

Gender-selective neural populations: evidence from event-related fMRI repetition suppression

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Abstract Accurate recognition of gender in another individual is integral to successful human social interaction and to mate selection. When we encounter another person, we are effortlessly able to identify their gender, most often through the information conveyed by their facial features. Faces comprise the most abundantly encountered cue used to classify human gender. Considering the importance of facial information in gender perception, relatively little is known about the mechanisms involved in perceiving gender through human facial cues. We used an event-related fMRI repetition suppression paradigm to explore the neural circuitry underlying gender perception from facial information. Participants viewed brief consecutive images consisting of either gender-same face pairings (two male faces or two female faces) or images of gender-different face pairings (a male face preceded or followed by a female face), while attending to facial attractiveness in both conditions. Using a region-of-interest approach, we found repetition suppression on gender-same trials within the left ventral temporal fusiform gyrus and in the right collateral sulcus.

Whole-brain voxel-wise analyses revealed selectivity for face gender again in the right collateral sulcus, in addition to the left cuneus and the right lateral occipital gyrus. Our results indicate that in addition to the face-selective FFA, cortical areas that are not traditionally considered to be “face-selective” are involved in the perception of gender-based facial cues.

Keywords Face perception · Gender perception · fMRI adaptation · Ensembles · Collateral sulcus · Fusiform gyrus

Introduction

Human faces provide a rich source of information, not only about identity and emotion, but also about other socially relevant information such as gender. The processing of visual facial cues for the purpose of gender perception arguably constitutes an essential human skill that supports appropriate social interaction and mate selection. Psychophysical evidence suggests that specific neural populations encode facial gender; however, only a few studies have investigated the brain regions supporting such gender-based decisions.

That specific neural populations may be engaged during the process of perceiving facial gender is supported by behavioral studies reporting psychophysical adaptation aftereffects in response to manipulations of facial gender (Rhodes et al. 2004; Webster et al. 2004; Ghuman et al. 2010). In these studies, prolonged exposure to male or female faces biases the perception of subsequently presented faces, such that “neutral-gendered” faces are perceived as looking more female or male, respectively. These psychophysical adaptation aftereffects are thought to reflect an opponent coding of faces at a neural level whereby neurons either fire to male faces or to female faces (Clifford and Rhodes 2005).

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Although the neural mechanisms underlying face perception have been widely studied, face perception literature has placed a predominant focus on examining the aspects of face processing, such as identity (Winston et al. 2004) and emotion (Anderson et al. 2000; Masuda et al. 2008). Current models of facial recognition have not incorporated higher-level categorical-level aspects of face encoding, such as gender. For example, in evaluating the current evidence for the neural basis of face recognition, Haxby et al. (2000) proposed a theoretical model of face processing involving a “core” and an “extended” network. According to this account, the early perception of identity and the changeable aspects of a face are mediated by the “core” network that includes the fusiform face area (FFA) (Kanwisher et al. 1997; Ishai et al. 1999), the occipital face area (OFA) (Rossion et al. 2003; Grill-Spector et al. 2004; Steeves et al. 2006), and the superior temporal sulcus (STS) (Pruce et al. 1998; Hoffman and Haxby 2000). In contrast, the “extended” face-processing network, which includes the amygdala (AMG) and insula (INS), anterior temporal regions, and frontal areas, processes emotion (Adolphs et al. 1994) and expression (Ishai et al. 2005), semantic aspects of faces (Gobbini and Haxby 2007), and decisions such as attractiveness (O’Doherty et al. 2003), respectively. The Haxby et al. (2000) model, however, is silent about brain regions that are critical for the perception of gender. Accordingly, there have been few attempts to isolate or localize brain areas involved in the perception of facial gender. This seems surprising, given the large number of fMRI studies dedicated to localizing brain regions that support the processing of other facial cues, such as identity and emotion.

To date, only a handful of studies have specifically addressed the neural basis of gender recognition. An early examination of brain regions involved in face-gender perception was conducted by Sergent et al. (1992), using positron emission tomography. These authors asked participants to overtly categorize the gender of a number of male and female faces in one condition and to attend to identity in another. The gender discrimination task produced activation in regions of extra-striate cortex, including the right cuneus and the left lateral occipital area, whereas the identity task revealed activation in the right lingual gyrus, anterior temporal regions, and bilateral fusiform gyrus (Sergent et al. 1992).

Further support for the possibility that there may be a network of cortical areas that encode face gender is supported by a study by Freeman et al. (2010) in which participants were asked to discriminate gender with faces that morphed between male and female. Activity in the fusiform face area and lateral fusiform gyrus increased a function of how objectively male or female the faces appeared to be. Conversely, activity in the orbitofrontal cortex increased as the decision became more subjective and difficult, that is, when

the morphed faces were more androgynous. On the basis of these findings, Freeman et al. (2010) argue that gender is a static categorical cue, dependent on visual features that are analyzed within fusiform gyrus.

