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The Neural Basis of Haptic Object Processing

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Abstract We review the organization of the neural networks that underlie haptic object processing and compare that organization with the visual system. Haptic object processing is separated into at least two neural pathways, one for geometric properties or shape, and one for material properties, including texture. Like vision, haptic processing pathways are organized into a hierarchy of processing stages, with different stages represented by different brain areas. In addition, the haptic pathway for shape processing may be further subdivided into different streams for action and perception. These streams may be analogous to the action and perception streams of the visual system and represent two points of neural convergence for vision and haptics.

Résumé We review the organization of the neural networks that underlie haptic object processing and compare that organization with the visual system. Haptic object processing is separated into at least two neural pathways, one for geometric properties or shape, and one for material properties, including texture. Like vision, haptic processing pathways are organized into a hierarchy of processing stages, with different stages represented by different brain areas. In addition, the haptic pathway for shape processing may be further subdivided into different streams for action and perception. These streams may be analogous to the action and perception streams of the visual system and represent two points of neural convergence for vision and haptics.

Object recognition is a fundamental cognitive operation performed countless times each day. Yet despite decades of research into the mechanisms of human object recognition, we have only the barest idea of how this complex problem is solved so efficiently by the brain. Routine object recognition seems effortless and automatic to us, yet attempts to create artificial systems that recognize objects in the way that humans do have had little practical success. One suggestion for the slow progress of artificial recognition systems is the reliance of those systems on purely visual input, even though objects in our environment are a source of incredibly rich *multisensory* stimulation. For instance, a glass containing a soft drink can produce sensations of taste and smell, but you can also see the glass, watch the bubbles move, reach out and feel the bubbles burst against your skin and even hear them fizz.

It is not a stretch to suggest that objects such as the soft drink are the rule, as opposed to the exception, in our world. It seems equally likely that when we are attempting to ascertain the identity of an object in our environment, we use all the information available, regardless of the sensory modality. However, despite the multisensory nature of real-world object recognition, until recently object recognition was almost exclusively studied using unisensory stimuli. Furthermore, the majority of those unisensory experiments used *visual* stimuli. Recently, though, there has been a surge of interest in multisensory phenomena, including multisensory object recognition (Calvert, Spence, & Stein, 2004). Because relatively less is known about how object recognition occurs using sensory inputs besides vision, the increased interest in multisensory recognition has led to increased interest in nonvisual unisensory object recognition.

Of the various candidate sensory systems besides vision by which objects can be recognized, perhaps the most actively studied has been touch. Here, we will distinguish between passive touch and haptics, which we define as active use of the hands to retrieve the attributes of an object stimulus, using both cutaneous and kinesthetic inputs. Haptic object recognition has been studied behaviourally and in patients with brain damage for many decades. It has been studied using neurophysiologic and neuroimaging techniques since their inception. The intent of this chapter is to present an overview of the neural mechanisms of haptic object recognition. We will focus particularly on mechanisms involving the object attributes of shape and surface texture.

Neural Mechanisms of Shape Recognition

One self-imposed limitation on the breadth of object recognition research has been an emphasis on analyzing the geometric characteristics of objects (e.g., size or shape). Like the preferential study of vision over

