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Review

Vision and touch: Independent or integrated systems for the perception of texture?

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ABSTRACT

In the following review, we discuss the evidence for the role of vision and touch in the perception of texture with the particular aim of evaluating whether these systems contribute information to texture perception in either an independent or integrated manner. Although texture is perceived by both vision and touch, several behavioural and neuroimaging studies have suggested that texture information is processed in qualitatively different ways, such that the type of information encoded and the manner in which it is encoded differs across these sensory systems. Furthermore, vision and touch perceive different aspects of texture information with vision the more appropriate modality for discriminating texture boundaries and touch the more appropriate modality for discriminating stimulus roughness and compliance. Differences also exist in the neural structures and functions which underlie these systems, further suggesting independence of these modalities in the perception of texture. Accordingly, recent evidence suggests that behavioural tasks involving texture perception do not benefit from integration across the senses, suggesting that qualitatively different information is represented across vision and touch which cannot be combined to enhance perceptual performance. Research using more familiar objects, however, does suggest a role for sensory integration on texture perception, although these effects may be due to more cognitive influences rather than basic sensory encoding. In sum, we suggest that unlike shape perception, vision and touch contribute information to the perception of texture in an independent but complementary manner.

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Contents

1.	Introduction	60
2.	Tactile and visual sensory exploration of texture	61
3.	Stimulus properties encoded by touch and vision	61
4.	Behavioural evidence for cross-modal interactions in texture perception	63
5.	Neural correlates of unimodal tactile and visual texture perception	65
6.	Neural correlates of multisensory texture perception	67

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7.	Conclusions and future directions	68
Ack	nowledgments	69
Ref	erences	69

1. Introduction

When we see or touch the surface of an object we encode information that allows us to make perceptual decisions about that object for the purpose of recognition or action, or for more aesthetic judgements such as the quality or attractiveness of the item. Object information can be based on both geometric, (e.g. shape, size, orientation and curvature), and material properties, (e.g. temperature, compliance, texture, and weight) and both the visual and tactile modalities contribute to the representation of objects based on these characteristics. Texture information in particular is an inherent material characteristic of the surface of any object and provides an important cue for its perception. For instance, the scaly skin of a snake or the hairy skin of a kiwifruit can help us distinguish these objects through touch or vision, even when shape information is not fully available. Yet, despite a growing interest in recent years on the behavioural and neural correlates of object recognition across modalities, relatively less attention has been given to the multisensory perception of material properties such as texture and roughness.

Although a number of review articles have considered texture perception in general (e.g. Landy, 1996; Lederman and Klatzky, 2004), or tactile texture perception (Taylor et al., 1973; Lederman, 1982; Hollins and Bensmaïa, 2007), and visual texture perception (Bergen, 1991; Landy and Graham, 2004) in particular, none have looked specifically at the effects of multisensory inputs on texture perception from both a behavioural and neuroimaging perspective. In the following review, we specifically aim to investigate to what extent vision and touch contribute independent information to the representation of an object surface or whether this information is integrated into a single representation.

Texture (n.) is defined as the feel, appearance, or consistency of a surface, substance, or fabric (Oxford English Dictionary, 2008). Consequently, texture information is distinct from more global shape information but can nevertheless contribute to the perception of an object. Evidence that texture perception is distinct from shape perception comes from a variety of sources, including behavioural, neuroimaging and neuropsychological literatures (e.g. Zhang et al., 2004; Amedi et al., 2005). For example, Milner and colleagues (Milner et al., 1991; James et al., 2003) have studied the sensory and perceptual abilities of patient D.F., who has visual form agnosia as a result of carbon monoxide poisoning. D.F. presents severe visual deficits including visual form perception, brightness, motion and depth. However, D.F. maintains the ability to use pattern information to aid suitable preshaping and hand rotation when reaching for an object (Milner et al., 1991). Along with her ability to discriminate colour, D.F. is able to use surface properties to identify objects despite remaining perceptually unaware of their form (Humphrey et al., 1994), suggesting that texture processing is distinct from global shape processing.

Historically, each of the senses has been studied in isolation; although there has been an increased interest towards exploring multisensory interactions on perception (see Marks, 1978). With regards to texture perception in particular, a number of studies have provided some evidence of multisensory influences. Information about the texture of a surface or object can be mediated through different sensory modalities such as touch, vision and audition. Although touch and vision are the more obvious senses for perceiving texture, audition can also play a role in texture perception. For example, the sound of someone rubbing their fingers on a surface provides valuable information about the roughness of that surface (Lederman, 1979; for a review see Lederman and Klatzky, 2004). Similarly, von Scheiller (1932) noted that noise bursts or tones repeated at regular intervals influence the perception of roughness by touch. More recent demonstrations of audiotactile integration in texture perception include the so-called parchment-skin illusion (Jousmaki and Forss, 1998; Guest et al., 2002), where distorted auditory feedback affects the perceived roughness or smoothness of the hands rubbing together.

Although audition can influence tactile perception of texture, the extent to which vision and touch influence each other for texture perception is not well understood. For example, some studies have revealed sufficient differences in behavioural performance (e.g. Bergmann Tiest and Kappers, 2007), and neural activations (e.g. Randolph and Semmes, 1974; Servos et al., 2001) across these modalities, while others have demonstrated no difference in performance across modalities (e.g. Lederman and Abbott, 1981; Guest and Spence, 2003). Moreover, other studies have suggested that different texture information is encoded across vision and touch (Klatzky et al., 1987; Heller, 1989; Sailer et al., 2003). As such, it is possible that the representation of an object's material properties benefits from qualitatively unique information, rather than the integration of redundant information encoded across these modalities (Millar, 1994). However, evidence for complete independence across the visual and tactile systems for the perception of texture is not consistent as some studies have reported that texture information can be shared across modalities. This evidence raises the question of whether it is the nature of the information or the particular perceptual process that determines whether texture information can be integrated across the senses. In the following sections we review the evidence from the literature on the perception of texture across vision and touch with the aim of elucidating the nature of the relationship between these modalities for texture perception. We focus specifically on texture perception for the purpose of recognition and discrimination, and have considered the literature on the affective aspects of texture perception to be outside the scope of this review (for a review see McGlone et al., 2007). In the following sections, we compare the visual and tactile senses according to the manner in which information is encoded, the nature of the information

processed, and the neural systems underlying texture perception within and across these modalities. Finally, we suggest directions for future research which will help us better determine the relative contributions of these sensory modalities to our perception of texture.

2. Tactile and visual sensory exploration of texture

The haptic system makes use of particular stereotyped motor patterns or exploratory procedures (EP) when examining an object or surface (Klatzky and Lederman, 1987; Lederman and Klatzky, 1987) and each EP optimally extracts information about a particular property for the benefit of subsequent perceptual performance (Klatzky et al., 1989). The EP typically performed for encoding texture is lateral motion, that is, the fingertips move back and forth over a textured surface (Lederman and Klatzky, 1987). Accordingly, the fingertips have a high density of specialised mechanoreceptors ideal for this task (Johansson and Vallbo, 1979; Vallbo and Johansson, 1984), as well as a large area within the somatosensory cortex dedicated to processing stimulation from the fingers relative to other body parts (Sutherling et al., 1992).

For texture, it is apparent that motion plays a key role in tactile perception. For example, early research on the role of motion in texture perception, using varying paper surfaces, demonstrated that observers rated their sensations as different depending on whether static touch or dynamic passive touch (i.e. movement of the surface over a stationary fingertip) was used (Menees and Zigler, 1923). Accordingly, Hollins and Risner (2000) demonstrated that the discrimination of sandpaper samples was more difficult using static touch rather than dynamic passive touch for fine textures; a finding that led to the duplex theory of texture perception (which we discuss later). However, of interest is whether active touch (i.e. movement of the hand over a surface) is necessary for efficient encoding, or whether dynamic passive touch is sufficient for tactile texture perception. When investigating the haptic perception of roughness in sighted and blind observers, Heller (1989) observed no difference in performance between these groups, and notably, no difference in performance between active touch and dynamic passive touch. Furthermore, roughness perception (Lederman, 1981, 1983; Verrillo, 1999) and roughness discrimination (Lamb, 1983) do not vary as a function of whether active or passive dynamic touch is used. From these findings we conclude that relative motion, rather than hand movement, is important for encoding texture information.

Although texture perception is successfully conveyed through touch, in everyday experience textures are rarely encountered by touch alone. The visual perception of texture gives the observer important information about the surface of an object or even the depth of a plane (Gibson, 1933; Gibson and Radner, 1937). Moreover, the surface properties of an object are often primarily perceived through vision (Schifferstein and Cleiren, 2005; Schifferstein, 2006) which then may guide the tactile system to explore the surface. Thus, when we see an object, we may then reach out our hand to further investigate the properties of its surface.

Like touch, the visual system explores external information in an active, dynamic way through a series of eye movements and fixations over the stimulus of interest (for a review see Findlay and Gilchrist, 2003). However, a recent study comparing exploration strategies across vision and touch for texture perception, suggests that these strategies may be modality-specific. Sailer et al. (2003) reported that whilst different textures affected the nature of haptic exploration procedures these had no effect on visual exploration. Moreover, their study indicates that as a consequence of these modality-specific exploratory procedures, different information about texture may be encoded by vision and touch.

3. Stimulus properties encoded by touch and vision

Our daily experience of textures may involve many vast types of surfaces such as fabric, stone and sandpaper to name a few. The variation in the perceived roughness of these textures is reflected in the sensory mechanisms that encode this information. In 1925, Katz proposed that both spatial and temporal cues mediate tactile texture perception. Katz argued that spatial cues such as size, shape and distribution of surface elements, are responsible for our perception of coarse textures such as Braille characters, whereas vibrational cues elicited by the movement of the finger as it moves on a surface are used for fine texture perception (Katz, 1925). Although his views were relatively ignored over many decades, his idea was later to become the basis of much research activity that led to the so-called duplex theory of tactile texture perception pioneered by Hollins and colleagues (Hollins et al., 1998; Hollins and Risner, 2000). According to this theory coarse and fine textures are mediated by a distinct receptor system (Hollins et al., 1998, 2000b, 2001, 2002; Hollins and Risner, 2000; Bensmaïa and Hollins, 2003; for a review see Hollins and Bensmaïa, 2007). The systems and their underlying neurophysiological mechanisms have been wellcharacterised by psychophysical experiments conducted by Gescheider, Verrillo and colleagues (e.g. Bolanowski et al., 1988; Gescheider et al., 2001; 2002; Verrillo and Gescheider, 1975, 1977; Verrillo et al., 1983).

