Chapter 15
Haptic Face Processing and Its Relation to Vision

Susan J. Lederman, Roberta L. Klatzky, and Ryo Kitada

15.1 Overview

Visual face processing has strong evolutionary significance for many biological species because the face conveys information that is critically important to biological survival: predator or prey? friend or enemy? potential mate? A substantial research literature in cognitive psychology, cognitive science, and cognitive neuroscience has established that face processing is an essential function of visual perception, to such an extent that a subset of visual abilities, sometimes referred to as a "face module," may be dedicated to it. Criteria for such face skills are often derived from arguments that face processing is not only universal in humans but also observed in other species, developmentally early to emerge, and performed by highly specialized cortical areas.

Numerous detailed published reviews and books have been published on visual face processing (e.g., Adolphs, 2002; Bruce and Young, 1998; Peterson and Rhodes, 2003). Compared to other object categories, the general hallmarks of visual processing for facial identity are that it is (a) highly practiced (Gauthier et al., 2003; see also McKone and Kanwisher, 2004); (b) predominantly based on overall configuration (de Gelder and Rouw, 2000; Farah et al., 1995; Maurer et al. 2002); (c) orientation specific (e.g., Diamond and Carey, 1986; Farah et al., 1995; Freire et al., 2000; Leder and Bruce, 2000; Maurer et al., 2002; Sergent, 1984); and (d) identity specific (Bruce and Young, 1998).

Not surprisingly, almost all of the face research from which these general principles derive involves the visual system. However, recent research reveals that humans are also capable of haptically recognizing both facial identity and facial expressions of emotion in live faces, 3-D face masks (rigid molds taken from live faces) and 2-D raised-line depictions. Such results clearly confirm that face processing is not unique to vision.

S.J. Lederman (✉)
Department of Psychology, Queen's University, Kingston, ON K7L 3N6, Canada
e-mail: susan.lederman@queensu.ca

M.J. Naumer, J. Kaiser (eds.), *Multisensory Object Perception in the Primate Brain*,
DOI 10.1007/978-1-4419-5615-6_15,

The current chapter will focus primarily on the research literature pertaining to the haptic extraction of facial identity and facial expressions of emotion, two aspects of face perception that have received considerable attention from vision scientists. In particular, we will address a number of questions concerning functional aspects that pertain to how humans *process* and *represent* facial identity and emotional expressions, together with the *neural mechanisms* that underlie these functions. We note that information-processing theorists make a fundamental distinction between representation and process: whereas "representation" refers to the data on which computational operations are performed, "process" refers to the operations themselves.

Theoretically, we conceptualize face processing as involving haptic or visual object-recognition systems that are likely to show both commonalities *and* differences in facial processes and representations, whether expressed in functional or neural terms. Hence, our discussions of facial identity and emotion perception will each begin with a brief survey of the relevant vision literature, followed by a more extensive consideration of haptic face processing, on its own and as it relates to vision.

15.2 Facial Identity

15.2.1 Visual Perception of Facial Identity

Humans are clearly highly effective at perceiving, recognizing, and identifying individuals on the basis of information that is visually extracted from faces.

15.2.1.1 How Does the Visual System *Process* Facial Identity?

Of critical concern to vision researchers is whether face processing is based primarily on the facial configuration (i.e., features *and* their spatial interrelations) or more on the features themselves. Much of the visual face research has unequivocally emphasized the primacy of configural processes (Maurer et al., 2002).

Early studies used evidence of the "face inversion effect" (i.e., upright faces are better recognized than inverted faces) to confirm the importance of configural processing, arguing that inverting faces impair the viewer's ability to process faces configurally (e.g., Diamond and Carey, 1986; Sergent, 1984; Yin, 1969). However, Maurer et al. (2002) have since noted that on its own, the face inversion paradigm does not unambiguously evaluate the contribution of configural processing. After all, face inversion may impair performance for other reasons, such as disrupting information about the features *per se*, or because of inexperience in identifying inverted faces.

A number of subsequent studies have included other experimental manipulations in conjunction with the face inversion paradigm to provide stronger support for the claim that inverting the face interferes with configural processing. For example, Farah et al. (1995) first trained participants to identify a series of upright faces by name, based on either the whole face or only one part (e.g., nose). In a subsequent identification test using new upright or inverted versions of the training faces, "whole-face" training produced an inversion effect, but "part-face" training failed to do so (see Fig. 15.1). The latter result suggests that the initial part-face presentation impeded configural processing.

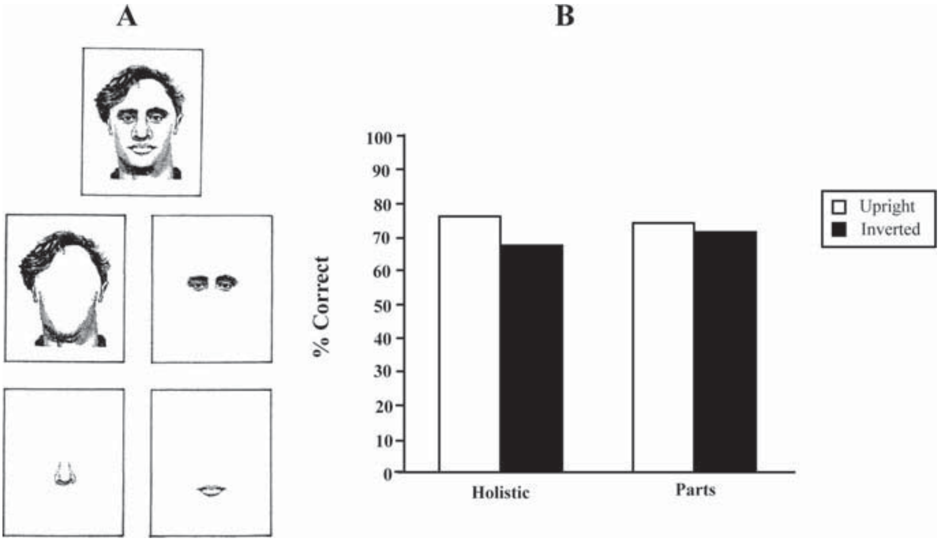

Fig. 15.1 One of the stimulus faces employed by Farah et al. (1995) Experiment 2. (**a**) The top is a sample "holistic" face; below are four "part" versions of the same face. Note that during the subsequent test phase, only the holistic versions were presented. (**b**) Results from Farah et al. (Experiment 2) indicate that the face inversion effect was eliminated when participants were trained to encode faces by their parts. Reprinted with permission of the American Psychological Association

Freire et al. (2000) asked participants to discriminate upright or inverted faces that differed in configural information, that is, the eyes and mouths were slightly shifted in their locations although the features remained unchanged. Using the figural discrepancies, they could easily discriminate the upright faces but not the inverted ones. In contrast, participants could discriminate faces that differed in their features equally well in upright and inverted conditions. This pattern of results further suggests that face inversion disrupts configural, but not featural, processes.

Researchers have also used several other experimental paradigms that strongly support the primacy of the face configuration in processing upright faces. For example, "scrambling" facial features (e.g., Collishaw and Hole, 2000) and combining or "morphing" the halves of different faces (e.g., Hole, 1994) both alter the normal facial configuration while leaving the features unchanged. Inverting features within a face (the "Thatcher effect") also appears to disrupt configural processing (Boutsen and Humphreys, 2003). Conversely, "blurring" facial features alter the features themselves while leaving the face configuration unchanged. Collectively, the results of such studies confirm that the accuracy with which facial identity is recognized is disrupted more when the configuration of the face is altered, as opposed to the features themselves.

In addition to studying those who are neurologically intact, visual face researchers have focused on a clinical population of persons diagnosed with "prosopagnosia." While such people can identify faces at the "basic" category level (Rosch et al., 1976), they demonstrate limited, if any, success in visually differentiating individual faces. Some have sustained clear trauma through acute accident or disease ("adventitious" prosopagnosia); in contrast, others have no known brain damage and normal early visual processing systems ("developmental" prosopagnosia). While all researchers concur that some aspects of the visual system are not functioning appropriately, they disagree as to the domain of mechanisms that are damaged, and thus, on the object classes that those mechanisms regulate (Duchaine et al., 2006). In this chapter, we limit discussion of prosopagnosia to how it informs us about our primary focus, namely, haptic face perception.

15.2.1.2 How Does the Visual System R*epresent* Facial Identity?

The nature of visual representation of facial identity has been functionally addressed by asking two important questions: (a) Is any specific face orientation "privileged" (i.e., more accessible to perception and memory)? and (b) Do features of the face differ with respect to their salience in the facial representation; if so, how?

The first of these issues is not independent from process, as discussed in the previous section. In addition to indicating configuration-based processing of facial identity, a strong face inversion effect speaks to the role of orientation in the facial representation. That the identity of upright visually presented faces is commonly recognized more accurately than inverted faces suggests that the upright orientation is canonical or "privileged."

With respect to the second question, a variety of techniques have been employed to assess the relative salience of facial features. These include, for example, the study of eye movements, psychophysical experiments with spatially filtered stimuli, multidimensional scaling, and the use of subjective questionnaires. In general, the region around the eyes appears to be most important for visual face recognition (e.g., Keating and Keating, 1982; Leder et al., 2001; Mangini and Biederman, 2004; Schyns et al., 2002; Sekuler et al., 2004); more precisely, people visually attend foremost to the eyebrows (Schyns et al., 2002), followed in descending order of importance by the eyes, mouth, and, finally, nose (Fraser et al., 1990; Haig, 1986; Janik et al., 1978).

15.2.1.3 What Are the *Neural Mechan*isms that Underlie Visual Perception of Facial Identity?

Visual neuroscience has further contributed to our understanding of human face perception by investigating the neural mechanisms that underlie a variety of important functions, including but not restricted to the perception of facial identity. This topic has received much attention, and the interested reader may consult Haxby et al. (2000) and Posamentier and Abdi, (2003).