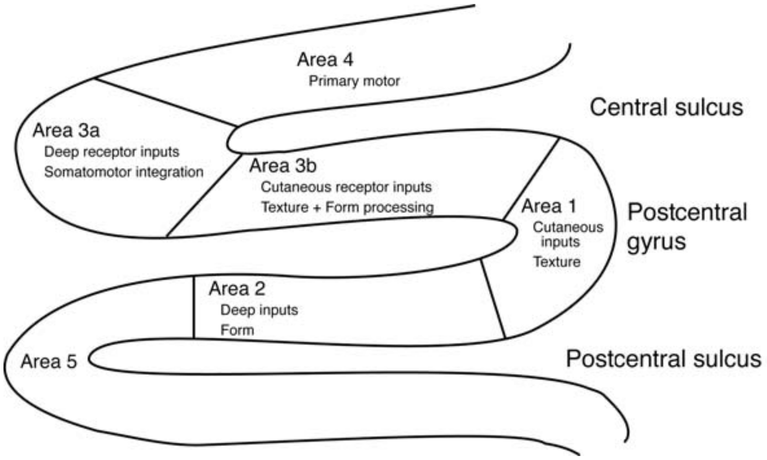

Figure 1. Cytoarchitectonic divisions of the human postcentral gyrus. Numbers indicate the corresponding Brodmann's areas. Areas 3a, 3b, 1, and 2 constitute primary somatosensory cortex (SI). Approximate placement of the divisions was taken from Grefkes, Geyer, Schormann, Roland, and Zilles, 2001. Functional properties of the different areas were derived from our review of studies with nonhuman primates.

other sensory systems, there are some potentially acceptable reasons for the bias toward the study of shape over other object characteristics. First, shape information by itself is sufficient for highly efficient object recognition (Biederman, 1987); it does not need to be combined with other object characteristics. Second, one of the strongest indicators of category membership for an object is the configuration of its parts or features, that is, its geometric or spatial properties (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). As it turns out, vision is better suited to retrieving an object's shape than any other sensory system; this perhaps explains the predominance of visual shape studies in the object recognition literature. But, haptics can also extract useful shape information from objects and use it for the purposes of recognition (Klatzky, Lederman, & Reed, 1987), particularly for recognition at the basic level of categorization (Lederman & Klatzky, 1990).

Differences in the ability of the visual and haptic systems to extract shape information from an object begin at the level of the receptors, especially the way that the two systems are able to move the receptor surfaces. The receptor surfaces of both the visual and haptic systems have regions of low and high acuity. For vision, the high-acuity region is the fovea; for haptics, the high-acuity regions are the fingertips. When an object is explored, either visually or haptically, it is usually these high-acuity regions that are brought to bear on an object. The movements involved in haptic object recognition are relatively stereotypical and are different depending on whether the intent is to categorize based on geometric or material properties (e.g., roughness, hardness, temperature, etc.). One particularly interesting characteristic of these movements is that movements used to determine an object's geometric properties tend to require significant time and to be executed in a sequential manner. On the other hand, exploratory movements used to determine an object's material properties tend to be brief, single movements (Lederman & Klatzky, 1987, 1993).

Difficult visual recognition tasks may also require an exploration strategy, but because a saccadic eye movement can be planned and executed in under 200 ms, whereas moving the fingers to a new location of an object takes much longer, vision has a decided speed advantage over haptics for sequential sampling of a stimulus. The visual system also has another advantage when it comes to quickly accessing the *geometric* properties of an object: The visual system is capable of carrying out a coarse-grained analysis using the peripheral retina simultaneously with the fine-grained analysis carried out with the fovea. In contrast, except for extremely small objects, it is difficult for the haptic system to carry out a coarse-grained analysis using the palms simultaneously with a fine-grained analysis with the fingers. In general, the spatial extent of an object that can be processed simultaneously by vision is greater than that by haptics (Loomis, 1981), which will often obviate the need for time-consuming sequential processing altogether.

Thus, for recognition of objects by their shape, haptic exploration can require considerable time, especially when compared with vision. The longer it takes

