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To cite this article: Jasmin Cloutier , David J. Turk & C. Neil Macrae (2008) Extracting variant and invariant information from faces: The neural substrates of gaze detection and sex categorization, *Social Neuroscience*, 3:1, 69-78, DOI: [10.1080/17470910701563483](https://doi.org/10.1080/17470910701563483)

To link to this article: <http://dx.doi.org/10.1080/17470910701563483>



Published online: 14 Mar 2008.



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Extracting variant and invariant information from faces: The neural substrates of gaze detection and sex categorization

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Guided by influential models of face processing, efforts have been expended to uncover the neural substrates subserving the many facets of face perception. Extending this work, the present study used functional brain imaging (fMRI) to explore the relationship between the operations supporting the explicit extraction of sex and gaze-related information from faces. The brain imaging data showed the right superior temporal sulcus to be preferentially involved during assessments of gaze direction and a region of the left fusiform gyrus to be involved during sex categorization. These results provide support for the distributed face-processing model advanced by Haxby and colleagues (2000).

Upon encountering other social agents, a simple glance at their face is all that it takes to extract a wealth of useful information (Bruce & Young, 1998). For example, brief exposure to available facial cues is sufficient to categorize faces according to their sex or race, to determine their current emotional state or to compute their gaze direction (i.e., direction of social attention), hence possible behavioral intentions (Cloutier, Mason, & Macrae, 2005; Friesen & Kingstone, 1998; Willis & Todorov, 2006). If the face belongs to a familiar individual, perceivers will also readily access specific personalized information, such as the person's name, occupation, likes and dislikes. Aside of a few exceptions (e.g., the study of attractiveness and emotions), the pivotal role of face processing has only recently been established in many areas of social cognition (Bodenhausen &

Macrae, 2006; Zebrowitz, 2006). Arguably, faces are the most prevalent cues used during social interactions. This is especially true when no other source of information (i.e., biographical knowledge) is available to guide the interactions. Therefore, a better understanding of the perceptual mechanisms mediating face processing is essential to appreciate our remarkable person perception abilities. Accordingly, with the help of behavioral, neuroimaging and patient studies, great strides have been made in unraveling the underlying mechanisms of face processing (Adolphs, 1999; Allison, Puce, & McCarthy, 2000; Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2002).

Investigations using brain-imaging techniques have worked towards identifying the neural substrates that subserve various aspects of face processing. Multiple brain areas have been found

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During this research, CNM was supported by a Royal Society-Wolfson Fellowship. This research was funded by the Dartmouth Brain Imaging Center.

We thank Joe Moran, Leah Somerville, Julian P. Keenan and several anonymous reviewers for their comments and advice.

to be involved in perceiving faces (Haxby, Gobbini, & Montgomery, 2004; Ishai, Schmidt, & Boesiger, 2005). Among these brain areas, some seem to be uniquely dedicated to the recognition of faces (Kanwisher, 2006). In particular, an area of the fusiform gyrus has been shown to preferentially support face recognition (Grill-Spector, Knouf, & Kanwisher, 2004; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992). The privileged status of faces in this brain area could be due to their biological relevance and to the tremendous number of exemplars processed throughout our lives. Other components of this face-responsive brain network have been shown to be involved in extracting specific facial properties. Indeed, some brain regions have been shown to be active when processing the race (Golby, Gabrieli, Chiao, & Eberhardt, 2001; Phelps et al., 2000), emotional expression (Adolphs, 2002; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000), familiarity (Gobbini, Leibenluft, Santiago, & Haxby, 2004; Gorno-Tempini & Price, 2001) and direction of attention (Hooker et al., 2003; Pelphrey, Singerman, Allison, & McCarthy, 2003b; Pelphrey, Viola, & McCarthy, 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998) of faces.

In the face-processing literature, an important functional distinction has been drawn between featural and configural encoding operations. Whereas featural operations code the constituent elements of faces (e.g., nose, eyes, hairstyle), configural operations code the spatial relations among features of the face (see Maurer, Le Grand, & Mondloch, 2002). Although categorical judgments can be executed by extracting single facial features (Brown & Perrett, 1993; Goshen-Gottstein & Ganel, 2000), the processing of identity relies on the extraction of configural information (i.e., second-order featural relations, see Maurer et al., 2002). A similar distinction has been suggested to explain hemispheric differences in the brain's capacity to process local and global aspects of a stimulus (Fink et al., 1996; Robertson & Lamb, 1991). It has been proposed that the right hemisphere preferentially supports global processing and that the left hemisphere preferentially supports the processing of local elements of stimuli. Support for this framework has also been noted in the face-processing literature. Indeed, it has been suggested that facial dimensions requiring configural processing are supported by the right hemisphere, and that

dimensions requiring featural processing are supported by the left hemisphere (Hillger & Koenig, 1991; Mason & Macrae, 2004; Rossion et al., 2000).

