The Fusiform and Occipital Face Areas Can Process a Nonface Category Equivalently to Faces

Valentinos Zachariou, Zaid N. Safiullah, and Leslie G. Ungerleider

Abstract

■ The fusiform and occipital face areas (FFA and OFA) are functionally defined brain regions in human ventral occipito-temporal cortex associated with face perception. There is an ongoing debate, however, whether these regions are face-specific or whether they also facilitate the perception of non-face object categories. Here, we present evidence that, under certain conditions, bilateral FFA and OFA respond to a nonface category equivalently to faces. In two fMRI sessions, participants performed same–different judgments on two object categories (faces and chairs). In one session, participants differentiated between distinct exemplars of each category, and in the other session, participants differentiated between exemplars that differed only in the shape or spatial configuration of their features (featural/configural differences). During the latter session, the within-category similarity was comparable for both object categories. When differentiating between distinct exemplars of each category, bilateral FFA and OFA responded more strongly to faces than to chairs. In contrast, during featural/configural difference judgments, bilateral FFA and OFA responded equivalently to both object categories. Importantly, during featural/configural difference judgments, the magnitude of activity within FFA and OFA evoked by the chair task predicted the participants' behavioral performance. In contrast, when participants differentiated between distinct chair exemplars, activity within these face regions did not predict the behavioral performance of the chair task. We conclude that, when the within-category similarity of a face and a nonface category is comparable and when the same cognitive strategies used to process a face are applied to a nonface category, the FFA and OFA respond equivalently to that nonface category and faces. ■

INTRODUCTION

It is generally agreed that the neural substrates that mediate face perception are separate from those that mediate the perception of other object categories. For example, a network of functionally defined brain regions spanning the ventral visual cortex is specialized in face processing. This network comprises regions such as the occipital face area (OFA; Gauthier et al., 2000), the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997), and the anterior inferior temporal face area (Rajimehr, Young, & Tootell, 2009; Haxby, Hoffman, & Gobbini, 2000; Sergent, Ohta, & MacDonald, 1992). All of these regions exhibit disproportionately stronger activation to faces than to nonface objects (Rossion et al., 2003; Kanwisher et al., 1997). Importantly, damage to this face-processing network can lead to prosopagnosia, a face-specific perceptual impairment (Duchaine, Yovel, Butterworth, & Nakayama, 2006; Della Sala & Young, 2003). Prosopagnosic patients are aware that a face is present but are unable to assign identity to the face; in contrast, they have no problem identifying objects belonging to nonface categories (Busigny, Graf, Mayer, & Rossion, 2010). Conversely, impairments in identifying

nonface categories of objects can occur without deficits in face recognition (e.g., Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Moscovitch, Winocur, & Behrmann, 1997; Feinberg, Schindler, Ochoa, Kwan, & Farah, 1994). This double dissociation between impairments in face and nonface recognition strongly suggests the existence of separate neural substrates for their processing.

Despite the evidence that face and nonface categories of objects are mediated by separate neural substrates, the reasons for this segregation are less clear. One hypothesis is that this face/nonface segregation is related to the high, within-category visual similarity of faces, as compared with nonface objects, which led to the evolution of specialized neural mechanisms to individuate among different faces (Diamond & Carey, 1986). However, the specific cognitive processes this specialized neural machinery might mediate remain unclear. One theory suggests that face processing involves at least two cognitive processes: featural processing, which entails perceiving the features of a face, such as the shape of the eyes, nose, and mouth, and configural processing, which entails perceiving the spatial arrangement among facial features, such as the distance between the eyes, nose, and mouth (Zachariou, Nikas, Safiullah, Gotts, & Ungerleider, 2016; Zhang, Liu, & Xu, 2015; Maurer et al., 2007; Yovel & Kanwisher, 2004; Maurer, Le Grand, & Mondloch, 2002).

National Institute of Mental Health, National Institutes of Health

A remaining topic of debate is whether this specialized neural machinery and the cognitive processes it mediates are specific to faces or can generalize to nonface categories of objects. One side of the debate argues that faces are a unique category of objects, crucial to the survival of human and nonhuman primates, and the neural substrates that mediate face perception evolved specifically for their processing and are thus domain-specific; they cannot mediate the processing of nonface categories of objects (Busigny et al., 2010; Grill-Spector, Knouf, & Kanwisher, 2004; Yovel & Kanwisher, 2004; Kanwisher et al., 1997; for a review, see Kanwisher & Yovel, 2006). The other side of the debate argues that the face-processing system is domain-general and engages as a function of expertise/ experience in the processing of any object category with very similar, within-category exemplars (Gauthier, Curran, Curby, & Collins, 2003; Tarr & Gauthier, 2000; for a review, see Gauthier & Nelson, 2001). More specifically, previous studies have demonstrated (e.g., McGugin, Gatenby, Gore, & Gauthier, 2012) that the nonface object selectivity of the face-processing system increases with training on differentiating between exemplars of a nonface object category.

Here, we reevaluated the domain-general and domain-specific hypotheses of face perception from two perspectives: (1) the high degree of within-category similarity of faces, considered to be a key factor for the evolution of the face-specific processing system, and (2) the featural/ configural cognitive processes this system mediates. More precisely, we explored the degree to which the face-processing regions of the ventral visual pathway (namely bilateral FFA and OFA) are activated when participants differentiate between exemplars of a face and a nonface category of objects (chairs) with comparable within-category similarity that differ only in their shape features or configuration. Although the domain-general and domain-specific hypotheses of face perception have been studied in previous experiments (e.g., Pitcher, Walsh, Yovel, & Duchaine, 2007; Duchaine et al., 2006; Yovel & Duchaine, 2006; Yue, Tjan, & Biederman, 2006; Rhodes, Byatt, Michie, & Puce, 2004; Yovel & Kanwisher, 2004), within-category similarity, behavioral performance, and type of cognitive processing engaged in differentiating between exemplars of the nonface category have not been adequately controlled (e.g., Kanwisher & Yovel, 2006; Rhodes et al., 2004).

In our experiments, we used tasks similar to those used previously (e.g., Renzi et al., 2013; Liu, Harris, & Kanwisher, 2010; Barton, 2008; Maurer et al., 2007; Pitcher et al., 2007; Duchaine et al., 2006; Yovel & Duchaine, 2006; Yovel & Kanwisher, 2004) with the following modifications. First, we used a larger set of distinct exemplars for both the face and nonface categories compared with prior studies, thus making it more difficult to memorize differences associated with specific face and nonface stimuli. Second, we ensured that, within each object category, low-level features such as luminance were matched, preventing their use when per-

forming the tasks. Third, we matched the in-scanner behavioral performance on the face and nonface categories of objects to exclude processing difficulty as a confounding factor. Lastly, we used the Structural Similarity Index Measure (SSIM; Wang, Bovik, Sheikh, & Simoncelli, 2004) to quantify and subsequently match, as much as possible, the within-category similarity of the face and nonface categories of objects. These modifications turned out to have a profound impact on the response of the face-processing regions to the nonface category, and our conclusions regarding domain-specific and domain-general processing of the face-processing system of the brain.

METHODS

Experimental Design

The experiment consisted of three fMRI sessions: a localizer, a same–different object task, and a border detection task session. During the localizer session, participants were presented with a face localizer task (adapted from Kanwisher et al., 1997), which localized brain regions that responded more strongly to faces than to houses and vice versa. Within the same session, participants also performed a task similar to the face localizer, in which activity evoked by different face exemplars (different face images were used here compared with the face localizer task) was contrasted to that evoked by different chair exemplars. Activations from this faces–chairs task were used to establish a baseline BOLD signal magnitude measure for the response of the localized face- and nonface-selective areas to the face and chair stimuli before matching them on within-category similarity and type of cognitive processing. As such, we contrasted this baseline activity with activations during the same–different object task and border detection task session, when the within-category similarities were comparable and the stimuli differed only in their features or configurations.

During the same–different object task session, we modified the face and chair stimuli presented during the localizer session, so they only differed in one of two dimensions: either in the shape of the object's features (featural differences) or in the spatial configuration of those features (configural differences; see below). By constraining differences between the stimuli, we increased the within-category similarity of both faces and chairs, but more dramatically for chairs (see Results). As a result, in the same–different object task session, the face and nonface categories had comparable within-category similarities, as measured by SSIM (see Methods below).

Following these modifications, we retested the same group of participants on the face and chair stimuli and measured the magnitude of activations within the localized face- and nonface-selective brain regions compared with the baseline measures obtained during the localizer session.

Lastly, during the border detection task session, we investigated whether the findings of the same–different

object task session were driven solely by the stimuli per se (comparable within-category similarity) or whether task-related, cognitive processes (featural and configural processing) were also necessary. To distinguish between these two alternatives, we used a procedure almost identical to that of the same–different object task session but, instead of performing same–different judgments between exemplars, participants passively viewed the face and nonface stimuli (the same stimuli as the ones used in the same–different object task session) and pressed a button when a border appeared around the stimuli (see Methods below). If the chair stimuli were sufficient to drive the effects observed in the same–different object task session, then passively viewing the same images should replicate the main findings. Alternatively, if the findings of the same–different object task session required the cognitive processes engaged during the configural/featural difference judgments, then passively viewing the stimuli should not replicate the findings of the same–different object task session, as those cognitive processes were absent during passive viewing.