Haxby et al. (2000) have proposed that human face perception is mediated by a hierarchically organized, distributed neural network that involves multiple bilateral regions (Fig. 15.2), including but not limited to the FFA. This model functionally distinguishes between the representation of invariant facial characteristics, such as identity, and variable aspects such as expression, eye gaze, and lip movement that all contribute to social communication. Collectively, fMRI studies have revealed the significance of three regions in the occipitotemporal extrastriate area: (a) bilateral regions in the lateral fusiform gyrus (i.e., fusiform face area, or FFA: Clark et al., 1996; Hadjikhani and de Gelder, 2002; Halgren et al., 1999; Haxby et al., 1994; Kanwisher et al., 1997; McCarthy et al., 1997), (b) lateral inferior occipital gyri (Hadjikhani and de Gelder, 2002; Halgren et al., 1999; Hoffman and Haxby, 2000; Levy et al., 2001; Puce et al., 1996), and (c) posterior superior temporal sulcus (Halgren et al., 1999; Haxby et al., 1999; Hoffman and Haxby, 2000; McCarthy et al., 1997; Puce et al., 1998). Researchers have long argued that the FFA uniquely contributes to face recognition, although others have recast its role in terms of a module for the perception of faces *and* non-face objects for which the observer possesses a high degree of expertise (Gauthier et al., 1999).

Ultimately, the ever-increasing sophistication in technologies (e.g., combination of different neuroimaging techniques, multi-electrode stimulation/recording techniques, and computational modeling) will enhance our understanding of the distributed neural networks and computations that underlie the multiple functions of face perception.

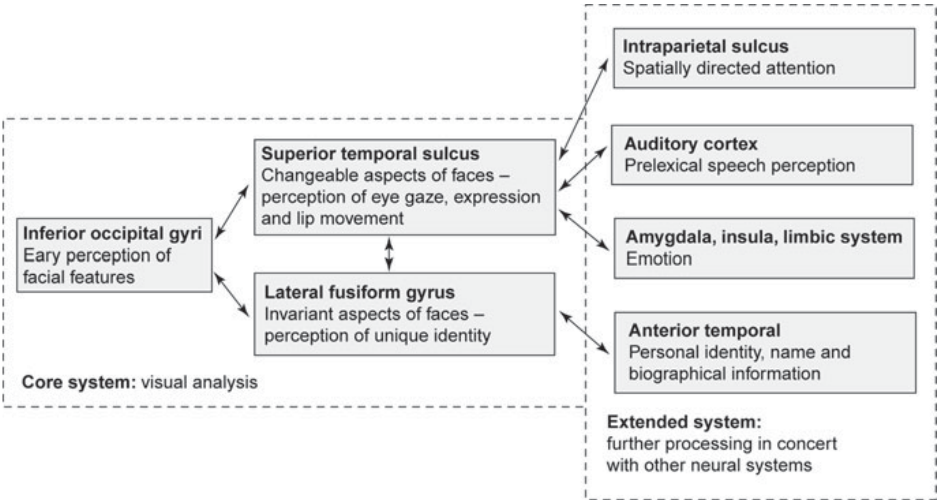

Fig. 15.2 Haxby et al.'s model of a distributed neural system for perceiving human faces. The system is composed of a core system used for visual face analysis and an extended system used for additional processing of the meaning of the facial information. Reprinted from Haxby et al. (2000) with permission of Elsevier Ltd

15.2.2 Haptic Perception of Facial Identity

Whether sighted or blind, individuals rarely choose to recognize a person by manually exploring their face. While this may be true, are they *capable* of doing so; alternatively, is face perception strictly a visual phenomenon? We now know that people can haptically discriminate and identify both unfamiliar and familiar live faces and corresponding clay face masks at levels considerably above chance (Kilgour and Lederman, 2002; see also Casey and Newell, 2003; Pietrini et al., 2004). In the Kilgour and Lederman (2002) study, blindfolded sighted college students haptically matched the facial identity of live actors with a success rate of 80% (chance = 33%), as shown in Fig. 15.3. When rigid face masks were used, accuracy declined to about 60%; nevertheless, performance remained well above chance. Kilgour et al. (2005) subsequently showed that with considerable training, people could learn to identify face masks by name perfectly. More recently, McGregor et al. (2010) have shown that such individuals are also capable of learning to name individual 2-D raised-line drawings of individual faces, with accuracy improving by ∼ 60% after only five blocks of training with feedback. Finally, Kilgour et al. (2004) have confirmed the first known case of haptic prosopagnosia, a condition in which the individual was unable to haptically differentiate faces.

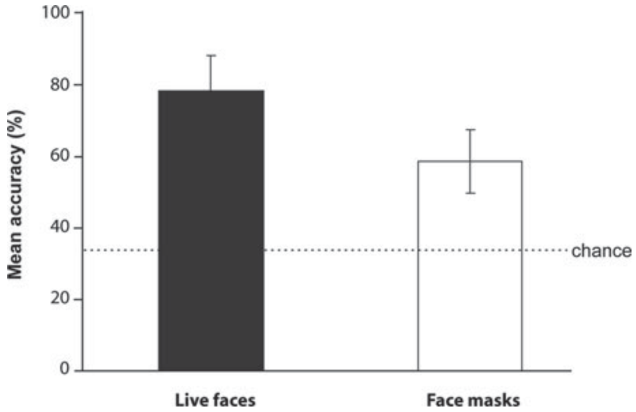

Fig. 15.3 Face recognition accuracy for live faces and 3-D face masks in a same–different matching task. Revised from Kilgour and Lederman (2002) with permission from the Psychonomic Society

15.2.2.1 How Does the Haptic System *Process* Facial Identity and How Does This Relate to Vision?

Two noteworthy questions about haptic face processing have been considered to date: (a) what is the relative importance of configural, as opposed to feature-based, processes in the haptic perception of facial identity and (b) to what extent is visual mediation used to process facial information haptically?

In Section 15.2.1.1, we noted that vision scientists have used evidence of a "face inversion effect" – upright faces are better recognized than inverted faces – to argue that the recognition of upright faces strongly involves configural processing. Recent studies indicate a parallel in haptic face processing for neurologically intact individuals. People haptically differentiate the identity of 3-D face masks better when they are presented upright, as opposed to inverted (Kilgour and Lederman, 2006). It is further noteworthy that in addition to being unable to haptically differentiate upright faces at levels above chance, the prosopagnosic individual (LH) in the Kilgour et al. (2004) study demonstrated a paradoxical inversion effect (i.e., *better* performance for inverted than upright faces) haptically (Fig. 15.4), as well as visually (for possible neural explanations of the paradoxical inversion effect, see Farah et al., 1998; de Gelder and Rouw, 2000). To this extent, then, haptic processing and visual processing of facial identity are similarly influenced by orientation.

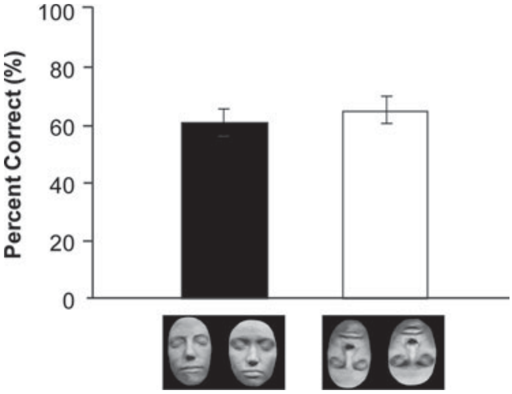

Fig. 15.4 Recognition accuracy for a prosopagnosic individual (LH) for upright and inverted face masks in a same/different matching task. Performance was at chance level for upright faces and higher than chance for inverted faces, reflecting a paradoxical face-inversion effect. Revised and reprinted from Kilgour et al. (2004) with permission from Elsevier Ltd

Acknowledging the caveat raised by Maurer et al. (2002) with respect to using the face inversion paradigm on its own to assess the role of configural processing, it would be desirable to employ one of the more direct methodologies (morphing, scrambling, blurring, etc.). Accordingly, McGregor et al. (2010) used 2-D raised-line drawings in a face-identity learning task involving scrambled, as well as upright and inverted faces. The upright and scrambled displays produced equivalent performance. Because scrambling faces alters the global facial configuration, McGregor et al. concluded that it was not used to haptically process facial identity portrayed in 2-D raised-line drawings. Scrambled faces also produced higher accuracy than inverted faces. Because face inversion alters the local configural information about the features, McGregor et al. further concluded that participants haptically processed only *local* configural information about the 2-D features, the features themselves being treated as oriented objects within a body-centered frame of reference. Because this study focused on the haptic system, a visual control was not included; however, a parallel visual study would clearly be informative.

Casey and Newell (2007) also used more direct methods to assess cross-modal transfer and the contribution of configural processing to such transfer. Participants in a haptic–visual cross-modal transfer task matched a haptically presented unfamiliar 3-D face mask to one of three subsequently presented colored 2-D visual displays that were normal, blurred, or scrambled. As mentioned earlier, blurring the image leaves the global configural arrangement of the features unchanged, while altering details about the features *per se*. Conversely, scrambling the features alters the facial configuration while leaving the features unaffected. Although only limited haptic–visual cross-modal transfer was observed, performance in the normal and blurred conditions was equivalent. The authors concluded that to the limited extent that cross-modal transfer did occur in processing facial identity, both modalities used global configuration – as opposed to feature-based processing.