When focusing on the perceptual cues required for the extraction of various facial dimensions, facial properties have also been divided into two basic categories: invariant facial properties, such as the identity and sex of a face; and dynamic, changeable facial properties, such as the emotional expression or gaze direction conveyed by a face. Based on this distinction, Haxby and colleagues (2002) have developed a distributed neuro-cognitive model of face processing. The model suggests the existence of a core system for face processing involving the fusiform gyrus (FG) for the representation of invariant facial dimensions (e.g., identity) and the superior temporal sulcus (STS) for the representation of dynamic facial dimensions (e.g., gaze direction). These early visual components of face processing are complemented by an extended network composed of brain regions (e.g., medial temporal lobe, anterior temporal cortex) that support the extraction of further meaningful information from faces (e.g., biographical details).

Initial evidence for the core components of this distributed neuro-cognitive model was gathered by directly comparing the brain regions involved in processing the identity and/or gaze direction of unfamiliar faces (Hoffman & Haxby, 2000). The results of this investigation supported the notion that processing identity is mediated by the FG while computing gaze direction is supported by activity in the STS (see also Haxby et al., 2002). Although other researchers have adopted a similar framework to guide their investigations (Andrews & Ewbank, 2004; Winston, Henson, Fine-Goulden, & Dolan, 2004), to our knowledge only one fMRI study has directly compared the neural operations that support the extraction of invariant and dynamic information from faces (Hoffman & Haxby, 2000). Moreover, there are reasons to believe that the task used by Hoffman and Haxby (2000) to examine the extraction of invariant information from faces might not have been representative of this type of processing. Specifically, participants were asked to match the gaze direction (i.e., same or different direction) or the perceptual identity (i.e., same or different face) of unfamiliar faces in an n -back task (i.e., 1-back task). Typically, identity-based processing is characterized as the extraction of perceptual information necessary to recognize a

specific individual across multiple viewpoints and contexts (Bruce & Young, 1986). As such, people are usually required to match identities across different facial viewpoints. However, Hoffman and Haxby (2000) presented to-be-matched faces in identical viewpoints, thereby making it possible that recognition could be based on perceptual matching not person identification per se (Bruce & Young, 1986; Mason & Macrae, 2004). That is, there is no way to confirm that the identities of the faces were ever processed during this experiment. Instead, subjects might have based their positive identity judgments on the repetition of superficial aspects of the identical stimuli.

In addition, comparing the extraction of identity with gaze-related information is also potentially problematic. Put simply, processing the identity of a face is more perceptually demanding than computing the gaze direction signaled by the face. Face recognition is believed to rely on configural information (i.e., the relationship among facial features; Collishaw & Hole, 2002; Leder & Bruce, 2000; Maurer, Le Grand, & Mondloch, 2002; Searcy & Bartlett, 1996), whereas the unique morphology of the human eye (Kobayashi & Kohshima, 1997) makes the computation of gaze direction a relatively straightforward feature-based task (Driver et al., 1999; Friesen & Kingstone, 1998; Friesen, Ristic, & Kingstone, 2004; Quadflieg, Mason, & Macrae, 2004). It is possible, therefore, that the activity observed in FG and STS may reveal more about differences in the complexity of different aspects of face processing than the extraction of invariant and dynamic knowledge from faces.