Participants

Twenty-five healthy adults were recruited for the experiment (18 women, age range 22–42 years). Four participants, however, failed training during the same–different object task session (see Methods below) and were not scanned. Thus, 21 healthy adults (15 women, age range 22–42 years) participated in the localizer and same–different object task sessions of the experiment. Sixteen of these 21 participants also participated in the border detection task session (10 women, age range 22–42 years). The remaining five participants moved away from the NIH and could not participate. All were right-handed and had normal vision (corrected, if necessary). All gave informed consent under a protocol approved by the institutional review board of the National Institute of Mental Health. Before testing, all participants were asked whether they considered themselves to be experts on houses, chairs, or furniture, in general, to determine whether any of our participants had substantial previous experience on the nonface categories of objects we used. This interview was intended to exclude obvious outliers where expertise with one of the nonface object categories could affect brain activity in face-selective regions (see McGugin et al., 2012). None of the participants, however, identified himself or herself as a house, chair, or furniture expert. At the end of the experiment, all participants were also asked whether they perceived the chair stimuli as face-like or having any face-like properties, and none did.

Procedure

The experiment, implemented using E-Prime 2.0 (Psychology Software Tools, Inc.), was run on a Windows 7–based PC. Stimuli were presented via an analog projector on a 240 × 180 mm screen (15° visual angle horizontally by 11° vertically at a distance of 92 cm away from the participants' eyes), situated at the bore opening of the MRI scanner at a resolution of 1024 × 768 pixels (0.015° per pixel). Participants viewed the projection screen through a mirror attached to the head coil of the MRI scanner.

The localizer, same–different object task, and border detection task sessions occurred on three 60-min scan sessions on different days, with the localizer session first, followed by the same–different object task session, followed by the border detection task session. During the localizer session, there were four functional runs for the face localizer and another four runs for the faces–chairs task. The order of the runs was counterbalanced across participants. Consequently, four of these runs consisted of same–different face or same–different house judgments, and the remaining four consisted of same–different face judgments from a different set of face images and same–different chair judgments (separate, counterbalanced blocks per condition). During the same–different object task and border detection task sessions, there were eight functional runs with counterbalanced order across participants: Four runs consisted of either same–different face judgments (same–different object task session) or passive viewing of face stimuli (border detection task session), and the remaining four consisted of same–different chair judgments or passive viewing of the chair stimuli.

For all sessions, a functional run consisted of twelve 32-sec blocks, six blocks per object category for the localizer session and six blocks per type of difference (configural or featural) for the same–different object task and border detection task sessions. Each run was preceded and followed by 8 sec of fixation. Each trial lasted 2700 msec, and trials within a block were separated by a 300-msec intertrial interval.

On each trial of both the localizer and same–different object tasks, participants compared two images presented simultaneously on either side of the screen center and indicated with a button press if they differed. If they did not differ, participants did not respond. The border detection task session used a similar procedure as the same–different object task session, with two important difference: (1) In 2 out of the 10 trials of a block, both images in the stimulus display (face or nonface) were presented with a thin black border around them. We will refer to these trials as border trials. (2) Participants passively viewed the stimuli in the display and pressed a button when these border trials occurred. Participants withheld responses on nonborder trials. The border trials ensured that participants paid attention to the face and nonface stimuli on the screen. In the scanner, RT and accuracy in response to the border trials were recorded as a measure of the participants' level of attention.

Across trials, the two images appeared in one of two possible spatial configurations: In half the trials, images

appeared in a top-left, bottom-right configuration, and in the remaining half, in a top-right, bottom-left configuration. All stimuli were 4.5° wide by 5° tall and were separated by 4° of visual angle, 2° on either side of the screen center (2° of horizontal and vertical offsets, measured from the center of the screen to the center of an image). This presentation arrangement allowed us to display stimuli across the entire visual field (top/bottom/left/right). Participants were not required to maintain fixation during these tasks and could freely look at the stimuli in the display.
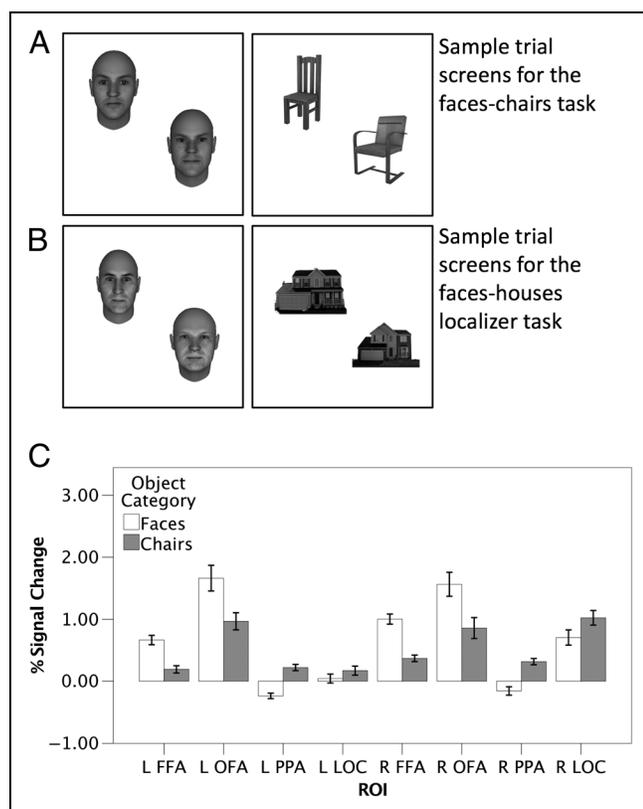
Localizer Session

The localizer session comprised two tasks with identical procedures. In one, we contrasted BOLD activations evoked by same–different face judgments to activations


Figure 1. Sample trial displays and stimuli used during the localizer session and the corresponding beta-weight coefficients (percent signal change) in response to face and chair difference judgments for bilateral FFA, OFA, PPA, and LOC ROIs. (A) Sample displays for the face and nonface categories used in the faces–chairs localizer task. (B) Sample displays for the face and nonface categories used in the faces–houses localizer task. (A and B) Trials in which the face and nonface exemplars differed and participants responded. (C) Beta-weight coefficients (percent signal change) in response to the faces–chairs task of the localizer session, within bilateral FFA, OFA, PPA and LOC. These ROIs were defined using BOLD activity from the faces–houses and whole-object versus scrambled object localizer tasks at the individual participant level. The error bars denote ±1 *SEM*.

evoked by same–different house judgments. In the other, we contrasted BOLD activations evoked by same–different face judgments, using a different set of face images, to activations evoked by same–different chair judgments (tasks were adapted from Kanwisher et al., 1997, and also used in Zachariou et al., 2015, 2016).

For each of the two face tasks, in separate blocks with counterbalanced order, the stimuli depicted grayscale images of either faces or the nonface category (houses or chairs; 20 images per object category). In half the trials of each block, the two exemplars differed (Figure 1A), and participants indicated detection of this difference by button press. At the beginning of each block, a dummy trial consisting of two different faces, houses or chairs (presented for 2.7 sec) informed participants of the task in the upcoming block.

We were unable to localize the lateral occipital complex (LOC; Grill-Spector et al., 1999) using the faces > houses contrast, as those stimuli evoked comparable activations. Consequently, we used fMRI data obtained from a whole versus phase-scrambled object localizer task performed by the same group of participants in the same MRI scanner for a different study (a few weeks earlier) to localize LOC at the individual participant level. The procedure of this shape localizer task was identical to that of the faces–houses task of the localizer session, but the images depicted either whole or phase-scrambled common objects (sample stimuli are shown in Zachariou, Klatzky, & Behrmann, 2014). Hence, LOC was localized using the contrast of activations evoked by same–different whole-object judgments > activations evoked by same–different phase-scrambled object judgments.

Same–Different Object Task and Border Detection Task Sessions

The same–different object and border detection task procedures were nearly identical to those used previously (Zachariou et al., 2016), but with the addition of chair stimuli. In each trial of the same–different object task session, participants compared two faces or two chairs (separate, counterbalanced runs for faces and chairs) presented simultaneously on either side of the screen center and, like the localizer session, indicated with a button press if they differed. If they did not differ, participants did not respond. During the border detection task session, participants passively viewed the stimuli in the display and pressed a button only when border trials occurred.

For the same–different object and border detection task sessions, we used the same face and chair stimuli (Figure 2) used in the localizer session, but the exemplars from each category now only differed across one of two dimensions: the shape of their features (featural differences) or the configuration of those features (configural differences). These differences were blocked

