McGraw-Hill, New York, p 498–529.

[12] Sinclair RJ, Burton H (1991) Neuronal activity in the primary somatosensory cortex in monkeys (*Macaca mulatta*) during active touch of textured surface gratings: responses to groove width, applied force, and velocity of motion. J Neurophysiol 66:153–169.

[13] Chapman CE, Tremblay F, Jiang W, Belingard L, Meftah el M (2002) Central neural mechanisms contributing to the perception of tactile roughness. Behav Brain Res 135:225–233.

[14] Warren S, Hamalainen HA, Gardner EP (1986) Objective classification of motion- and direction-sensitive neurons in primary somatosensory cortex of awake monkeys. J Neurophysiol 56:598–622.

[15] Pei YC, Bensmaia SJ (2014) The neural basis of tactile motion perception. J Neurophysiol 112:3023–3032.

[16] Yau JM, Connor CE, Hsiao SS (2013) Representation of tactile curvature in macaque somatosensory area 2. J Neurophysiol 109:2999–3012.

[17] Amedi A, von Kriegstein K, van Atteveldt NM, Beauchamp MS, Naumer MJ (2005) Functional imaging of human crossmodal identification and object recognition. Exp Brain Res 166:559–571.

[18] Beauchamp MS (2005) See me, hear me, touch me: multisensory integration in lateral occipital-temporal cortex. Curr Opin Neurobiol 15:145–153.

[19] James TW, Kim S, Fisher JS (2007) The neural basis of haptic object processing. Can J Exp Psychol 61:219–229.

[20] Lacey S, Sathian K (2014) Visuo-haptic multisensory object recognition, categorization, and representation. Front Psychol 5:730.

[21] Sadato N, Pascual-Leone A, Grafman J, Ibanez V, Deiber MP, Dold G, Hallett M (1996) Activation of the primary visual cortex by Braille reading in blind subjects. Nature 380:526–528.

[22] Cohen LG, Celnik P, Pascual-Leone A, Corwell B, Falz L, Dambrosia J, Honda M, Sadato N, Gerloff C, Catala MD, Hallett M (1997) Functional relevance of cross-modal plasticity in blind humans. Nature 389:180–183.

[23] Sathian K, Zangaladze A, Hoffman JM, Grafton ST (1997) Feeling with the mind's

eye. Neuroreport 8:3877–3881.

[24] Deibert E, Kraut M, Kremen S, Hart J, Jr. (1999) Neural pathways in tactile object recognition. Neurology 52:1413–1417.

[25] Puce A, Allison T, Asgari M, Gore JC, McCarthy G (1996) Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J Neurosci 16:5205–5215.

[26] Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311.

[27] Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW (2000) The fusiform “face area” is part of a network that processes faces at the individual level. J Cogn Neurosci 12:495–504.

[28] Downing PE, Jiang Y, Shuman M, Kanwisher N (2001) A cortical area selective for visual processing of the human body. Science 293:2470–2473.

[29] Peelen MV, Downing PE (2005) Selectivity for the human body in the fusiform gyrus. J Neurophysiol 93:603–608.

[30] Epstein R, Kanwisher N (1998) A cortical representation of the local visual environment. Nature 392:598–601.

[31] Cohen L, Dehaene S, Naccache L, Lehericy S, Dehaene-Lambertz G, Henaff MA, Michel F (2000) The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123:291–307.

[32] Costantini M, Urgesi C, Galati G, Romani GL, Aglioti SM (2011) Haptic perception and body representation in lateral and medial occipito-temporal cortices. Neuropsychologia 49:821–829.

[33] Wolbers T, Klatzky RL, Loomis JM, Wutte MG, Giudice NA (2011) Modality-independent coding of spatial layout in the human brain. Curr Biol 21:984–989.

[34] Reich L, Szwed M, Cohen L, Amedi A (2011) A ventral visual stream reading center independent of visual experience. Curr Biol 21:363–368.

[35] Pietrini P, Furey ML, Ricciardi E, Gobbini MI, Wu WH, Cohen L, Guazzelli M, Haxby JV (2004) Beyond sensory images: Object-based representation in the human ventral pathway. Proc Natl Acad Sci USA 101:5658–5663.

[36] Gilbert CD (2012). 25. The constructive Nature of Visual Processing. In: Kandel ER, Schwartz JH, Jessell TM, Siegelbaum SA, Hudspeth AJ (eds) Principles of Neural Science. 5th edn. McGraw-Hill, New York, p 556–576.