Although many researchers have been guided by Haxby and colleagues' neuro-cognitive model of face processing, very few studies have directly tested its core components. Considering its broad influence in both social and cognitive neuroscience, this state of affairs is somewhat surprising. In order to remedy the potential difficulties previously noted with the Hoffman and Haxby (2000) study, a task is required in which both the extraction of invariant and dynamic facial information is supported by simple, feature-based processing. Comparing sex categorization and the computation of gaze direction offers just such a possibility. It is widely acknowledged that hair-related information (e.g., hairstyle, length of hair) is a dominant cue when people are faced with the task of determining the sex of a face (Brown & Perrett, 1993; Burton, Bruce, & Dench,

1993; Cloutier et al., 2005; Cloutier & Macrae, in press; Macrae & Martin, in press). Thus, just like gaze direction, sex categorization relies on feature-based processing. If Haxby and colleague's model is correct, as an invariant facial property, sex construal should be supported by activity in FG. In contrast, the computation of gaze direction should be supported by activity in STS (Hoffman & Haxby, 2000). To establish the generality of the core component of Haxby et al's (2002) model of face processing and add to the preliminary evidence in its support, we tested this prediction in the present study.

METHOD

Participants

Thirteen participants (9 female), all Dartmouth College undergraduate or graduate students, completed the study for course credit or \$10. Participants were right-handed, reported no significant abnormal neurological history and had normal or corrected-to-normal visual acuity. Informed written consent for all participants was obtained prior to the experiment in accordance with the guidelines established by the Committee for the Protection of Human Subjects at Dartmouth College.

Behavioral procedure

Participants performed four simple blocks of categorization trials for each type of judgment (i.e., sex categorization or gaze direction). In both conditions, participants responded, via a button press, by making match or mismatch judgments on presented faces. In the sex task, they were required to report if the sex of a presented face matched the sex of the previous face (1-back task). In the gaze-direction task, they were required to report if the gaze direction of a presented face (i.e., averted or direct) matched the gaze direction of the preceding face. This ensured that participants were explicitly processing the dimensions of interest. Each block of trials was composed of 20 unfamiliar faces (10 men and 10 women) presented in a pseudo-random fashion. The faces were 6.2×8.8 cm in size. Faces appeared in the center of the screen for 1000 ms and were then replaced by a fixation cross that remained in the center of the screen for

1500 ms. In both conditions, the faces displayed direct and averted eye gaze equally often. Reaction times and response accuracy were recorded. In a control task, scrambled color images created from the face stimuli were presented at the same rate and in the same format as the stimuli in the sex and gaze-direction tasks. In these trials subjects were required to press both right and left buttons simultaneously when the stimuli appeared. As in Hoffman and Haxby (2000), the blocks of control task alternated with each task block for a total presentation of nine control blocks.

Image acquisition

Imaging was performed on a 1.5-T whole body scanner (General Electric Medical Systems Signa, Milwaukee, WI) with a standard head coil. Visual stimuli were generated using an Apple G4 laptop computer running PsyScope software (Cohen, MacWhinney, Flatt, & Provost, 1993). Stimuli were projected to participants with an Epson (model ELP-700) LCD projector onto a screen positioned at the head end of the bore. Participants viewed the screen through a mirror. A fiberoptic light-sensitive key press, interfaced with the PsyScope Button Box (New Micros, Dallas, TX) was used to record participants' behavioral performance.

Anatomical images were acquired using a high-resolution 3D spoiled gradient recovery sequence (SPGR; 124 sagittal slices, TE = 3.2 ms, TR = 8 ms, flip angle = 15°, voxel size = 1 × 1 × 1.2 mm). Functional images were collected in 4 runs using a gradient spin-echo, echo-planar sequence sensitive to BOLD contrast (T2*) (TR = 2500 ms, T2* echo time = 35 ms, flip angle = 90°, 3.75 × 3.75 in-plane resolution). During each functional run, 240 sets of axial images (25 slices; 4.5 mm slice thickness, 1 mm skip between slices) were acquired, allowing for whole-brain coverage.

Image analysis

All data were analyzed using SPM99 software (Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1995). Functional data were realigned within and across runs to correct for head movement, and coregistered with each participant's anatomical data. Functional data

were then transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurologic Institute), which approximates Talairach and Tournoux's (1988) atlas space. Normalized data were then spatially smoothed (6 mm full width-at-half-maximum; FWHM) using a Gaussian kernel. The normalized and smoothed images were then used for statistical analysis.