**Figure 2.** All object images used. (A) The 20 face exemplars used. (B) The 20 chair exemplars used.
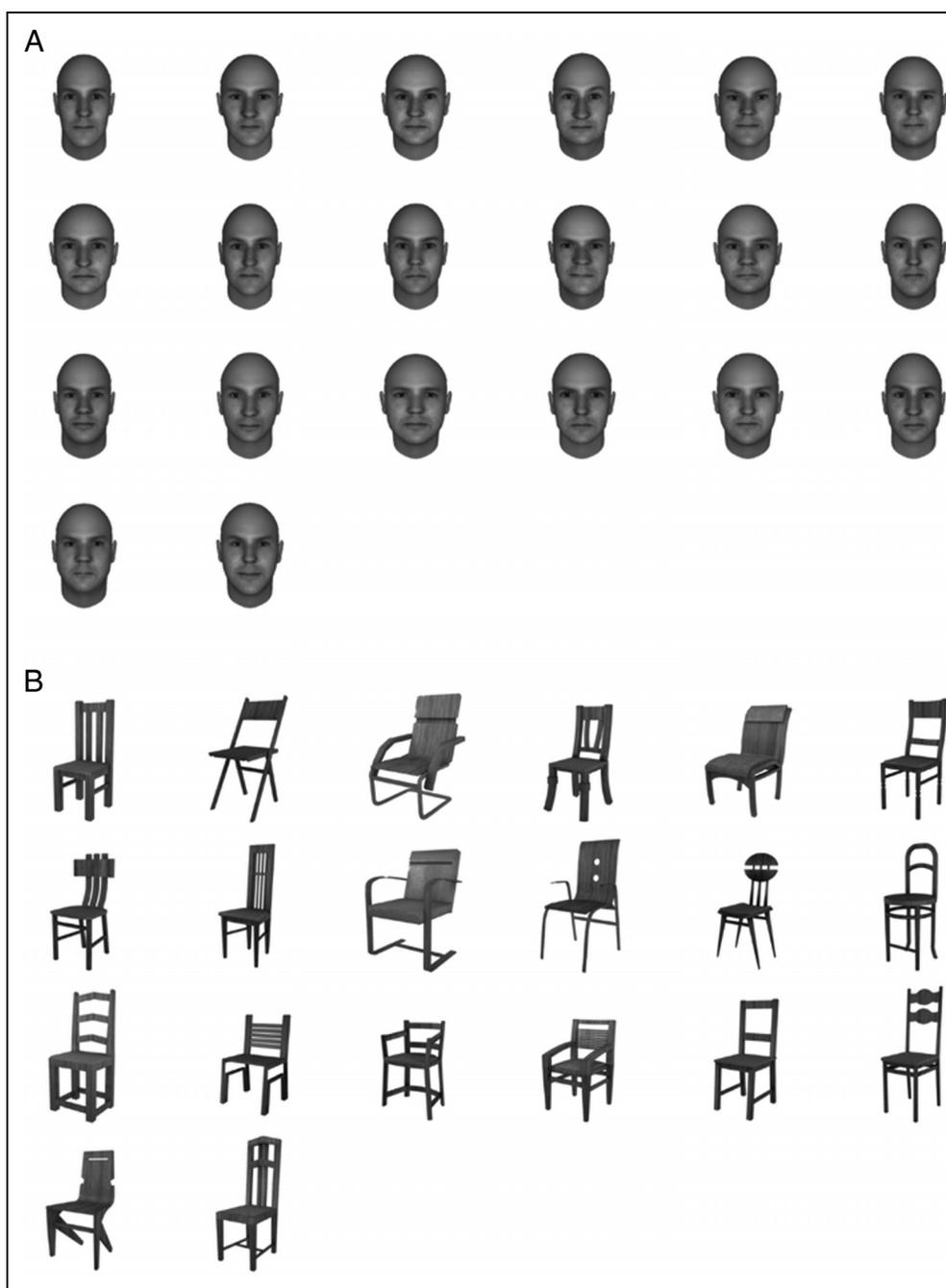
within the runs of each object category, and their order was counterbalanced between runs and across participants. During the same–different object task session, participants were not instructed to detect featural or configural differences; rather, they were instructed to make same–different judgments between the stimuli in the display. A postexperiment interview, however, indicated that all participants were aware of the two types of differences. All participants indicated that the eyes and nose of face images or the legs and backrest of chair images had different shapes on some trials. Similarly, participants also indicated that the eyes and nose of face images

and the legs and backrest of chair images were closer together or farther apart on some trials.

Each face exemplar appeared in two variants, which differed only in the shape of the eyes or of the nose. Each chair exemplar also appeared in two variants, which differed only in the shape of the backrest or of the chair legs. We will refer to the two variants of a category that differed in shape as S_1 and S_2 (Figure 3A).

We also assigned two different spatial configurations to each exemplar: the distance between the eyes or between the nose and mouth for the face stimuli and the distance between the backrest and seat of a chair
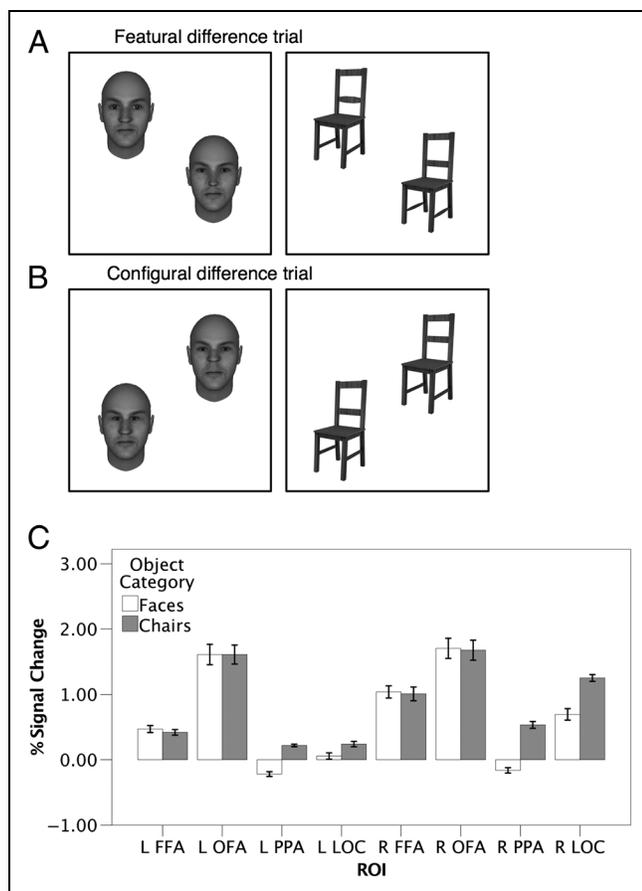
Figure 3. Sample trial displays and stimuli used during the same–different object task session and the corresponding beta-weight coefficients (percent signal change) in response to face and chair difference judgments for bilateral FFA, OFA, PPA and LOC ROIs. (A) Sample displays for the face and chair categories of the same–different object task session, in which the exemplars differed in features (featural difference). (B) Sample stimulus in which the exemplars differed in configuration (configural difference). (A and B) Trials in which the face and onface exemplars differed and participants responded. (C) Beta-weight coefficients (percent signal change) in response to the face and chair difference detection task, within bilateral FFA, OFA, PPA, and LOC ROIs. These ROIs were defined using BOLD activity from the faces–houses and whole-object versus scrambled object localizer tasks at the individual participant level. The error bars denote ±1 *SEM*.

or between the chair legs and the seat for the chair stimuli. Typical distance differences for both faces and chairs were between 0.5° and 0.9° of visual angle. Consequently, the shape features of an exemplar (face or chair) appeared with two different spatial configurations. We will refer to these two different spatial configurations as C_1 and C_2 (Figure 3B).

A featural difference occurred by presenting both the S_1 and S_2 variants of an exemplar in the stimulus display of a trial while holding spatial configuration (i.e., C_1 or C_2) constant between the images. Like the featural difference trials, configural difference trials occurred when both the C_1 and C_2 spatial configurations of an exemplar

were presented in a stimulus display whereas S_1 or S_2 (randomly selected) was held constant between the images.

In no-difference trials, both exemplars in the stimulus display (faces or chairs) were assigned the same combination of features ($S_{1\ or\ 2}$) and configuration ($C_{1\ or\ 2}$), which were randomly selected. In each block, no difference was present in half the trials.

For the same–different object task session, before scanning, participants completed a training session that lasted 30–45 min. During training, the running average RT for the four types of differences (face featural/configural and chair featural/configural) was compared. Then, the ratio of featural/configural difference blocks of each category was adjusted to allow more practice for the type and category of difference with the slower RT, until the absolute difference in RT was within 100 msec. The RT of a training block was included in the running average only if accuracy was above 90%; if accuracy was below 90%, the training block repeated. If the matching on RT, within the 100-msec criterion, was not achieved within 20 min of training, participants were presented with configural difference blocks only (of one or both categories, depending on which block type was slower) and the difficulty level of the configural difference trials was adjusted to match the RT of featural difference trials. Adjustments in difficulty were made after each block presentation, but if RT could not be matched within a total of 45 min, training was aborted and the participant was excluded from the study. Four participants were excluded for this reason and were not scanned. The difficulty level was controlled automatically and in real time by the training program and was adjusted by making the two spatial configuration sets, which were assigned to each exemplar (C_1, C_2) either more similar (increase in difficulty) or more dissimilar (decrease in difficulty). Altering the distance between the eyes and between the nose and mouth controlled the similarity/dissimilarity between spatial configurations for the faces. Similarly, altering the distance between the backrest and the seat of a chair and between the chair legs and the seat controlled the similarity/dissimilarity between spatial configurations for the chairs. If difficulty changes occurred for a category (face or chair), they did so for all configuration sets, across all feature sets of the category.