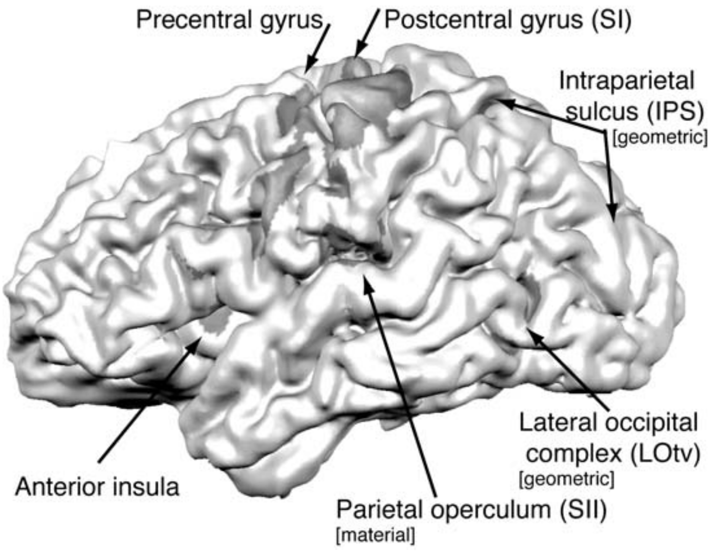

Figure 2. Brain areas involved in haptic object exploration. A rendering of the grey matter surface of a left cerebral hemisphere. Superimposed red/yellow is a statistical parametric map derived by contrasting haptic exploration of real objects with rest in one representative subject. Functional properties, shown in square brackets, were derived from our review of the human neuroimaging literature.

to gather the necessary sensory information to create a whole percept, the more demand is placed on other cognitive resources such as spatial and temporal integration, working memory, and attention. When presentation time is limited, these demands may become too high and recognition may fail. However, with enough time for thorough exploration, haptic inputs contain enough information to construct robust three-dimensional object representations, representations that are quite similar to those used by vision and that may even share similar neural substrates (James, James, Humphrey, & Goodale, 2005). One focus of this review will be to compare the primate visual and somatosensory cortical systems and examine their organization for similarities and differences.

For several decades, evidence has accumulated that the primate visual system is organized hierarchically, that is, information that comes from the eye is processed in a series of stages. Information is passed from lower stages to higher stages of processing and sometimes is also fed backward. Functional and anatomical evidence suggests that the hierarchical stages are often represented by architecturally distinct cortical areas and that connections between these areas represent the flow of information through the hierarchy (for reviews, see Felleman & Van Essen, 1991; Lennie, 1998; Orban, Van Essen, & Vanduffel, 2004; Tootell, Tsao, & Vanduffel, 2003).

Although the volume of evidence for a somatosensory hierarchy is smaller than that for vision, it is compelling. The primate anterior parietal lobe has architecturally distinct areas along the postcentral gyrus that are also functionally distinct (Figure 1). Areas 1, 2, 3a, and 3b form primary somatosensory cortex (SI), which is found on the postcentral gyrus in humans and macaques. Information from the periphery enters SI via thalamocortical connections at Areas 3a, 3b, 1, and 2 (DiCarlo, Johnson, & Hsiao, 1998; Hsiao, Johnson, & Twombly, 1993; Huffman & Krubitzer, 2001; Krubitzer, Huffman, Disbrow, & Recanzone, 2004). Neurons in Areas 1 and 2, however, also receive input from neurons in Areas 3a and 3b (Hyvärinen & Poranen, 1978; Iwamura & Tanaka, 1978), suggesting that although Areas 1 and 2 receive input from the periphery, they may actually represent a higher stage of processing than Areas 3a and 3b. Areas 1 and 2 may process information at the same stage of the hierarchy as each other, or may process information in serial, with Area 2 representing a higher stage or processing than Area 1 (for discussion, see Bodegard, Geyer, Grefkes, Zilles, & Roland, 2001). Similar to vision, the receptive field properties of neurons in somatosensory areas increase in size and complexity from lower to higher levels of the hierarchy (Iwamura, 1998). Neurons in Area 1 are sensitive to differences in roughness (Hsiao et al., 1993; Randolph & Semmes, 1974), whereas neurons in Area 2 are sensitive to differences in edge, curvature or form features (Iwamura & Tanaka, 1978; Randolph & Semmes, 1974), suggesting that somatosensory processing may be divided into channels for form and texture as early as SI.

Beyond the primary somatosensory cortex, SI projects to several different brain areas, but most notably to the secondary somatosensory cortex (SII; Figure 2), which is located on the superior bank of the lateral fissure (parietal operculum), and Area 5, which is located posterior to Area 2 in the superior parietal lobule (Duffy & Burchfiel, 1971; Iwamura, 2003; Murray & Mishkin, 1984; Sakata, Takaoka, Kawarasaki, & Shibutani, 1973). The receptive field properties of these two areas appear to further increase in size and complexity compared to the properties of receptive fields in SI, suggesting that SII and Area 5 represent higher levels of somatosensory processing. Despite the increase in size of the receptive fields, SII still has a well-represented somatotopic map. In fact, similar to SI, SII has multiple complete somatotopic maps that appear to be differentially responsive to cutaneous or proprioceptive input (Fitzgerald, Lane, Thakur, & Hsiao, 2004).