[37] Lederman SJ, Klatzky RL (1997) Relative availability of surface and object

properties during early haptic processing. J Exp Psychol Hum Percept Perform 23:1680–1707.

[38] Roland PE, O’Sullivan B, Kawashima R (1998) Shape and roughness activate different somatosensory areas in the human brain. Proc Natl Acad Sci USA 95:3295–3300.

[39] Bodegård A, Geyer S, Grefkes C, Zilles K, Roland PE (2001) Hierarchical processing of tactile shape in the human brain. Neuron 31:317–328.

[40] Kitada R, Kito T, Saito DN, Kochiyama T, Matsumura M, Sadato N, Lederman SJ (2006) Multisensory activation of the intraparietal area when classifying grating orientation: a functional magnetic resonance imaging study. J Neurosci 26:7491–7501.

[41] Kitada R, Sasaki AT, Okamoto Y, Kochiyama T, Sadato N (2014) Role of the precuneus in the detection of incongruency between tactile and visual texture information: A functional MRI study. Neuropsychologia 64C:252–262.

[42] Stilla R, Sathian K (2008) Selective visuo-haptic processing of shape and texture. Hum Brain Mapp 29:1123–1138.

[43] Lederman SJ, Klatzky RL (1987) Hand movements: a window into haptic object recognition. Cogn Psychol 19:342-368.

[44] Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annu Rev Neurosci 20:303–330.

[45] Amedi A, Malach R, Hendler T, Peled S, Zohary E (2001) Visuo-haptic object-related activation in the ventral visual pathway. Nat Neurosci 4:324–330.

[46] James TW, Humphrey GK, Gati JS, Servos P, Menon RS, Goodale MA (2002) Haptic study of three-dimensional objects activates extrastriate visual areas. Neuropsychologia 40:1706–1714.

[47] Peltier S, Stilla R, Mariola E, LaConte S, Hu X, Sathian K (2007) Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. Neuropsychologia 45:476–483.

[48] Kim S, James TW (2010) Enhanced effectiveness in visuo-haptic object-selective brain regions with increasing stimulus salience. Hum Brain Mapp 31:678–693.

[49] Zhang M, Mariola E, Stilla R, Stoesz M, Mao H, Hu X, Sathian K (2005) Tactile discrimination of grating orientation: fMRI activation patterns. Hum Brain Mapp 25:370–377.

[50] Sathian K, Lacey S, Stilla R, Gibson GO, Deshpande G, Hu X, Laconte S, Glielmi C (2011) Dual pathways for haptic and visual perception of spatial and texture

information. Neuroimage 57:462–475.

[51] Kitada R, Hashimoto T, Kochiyama T, Kito T, Okada T, Matsumura M, Lederman SJ, Sadato N (2005) Tactile estimation of the roughness of gratings yields a graded response in the human brain: an fMRI study. Neuroimage 25:90-100.

[52] Craig AD, Chen K, Bandy D, Reiman EM (2000) Thermosensory activation of insular cortex. Nat Neurosci 3:184–190.

[53] Servos P, Lederman S, Wilson D, Gati J (2001) fMRI-derived cortical maps for haptic shape, texture, and hardness. Brain Res Cogn Brain Res 12:307–313.

[54] Fitzgerald PJ, Lane JW, Thakur PH, Hsiao SS (2006) Receptive field properties of the macaque second somatosensory cortex: representation of orientation on different finger pads. J Neurosci 26:6473-6484.

[55] Rizzolatti G, Craighero L (2004) The mirror-neuron system. Annu Rev Neurosci 27:169–192.

[56] Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999) Cortical mechanisms of human imitation. Science 286:2526–2528.

[57] Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL (2003) Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. Proc Natl Acad Sci USA 100:5497–5502.

[58] Calvert GA, Campbell R, Brammer MJ (2000) Evidence from functional magnetic resonance imaging of crossmodal binding in the human heteromodal cortex. Curr Biol 10:649–657.

[59] Raij T, Uutela K, Hari R (2000) Audiovisual integration of letters in the human brain. Neuron 28:617–625.

[60] Grill-Spector K, Malach R (2001) fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol (Amst) 107:293–321.

[61] Segaert K, Weber K, de Lange FP, Petersson KM, Hagoort P (2013) The suppression of repetition enhancement: a review of fMRI studies. Neuropsychologia 51:59–66.

[62] Oosterhof NN, Tipper SP, Downing PE (2013) Crossmodal and action-specific: neuroimaging the human mirror neuron system. Trends Cogn Sci 17:311–318.