The on-screen sizes of the face and chair exemplars were matched. All images used were in grayscale (each pixel only carried intensity information, a value from 0 to 255 converted to a percentage here for clarity). To ensure that the low-level features of both object categories were comparable, we used Photoshop to extract the per-pixel intensity values of one face image (we used the "save image statistics" function in Photoshop), which acted as the template image. We then applied this pixel intensity template (using the same plugin) to every other image (including the chair images). Consequently, every image (face and chair) was very similar in luminance to

the template face image. The mean luminance value of the face images was 41% and of the chair images 41.5%. An independent samples t test (two-tailed) on the luminance values between the object categories (faces and chairs) did not yield a significant main effect ($t(38) = -0.39, p = .7$) indicating that the face and chair stimuli were closely matched on luminance, as intended. The contrast of the face and chair stimuli, defined as the standard deviation of the luminance values of an image, differed between the two object categories: The standard deviation of the luminance values for the face images was 0.70%, and the standard deviation of the luminance values for the chair images was 4.4% ($t(38) = 2.2, p = .0004$). The reason the contrast values are higher for the chair stimuli is because, unlike faces, chairs have gaps through which the background is visible. At these gaps, there is an abrupt change in luminance, which affects the overall contrast values of the chairs. The effect of this difference in contrast between the two object categories was evaluated in the border detection task session in which we investigated whether the findings of the same–different object task session were driven solely by the stimuli per se and differences in their lower-level features.

fMRI Acquisition

Participants were scanned in a General Electric MR750 3T scanner with a 32-channel head coil. Functional images were acquired with an EPI sequence (repetition time = 2 sec, echo time = 27 msec, flip angle = 79°, 3.2 mm isotropic voxels, 72 × 72 matrix, field of view = 230 mm, 45 axial slices covering the whole brain). The 45 slices were acquired with in-plane acceleration, using the GE protocol ASSET (www.gehealthcare.com/usen/education/tip_app/docs/fieldnotes_volume1-1_asset.pdf) with an acceleration factor of 2. An MPRAGE and a proton density sequence (1 mm^3 voxels, 176 slices, field of view = 256 mm) were used for anatomical imaging and were acquired within the same scan session (MPRAGE and proton density scans were collected in both the localizer and same–different object task sessions).

fMRI Preprocessing

Anatomical scans were first corrected for the 32-channel head coil contrast artifacts using the proton density scan acquired during each session. The functional scans were slice scan time-corrected, motion-corrected, coregistered to their constituent contrast-corrected anatomical image, normalized to Talairach space (Talairach & Tournoux, 1988) using a nonlinear transformation (3dQwarp; afni.nimh.nih.gov/pub/dist/doc/program_help/3dQwarp.html), smoothed with a Gaussian kernel of 6 mm FWHM, and mean-based intensity normalized (all volumes by the same factor) using AFNI (Cox, 1996). In addition, linear and nonlinear trends were removed during preprocess-

ing of the data. The motion parameters from the output of the volume registration step were regressed out in all AFNI analyses.

fMRI Statistical Analyses

All imaging data were analyzed using AFNI (Cox, 1996). Group-level analyses were conducted using linear mixed-effects models (*3dLME*; Chen, Saad, Britton, Pine, & Cox, 2013). The resulting statistical maps were thresholded at qFDR < 0.05 using the false discovery rate approach for multiple comparison correction (Genovese, Lazar, & Nichols, 2002). Group-level analyses were only conducted on the faces–houses and the whole versus phase-scrambled object localizer tasks. These group-level analyses were used to identify the group average size/volume of the face- and nonface-selective areas in ventral occipitotemporal cortex (VOTC) so we could determine an appropriate size/volume for the individual participant ROIs. All subsequent analyses were conducted using these individual participant ROIs to avoid issues related to between-participant variability in the anatomical location of the face-selective regions in VOTC (see Saxe, Brett, & Kanwisher, 2006). To define individual participant ROIs, the whole-brain statistical maps of each participant were thresholded at a family-wise error corrected $\alpha < .01$ at $p < .001$, using the AFNI program *3dClustSim* (2016 version, which addresses issues raised in Eklund, Nichols, & Knutsson, 2016; see Cox, Chen, Glen, Reynolds, & Taylor, 2017; afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html). Alpha (α) denotes the false-positive rate at the cluster level. That is, α is the probability of false positives associated with all the clusters that are above the minimum cluster size (estimated from 3dClustSim using Monte Carlo simulations) for a specific voxel-wise (uncorrected) p value threshold.

By using the fMRI contrast of faces > houses from the face localizer task and the contrast of whole > phase-scrambled objects from the shape/object localizer task, we identified clusters of activity (at qFDR < 0.05) within VOTC, at the group level, in which activations evoked by face difference judgments were greater than those evoked by house difference judgments (and vice versa) and activations in LOC in which activations evoked by same–different whole-object judgments were greater than those evoked by same–different phase-scrabbled object judgments. Positively activated regions from the faces > houses contrast included bilateral FFA (BA 20 and BA 37; center of mass Talairach coordinates in the right hemisphere: 40, −48, −17; volume: 60 voxels, 1.96 cm^3; left hemisphere: −37, −45, −16; volume: 50 voxels, 1.63 cm^3) and bilateral OFA (BA 19; center of mass Talairach coordinates in the right hemisphere: 43, −73, −5; volume: 60 voxels, 1.96 cm^3; left hemisphere: −42, −73, −4; volume: 45 voxels, 1.47 cm^3). Negatively activated regions (houses > faces) included bilateral parahippocampal place area (PPA) (BA 36 and BA 37; center

of mass Talairach coordinates in the right hemisphere: 27, −45, −8; volume: 100 voxels, 3.27 cm³; left hemisphere: −26, −42, −7; volume: 100 voxels, 3.27 cm³). Positively activated regions from the whole objects > phase-scrambled objects contrast included bilateral LOC (Talairach coordinates in the right hemisphere: 38, −81, 10; volume: 45 voxels, 1.44 cm³; left hemisphere: −43, −71, 9; volume: 40 voxels, 1.31 cm³).

Analyses at the individual participant level were performed as follows. First, we ran the AFNI program 3dClustSim at the individual participant level to obtain family-wise, error-corrected clusters for each participant, corresponding to the contrast of faces > houses. Then, for each participant, we identified positively activated clusters within the VOTC in which activations evoked by faces were greater than those evoked by the houses. Lastly, we increased the significance threshold separately for each cluster, until the number of voxels in a cluster matched the number of voxels of the corresponding group-level ROI (the group-level left/right FFA and OFA; on average, this occurred at $p < 1 \times 10^{-9}$). Using this method, we were able to localize bilateral FFA and OFA consistently across participants. Based on the Talairach coordinates of FFA-1 and FFA-2 provided in Pinsk et al. (2009), the individual participant FFA ROIs we selected appear to correspond to FFA-1 (Pinsk et al., 2009, average Talairach coordinates in the left hemisphere: −38 ($SEM = 1$), −56 ($SEM = 6$), −13 ($SEM = 1$); right hemisphere: 40 ($SEM = 1$), −58 ($SEM = 6$), −13 ($SEM = 1$); average (center of mass) Talairach coordinates of the FFA-1 we localized in left hemisphere: −38 ($SEM = 1.07$), −45 ($SEM = 1.01$), −17 ($SEM = 0.5$); right hemisphere: 39 ($SEM = 1.02$), −44 ($SEM = 0.39$), −16 ($SEM = 0.56$)). Unfortunately, we failed to localize FFA-2 either at the group level and consistently across all participants at the individual participant level.

The same procedure was used to identify bilateral LOC and PPA ROIs at the individual participant level using the contrasts of whole > phase-scrambled objects and of houses > faces, respectively. All individual participant ROIs were used to extract beta-weight coefficients from the faces–chairs task of the localizer, same–different object task and border detection task sessions, separately for each category (face or chair) and task type (configural or featural)

Statistical Analyses of Behavioral Measures

Behavioral data collected during the scans were analyzed using SPSS and a general linear mixed-effects model (with participants added as a random variable). Multiple comparisons used Sidak corrections where necessary.

Brain Activity–Behavior Correlations

Brain activity–behavior correlations were analyzed in SPSS using linear regression ANCOVAs with Session (localizer and same–different object task sessions) added as an interaction term. Brain activity (percent signal change) for these regression analyses was extracted using masks comprised from the individual participant bilateral FFA and OFA ROIs, separately for each participant, object category, and session. We used RT (msec) as the behavioral measure for these correlations because it had greater variability compared with accuracy and was therefore a good candidate. More importantly, in contrast to RT (msec), the accuracy (percent correct) measures collected during the same–different object task session were not normally distributed (Kolmogorov–Smirnov test for normality: RT for faces $p = .586$, chairs $p = .170$; accuracy for faces $p = .012$, chairs, $p = .001$). In addition, during the same–different object task session, the accuracy measures failed the Levene's test of equality of variance ($p = .040$) whereas the RT measures did not ($p = .06$). These issues with the accuracy measures of the same–different object task session were not unexpected. Participants were trained to criterion (90% accuracy) right before the same–different object task session, which affected both the variance and the normality of this measure. The face and chair tasks, however, did not differ significantly in accuracy (see Results section below).

Structural Similarity Index Measure

The SSIM (Wang et al., 2004) compares the visual similarity between two images across three independent image characteristics: luminance, contrast, and structure. The luminance component is a measure of the difference in the average luminance intensity between two images (across all the pixels of an image, measured as a value between 0 and 255). The contrast component is a comparison of the standard deviations of the luminance values between two images, and the structure component is a comparison of the covariance of the luminance values between two images. That is, the structure component is the correlation between the normalized (divided by the standard deviation) luminance value of a pixel in one image to the same pixel in another image (of the same resolution/size), averaged across all pixels. These three components are then combined into a single SSIM value that can vary between 0 and 1, with 0 indicating that two images are completely different from each other and 1 indicating that two images are identical.

To calculate the SSIM values for the face and chair stimuli, we first loaded all images in Matlab as matrices: 562 × 649 pixel/element matrices corresponded to the native resolution of the images. We then cropped each image matrix to include only those pixels within a 458-pixel wide by 583-pixel tall rectangle to eliminate as much of the background of an image as possible. We then calculated SSIM within these smaller rectangles using a moving 11 × 11-pixel circular symmetric Gaussian-weighted function window (see Wang et al., 2004).

RESULTS

Localizer Session

ROI Analysis

These ROI-level ANOVAs used fMRI activity from the faces–chairs task of the localizer session, extracted from the bilateral FFA, OFA, PPA, and LOC individual participant ROIs, defined using activity from the faces–houses and the whole versus phase-scrambled objects localizer tasks. The ANOVA model comprised Object category (face or chair) and ROI (bilateral FFA, OFA, PPA, and LOC) as factors.