Neuroimaging and neuropsychological research in humans support and extend the account of research in nonhuman primates that somatosensory information travels through a hierarchy of processing stages to accomplish haptic object recognition tasks. Research with vibratory stimulation and palpation of simple ellipsoid objects has confirmed that the human postcentral gyrus contains four separate somatotopic maps corresponding to Areas 3a, 3b, 1, and 2 (Bodegard et al., 2001; Burton, MacLeod, Videen, & Raichle, 1997a; McGlone et al., 2002). Likewise, human post-mortem and neuroimaging studies suggest the existence of at least four separate somatotopic maps in SII (Eickhoff, Amunts, Mohlberg, & Zilles, 2006; Eickhoff, Schleicher, Zilles, & Amunts, 2006).

Patients with damage to various parts of the parietal lobe sometimes display symptoms of tactile agnosia, that is, a difficulty identifying objects based on touch in the absence of a primary sensory dysfunction. Thus, these patients can perform simple detection or discrimination tasks, but cannot identify objects by touch in the absence of vision. Evidence from several studies converges to suggest that SII is a critical brain region involved in producing the deficit in haptic object recognition (Bohlhalter, Fretz, & Weder, 2002; Caselli, 1991; Reed & Caselli, 1994). In these patients, the sparing of SI may be enough to accomplish simple tasks (Roland, 1976), but damage to SII makes complex object recognition difficult (Bohlhalter et al., 2002). One limitation on the conclusions that can be made based on these studies is that the stimuli were usually real objects, which could be differentiated based on a combination of many different object characteristics. This is not always seen as a limitation (Reed, Shoham, & Halgren, 2004), because outside the laboratory, objects are recognized using many different characteristics. To study the neural networks that are used for object recognition in real-world settings, it may be necessary to relinquish control over the various characteristics that make up real objects. Of course, a combination of methods will likely be the most promising path; therefore, the lack of patient studies investigating the separate contribution of geometric and material properties to object recognition could be seen at this point to be a limitation.

A similar limitation exists for most neuroimaging studies, which also tend to use objects that can be individuated using more than one object characteristic. The neuroimaging studies converge with the patient studies to indicate that SII is involved in haptic object recognition (Bonda, Petrides, & Evans, 1996; Pietrini et al., 2004; Reed et al., 2004; Roland, O'Sullivan, & Kawashima, 1998) and that SII is likely higher in the hierarchy of processing stages than is SI. Additionally, four studies (Kitada et al., 2006; Roland et al., 1998; Servos, Lederman, Wilson, & Gati, 2001; Stoesz et al., 2003) made direct comparisons of the networks involved in analyzing the micro- and macrogeometry of the objects. Although the findings are not completely consistent, they do add to what we know based on the patient data. Importantly, none of the three studies found evidence for shape processing in SII, whereas two of the studies found evidence for processing of material properties, specifically texture and hardness (Roland et al., 1998; Servos et al., 2001). Thus, SII is an important, high-level processing stage in haptic object recognition, but the evidence suggests that it is not involved in shape processing.

Based on the neuroimaging evidence, there are other brain areas that have been implicated in haptic shape processing. One of these areas is the anterior aspect of the intraparietal sulcus (aIPS; Figure 2). In three studies, area aIPS produced greater activation with length or shape discriminations than with roughness discriminations (Bodegard et al., 2001; Kitada et al., 2006; Roland et al., 1998). However, two other studies that made similar comparisons did not find activation in area aIPS (Servos et al., 2001; Stoesz et al., 2003). One potential reason for this discrepancy involves findings from another group of studies (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999; Binkofski et al., 1998) that investigated the neural mechanisms of haptic object recognition from a slightly different perspective, namely, that haptic exploration requires a unique interaction between somatosensory and motor systems. The conclusion they draw from their findings is that aIPS is not a purely somatosensory processing region, but instead integrates somatosensory and motor information. This conclusion is supported by neuropsychological findings; patients with damage in the aIPS region of the parietal lobe suffer from tactile apraxia, which is characterized by an inability to recognize objects haptically due to inappropriate use of exploratory movements (Binkofski, Kunesch, Classen, Seitz, & Freund, 2001; Binkofski et al., 1998; Pause, Kunesch, Binkofsky, & Freund, 1989).

