Object recognition is one of the most important cognitive operations that people perform. Objects surround us constantly and to direct the appropriate actions toward these objects first requires successful identification. From an evolutionary perspective, the ability to reliably recognize objects is extremely adaptive because of the need to identify predators, edible foods and conspecifics. Furthermore, for social organisms such as humans, specialized forms of object recognition such as face recognition are extremely important for maintaining normal social interactions. The fact that face recognition seems relatively effortless is a clue to its special nature. Despite the similarity in geometric structure between different human faces, which should make face recognition extremely difficult, we tend to recognize faces with the same facility as other objects that are less similar [30,31]. Most of the evidence points to the existence of specialized brain systems in humans for processing visual stimuli of special significance, such as faces [9,13,28].

The majority of studies investigating object recognition in humans use visual stimuli, because humans are predominantly visual animals. Nevertheless, to attain a more thorough understanding of object recognition processes, they should be studied using input through multiple sensory systems. Theories of object recognition, which have been developed largely based on visual data, can be elaborated or constrained by the inclusion of data from other sensory systems. Of the other possible sensory inputs, recognition through haptic exploration (active touch) may be the most informative, because vision and touch share the ability to extract information about the complex geometric structure of objects [2,3,20,22,23,26]. Furthermore, there is ample evidence that object recognition tasks carried out using visual or haptic information rely on overlapping brain regions. In particular, parts of the lateral occipital complex (LOC [21]) appear to be involved in both visual and haptic exploration of objects [11,25] and these same brain regions are more responsive to objects than to textures [1] or nonsense objects [27]. Responses in LOC are also modulated by previous experience. Previous haptic or visual experience with objects increased activation in these regions when the same objects were subsequently viewed [11]. Finally, visual and haptic object activations in ventral occipital and tem-
poral cortex show patterns that are distinctly category-specific [25]. Together, these studies suggest that there are significant similarities between visual and haptic object recognition for both behavioral and neural measures, not just for object recognition in general, but also for specific categories of objects.

The general aim of the present study was to investigate the neural substrates involved in haptic face processing. Previous work [17] shows that haptic exploration of a face can convey sufficient information to successfully perform a face identification task. Furthermore, a study of an individual with prosopagnosia (inability to recognize visual faces) revealed that the individual also had difficulty recognizing faces haptically, even though control objects were recognized normally [15]. Prosopagnosia is thought to involve injury to the ventral temporal cortex and in particular the fusiform gyrus, predominantly in the right hemisphere [4,32]. The lesion data is consistent with fMRI studies that find stronger activation in the fusiform gyrus for faces than for other objects, with a stronger selectivity in the right hemisphere [13,28]. A recent fMRI study, however, found unilateral activation of only the left fusiform gyrus during haptic face identification [16]. Therefore, haptic face identification, like visual face identification, involves the fusiform gyrus, although the subregions of the fusiform gyrus that are recruited by visual and haptic face identification may be different.

The majority of studies investigating the role of the fusiform gyrus in face identification use unfamiliar faces; however, several studies [6,14,18,29] suggest that activation in the fusiform gyrus is influenced by familiarity of object stimuli. These findings, however, have come exclusively from visual experiments and, as mentioned earlier, to further our understanding of cognitive processes, it is important to include different sensory inputs. The role of the fusiform gyrus was previously investigated in its relation to haptic face identification [15,16]. In the following experiment, we extend these results by investigating the influence of familiarity on brain activation during haptic face exploration. Whether or not familiar faces produce greater or lesser activation than unfamiliar faces is somewhat ambiguous based on previous studies of visual face recognition; however, in most studies, experience with unfamiliar faces caused an increase in activation [10,12,14,18] (but see [29]). Thus, we predict an increase in activation in the left fusiform gyrus for familiar faces over unfamiliar faces when haptically explored.

Fourteen volunteers (seven male and seven female) between the ages of 22 and 30, all of whom gave written informed consent in accordance with the Declaration of Helsinki, participated in this study. The study was approved by the ethical review boards of both Queen’s University and the University of Western Ontario. All subjects reported right-handedness, normal tactile sensation and no history of neurological disorders.

A set of 36 3-D clay facemasks were used as stimuli. As described in detail elsewhere [17], these facemasks were created using plaster molds of live faces. Examples are shown in Fig. 1. For each subject, 18 of the 36 facemasks were randomly chosen for use during the training phase leaving 18 facemasks that remained unfamiliar to the subject. During the scanning phase, subjects lay in a supine position within the scanner bore with a Plexiglas “table” placed over the lower half of the body, with the front edge at about the level of the abdomen (Fig. 2). On top of the table was a guide with a sliding platform that supported one of the facemasks. Use of the table apparatus allowed the experimenter (who stood next to the scanner) to slide a new facemask into the bore within the reach of the subject’s hand for each trial.

