

Rapid publication

Haptic face recognition and prosopagnosia

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Abstract

Cases of cross-modal influence have been observed since the beginning of psychological science. Yet some abilities like face recognition are traditionally only investigated in the visual domain. People with normal visual face-recognition capacities identify inverted faces more poorly than upright faces. An abnormal pattern of performance with inverted faces by prosopagnosic individuals is characteristically interpreted as evidence for a deficit in configural processing essential for normal face recognition. We investigated whether such problems are unique to vision by examining face processing *by hand* in a prosopagnosic individual. We used the haptic equivalent of the visual-inversion paradigm to investigate haptic face recognition. If face processing is specific to vision, our participant should not show difficulty processing faces haptically and should perform with the same ease as normal controls. Instead, we show that a prosopagnosic individual cannot haptically recognize faces. Moreover, he shows similar abnormal inversion effects by hand and eye. These results suggest that face-processing deficits can be found across different input modalities. Our findings also extend the notion of configural processing to haptic face and object recognition.

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1. Introduction

Cases of cross-modal influence have been noted since the beginning of psychological science. In 1839, Brewster reported that observers who saw indented objects (e.g., engraved seals) through an optical device that inverted apparent concavity, also experienced a haptic inversion effect when they explored these objects simultaneously by touch (Brewster, 1839). The corresponding question—is failure to recognize what one sees also associated with a failure to recognize what one touches—has rarely been raised. In light of the ongoing debate on face specificity and the importance of prosopagnosia to this discussion, it appears highly relevant to ask whether a deficit in face recognition by vision might be associated with a deficit in face recognition by touch (i.e., the haptic system).

Neurologically intact individuals process faces more by their overall configuration than by their local features (de Gelder & Rouw, 2000a; Freire, Lee, & Symons, 2000). To investigate this configural or holistic (Tanaka & Farah, 1993) recognition strategy, researchers have predominantly

used the inversion effect, which is defined as a decrease in performance when recognizing inverted as oppose to upright faces (Valentine, 1988; Yin, 1969). Results that show a relatively stronger inversion effect for faces than for other mono-oriented objects have also been interpreted as evidence that faces occupy a special status (Diamond & Carey, 1986) among visually apprehended objects. This weaker inversion effect for non-face objects is presumably due to recognition that is more strongly based on features and less disrupted by inversion (Leder & Bruce, 2000).

The inversion effect plays an important role in understanding the visual deficits of patients with a category-specific recognition deficit for faces (prosopagnosia). Some prosopagnosic individuals do not demonstrate the typical inversion effect, while others process inverted faces better than upright faces (de Gelder & Rouw, 2000b; Farah, Wilson, Drain, & Tanaka, 1998). The paradoxical inversion effect (de Gelder & Rouw, 2000b) indicates that configural processing is disrupted but not totally absent. When the need for configural processing is removed (by inverting the face), a feature-based analysis can be performed more easily.

Previous studies have been confined to investigating face recognition and its deficits in the visual modality only. Yet there is no intrinsic link between vision and face recognition

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or prosopagnosia. In fact, intact lower-level visual abilities figure prominently among the diagnostic criteria for prosopagnosia. And disorders of higher cognition can either be limited to a single sensory modality or occur across more than one modality (Feinberg, Gonzalez-Rothi, & Heilman, 1986), depending on whether the information is available to more than one sensory system. Haptic face recognition has recently been demonstrated in normal individuals (Kilgour & Lederman, 2002); however, it has never been studied in prosopagnosics.

Can a prosopagnosic individual recognize faces solely by touch? We investigated this question using a haptic inversion paradigm in which our prosopagnosic participant, LH, was required to decide whether two faces (or two non-faces) were the same or different from one another. To date, LH's sense of touch has never been assessed formally. We therefore also evaluated his sensorimotor hand function.

2. Method

2.1. Participants

2.1.1. Patient

LH is a 51-year-old man who sustained bilateral occipito-temporal, right frontal, and anterior temporal lesions subsequent to a motor vehicle accident in 1968. He has been prosopagnosic since that time. Detailed neuropsychological information can be obtained in other reports (Etcoff, Freeman, & Cave, 1991; Farah, Levinson, & Klein, 1995; Farah, Tanaka, & Drain, 1995; Levine, Calvanio, & Wolf, 1980).