For each participant, a general linear model, incorporating task effects (modeled as a box-car function convolved with the canonical hemodynamic response function), a mean, and a linear trend were used to compute parameter estimates and *t*-contrast images (containing weighted-parameter estimates) for each comparison at each voxel. A random-effects analysis (one sample *t*-test, hypothesized mean = 0) was then applied to the individual subject *t*-contrast images to create mean *t*-images. An automated peak search algorithm identified the location of peak activations and deactivations based on *t*-value and cluster size (10 voxel minimum). This analysis enabled individual trial types to be directly compared to identify activations that differ between conditions (e.g., gaze > sex). Parameter estimates were extracted for the STS and fusiform gyrus clusters reported in Table 1 and were graphically displayed in Figures 1 and 2, respectively. All reported stereotaxic coordinates of significant activations have been converted to Talairach atlas space (Talairach & Tournoux, 1988).

RESULTS

Behavioral results

No differences were observed on the mean reaction times taken to perform the sex-identification or gaze-direction tasks (respective *M*s and *SD*s: 977 ms and 158 ms vs. 1011 ms and 168 ms), $t(12) = 1.33$, *ns*. Although all participants performed above 75% accuracy on both tasks, participants were less accurate in the sex identification than in the gaze-direction task (respective *M*s and *SD*s: 86% and 7% vs. 90% and 6%), $t(12) = 2.36$, $p = .036$.

Imaging results

To examine whether the sex-identification and gaze-direction tasks were associated with

TABLE 1
Regions of increased activity associated with gaze discrimination specifically

Brain areas	Hemisphere	Coordinates			T	Cluster size
		x	y	z		
<i>Eye gaze > sex (p < .005)</i>						
Superior temporal sulcus (BA 21, 22)	R	53	-41	5	4.34	10
Precentral gyrus (BA 4)	L	-50	-5	17	4.22	13

different patterns of neural activity, the BOLD response associated with the blocked presentation of both tasks was contrasted. The direct contrast of gaze direction versus sex identification ($p < .005$ with cluster size of a minimum of 10 voxels) revealed only two brain areas preferentially active for the processing of eye gaze. A direct contrast of sex identification versus gaze direction ($p < .001$ with cluster size of a minimum of 10 voxels) revealed only four brain areas preferentially active for the processing of sex. The coordinates, t -values and cluster sizes of these

activations are reported in Tables 1 and 2 respectively. Of particular interest, although both tasks recruited a similar network of brain regions, these contrasts revealed that the right STS demonstrated significantly more activity during judgments of gaze direction than sex ($t = 4.34$, $p < .005$) (see Figure 1). Conversely, a region of the left FG was more active during judgments of sex than gaze direction ($t = 5.48$, $p < .001$) (see Figure 2). The mean-beta values of the STS and the FG ROIs were derived from the respective contrasts and are plotted in Figures 1 and 2.