The studies outlined above have provided preliminary insights into the neural substrates for gender discrimination, which may or may not be shared with other facial processing networks. One way to identify the structures that are *specific* for gender discrimination is to use fMRI repetition suppression. This technique utilizes the characteristic reduction in fMRI signal strength that follows the repetition of a particular stimulus attribute to isolate the neural structures that are specific to the processing of that attribute (for reviews, see Grill-Spector and Malach 2001). Ng et al. (2006) recently used a variant of this technique to identify gender-selective neural populations. The four participants in their study were presented with set of faces that varied in gender and ethnicity. Using a region-of-interest (ROI) approach, they found evidence of repetition suppression for both gender and ethnicity in the fusiform gyrus and inferior occipital cortex. The repetition suppression effects in these regions correspond to Haxby et al.’s (2000) “core” regions in the face network. Ng et al. (2006) also found repetition suppression in the cingulate gyrus, a region located outside of the face network. However, in their study, Ng et al. used an unusually lengthy delay (3 min) between stimulus repetitions. It is not clear whether the reduction in the signal that one observes with these long-interval repetitions captures the effects that one would observe using standard fMRI-A designs, in which the interval between stimulus repetitions is typically on the order of seconds or less. For example, Fang et al. (2007) directly compared results using a short- and long-term repetition suppression paradigm and found that repetition suppression effects were contingent on the duration of stimuli presentation during the preadaptation phase. This group concluded that short- and long-term repetition suppression effects rely on different neural mechanisms. Indeed, it has been argued that short-interval designs are more likely to identify neural structures that are specific to the processing of the relevant stimulus attribute. Longer intervals, on the other hand, are more likely to tap into higher-level mechanisms, such as memory and other cognitive operations (Weiner et al. 2010).

Using a multivariate fMRI approach, Kaul et al. (2011) found gender-specific activation patterns that were not limited to face-selective regions within the fusiform gyrus, but also across the entire “face network,” including the inferior occipital gyrus (IOG), superior temporal sulcus, inferior frontal gyrus, insula, and orbitofrontal cortex. These areas may all be involved in the processing of facial features; however, it is unclear whether all are involved in encoding gender, per se. The activation in these areas could instead

reflect factors related to but not essential for gender perception. For instance, the gender-specific activity in the insula, as reported by Kaul's group, could reflect individual participants' emotional associations with the faces of different genders (Singer et al. 2009). Similarly, the activation in the IOG has been arguably linked to the perception of early structural properties of a face (Haxby et al. 2000; Fox et al. 2009) rather than gender. Many different aspects of perception are involved in the perception of gender from a face, making it difficult to dissociate, with certainty, the function of each brain region reported by the Kaul group. In short, it is difficult to determine which particular areas were linked to gender discrimination in this study.

Previous studies that have examined the aspects of face-gender selectivity in the brain have been varied in their reports of brain areas that encode gender. Areas that have been found to be involved in the processing face-based cues for gender include frontal areas (Ng et al. 2006; Kaul et al. 2011; Freeman et al. 2010), the insula (INS) and the inferior occipital gyrus (IOG) (Kaul et al. 2011), and the cingulate cortex (CC) (Ng et al. 2006). The activation in these areas, however, could reflect factors related to but not essential for gender perception. For instance, the cingulate cortex subserves voluntary choices based on prior knowledge (Kennerley et al. 2006). The cingulate cortex activation reported by Ng et al. (2006) may reflect the gender discrimination decision that is made when viewing a face rather than gender encoding. The activity in the orbitofrontal cortex reported by Freeman et al. and Kaul et al. may also reflect gender discrimination decisions, rather than the perception of face gender itself (Bechara et al. 2000; Manes et al. 2002). Although all of these areas may contribute in some fashion to the perception of gender, it is not clear whether there is a particular region of the brain that somehow integrates all these cues and related processes into an overall perception of face gender. The main goal of the present study was to address these problems by attempting to identify the neural structures specifically related to the encoding of gender and to isolate those structures from those mediating the kinds of processes described above.

To isolate activity in neural structures specifically related to the encoding of gender, we used an fMRI repetition suppression design with a 200-ms interval between stimuli in the paired presentations of faces. The use of a short inter-stimulus interval helped to minimize the adaptation of high-level cognitive mechanisms (Ganel et al. 2006). To determine the specificity of face-based gender processing, we first measured repetition suppression in functionally defined regions of interest (ROIs) identified using a separate localizer task to identify face-, place-, body-, and object-related regions. In addition, we also use a voxel-wise approach to identify brain regions showing gender-selective activity at the whole-brain level.

Methods

Participants

Sixteen right-handed individuals age 19 to 42 ($M = 24.56$, $SE = 1.58$; 9 female) with normal or corrected-to-normal vision participated in the study. Written informed consent was collected in accordance with the guidelines approved by the University of Western Ontario Health Sciences Research Ethics Board and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants were compensated \$25 for each hour of their time.

Face stimuli

Stimuli consisted of gray scale frontal-view photographs of 164 different faces with neutral expressions. Face stimuli were selected from the COLOR FERET face database (Phillips et al. (1998), <http://face.nist.gov/colorferet/>) and the NIMSTIM database (Tottenham et al. (2009), <http://www.macbrain.org/resources/htm>); the remaining photographs were drawn from a collection of one of the researchers. Each face image was converted to gray scale and sized to fill a 500×471 pixel canvas using Adobe Photoshop software. The hair and neck remained visible to keep the faces as naturalistic as possible. Face images (15.2° high by 12.5° wide) were presented on a rear-projection screen located 21 cm from the participant, via a mirror system that was attached to the top of a head coil within the scanner.

Experimental procedure and design

We used an event-related fMRI-A paradigm with two conditions: gender-same trials (where the two faces in the trial were of the same gender) and gender-different trials (where the two faces in the trial differed in gender). In addition, there was a "baseline" fixation condition in which participants passively viewed a black fixation cross on a gray background.