Whether or not haptic processing of facial identity involves the use of visual mediation is highly controversial among touch and vision scientists. Any performance similarities between the two modalities may be attributed to the transformation of haptic inputs into a visual image that is subsequently re-processed by visual mechanisms and/or to the modalities' sharing common supra-modal processes. If vision does mediate haptic face processing (or, more generally, haptic object processing), then the ability to perform a haptic face task well is likely the result of the haptic system "piggybacking" onto the underlying functionalities, representations, and brain structures used by the visual system. If vision does not mediate performance in a haptic face task, people must rely on the basic processing mechanisms associated with the sense of touch.

What little behavioral data on this topic exists reveals little support for the use of visual mediation in the haptic perception of facial identity. Minimal correlation was observed between VVIQ test results (Visual Vividness Imagery Questionnaire: Marks, 1973) and performance on a haptic face-identity task involving 3-D face masks (e.g., Kilgour and Lederman, 2002). Moreover, Pietrini et al. (2004) demonstrated that totally blind subjects (two congenital; two early blind with no memory of any visual experiences) achieved >90% accuracy in a one-back haptic discrimination task also involving lifelike face masks. We will present additional converging neuroimaging evidence from Kitada et al. (2009) in Section 15.2.2.3.

15.2.2.2 How Does the Haptic System *Represent* Facial Identity and How Does This Relate to Vision?

When considering the nature of haptically derived representations of facial identity, it is important to note the greater efficiency with which the haptic system can process material, as opposed to geometric, properties. This is likely due to several factors: the haptic system's low spatial acuity, the relative costs and benefits of different manual exploratory procedures (Lederman and Klatzky, 1987), and the high demands on spatiotemporal integration and memory given that haptic exploration is typically sequential. The converse is generally true for vision, that is, vision's excellent spatial acuity and its ability to process edges in an object or display simultaneously render this modality particularly efficient when processing geometric, as opposed to material, properties. Such differences in efficiency in turn affect the relative salience of material and geometric features for the haptic and visual systems, respectively (see, e.g., Klatzky et al., 1987; Lederman et al., 1996).

In keeping with this material/geometry distinction, recall that haptic face matching was 20% more accurate with live faces than with face masks (Kilgour and Lederman, 2002). This finding implicates material-specific properties of the face as important sources of haptic information about facial identity. It is important to note as well that haptic performance with the 3-D masks remained well above chance, confirming the importance of 3-D structural information. Evidence of bi-directional cross-modal transfer (whether partial or complete) in priming studies using homogeneous non-face objects and face masks (Reales and Ballesteros, 1999; Easton et al., 1997a, b; Hadjikhani and Roland, 1998; Kilgour and Lederman, 2002; Casey and Newell, 2003, 2007; Norman et al., 2004) further confirms that vision and touch processes have access to at least some common structural representations. However, to the extent that the transfer is incomplete (particularly for faces), the two modalities may well represent different aspects of the object in light of the material–geometry distinction above, that is, a relatively stronger emphasis on structure for vision and material for touch.

We turn now to the role of orientation in representations of facial identity derived from haptic inputs and comparisons with vision (see Section 15.2.1.2). Collective evidence of a haptic face inversion effect for facial identity (McGregor et al., 2010; Kilgour and Lederman, 2006; Kilgour et al., 2004) suggests that with respect to facial orientation, vision and haptics share a common constraint in representing facial identity: Representations derived from exploring 3-D face masks and 2-D drawings are orientation dependent within the *x–y* fronto-parallel plane; thus, like vision, the upright face is "preferred" or "canonical" for haptics (but see Newell et al., 2001, which has shown different orientation preferences in the sagittal plane for 3-D nonsense objects).

15.2.2.3 What Are the *Neural Mechanisms* that Underlie Haptic Perception of Facial Identity and How Does This Relate to Vision?

Several studies have now begun to employ neuroimaging techniques (e.g., fMRI) to determine the underlying components of the distributed neural network recruited by haptic identification of faces (vs. non-face control objects) and by faces presented haptically vs. visually. Thus, in this section we address (a) studies that have focused on brain activity specifically induced by haptically presented faces and (b) studies that have compared brain activity elicited by haptic vs. visual face presentation.

We begin by noting that a number of fMRI studies have collectively shown that haptic processing of common non-face objects activates extrastriate areas (e.g., lateral occipital complex) traditionally believed to serve only visual functions (Amedi et al., 2001; Deibert et al., 1999; James et al., 2002; Reed et al., 2004). Researchers have now extended this work by examining haptic processing of face masks by both blindfolded neurologically intact and congenitally blind observers (Kilgour et al., 2004; Pietrini et al., 2004; Kilgour et al., 2005).

In one study (Kilgour et al., 2005), after learning to successfully identify a set of 3-D face masks by name via unimanual exploration with the left hand, neurologically intact individuals performed the same task in the scanner with a subset of those masks. Among other findings, the fusiform gyrus (left) was activated more strongly when faces, as opposed to non-face nonsense objects of similar shape and size, were explored haptically. The study by Kilgour et al. (2004) (see Section 15.2.2.2), which required a prosopagnosic individual (LH) and neurologically intact controls to haptically match 3-D face masks, complements the fMRI findings obtained by Kilgour et al. (2005) with neurologically intact individuals. Kilgour et al. (2004) proposed that LH's inability to haptically match faces was due to damage in the occipitotemporal cortex. Together, these two studies suggest that the occipitotemporal region plays an important role in haptic processing of faces, as well as other objects.

An additional fMRI study that further extends our inchoate understanding of the neural basis of haptic processing of facial identity specifically investigated the influence of familiarity on haptic face identification (James et al., 2006). Subjects were carefully trained to unimanually identify a subset of 3-D plaster face masks ("familiar" subset) using their left hand. In the scanner, they were then haptically presented with old and new objects to judge for familiarity. The left fusiform gyrus was activated more strongly by the haptic presentation of familiar (cf. unfamiliar) objects, suggesting that this area specifically differentiates between haptically familiar and unfamiliar faces.

We now compare brain organization and neural substrates in face identification under haptic vs. visual face presentations. The studies by Kilgour et al. (2005) and James et al. (2006) suggest that both haptic and visual identification of faces activate the left fusiform gyrus, although the sub-regions that are activated within that area by each modality may be different. In contrast, it is well known that visually presented faces recruit the right hemisphere more strongly than the left (Gauthier et al., 1999; Kanwisher et al., 1997). Because a corresponding visual face-presentation condition was not included in the initial exploratory studies on haptic face processing (James et al., 2006; Kilgour et al., 2005), it is possible that regions activated by haptic have been activated by visual face presentations. The occurrence of strong activation in the left hemisphere coupled with no significant right hemisphere activation suggests, rather, that the neural systems that mediate haptic and visual face recognition diverge. Because manual exploration is so often sequential, perhaps activation in the left fusiform gyrus was greater than in the right because haptically derived inputs about the facial configuration must be integrated over time. Conversely, visually derived inputs about the face may be simultaneously integrated over space. Dissociation of temporal- and spatial-integration processes in left and right hemispheres, respectively, has received support from theories of brain lateralization (Kolb and Whishaw, 2003) (for alterative explanations, see James et al., 2006).

Two additional fMRI studies offer complementary evidence for the suggestion that there is some overlap between vision and touch in their neural representations of facial identity, but that at least some information is preserved in separate modality-specific channels. Pietrini et al. (2004) used pattern classification methods (drawn from the fields of statistics and machine learning) in conjunction with fMRI data to determine if the specific class of object (bottles, shoes, faces) could be predicted from patterns of activity in ventral temporal extrastriate cortex that were derived during match-to-sample and simple exploration tasks involving visual vs. haptic presentations. While there was strong overlap and correlation between visual and haptic activation patterns for the non-biological categories (bottles, shoes), this was not the case for faces. Thus, the representation of biological common objects (i.e., the face) may not be fully cross-modally shared by the widely distributed neural network proposed by Haxby et al. (2002).

In a related study, Kitada et al. (2009) examined brain organization for haptic and visual identification of human body parts (faces, hands and feet) vs. a non-biological category of control objects (bottles). In accord with Pietrini et al. (2004), haptic and visual object identification activated largely disjoint networks (Fig. 15.5a). However, it is possible that face sensitivity may be shared across sensory modalities in small regions, of which locations are spatially varied across subjects. The authors examined two regions which produced the strongest activation in haptic and visual face identification. These two discrete areas, HFR (“haptic face region”) and FFA (“fusiform face area”), were sensitive to 3-D face masks (cf. controls) whether presented haptically or visually. Nevertheless, the corresponding activation patterns across object categories (faces, feet, hands, and bottles) were different for FFA and HFR regions (Fig. 15.5). Kitada et al. concluded that although both regions within the fusiform gyrus are sensitive to faces, independent of sensory modality, the sub-region that is most sensitive to haptically presented faces (HFR) is functionally distinct from that which is most sensitive to visually presented faces.

A number of tactile/haptic functional neuroimaging studies with non-face patterns and objects have now confirmed that the visual cortex is generally involved in normal tactual perception by sighted and blind observers (for further details, see review by Sathian and Lacey, 2007). What remains unclear for both non-face and face objects, however, is whether this visual involvement consists of knowledge-directed processes (e.g., anticipatory visual imagery or visual memory) that may assist or mediate tactual performance, stimulus-directed activation of visual cortical areas by tactual inputs, which in turn implies that these putative “visual” areas are in fact “multisensory,” or both stimulus-driven and knowledge-driven processes (Lacey, Campbell and Sathian, 2007; Sathian and Lacey, 2008). Further research on this issue is clearly required.