Coarse surfaces, with spatial period above the interval 0.1-0.2 mm (Hollins and Risner, 2000; Hollins and Bensmaïa, 2007), are perceived based on their spatial variation by the afferent firing rates of slowly adapting type I mechanoreceptors, such as Merkel receptors (Connor et al., 1990; Connor and Johnson, 1992; Blake et al., 1997; Yoshioka et al., 2001). A common stimulus used when studying coarse texture perception is grooved metal plates, as they can be easily modified depending on the investigation at hand. In a series of studies using these stimuli with monkeys, Goodwin and Morley (1987a,b; Morley and Goodwin, 1987) characterised the responses of the cutaneous mechanoreceptive afferents in terms of the spatial period of the gratings and the movement characteristics. A number of studies have demonstrated that the degree of spacing between grooves is an important spatial feature for tactile roughness perception such that as spacing increases so does the perceived roughness (e.g. Lederman and Taylor, 1972; Goodwin et al., 1989; Sathian et al., 1989). Temporal cues have also been reported to play a role in the perception of coarse textures (Cascio and Sathian, 2001; Gamzu and Ahissar, 2001), although this effect is modest. Despite both spatial and temporal information being available during the exploration of coarse surfaces through touch, spatial information appears to be sufficient for the perception of coarse surfaces (Hollins et al., 2006).

Relative to coarse surfaces, fine textures seem to be encoded differently in the tactile system. Fine surfaces, with spatial period below 0.1 mm-0.2 mm (Hollins and Risner, 2000; Hollins and Bensmaïa, 2007) seem to be perceived on the basis of vibrations elicited on the skin during exploration. This signal is mediated by rapidly adapting mechanoreceptors, such as Pacinian or Meissner corpuscles in the skin (see Bensmaïa and Hollins, 2003). The observation that discrimination of fine surfaces is better when the surface moves across the finger tip, therefore inducing vibration, compared to when it is in stationary contact with the fingertip supports the role of cutaneous vibration in the tactile perception of fine textures (Hollins and Risner, 2000). Additionally, a surface that is vibrating, in the Pacinian-sensitive range of 150-400 Hz, is perceived as rougher than an identical surface that is not vibrating (Hollins et al., 2000b). Furthermore, by reducing the sensitivity of the vibrotactile channels through vibratory adaptation, discrimination of fine surfaces is impaired relative to a no-adaptation condition (Hollins et al., 1998, 2002).

Together, these results indicate that vibrotaction plays an important role in the perception of fine textures. However texture-elicited vibrations can be perceived in terms of either their temporal or intensive properties. For example, roughness can be determined temporally, as a function of the frequency of the texture-induced vibrations elicited on the skin, or roughness can be determined by the intensity of these vibrations. Empirical findings tend to support the reliance on an intensity code. For example, although the frequency hypothesis predicts that as the frequency of vibrations elicited on the skin increases then the stimulus surface would be perceived as increasingly smoother, Bensmaïa and Hollins (2003) reported that this is not necessarily the case. Furthermore, the tendency to judge a vibrating surface as rougher increases as the amplitude of the vibrations increase, independent of the frequency of those vibrations (Hollins et al., 2000b). Moreover, Miyaoka et al. (1999) demonstrated in a discrimination task that when typical scanning velocities were used the temporal frequencies that would be elicited by their surfaces were outside the range that could be determined by the vibrotactile system (i.e. <1 kHz). In support of the intensity hypothesis, difference thresholds of the perceived roughness of fine abrasive surfaces were found to be in the same range as those obtained in a height-discrimination involving varying ridge heights (Miyaoka et al., 1999), suggesting that roughness perception relied on amplitude rather than frequency information. In sum, the findings are in favour of the intensity theory of roughness for fine texture perception.

Although roughness, a highly prominent perceptual dimension of texture, has been the main focus of tactile texture perception (Jones and Lederman, 2006; Hollins and Bensmaïa, 2007), this is clearly not the only dimension of texture. Other studies have found that properties other than frequency information or vibrotactile intensity can also contribute to the perception of surface texture. For example, a power relation between subjective roughness judgements and stimulus fric-

tion has been observed using abrasive papers (Ekman et al., 1965). Also, Smith et al. (2002) found that perceived roughness correlated with the average rate of change of the tangential touching force. Furthermore, compressibility has been found to be an important cue for texture perception in touch, albeit to a lesser extent than roughness (Bergmann Tiest and Kappers, 2006).

Many studies investigating the role of touch in texture perception have used artificially produced surfaces such as gratings, sandpaper, raised-dot patterns and etched surfaces (e.g., Lederman and Abbott, 1981; Klatzky et al., 1989; Connor et al., 1990; Gescheider et al., 2005), however few have investigated tactile texture perception using more high-level or 'natural' stimuli. This may largely be due to the difficulty in quantifying the physical properties of natural materials. Some exceptions include studies by Hollins and colleagues (1993, 2000a) which have investigated the perceptual dimensions of tactile surface textures using various familiar materials (including wood and straw). Hollins and colleagues used multidimensional scaling (MDS) methods along with dynamic passive touch and found evidence for two main orthogonal dimensions in texture perception; namely, rough-smooth and soft-hard, and a number of relatively weaker dimensions, sticky-slippery (Hollins et al., 1993, 2000a), flat-bumpy, and warm-cool (Hollins et al., 1993). Earlier, Yoshida (1968a,b) used MDS with 25 different familiar materials (including glass and different fabrics), and found that the main contrast for their samples was between metallicness and fibrelikeness. More recently, Ballesteros et al. (2005) used a number of convergent methods to study the dimensions of perceptual haptic space for various ecological textures (including plastics, cork and fur). Their results, based on both a spatial arrangement task (SAT) and a free classification task (FCT), indicated a two-dimensional space solution with bipolar dimensions. While the SAT revealed the combined dimensions of rough-smooth and slippery-adherent, the CFT revealed the dimensions of smooth-adherent, and rough-slippery. The authors suggested that, depending on the task, the extremes of the dimensions are combined differently. In a similar study, Picard et al. (2003) investigated the influence of semantics on haptic texture space of 24 seat cover materials using a similarity classification task. They observed 3 to 4 continuous perceptual dimensions, including orthogonal dimensions soft-harsh, and thin-thick, and to a lesser extent, the separate dimensions of relief and hardness. The dimensions revealed by these different studies may be based on the particular properties of the stimuli used in the tasks. Since the materials used by Picard et al. (2003) were all fabrics, it is difficult to compare their results with previous findings. Furthermore, many previous investigations have used too few materials to make realistic judgements on the number of dimensions that exist in the representation of haptic texture. To address this, Bergmann Tiest and Kappers (2006) tested participants on a free-sorting task of 124 varying, common materials using active touch. Using such a broad set of stimuli elicited a four-dimensional haptic material space, which as the authors interpreted involves dimensions such as roughness and compressibility. However, although our understanding of the tactile perceptual space for ecological surfaces is growing, the role of vision has received relatively less attention. As such, our knowledge of how vision may affect the tactile perception of ecological textures is relatively poor.

Whilst the information encoded from a surface leads to the perception of its roughness or texture, attention can also play a role in both tactile and visual texture perception. The role of spatially-selective attention in tactile texture perception was investigated by Sathian and Burton (1991). They demonstrated using grooved metal plates that although spatial attention may be useful in detecting the absence of a texture change, discerning its direction, and discriminating between different textures, it plays a minimal role in the detection of an abrupt change in texture. However, this ability to detect a change in texture is a key characteristic of visual perception along with a number of other dimensions, including contrast changes, reflectance, luminance, and cluster. In particular, the ability to detect borders between different textures is an important aspect of visual object segregation. This enables the observer to determine whether a scene contains two or more textured regions. A real-world example of this is an animal determining the location of its prey in a visually complex environment; by using camouflage many animals can disguise themselves from their predator. A texture boundary arises if two adjacent image regions are distinguished as having distinct surface textures. These boundaries may then be used to identify and segment the figure from the background which can subsequently aid in

The visual texture segregation literature mainly focuses on the ability of the observer to effortlessly discriminate pairs of texture regions. Early investigations focussed on defining what aspects of image structure and features give rise to preattentive texture segregation. As such, the distribution of properties, such as brightness, colour, size, contour, slope, and contour termination were found to affect textural segmentation (Olson and Attneave, 1970; Beck, 1972, 1973; Marr, 1976). Later, Julesz (1981) and Julesz et al. (1978) proposed the idea of 'textons', which represent such features as size, orientation, line terminations and line crossings, and which they argued, formed the basis of texture segregation. Alternatively, it was suggested that the orientation and spatial frequency-tuned channels mentioned in the spatial vision literature (De Valois and De Valois, 1988; Graham, 1989, 1992) may be sufficient for modelling texture segregation. Since then, a number of similar models, based on selective filtering for orientation and spatial frequency in a visual scene, have been suggested to account for the ability of the visual system to segment texture information in a visual scene into meaningful wholes (for a review see Landy and Graham, 2004).

The perceptual representation of the spatial information present in irregular textures, such as those found in the real world, have often been examined using scatter-dot displays. These enable the investigation of the perception of spatial texture attributes in isolation from other properties of surfaces such as luminance, colour and spatial frequency. Scatter-dot displays may be manipulated such that they differ in terms of apparent number of dots (i.e. numerosity), and spacing (i.e. cluster), which each may contribute to the perception of texture density (for a review see Durgin, 1995). Texture density, that is the number of elements per unit of area, is a simple way of describing a textured area and is thus an important cue for surface segregation (Barlow, 1978; Marr, 1982). Cluster can be thought of as a measure of the variance of densities present in a texture (Ginsburg and Goldstein, 1987). Durgin (1995) suggests

that the visual system represents texture density independent of number, and that the representation of perceived cluster depends, in part, on the processes underlying the perception of texture density. In any case, both cluster and numerosity seem to be important featural dimensions that are independently encoded by the visual system for the perception of texture, particularly surface or two-dimensional texture.