The sensorimotor nature of aIPS is not its only intriguing feature; other neuroimaging and neurophysiologic studies suggest that aIPS is actually a bimodal sensory region that also receives inputs from the visual system (Culham & Kanwisher, 2001; Grefkes, Weiss, Zilles, & Fink, 2002; Zhang, Weisser, Stilla, Prather, & Sathian, 2004). There is evidence that aIPS is involved in mental rotation of both visually and tactilely presented stimuli (Alivisatos & Petrides, 1996; Prather, Votaw, & Sathian, 2004). Also, visually, area aIPS is thought to process shape information for the purpose of generating and executing goal-directed actions such as visually guided reaching and grasping movements (James, Culham, Humphrey, Milner, & Goodale, 2003). Thus, aIPS may be a site of convergence for several interrelated sensorimotor processes that rely on visual, haptic and motor information to analyze object shape.

Another brain area implicated in haptic shape processing, based on neuroimaging evidence, is LOtv (Figure 2). Several neuroimaging studies have found evidence that LOtv is activated more by object exploration than by a variety of control conditions (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; Amedi, Malach, Hendler, Peled, & Zohary, 2001; James et al., 2002; Peltier et al., 2007; Pietrini et al., 2004; Prather et al., 2004; Reed et al., 2004; Stoesz et al., 2003; Zhang et al., 2004). Five of these studies (James et al., 2002; Peltier et al., 2007; Prather et al., 2004; Stoesz et al., 2003; Zhang et al., 2004) used objects that could not be distinguished based on their material properties, that is, they could only be distinguished based on their shape, suggesting that LOtv is involved in shape processing, but may not be involved in processing other characteristics of objects. Area LOtv is part of a larger complex of *visual* processing areas called the lateral occipital complex (Malach et al., 1995). Many neuroimaging studies have found that LOtv, like the neighbouring areas, is activated by visual input (Amedi et al., 2001; James et al., 2002; Peltier et al., 2007; Pietrini et al., 2004; Stoesz et al., 2003; Zhang et al., 2004); therefore, like aIPS, LOtv is bimodal and involved in processing visual and haptic shape information about objects.

The cases of tactile agnosia reported above were all caused by damage to SII and other areas of parietal cortex. Thus, it is interesting to note a report on a patient (D.F.) with *visual* agnosia who, in addition to a problem with visual object recognition, also has a problem with haptic object recognition (James et al., 2005). The case is interesting, because like many patients with visual agnosia, DF's lesion was in the occipital cortex, not in parietal cortex. In fact, high-resolution MRI showed the lesion to be in an area resembling the lateral occipital complex (LOC). Because the LOC is a functionally defined region, it was not possible to locate it in DF due to her problems with object recognition; therefore, the location of her lesion was compared in stereotaxic space with the location of LOC in healthy controls.

A preliminary comparison of her haptic abilities suggested that her problems with haptic recognition were as great as her well-established problems with visual recognition. DF was asked to perform three different tasks either visually or haptically with novel objects, sequential matching, old/new recognition or paired associate learning. Her performance on all three tasks was matched for visual and haptic presentation. Importantly, the objects could only be distinguished by their shape, not by their material properties. These findings suggest that a better classification for DF's particular deficit is bimodal visual-haptic form agnosia. Furthermore, DF's case study suggests that LOtv is not only *involved* in bimodal shape recognition, but is *necessary* for either visual or haptic shape recognition to proceed. It should be noted that DF's brain damage was due to carbon monoxide poisoning, which causes diffuse damage throughout the brain. In DF's case, lesions are mostly confined to the lateral occipital complex, but there is evidence of atrophy elsewhere and also a small unilateral lesion in the caudal intraparietal sulcus (James et al., 2003). However, there are several other reported cases of bimodal visual-haptic agnosia in the literature, most of which were caused by damage to the temporal-occipital region (Feinberg, Gonzalez Rothi, & Heilman, 1986; Morin, Rivrain, Eustache, Lambert, & Courtheoux, 1984; Ohtake et al., 2001), which suggests that DF's deficit stems from her lesion to LOtv and not from another consequence of anoxia. Nonetheless, it would be interesting to test DF on cross-modal *matching* task, which neuroimaging suggests may involve the caudal IPS region (Saito, Okada, Morita, Yonekura, & Sadato, 2003), and which may be more sensitive to damage in that region than the within-modality tasks that we used. In sum, the combination of the neuropsychological and neuroimaging studies suggest that LOtv and aIPS may represent a stage of the hierarchy where an object's shape is abstracted to the point that it is inconsequential whether the sensory information was originally visual or haptic.