Each scan consisted of 96 experimental trials, with 32 trials per condition (gender-same, gender-different, and baseline fixation). In the gender-same and gender-different conditions, 128 faces were randomized across trials, with each face appearing once per trial type (gender-different (Male–Female; Female–Male) and gender-same (Male–Male; Female–Female) across the four experimental runs (Fig. 1). Importantly, face identity was not repeated within any run. Trials lasted for a total of 4,000 ms and involved the consecutive presentation of two faces displayed for 400 ms each. The two faces in each trial were separated by a brief 200 ms inter-stimulus fixation cross and an inter-trial interval of 3,000 ms followed each trial. Run order was counterbalanced within and between observers using a balanced Latin square design (Bradley 1958).

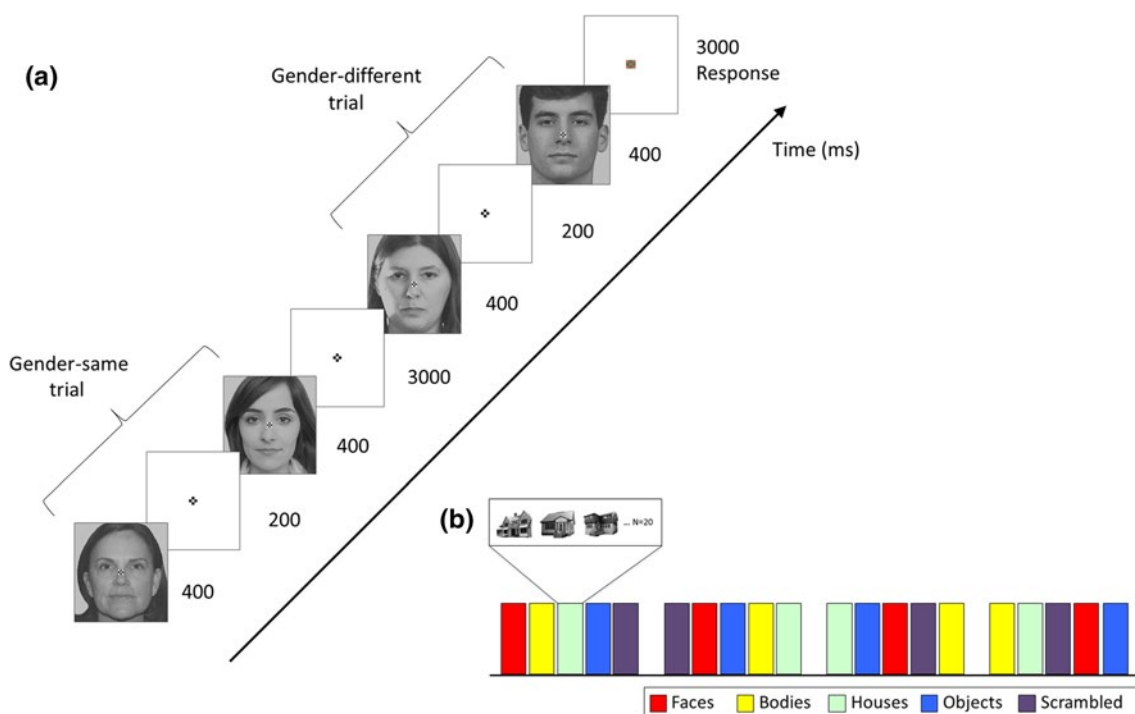


Fig. 1 a Experimental design for the face repetition suppression experiment. Two trials, one with gender-same and the other with gender-different face pairs, are illustrated. On randomly occurring response trials, participants were asked to provide an attractiveness rating for a face that preceded a change in the color of the fixation cross. **b** fMRI protocol for the localizer task, in which we function-

ally isolated face, body, object, and house-selective regions in each observer. Primary visual cortex was isolated by contrasting activation for images of scrambled objects with the baseline fixation condition. Condition types are color coded. Each run consisted of four stimulus epochs, each comprising 1 block of trials (20 different images) from each condition (objects, faces, bodies, houses, scrambled objects)

On six random trials within each run, participants were prompted to complete a 1-back task when the central fixation cross flashed red for 50 ms (Fig. 1a). On these response trials, participants provided an attractiveness rating of the face preceding the fixation cross color change, indicating whether they perceived the face as being “attractive” or “not attractive.” Response trials were counterbalanced for their order of appearance relative to position in the pair of faces (1st or 2nd) and to the gender of the face to be rated (M/F). Participants made a button-press response with the index finger of the right hand, using “left” and “right” keys on an fMRI-compatible response box. Response button mapping was counterbalanced across participants.

Localizers

In addition to the main fMRI-A experiment, participants also completed a separate localizer task designed to functionally isolate face-, object-, body-, and place-selective regions within lateral and ventral occipito-temporal cortex. Stimuli for the localizer task consisted of gray scale images of frontal-view neutral-expression faces, front-facing bodies (cropped to remove the head), houses, common objects, and scrambled objects. Each run consisted of four 80 s blocks of

stimuli from each of the five image conditions, each interleaved with a 16-s of baseline fixation (Fig. 1b). Each epoch contained five 16-s blocks, in which 20 different images from the same stimulus category were presented for 300 ms each. The order of stimulus category presentation was balanced within and across runs, again using a balanced Latin square design (Bradley 1958).

Participants completed a 1-back task using a key-press response to indicate when two identical images were repeated in an epoch. Two response trials were included in each epoch (10 response trials per block).