2.1.2. Control group

We tested seven gender-, age- and education-matched, neurologically intact participants as controls for LH (mean age = 51.3 years, S.D. = 2.3). These participants completed four blocks (18 trials/block) with the same stimuli that we presented to LH. The blocks consisted of faces and teapots, each presented in upright and inverted positions. Additionally, each control-group participant completed a visual face-recognition test (Benton, Sivan, Hamsner, Varney, & Spreen, 1994), and was within normal limits.

All participants provided informed consent. The General Ethics Research Board of Queen's University has given approval to this study.

2.2. Materials and procedures

2.2.1. Assessment of sensorimotor hand function

LH was blindfolded in all conditions but for visual face recognition. Four preliminary tests assessed LH's cutaneous thresholds, fine motor dexterity and haptic object-recognition capabilities. To determine LH's tactile sensitivity, we used von Frey hairs, consisting of nylon monofilaments of varying diameters, each calibrated to

bend with the application of a specific pressure. The stimuli were applied to the volar surface of the index finger of each hand. LH was required to state whether or not he detected the stimulus. A two-alternative (Y/N) adaptive forced-choice procedure was used, with the pressure threshold calculated as the average of the pressures corresponding to five changes in response direction.

We measured LH's tactile acuity using a two-point discrimination test. We used a set of four octagonal-shaped disks, each containing pairs of rounded metal prongs (1 mm diameter) arranged around the disk circumference in order of increasing inter-prong separation. The inter-prong distance was measured from the center of each prong and ranged from 1.2 to 9.0 mm in 0.2-mm steps. The prongs were applied perpendicularly to the long axis of the volar surface of the index finger with just enough pressure for LH to determine that he was being stimulated. LH's task was to decide whether he felt one or two points. A two-alternative adaptive forced-choice procedure was used, with the two-point touch threshold calculated as the average of the inter-gap distances corresponding to five changes in response direction.

LH's fine motor control was assessed using the Grooved Pegboard Test (Lafayette Instrument, 1970), a task that requires the participant to unimanually place 25 metal pegs into holes as quickly as possible.

LH's ability to haptically identify common objects was tested using a set of 24 household objects presented to his right (dominant) hand. He was required to name these objects as quickly and as accurately as possible.

2.2.2. Discrimination of face and non-face objects

We assessed LH's haptic ability to discriminate whether an object was an upright facemask, inverted facemask, upright teapot, or inverted teapot. All the faces and the teapots were made of stoneware clay. Fig. 1 shows three pairs of both the facemasks and the teapots. The clay facemasks were models of 36 female volunteers (for details see Kilgour & Lederman, 2002). We presented an exemplar from one of these four categories of stimuli one at a time and asked LH to identify the category to which it belonged. Each combination of object-type by orientation was presented on one quarter of the 64 trials. LH was required to state whether or not the object was an upright face.

2.2.3. Visual face-matching

We also tested LH's ability to discriminate the facemasks visually. This task was completed after the primary face/nonface experiment. The methodology was identical to that described below for the haptic task.

2.2.4. Haptic inversion paradigm

LH performed a 2AFC same/different face discrimination task. A "standard" facemask was presented to LH, who manually explored it with no time restriction. The standard face was then replaced with a second "comparison" facemask to explore. LH was required to state whether the two



Fig. 1. Examples of the facemask and teapot stimuli used. The three rows on the left of the figure show three different pairs of faces selected to be similar to one another. The three rows on the right are pairs of teapots designed to be similar to one another.

faces were the “same” or “different”. Thirty-six different clay facemasks were paired together based on their being both visually and tactually similar to one another. There were a total of 108 trials consisting of different combinations. One half of the trials were presented in an upright orientation, and the other half were presented in an inverted orientation. Within each orientation, one half of the trials consisted of the same face presented twice; during the remaining trials, two different faces were presented. The experiment was carried out in blocks, which alternated between upright and inverted orientations. The ‘same’ and ‘different’ trials were presented in random order. As the control condition, we tested LH’s ability to discriminate between teapots presented in both upright and inverted orientations. The experimental design was identical to that of the faces, with the exception that LH completed only 36 trials in total, with 18 upright and 18 inverted pairs. Teapots were chosen as control stimuli because they shared some critical characteristics with faces (canonical orientation, common configuration, overall feature similarity, and exemplar-level recognition).