Each subject was individually trained at the Touch Laboratory of Queen’s University (Kingston, Canada) to identify a set of 18 facemasks by name. During training, subjects were kept under conditions similar to those under which they would be tested during the scanning phase. That is, each subject lay blindfolded on a bench in a supine position and the stimuli were presented at approximately abdomen level. Subjects explored the facemasks with their left hand. Training continued until subjects were able to identify facemasks with 100% accuracy and within ~7–8 s. On average, it took 10–12 h of training to satisfy our highly demanding criteria for acceptable haptic identification.

During the scanning phase of the study, subjects performed a haptic face recognition task while brain activation was measured using fMRI. Facemasks were presented to the subject in a slow event-related design using the table apparatus described above. Subjects lay supine within the scanner bore, blindfolded, with their head secured firmly in the head coil with foam padding.
Fig. 2. MR compatible haptic stimulus-delivery “table” apparatus. The subject lay within the scanner bore while the experimenter operated the apparatus from beside the scanner. Facemasks were fixed to a platform and pushed to within the subject’s reach. Because they used their left hand to explore the facemasks, their left shoulder and upper arm were supported with foam padding in order to minimize transduction of movement to the head. The Plexiglas “table” described above was placed over the lower half of the subject’s body, with the front edge at about the level of their abdomen so that the facemasks were presented in roughly the same position during both training and scanning phases.

Between each trial, the experimenter selected the next facemask for presentation, fixed it to the guided platform on the table and pushed it into the bore to the end of the guide. A tone, audible to both the experimenter and the subject, signaled the subject to begin exploring the facemask with their left hand. The subject’s task was to determine if the facemask was one they had encountered during the training phase (familiar) or not (unfamiliar). They responded with one of two buttons using their right hand. After making their response, subjects continued to explore the facemask with their left hand until a second tone sounded, signaling the end of the trial. At that point, the experimenter retracted the guided platform and the trial sequence began again.

Functional data were analyzed using the BrainVoyager™ multi-study GLM (general linear model) procedure and in-house Matlab routines. Three statistical parametric maps (SPMs) were created. For all of these, predictor functions were a series of gamma functions (\( \Delta = 2.5, \tau = 1.25 \)) spaced in time based on the event-related stimulus presentation protocol. (1) A group random-effects model was used to compare familiar facemasks with unfamiliar facemasks. (2) A group random-effects model was used to compare familiar responses (“hits” and “false alarms”) with unfamiliar responses. (3) A group random-effects model was used to compare correct responses (“hits” and “correct rejections”) with incorrect responses. For 3 of the 14 subjects, one or more of the possible response conditions was not represented (for example, one subject made no errors). Therefore, the three analyses described above were carried out on the remaining 11 subjects for whom all possible response conditions were represented. Random-effects SPM analyses were thresholded using an uncorrected \( t \)-value of 4.4 (\( t_{10} = 4.4, p < .001 \)) and cluster filter size 540 mm\(^3\) (10 voxels). Peak statistical values for clusters were reported with Bonferroni correction of associated Type I error rates.

Fig. 3 shows an SPM analysis comparing familiar facemasks with unfamiliar facemasks. At our predefined threshold (\( t_{10} = 4.4, p < .001 \), uncorrected), only one cluster showed a significant difference in activation between conditions. At that threshold, the volume of the cluster was 1126 mm\(^3\). The closest anatomical landmark to the significant cluster was the left fusiform gyrus, which lies along the ventral surface of the posterior cortex. The inset panel in Fig. 3 shows a mag-
nified view of the area surrounding the cluster and indicates the fusiform gyrus and its two flanking sulci. The cluster sits deep within the collateral sulcus on the medial bank of the left fusiform gyrus. It is worthwhile noting that, even at a liberal threshold (t(12) = 2.0, p < .10, uncorrected), the right fusiform gyrus did not show a significant difference between conditions. This finding was observed despite the fact that subjects explored the facemasks with their left hand, which (if anything) should have biased activation toward the right hemisphere.

Two other SPM analyses, one comparing familiar responses with unfamiliar responses and one comparing correct responses with error responses did not show significant differences between conditions at the same threshold used in Fig. 3 (t(12) = 4.4, p < .001, uncorrected).

In agreement with previous work [16], we found that the left fusiform gyrus was involved in haptic face processing. More specifically, though, we determined that activation in the left fusiform gyrus distinguishes between familiar and unfamiliar faces. Together with the previous studies, our findings suggest that haptic object recognition and visual object recognition share one or more common neural substrates. Furthermore, like visual objects, haptic objects appear to be processed in a hierarchy of processing stages, with the specificity of these stages dependent on the class of stimulus.