[63] Grefkes C, Weiss PH, Zilles K, Fink GR (2002) Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. Neuron 35:173–184.

[64] Nakashita S, Saito DN, Kochiyama T, Honda M, Tanabe HC, Sadato N (2008) Tactile-visual integration in the posterior parietal cortex: a functional magnetic

resonance imaging study. Brain Res Bull 75:513–525.

[65] Saito DN, Okada T, Morita Y, Yonekura Y, Sadato N (2003) Tactile-visual cross-modal shape matching: a functional MRI study. Brain Res Cogn Brain Res 17:14–25.

[66] Tal N, Amedi A (2009) Multisensory visual-tactile object related network in humans: insights gained using a novel crossmodal adaptation approach. Exp Brain Res 198:165–182.

[67] Hadjikhani N, Roland PE (1998) Cross-modal transfer of information between the tactile and the visual representations in the human brain: A positron emission tomographic study. J Neurosci 18:1072–1084.

[68] Kassuba T, Klinge C, Holig C, Roder B, Siebner HR (2013) Vision holds a greater share in visuo-haptic object recognition than touch. Neuroimage 65:59–68.

[69] Whitaker TA, Simoes-Franklin C, Newell FN (2008) Vision and touch: independent or integrated systems for the perception of texture? Brain Res 1242:59–72.

[70] Fleming RW (2014) Visual perception of materials and their properties. Vision Res 94:62–75.

[71] Eck J, Kaas AL, Goebel R (2013) Crossmodal interactions of haptic and visual texture information in early sensory cortex. Neuroimage 75:123–135.

[72] Gonzalo D, Shallice T, Dolan R (2000) Time-dependent changes in learning audiovisual associations: a single-trial fMRI study. Neuroimage 11:243–255.

[73] Naya Y, Yoshida M, Miyashita Y (2001) Backward spreading of memory-retrieval signal in the primate temporal cortex. Science 291:661–664.

[74] Ranganath C, Cohen MX, Dam C, D’Esposito M (2004) Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. J Neurosci 24:3917–3925.

[75] Tanabe HC, Honda M, Sadato N (2005) Functionally segregated neural substrates for arbitrary audiovisual paired-association learning. J Neurosci 25:6409–6418.

[76] Weniger G, Boucsein K, Irle E (2004) Impaired associative memory in temporal lobe epilepsy subjects after lesions of hippocampus, parahippocampal gyrus, and amygdala. Hippocampus 14:785–796.

[77] Fuster JM, Bodner M, Kroger JK (2000) Cross-modal and cross-temporal association in neurons of frontal cortex. Nature 405:347–351.

[78] Hasegawa I, Fukushima T, Ihara T, Miyashita Y (1998) Callosal window between prefrontal cortices: cognitive interaction to retrieve long-term memory. Science 281:814–818.

[79] Krause BJ, Schmidt D, Mottaghy FM, Taylor J, Halsband U, Herzog H, Tellmann L, Muller-Gartner HW (1999) Episodic retrieval activates the precuneus irrespective of the imagery content of word pair associates. A PET study. Brain 122:255–263.

[80] Tanabe HC, Sadato N (2009) Ventrolateral prefrontal cortex activity associated with individual differences in arbitrary delayed paired-association learning performance: a functional magnetic resonance imaging study. Neuroscience 160:688–697.

[81] Holdstock JS, Hocking J, Notley P, Devlin JT, Price CJ (2009) Integrating visual and tactile information in the perirhinal cortex. Cereb Cortex 19:2993–3000.

[82] Ekman G, Hosman J, Lindstroem B (1965) Roughness, Smoothness, and Preference: A Study of Quantitative Relations in Individual Subjects. J Exp Psychol 70:18–26.

[83] Verrillo RT, Bolanowski SJ, McGlone FP (1999) Subjective magnitude of tactile roughness. Somatosens Mot Res 16:352–360.

[84] Kitada R, Sadato N, Lederman SJ (2012) Tactile perception of nonpainful unpleasantness in relation to perceived roughness: effects of inter-element spacing and speed of relative motion of rigid 2-D raised-dot patterns at two body loci. Perception 41:204–220.

[85] Klocker A, Oddo CM, Camboni D, Penta M, Thonnard JL (2014) Physical factors influencing pleasant touch during passive fingertip stimulation. PLoS One 9:e101361.