The visual system can also perceive three-dimensional texture patterns. For example, Ho et al. (2007) found that the visual perception of three-dimensional texture is affected by the interaction of the illuminant and local height variations in the texture. They also observed that roughness constancy was not always consistent across varying viewpoints of the observer. In particular, they found that a surface was consistently judged to be rougher as it was illuminated from a more oblique angle, even when more cues to the illuminant position were provided. In other words, the perception of three-dimensional texture in vision is not invariant to changes in view or illumination. Clearly illumination changes would not affect the perception of texture through touch, however it remains to be seen whether observer viewpoint affects tactile texture perception in the same way as it does for visual texture perception.

4. Behavioural evidence for cross-modal interactions in texture perception

From the evidence discussed above, it seems that although the properties the surface of an object are readily discriminable by touch and vision, these modalities encode and process texture information in distinct ways. For example, although the spatial properties of objects, such as shape, volume or size, are most efficiently recognised by vision, surface roughness is particularly salient to the tactile sense (Klatzky et al., 1987) and may be better assessed using touch than vision (Heller, 1989), suggesting performance differences across these modalities in the perception of texture.

Early comparative investigations between visual and tactile texture perception, however, indicate no clear difference in discrimination performance across these modalities (e.g. Binns, 1936). Similarly, a number of more recent studies have indicated that differences in performance between the modalities in discriminating textures, such as sandpaper, are small to nonexistent (Bjorkman, 1967; Lederman and Abbott, 1981; Heller, 1982; Jones and O'Neill, 1985; Rexroad and White, 1987). For example, Brown (1960) observed no difference between tactile, visual and visuo-tactile performance in a roughness pairedcomparison task using wood samples of varying roughness. Moreover, Guest and Spence (2003) reported finding no difference between tactile and visual performance on roughness discrimination of fabrics. However, Bergmann Tiest and Kappers (2007) used a wide variety of familiar textures in a free-sorting task, and reported a performance benefit for tactile over visual texture perception. According to their findings, the medium frequency roughness band (i.e., 0.1 mm) was important for judgements of roughness in the tactile rather than the visual system, for which a larger spatial scale (i.e., 1.0 mm) was preferred. This is in line with the known detection thresholds across the modalities for touch, measured as 0.98 mm on a static grating orientation discrimination task (Van Boven and

Johnson, 1994) whereas for vision, features at length scale of 0.2 mm are at or below threshold.

Differences between the senses in texture discrimination and recognition performance suggest that information encoded across vision and touch may not transfer efficiently across modalities. Although the recognition of both familiar and unfamiliar object shapes is possible when explored through one modality, e.g. touch, and identified in another, e.g. vision (see Easton et al., 1997; Newell et al., 2001; Ernst et al., 2007), the extent to which information about texture can be efficiently shared across modalities is not as well understood.

The efficient transfer of texture information between touch to vision has been shown in both newborn infants (Molina and Jouen, 2001; Sann and Streri, 2007), and 1-month old infants (Meltzoff and Borton, 1979). In a series of experiments, Picard (2007) investigated intra-modal and cross-modal performance in the perception of texture in older children (5 and 8 year olds) using fabric samples. For both age groups, performance was equivalent across vision and touch when the task was relatively easy (i.e. the sample and distracter textures shared different degrees of softness and thickness). However, when the test stimuli shared similar tactile properties, visual recognition was better than tactile recognition performance. Interestingly, stimulus context did not affect cross-modal (visuo-tactile) performance, suggesting that cross-modal recognition was resolved using mainly bottom-up perceptual processing of the test stimuli.

Picard (2007) also found that visual to tactile (VT) performance improved between the ages of 5 and 8 years using difficult to discriminate textures although there was no corresponding improvement in unimodal or tactile to visual (TV) performance. Picard (2007) argued that this relative improvement in VT performance was indicative of a shift to more efficient top-down processing in the older children. However, Picard (2006) also reported differences between VT and TV performance in adults in texture recognition tasks. As such, a difference in the encoding of information across these modalities is likely to account for the poor transfer of information from touch to vision relative to from vision to touch.

In addition to how information is transferred across modalities, another pertinent issue is understanding how the senses act together for the perception of texture. Several studies have investigated multisensory interactions for texture perception, although the evidence is generally inconsistent regarding whether the senses optimally combine information to enhance perception. For example, Ballesteros et al. (2005) explored whether bimodal exploration of the same texture stimuli affected the perceptual dimensions produced by participants relative to unimodal exploration. They found that across both a spatial arrangement task (SAT) and a free classification task (FCT) the goodness of fit was better in the bimodal condition than the unimodal, haptic condition.

On the other hand, studies which have used a sensory conflict paradigm have suggested little interaction between the senses in texture perception. The idea behind this paradigm is that if a common multisensory representation of texture exists, then this representation will be based on an optimal combination of information from across the two senses (e.g. Ernst and Banks, 2002) or, if information in one sense is more reliable than

the other than that one sense may dominate the other for perception (Lederman and Abbott, 1981). An example of sensory dominance has been demonstrated by Rock and Victor (1964) for shape perception: when a conflict between visual and tactile information arises, visual information can 'capture' the tactile input such that the visual experience dominates the tactile interpretation of the size of an object.

Using a conflict paradigm similar to that of Rock and Victor, Lederman and Abbott (1981) examined how a discrepancy between visual and tactile inputs affected texture perception. They found that when discrepant visual and tactile texture information was available, the texture percept was based on an equal weighting across these modalities. However, Lederman and Abbott found no difference in a range of tasks involving judgements of roughness across unimodal visual and tactile and bimodal visuo-tactile conditions. In other words, they did not find evidence of multisensory enhancement in behavioural performance involving texture perception. Similarly, Jones and O'Neill (1985) compared roughness judgements across unimodal, visual and tactile, and bimodal conditions and found no difference between these conditions on accuracy performance. Jones and O'Neill reported that decision speed was quicker in vision than in touch but that decision speed in the bimodal condition was the average of these two conditions. In contrast, Heller (1982) observed that using vision and touch together improved accuracy on a three-alternative smoothness rating task, relative to the unimodal conditions; although on closer examination this benefit for the bimodal condition was the result of the observer viewing their hand movements during the task rather than any benefit on the perception of texture per se. Finally, Guest and Spence (2003) reported evidence for tactile dominance in texture perception. Using a sensory conflict paradigm, they observed that visual discrimination performance was affected by incongruent tactile distracters but that tactile performance was not affected by congruent or incongruent visual information. Collectively, these studies suggest that using both the visual and tactile modalities together does not seem to benefit texture perception relative to unimodal inputs. These findings further suggest that information may not be optimally integrated as this information may be qualitatively different across modalities. Indeed, our review of the nature of the stimulus properties encoded across these modalities suggests that this is the case and that each modality encodes texture information in a specific manner that is most appropriate to the physiology of that system. As such, it may not be entirely unexpected that texture information is not combined into a multisensory representation.

According to the *modality precision* or *modality appropriateness* hypothesis (Welch and Warren, 1980) input from different modalities is weighted as a function of the relative unimodal capabilities with respect to the task demands. For example, vision is thought of as the spatial sense and consequently, visual perception has been shown to be more accurate and precise on spatial tasks, such as form-matching, than tactile perception (e.g. Cashdan, 1968; Milner and Bryant, 1970; Bryant and Raz, 1975). Visuo-spatial superiority may be due to the fact that spatial information can be encoded in a parallel manner by vision whereas the tactile system has to rely on sequential encoding of spatial information, a task that is clearly demanding

on memory resources because of the need to integrate spatial information over time. However, unimodal tactile and visual performance have been found to be similar on texture perception tasks (e.g. Lederman and Abbott, 1981), although that is not to say that participants did not encode different properties of texture in a modality-specific manner, i.e. in a way most appropriate to the sensitivities of each modality.

As such, the lack of evidence of better performance in bimodal relative to unimodal conditions may be due to different information encoded in each modality. Furthermore, this difference in encoded information may be mediated by attention, such that some features are more salient and are more easily attended to in one modality rather than another. This so-called directed attention hypothesis (Welch et al., 1979) has received some support in the literature (Cannon, 1970; Kelso et al., 1975; Warren, 1979), although it is not known to what extent attention affects multisensory texture perception. However, Lederman (1979) proposed a variant of this theory, namely the ecological validity hypothesis, where cues from one modality (e.g. touch) may be more ecologically valid to, or reliably encoded by one modality than cues from another modality (e.g. vision) for the purpose of the task, and may therefore dominate perception.

Interestingly, several studies have suggested that when vision and touch are combined for the purpose of texture perception, task demands can affect the relative dominance of each modality to the percept. For example, Lederman et al. (1986) demonstrated that when a judgement dimension was altered, e.g. from judgements of spatial density to roughness, the relative weighting of visual and haptic inputs on the decision changed. Later, in a similarity grouping task, Klatzky et al. (1987) showed that when participants were given instructions that biased them towards visual inputs, they sorted the stimuli initially by shape. On the other hand, when participants were biased toward tactile similarity, objects were sorted primarily in terms of material properties, such as texture. Furthermore, when discriminating between objects that varied in terms of material properties (i.e. roughness, hardness, thermal properties, and weight), observers used tactile information to guide their visual decisions (Klatzky et al., 1987).