Recently, Kitada et al. (2009) addressed the use of visual imaging vs. multisensory processing of faces and other body parts by including a third condition in which subjects were required to visually image targeted exemplars of face masks (as well as other body parts). Several measures of visual imagery were obtained, involving both behavioral (i.e., VVIQ: Marks, 1973; subjective reports regarding the extent to which subjects used visual imagery) and neuroimaging measures (i.e., neural activation in visual imagery vs. haptic conditions). Various correlational analyses converged in showing that at best, visual mediation could account for only a

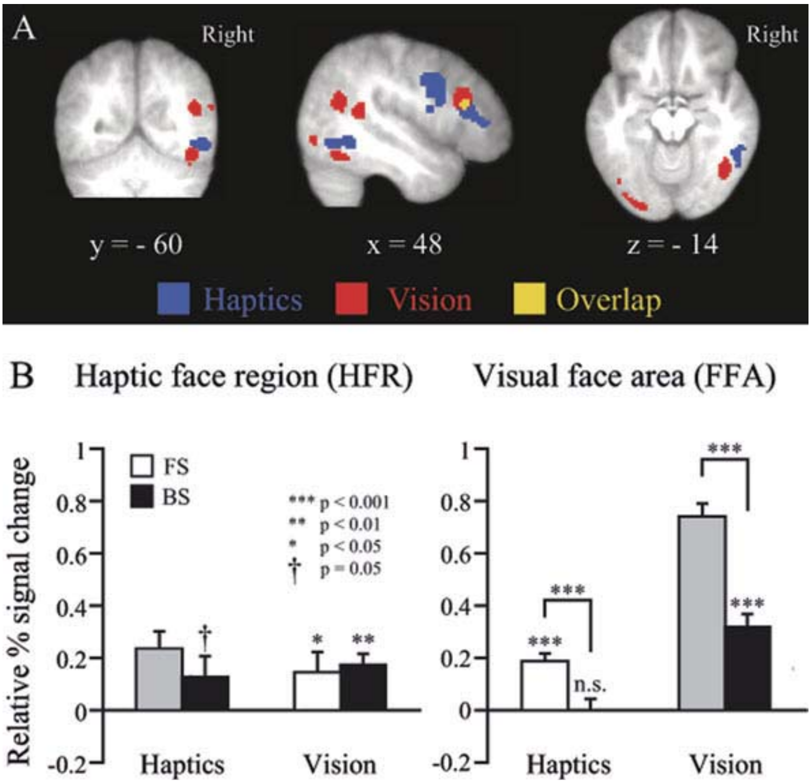

Fig. 15.5 (**a**) Group analysis. Activation patterns during identification of faces compared to control objects were superimposed on the coronal, sagittal, and transverse planes of the anatomical image averaged across the subjects. (**b**) Signal change of faces and other body parts relative to the control objects in HFR and FFA. The *gray bar* indicates the condition used to define the region. Data are presented as the mean ± SEM. *Asterisks and n.s.* above each bar indicate the result of a one-sample *t*-test on the sensitivity score for faces (FS) and other body parts (BS). *Asterisks* above a pair of bars show the result of a post hoc pair-wise comparison. Reprinted from Kitada et al. (2009) with permission of the MIT Press and the Cognitive Neuroscience Society

relatively minor portion of the increase in category-specific signal observed with haptically presented faces (and other body parts) (for further details, see Kitada et al., 2009). The authors concluded that visual imagery is not *necessary* to achieve good haptic perception of facial identity (or other body parts).

15.2.3 Summary

In Section 15.2 we considered how facial identity is visually vs. haptically processed, focusing specifically on the relative importance of configural vs. feature-based processes and the extent to which visual mediation is used to process haptically derived inputs about facial identity and the extent and nature of cross-modal transfer between visual and haptic processing of facial identity. We then considered the nature of visual and haptic face representations, addressing primary issues pertaining to whether a specific face orientation is “privileged,” and whether and how facial features differ with respect to their salience in facial representations. Finally, we examined the unisensory and multisensory neural substrates that underlie facial identity. In Section 15.3, we address many of the same questions as they pertain to facial expressions of emotion.

15.3 Facial Expressions of Emotion

15.3.1 Visual Perception of Emotion from Facial Expressions

A second critical component of visual face processing that has attracted much attention by vision researchers concerns how people communicate their emotions nonverbally by means of varying their facial expressions (Darwin, 1972/1955). Facial expressions exhibit invariant features with respect to both the static musculoskeletal pattern when the expression is fully formed and from brief changes in these patterns over time. A small set of facial expressions of emotion that include anger, disgust, fear, happiness, sadness, and surprise are universally recognized (Ekman et al., 1987). Details of these expressions have been expressed in terms of specific “facial action patterns” (Ekman and Friesen, 1975), with visually detectable consequences that are used to process facial expressions of emotion in static photographs, line drawings, and artificial dynamic displays. In keeping with the organization of Section 15.2.1, we now address significant issues pertaining to facial processing and representations of facial expressions of emotion and to their underlying neural substrates.

15.3.1.1 How Does the Visual System *Process* Facial Expressions of Emotion?

As previously noted, one of the hallmarks of face processing is the influence of face orientation on face perception and recognition, with important implications for how faces are processed and for the manner in which the visual inputs are represented. With respect to process, several studies have demonstrated clear face inversion effects relating to the visual perception of facial expressions of emotion by both neurologically intact and almost all prosopagnosic observers (Calder et al., 2000; de Gelder et al., 2003; Fallshore and Bartholow, 2003; Prkachin, 2003). Such studies suggest that global face configuration plays a primary role in processing facial expressions of emotion. Thus, neurologically intact individuals consistently show standard inversion effects in face identity and emotion tasks. Prosopagnosic participants, however, do not. Although unable to identify faces, they are still capable of perceiving and identifying facial expressions of emotion and do show inversion effects. Such performance differences in the prosopagnosic group support traditional claims of functional dissociation between identity and emotion (Bruce and

Young, 1986). However, such putative independence has been challenged by de Gelder and colleagues (2003), who showed that facial expressions of emotion modulate facial identification by neurologically intact and prosopagnosic participants (although in opposite directions).

15.3.1.2 How Does the Visual System *Represen*t Facial Expressions of Emotion?

We now address three important issues with regard to how facial expressions of emotion are represented. Paralleling Section 15.2.2.2 on facial identity, we begin by considering two issues (a) Are face representations orientation independent; if the answer to this question is affirmative, is a specific orientation "privileged"? (b) What is the relative salience of facial features? A third significant issue (c) pertains to theoretical approaches used to address the visual representation of facial expressions of emotion. With respect to the first issue, we briefly note that evidence of inversion effects for emotions implies that orientation is important in the representation of emotional expressions, and more particularly, that the upright orientation is privileged. This point will be discussed further below.

As for the second issue, studies show that people use a combination of features to recognize emotions, including the local shape of face components (e.g., eyes wide open/narrowed, brows raised/lowered, corners raised/lowered) and pigmentation or texture differences (e.g., mouth open/closed; teeth showing/behind the lips) (for summaries, see e.g., Ekman and Friesen, 1975; Bruce and Young, 1986). While shape plays a very important role in visual recognition of facial expressions of emotion, the contributions of surface features (e.g., skin pigmentation) are more limited (Bruce and Young, 1998).

Turning to theoretical approaches, researchers in the area of social psychology have proposed both category-based and dimension-based models of the visual recognition of facial expressions of emotion. Category-based models generally argue for a limited set of cross-culturally recognizable expressions that most frequently include happiness, sadness, anger, disgust, fear, and surprise (Ekman et al., 1987). People are very good at classifying these primary categories of facial emotions when visually presented in static photographs (e.g., Ekman, 1972; Wehrle et al., 2000), line drawings (Etcoff and Magee, 1992) and simulated dynamic presentations (e.g., Calder et al., 1996; Ekman, 1972; Etcoff and Magee, 1992).

In contrast, dimension-based models have argued that visual recognition of facial emotions is based on the location of faces within an *n*-dimensional continuous psychological space, typically described by a 2-D solution (Galati et al., 1997; Katsikitis, 1997; Russell, 1980). For example, Katsikitis (1997) conducted multidimensional scaling of the similarity structure of facial-emotion space using photos of six primary emotions plus a neutral expression. In a 2-D solution, the expressions were approximately distributed in a circle with "neutral" close to the centre, as shown in Fig. 15.6. One dimension was identified as pleasant/unpleasant (i.e., going from happiness and surprise to disgust, anger, and sadness). Katsikitis further proposed that participants used landmark features on a second dimension (upper

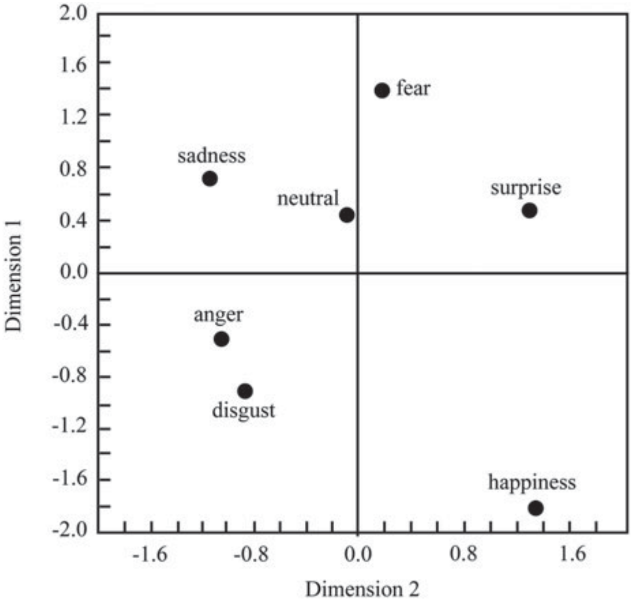

Fig. 15.6 Visual face space for facial expressions of emotion in 2-D line drawings based on a 2-D MDS solution. Reprinted from Katsikitis (1997) with permission from Pion Ltd

face/lower face) as clues for differentiating emotions, with surprise, fear, and sadness tending to involve the upper face, and happiness, disgust, and anger the lower face (see also Galati et al., 1997). In Russell's (1980) "circumplex" model, the two dimensions are pleasure–displeasure and arousal–sleepiness.