MRI acquisition

Scanning was carried out on a 3 Tesla Siemens Magnetom Tim Trio imaging system at the Robarts Research Institute at the Western University (London, Ontario, Canada). The functional data were acquired with a T2*-weighted single-shot gradient-echo echo-planar imaging sequence with interleaved slice acquisition. Foam padding was used to reduce head motion. The parameters for obtaining functional data were as follows: field of view (FOV) = 192 mm × 192 mm; in-plane resolution = 3.0 mm × 3.5 mm, slice thickness = 3.5 mm (zero gap); 19 axial slices; echo time (TE) = 30 ms; repetition

time (TR) = 1,000 ms; flip angle (FA) = 43°. Functional data were aligned to high-resolution anatomical images obtained using a 3D T1-weighted MPRAGE sequence (TE = 2.98 ms TR = 2,300 ms; TI (inversion time) = 900 ms; FA = 9°; 192 contiguous slices of 1 mm thickness; FOV = 240 mm × 256 mm²). Localizer parameters were the identical to the main experimental scan runs except for slice thickness = 2 mm (4 mm gap) and TR = 2,000 ms.

Data preprocessing and region-of-interest analysis

Data were preprocessed and analyzed using Brain Voyager QX (version 1.10.2, Brain Innovation, Maastricht, the Netherlands). Functional data were assessed for head motion and/or magnet artefacts by viewing cine-loop animation and examining motion-detection parameter plots following 3D motion correction algorithms on the untransformed two-dimensional data, aligned to the functional volume closest in time to the anatomical scan. Data from one participant were excluded due to excessive head motion (greater than 3 mm within a run). Response trials were excluded from the analysis. The event-related responses were processed using a deconvolution analysis whereby each voxel's full response time course was estimated using a general linear model. Functional data were preprocessed with high-pass temporal filtering to remove frequencies below 3 cycles/run. Functional volumes were then superimposed on anatomical brain images transformed into Talairach space (Talairach and Tournoux 1988).

Region-of-interest (ROI) analysis

Localizer data were used to functionally define regions of interest separately for each participant. To examine the possible influence of low-level visual properties of our face stimuli on repetition suppression effects, we also defined an additional ROI within early visual cortex around the occipital pole (corresponding to V1 and perhaps V2), according to both anatomical location and higher activation in response to scrambled images versus fixation. We first functionally localized face- and body-selective regions within each hemisphere (Table 1). Face-selective regions (fusiform face area (FFA) and occipital face area (OFA)) were selected by identifying those regions that showed greater activation to images of faces versus houses in within the ventral temporal fusiform gyrus and ventral occipital cortex (Kanwisher et al. 1997; Gauthier et al. 2000). Extrastriate body area (EBA) and fusiform body areas (FBA) were identified as those regions that showed preferential activation for bodies over houses within the lateral occipital and ventral fusiform gyrus, respectively (Downing et al. 2001; Peelen and Downing 2005). Object-selective regions within the lateral occipital complex (LOC) were defined as the regions within

the lateral occipital surface (area LO) and ventral temporal surface within the posterior fusiform sulcus (pFs) that showed greater activation to intact versus scrambled images of objects (Kourtzi and Kanwisher 2001). House-selective populations were defined as those regions within the collateral sulcus that were activated using the contrast house images as compared to all other image types (Epstein and Kanwisher 1998). ROIs were defined by first selecting the peak voxel of functional activation within each anatomically defined area. ROI size was constrained by setting a minimum statistical threshold ($t > 3.0$, $p < 0.001$) before selecting a volume of interest up to 10 mm³ (i.e., 1,000 voxels), around the peak voxel.

De-convolved time courses were extracted from all ROIs in each of the 15 participants, and all subsequent analyses were performed on unsmoothed data. Beta-weights were averaged across the group for both the gender-same and gender-different image conditions. The mean of peak activations of the response time courses (time points 7 and 8) in the gender-same and gender-different trials were contrasted using a paired-samples *t* test for body and face areas, in addition to object-selective, place-selective, and early visual areas. Because we had a priori predictions about the activity in particular regions, Bonferroni corrections for multiple comparisons were not applied.

Voxel-wise group analysis

Next, we performed whole-volume voxel-wise analyses on the group data for the adaptation experiment. fMRI signals for each subject were spatially smoothed (6 mm, full-width at half-maximum Gaussian kernel). Individual subject data were analyzed using a single-subjects general linear model (GLM). Data for each participant were processed using a percent-signal-change (%SC) transformation and a correction for serial (temporal) correlations. Group data were then analyzed using a random effects (RFX) general linear model (GLM). To identify repetition-based effects in face gender-selective neural populations, a contrast was performed at the peak of the response time course (time points 7 and 8) to reveal areas in which activation on gender-different trials was greater than gender-same trials [gender-different > gender-same]. The resultant group activation map was set to a statistical threshold of $p < 0.01$ (using a cluster size threshold of $p < 0.05$).