[86] Chatonnet J, Cabanac M (1965) The perception of thermal comfort. Int J Biometeorol 9:183–193.

[87] Mower GD (1976) Perceived intensity of peripheral thermal stimuli is independent of internal body temperature. J Comp Physiol Psychol 90:1152–1155.

[88] Attia M, Engel P (1982) Thermal pleasantness sensation: an indicator of thermal stress. Eur J Appl Physiol 50:55–70.

[89] Nakamura M, Yoda T, Crawshaw LI, Yasuhara S, Saito Y, Kasuga M, Nagashima K, Kanosue K (2008) Regional differences in temperature sensation and thermal comfort in humans. J Appl Physiol 105:1897-1906.

[90] Craig AD (2002) How do you feel? Interoception: the sense of the physiological condition of the body. Nat Rev Neurosci 3:655–666.

[91] Olausson H, Lamarre Y, Backlund H, Morin C, Wallin BG, Starck G, Ekholm S, Strigo I, Worsley K, Vallbo AB, Bushnell MC (2002) Unmyelinated tactile afferents signal touch and project to insular cortex. Nat Neurosci 5:900–904.

[92] McGlone F, Wessberg J, Olausson H (2014) Discriminative and affective touch: sensing and feeling. Neuron 82:737-755.

[93] Rolls ET, O’Doherty J, Kringelbach ML, Francis S, Bowtell R, McGlone F (2003) Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. Cereb Cortex 13:308–317.

[94] Rolls ET, Grabenhorst F, Parris BA (2008) Warm pleasant feelings in the brain. Neuroimage 41:1504–1513.

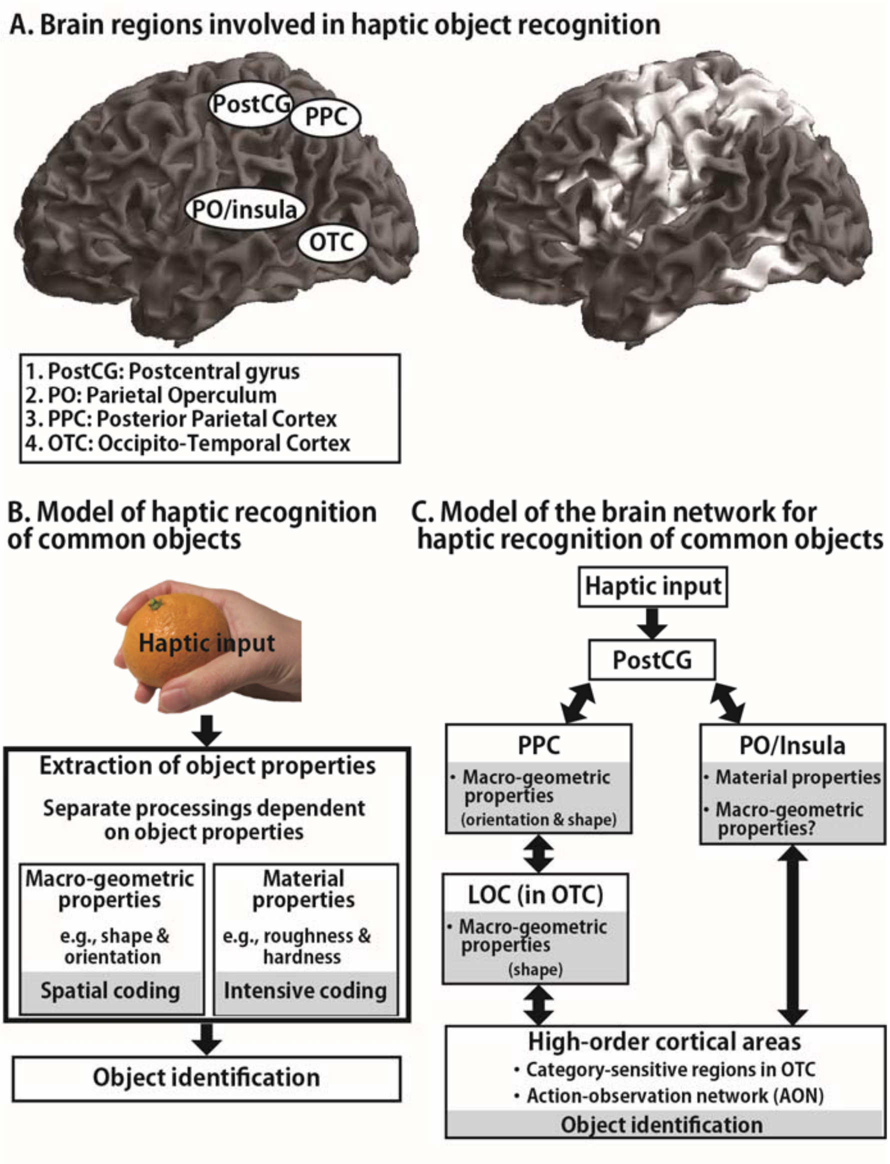

Figure 1. Model of the brain network for haptic recognition of common objects.

a. Brain regions involved in haptic object recognition.