The results showed both Object category ($F(1, 20) = 7.6$, $p < .01$) and ROI ($F(7, 20) = 51.9$, $p < .01$) as significant main effects and a significant interaction between the factors ($F(7, 20) = 13.7$, $p < .01$). To unpack the significant interaction, we repeated the analysis separately for each ROI (Figure 1C), with Object category as the sole factor. Analysis of the right FFA ($F(1, 20) = 132.1$, $p < .01$), right OFA ($F(1, 20) = 62.1$, $p < .01$), left FFA ($F(1, 20) = 77.6$, $p < .01$), and left OFA ($F(1, 20) = 31.1$, $p < .01$) ROIs yielded Object category as a significant main effect, with all these ROIs more strongly activated by same–different face judgments than chair judgments. Analysis of the right PPA ($F(1, 20) = 150.8$, $p < .01$), right LOC ($F(1, 20) = 17.2$, $p < .01$), left PPA ($F(1, 20) = 140.7$, $p < .01$), and left LOC ($F(1, 20) = 12.8$, $p < .01$) ROIs also yielded a significant main effect of Object category, but these ROIs were more strongly activated by same–different chair judgments than face judgments.

In summary, as anticipated from previous literature, face-selective ROIs responded significantly more to face than to chair difference judgments, whereas bilateral PPA and bilateral LOC responded significantly more to chair than to face difference judgments.

Localizer SSIM Analysis

Here, we only compared the SSIM values between the face and chair stimuli used in the faces–chairs localizer task, because the stimuli of the faces–houses task were not used in the same–different object task session. The SSIM was calculated between all possible pairs of images within a category, separately for faces and chairs. The results of a two-tailed t test between the SSIM values of the face and chair stimuli indicated a significant difference ($t(378) = 70.35$, $p < .01$), such that faces had a higher SSIM value than chairs (mean face SSIM = 0.89, $SD = 0.03$; mean chair SSIM = 0.60, $SD = 0.05$). In other words, the faces were 11% different from each other, whereas the chairs were 40% different from each other. As anticipated, before controlling for within-category similarity, the face images were substantially more visually similar to each other than were the chair images.

Face–Chair Localizer Behavioral Performance

We also compared the participants' in-scanner behavioral performance on the face and chair difference detection tasks of the localizer session, with the goal of establishing a measure of task difficulty for the two tasks. For these analyses, we conducted univariate repeated-measures ANOVAs on RT and Accuracy (percent correct) using mixed-effects models and Object category (face or chair) as the sole factor. For RT, we excluded incorrect trials.

Analysis of both RT ($F(1, 20) = 1267$, $p < .01$) and accuracy ($F(1, 20) = 185$, $p < .01$) showed a significant main effect of Object category, with participants both faster and more accurate during same–different chair judgments than face judgments (average RT for faces = 1021 msec; even–odd trial, split-half Cronbach's alpha = .46, $SEM = 31.6$ msec; average accuracy for faces = 91%, $SEM = 6.4\%$; average RT for chairs 802 msec; even–odd trial, split-half Cronbach's alpha = .75, $SEM = 45.4$ msec; average accuracy for chairs 97%, $SEM = 3.3\%$). This difference in RT and Accuracy is consistent with the faces being more similar to each other than were the chairs (see SSIM results).

Same–Different Object Task Session

ROI Analysis

Here, we used the same ROIs as in the analyses of the localizer session to compare beta-weight coefficients (percent signal change) from the two same–different detection tasks, faces and chairs, with the exemplars from each category differing in either the shape of their features or their configuration (featural or configural differences). A repeated-measures ANOVA was conducted with ROI (bilateral FFA, OFA, PPA, and LOC), Object category (face or chair), and Type of difference (featural or configural) as factors. The analysis yielded significant main effects of ROI ($F(7, 20) = 99.2$, $p < .01$) and Object category ($F(1, 20) = 21.9$, $p < .01$) and a significant interaction between ROI and Object category ($F(7, 20) = 5.1$, $p = .01$). Type of difference was not significant ($F(1, 20) = 0.02$, $p = .96$) and did not interact significantly with any of the other factors (ROI × Type of difference: $F(2, 20) = 0.04$, $p = 1.00$; Object category × Type of difference: $F(1, 20) = 0.01$, $p = .91$; ROI × Object category × Type of difference: $F(2, 20) = 0.02$ $p = 1.00$). To further explore the significant interaction between ROI and Object category, we conducted separate ANOVAs for each of the ROIs, with Object category as the sole factor (Figure 3C).

The analysis of the right FFA ($F(1, 20) = 0.35$, $p = .56$), right OFA ($F(1, 20) = 0.36$, $p = .55$), left FFA ($F(1, 20) = 1.3$, $p = .25$), and left OFA ($F(1, 20) = 0$, $p = .99$) ROIs did not yield a significant main effect of Object category ($F(1, 20) = 0.37$, $p = .56$), such that activations evoked by face difference judgments were comparable to those evoked by chair difference judgments (Figure 3C). Analysis of the right PPA ($F(1, 20) = 681.2$, $p < .01$), right LOC ($F(1, 20) = 79$, $p < .01$), left PPA ($F(1, 20) = 179.4$, $p < .01$), and left LOC ($F(1, 20) = 25.4$, $p < .01$)

ROIs, by contrast, did indicate a significant main effect of object category, such that activations evoked by chair difference judgments were greater than those evoked by face difference judgments.

To more closely examine the similarity in the strength of activations evoked by face and chair difference judgments within bilateral FFA and OFA, we conducted Bayesian paired t tests (using SPSS) within each of these face-selective ROIs, comparing the magnitude of activity between the face and chair tasks. Unlike the traditional general linear model analysis, the Bayesian paired t tests allowed us to calculate the Bayes factor, which, in this case, was the likelihood of the alternative hypothesis (H1: Face activity is different from chair activity) relative to the null hypothesis (H0: No difference between the face and chair activity) expressed as a ratio (H1/H0). As such, Bayes factor values greater than 1 indicate that the alternative hypothesis is more likely, and values less than 1 indicate that the null hypothesis is more likely. The Bayesian t test within the right FFA yielded a Bayes factor of 0.24 (with a prior scale of 0.707; default value for SPSS), providing evidence in favor of the null hypothesis. That is, activity evoked by face and chair difference judgments in right FFA is more likely to be comparable than different. Similarly, the Bayesian paired t test within the right OFA yielded a Bayes factor of 0.25, the left FFA yielded a Bayes factor of 0.28, and the left OFA yielded a Bayes factor of 0.22.

In summary, not only did we not find significant differences between the face and chair activity in bilateral FFA and OFA, according to the Bayesian paired t tests, but we also provide evidence to support the null hypothesis.

Comparison of fMRI Activity for Face and Chair Difference Judgments within the 10 Most Significantly Active Voxels in Right FFA (FFA-1)

The results of the ROI analyses of the same–different object task session indicated that bilateral FFA and OFA responded equivalently to face and chair difference judgments. It remains possible, however, that this finding might be due to the relatively large size of the face-selective ROIs we used (e.g., the right FFA is close to 2000 mm³). To account for this possibility, we conducted a control analysis in which we contrasted brain activity from the same–different face/chair detection tasks within the 10 most face-selective voxels of the right FFA. We selected the right FFA for this control analysis because it is considered to be the most face-selective region in VOTC.

For this analysis, we relocalized the right FFA at the individual participant level, using the faces > houses fMRI contrast as previously but increased the significance threshold further until only the 10 most significantly active voxels remained (on average, this occurred at $p < 1 \times 10^{-41}$). Then, as with the previous ROI analyses, these 10 most face-selective voxels within the right FFA were used to extract fMRI activity (percent signal change)

from the same–different object task session of the experiment, separately for each object category (face or chair) and task type (configural or featural). We then conducted a linear mixed-effects ANOVA on this peak, fMRI activity with object category and task type as factors.

This ANOVA, however, did not yield any significant main effects (object category: $F(1, 60) = 0.337$, $p = .564$; task type: $F(1, 60) = 0.025$, $p = .876$), and the interaction between the factors was not significant ($F(1, 60) = 0.243$, $p = .624$). Consequently, brain activity for the same–different face detection task (1.14% signal change) within the 10 most face-selective voxels of the right FFA was comparable to that of the same–different chair detection task (1.11% signal change). Bayesian paired t tests between the activity for faces and chairs within these 10 peak voxels verified the analysis of the previous ANOVA (Bayes factor of 0.242, prior scale 0.707). Consequently, the size of the face-selective ROIs does not appear to be the driving factor for the effects we observed.

Comparison of fMRI Activations between the Localizer and Same–Different Object Task Sessions

The ROI-level analyses of the localizer and same–different object task sessions suggest significant differences in the magnitude of activity within face-selective ROIs of VOTC between the face–chair difference judgments performed during the localizer session and those performed during the same–different object task session. To explore these differences statistically, we conducted a repeated-measures ANOVA (mixed-effects model with participants added as a random variable) with Object category (face or chair), Session (localizer or same–different object task session), and ROI (bilateral FFA, OFA, PPA, and LOC) as factors. The type of difference factor (featural or configural) was excluded from this analysis as it was not present during the localizer session (which would prevent us from running this ANOVA) and also had no impact in any previous test.