Results

ROI analyses

We were primarily interested in whether gender-selective fMRI responses would be observed within face- and

Table 1 Regions of interest identified in the functional localizer task

Brain region	Talairach coordinates			No. voxels (mm ³)	Stat max	No. participants
	X	Y	Z			
Face selective						
Fusiform face area						
L	-37 (1.1)	-51 (2.2)	-17 (1.0)	349	9.30	15
R	+38 (0.8)	-50 (1.8)	-16 (0.7)	408	11.76	15
Occipital face area						
L	-36 (1.4)	-74 (2.2)	-16 (1.6)	224	7.99	10
R	+40 (1.6)	-72 (1.7)	-13 (2.2)	320	8.35	13
Body selective						
Extrastriate body area						
L	-43 (0.9)	-74 (1.3)	0 (1.2)	776	13.98	15
R	+44 (0.8)	-68 (1.1)	-2 (1.2)	810	13.82	15
Fusiform body area						
L	-38 (1.3)	-49 (2.2)	-15 (0.9)	444	8.77	13
R	+39 (1.0)	-49 (2.0)	-12 (0.8)	501	10.27	13
Object selective						
Lateral occipital complex						
L	-42 (1.1)	-70 (2.2)	-5 (1.4)	780	10.58	15
R	+42 (1.0)	-70 (1.4)	-6 (1.4)	744	10.62	15
Posterior fusiform sulcus						
L	-40 (0.6)	-70 (0.9)	-12 (0.7)	675	10.64	15
R	+41 (0.9)	-69 (0.8)	-13 (0.7)	717	10.75	14
Place selective						
Collateral sulcus						
L	-23 (0.8)	-46 (2.1)	-8 (0.5)	676	10.85	15
R	+25 (0.9)	-50 (1.8)	-9 (0.6)	580	10.18	15
Early visual						
VI, V2						
L	-6 (0.7)	-88 (1.0)	-4 (1.1)	790	10.23	14
R	+9 (0.7)	-88 (1.0)	-3 (1.0)	749	11.00	15

For each ROI, the Talairach coordinates, number of volumes, and peak activity level (Stat max) were averaged across all participants. The standard deviation of each coordinate is indicated in parentheses. Stat max refers to the maximum t value within each region of interest, averaged across all subjects. No. participants refer to the number of participants in which we were able to localize each region of interest. Left (L), right (R)

body-selective regions of interest in the temporal and occipital cortex. Additionally, we examined the extent to which category-selective regions outside the face and body areas, including the collateral sulcus (CoS), lateral occipital cortex (LO), posterior fusiform (pFs), and early visual areas, showed evidence of selectivity to facial gender cues. We identified four body- and object-selective regions of interest, based on fMRI responses collected using a separate localizer scan. These areas included the fusiform face area (FFA), occipital face area (OFA), fusiform body area (FBA), and extra-striate body area (EBA). We were confident that our ROI's were situated within face-selective areas of the fusiform gyrus because when we ran the contrast

[Faces > Baseline Fixation] in our fMRI-A experiment, the region of maximal activation overlapped with that identified in the faces versus houses contrast of the localizer task.

Significantly greater activation was observed for gender-different as compared to gender-same face trials in the left FFA ($t(15) = 2.80$, $p = 0.01$) (Fig. 2) and in the right CoS ($t(15) = 2.40$, $p = 0.03$) (Fig. 3). We did not however find significant repetition suppression in any of the other ROIs (right FFA, $p = 0.99$; left CoS, $p = 0.65$; right OFA, $p = 0.12$; left OFA, $p = 0.30$; right EBA, $p = 0.66$; left EBA, $p = 0.94$; right FBA, $p = 0.09$; left FBA, $p = 0.34$; right LO, $p = 0.26$; left LO, $p = 0.07$; right pFus, $p = 0.25$; left pFus, $p = 0.04$).

Fig. 2 Activation to gender-same (*green*) and gender-different (*blue*) trials in bilateral face- and body-selective ROIs in the fusiform and occipital regions. The relevant contrast used to localize each region of interest is indicated pictorially above the graph. Beta-weights were extracted from participants individually and averaged across the group at the peak of the response time course (time points 7 and 8). A significant difference between gender-same and gender-different trials was observed only in the left fusiform. Standard error of the mean is indicated by *error bars*

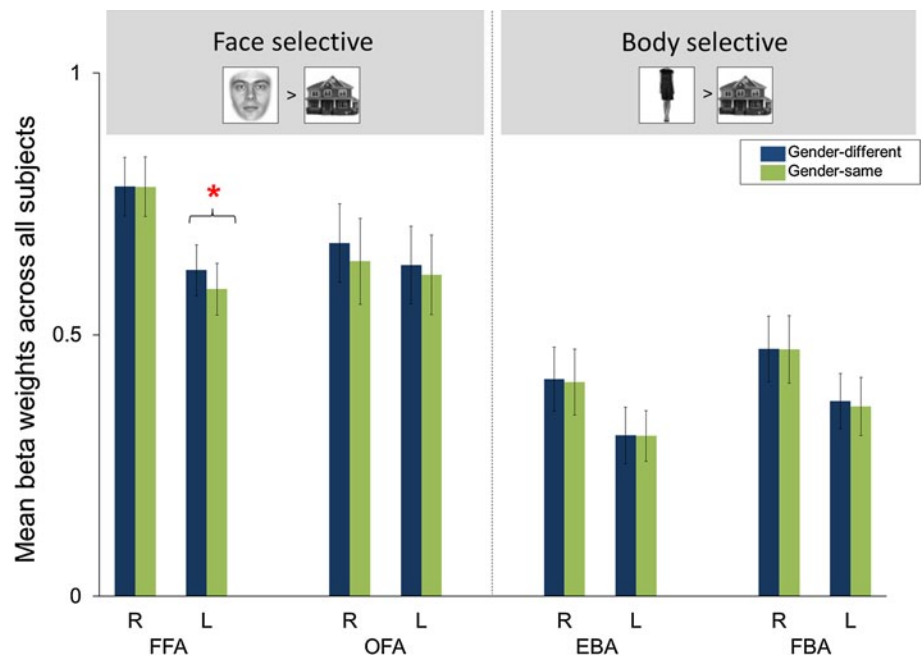
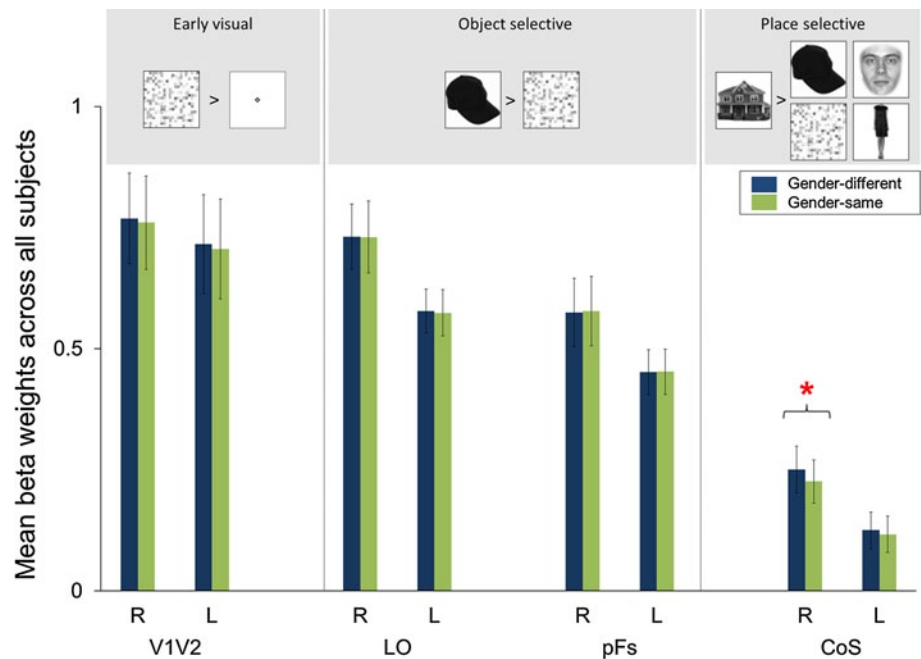