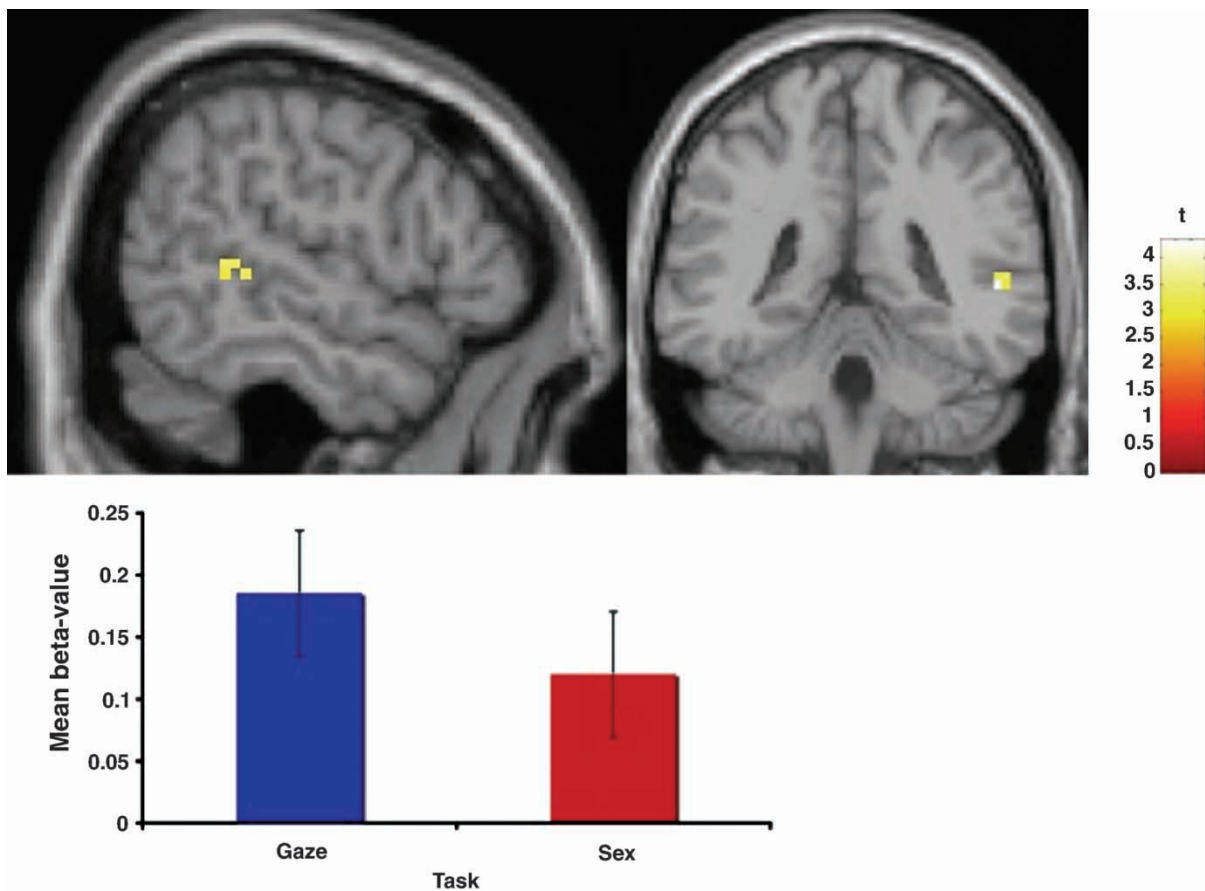


Figure 1. STS activity is significantly greater when making eye-gaze judgments compared to sex judgments (Talairach coordinates of peak: 53, -41, 5; image threshold, $p < .005$, uncorrected, image not masked). The graph displays β values (M and SE) for sex and gaze judgments from the right STS ROI derived from the gaze versus sex contrast.