3. Results

3.1. Assessment of sensorimotor hand function

LH’s sensory thresholds for tactile pressure sensitivity and tactile spatial acuity were both within normal limits (2.69 mg, and 3.2 mm, respectively). LH showed some impairment on the Grooved Pegboard Test (Lafayette Instrument, 1970) of fine motor control inasmuch as his

performance was slower than that of an age-matched normative sample. He performed the test with the dominant and non-dominant hands in 217 and 236 s, respectively. The data for the normative sample are 68 s (S.D. = 9.4) and 75 s (S.D. = 10.5), respectively. However, like normals, LH made no errors.

LH successfully identified 19 of 24 (79%) common household objects by touch alone. For two of the five incorrectly named objects, LH described their function. Moreover, the three remaining unidentified objects were also identified relatively poorly by a neurologically intact sample (Jessel, 1985): 52, 43, and 18% correct. Thus, LH’s accuracy was comparable to that of the neurologically intact sample (overall 88% accuracy). However, he was relatively impaired in terms of his response times for naming the common objects: the mean response time for the neurologically intact sample ($n = 23$) was 3.3 s (S.D. = 1.9), whereas LH’s mean response time was 5.6 s (S.D. = 6.5). With these preliminary tests we conclude that the accuracy of LH’s haptic performance on the face-processing task was not due to impairments in sensory-motor hand function. His sensory thresholds fell within normal limits. However, we expected LH’s performance with the faces to be slower than the control group.

3.2. Discrimination of face and non-face objects

We tested LH’s ability to haptically discriminate upright faces from a set of upright faces, inverted faces, upright non-face objects (teapots), and inverted non-face objects (teapots). Of 64 presentations, LH made one error when he failed to identify an upright facemask as such.

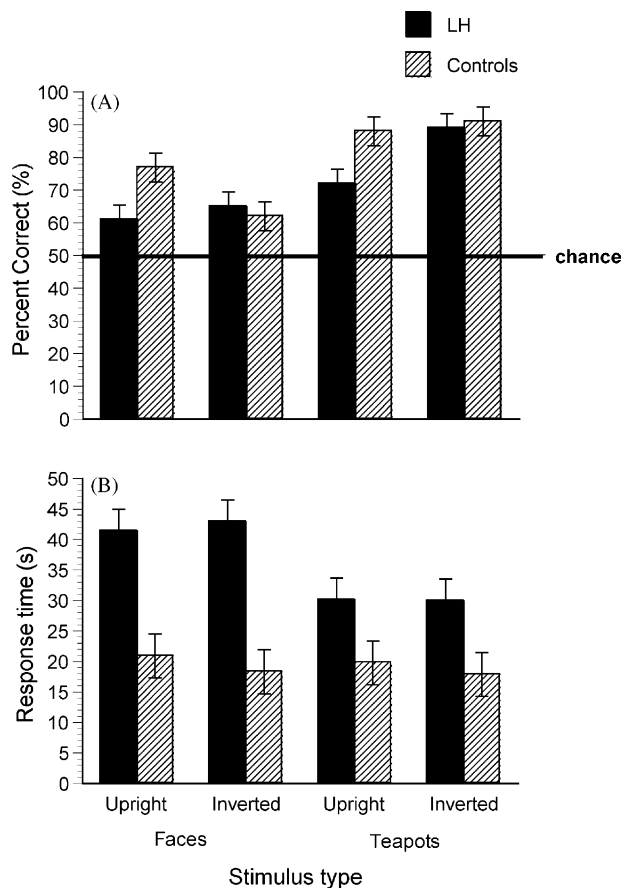


Fig. 2. Mean accuracy (%; panel A) and response time (s; panel B) as a function of stimulus type by participant. Error bars represent S.E.M.