Fig. 3 Activation to gender-same (*green*) and gender-different (*blue*) trials in bilateral place-selective, object-selective, and early visual areas of the temporal and occipital cortex. The relevant contrast used to localize each region of interest is indicated pictorially above the graph. Beta-weights were extracted from participants individually and averaged across the group at the peak of the response time course (time points 7 and 8). A significant difference between gender-same and gender-different trials was observed only in the right collateral sulcus. Standard error of the mean is indicated by *error bars*



Early visual areas were localized bilaterally to rule out any repetition suppression effects that might have been due to low-level features of face stimuli. We did not find significant repetition suppression to repeats in face gender in early visual areas in either the left ($t(14) = 0.06$, NS) or the right hemisphere ($t(15) = 0.75$, NS). This suggests that the repetition suppression effects found in the left fusiform face area and right collateral sulcus were not likely due to low-level structural similarities in the face stimuli used in the gender-same trials.

Whole-brain random effects analysis

In the voxel-wise group analysis, significant activation was found in the left precuneus, the right lateral occipital gyrus, the right collateral sulcus, and a small cluster of activation was also found in the right putamen (Fig. 4).

In summary, a region-of-interest analysis identified the left fusiform face area (FFA) and the right collateral sulcus (CoS) as selectively coding for changes in face gender. A whole-brain group RFX analysis again identified the right