Other studies have also found evidence that visual cortical areas are activated by haptic object recognition tasks (Deibert, Kraut, Kremen, & Hart, 1999; Sathian, Zangaladze, Hoffman, & Grafton, 1997), but it seems that these areas correspond to neither LOtv or aIPS. The exact functionality of these brain areas and their relationship to LOtv and aIPS will require further investigation. Another brain area implicated in haptic object recognition is the anterior insula (Figure 2). The insula is a polysensory area that may receive a direct input from SII (Bonda et al., 1996). Whether or not the insula processes shape information, other characteristics of objects, or some combination of characteristics is unknown. It is likely, though, that the insula represents a very high level in the hierarchy of object recognition stages.

One aspect of the organization of brain areas involved in haptic object recognition poses an interesting question. Why are there two brain areas devoted to processing bimodal haptic and visual shape information? Are area aIPS in the parietal lobe and area LOtv in the ventral temporal-occipital junction redundant? One hypothesis is that these two areas process shape information differently and that the difference is similar to the difference in processing represented in the dorsal “where/how” and ventral “what” pathways of the visual system (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). Briefly, this “two pathways” theory of visual processing suggests that visual information is processed along two separate streams because of the necessity for two distinct types of outputs. The ventral stream is responsible for generating our phenomenological experience of the world or, more practically speaking, recognition of objects and scenes in our environment. The dorsal stream is responsible for coordinating locomotion and other visually guided actions such as reaching and grasping movements. Visual shape information is important for both streams, which partially explains why both LOtv and aIPS are involved in visual shape processing. It is interesting to speculate that the haptic shape processing system may also be organized into dorsal and ventral streams of processing that overlap partially with the visual streams. In fact, it has been previously hypothesized that the haptic system is organized into two streams that have functional similarities to the two visual streams (Reed, Klatzky, & Halgren, 2005). This study, however, did not test all aspects of the functions ascribed to the two visual streams and also did not test for neural overlap between vision and haptics. Thus, considerable research is needed to establish a link between converging dorsal and ventral streams of haptic and visual processing.

Neural Mechanisms of Texture Recognition

Shape information is very useful for efficient object recognition, but other object characteristics can also be used to successfully recognize an object. The haptic system can apprehend a number of object characteristics in addition to shape, for instance, an object’s weight, compliance, temperature, and different aspects of its surface texture (Lederman & Klatzky, 1993). These characteristics can be generalized into a category of features that allow an assessment of the material from which an object is made, namely, its material properties. Objects can be efficiently recognized based on different combinations of material properties. Here, we will focus on surface texture, which is the material property that has been studied the most as it relates to haptic object recognition.

As with shape processing, differences in the ability of the visual and haptic systems to extract texture information from an object begin at the level of the receptors and especially in the types of exploratory movements that are used by the two systems. For vision, the same saccadic eye movements that produce a speed advantage when analyzing spatially disparate features of an object prove to be a disadvantage when analyzing the surface texture of an object. Because a saccade is a jump from one location to another, it is difficult (or impossible) for the visual system to slowly move the high-acuity portion of its receptors over a surface. Even the smooth pursuit movements of the visual system are not designed for this purpose; they are designed to keep a moving target static. In other words, eye movements excel at keeping the visual world static on the retina for brief periods of time; therefore, vision can provide a static analysis of an object’s parts and surfaces, but not a dynamic analysis. The haptic system, on the other hand, is largely unrestricted in the manner that the high-acuity portion of its receptors can be moved over an object. Unlike vision, haptics can perform either static or dynamic analyses by moving the fingerpads over a surface. The use of dynamic analysis helps determine the qualities of the texture that are useful for recognition (Lederman & Klatzky, 1993). Thus, the haptic system is highly efficient at extracting texture information from an object and using it for recognition (Klatzky et al., 1987; Lederman & Klatzky, 1990).