3.3. Haptic face-matching accuracy

Fig. 2 (panel A) shows how accurate LH and the control group were when required to judge members of face pairs presented in the same orientation as being the same or different. Given that each trial produced a response that was either correct or incorrect, the data were analyzed using the binomial distribution. Analysis of variance could not be used to compare means as our dichotomous data violated the assumptions of that statistical technique. Of the four conditions—upright faces, inverted faces, upright teapots, and inverted teapots—LH's ability to determine whether two stimuli were the same or different was at chance level only for the upright faces ($P = 0.14$). His performance with the inverted faces was not statistically different from that with the upright faces ($P = 0.33$), but it was better than chance ($P = 0.04$). LH's accuracy in discriminating between the upright teapots was significantly above chance ($P = 0.04$). The inverted-teapot condition was statistically better than the upright-face condition ($P = 0.01$) in addition to being significantly better than chance ($P = 0.001$). The superior performance with inverted non-face objects is consistent with earlier findings that LH was significantly better when visually matching non-face objects (de Gelder & Rouw, 2000b).

LH did not show any advantage when touching as opposed to seeing upright facemasks: his ability to haptically discriminate between two upright faces was at chance, as it was when he looked at them.

The control group performed above chance in all four conditions: upright facemasks ($t(6) = 4.7$, $P = 0.005$); inverted facemasks ($t(6) = 11.2$, $P < 0.0001$); upright teapots ($t(6) = 12.1$, $P < 0.0001$); inverted teapots ($t(6) = 23.0$, $P < 0.0001$). However, the control group showed a different pattern of results than LH: they demonstrated the inversion effect that is typically found with visual face stimuli. That is, the control group performed better with upright faces than with inverted faces ($t(6) = 2.6$, $P = 0.04$). However, there was no inversion effect with the teapots: the accuracy of discriminating between teapots did not differ with orientation, ($t = -1.08$, $P = 0.32$). We therefore note that the control group generally had no difficulty discriminating between two upright faces, but their performance deteriorated when the faces were inverted. LH, on the other hand, was unable to discriminate between faces above chance level when they were presented in the upright position; his performance was 1.5 standard deviations below that of the mean of the control group. Furthermore, contrary to the control group, LH improved slightly (i.e., relative to chance) when the faces were presented in the inverted position, and his performance was closer to that of the control group ($z = -0.9$). Although LH had difficulty discriminating between upright teapots ($z = -2.0$, relative to controls), he had no difficulty when they were inverted and his performance was similar to that of the control group ($z = -0.2$).

3.4. Haptic face-matching response time

LH's deficit in haptic-face processing is clearly apparent in the data shown in Fig. 2 (panel B), which presents the response times corresponding to the accuracy results (panel A). Response time was calculated as the total time spent haptically exploring the first and second stimulus objects prior to responding whether they were the same or different. We entered these data into a $2 \times 2 \times 2$ analysis of variance, with Participant (LH versus controls) as the between-subjects factor, and stimulus (faces versus teapots) and orientation (upright versus inverted) as the within-subjects factors. Averaged across participants and conditions, mean response time for incorrect trials (29.8 s, S.D. = 16.2) and correct trials (22.8 s, S.D. = 11.5) were not statistically different from one another ($t(31) = 1.91$, $P > 0.05$); therefore, all trials were analyzed. Although not statistically significant, there was a trend for incorrect trials to be slower than correct trials. Table 1 shows a breakdown of the response times by condition and participant. There was a main effect of Participant, $F(1, 6) = 22.34$, $P = 0.003$: overall, LH was slower than the control group. There was also a main effect of Stimulus, $F(1, 6) = 18.04$, $P = 0.005$: all participants (LH and controls) were faster responding to teapots than

Table 1
Mean response times (s) and standard deviations (in parentheses) for correct and incorrect trials as a function of condition and participant

Condition	LH		Control group	
	Correct	Incorrect	Correct	Incorrect
Facemasks				
Upright	40.5 (15.1)	43.8 (17.5)	19.77 (5.5)	22.22 (6.4)
Inverted	40.7 (11.5)	46.8 (15.0)	19.34 (6.2)	19.35 (6.5)
Teapots				
Upright	29.0 (7.5)	30.0 (3.8)	19.1 (5.1)	20.5 (4.4)
Inverted	29.7 (6.9)	36.4 (23.4) ^a	16.7 (4.8)	20.7 (6.7)

^a The large S.D. in this condition is attributable to the fact that only two trials contributed to this mean, one of which was anomalously large (52.9 s).