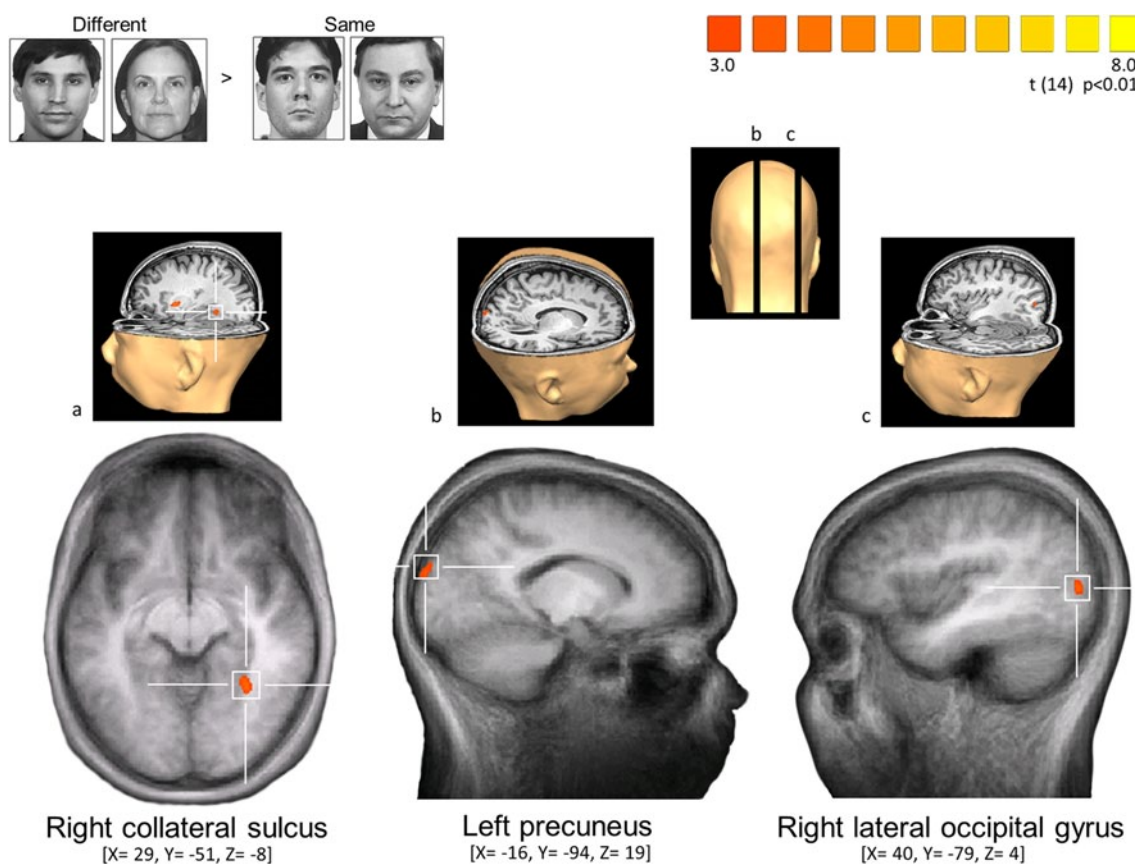


Fig. 4 Voxel-wise group random effects activation for a sample of 15 participants. The respective contrast of (gender-change > gender-repeat trials) is indicated in the *top left corner*. The group contrast was performed on smoothed data at $p < 0.01$, indicated in the *top right corner* of the image, with a cluster correction threshold of 7. **a** Activation in the right collateral sulcus is indicated in both the sagittal and horizontal plane. The sagittal full-head view indicates the height at which the horizontal slice was taken. **b** The activation in the left precuneus is indicated in the sagittal view at the intersection of the cross-hairs. A 3D reconstruction of the left hemisphere is

displayed above the sagittal MRI image. **c** The activation in the right lateral occipital gyrus is indicated in the sagittal view at the intersection of the cross-hairs. A 3D reconstruction of the right hemisphere is displayed above the sagittal MRI image. The different sagittal planes are indicated in a 3D skull reconstruction above **b** and **c**. Talairach coordinates for each activated region are indicated below the *images*. The right collateral sulcus, left precuneus, and the right lateral occipital gyrus all showed greater activation when face gender changed, as opposed to when gender stayed the same across the group

collateral sulcus, in addition to the left precuneus and the right lateral occipital gyrus, as being gender-selective. These effects were not related to low-level features of the stimuli used, since we did not find corresponding repetition suppression effects in primary visual cortex. Interestingly, the right FFA and the left CoS did not show selectivity to face gender, nor did neighboring body-, object-, and place-selective regions.

Discussion

We used an event-related fMRI repetition suppression design to identify brain regions involved in processing gender-based facial cues. Using a region-of-interest approach, we found a significant reduction in fMRI responses with

repetitions of face gender within the fusiform face area (FFA) of the left hemisphere. The fact that the gender-selective fMRI responses were observed only in the left FFA contrasts with the commonly reported observation that responses associated with facial identity are typically right-lateralized (Kanwisher et al. 1997). We did not find any above-threshold FFA activation in the voxel-wise group analysis. One reason for this discrepancy is that the anatomical coordinates of small areas like the FFA typically differ from participant to participant, and therefore are not always apparent in a group analysis that relies on overlap of activation across participants. Moreover, because participants in our experiment were engaged in a task that was quite orthogonal to gender identification (i.e., rating attractiveness), the magnitude of the adaptation effects might have been attenuated. Nevertheless, we chose this approach to

ensure that any differences in activation that we observed were not due to differences in attention or strategy.

Gender-based repetition effects were also observed within the right “parahippocampal place area” (PPA) located along the anterior branch of the collateral sulcus. Using a voxel-wise approach, we observed gender-based repetition effects in the right anterior collateral sulcus (CoS). Interestingly, the location of this activity in the right CoS corresponds to the location of the activity we observed in the right PPA as functionally localized in our region-of-interest analysis. The voxel-wise analysis also revealed gender-related repetition effects within the left precuneus and right lateral occipital gyrus. Taken together, our results suggest that visual cues associated with the gender of human faces are processed within the ventral visual stream, in areas that lie both within, and outside of, the classical face-selective processing network (Haxby et al. 2000).

Although key areas within the face-processing network (Haxby et al. 2000), particularly the FFA, have been studied extensively, the functional roles of other areas within the network remain poorly understood. In the present study, we found evidence of gender-related activity in the left FFA. This activity appeared to be specific to the facial cues associated with gender since identity was always varied and all the faces had neutral expressions. The gender-selective responses we observed in the FFA coincide with previous fMRI studies that have reported gender-related activation in this area (Freeman et al. 2010; Ng et al. 2006). Our results, taken together with the results reported by Ng et al. (2006), establish that the FFA contains gender-selective neural populations.

One can ask why gender-selective activity, unlike activity related to identity and other facial features, appears to be largely limited to the FFA and has not been reported in comparatively more posterior regions of the cortical face-processing network—particularly the occipital face area (OFA). This may be because the OFA serves as an initial processing stage in the face perception network, with a preferential sensitivity for basic facial components such as the eyes, nose, and mouth—and not for high-level configural or conceptual information such as identity or expression (Steeves et al. 2006; Gilaie-Dotan et al. 2010; Pitcher et al. 2011). For example, Gilaie-Dotan et al. (2010) examined the effects of TMS-induced disruption of the occipital face area (OFA) on observers’ ability to match the identity of familiar faces.