The analysis indicated that Session ($F(1, 20) = 16.5$, $p < .01$) and ROI ($F(7, 20) = 105.9$, $p < .01$) were significant main effects, whereas Object category was not ($F(1, 20) = 0.98$, $p = .32$). In addition, all two- and three-way interactions between the factors were significant: Session × Object category ($F(1, 20) = 19.8$, $p < .01$), Session × ROI ($F(7, 20) = 2.35$, $p = .02$), Object category × ROI ($F(7, 20) = 12.7$, $p < .01$), Session × Object category × ROI ($F(14, 20) = 6.9$, $p < .01$). To unpack the significant three-way interaction between Session, Object category, and ROI, we conducted separate analyses for each object category (face or chair) with ROI and session as factors. For face difference judgments, ROI was the only significant main effect ($F(7, 20) = 75.1$, $p < .01$). Session was not a significant main effect ($F(1, 20) = 0.06$, $p = .79$), and there was no significant interaction between the two factors ($F(7, 20) = 0.31$, $p = .95$). In contrast, for chair difference judgments, all main effects and the interaction

between the factors were significant (session: $F(1, 20) = 40.5, p < .01$; ROI: $F(7, 20) = 37.5, p < .01$; Session × ROI: $F(7, 20) = 3.8, p < .01$).

To unpack the significant interaction between session and ROI for chair difference judgments, we conducted separate analyses within each ROI with session as the sole factor. For the right FFA ($F(1, 20) = 15.0, p < .01$), right OFA ($F(1, 20) = 9.4, p < .01$), left FFA ($F(1, 20) = 8.2, p < .01$), and left OFA ($F(1, 20) = 14.15, p < .01$), Session was a significant main effect: Activity for chair difference judgments in these ROIs was significantly greater during the same–different object task session compared with the localizer session. In contrast, for the right PPA ($F(1, 20) = 3.97, p = .06$), right LOC ($F(1, 20) = 2.7, p = .11$), left PPA ($F(1, 20) = 0.05, p = .94$), and left LOC ($F(1, 20) = 0.54, p = .47$) ROIs, Session was not a significant main effect.

In summary, activations evoked by face difference judgments within all VOTC ROIs were not affected by session: Activations were comparable whether different face exemplars were presented (localizer session) or faces differed only in their shape features or configuration (same–different object task session). In striking contrast, activations evoked by chair difference judgments were affected by session, but only within the face-selective ROIs of VOTC (bilateral FFA and OFA): activations increased almost threefold when chairs differed only in shape features or configuration (same–different object task session) compared with when different chair exemplars were presented (localizer session). Activations evoked by chair difference judgments within bilateral PPA and LOC were not affected by session, similar to activations evoked by face difference judgments. Consequently, only the face-selective ROIs were effected by whether different chair exemplars were presented (localizer session) or chairs differed only in their shape features or configuration (same–different object task session).

Same–Different Object Task Session Behavioral Performance

To ensure the behavioral performance for the face and chair same–different tasks was comparable, we conducted a repeated-measures ANOVA separately for RT and Accuracy. Object category (face or chair) and Type of difference (configural or featural) were the factors for these analyses.

Analysis of RT yielded no significant main effects or interaction: Object category ($F(1, 20) = 0.6, p = .44$; 1459 msec for face difference judgments; even–odd trial, split-half Cronbach's alpha = .53, $SEM = 49.6$ msec; 1429 msec for chair difference judgments; even–odd trial, split-half Cronbach's alpha = .41, $SEM = 32.1$ msec), Type of difference ($F(1, 20) = 1.5, p = .23$; 1467 msec for configural differences, $SEM = 60.3$ msec; 1420 msec for featural differences, $SEM = 59.1$ msec), Object category × Type of difference ($F(1, 20) = 0.04, p = .85$).

Analysis of accuracy yielded similar results, with no significant main effects or interaction: Object category ($F(1, 20) = 3.8, p = .06$; 93% correct for face difference judgments, $SEM = 0.9\%$; 94% correct for chair difference judgments, $SEM = 0.7\%$), Type of difference ($F(1, 20) = 0.14, p = .71$; 93% correct for configural differences, $SEM = 0.56\%$; 93% correct for featural differences; $SEM = 0.5\%$), Object category × Type of difference ($F(1, 20) = 3.53, p = .07$).

Brain Activity–Behavior Correlations

To examine the functional contribution of VOTC face-selective areas to the same–different face and chair tasks, we conducted linear regression ANCOVAs, separately for each object category, between fMRI activity (percent signal change) corresponding to these tasks (extracted from bilateral FFA and OFA) and behavioral performance, using RT (msec) as the behavioral measure. Session (localizer or same–different object task session) was added as an interaction term in these linear regression analyses to explore whether or not the functional contribution of these brain regions to face and chair difference judgments changed between sessions. For these analyses, we excluded type of difference as a factor (configural or featural difference) because this factor had no impact on either the magnitude of activity or behavioral performance in all previous analyses.

In the linear regression analysis on the same–different face tasks (Figure 4A, B), session did not interact with the correlation between fMRI activity (percent signal change[1]) for face difference judgments and RT performance on the face task ($p = .1$). Irrespective of session, fMRI activity in response to same–different face judgments positively correlated with RT performance ($t(1, 41) = 2.041, r^2 = .10, p = .04$). Participants with greater activation during face difference judgments were slower (longer RTs) at detecting differences between the faces. This finding is consistent with previous literature showing that longer RTs correlate with greater magnitude of task-related fMRI activation (Domagalik, Beldzik, Oginska, Marek, & Fafrowicz, 2014; Rao, Motes, & Rypma, 2014; Yarkoni, Barch, Gray, Conturo, & Braver, 2009).

Conversely, for the same–different chair tasks, session interacted significantly with the correlation between fMRI activity for chair difference judgments and RT performance ($p < .0001$) on the chair task. To unpack this significant interaction, we performed partial correlations between fMRI activity and RT performance, separately for each session (localizer and same–different object task sessions). In each of these partial correlations, the RT measures for the same–different chair task in one session was correlated with the fMRI activity of the same task while controlling for the effects of the RT performance of the chair task in the other session. The reason for these partial correlations was to account for the impact of general ability, namely how good a participant is in
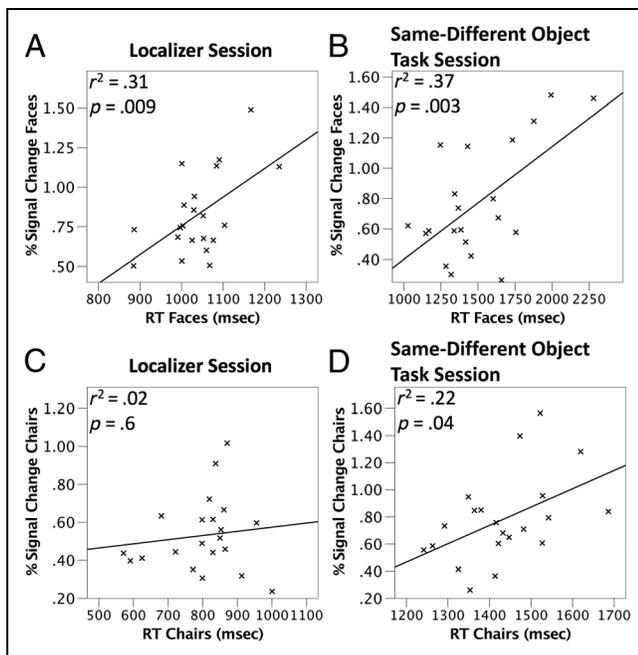
Figure 4. Scatterplots of the brain activity–behavior correlations for face and chair difference judgments for the localizer and same–different object task sessions. The fMRI activity used in these correlations was extracted from the individually defined bilateral FFA and OFA ROIs. (A) Brain activity–behavior correlation across participants between fMRI activity (percent signal change) evoked by the same–different face task of the localizer session and RT on the face task. (B) Brain activity–behavior correlation across participants between fMRI activity (percent signal change) evoked by the same–different face task of the same–different object task session and RT on the face task. (C) Brain activity–behavior correlation across participants between fMRI activity (percent signal change) evoked by the same–different chair task of the localizer session and RT on the chair task. (D) Brain activity–behavior correlation across participants between fMRI activity (percent signal change) evoked by the same–different chair task of the same–different object task session and RT on the chair task.

general in same–different object tasks, irrespective of object category and session that can affect the correlation between RT and percent signal change. For the localizer session (Figure 4C), the brain activity[2] within the face-selective regions corresponding to same different chair judgments did not predict RT performance ($t(1, 21) = 0.556$, $r^2 = .016$, $p_{partial} = .603$). In contrast to the analysis of the localizer session, during the same–different object task session (Figure 4D), brain activity corresponding to the same–different chair task positively predicted RT performance ($t(1, 21) = 2.372$, $r^2 = .229$, $p_{partial} = .038$). Participants with greater activation on the chair task of the same–different object task session were slower (longer RTs) at detecting differences between the chairs.

In summary, for the face tasks, brain activity within the face-selective regions of VOTC positively predicted the participants' RT performance on the task, irrespective of session. Conversely, brain activity related with the chair tasks predicted RT performance during the same–

different object task session only. That is, moving from the localizer to the same–different object task session, bilateral FFA and OFA not only responded equally to both faces and chairs but also predicted the behavioral performance of the nonface task.

Same–Different Object Task Session Analysis

For the analysis of the same–different object task session, we first compared the SSIM values between the object categories (faces and chairs) using a two-tailed, independent samples t test. Subsequently, we conducted a univariate ANOVA between Object category and Session (localizer and same–different object task sessions) to explore how the SSIM values varied between the two sessions.

For the t-test analysis, we calculated the SSIM values between all possible pairs of images within a category, separately for each object category (faces or chairs) and type of difference (configural or featural), because participants were only presented with exemplars that differed in either the features of a category or their configuration, but not both. The type of difference factor (configural or featural) was not included in the analyses for two reasons: (1) type of difference was not a significant factor in the previous analyses of fMRI activation and behavioral performance and (2) the removal of type of difference allowed us to compare the SSIM values between the localizer and same–different object task sessions, because the localizer session did not have type of difference as a variable.