Left, The regions used in the proposed model. PostCG, postcentral gyrus containing the primary somatosensory cortex (SI); PO/Insula, parietal operculum including the secondary somatosensory cortex (SII) and adjacent insula; PPC, posterior parietal cortex including the intraparietal sulcus (IPS); OTC, occipito-temporal cortex**.**

Right, Brain regions that are active during haptic object recognition with the right hand (relative to rest condition) (Kitada et al. unpublished data; Z > 2.58 corrected for multiple comparisons at cluster level). Only the left side of the brain is shown.

b. Model of haptic recognition of common objects.

c. Model of the brain network for haptic recognition of common objects.

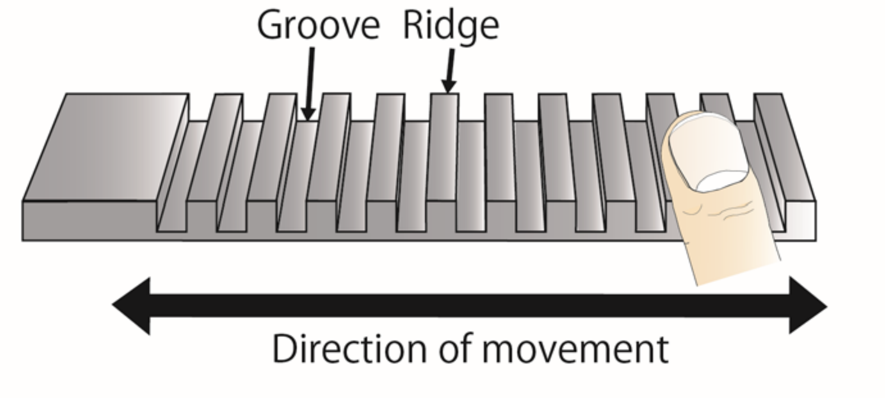

Figure 2. Linear gratings

These comprise a series of ridges and grooves. Changing the groove width changes the perceived magnitude of roughness, whereas changing the orientation of ridges and grooves changes the orientation perception. Different brain activation patterns between macro-geometric and material properties can be tested by controlling factors such as hand movement and stimuli.