5. Neural correlates of unimodal tactile and visual texture perception

As well as behavioural differences between vision and touch in the perception of texture, these systems are supported by different neural substrates in the brain. For example, the major cortical regions underlying tactile texture perception are the primary and secondary somatosensory areas, the posterior parietal cortex as well as other more anterior brain regions such as the pre-frontal cortex. The visual processing of texture, on the other hand, involves cortical areas of the brain that are generally distinct from those involved in tactile perception such as primary visual cortex, the collateral sulcus and other higher visual areas such as the fusiform gyrus. In the following paragraphs we will give an overview of the main brain regions that have been reported to be activated during texture perception across vision and touch and assess to what extent these neural systems work together or independently. These studies will include both

electrophysiological and neuroimaging data in both monkeys and humans.

In touch, the primary somatosensory cortex (SI) receives primary afferent connections from the thalamus and is located in the post-central gyrus (PCG) of the human brain. Based on its cytoarchitectonic characteristics, SI can be further divided into areas 3a, 3b, 1 and 2. Early lesion work in monkeys suggested that several of these cytoarchitectonic areas might be responsible for texture perception. For example, work by Randolph and Semmes (1974) on SI indicated that an ablation of area 3b impaired shape and texture discrimination in the monkey, whereas ablation in area 1 only impaired texture perception.

In agreement with these lesion works, studies based on single unit recordings have also confirmed the involvement of these areas in texture perception. For example, neuronal activity in areas 3b, 1 and 2 signal differences in textures explored through active touch. Darian-Smith et al. (1982) reported that single neurons in areas 3b and 1 discharge when the monkey rubs the contra-lateral finger pad across a textured surface. In a further set of electrophysiological studies, where monkeys were trained to detect differences between smooth and rough textures, such as raised Braille characters, texture-related activity was observed in areas 3b, 1 and 2 (Chapman and Ageranioti-Belanger, 1991; Ageranioti-Belanger and Chapman, 1992). Texture-sensitive neurons can be further classified as graded, if their discharge rate is proportional to the changes in spatial period, or non-graded, if the discharge rate varies with a change in spatial period but does not provide information about the magnitude of this change. In SI, texture-related neurons exhibit graded responses, i.e. their firing rate increases with increasing spatial period of gratings (Sinclair and Burton, 1988) and of raised-dot surfaces (Jiang et al., 1997), suggesting that SI encodes texture based on mean firing rates.

With the advance of non-invasive neuroimaging techniques, it is possible to gain insight on which areas of the cortex are being recruited during texture discrimination in the human brain. Notably, SI is systematically activated in texture perception studies, independently of the specific stimuli or task, and temporary disruption of SI by transcranial magnetic stimulation (TMS) over the SI cortex impaired the discrimination of grating textures (Zangaladze et al., 1999). Using fMRI, Servos et al. (2001) investigated the neural subtracts of haptic texture, shape and hardness perception. They observed activity in the PCG contralaterally to the exploring hand for all three classification tasks. They also reported a common posterior region for shape and texture discrimination, whereas hardness discrimination activated a more anterior location of SI. In the previous studies, the stimuli used would be classified as coarse textures, since their spatial period is above the range 0.1-0.2 mm. Although, as previously discussed, vibrations elicited when the fingers move across a textured surface, which then activate the Pacinian system, may underlie roughness perception of fine surfaces. A way of specifically targeting this system is by passively applying vibratory stimuli to the fingertips. By using fMRI and vibrotactile stimuli Nelson et al. (2004) observed that activations in SI reflect the changes in the vibrotactile amplitude which further confirms both the important role of SI in texture perception, and lends support to the idea of intensity coding for fine texture perception.

Another brain region consistently activated by tactile texture perception is the secondary somatosensory cortex (SII) which is located in the parietal operculum (PO). In contrast to SI, SII shows bilateral activation after unilateral stimulation and its neurons show larger and widely overlapping receptive fields (Burton, 1986), in line with its integrative role in somatosensory processing. Electrophysiological and histological studies in primates and humans have greatly contributed to our understanding of the structure and function of SII over the last two decades. Cytoarchitectonic studies in primates have revealed three distinct subdivisions in the SII cortex, each one of which with a complete somatotopic map (for a review see Kaas and Collins, 2003). More recently, Eickhoff and colleagues (Eickhoff et al., 2006a, 2007) studied the cytoarchitectonic organization of 10 human post-mortem brains and identified four distinct cytoarchitectonic areas in the parietal operculum (OP1-4). They further compared the SII locations reported in 57 fMRI and PET studies with the four OP subdivisions and observed a wide overlap between the two (Eickhoff et al., 2006b), concluding that the histological defined maps OP1-4 of the human parietal operculum can be interpreted as an anatomical correlate of the functionally defined SII region.

Unilateral and bilateral ablation of SII has been shown to impair texture discrimination in monkeys (Ridley and Ettlinger, 1976, 1978; Garcha and Ettlinger, 1980). Interestingly, Ridley and Ettlinger (1976) found that roughness discrimination did not appear to be affected by a bilateral removal of SII. In contrast, Murray and Mishkin (1984) reported that monkeys with bilateral SII removal were severely impaired in learning a texture discrimination task and had increased roughness discrimination thresholds. The distinction in these results may be due to the different extent of the lesions across studies.

The involvement of SII in texture perception has been further confirmed by single-unit recordings in SII neurons in monkeys (Sinclair and Burton, 1993; Jiang et al., 1997; Pruett et al., 2000, 2001). Sinclair and Burton (1993) recorded activity of SII neurons while the monkeys actively explored pairs of gratings differing in spatial period (0.75-3.15 mm) and indicated which grating was smoother. They observed that texture-sensitive SII neurons exhibited both positive and negative graded changes in firing rate with changes in the spatial period of the gratings. In another study, two monkeys were trained to discriminate a standard surface of spatial period 2.0 mm, from three other modified surfaces of spatial period 3.0, 4.0, and 5.0 mm (Jiang et al., 1997). Their results revealed that activity in the majority of the texturesensitive SI neurons was graded, while the larger majority of activation from the texture-sensitive neurons in SII was nongraded. According to the authors, one possible explanation for the discrepancy in the results is that the non-graded response from SII cells in their study may be due to SII neurons being tuned for finer textures.

More recently a series of neuroimaging studies have also revealed the involvement of PO and insula in tactile texture processing in healthy humans. In a recent fMRI study by Stilla and Sathian (in press), activity in the insula and PO was observed when subjects haptically explored different textures. Using a different approach, Kitada et al. (2005) looked at the brain activity during a tactile roughness-estimation task using fMRI. Participants were asked to estimate the roughness of three different gratings, each with a spatial period of 0.5, 1.2, or

1.5 mm, with a tactile control condition using the same textures but without performing the estimation task. Activity during the estimation task was observed in the PO and insula bilaterally and in the right, lateral, pre-frontal cortex. The PO and insula also showed significant activation in the control condition, indicating that these areas are involved in the sensory processing of the gratings rather than in the cognitive task or rating the roughness. Furthermore, graded activity was observed in the PO according to the spatial properties of the encoded stimulus.

Three different PET studies have compared roughness discrimination with length discrimination (O'Sullivan et al., 1994; Ledberg et al., 1995; Roland et al., 1998). In these studies, roughness discrimination activated PO more than length discrimination, whereas length discrimination activated the intraparietal sulcus (IPS) (O'Sullivan et al., 1994; Roland et al., 1998). These series of studies stresses that the involvement of the PO is discrimination of microgeometric properties of objects (texture) rather than their macro-geometric properties (shape and length).

The posterior parietal cortex (PPC) has also been implicated in tactile processing of texture. In monkeys it contains Brodmann's areas 5 and 7, whereas in humans these two areas only correspond to the superior part of PPC, above the intraparietal sulcus, while the inferior part of PPC includes the human specific Brodmann's areas 39 and 40 (Zilles and Palomero-Gallagher, 2001). The PPC is known as the "parietal association area" and is considered as a multisensory area that integrates tactile information with other sensory modalities (for a review see Culham and Valyear, 2006). Although activation in the IPS has been observed during grating orientation discrimination tasks (Harada et al., 2004; Van Boven et al., 2005; Zhang et al., 2005), this region seems to be specific for haptic shape rather than texture perception (O'Sullivan et al., 1994; Roland et al., 1998; Bodegard et al., 2001), as well as cross-modal shape perception (Zhang et al., 2004). For example, Roland et al. (1998) observed IPS activation during shape and length discrimination but not during roughness discrimination.

Other brain regions have also been implicated in roughness-estimation tasks, such as the right pre-frontal cortex (Kitada et al., 2005; Van Boven et al., 2005; Zhang et al., 2005). Activation in the pre-frontal cortex has been observed during the discrimination of the speed of a brush on the palm of the hand (Bodegard et al., 2000), discrimination of the length of parallelepipeds (Stoeckel et al., 2003), and discrimination of two-dot Braille characters (Harada et al., 2004). Although these areas are activated during tactile discrimination, activation seems more related to the cognitive component of the task rather than the sensory processing necessary for texture estimation.

Over the past 10 years, a large number of neuroimaging studies have focused on identifying the neural substrates of object recognition by vision, and very few studies have directly investigated visual texture perception. In any case, texture perception by vision is thought to occur in the early stages of visual processing, although the underlying mechanism or regions involved in this type of perception are not well understood. Bergen and Adelson (1988) suggest that early vision can be thought of as a process that extracts information about the material properties of an object. More recently, Landy and Graham (2004) proposed different processing mechanisms for

patterns that differ in their luminance intensity (i.e. first-order patterns) and patterns that differ in contrast or texture (i.e. second-order patterns). Based on this theory, several fMRI studies have tried to identify the brain regions involved in the processing of first- and second-order patterns (e.g. Kastner et al., 2000; Schira et al., 2004, Larsson et al., 2006, Thielscher et al., 2008). They all observed that the output of the first-stage filters in the primary visual cortex (V1) was subject to further analysis (second-stage filter) in the extrastriate cortex. Furthermore, Thielscher et al. (2008) observed parametric modulation of orientation contrast in area V4.