Surprisingly, disruption of the OFA did not affect face recognition—an effect the authors argued to reflect that the OFA is involved in processing basic shape-related cues, rather than high-level conceptual information relating to facial identity (Gilaie-Dotan et al. 2010). The latter results concur with those of Pitcher et al. (2009), who reported that TMS-induced deactivation of the OFA resulted in impaired

discrimination of *unfamiliar* faces, a process that could rely more heavily on low-level featural processing. Thus, the lack of gender-based repetition effects in the OFA in our study is not surprising, given that different face-identity pairs were presented on every trial, thereby ensuring that basic facial features that cue gender were constantly changing and therefore should not elicit repetition-related effects on measured fMRI responses. Taken together, our results suggest that facial gender is a relatively complex aspect of face processing that engages regions that encode higher-level configural information within the face-processing network, such as the FFA.

We observed gender-related repetition effects within the left, but not the right FFA. This result seems surprising, given that the right fusiform face area is more frequently reported to be involved in the processing of facial identity (Kanwisher et al. 1997; Gauthier et al. 2000) and expression (Ganel et al. 2006). Unlike identity, gender discrimination could be seen as more conceptual and categorical process that requires generalization as well as differences across an enormous range of exemplars. In line with this idea, it is interesting to note that human neuropsychological work has shown that lesions of the left hemisphere, but not the right, are frequently associated with a deterioration in semantic concept formation. These conceptual deficits frequently manifest as poor performance on tests of nonverbal as well as verbal comprehension (Patterson et al. 2007). The categorization of faces as male or female is based on our concepts of “maleness” and “femaleness,” where individuals can be placed in one or the other of these categories based on any one or more of a broad range of features. This account would appear to contrast with a recent study by Meng et al. (2012) showing that the pattern of activation in the right FFA is related to categorical face versus non-face judgments, whereas the pattern of activation in the left FFA is related to more subtle (graded) similarities between “face” images. The authors speculate that graded image-level processing in the left FFA is a necessary precursor to the more categorical processing in the right FFA. By the same token, one could also speculate that the same kind of subtle processing in the left FFA is required for categorical judgements of gender that are mediated, not by the right FFA, but by more high-level decision-related structures located elsewhere in the brain.

It should be noted that the relationship between fMRI adaptation and changes at the neural level is not entirely clear, particularly when only one feature of a complex object is manipulated (e.g., Sawamura et al. 2006). Nevertheless, this technique has been enormously effective in unravelling the way in which complex stimuli, such as faces, objects, and scenes, are coded in occipito-temporal cortex (e.g., Grill-Spector 2006; Kourtzi and Kanwisher 2001; Epstein et al. 2003). fMRI adaptation is well suited to the study of gender,

which arguably is even more complex in its representation than facial identity and emotion, where there is a long history of adaptation studies (e.g., Winston et al. 2004). Future studies could examine the extent to which the effects we report can be replicated using other fMRI techniques, such as multi-voxel pattern analysis (Kriegeskorte et al. 2007).

In addition to the FFA, which is a key area in the face-processing network, we also observed activation in areas outside this network. Specifically, in the whole-brain analysis, we observed activation in the right precuneus and the right lateral occipital cortex areas that are frequently implicated in visual processing (Cavanna and Trimble 2006; Murray and Wojciulik 2003). At present, the contribution of these areas to gender perception is not clear and remains to be investigated. Interestingly, however, another area outside the classical face-processing network showed robust activation in both the region-of-interest and the whole-brain analyses. The collateral sulcus has been implicated in a range of visual processes, each of which could play a role in gender categorization. First, the CoS has been shown to be involved in configural aspects of scene perception (Oliva and Torralba 2001). Gender perception could arguably rely in part up on such configural processes. For example, gender perception is disrupted with face inversion, a manipulation that is thought to interfere significantly with configural processing (Zhao and Hayward 2010). Second, the CoS has been implicated in the processing of surface properties such as visual texture (Cant and Goodale 2007). It is likely that the prominent difference in the visual textures of male and female faces is a key component in gender classification. For example, male faces tend to have thicker and coarser eyebrows than female faces, while female faces tend to have darker shaded skin around the eyes as compared to male faces (Liggett 1974). Finally, there is recent evidence from fMRI that regions within the CoS are involved in the processing of visual “ensembles” (Cant and Xu 2012). The term ensemble relates to the observation that a highly heterogeneous group of objects can be categorized as being members of the same set, regardless of the fact that the exemplars within the set differ from one another at a feature-based level (Williams and Sekuler 1984; Portilla and Simoncelli 2000). For instance, a collection of seashells can be categorized as belonging to the same object group, even though no two shells need share the same features. Similarly, the categorization of individual human faces into males or females could be regarded as the creation of two ensembles, where the cues determining membership of the ensemble (in this case, gender) can differ enormously. Moreover, the set of cues that are used to determine gender presumably vary both within and between cultures. For example, the presence of facial hair, tattoos, makeup, and other alterable features can vary from one culture to the next. Importantly, the faces used as stimuli in our study included many of these

alterable features, such as differences in hair and makeup. This contrasts with the majority of studies that have examined facial representations of gender, which have tended to use impoverished stimuli, such as cropped faces with face outline, makeup, hair, and other real-world features removed (Ng et al. 2006; Freeman et al. 2010). In other words, we tried to insure that the implicit categorization process that was engaged during our task was as realistic as possible. In future, it would be interesting to investigate the extent to which other gender-based cues, such as gait patterns (Troje et al. 2006), body shape and clothing (Ghuman et al. 2010), and vocal cues (Van der Zwan et al. 2009), amplify the activation we observed CoS.

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Conflict of interest The authors declare that they have no conflict of interest.

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