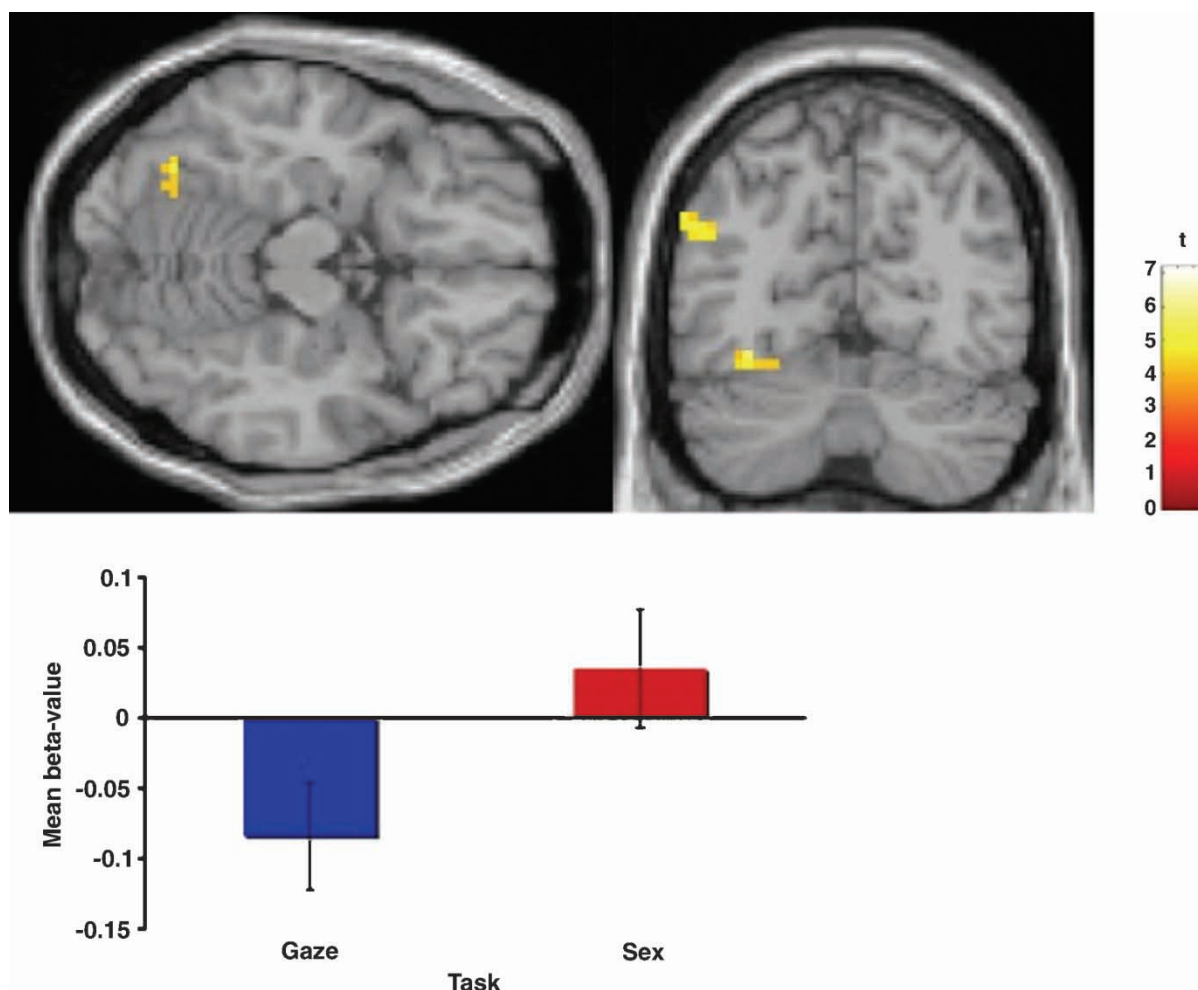


Figure 2. Fusiform activity is significantly greater when making sex judgments compared to eye-gaze judgments (Talairach coordinates of peak: $-33, -64, -7$; image threshold, $p < .001$, uncorrected, image not masked). The graph displays β values (M and SE) for sex and gaze judgments from the left fusiform ROI derived from the sex versus gaze contrast.

DISCUSSION

Notwithstanding the fact that perceiving faces entails the recruitment of a complex network of brain regions (Haxby et al., 2004; Ishai et al., 2005), components of this network have been shown to be preferentially involved in extracting

specific facial properties. In this respect, the current findings are in agreement with the distributed face-processing model advanced by Haxby and colleagues (2002). Corroborating the predictions of the model, we found that the STS preferentially supports the processing of a dynamic facial property (i.e., gaze direction) and

TABLE 2
Regions of increased activity associated with sex discrimination specifically

Brain areas	Hemisphere	Coordinates			T	Cluster size
		x	y	z		
<i>Sex > eye gaze ($p < .001$)</i>						
Calcarine sulcus (BA 17)	L	-21	-84	12	5.14	15
Angular gyrus (BA 39)	L	-50	-65	31	5.89	18
Fusiform gyrus (BA 19)	L	-33	-64	-7	5.48	10
Inferior parietal lobule (BA 7)	L	-24	-56	39	5.28	14

that an area of the FG preferentially supports the processing of an invariant facial property (i.e., sex). Interestingly, these effects were obtained by contrasting tasks that are both believed to be performed using feature-based processing (cf. Hoffman & Haxby, 2000). This reinforces the assumption that the static and dynamic nature of the respective facial dimensions captures the difference between these two tasks rather than other functional differences (e.g., featural vs. configural).

Importantly, the current study replicates numerous neuroimaging findings implicating the STS in the processing of gaze-related information (Hoffman & Haxby, 2000; Hooker et al., 2003; Pelphrey et al., 2003b; Puce et al., 1998). Evidence from single-cell recordings in monkeys further supports the proposed role of this region in the extraction of gaze-related information from faces (Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1985). Interestingly, there has been increasing evidence of STS involvement in the processing of meaningful social information (Allison et al., 2000). For example, this region shows increased activity when biological motion is perceived, as compared to non-biological motion (Pelphrey et al., 2003a; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Additionally, STS appears to be involved in inferring the mental states of others (Gallagher & Frith, 2003) and in attributing diagnostic information to individuals (Harris, Todorov, & Fiske, 2005; Mitchell, Cloutier, Banaji, & Macrae, 2006). In light of these and other findings, it appears that the role of the STS in extracting dynamic information from faces (e.g., gaze direction) could support the computations necessary to infer the attentional focus and intentions of social agents (Baron-Cohen, 1995; Haxby et al., 2002, 2004).