A recent fMRI study by Peuskens et al. (2004) investigated the processing of surface texture by asking participants to attend to either the shape or the surface texture of randomly deformed spheres presented visually. The texture specific areas, i.e. the areas that were exclusively activated by texture, were located in the collateral sulcus (CoS) and the lingual gyrus of the cortex, while shape specific areas included the lateral occipital complex (LOC) and IPS. Notably, attention to the surface properties preferentially activated regions in the ventral stream only, whereas attention to object shape activated regions in both the ventral and dorsal streams. The involvement of the CoS in visual texture perception is in line with results demonstrating that this region responds specifically to texture patterns compared to faces and letter strings (Puce et al., 1996). Similar results were obtained by Cant and Goodale (2007) during an fMRI investigation of the neural correlates of visual texture perception. They observed that the processing of the surface properties selectively activated the inferior occipital gyrus (IOG) and CoS, relative to shape tasks which selectively activated the LOC. In accordance with this, in a behavioural equivalent paper, Cant et al. (2008) observed that form and surface properties were processed independently. Here, changes in colour were successfully ignored while attending to changes in texture and vice versa. This set of neuroimaging results indicate that the CoS is a crucial brain area for texture processing by vision. Furthermore, its close anatomical proximity to the parahippocampal place area (PPA), an area normally associated with scene processing (Epstein and Kanwisher, 1998; Epstein et al., 1999) as well as behavioural evidence that surface properties aid to scene recognition, hint at the possibility of the PPA also be a part of this network of areas involved in the analysis of surface properties.

These results also confirm the existence of two different pathways in object recognition: the dorsal pathway for processing surface properties and the ventral pathways for processing geometric properties. This dissociation is further confirmed by lesion studies affecting one pathway and leaving the other intact. For example, patient D.F. who has impaired shape but not texture discrimination presents large bilateral lesions that include LOC, although her fusiform gyrus and parahippocampal cortex remain largely intact (Milner et al., 1991; Humphrey et al., 1994; James et al., 2003). Further evidence for the role of the fusiform gyrus in visual texture perception has been observed (Beason-Held et al., 1998), along with the lingual gyrus (Beason-Held et al., 1998; Peuskens et al., 2004) and other regions in the parieto-occipital cortex (POC), although these areas are not thought to be specific for texture processing per se.

The studies mentioned suggest that cortical areas of the brain that are specific for the perception of texture within each

modality. However, none of the studies mentioned investigated the role of both vision and touch on neural activity during texture perception. In the following section we address what cortical areas are involved in the common processing of texture across modalities.

6. Neural correlates of multisensory texture perception

Some studies have suggested that, in humans, activity in the visual cortex is present during tactile perception. However, many of these studies used specific shapes as stimuli, therefore, it is difficult to determine whether visual activation is due to imagery or multisensory processing. However, Sathian et al. (1997) suggest that although visual imagery has been implicated in the tactile perception of some macro-geometric properties of objects, such as shape and size, its involvement in the perception of texture is thought to be minimal. For example, they used PET during tactile discrimination of grating orientation and assessed the role of visual imagery in this task. The task was contrasted against a control spacing task where participants judged whether the ridges were too large or too small. The results revealed that the tactile grating orientation task, and not the tactile grating spacing task, significantly increased regional cerebral blood flow in the contralateral POC, a cortical region considered to be part of the visual cortex (see also Sergent et al., 1992). In a later study, Zangaladze et al. (1999) used TMS to temporarily inactivate the POC and the SI area during tactile orientation and spacing tasks. They found that disrupting the function in the POC area interfered with the discrimination of grating orientation but not the spacing task, suggesting that activation in visual areas is specific to some tactile tasks but perhaps not those involving texture. On the other hand, Merabet et al. (2004) used repetitive-TMS over the occipital cortex while subjects performed a tactile roughness discrimination task and an inter-dot spacing task. They observed that functional disruption of the occipital areas (V1/V2) impaired the spacing task but not the roughness task. This study suggests that visual areas are activated during specific tactile tasks involving texture perception, although the role of visual imagery can probably not be ruled out. For example, in another recent study by Merabet et al. (2007) tactile exploration of raised-dots patterns resulted in activation of V1 and deactivation of the extrastriate cortical regions. The results of this set of studies may indicate the involvement of visual imagery when participants are conducting a task based on more geometric (i.e. orientation) rather than material (i.e. texture) properties of a stimulus. This suggests that these two properties, orientation and roughness are distinct and are further underpinned by distinct regions of activation in the human brain.

Newman et al. (2005) specifically investigated the role of visual imagery of material and geometric properties on cortical activation when information about familiar objects was retrieved from memory. In this experiment, participants were instructed to mentally evaluate a pair of objects along either a material dimension (roughness, hardness and temperature; e.g. "what is rougher: pear or egg?") or a geometric dimension (size and shape; e.g. "what is bigger: marble or grape?"). The fMRI results showed that, although the same network of brain

areas was activated for both material and geometric properties, the IPS was more activated when participants were asked about geometric properties, whereas the extrastriate cortex was more activated for material properties. Interestingly, imagery of material properties also resulted in a small activation in the right somatosensory and pre- motor areas, although no haptic input was present. On the other hand, area LOC was equally activated for both material and geometric properties, although a trend was observed for slightly larger activation for geometric properties. Several studies have argued that LOC is a multisensory processing region involved in shape processing (see Amedi et al., 2005). However, in this study LOC was also activated for roughness imagery, but not for hardness and temperature. This might be due to the fact that roughness, although a material property, relies heavily on shape processing (i.e. the visualization of an object may provide cues to the roughness of its surface). Therefore, it is not clear whether the LOC was activated during roughness processing because of associations with object shape.

Most neuroimaging research in this area has not specifically addressed multisensory perception of texture. In a recent exception, Stilla and Sathian (in press) used fMRI to investigate visuo-tactile processing of shape and texture. Here, the authors used two sets of stimuli including objects with the same shape but with different textures, to study texture perception independently of shape. For texture, the right medial occipital cortex (MOC) in a region close to V2 was the area commonly activated by touch and vision. Although this region was more responsive to visual than to haptic textures, it had a significant activation above baseline for textures explored through touch. Despite an overlap in MOC for vision and touch in texture perception, the absence of a correlated activity between these modalities led the authors to suggest that this region is not multisensory, but may reflect the coexistence of unimodal neuronal populations.

Despite an abundant behavioural literature investigating texture perception, neuroimaging studies with this focus are still relatively sparse. Apart from utilising similar stimuli as their behavioural counterparts (e.g. gratings, raised-dot patterns), the behavioural and neuroimaging texture perception studies are reasonably distinct, and little connection is made. As the neuroimaging literature mainly investigates texture perception using vision and touch in isolation, it is difficult to conclude whether these senses are independent or integrated for texture perception. However, recent work by Stilla and Sathian (in press) which specifically looks at texture using both modalities, may hint at the senses being independent, in parallel with what can be drawn from behavioural studies. Further research is needed to better understand the relationship between both unimodal and multisensory texture perception, and activation in the brain. Other areas for future study are suggested in the following section.

7. Conclusions and future directions

Over the past century research investigating objects and their material properties has been growing. Texture perception in particular has received a great amount of attention; specifically, the ability of different senses to discriminate textures which may aid the recognition of objects has been investigated. From these explorations, it appears that few differences exist in terms of behavioural performance in texture perception across vision and touch for texture discrimination. However, the results of several studies investigating crossmodal and multisensory perception suggest that these modalities perceive texture in qualitatively different ways. As a consequence, cross-modal performance is often not as good as unimodal texture perception (e.g. Picard, 2007). Furthermore, texture discrimination does not seem to benefit from an integration of information across modalities (Lederman and Abbott, 1981; Jones and O'Neill, 1985). Evidence from neuroimaging studies suggests few cortical regions in common for touch and vision during unimodal texture perception. On the other hand, bimodal or multisensory processing of texture information seem to activate areas commonly thought of as visual areas, such as the lateral and medial occipital cortices (e.g. Stilla and Sathian, in press).

A number of potential directions for future research were apparent to the authors whilst reviewing the literature. Many studies to date on the perception of texture have used artificial stimuli, such as gratings and raised-dot patterns, where the physical parameters such as spatial frequency and amplitude can be highly controlled. However, given our remarkable ability of perceiving natural textures, especially considering the irregularities in texture information across these types of stimuli, investigations of more everyday texture perception are now very timely. A shift towards exploring the perception of more natural materials may provide beneficial information for the development of virtual environments and have important implications for industry in the design and manufacture of products with appealing textures. Utilising real materials is challenging, as the ability to control the physical characteristics of the stimulus is more difficult than for artificial stimuli. Most of the literature on texture perception focuses on the concept of roughness, while ignoring other important dimensions of texture. Ideally, it would be desirable to select a set of stimuli which, although similar, would differ across a number of dimensions such as roughness, compressibility, temperature, and luminance and examine the influence that altering one dimension at a time has on behavioural and neurophysiological results.

Additionally, although we have seen that the lateral motion exploratory procedure is optimal for texture perception (Lederman and Klatzky, 1987), of interest is whether this will hold when real textures are used. For example, a wood surface may have particular features (such as a knot) which would focus the attention of the explorer. While previous studies in tactile texture perception often control the subjects' exploration of the stimuli, this is no longer valid for visual exploration. To this end, it would be interesting to examine if unconstrained tactile and visual exploration of real textures focus on the same features (e.g. asymmetries).

Future directions in texture perception research must also involve convergent methodologies, such as behavioural studies, neuroimaging and electrophysiology. Open questions, such as the role of temporal cues in texture perception could be explored by combining techniques such as fMRI and EEG, which provide complementary information about accurate location and timings of activation. Behavioural results

have shown that, although temporal cues are available, they do not seem to be necessary for coarse or fine texture perception. Moreover, the neural underpinnings involved in temporal processing of texture information are, as yet, unknown.

Finally, in order to complement the wealth of behavioural studies, more studies investigating the neural correlates of multisensory texture perception across a range of stimuli and tasks are required. However, this is not without its challenges as one major difficulty with neuroimaging bimodal protocols is that the visual stimulus must either be displayed as an image (and therefore incurs artificiality), or the hand of the observer will be in view. This poses a problem for the design of the experiment, and introduces the limitation of manipulating the visual stimulus on dimensions such as luminance and viewpoint. Addressing these issues and moving in these directions would, in our opinion, be advantageous for the area of texture perception.