to faces. However, the stimulus \times participant interaction term was also statistically significant, $F(1, 6) = 14.05$, $P = 0.01$: LH was notably and statistically slower than the control group when responding to the faces but statistically equivalent when responding to the teapots. Although there was no inversion effect apparent in the response–time data for either LH or the control group, our data strongly support a face-specific processing deficit in LH. One reviewer suggested that LH might have been slower with faces than teapots simply because he might have experienced more hesitancy when touching faces as opposed to teapots. We do not believe this to be the case for two reasons. First, it is not clear why this would occur inasmuch as the faces were inanimate masks, as opposed to real faces. Second, the videotapes indicated that LH began exploring faces immediately and without interruption. It is difficult to interpret these response–time data further. Ideally, we would have found a face-inversion effect for the control group consistent with the accuracy data for the face-inversion effect. Similarly, we would have found a paradoxical teapot-inversion effect for LH corresponding to his accuracy data. The inherent variability of response–time data and the limited number of participants may have contributed to the absence of these effects.

3.4.1. Visual face-matching

To ensure that LH was processing the facemasks as faces per se, as opposed to non-face objects, we also tested LH's ability to perform the same/different task with the facemasks visually. His visual accuracy was similar to his haptic performance. When the faces were presented in the upright orientation, his accuracy was only 55% (chance = 50%). He also performed at chance level when the faces were inverted (61% correct). The control group was not tested visually with the facemasks for two reasons. First, they were tested with a standardized visual face recognition test (Benton et al., 1994). Second, previous research (Kilgour & Lederman, 2002) on a visual match-to-sample task with the same set of facemasks showed a ceiling effect.

4. Discussion

LH's visual prosopagnosia has been well documented. To our knowledge, LH is also the first documented case of *haptic* prosopagnosia. Our data confirm that LH's ability to identify faces haptically was as deficient as it was visually; moreover, the patterns of matching impairment were very similar. LH did not demonstrate the normal inversion effect that is found with control participants either visually or haptically. Although he demonstrated some general deficits in terms speed of information processing, his accuracy in matching two upright non-face objects was 72% correct, and he did so as quickly as the control group. In contrast, LH's ability to match two upright faces was only at chance level and he was significantly slower than normal controls in doing so. Moreover, his ability to match two inverted faces was somewhat better, being above chance level.

Similar to previous findings in the visual domain of a paradoxical inversion effect for objects (de Gelder & Rouw, 2000b), LH showed a haptic paradoxical inversion effect for the teapots. We did not test his ability to match teapots visually for two reasons. First, logistical constraints limited the amount of time available with LH. Second, as stated earlier, de Gelder and Rouw (2000b) have documented this effect with LH. They argued that configural processing mechanisms are applied to non-face objects, as well as faces. They interpreted their findings of a paradoxical object-inversion effect as due to deficient configural-processing mechanisms that interfere with intact feature-based processing mechanisms. Our data are consistent with this interpretation. This also raises a question as to whether our findings reflect an impairment of subordinate-level object recognition rather than an impairment of face recognition. If this were the case, however, LH would not have shown normal processing of the inverted teapots, as they are also processed at the subordinate level.

The existence of visual prosopagnosia is used as evidence of a face-specific neural system that is independent of the visual object-recognition system used to process non-face objects (Farah, Levinson, et al., 1995). Observations of prosopagnosics' behavior and how far it deviates from "normal" only allow us to indirectly infer an association between the brain damage and behavior. Our observations of LH's haptic behavior similarly allow us to speculate about the neural substrates that underlie the ability to process faces haptically. Several brain regions are possible candidates.

One possibility is that haptic presentation of faces may activate neural substrates that are also involved in visual face recognition. There has been considerable research implicating the involvement of the fusiform gyrus (Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995). As this area is included in the areas that are damaged in LH, the fusiform gyrus probably fails to provide proper functional support when LH is attempting to recognize faces by touch.

As there is additional evidence that other extrastriate visual regions are activated in haptic object recognition tasks (Deibert, Kraut, Kremen, & Hart, 1999; James et al., 2002; Ostry & Romo, 2001), these cortical areas may also be involved in haptic face recognition. The regions traditionally include areas within the parietal lobes (supramarginal and angular gyri; Deibert et al., 1999). More recently, the lateral occipital complex (LOC), which was thought to be a visual area, has been implicated as part of a multimodal object-related network involved in haptic object processing (Amedi, Malach, Kendler, Peled, & Zohary, 2001; James et al., 2002).