The results of this t-test analysis indicated a significant difference between the SSIM values of faces and chairs ($t(78) = 5.96, p < .01$), with the face stimuli having a slightly higher SSIM value (average SSIM = 0.98, SD = 0.01) and were thus slightly more similar to each other than were the chair stimuli (average SSIM = 0.95, SD = 0.04).

The univariate ANOVA on SSIM between Object category (faces or chairs) and Session (localizer or same–different object task session) yielded both factors as significant main effects (Object category: $F(1, 456) = 1207, p < .01$; Session: $F(1, 456) = 2014, p < .01$). There was also a significant interaction between Object category and Session ($F(1, 456) = 677, p < .01$). To unpack the significant interaction, we ran two separate, independent samples t tests, one for faces and the other for chairs, comparing the SSIM values of each object category between the localizer and same–different object task sessions. The t test on the SSIM values of the face stimuli showed a significant but small difference between the localizer and same–different object task sessions ($t(228) = 21.7, p < .01$), such that the face stimuli were more similar to each other during the same–different object task session (average SSIM = 0.98, SD = 0.01) than the localizer session (average SSIM = 0.89, SD = 0.03). Faces during the same–different object task session were 2% different from each other, whereas they were 11% different from each other during the localizer session.

The *t* test on the SSIM values of the chair stimuli showed a significant and large difference between the localizer and same–different object task sessions ($t(228) = 239, p < .01$). The chair stimuli were far more similar to each other during the same–different object task session (average SSIM = 0.95, SD = 0.04) than during the localizer session (average SSIM = 0.60, SD = 0.05). The chair stimuli were 5% different from each other during the same–different object task session, whereas they were 40% different from each other during the localizer session.

In summary, during both the localizer and same–different object task sessions, the face stimuli were more similar to each other than were the chair stimuli. During the same–different object task session, however, the within-category similarity of the faces and chairs was comparable (2% difference for faces vs. 5% difference for chairs) compared with the localizer session (11% difference for faces vs. 40% difference for chairs). It should be noted that, for the face category, an increase in SSIM of 9% (11% difference during the localizer session vs. 2% difference during the same–different object task session) was not sufficiently large to cause any measurable differences in BOLD magnitude in any of the ROIs we tested. Consequently, a difference of 3% in SSIM between the face and chair stimuli of the same–different object task session is unlikely to have a substantial impact on the interpretation of the findings compared with the 35% change in SSIM for the chair stimuli between the localizer and same–different object task sessions.

It should also be noted that, even though during the same–different object task session the face stimuli were more similar to each other compared with the chair stimuli, the participants' behavioral performance on the same–different detection tasks was comparable between the two object categories. Consequently, the participants were able to perform finer discriminations between the faces compared with the chairs, likely due to having a lifetime of experience with differentiating small differences between faces.

Does SSIM Predict Psychophysical Similarity?

To examine whether the SSIM values we calculated for the face and chair stimuli could predict psychophysical similarity, we conducted bivariate correlation analyses between the SSIM values of the face and chair stimuli presented during the same–different object task session (separately for configural and featural differences) and corresponding RT performance for the same stimuli in the same session. All resulting correlations between the SSIM values of the face and chair stimuli and corresponding RT performance were significant: configural faces: $F(1, 19) = 8.796, p = .008, r^2 = .32$; featural faces: $F(1, 19) = 4.6, p = .04, r^2 = .204$; configural chairs: $F(1, 19) = 7.701, p = .01, r^2 = .3$; featural chairs: $F(1, 19) = 6.39, p = .02, r^2 = .26$. All correlations were positive, indicating that the higher the SSIM value (i.e., the more similar

the image pairs), the slower the RTs. Consequently, the SSIM values reliably predicted psychophysical similarity.

Border Detection Task Session

This session was conducted to test whether the comparable magnitudes of activation between face and chair difference judgments in the face-selective ROIs, observed in the same–different object task session, was the consequence of the stimuli per se or if the cognitive strategies the participants used during configural and featural difference judgments were also a factor. Consequently, we used the same stimuli as those used in the same–different object task session, but participants passively viewed the stimuli (Figure 5A, B) instead of performing same–different judgments between them.
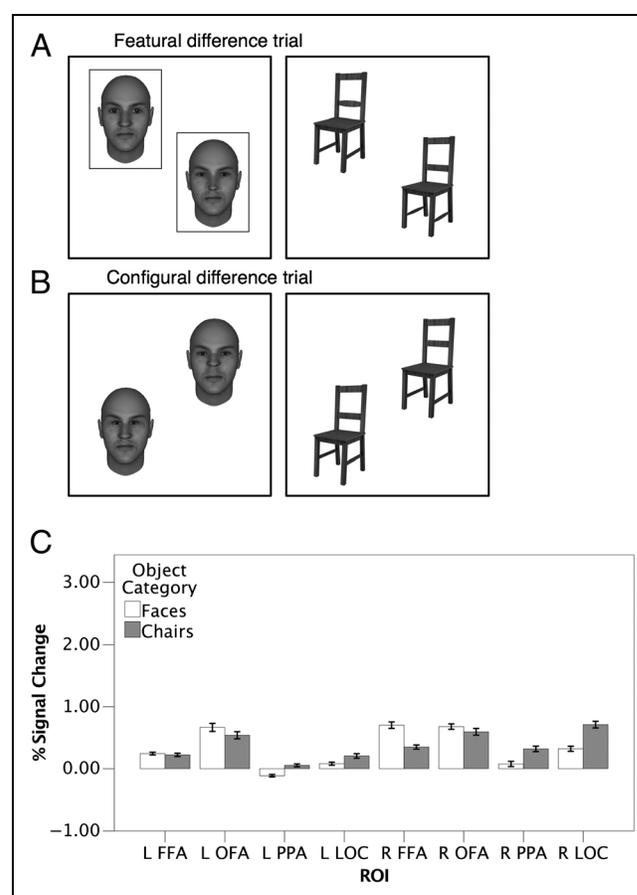
Figure 5. Sample trial displays and stimuli used during the border detection task session and the corresponding beta-weight coefficients (percent signal change) across ROIs. (A) Sample stimulus displays for the face and chair categories of the border detection task session, in which the exemplars differed in features (featural difference). Left (face panel): (A) Border trial in which participants responded. (B) Sample stimulus displays for the face and chair categories in which the exemplars differed in configuration (configural difference). (C) Beta-weight coefficients in response to passively viewing the face and chair stimuli in bilateral FFA, OFA, PPA, and LOC ROIs. These ROIs were defined using BOLD activity from the faces–houses and whole-object versus scrambled object localizer tasks at the individual participant level. The error bars denote ±1 *SEM*.

ROI Level Analysis

First, a repeated-measures ANOVA was conducted with ROI (bilateral FFA, OFA, PPA, and LOC), Object category (face or chair), and Type of difference (configural or featural) as factors. This analysis yielded a significant main effect of ROI ($F(7, 15) = 94.3$, $p < .01$) and Object category ($F(1, 15) = 27.8$, $p < .01$) and a significant interaction of ROI × Object category ($F(7, 15) = 18.0$, $p < .01$). The main effect of Type of difference and the remaining interactions between the factors were not significant (Type of difference: $F(1, 15) = 0.16$, $p = .69$; Object category × Type of difference: $F(1, 15) = 0.1$, $p = .77$; Type of difference × ROI: $F(7, 15) = 0.04$, $p = 1.00$; Object category × Type of difference × ROI: $F(7, 15) = 0.02$, $p = 1.00$).

To unpack the significant interaction between Object category and ROI, we ran separate, repeated-measures ANOVAs within each ROI, using Object category as the sole factor (Figure 5C). For the right FFA ($F(1, 15) = 113$, $p < .01$), right OFA ($F(1, 15) = 4.2$, $p = .04$), and left OFA ($F(1, 15) = 8.8$, $p < .01$), there was a significant main effect of Object category: activations when passively viewing faces were significantly greater than when viewing chairs. Within left FFA, the main effect of Object category was not significant ($F(1, 15) = 0.15$, $p = .29$). Within the right PPA ($F(1, 15) = 257$, $p < .01$), right LOC ($F(1, 15) = 173$, $p < .01$), left PPA ($F(1, 15) = 98.8$, $p < .01$), and left LOC ($F(1, 15) = 50.8$, $p < .01$), activations when passively viewing chairs were greater than when viewing faces.

In summary, the findings from the border detection task session were similar to those from the localizer session. When passively viewing the face and chair stimuli used in the same–different object task session, the face-selective brain regions of VOTC no longer responded equivalently to those stimuli but rather showed a preference for faces. Thus, the results of the same–different object task session cannot be attributed to the stimuli per se or to differences in their lower-level features.

Behavioral Performance of Border Trials

To confirm that participants paid attention while passively viewing the face and chair stimuli, we conducted repeated-measures ANOVAs separately for RT and accuracy on border trials, namely, those in which a face or nonface stimulus appeared with a thin black border around it and participants responded. Object category (face or chair) and Type of difference (configural or featural) were the factors for these analyses.

Analysis of RT yielded no significant main effects or interaction: Object category ($F(1, 15) = 0.09$, $p = .79$; 611 msec for face judgments; 631 msec for chair judgments), Type of difference ($F(1, 15) = 0.08$, $p = .78$; 620 msec for border trials with a configural difference; 623 msec for border trials with a featural difference), Object category × Type of difference ($F(1, 15) = 0.03$, $p = .87$).

Analysis of accuracy yielded similar results, with no significant main effects or interaction between the factors: Object category ($F(1, 15) = 0.7$, $p = .40$; 99.5% correct for face judgments; 99.2% correct for chair judgments), Type of difference ($F(1, 15) = 1.05$, $p = .31$; 99.4% correct for trials with a configural difference; 99.3% correct for with a featural difference), Object category × Type of difference ($F(1, 15) = 0.67$, $p = .41$). Hence, both RT and accuracy results confirmed that participants attended equally to the stimuli, irrespective of object category or type of difference.