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REFERENCES

- Ageranioti-Belanger, S.A., Chapman, C.E., 1992. Discharge properties of neurones in the hand area of primary somatosensory cortex in monkeys in relation to the performance of an active tactile discrimination task. II. Area 2 as compared to areas 3b and 1. Exp. Brain Res. 91, 207–228.
- Amedi, A., von Kriegstein, K., van Atteveldt, N.M., Beauchamp, M.S., Naumer, M.J., 2005. Functional imaging of human crossmodal identification and object recognition. Exp. Brain Res. 166, 559–571.
- Ballesteros, S., Reales, J.M., Poncé de Leon, L., García, B., 2005. The perception ofecological textures by touch: does the perceptual space change under bimodal visual and haptic exploration? Proceedings of the First Joint Eurohaptics Conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems (World Haptics).
- Barlow, H.B., 1978. The efficiency of detecting changes of density in random dot patterns. Vis. Res. 18, 637–650.
- Beason-Held, L.L., Purpura, K.P., Krasuski, J.S., Maisog, J.M., Daly, E.M., Mangot, D.J., Desmond, R.E., Optican, L.M., Schapiro, M.B., VanMeter, J.W., 1998. Cortical regions involved in visual texture perception: A fMRI study. Cogn. Brain Res. 7, 111–118.
- Beck, J., 1972. Similarity grouping and peripheral discriminability under uncertainty. Am. J. Psychol. 85, 1–19.
- Beck, J., 1973. Similarity grouping of curves. Percept. Mot. Skills 36, 1331–1341.
- Bensmaïa, S.J., Hollins, M., 2003. The vibrations of texture. Somatosens Motor Res. 20, 33–43.
- Bergen, J.R., 1991. Theories of visual texture perception. In: Regan, D. (Ed.), Vision and Visual Dysfunction. Macmillan, New York, pp. 114–134.
- Bergen, J.R., Adelson, E.H., 1988. Early vision and texture perception. Nature 333, 363–364.

- Bergmann Tiest, W.M., Kappers, A.M.L., 2006. Analysis of haptic perception of materials by multidimensional scaling and physical measurements of roughness and compressibility. Acta Psychol. (Amst). 121, 1–20.
- Bergmann Tiest, W.M., Kappers, A.M.L., 2007. Haptic and visual perception of roughness. Acta Psychol. (Amst). 124, 177–189.
- Binns, H., 1936. Visual and tactual 'judgement' as illustrated in a practical experiment. Brit. J. Psychol. 27, 404–410.
- Bjorkman, M., 1967. Relations between intra-modal and cross-modal matching. Scand. J. Psychol. 8, 65–76.
- Blake, D.T., Hsiao, S.S., Johnson, K.O., 1997. Neural coding mechanisms in tactile pattern recognition: the relative contributions of slowly and rapidly adapting mechanoreceptors to perceived roughness. J. Neurosci. 17, 7480–7489
- Bodegard, A., Geyer, S., Grefkes, C., Zilles, K., Roland, P.E., 2001. Hierarchical processing of tactile shape in the human brain. Neuron 31, 317–328.
- Bodegard, A., Geyer, S., Naito, E., Zilles, K., Roland, P.E., 2000. Somatosensory areas in man activated by moving stimuli: cytoarchitectonic mapping and pet. NeuroReport 11, 187–191.
- Bolanowski, S.J., Gescheider, G.A., Verrillo, R.T., Checkosky, C.M., 1988. Four channels mediate the mechanical aspects of touch. J. Acoust. Soc. Am. 84, 1680–1694.
- Brown, I.D., 1960. Visual and tactual judgments of surface roughness. Ergonomics 3, 51–61.
- Bryant, P.E., Raz, I., 1975. Visual and tactual perception of shape by young children. Dev. Psychol. 11, 525–526.
- Burton, H., 1986. Second somatosensory cortex and related areas. In: Jones, E., Peters, A. (Eds.), Cerebral Cortex: Sensory-Motor Areas and Aspects of Cortical Connectivity. Plenum, New York, pp. 31–99.
- Cannon, L.K., 1970. Intermodality inconsistency of input and directed attention as determinants of the nature of adaptation. J. Exp. Psychol. 84, 141–147.
- Cant, J.S., Goodale, M.A., 2007. Attention to form or surface properties modulates different regions of human occipitotemporal cortex. Cereb. Cortex. 17, 713–731.
- Cant, J.S., Large, M.-E., McCall, L., Goodale, M.A., 2008. Independent processing of form, colour, and texture in object perception. Perception 37, 57–78.
- Cascio, C.J., Sathian, K., 2001. Temporal cues contribute to tactile perception of roughness. J. Neurosci. 21, 5289–5296.
- Cashdan, S., 1968. Visual and haptic form discrimination under conditions of successive stimulation. J. Exp. Psychol. 76, 215–218.
- Chapman, C.E., Ageranioti-Belanger, S.A., 1991. Discharge properties of neurones in the hand area of primary somatosensory cortex in monkeys in relation to the performance of an active tactile discrimination task. I. Areas 3b and 1. Exp. Brain Res. 87, 319–339.
- Connor, C.E., Johnson, K.O., 1992. Neural coding of tactile texture: comparison of spatial and temporal mechanisms for roughness perception. J. Neurosci. 12, 3414–3426.
- Connor, C.E., Hsiao, S.S., Phillips, J.R., Johnson, K.O., 1990. Tactile roughness: neural codes that account for psychophysical magnitude estimates. J. Neurosci. 10, 3823–3836.
- Culham, J.C., Valyear, K.F., 2006. Human parietal cortex in action. Curr. Opin. Neurobiol. 16, 205–212.
- Darian-Smith, I., Sugitani, M., Heywood, J., Karita, K., Goodwin, A.W., 1982. Touching textured surfaces: cells in somatosensory cortex respond both to finger movement and to surface features. Science 218, 906–909.
- De Valois, R.L., De Valois, K.K., 1988. Spatial Vision. Oxford University Press, New York.
- Durgin, F.H., 1995. Texture density adaptation and the perceived numerosity and disctribution of texture. J. Exp. Psychol. 21, 149–169.

- Easton, R.D., Greene, A.J., Srinivas, K., 1997. Transfer between vision and haptics: memory for 2-d and 3-d objects. Psychon. Bull. Rev. 4, 403–410.
- Eickhoff, S.B., Amunts, K., Mohlberg, H., Zilles, K., 2006a. The human parietal operculum. II. Stereotaxic maps and correlation with functional imaging results. Cereb. Cortex. 16, 268–279.
- Eickhoff, S.B., Schleicher, A., Zilles, K., Amunts, K., 2006b. The human parietal operculum. I. Cytoarchitectonic mapping of subdivisions. Cereb. Cortex. 16, 254–267.
- Eickhoff, S.B., Grefkes, C., Zilles, K., Fink, G.R., 2007. The somatotopic organization of cytoarchitectonic areas on the human parietal operculum. Gereb. Cortex. 17, 1800–1811.
- Ekman, G., Hosman, J., Lindstrom, B., 1965. Roughness, smoothness, and preference: a study of quantitative relations in individual subjects. J. Exp. Psychol. 70, 18–26.
- Epstein, R., Harris, A., Stanley, D., Kanwisher, N., 1999. The parahippocampal place area: recognition, navigation, or encoding? Neuron 23, 115–125.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. Nature 392, 598–601.
- Ernst, M.O., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415, 429–433.
- Ernst, M.O., Lange, C., Newell, F.N., 2007. Multisensory recognition of actively explored objects. Can. J. Exp. Psycyhol. 61, 242–253.
- Findlay, J.M., Gilchrist, I.D., 2003. Active Vision: The Psychology of Looking and Seeing. Oxford University Press, Oxford, UK.
- Gamzu, E., Ahissar, E., 2001. Importance of temporal cues for tactile spatial-frequency discrimination. J. Neurosci. 21, 7416–7427.
- Garcha, H.S., Ettlinger, G., 1980. Tactile discrimination learning in the monkey: The effects of unilateral or bilateral removals of the second somatosensory cortex (area SII). Cortex 16, 397–412.
- Gescheider, G.A., Bolanowski Jr., S.J., Greenfield, T.C., Brunette, K.E., 2005. Perception of the tactile texture of raised dot patterns: a multidimensional analysis. Somatosens. Motor Res. 22, 127–140.
- Gescheider, G.A., Bolanowski, S.J., Hardick, K., 2001. The frequency selectivity of information-processing channels in the tactile sensory system. Somatosens. Motor Res. 18, 191–201.
- Gescheider, G.A., Bolanowski, S.J., Pope, J., Verrillo, R.T., 2002. A four-channel analysis of the tactile sensitivity of the fingertip: frequency selectivity, spatial summation, and temporal summation. Somatosens. Motor Res. 19, 114–124.
- Gibson, J.J., 1933. Adaptation, after-effect, and contrast in the perception of curved lines. J. Exp. Psychol. 16, 1–31.
- Gibson, J.J., Radner, M., 1937. Adaptation, after-effect, and contrast in the perception of tilted lines: I. Quantitative studies. J. Exp. Psychol. 20, 453–467.
- Ginsburg, N., Goldstein, S.R., 1987. Measurement of visual cluster. Am. J. Psychol. 100, 193–203.
- Goodwin, A.W., Morley, J.W., 1987a. Sinusoidal movement of a grating across the monkey's fingerpad: Representation of grating and movement features in afferent fiber responses. J. Neurosci. 7, 2168–2180.
- Goodwin, A.W., Morley, J.W., 1987b. Sinusoidal movement of a grating across the monkey's fingerpad: effect of contact angle and force of grating on afferent fiber responses. J. Neurosci. 7, 2192–2202.
- Goodwin, A.W., John, K.T., Sathian, K., Darian-Smith, I., 1989. Spatial and temporal factors determining afferent fiber responses to a grating moving sinusoidally over the monkey's fingerpad. J. Neurosci. 9, 1280–1293.
- Graham, N.V.S., 1989. Visual Pattern Analyzers. Oxford University Press, New York.
- Graham, N.V.S., 1992. Breaking the visual stimulus into parts. Curr. Dir. Psychol. Sci. 1, 55–61.
- Guest, S., Spence, C., 2003. What role does multisensory integration play in the visuotactile perception of texture? Int. J. Psychophysiol. 50, 63–80.