LH's brain damage does not include sensorimotor areas in the parietal lobes presently known to be involved in haptic (real) object recognition (Deibert et al., 1999; Ostry & Romo, 2001). This sparing is underscored by his normal performance when recognizing teapots haptically. Another possibility is that his intact LOC is recruited when both faces and teapots are processed haptically. Recruitment of this area may be sufficient for processing teapots; however, haptic face processing may require the additional involvement of the fusiform gyrus, which is not functionally available to LH.

Another possibility is that haptic face-recognition implicates the claustrum, which has been shown to be involved in haptic-visual cross-modal transfer (Hadjikhani & Roland, 1998) and is intact in LH. Therefore, it is not unreasonable to suggest that haptic information may be processed normally, relayed to the claustrum and from there to the inferotemporal cortex involved in visual face recognition. Again, we propose that LH's damaged inferotemporal cortex may prevent apprehension of the haptic face representation.

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References

- Amedi, A., Malach, R., Kendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience*, *4*, 324–330.
- Benton, A. L., Sivan, A. B., Hamsher, K. de S., Varney, N. R., & Spreen, O. (1994). *Contributions to neuropsychological assessment. A clinical manual* (2nd ed.). New York: Oxford University Press.
- Brewster, D. (1839). *Letters on Natural Magic*. New York: Harper.
- de Gelder, B., & Rouw, R. (2000a). Configural face processes in acquired and developmental prosopagnosia: Evidence for two separate face systems? *Cognitive Neuroscience*, *11*, 3145–3150.
- de Gelder, B., & Rouw, R. (2000b). Paradoxical configuration effects for faces and objects in prosopagnosia. *Neuropsychologia*, *38*, 1271–1279.
- Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*, 107–117.
- Deibert, E., Kraut, M., Kremen, S., & Hart Jr., J. (1999). Neural pathways in tactile object recognition. *Neurology*, *52*, 1413–1417.
- Etcoff, N. L., Freeman, R., & Cave, K. R. (1991). Can we lose memory for faces? Content specificity and awareness in a prosopagnosic. *Journal of Cognitive Neuroscience*, *3*, 25–41.
- Farah, M. J., Levinson, K. L., & Klein, K. L. (1995a). Face perception and within-category discrimination in prosopagnosia. *Neuropsychologia*, *33*, 661–674.
- Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995b). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception & Performance*, *21*, 628–634.
- Farah, M. J., Wilson, K. D., Drain, H. M., & Tanaka, J. W. (1998). The inverted face inversion effect in prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms. *Vision Research*, *35*, 2089–2093.
- Feinberg, T. E., Gonzalez-Rothi, L. J., & Heilman, K. M. (1986). Multimodal agnosia after unilateral left hemisphere lesion. *Neurology*, *36*, 864–867.
- Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, *29*, 159–170.
- Hadjikhani, N., & Roland, P. E. (1998). Cross-modal transfer of information between the tactile and visual representations in the human brain: A positron emission tomographic study. *Journal of Neuroscience*, *18*, 1072–1084.
- Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. Ma., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *The Journal of Neuroscience*, *14*, 6336–6353.
- James, T. W. et al. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia*, *40*, 1706–1714.
- Jessel, A. (1985). *Cutaneous spatial resolution and haptic recognition of common objects in elderly and young adults*. Unpublished Honours thesis, Queen's University, Kingston, Ont., Canada.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*, 4302–4311.
- Kilgour, A. R., & Lederman, S. J. (2002). Face recognition by hand. *Perception & Psychophysics*, *64*, 339–352.
- Lafayette Instrument. (1970). *Grooved Pegboard Test*. Lafayette, IN: author.
- Leder, H., & Bruce, V. (2000). When inverted faces are recognized: The role of configural information in face recognition. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *53A*, 513–536.
- Levine, D. N., Calvanio, R., & Wolf, E. (1980). Disorders of visual behavior following bilateral posterior cerebral lesions. *Psychological Research*, *41*, 217–234.
- Ostry, D. J., & Romo, R. (2001). Tactile shape processing. *Neuron*, *31*, 173–174.
- Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, *74*, 1192–1199.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *46A*, 225–245.
- Valentine, T. (1988). Upside-down faces: A review of the effects of inversion upon face recognition. *British Journal of Psychology*, *79*, 471–491.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*, 141–145.