Previous studies of haptic non-face object recognition found a region of putative visual cortex, the lateral occipital complex, that was also found to be sensitive to familiarity [11]. The LOC is suggested as the site for convergence of visual and haptic 3-D shape representations [11] and is highly involved in the recognition of both generic objects and objects in more specialized, subordinate-level classes, such as faces. For visually presented faces and other within-class objects of expertise, it is well known that a region of the fusiform gyrus (the fusiform face area (FFA)) is recruited, more in the right hemisphere than in the left hemisphere [9,13]. This recruitment of additional cortex for processing a specialized class of objects illustrates the hierarchical organization of the visual system. Finding that the left fusiform gyrus is activated during haptic face recognition suggests that the same hierarchical organization exists for haptic object recognition as well. However, our findings, and those from previous studies, provide converging evidence that the specialized brain regions recruited for visual and haptic face recognition are not the same [16,25]. Visual face stimuli were not used in this study; therefore, we cannot determine absolutely that the regions involved in haptic face recognition would not also have been recruited for visual face recognition, but the fact that there was no significant activation in the right fusiform gyrus coupled with highly significant activation in the left fusiform gyrus suggests that the neural systems underlying vision and haptics diverge for face stimuli.

Like visual face stimuli, the facemasks used here share a common structural configuration; therefore, discriminating an individual face often requires analyzing differences in the geometric relationship of the parts [5]. For visual recognition, the right fusiform gyrus seems to be involved in processing learned configurations [7] by combining information from spatially distinct areas of a stimulus, which is called holistic processing [8]. Owing to the structure of their receptor surfaces, it is unlikely that the haptic system can process information over large areas of space as efficiently as vision [19]. In that case, it is perhaps not surprising that haptic face processing does not recruit the strong holistic processing capacity of the right fusiform gyrus.

The most significant behavioral difference between visual and haptic face recognition was the longer time to recognize the faces haptically (∼7–8 s). Perhaps the role of the left fusiform gyrus is to piece together the configuration of a stimulus when the input is received sequentially over an extended period of time. In other words, perhaps the role of both the left and right fusiform gyrus is to process learned stimulus configurations, but the right fusiform gyrus processes a configuration by integrating stimulus information over space, whereas the left fusiform gyrus processes a configuration by integrating over time. A dissociation of spatial integration processes in the right hemisphere and temporal integration processes in the left hemisphere is certainly supported by theories of cerebral lateralization [32].

The above hypothesis is speculative and it cannot be tested within the present experimental design. In addition to the above hypothesis, there are other possible explanations of the left lateralized activation that should be explored. First, subjects may be using visual imagery during haptic exploration. But, visual face imagery, like actual face perception recruits the right fusiform gyrus to a greater extent than the left fusiform gyrus [24]; therefore, it is unlikely that visual imagery during haptic face exploration would consistently recruit only the left FFA.

Second, subjects have labels for the familiar facemasks and may be recalling these labels during testing, which may in turn recruit left hemisphere mechanisms more than right. But, the absence of an effect between faces with labels that are correctly recognized (hits) versus not (misses) suggests that labeling may not be driving this effect. Furthermore, in our previous work we compared facemasks with control objects, both of which were trained with labels and found that left fusiform gyrus activation was greater for facemasks [16].

Third, subjects may find it easier to categorize the familiar than the unfamiliar facemasks, which may also recruit left hemisphere mechanisms more than right. In our previous work, however, we found left fusiform gyrus activation even when subject’s performance on the task was equated. In that study, subjects silently named facemasks and control stimuli (categorizing at the individual level) while being scanned. Pre-testing showed that performance on the task was equivalent for facemasks and control objects [16].

In our previous study of haptic face recognition, the left fusiform gyrus responded more with facemasks than with control objects [16]. Before scanning in that study, subjects underwent 10–12 h of haptic training with facemasks and control objects. Likewise, in the present study, subjects underwent 10–12 h of haptic training. Although our finding of left fusiform gyrus activation could be indicative of a special interaction between vision and haptics for face stimuli, there is another explanation. In our previous study, a distinct difference between the facemasks and the control objects was that the facemasks
shared a common spatial configuration of features, whereas the control objects did not (or did not). Thus, the left fusiform gyrus may be recruited during haptic training with similar within-class stimuli, regardless of whether or not those stimuli are faces. Further evidence for this claim comes from visual expertise training studies. When subjects are trained for 10–12 h to individuate novel objects (called Greebles), they show increased activation with Greebles in the FFA [7]. Recent unpublished findings in our lab showed that 10–12 h of haptic training with Greebles is also sufficient for subjects to reach the same behavioral criterion used in the visual studies. Brain activation was not measured for the haptic Greeble experts; thus, we do not know what brain regions would be recruited during the acquisition of haptic Greeble expertise, but the speculation would be that 10–12 h of haptic training may be the requisite for recruiting the left fusiform gyrus. Thus, it is possible that the experimental design in our previous study and in the present study is testing haptic face “experts” and that this expertise has little to do with their visual face expertise.

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Appendix A. Supplementary data


References