15.3.1.3 What Are the *Neural* Mechanisms that Underlie Visual Perception of Facial Expressions of Emotion?

In this section, we briefly address two significant aspects: (a) localized neural regions vs. spatially distributed neural networks for visually perceiving emotional expressions and (b) dissociation vs. interaction in the visual processing of facial identity and emotional expressions.

In their model of visual face perception, Haxby et al. (2000) propose an extended neural network that is used in conjunction with the core system underlying facial identity (see Fig. 15.2) in order to extract social relevance. The extension is thought to be phylogenetically older and faster and to involve the amygdala, which receives inputs (especially those related to threat) from sub-cortical mechanisms via a retinal-collicular-pulvinar pathway (Morris et al., 1998). Much of the relevant fMRI research has implicated a strong role for the amygdala, particularly in processing negative facial expressions, namely fear and anger (e.g., Adams et al., 2003; Adolphs et al., 1999). However, Winston et al. (2003) used an event-related design to show that the amygdala (together with extrastriate and fusiform cortex and posterior STS) actually responds similarly across basic emotions with negative (disgust and fear) and positive (happiness and sadness) valences. Research has further implicated other areas, including the anterior insula (specifically for disgust, Phillips et al., 1997), as well as prefrontal cortical areas (usually orbitofrontal cortex: Rolls, 1996; also ventral prefrontal cortex (Hornak et al., 1996; Winston et al., 2003; Nomura et al., 2004) and sensorimotor cortex (especially right hemisphere), perhaps related to somatic cues associated with simulating the observed emotional expressions (Adolphs et al., 1999; Adams et al., 2003; Ohman, 2002; Winston et al., 2003).

Researchers have traditionally argued that parallel neural systems are used to process facial identity and emotion from facial expressions (e.g., Bruce and Young, 1986; Calder et al., 2001; Duchaine et al., 2003). However, in neurologically intact viewers, processing identity and emotion from expression can interact (Rotshtein et al., 2001; see also de Gelder et al., 2003; Ganel and Goshen-Gottstein, 2004). Overall, the results of such studies confirm that cross talk does occur between identity- and emotion-processing systems.

15.3.2 Haptic Processing of Emotion from Facial Expressions

Haptic researchers have shown that people are also capable of haptically perceiving and recognizing the six culturally universal facial expressions of emotion. Lederman et al. (2007) showed that with only 5–10 minutes training, young adults were able to use touch alone to classify these expressions at levels usually well above chance (17%). In one experiment, blindfolded subjects actively and bimanually explored the six emotional expressions portrayed statically by live actors. Classification accuracy was 51% and increased substantially to 74% in a second experiment when the live expressions were dynamically formed under the subjects' stationary hands (Fig. 15.7).

Clearly the perception of universal facial expressions of emotion is also bimodal. This finding seems reasonable inasmuch as the invariant features of the musculoskeletal facial displays of each emotion are accessible to the hands, as well as to the eyes. Subsequent studies have confirmed that people can haptically classify this same primary set of emotional expressions above chance levels when displayed on rigid 3-D face masks, which retain 3-D structure but not material information (Baron, 2008), and in 2-D raised-line drawings, which simplify the remaining 2-D information but eliminate both 3-D structural and material information normally available in static live faces (Lederman et al., 2008).

15.3.2.1 How Does the Haptic System *Process* Facial Expressions of Emotion and How Does This Relate to Vision?

Paralleling haptic research on facial identity, researchers have also investigated whether face inversion effects occur with respect to haptic processing of facial expressions of emotion. Sizable ($\sim$15%) inversion effects have been documented in

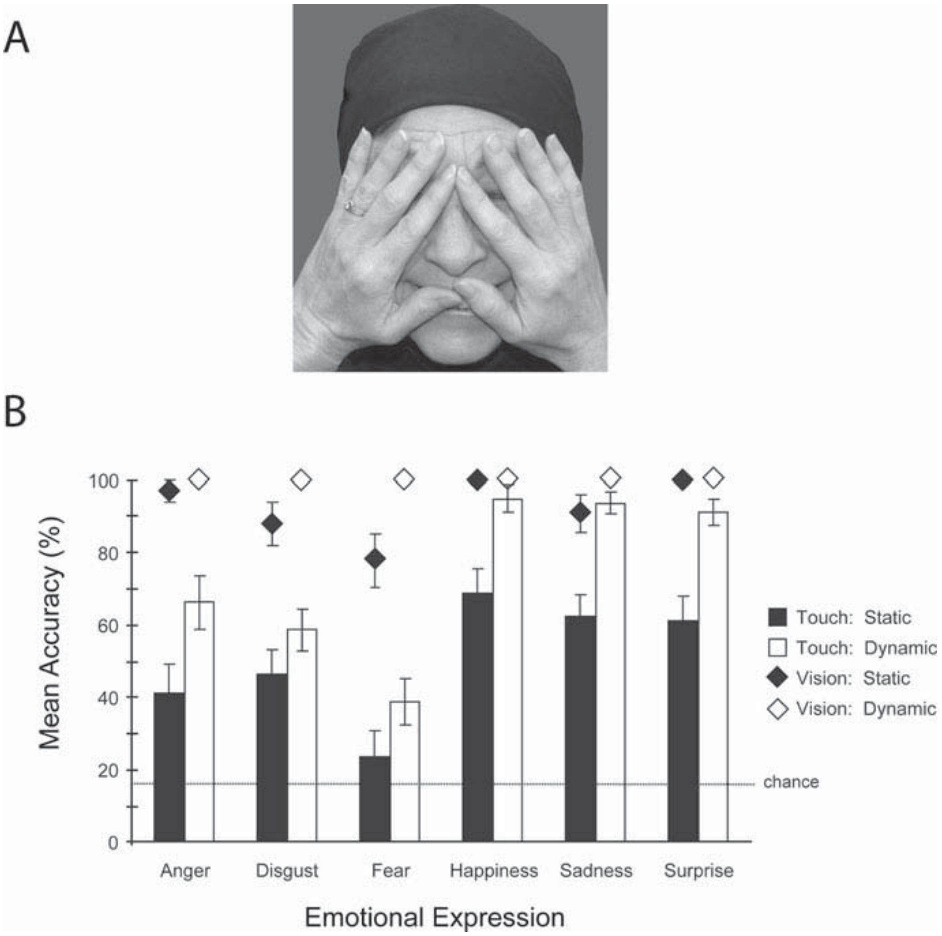

Fig. 15.7 (**a**) Initial or continuing hand positions used to haptically process happiness depicted statically and dynamically, respectively, by a live model; (**b**) haptic emotion-classification accuracy as function of emotional expression for static and dynamic displays. Reprinted from Lederman et al. (2007) with permission of Wiley and Sons Canada

studies involving seven-alternative-forced-choice classification (six primary emotional expressions + “neutral”) tasks with both live faces (Direnfeld, 2007) and 2-D raised-line drawings, for which it was possible to include a third scrambled-face condition (Lederman et al., 2008). In both studies, emotions were classified more accurately when faces were presented upright, as opposed to inverted. In the latter study, classification accuracy was higher for upright faces than for either scrambled or inverted faces, for which accuracy was equivalent. Collectively, these two studies suggest that as with vision, configural processing of facial expressions of emotion plays a very important role haptically. A notable exception to this statement is a study by Baron (2008), which presented expressions on 3-D face masks in upright or inverted orientations. For the masks, upright and inverted faces both produced excellent accuracies (81 and 84%, respectively), which were statistically equivalent. To confirm that the face mask displays were indeed effective, a parallel visual control experiment was also run. Unlike the haptic results, a face inversion effect was now observed.

An additional experiment in the Lederman et al. study (2008) focused on a different, but related, aspect of face inversion effects. Subjects were required to judge both the emotional valence (positive vs. negative) and the associated emotional magnitude (on a scale of 1–5) of each of seven expressions (six culturally universal expressions and neutral) in both upright and inverted 2-D orientations using either touch or vision. When faces were presented visually, an inversion effect (lower magnitude for inverted faces) reliably occurred across all emotions except for happy. The results for touch were not as clear-cut. Relative to vision, the signed emotional valence judgments for haptically explored faces were quite variable, with no reliable evidence of a face inversion effect (Fig. 15.8a). In contrast, when the unsigned magnitudes were considered, the haptic and visual judgments were equivalent (Fig. 15.8b).

The studies included in this section are also interesting for the similarities and differences in visual and haptic processing of facial expressions of emotion. Much like vision, configuration-based processes seem to play a critical role in the haptic processing of facial expressions of emotion in classification tasks using live faces and raised 2-D outline drawings. In contrast, when 3-D face masks are presented, the haptic system favors feature-based processing more strongly, while vision

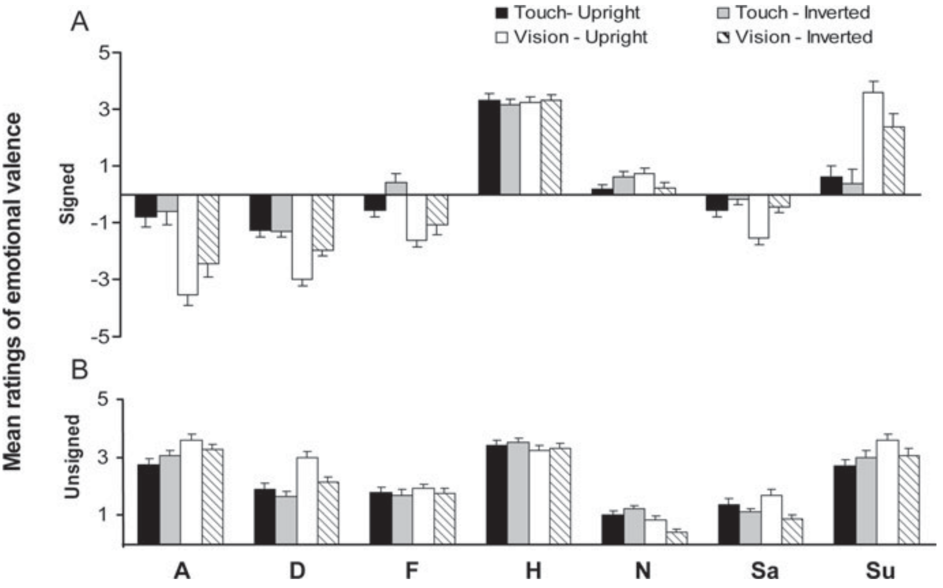

Fig. 15.8 Mean haptic and visual ratings of the emotional valence of facial expressions of emotion presented in upright vs. inverted orientations. (**a**) Signed ratings (+ 1 SEM); (**b**) unsigned ratings (+1 SEM). Reprinted from Lederman et al. (2008) with permission of the IEEE Computer Society

emphasizes configuration-based processes. Visual processing and haptic processing of facial expressions of emotion also differ with respect to judgments of emotional valence. Unlike vision, the haptic system appears unable to judge emotional valence consistently, likely because of the subtle differences in the spatial information available to a perceptual system with poor spatial resolving capacity (cf. vision). The two modalities are fairly similar in their ability to scale emotional magnitude of the relatively intense emotions portrayed in these studies, possibly because the magnitude of the differences along this dimension is more perceptually accessible to touch, as well as to vision.