- Guest, S., Catmur, C., Lloyd, D., Spence, C., 2002. Audiotactile interactions in roughness perception. Exp. Brain Res. 146, 161–171.
- Harada, T., Saito, D.N., Kashikura, K., Sato, T., Yonekura, Y., Honda, M., Sadato, N., 2004. Asymmetrical neural substrates of tactile discrimination in humans: a functional magnetic resonance imaging study. J. Neurosci. 24, 7524–7530.
- Heller, M.A., 1982. Visual and tactual texture perception: Intersensory cooperation. Percept. Psychophys. 31, 339–344.
- Heller, M.A., 1989. Texture perception in sighted and blind observers. Percept. Psychophys. 45, 49–54.
- Ho, Y.X., Maloney, L.T., Landy, M.S., 2007. The effect of viewpoint on perceived visual roughness. J. Vision. 7, 1.
- Hollins, M., Risner, S.R., 2000. Evidence of the duplex theory of tactile texture perception. Percept. Psychophys. 62, 695–705.
- Hollins, M., Bensmaïa, S.J., 2007. The coding of roughness. Can. J. Exp. Psycyhol. 61, 184–195.
- Hollins, M., Faldowski, R., Rao, S., Young, F., 1993. Perceptual dimensions of tactile surface texture: a multidimensional scaling analysis. Percept. Psychophys. 54, 697–705.
- Hollins, M., Bensmaïa, S.J., Risner, S.R., 1998. The duplex theory of tactile texture perception. In: Grondin, S., Lacouture, Y. (Eds.), Proceedings of the 14th Annual Meeting of the International Society for Psychophysics. The International Society for Psychophysics, Québec, Canada, pp. 115–120.
- Hollins, M., Bensmaïa, S.J., Karlof, K., Young, F., 2000a. Individual differences in perceptual space for tactile textures: evidence from multidimensional scaling. Percept. Psychophys. 62, 1534–1544.
- Hollins, M., Fox, A., Bishop, C., 2000b. Imposed vibration influences perceived tactile smoothness. Perception 29, 1455–1465.
- Hollins, M., Bensmaïa, S.J., Washburn, S., 2001. Vibrotactile adaptation impairs discrimination of fine, but not coarse, textures. Somatosens. Motor Res. 18, 253–262.
- Hollins, M., Bensmaïa, S.J., Roy, E.A., 2002. Vibrotaction and texture perception. Behav. Brain Res. 135, 51–56.
- Hollins, M., Lorenz, F., Harper, D., 2006. Somatosensory coding of roughness: the effect of texture adaptation in direct and indirect touch. J. Neurosci. 26, 5582–5588.
- Humphrey, G.K., Goodale, M.A., Jakobson, L.S., Servos, P., 1994. The role of surface information in object recognition: studies of a visual form agnosic and normal subjects. Perception 23, 1457, 1481
- James, T.W., Culham, J., Humphrey, G.K., Milner, A.D., Goodale, M.A., 2003. Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. Brain 126, 2463–2475.
- Jiang, W., Tremblay, F., Chapman, C.E., 1997. Neuronal encoding of texture changes in the primary and the secondary somatosensory cortical areas of monkeys during passive texture discrimination. J. Neurophysiol. 77, 1656–1662.
- Johansson, R.S., Vallbo, A.B., 1979. Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. J. Physiol. (Lond.) 286, 283–300
- Jones, L.A., Lederman, S.J., 2006. Human Hand Function. Oxford University Press, New York.
- Jones, B., O'Neill, S., 1985. Combining vision and touch in texture perception. Percept. Psychophys. 37, 66–72.
- Jousmaki, V., Forss, N., 1998. Effects of stimulus intensity on signals from human somatosensory cortices. NeuroReport 9, 3427–3431.
- Julesz, B., 1981. Textons, the elements of texture perception, and their interactions. Nature 290, 91–97.
- Julesz, B., Gilbert, E.N., Victor, J.D., 1978. Visual discrimination of textures with identical third-order statistics. Biol. Cybern. 31, 137–140.
- Kaas, J.H., Collins, C.F., 2003. The organization of somatosensory cortex in anthropoid primates. Adv. Neurol. 93, 57–67.

- Kastner, S., De Weerd, P., Ungerleider, L.G., 2000. Texture segregation in the human visual cortex: a functional MRI study. J. Neurophysiol. 83, 2453–2457.
- Katz, D., 1925. Der aufbau der tastwelt [the world of touch]. Z. Psychol. 11.
- Kelso, J., Cook, E., Olson, M., Epstein, W., 1975. Allocation of attention and the locus of adaptation to displaced vision. J. Exp. Psychol. Hum. Percept. Perform 1, 237–245.
- Kitada, R., Hashimoto, T., Kochiyama, T., Kito, T., Okada, T., Matsumura, M., Lederman, S.J., 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.
- Klatzky, R.L., Lederman, S.J., 1987. The Intelligent Hand. Academic Press, San Diego.
- Klatzky, R.L., Lederman, S.J., Reed, C.L., 1987. There's more to touch than meets the eye: the salience of object attributes for haptics with and without vision. J. Exp. Psychol. Gen. 116, 356–369.
- Klatzky, R.L., Lederman, S.J., Reed, C.L., 1989. Haptic integration of object properties: texture, hardness and planar contour. J. Exp. Psychol. Hum. Percept. Perform. 15, 45–57.
- Lamb, G.D., 1983. Tactile discrimination of textured surfaces: psychophysical performance measurements in humans. J. Physiol. 338, 551–565.
- Landy, M.S., 1996. Texture perception. In: Adelman, G. (Ed.), Encyclopedia of Neuroscience. Elsevier, Amsterdam.
- Landy, M.S., Graham, N., 2004. Visual perception of texture. In: Chalupa, L., Werner, J.S. (Eds.), The Visual Neurosciences. MIT Press, Cambridge, MA, pp. 1106–1118.
- Larsson, J., Landy, M.S., Heeger, D.J., 2006. Orientation-selective adaptation to first- and second-order patterns in human visual cortex. J. Neurophysiol. 95, 862–881.
- Ledberg, A., O'Sullivan, B.T., Kinomura, S., Roland, P.E., 1995.
 Somatosensory activations of the parietal operculum of man. A pet study. Eur. J. Neurosci. 7, 1934–1941.
- Lederman, S.J., Taylor, M.M., 1972. Fingertip force, surface geometry and the perception of roughness by active touch. Percept. Psychophys. 12, 401–408.
- Lederman, S.J., 1979. Auditory texture perception. Perception 8, 93–103
- Lederman, S.J., 1981. The perception of surface roughness by active and passive touch. Bull Psychon. Soc. 18, 253–255.
- Lederman, S.J., 1982. The perception of texture by touch. In: Schiff, W., Foulke, E. (Eds.), Tactual Perception. Cambridge University Press, Cambridge, UK, pp. 130–167.
- Lederman, S.J., 1983. Tactual roughness perception: spatial and temporal determinants. Can. J. Psychol. 37, 498–511.
- Lederman, S.J., Abbott, S.G., 1981. Texture perception: studies of intersensory organization using a discrepancy paradigm, and visual versus tactual psychophysics. J. Exp. Psychol. Hum. Percept. Perform. 7, 902–915.
- Lederman, S.J., Klatzky, R.L., 1987. Hand movements: a window into haptic object recognition. Cogn. Psychol. 19, 342–368.
- Lederman, S.J., Klatzky, R.L., 2004. Multisensory texture perception. In: Calvert, G.A., Spence, C., Stein, B.E. (Eds.), The Handbook of Multisensory Processes. MIT Press, London, UK.
- Lederman, S.J., Thorne, G., Jones, B., 1986. Perception of texture by vision and touch: multidimensionality and intersensory integration. J. Exp. Psychol. Hum. Percept. Perform. 12, 169–180.
- Marks, L.E., 1978. The Unity of the Senses: Interrelations Among the Modalities. Academic Press, New York.
- Marr, D., 1976. Early processing of visual information. Phil. T. R. Soc. B 275, 483–518.
- Marr, D., 1982. Vision: A Computational Investigation into the Human Representation and Processing of Visual Information. Freeman, San Francisco, CA.
- McGlone, F.P., Vallbo, A.B., Olausson, H., Loken, L., Wessberg, J., 2007. Discriminative touch and emotional touch. Can. J. Exp. Psycyhol. 61, 173–183.