In contrast to the STS, which seems to extract dynamic information from faces, the FG appears to support the extraction of invariant information from faces (Haxby et al., 2002, 2004). Indeed, it has been established that certain areas of the FG preferentially support face processing and face recognition (Grill-Spector et al., 2004; Ishai et al., 1999; Sergent et al., 1992). However, there are numerous debates as to the precise nature of the representational role played by these regions in supporting the processing of faces. For example, it has been argued that a specific region of the FG serves as a module uniquely specialized for face processing (Kanwisher et al., 1997). Other researchers posit that this so-called fusiform face

area (FFA) supports subordinate-level object recognition (Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Turk, Rosenblum, Gazzaniga, & Macrae, 2005). Alternatively, an object-form topography model posits that faces and other objects are represented in distributed and overlapping areas of the FG (Haxby et al., 2001). Interestingly, in the current experiment, increased activity in the left FG was observed when sex judgments, as compared to gaze judgments, were performed. This hemispheric asymmetry is in line with proposed differences in the functions of the right and left FG in face processing. Indeed, while the right FG has consistently been involved in face recognition and identity processing (Ishai et al., 2005; Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997), tasks which require configural or holistic processing, some findings suggest that regions of the left FG might preferentially process featural information from faces (Hillger & Koenig, 1991; Rossion et al., 2000). In an fMRI study by Rossion and colleagues (2000), increased activity in the right FG was observed when participants were asked to match whole faces. However, when matching parts of faces, increased activity in the left FG was reported. Therefore, the current results give additional support to a possible functional asymmetry between the right and left FG when processing distinct facial dimensions. The potential functional specialization of sub-areas of the FG based on which facial dimension is being processed is not necessarily incompatible with any existing representational theory of the ventral temporal cortex. Nevertheless, it raises interesting questions that should further be addressed in future studies.

Although the STS is the brain area that has been the most consistently shown to support eye-gaze processing, other brain areas are believed to play an important role in monitoring eye-gaze information (Calder et al., 2002; Hooker et al., 2003; Wicker, Perrett, Baron-Cohen, & Decety, 2003). For example, the amygdala has been found to be active in the detection of eye contact (Kawashima et al., 1999) and patients with bilateral amygdala damage show difficulty in identifying gaze direction (Young et al., 1995). Although the current study did not find evidence of greater amygdala activation for eye gaze than for sex identification, it is possible that such a difference would have emerged if an event-related rather than a blocked design had been utilized. By emulating the block design adopted by Hoffman and Haxby (2000), the current study

was well suited to contrast the processing of eye gaze and sex dimensions from faces but might have obscured other interesting findings. Indeed, in the current study we could not distinguish between the brain activation to direct and averted eye gaze or to female and male faces. Additionally, although our study was underpowered to perform such between-group analyses, future studies should investigate potential gender differences in the neural substrates recruited when processing same-sex and opposite-sex faces.

In the current study, we compared the processing of static and dynamic facial dimensions and obtained support for the core distinction of Haxby and colleague's neuro-cognitive face-processing model. Nevertheless, these results rely on the assumption that the processing of those facial dimensions was equated on all characteristics other than their inferred static/dynamic qualities. The assumption that the processing of eye-gaze direction from photographs recruits a brain area (e.g., STS) associated with the dimension's implied dynamic qualities is supported by the results of studies using truly dynamic eye-gaze stimuli (Hooker et al., 2003; Puce et al., 1998). Nevertheless, it would be interesting to directly compare the processing of various facial characteristics (e.g., eye gaze and sex) from faces displaying natural movements (e.g., from video clips) to confirm that the extraction of presumed static facial dimensions do not rely on dynamic information when it is available. Furthermore, the use of fMRI adaptation paradigms, which assume that brain areas supporting the processing of specific stimulus dimensions reduce their activity over time, should provide convergent evidence of the functional dissociation between the processing of dynamic and static facial dimensions (Winston et al., 2004).

To summarize, findings from the current study are compatible with a neuro-cognitive framework proposing that the FG is preferentially involved in the extraction of invariant information from faces and the STS is involved in processing dynamic facial information (Haxby et al., 2002). In addition, the results are consistent with the possibility that some areas of the left FG are preferentially involved in making explicit person-related judgments that rely primarily on featural information (Rossion et al., 2000).

Manuscript received 1 June 2006
 Manuscript accepted 21 June 2007
 First published online 28 August 2007

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