15.3.2.2 How Does the Haptic System *Represent* Facial Expressions of Emotion and How Does This Relate to Vision?

In this section, we return to several issues raised in Section 15.3.1.2 with respect to vision. We now ask (a) Is haptic perception of facial expressions of emotion dependent on orientation, and if so, is there a canonical orientation? (b) Which facial features are primary for the haptic system, and what is their relative salience? (c) Finally, we consider the relevance of two major theoretical approaches to visual representation of emotional expressions for touch.

Based on the above-mentioned orientation effects, we conclude that the upright orientation is generally "privileged" in the representations of haptically encoded facial expressions of emotion. However, this conclusion applies only to live faces and 2-D raised-line drawings, inasmuch as face orientation had no observable effect with rigid 3-D face masks (Baron, 2008). The excellent performance obtained with 3-D masks may be attributed to the availability of a variety of 2-D and 3-D features, including teeth within the mouth, a feature that was either available but not explored (live faces) or absent (2-D drawings).

Which features/regions of static live face displays are most important for haptic processing of facially expressed emotions? Abramowicz (2006) compared performance when exploration of live faces was restricted either to the eyes/brows/forehead/nose (upper two-thirds) or to the nose/mouth/jaw/chin region (lower two-thirds). She found that while neither region was *necessary* for above chance classification accuracy, both were *sufficient*, with the lower two-thirds of the face producing more accurate performance. Using raised-line drawings, Ho (2006) similarly found that participants tended to be more accurate (as well as faster and more confident) when the eye/brow/forehead contours were deleted, as opposed to the mouth/chin/jaw contours. Vision, which was also assessed in this study, showed a similar response pattern across emotional expressions (see also Sullivan and Kirkpatrick, 1996, for related results, but cf. Gouta and Miyamoto, 2000).

Execution of facial action patterns that underlie the facial communication of human emotions produces transient changes in the musculoskeletal structure of the face and in the associated material properties of the skin and underlying tissue. Thus, dynamic facial displays of emotion may offer additional valuable haptic information to the perceiver, particularly given the temporal acuity of the hand in comparison to the eye (Jones and Lederman, 2006). Lederman et al. (2008) directly compared static and dynamic facial displays of emotion and found a marked improvement in haptic accuracy with dynamic information (51 vs. 74%, respectively). Visual studies tend to confirm the importance of dynamic cues in the representations of basic facial expressions of emotion (see, e.g., Ambadar et al., 2005; Atkinson et al., 2004; Cunningham et al., 2005; Kamachi et al., 2001; but see Bassili, 1978).

Although it is too early in the investigation of haptic face processing to produce a detailed model of how facial expressions derived from haptic inputs are represented, we may still address this issue from the perspectives of dimensional and category models previously proposed with respect to vision. In terms of a dimensional approach (e.g., Calder et al., 2001; Russell, 1980; Woodworth and Schlossberg, 1959), we highlight the two dimensions along which Lederman et al. (2008) required participants to haptically judge emotional valence – emotional "mood" (scale sign) and emotional intensity (scale magnitude). These two dimensions would appear tangentially related to Russell's visual pleasure–displeasure and arousal–sleepiness dimensions, respectively.

In keeping with a categorical approach (Ekman et al., 1987), one may ask whether certain feature regions of the face are more salient than others when haptically judging facial expressions of emotion. Subjective reports of the relative importance of different regions of the face and videotapes of hand movements during manual face exploration in many of our earlier studies suggested that both the lower-level mouth and upper-level eye regions (cf. mid-level nose region) of live faces and 2-D facial depictions may prove to be of particular importance both haptically and visually. The experimental studies by Abramowicz (2006) and Ho (2006) provide empirical confirmation of these subjective observations.

15.3.2.3 What Are the *Neural Mechanisms* that Underlie Haptic Perception of Facial Expressions of Emotion and How Does This Relate to Vision?

We are aware of only one study that has addressed the underlying neural substrates of haptic identification of facial expressions of emotion. To date, visual studies have shown that the inferior frontal gyrus, inferior parietal lobe, and cortical areas within and near the superior temporal sulcus are components of a cortical network – possibly the human analogue of the "mirror-neuron system in animals" (e.g., Rizzolatti et al., 1996) – used to process visual information about human actions, including facial expressions of emotion (Carr et al., 2003; Montgomery and Haxby, 2008; see also Kilts et al., 2003). Using fMRI techniques, Kitada et al. (2010) hypothesized that these regions are also involved in the haptic identification of facial expressions of emotion portrayed on 3-D rigid face masks. Subjects identified three different emotional expressions (disgust, neutral, and happiness) and three different types of control objects (shoes) haptically vs. visually. In brief, this study found that haptic and visual identification of facial expressions of emotion activated overlapping, yet separate, neural mechanisms including the three hypothesized regions that form part of a cortical neural network for understanding human actions. On the basis of these results, the authors suggested that this action network may partly underlie the perception of facial expressions of emotion that are presented haptically, as well as visually.

15.3.3 Summary

In Section 15.3, we addressed how humans – both neurologically intact and prosopagnosic individuals – visually and haptically process and represent facial expressions of emotion and the nature of the underlying neural substrates that support these functions. With respect to process, we focused primarily on the debate regarding configural vs. feature-based processing. With respect to representation, we addressed three issues: (a) Are face representations orientation independent and if so, is any specific orientation “privileged”? (b) What is the relative salience of facial features? and (c) Finally, what theoretical approaches have been used to address visual representation of facial expressions of emotion? We then considered the nature of the underlying neural mechanisms (uni- and multisensory) that are involved in the visual and haptic perception of facial expressions of emotion.

15.4 General Summary, Conclusions, and Future Directions

We have considered functional issues pertaining to how humans *process* and *represent* facial identity and emotional expressions, together with the *neural mechanisms* that underlie these important functions. In this section, we review those issues as they pertain to haptic face processing and its relation to vision, and we suggest directions for future research.

Is face processing solely a visual phenomenon? Research described here highlights the fact that face processing is a bimodal perceptual phenomenon that is accessible through manual, as well as visual, exploration, as confirmed with live faces, rigid 3-D face masks, and even 2-D raised-line drawings.

Is face processing unique? Interpreting the results obtained in visual studies has proved highly controversial and is beyond the scope of the current chapter. At one end of the controversy, a number of studies with neurologically intact and prosopagnosic individuals have contributed empirical support for the uniqueness of face perception in haptic and visual modalities. At the other side of the controversy, some researchers have argued that any object class for which individuals have special expertise may be processed differently than other object classes. The validity of this alternate interpretation with respect to haptic face processing certainly deserves consideration.

15.4.1 How Are Faces Processed?

Configural vs. feature-based processing. The results of many studies collectively confirm that visual processing of facial identity and facial expressions of emotion is highly configural. Global configural processing appears to be a prominent aspect of haptic face processing as well, but haptic studies considered in this chapter have also implicated roles for haptic feature-based processing as befits an information-processing system that extracts information more sequentially than the visual system. Considering wholistic vs. feature-based processing dichotomously tends to mask the complexity of the issues and the answers. Further research should consider constraints on configural processing and effects of task and context.

Visual-mediation vs. multisensory processing. Current data suggest that even if visual imagery is sometimes used, it is not necessary to achieve excellent performance on haptic facial identity tasks. To expand our current understanding, the nature of visual imagery in face processing tasks must be further clarified; in this regard, a more extensive battery of evaluation tasks would prove very helpful.

Intersensory transfer. Only limited intersensory transfer between vision and haptics takes place with respect to facial identity. To the extent that such transfer occurs, it appears to be globally configural, as opposed to feature based. The amount and nature of intersensory transfer has yet to be addressed with respect to facial expressions of emotion.

15.4.2 How Are Faces Represented?

Role of orientation. Research reported in this chapter has obtained face inversion effects with both visually and haptically presented displays (with some exceptions: identity in 2-D face displays and emotion in 3-D face masks). To the extent that face perception is orientation dependent, it implies that the upright position is "canonical" in face representation.

Relative importance of different facial regions to visual vs. haptic face processing. Whereas the eye and brow regions of the face are emphasized relatively more in visual facial identity tasks, the mouth region appears to be favored somewhat more overall when haptics is used. In terms of its potential application, this issue could be more systematically compared across the three major types of haptic face display (compliant live faces, 3-D face masks and 2-D drawings), inasmuch as the type and the amount of information that can be extracted haptically will vary. Despite comparable evaluations of the intensity of facial emotions in 2-D drawings, only vision reliably judges the extent to which the valence is positive or negative. The performance with haptic displays is not surprising, given the subtlety of 2-D facial cues to emotional valence or mood.