Haptic processing of texture information has rarely been studied in isolation, but instead has been studied in the context of dissociating it from the processing of shape information. Findings from cortical ablation and single-unit recording studies in nonhuman primates show a remarkable amount of agreement on the functional division between the processing of macrogeometry (shape) and microgeometry (texture) in somatosensory brain areas. Neurons in Area 1 (of SI) are sensitive to object texture and ablation produces deficits in texture discrimination, but not angle discrimination (Randolph & Semmes, 1974). Ablation of Area 2 produces deficits in angle discrimination, but not texture discrimination (Randolph & Semmes, 1974). Similar to Area 1, neurons in SII are sensitive to object texture (Hsiao et al., 1993; Jiang, Tremblay, & Chapman, 1997; Pruett, Sinclair, & Burton, 2000, 2001; Randolph & Semmes, 1974), but ablation produces deficits in both shape and texture discrimination (Murray & Mishkin, 1984). These findings are largely consistent with a division of the somatosensory system into texture and shape processing pathways and are also consistent with a hierarchical system for texture processing. Texture information passes from Areas 3a and 3b to Area 1 and on to Area SII (Hsiao et al., 1993; Jiang et al., 1997).

The interpretation of findings from patients with tactile agnosia and from neuroimaging studies is less clear. As described above, one conclusive finding from studies of patients with tactile agnosia is that lesions to SII produce deficits in haptic object recognition that cannot be explained based on superficial sensory loss (Bohlhalter et al., 2002; Caselli, 1991; Reed & Caselli, 1994; Roland, 1987). But, whether or not the agnosia is due to deficits with shape processing, texture processing, the combination of shape and texture, or some other process involved in haptic object recognition, is less clear.

Several neuroimaging studies have investigated the role of SII in haptic object recognition, but the results have not been conclusive. Initial studies of tactile texture perception compared texture stimulation of the skin with no stimulation and found that SII was activated by texture stimulation (e.g., Burton, MacLeod, Videen, & Raichle, 1997b). A more recent group of studies directly compared tasks that required texture discrimination with tasks that required shape discrimination. The first of these studies (Roland et al., 1998) found that SII produced more activation when the relevant characteristic was texture as opposed to shape. But, a second study (Servos et al., 2001) that used similar methods and stimuli found different results. Rather than separate pathways for shape and texture, that study found extensive overlap between the brain regions recruited for shape and texture processing, which were located along the postcentral gyrus. The same study found activation in SII for discriminations of hardness, but not for texture or shape. A third study (Bodegard et al., 2001) found that SII produced more activation with *passive* shape than texture discrimination. Even more recent is a study that parametrically varied the roughness of the texture stimulus used for discrimination (Kitada et al., 2005). That study found that activation in SII and the insula was correlated with the parametric variations in roughness. In sum, although three of the five studies reported here suggest that SII is involved in texture discrimination, the exact role of SII in texture processing remains controversial.

Before we completely give up on the idea that there could be a separate texture-processing pathway, there is a final group of studies that needs to be addressed. This group of studies used more complicated objects to investigate the neural substrates of haptic object processing. Many of them, however, did not include a texture discrimination condition, or did not fully analyze brain regions that were activated during texture discrimination. On the other hand, some of the studies used objects that could be distinguished using texture, and some of the studies used objects that could not be distinguished using texture; therefore, a comparison of results across studies may be useful.