- Meltzoff, A.N., Borton, R.W., 1979. Intermodal matching by human neonates. Nature 282, 403–404.
- Menees, M., Zigler, M.J., 1923. An experimental study of the perceptions roughness and smoothness. Am. J. Psychol. 34, 542–549.
- Merabet, L., Thut, G., Murray, B., Andrews, J., Hsiao, S., Pascual-Leone, A., 2004. Feeling by sight or seeing by touch? Neuron 42, 173–179.
- Merabet, L.B., Swisher, J.D., McMains, S.A., Halko, M.A., Amedi, A., Pascual-Leone, A., Somers, D.C., 2007. Combined activation and deactivation of the visual cortex during tactile sensory processing. J. Neurophysiol. 97, 1633–1641.
- Millar, S., 1994. Understanding and Representing Space. Oxford University Press, Oxford, UK.
- Milner, A.D., Bryant, P.E., 1970. Cross-modal matching by young children. J. Comp. Physiol. Psych. 71, 453–458.
- Milner, A.D., Perrett, D.I., Johnston, R.S., Benson, P.J., Jordan, T.R., Heeley, D.W., et al., 1991. Perception and action in 'visual form agnosia'. Brain 114, 405–428.
- Miyaoka, T., Mano, T., Ohka, M., 1999. Mechanisms of fine-surface-texture discrimination in human tactile sensation. J. Acoust. Soc. Am. 105, 2485–2492.
- Molina, M., Jouen, F., 2001. Modulation of manual activity by vision in human newborns. Dev. Psychol. 38, 123–132.
- Morley, J.W., Goodwin, A.W., 1987. Sinusoidal movement of a grating across the monkey's fingerpad: temporal patterns of afferent fiber responses. J. Neurosci. 7, 2181–2191.
- Murray, E.A., Mishkin, M., 1984. Relative contributions of sii and area 5 to tactile discrimination in monkeys. Behav. Brain Res. 11, 67–83
- Nelson, A.J., Staines, W.R., Graham, S.J., McIlroy, W.E., 2004. Activation in SI and SII: the influence of vibrotactile amplitude during passive and task-relevant stimulation. Brain Res. Cogn. Brain Res. 19, 174–184.
- Newell, F.N., Ernst, M.O., Tjan, B.S., Bülthoff, H.H., 2001. Viewpoint dependence in visual and haptic object recognition. Psychol. Sci. 12, 37–42.
- Newman, S.D., Klatzky, R.L., Lederman, S.J., Just, M.A., 2005. Imagining material versus geometric properties of objects: an fMRI study. Cogn. Brain Res. 23, 235–246.
- Olson, R.K., Attneave, F., 1970. What variables produce similarity grouping? Am. J. Psychol. 83, 1–21.
- O'Sullivan, B.T., Roland, P.E., Kawashima, R., 1994. A PET study of somatosensory discrimination in man. Microgeometry versus macrogeometry. Eur. J. Neurosci. 6, 137–148.
- Oxford English Dictionary. Oxford University Press. Retrieved Jan. 30, 2008 from http://www.askoxford.com/concise_oed/texture.
- Peuskens, H., Claeys, K.G., Todd, J.T., Norman, J.F., Van Hecke, P., Orban, G.A., 2004. Attention to 3-D shape, 3-D motion, and texture in 3-D structure from motion displays. J. Cogn. Neurosci. 16, 665–682.
- Picard, D., 2006. Partial perceptual equivalence between vision and touch for texture information. Acta Psychol. (Amst.) 121, 227–248.
- Picard, D., 2007. Tactual, visual, and cross-modal transfer of texture in 5- and 8-year-old children. Perception 36, 722–736.
- Picard, D., Dacremont, C., Valentin, D., Giboreau, A., 2003. Perceptual dimensions of tactile textures. Acta Psychol. (Amst). 114, 165–184.
- Pruett Jr., J.R., Sinclair, R.J., Burton, H., 2000. Response patterns in second somatosensory cortex (SII) of awake monkeys to passively applied tactile gratings. J. Neurophysiol. 84, 780–797.
- Pruett Jr., J.R., Sinclair, R.J., Burton, H., 2001. Neural correlates for roughness choice in monkey second somatosensory cortex (SII). J. Neurophysiol. 86, 2069–2080.
- Puce, A., Allison, T., Asgari, M., Gore, J.C., 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.

- Randolph, M., Semmes, J., 1974. Behavioral consequences of selective subtotal ablations in the postcentral gyrus of macaca mulatta. Brain Res. 70, 55–70.
- Rexroad, K., White, H., 1987. Sex differences in visual and tactual modes of texture discrimination. J. Genet. Psychol. 149, 131–132
- Ridley, R.M., Ettlinger, G., 1976. Impaired tactile learning and retention after removals of the second somatic sensory projection cortex (SII) in the monkey. Brain Res. 109, 656–660.
- Ridley, R.M., Ettlinger, G., 1978. Further evidence of impaired tactile learning after removals of the second somatic sensory projection cortex (SII) in the monkey. Exp. Brain Res. 31, 475–488.
- Rock, I., Victor, J.D., 1964. Vision and touch: an experimentally created conflict between the two senses. Science 143, 594–596.
- Roland, P.E., O'Sullivan, B., Kawashima, R., 1998. Shape and roughness activate different somatosensory areas in the human brain. P. Natl. Acad. Sci. 95, 3295–3300.
- Sailer, U., Eggert, T., Ditterich, J., Hassenzahl, M., Straube, A., 2003. Haptic texture affects the kinematics of pointing movements, but not of eye movements. NeuroReport 14, 467–469.
- Sann, C., Streri, A., 2007. Perception of object shape and texture in human newborns: evidence from cross-modal transfer tasks. Dev. Sci. 10, 399–410.
- Sathian, K., Burton, H., 1991. The role of spatially selective attention in the tactile perception of texture. Percept. Psychophys. 50, 237–248.
- Sathian, K., Goodwin, A.W., John, K.T., Darian-Smith, I., 1989.
 Perceived roughness of a grating: correlation with responses of mechanoreceptive afferents innervating the monkey's fingerpad. J. Neurosci. 9, 1273–1279.
- Sathian, K., Zangaladze, A., Hoffman, J.M., Grafton, S.T., 1997. Feeling with the mind's eye. NeuroReport 8, 3877–3881.
- Schifferstein, H.N.J., 2006. The perceived importance of sensory modalities in product usage: a study of selfreports. Acta Psychol. (Amst.) 121, 41–64.
- Schifferstein, H.N.J., Cleiren, M.P.H.D., 2005. Capturing product experiences: a split-modality approach. Acta Psychol. (Amst.) 118, 293–318.
- Schira, M.M., Fahle, M., Donner, T.H., Kraft, A., Brandt, S.A., 2004. Differential contribution of early visual areas to the perceptual process of contour processing. J. Neurophysiol. 91, 1716–1721.
- Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 115, 15–36.
- 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.
- Sinclair, R., Burton, H., 1988. Responses from area 3b of somatosensory cortex to textured surfaces during active touch in primate. Somatosens. Res. 5, 283–310.
- Sinclair, R., Burton, H., 1993. Neuronal activity in the second somatosensory cortex of monkeys (macaca mulatta) during active touch of gratings. J. Neurophysiol. 70, 331–350.
- Smith, A.M., Chapman, C.E., Deslandes, M., Langlais, J.S., Thibodeau, M.P., 2002. Role of friction and tangential force variation in the subjective scaling of tactile roughness. Exp. Brain Res. 144, 211–223.
- Stilla, R., Sathian, K., in press. Selective visuo-haptic processing of shape and texture. Hum. Brain Mapp. Corrected proof.
- Stoeckel, M.C., Weder, B., Binkofski, F., Buccino, G., Shah, N.J., Seitz, R.J., 2003. A fronto-parietal circuit for tactile object

- discrimination: an event-related fMRI study. NeuroImage 19, 1103–1114.
- Sutherling, W.W., Levesque, M.F., Baumgartner, C., 1992. Cortical sensory representation of the human hand: size of finger regions and nonoverlapping digit somatotopy. Neurology 42, 1020–1028.
- Taylor, M.M., Lederman, S.J., Gibson, R.H., 1973. Tactual perception of texture. In: Carterette, E., Friedman, M. (Eds.), Handbook of Perception. Academic press, New York.
- Thielscher, A., Kölle, M., Neumann, H., Spitzer, M., Grön, G., 2008. Texture segmentation in human perception: a combined modelling and fMRI study. Neuroscience 151, 730–736.
- Vallbo, A.B., Johansson, R.S., 1984. Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. Hum. Neurobiol. 3, 3–14.
- Van Boven, R.W., Ingeholm, J.E., Beauchamp, M.S., Bikle, P.C., Ungerleider, L.G., 2005. Tactile form and location processing in the human brain. Proc. Natl. Acad. Sci. U. S. A. 102, 12601–12605.
- Van Boven, R.W., Johnson, K.O., 1994. The limit of tactile spatial resolution in humans: grating orientation discrimination at the lip, tongue, and finger. Neurology 44, 2361–2366.
- Verrillo, R.T., 1999. Subjective magnitude of tactile roughness. Somatosens. Motor Res. 16, 352–360.
- Verrillo, R.T., Gescheider, G.A., 1975. Enhancement and summation in the perception of two successive vibrotactile stimuli. Percept. Psychophys. 18, 128–136.
- Verrillo, R.T., Gescheider, G.A., 1977. Effect of prior stimulation on vibrotactile thresholds. Sens. Process 1, 292–300.
- Verrillo, R.T., Gescheider, G.A., Calman, B.G., Van Doren, C.L., 1983. Vibrotactile masking: effects of one and two-site stimulation. Percept. Psychophys. 33, 379–387.
- von Scheiller, P., 1932. Die rauhigkeit als intermodale erscheinung. [roughness as an intermodal phenomenon]. Z. Psychol. 127, 265–289.
- Warren, D.H., 1979. Spatial localization under conflict conditions-is there a single explanation? Perception 8, 323–338.
- Welch, R.B., Warren, D.H., 1980. Immediate perceptual response to intersensory discrepancy. Psychol. Bull. 88, 638–667.
- Welch, R.B., Widawski, M.H., Harrington, J., Warren, D.H., 1979. An examination of the relationship between visual capture and prism adaptation. Percept. Psychophys. 25, 126–132.
- Yoshida, M., 1968a. Dimensions of tactual impressions (1). Jpn. Psychol. Res. 10, 123–137.
- Yoshida, M., 1968b. Dimensions of tactual impressions (2). Jpn. Psychol. Res. 10, 157–173.
- Yoshioka, T., Gibb, B., Dorsch, A.K., Hsiao, S.S., Johnson, K.O., 2001. Neural coding mechanisms underlying perceived roughness of finely textured surfaces. J. Neurosci. 21, 6905–6916.
- Zangaladze, A., Epstein, C.M., Grafton, S.T., Sathian, K., 1999. Involvement of visual cortex in tactile discrimination of orientation. Nature 401, 587–590.
- Zhang, M., Weisser, V.D., Stilla, R., Prather, S.C., Sathian, K., 2004. Multisensory cortical processing of object shape and its relation to mental imagery. Cogn. Affect. Behav. Neurosci. 4, 251–259
- 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.
- Zilles, K., Palomero-Gallagher, N., 2001. Cyto-, myelo-, and receptor architectonics of the human parietal cortex. NeuroImage 14, S8–20.