Theoretical approaches to the study of human facial emotions. Although both category-based and dimensional models have been proposed for visual representations of facial expressions of emotion, we know of no such comparable investigations with respect to haptics to date.

15.4.3 What Are the Underlying Neural Mechanisms and How Does this Relate to Vision?

Although neuroimaging studies have shown that visual and haptic systems share similarities in face processing, it is not clear to what extent haptic and visual systems share neural substrates for face perception; whether other brain regions, such as the inferior occipital gyrus, are involved in processing in both vision and haptics; and how multiple brain regions communicate during face processing. Other neuroimaging techniques such as the electroencephalogram (EEG) or magnetoencephalogram (MEG) may be able to elucidate temporal processing of haptic, as well as visual, face recognition. Models of effective connectivity based on functional neuroimaging data (e.g., Friston et al., 2003) are also needed to understand how multiple areas interact.

Finally, since neural mechanisms underlying visual and haptic face recognition are similar, one may ask whether neural mechanisms dedicated to face perception still exist without visual experience. An fMRI study on congenitally blind individuals may be able to answer this question.

Acknowledgments This chapter was prepared with the financial assistance of a grant to SL from the Canadian Institutes for Health (CIHR). We thank Cheryl Hamilton for her help in preparing the manuscript for publication.

References

Abramowicz A (2006) Haptic identification of emotional expressions portrayed statically vs. dynamically on live faces: the effect of eliminating eye/eyebrow/forehead vs. mouth/jaw/chin regions. Undergraduate thesis, Queen’s University, Kingston, Ontario

Adolphs R (2002) Neural systems for recognizing emotion. Curr Opin Neurobiol 12:169–177

Adolphs R, Tranel D, Hamann S, Young AW, Calder AJ, Phelps EA, Anderson A, Lee GP, Damasio AR (1999) Recognition of facial emotion in nine individuals with bilateral amygdala damage. Neuropsychologia 37(10):1111–1117

Adams RB Jr, Gordon HL, Baird AA, Ambady N, Kleck RE (2003) Effects of gaze on amygdala sensitivity to anger and fear faces. Science 300(5625):1536

Ambadar Z, Schooler JW, Cohn JF (2005) Deciphering the enigmatic face: the importance of facial dynamics in interpreting subtle facial expressions. Psychol Sci 16(5):403–410

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

Atkinson AP, Dittrich WH, Gemmell AJ, Young AW (2004) Emotion perception from dynamic and static body expressions in point-light and full-light displays. Perception 33(6):717–746

Baron M (2008) Haptic classification of facial expressions of emotion on 3-D facemasks and the absence of a haptic face-inversion effect. Undergraduate honours thesis, Queen’s University, Kingston, Ontario

Bassili JN (1978) Facial motion in the perception of faces and of emotional expression. J Exp Psychol Human Percept Perform 4(3):373–379

Bousten L, Humphreys GW (2003) The effect of inversion on the encoding of normal and “thatcherized” faces. Q J Expt Psychol 56A(6):955–975

Bruce V, Young A (1986) Understanding face recognition. Br J Psychol 77(3):305–327

Bruce V, Young A (1998) In the eye of the beholder: the science of face perception. Oxford University Press, New York, NY

Calder AJ, Burton AM, Miller P, Young AW, Akamatsu S (2001) A principal component analysis of facial expressions. Vision Res 41(9):1179–1208

Calder AJ, Young AW, Keane J, Dean M (2000) Configural information in facial expression perception. J Exp Psychol Hum Percept 26(20):527–551

Calder AJ, Young AW, Perrett DI, Etcoff NL, Rowland D (1996) Categorical perception of morphed facial expressions. Vis Cognit 3(2):81–117

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

Casey S, Newell F (2003) Haptic own-face recognition. Proc 3rd Int Conf Eurohapt 2003:424–429

Casey SJ, Newell FN (2007) Are representations of unfamiliar faces independent of encoding modality? Neuropsychologia 45(3):506–513

Clark VP, Keil K, Maisog J Ma, Courtney S, Ungerleider LG, Haxby JV (1996) Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography. Neuroimage 4:1–15

Collishaw SM, Hole GJ (2000) Featural and configurational processes in the recognition of faces of different familiarity. Perception 29(8):893–909

Cunningham DW, Kleiner M, Wallraven C, Bulthoff HH (2005) Manipulating video sequences to determine the components of conversational facial expressions. ACM Trans Appl Percept 2(3):251–269

Darwin C (1872/1955). The expression of emotions in man and animals. Philosophical Library, New York

de Gelder B, Frissen I, Barton J, Hadjikhani N (2003) A modulatory role for facial expressions in prosopagnosia. Proc Natl Acad Sci U S A 100(22):13105–13110

de Gelder B, Rouw R (2000) Paradoxical configuration effects for faces and objects in prosopagnosia. Neuropsychologia 38:1271–1279

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

Diamond R, Carey S (1986) Why faces are and are not special: An effect of expertise. J Exp Psychol Gen 115:107–117

Direnfeld E (2007) Haptic classification of live facial expressions of emotion: a face-inversion effect. Undergraduate honours thesis, Queen's University, Kingston, Ontario

Duchaine BC, Parer H, Nakayama K (2003) Normal recognition of emotion in a prosopagnosic. Perception 32:827–838

Duchaine BC, Yovel G, Butterworth EJ, Nakayama K (2006) Prosopagnosia as an impairment to face-specific mechanisms: elimination of the alternative hypotheses in a developmental case. Cogn Neuropsychol 23(5):714–747

Easton RD, Greene AJ, Srinivas K (1997a) Transfer between vision and haptics: memory for 2-D patterns and 3-D objects. Psychon Bull Rev 4:403–410

Easton RD, Greene AJ, Srinivas K (1997b) Do vision and haptics share common representations? Implicit and explicit memory within and between modalities. J Exp Psychol Learn Mem Cognit 23:153–163

Ekman P (1972) Universals and cultural differences in facial expressions of emotion. In: Cole J (ed) Nebraska symposium on motivation. University of Nebraska Press, Lincoln, NE, pp 207–238

Ekman P, Friesen WV (1975) Unmasking the face: a guide to recognising emotions from facial clues. Prentice Hall, Engelwood Cliffs, NJ

Ekman P, Friesen WV, O'Sullivan M, Chan A, Diacoyanni-Tarlatzis I, Heider K et al. (1987) Universals and cultural differences in the judgment of facial expression of emotions. J Pers Soc Psychol 53:712–717

Etcoff NL, Magee JJ (1992) Categorical perception of facial expressions. Cognition 44(3):227–240

Fallshore M, Bartholow J (2003) Recognition of emotion from inverted schematic drawings of faces. Percept Mot Skills 96(1):236–244

Farah MJ, Tanaka JW, Drain HM (1995) What causes the face inversion effect? J Exp Psychol Hum Percept Perform 21:628–634

Farah MJ, Wilson KD, Drain HM, Tanaka JR (1995) The inverted face inversion effect in prosopagnosia: evidence for mandatory, face-specific perceptual mechanisms. Vis Res 35(14):2089–2093

Farah MJ Wilson KD, Drain M, Tanaka JN (1998) What is "special" about face perception? Psychol Rev 105:482–498

Fraser IH, Craig GL, Parker DM (1990) Reaction time measures of feature saliency in schematic faces. Perception 19(5):661–673

Freire A, Lee K, Symons LA (2000) The face-inversion effect as a deficit in the encoding of configural information: direct evidence. Perception 29:159–170

Galati D, Scherer KR, Ricci-Bitti PE (1997) Voluntary facial expression of emotion: comparing congenitally blind with normally sighted encoders. J Pers Soc Psychol 73(6):1363–1379

Ganel T, Goshen-Gottstein Y (2004) Effects of familiarity on the perceptual integrality of the identity and expression of faces: the parallel-route hypothesis revisited. J Exp Psychol Hum Percept Perform 30(3):583–597

Gauthier I, Tarr MJ, Anderson AW, Skudlarski P, Gore JC (1999) Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. Nat Neurosci 2:568–573

Gauthier I, Curran T, Curby KM, Collins D (2003) Perceptual interference supports a non-modular account of face processing. Nat Neurosci 6(4):428–432

Gouta K, Miyamoto M (2000) Emotion recognition: facial components associated with various emotions. Jpn J Psychol 71(3):211–218

Hadjikhani N, de Gelder B (2002) Neural basis of prosopagnosia: an fMRI study. Hum Brain Mapp 16(3):176–182

Hadjikhani N, Roland PE (1998) Crossmodal transfer of information between the tactile and visual representations in the human brain: a positron emission tomographic study. J Neurosci 18:1072–1084

Haig ND (1986) Exploring recognition with interchanged facial features. Perception 5(3):235–247

Halgren E, Dale AM, Sereno MI, Tootell RBH, Marinkovic K, Rosen BR (1999) Location of human face-selective cortex with respect to retinotopic areas. Hum Brain Mapp 7(1):29–37

Haxby JV, Hoffman EA, Gobbini MI (2000) The distributed human neural system for face perception. Trends Cogn Sci 4:223–233

Haxby JV, Hoffman EA, Gobbini MI (2002). Human neural systems for face recognition and social communication. Biol Psychiat 51(1):59–67

Haxby JV, Horwitz B, Ungerleider LG, Maisog J Ma, Pietrini P, Grady CL (1994) The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J Neurosci 14:6336–6353

Haxby JV, Ungerleider JG, Clark VP, Schouten JL, Hoffman EA, Martin A (1999) The effect of face inversion on activity in human neural systems for face and object perception. Neuron 22:189–199