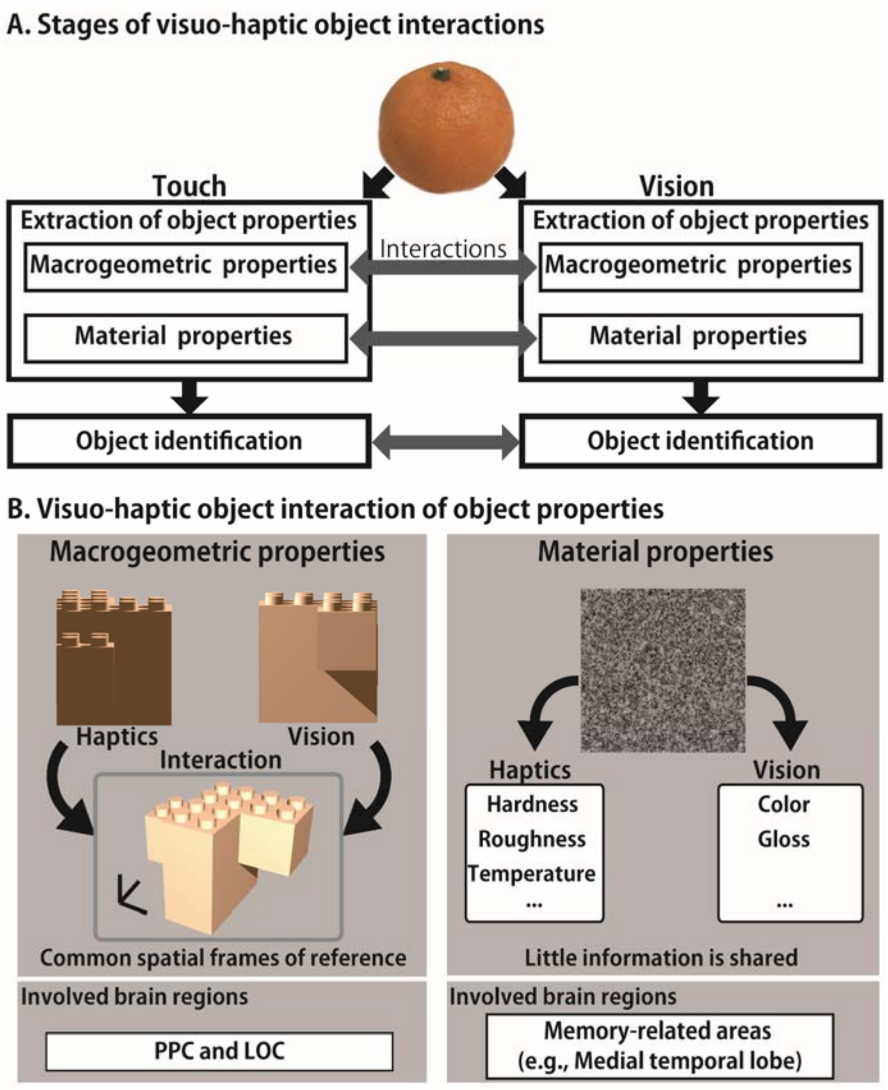

Figure 3. Model for visuo-haptic interactions

a. We frequently recognize objects using both vision and touch. Information originating from the two sensory modalities can interact at the level of extraction of object properties and at the level of object identification.

b. Difference in visuo-tactile interactions between macro-geometric and material properties. By employing common frames of reference, spatial information between the two sensory modalities can be directly compared. Previous studies suggest that the posterior parietal cortex (PPC) and lateral occipital complex (LOC) are involved in the visuo-haptic interaction of macro-geometric properties. By contrast, little information on material properties can be directly integrated between touch and vision. One possible heuristic is to compare physical object information extracted by touch and vision in the same “format”, after translating it from one sensory modality to the corresponding other. As previously learned physical associations between vision and touch are necessary for this translation, we can hypothesize that memory-related regions (such as the medial temporal lobe) are involved in visuo-haptic interactions of material properties.

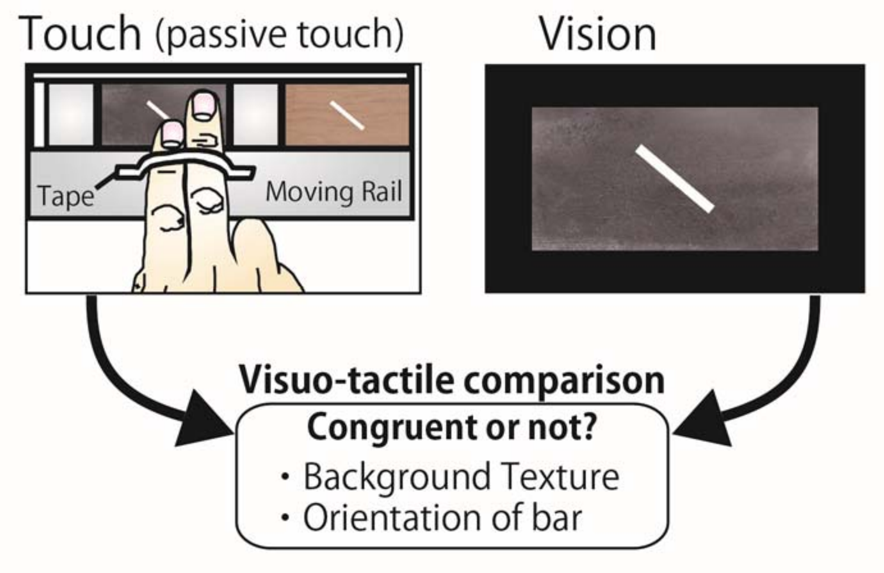

Figure 4. Task design of the visuo-tactile comparisons in Kitada et al. (2014) [41]
The stimuli consisted of surfaces on which an oriented plastic bar was placed on a background texture. The subject determined whether the orientations of visually- and tactually-presented bar stimuli were congruent in the orientation conditions, and whether visually- and tactually-presented background textures were congruent in the texture conditions. Brain activity in the texture conditions was compared with that in the orientation conditions.