Three of the studies (Amedi et al., 2001; Pietrini et al., 2004; Reed et al., 2004) compared haptic recognition of real objects with a control condition. Real objects, of course, can be distinguished using all of their many different properties, including material properties such as texture. The results for LOtv showed remarkably consistent results: In all three cases, LOtv produced more activation for haptic object recognition than for the control condition. Two of the three studies (Pietrini et al., 2004; Reed et al., 2004) showed that SII produced more activation for haptic object recognition than for the control condition. Although it was not reported, examination of the activation maps from the third study (Amedi et al., 2001) reveal that SII may have produced consistent results across the studies. The results of these three studies, however, do not distinguish between the processing of different object characteristics; they did not analyze different object characteristics in isolation. Three different studies (James et al., 2002; Peltier et al., 2007; Stoesz et al., 2003) focused on the processing of object shape without texture. Those studies used meaningless objects that were all made from the same material and had the same surface texture; therefore, texture could not be used to distinguish them. These three studies also showed very consistent results: In all cases, area LOtv, but *not* SII, produced more activation for haptic object recognition than the control condition. A significant difference between the real objects and the meaningless objects in these studies was that the former could be distinguished based on material properties, while the latter could not. One hypothesis based on the comparison of these results is that SII, which only produced activation with the real objects that could be distinguished by texture, is part of a texture processing pathway (Roland et al., 1998). Because the real objects could also be distinguished using several other material properties besides texture, a more general hypothesis would be that SII is a critical stage in a neural pathway for processing material properties.

It should be pointed out that one of the studies (Reed et al., 2004) compared real and meaningless objects directly and found that both SII and LOtv were more strongly activated with real objects than meaningless objects. The meaningless objects in that study differed significantly from the meaningless objects in the other three studies in that they could be distinguished using texture. Thus, the increased activation with real over meaningless objects suggests that activation in SII and LOtv may not be determined only by the ability to distinguish objects based on texture or shape, but may also be influenced by the familiarity of the object.

Also of interest is that one study (Pietrini et al., 2004) included SII in its analysis of visual and haptic object recognition. That study found that SII produced activation only for haptic recognition, not visual. A recent study on visual texture recognition suggests that areas in the ventral occipital lobe are responsible for visual object recognition using texture information (Cant & Goodale, 2007). Although this suggests a lack of overlap between haptic and visual texture processing pathways, two studies do not constitute sufficient evidence to make any strong claims. In fact, there is some evidence that haptic object recognition activates the anterior insular cortex (Figure 2), a known polysensory area, and that this area received projections from SII (Bonda et al., 1996).

Taken together, these findings suggest SII may represent a critical stage in a pathway specialized for processing the material properties of objects, of which texture is one example. The findings are not entirely conclusive, and more investigation is warranted. Unlike shape processing, there is little evidence for bimodal visual-haptic processing of texture.

Conclusions

To fully understand the neural basis of haptic object processing and the interconnection of the visual and haptic systems will require further study, especially of subjects that have, until recently, been somewhat neglected. For instance, the investigation of visual shape processing to the exclusion of other object attributes has proved worthwhile, but it is time to re-energize the investigation of the neural mechanisms involved in processing other visual object attributes such as texture and colour. In addition, increasing our knowledge of object recognition by studying it through multiple sensory inputs will increase our command of the mechanisms underlying object recognition in a way that studying only visual object recognition cannot.

By distilling the literature on the neural basis of haptic object processing, we have come to several conclusions about the state of the field. There is considerable evidence that haptic object recognition proceeds by two separate neural pathways, one specialized for material properties and the other for geometric properties of objects. These pathways may diverge as early as SI, where Area 1 is specialized for microgeometry and Area 2 for macrogeometry. There is also considerable evidence that the haptic/somatosensory system is organized in a series of hierarchical processing stages, with each stage represented by a different anatomical brain region. SII likely represents a higher stage in the hierarchy along the material properties processing pathway. Proposed counterparts to SII in the geometric properties pathway are aIPS and LOtv. Areas aIPS and LOtv may themselves represent the branching of two streams within the shape-processing pathway. Both aIPS and LOtv are bimodal visual-haptic processing centres and may represent the convergence of visual action and perception streams with similar haptic processing streams. Unlike aIPS and LOtv, SII is not bimodal, which may suggest that the systems for visual and haptic texture processing are non-overlapping.

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