Ho E (2006) Haptic and visual identification of facial expressions of emotion in 2-D raised-line depictions: relative importance of mouth versus eyes + eyebrow regions. Undergraduate honours thesis, Queen's University, Kingston, Ontario

Hoffman EA, Haxby JV (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat Neurosci 3(1):80–84

Hole GJ (1994) Configurational factors in the perception of unfamiliar faces. Perception 23(1): 65–74

Hornak J, Rolls ET, Wade D (1996) Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. Neuropsychologia 34(4):247–261

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

James TW, Servos P, Huh E, Kilgour A, Lederman SJ (2006) The influence of familiarity on brain activation during haptic exploration of 3-D facemasks. Neurosci Lett 397:269–273

Janik SW, Wellens AR, Goldberg ML, Dell'Osso LF (1978) Eyes as the center of focus in the visual examination of human faces. Percept Mot Skills 47(3):857–858

Jones LA, Lederman SJ (2006) Human hand function. Oxford University Press, New York

Kamachi M, Bruce V, Mukaida S, Gyoba J, Yoshikawa S, Adamatsu S (2001) Dynamic properties influence the perception of facial expressions. Perception 30(7):875–887

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

Katsikitis M (1997) The classification of facial expressions of emotion: a multidimensional-scaling approach. Perception 26(5):613–626

Keating CF, Keating EG (1982) Visual scan patterns of rhesus monkeys viewing faces. Perception 11(2):211–219

Kilgour A, Lederman S (2002) Face recognition by hand. Percept Psychophys 64(3):339–352

Kilgour A, Lederman SJ (2006) A haptic face-inversion effect. Perception 35:921–931

Kilgour AK, de Gelder B, Lederman SJ (2004) Haptic face recognition and prosopagnosia. Neuropsychologia 42:707–712

Kilgour A, Kitada R, Servos P, James T, Lederman SJ (2005) Haptic face identification activates ventral occipital and temporal areas: an fMRI study. Brain Cogn 59:246–257

Kilts CD, Egan G, Gideon DA, Ely TD, Hoffman JM (2003) Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. Neuroimage 18(1):156–68

Kitada R, Johnsrude I, Kochiyama T, Lederman SJ (2009) Functional specialization and convergence in the occipitotemporal cortex supporting haptic and visual identification of human faces and body parts: an fMRI study. J Cogn Neurosci 21(10):2027–2045

Kitada R, Johnsrude I, Kochiyama T, Lederman SJ (2010). Brain networks involved in haptic and visual identification of facial expressions of emotion: an fMRI study. Neuroimage 49(2): 1677–1689

Klatzky RL, Lederman SJ, Reed C (1987) There's more to touch than meets the eye: relative salience of object dimensions for touch with and without vision. J Exp Psychol Gen 116(4):356–369

Kolb B, Whishaw IQ (2003) Fundamentals of human neuropsychology, 5th edn.: Worth Publishers, New York, NY

Lacey S, Campbell C, Sathian, K (2007) Vision and touch: multiple or multisensory representations of objects? Perception 36(10):1513–1521

Leder H, Bruce V (2000) When inverted faces are recognized: the role of configural information in face recognition. Quart J Exp Psychol A Hum Exp Psychol 53A(2):513–536

Leder H, Candrian G, Huber O, Bruce V (2001) Configural features in the context of upright and inverted faces. Perception 30(1):73–83

Lederman SJ, Klatzky RL (1987) Hand movements: a window into haptic object recognition. Cogn Psychol 19(3):342–368

Lederman SJ, Klatzky RL, Abramowicz A, Salsman K, Kitada R, Hamilton C (2007) Haptic recognition of static and dynamic expressions of emotion in the live face. Psyc Sci 1 18(2):158–164

Lederman SJ, Klatzky RL, Rennert-May E, Lee JH, Ng K, Hamilton C (2008) Haptic processing of facial expressions of emotion in 2-D raised-line drawings. IEEE Trans Haptics 1:27–38

Lederman S, Summers C, Klatzky R (1996) Cognitive salience of haptic object properties: role of modality-encoding bias. Perception 25(8):983–998

Levy I, Hasson U, Avidan G, Hendler T, Malach R (2001) Center-periphery organization of human object areas. Nat Neurosci 4:533–539

Mangini MC, Biederman I (2004) Making the ineffable explicit: estimating the information employed for face classifications. Cogn Sci 28:209–226

Maurer D, Le Grand R, Mondloch CJ (2002) The many faces of configural processing. Trends Cogn Sci 6:255–226

Marks D (2003) Visual imagery differences in the recall of pictures. Brit J Psychol 64:17–24

McCarthy G, Puce A, Gore JC, Allison T (1997) Face specific processing in human fusiform gyrus. J Cogn Neurosci 9:605–610

McGregor TA, Klatzky RL, Hamilton C, Lederman SJ (2010). Haptic classification of facial identity in 2-D displays: learning and inversion effects. IEEE: Transactions on Haptics 1(2):48–55

McKone E, Kanwisher N (2004) Does the human brain process objects of expertise like faces? A review of the evidence. In: Dehaene S, Duhamel JR, Hauser M, Rizzolatti (eds) From monkey brain to human brain MIT Press, Boston

Montgomery K, Haxby JV (2008) Mirror neuron system differentially activated by facial expressions and social hand gestures: a functional magnetic resonance imaging study. J Cogn Neurosci 20(10):1866–1877

Morris JS, Öhman A, Dolan RJ (1998) Conscious and unconscious emotional learning in the human amygdala. Nature 393:467–470

Newell FN, Ernst MO, Tjan BJ, Bülthoff HH (2001) View-dependence in visual and haptic object recognition. Psyc Sci 12:37–42

Nomura M, Ohira H, Haneda K, Iidaka T, Sadato N, Okada T et al. (2004) Functional association of the amygdala and ventral prefrontal cortex during cognitive evaluation of facial expressions primed by masked angry faces: an event-related fMRI study. Neuroimage 21(1):352–363

Norman JF, Norman HF, Clayton AM, Lianekhammy J, Zielke G (2004) The visual and haptic perception of natural object shape. Percept Psychophys 66(2):342–351

Ohman A (2002) Automaticity and the amygdala: Nonconscious responses to emotional faces. Curr Dir Psychol Sci 11(2):62–66

Peterson MA, Rhodes G (2003) Perception of faces, objects, and scenes: analytic and holistic processes. Advances in visual cognition. Oxford University Press, New York

Phillips ML, Young AW, Senior C, Brammer M., Andrews C, Calder AJ et al. (1997) A specific neural substrate for perceiving facial expressions of disgust. Nature 389(6650):495–498

Pietrini P, Furey ML, Ricciardi E, Gobbini MI, Wu WH, Cohen L et al. (2004) Beyond sensory images: object-based representation in the human ventral pathway. Proc Natl Acad Sci U S A 101:5658–5663

Posamentier MT, Abdi H (2003) Processing faces and facial expressions. Neuropsychol Rev 13(3):113–143

Prkachin GC (2003) The effects of orientation on detection and identification of facial expressions of emotion. Br J Psychol 94(1):45–62

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

Puce A, Allison T, Bentin S, Gore JC, McCarthy G (1998) Temporal cortex activation in humans viewing eye and mouth movements. J Neurosci 18(6):2188–2199

Reales JM, Ballesteros S (1999) Implicit and explicit memory for visual and haptic objects: cross-modal priming depends on structural descriptions. J Exp Psychol Learn Mem Cogn 25(3): 644–663

Reed CL, Shoham S, Halgren E (2004) Neural substrates of tactile object recognition: an fMRI study. Hum Brain Mapp 21:236–246

Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. Brain Res Cogn Brain Res 3(2):131–141

Rolls E (1996) The orbitofrontal cortex. Philos Trans R Soc Lond B Biol Sci B351:1433–1444

Rosch E, Mervis C, Gray W, Johnson D, Boyes-Braem P (1976) Basic objects in natural categories. Cogn Psychol 8:382–439

Rotshtein P, Malach R, Hadar U, Graif M, Hendler T (2001) Feeling or features: different sensitivity to emotion in high-order visual cortex and amygdala. Neuron 32(4):747–757

Russell J (1980) A circumplex model of affect. J Pers Soc Psychol 39(6):1161–1178

Sathian K, Lacey S (2007). Journeying beyond classical somatosensory cortex. Can J Exp Psychol 61(3):254–264

Sathian K, Lacey S (2008) Visual cortical involvement during tactile perception in blind and sighted individuals. In: Rieser JJ, Ashmead DH, Ebner FF, Corn AL (eds) Blindness and brain plasticity in navigation and object perception. Erlbaum, Mahwah, NJ, pp 113–125

Schyns PG, Bonnar L, Gosselin F (2002) Show me the features! Understanding recognition from the use of visual information. Psychol Sci 13(5):402–409

Sekuler AB, Gaspar CM, Gold JM, Bennett PJ (2004) Inversion leads to quantitative, not qualitative changes in face processing. Curr Biol 14(5):391–396

Sergent J (1984) An investigation into component and configural processes underlying face perception. Br J Psychol 75(2):221–242

Sullivan LA, Kirkpatrick SW (1996) Facial interpretation and component consistency. Genet Soc Gen Psychol Monogr 122(4):389–404

Wehrle T, Kaiser S, Schmidt S, Scherer KR (2000) Studying the dynamics of emotional expression using synthesized facial muscle movements. J Pers Soc Psychol 78(1):105–119

Winston RS, O'Doherty J, Dolan RJ (2003) Common and distinct neural responses during direct and incidental processing of multiple facial emotions. Neuroimage 20(1):84–97

Woodworth RS, Schlosberg H (1959) Experimental psychology. Slovenska Akademia Vied, Oxford, England

Yin RK (1969) Looking at upside-down faces. J Exp Psychol 81(1):141–145