DISCUSSION

The aim of this study was to reexamine whether face-selective regions within VOTC, such as bilateral FFA and OFA are better described as domain-specific or domain-general. To this end, we first established a baseline measure for evoked activity by face and nonface (chair) stimuli within individually defined bilateral FFA and OFA, using a face localizer task routinely used in the literature (e.g., Busigny et al., 2010; Kanwisher & Yovel, 2006; Grill-Spector et al., 2004; Kanwisher et al., 1997). Then, in a same–different object task session, we equated, as much as possible, the within-category similarity of the face and chair stimuli and the type of cognitive processing (featural and configural processing) in differentiating between exemplars of the two object categories. We then evaluated how brain activity within bilateral FFA and OFA and in control brain regions (bilateral PPA and LOC) changed in the same–different object task session relative to the localizer session. For the same–different object task session, we used featural and configural difference detection tasks similar to those used previously in the face literature (e.g., Pitcher et al., 2007; Duchaine et al., 2006; Yovel & Duchaine, 2006; Rhodes et al., 2004; Yovel & Kanwisher, 2004). Finally, we ran a third scan session, in which participants passively viewed the same stimuli used in the same–different object task session. In this border detection task session, we explored whether the findings of the same–different object task session were driven solely by the chair stimuli per se (comparable within-category similarity to faces) or whether task-related, cognitive processes (featural and configural processing) were also necessary.

We found the following: (1) During the localizer session, when participants differentiated between distinct exemplars of the face and chair categories, bilateral FFA[3] (specifically FFA-1) and OFA responded more strongly to faces than to chairs, whereas bilateral PPA and LOC responded more strongly to chairs. In this localizer session, the within-category similarity of the faces was substantially greater compared with the chairs. (2) By contrast, during the same–different object task session, when participants differentiated between exemplars of the face and chair categories that had comparable within-category similarity and differed only in their features or

configuration, bilateral FFA and OFA responded equally strongly to faces and chairs. However, activa- tions evoked by face and chair difference judgments within bilateral PPA and LOC did not change between the localizer and same–different object task sessions: Bilateral PPA and LOC were more strongly activated by chair compared with face difference judgments during both the localizer and same–different object task sessions, and importantly, the magnitude of activations to both object categories did not change from the localizer to the same–different object task session. Consequently, the increased magnitude of activation for chair difference judgments in face-selective regions was not due to an overall increase in brain activity within VOTC, thereby excluding differences in attentional load between the two tasks as the source of the same–different object task session findings. (3) In addition, as expected from previous literature, fMRI activity evoked by same–different face judgments within bilateral FFA and OFA predicted the participants' behavioral performance (RT) on the face task (significant positive correlation) irrespective of session (localizer or same–different object task session). In contrast to the findings of the face task, fMRI activity evoked by same– different chair judgments within the same regions predicted the participants' behavioral performance on the chair task during the same–different object task session only. Consequently, during the same–different object task session, bilateral FFA and OFA contributed to the processing of the chair task, whereas during the localizer session they did not. (4) Lastly, during the border detection task session, when participants viewed the same stimuli used in the same–different object task session, all face-selective regions except for the left FFA responded more strongly to faces than to chairs. Thus, the increase in the magnitude of activity for chair difference judgments in the face-selective regions during the same–different object task session was not driven by the chair stimuli per se; the cognitive strategies the participants used during the same–different object task session were important in driving the effect.

Analyses of the participants' behavioral performance during the same–different object task session indicate comparable levels of difficulty between the face and nonface tasks: Participants were equally fast and accurate in responding to both face and chair difference judgments. In short, difficulty of processing, differences in low-level features of the stimuli, and the participants' level of attention on the tasks cannot be the reason why bilateral FFA and OFA responded equivalently to face and chair difference judgments during the same–different object task session.

Taken together, the findings indicate two separate properties of FFA and OFA. First, when differentiating between distinct exemplars of face and nonface categories (as in the localizer session) or when passively viewing exemplars of a nonface category with comparable within-category similarity to faces (as in the border detection task session), FFA and OFA are face-selective,

responding more strongly to faces than to nonface objects. Second, when exemplars of a nonface category are both extremely similar to each other (comparable within-category similarity as faces) and differ in such a way that participants are forced to employ a strategy typically used to process faces (e.g., featural/configural processing, as in the same–different object task session; see Zhang et al., 2015; Maurer et al., 2002, 2007; Yovel & Kanwisher, 2004), both FFA and OFA are no longer face-selective and respond equally strongly to the face and nonface categories.

Interestingly, requiring participants to process faces in a featural/configural manner did not affect the magnitude of activation in FFA and OFA (or PPA and LOC), compared with when participants differentiated between distinct face exemplars in the localizer session. This suggests that these face regions may naturally process faces in a featural and/or configural manner. As such, constraining the face exemplars to differ only in features or configuration did not affect the magnitude of activation to faces in FFA and OFA or the degree to which this activity could predict behavioral performance on the face tasks.

It is also of interest that the nonface-selective aspect of the FFA and OFA observed in the same–different object task session did not require expertise with the nonface category. For example, numerous studies have shown that face-selective areas, such as the right FFA, increase their response to nonface object categories as a function of expertise[4] (e.g., McGugin et al., 2012; Gauthier et al., 2003; Gauthier & Nelson, 2001; Tarr & Gauthier, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). In our experiment, however, we observed an increase in the magnitude of activity in bilateral FFA and OFA in response to chair difference judgments even though none of our participants identified himself or herself as a chair or furniture expert. Even though there may not be a single cognitive strategy related to visual expertise in object recognition (Harel, 2016), it is possible that the cognitive strategies we forced our participants to use (by constraining the type of differences between the chair exemplars) share similarities to some of the cognitive strategies visual object recognition experts use. That is, identifying differences in features or configuration may be a good strategy for differentiating between very similar nonface object exemplars (e.g., sexing day-old chicks; Biederman & Shiffrar, 1987). Visual object recognition experts may have acquired these cognitive strategies through extensive training and can implement these automatically when distinguishing among exemplars in the object category of their expertise.

Although the domain-specific nature of face-processing regions has been demonstrated in many previous experiments very similar to ours (e.g., Liu et al., 2010; Barton, 2008; Maurer et al., 2007; Pitcher et al., 2007; Duchaine et al., 2006; Yovel & Duchaine, 2006; Yue et al., 2006; Rhodes et al., 2004; Yovel & Kanwisher, 2004), our study is the first to so closely match the face and nonface categories on a number of dimensions including low-level

features, difficulty of processing (on both RT and accuracy), and, most importantly, within-category similarity. For instance, Yovel and Kanwisher (2004) reported that their house stimuli had six times the Euclidian distance difference compared with their face stimuli. These same stimuli have since been used in multiple studies (e.g., Pitcher et al., 2007; Yovel & Duchaine, 2006).

Another example is the study by Yue et al. (2006). Unlike similar studies, Yue et al. (2006) contrasted faces to blobs, which were matched on similarity and on essential low-level shape characteristics to the face stimuli, but not on behavioral performance like we did here. The authors found no sensitivity in bilateral FFA to these blobs, either in the magnitude of the BOLD activity or in release from adaptation. The blob stimuli used in Yue et al. (2006), however, yielded very low levels of BOLD activity in both right FFA (0.2% signal change) and in right LOC (0.3% signal change), compared with other nonface common objects. As such, it remains possible that these blob stimuli may not have been complex enough to drive the face-/object-selective cortex sufficiently, irrespective of similarity. In short, there are substantial differences between the blob stimuli used in Yue et al. (2006) and the chair stimuli used here to account for the differences between our findings.

Another remaining question is whether the increased magnitude of activity observed in FFA and OFA for chair difference judgments during the same–different object task session was driven by the nonface object category (and associated cognitive processes related to it) or simply because participants were forced to compare visual stimuli with very small differences between them in a featural/configural manner. More specifically, could we replicate the same–different object task session findings if we were to use texture patterns or fractal images with comparable within-category similarity to that of faces, instead of a nonface object category? Although this possibility cannot be ruled out by our findings, we think it unlikely: Nonobject stimuli, such as texture patterns, or even abstract shape patterns (e.g., the blob stimuli used in Yue et al., 2006) do not yield robust activation within face-selective areas of VOTC, compared with both faces and nonface object categories (e.g., Rossion, Hanseeuw, & Dricot, 2012; Grill-Spector et al., 2004). For example, Rossion et al. (2012) contrasted, in their FFA localizer task, activity evoked by whole-face images versus their Fourier phase-scrambled counterparts versus car images. The Fourier phase-scrambled face images resemble texture patterns but have comparable within-category similarity to the faces they were created from. Rossion et al. (2012) reported that the activity within the right FFA in response to the Fourier phase-scrambled face images was considerably less (0.2% signal change) compared with activity in response to the whole-face images (1.1–1.2% signal change) and also considerably less compared with activity in response to the car images (0.6–0.7% signal change). Consequently, the right FFA does not appear

to respond robustly to scrambled shapes or fractal/texture patterns irrespective of their within-category similarity. As such, it would be very difficult, if not impossible, to demonstrate equivalent activation for faces and fractal/texture patterns within face-selective regions, irrespective of how well the within-category similarity is matched, simply because nonobject/shape stimuli do not activate these face areas robustly. In the same–different object task session of our experiment, activity for face and chair difference judgments, within the face-selective areas, was robust (activity > 1% signal change, similar to Rossion et al., 2012). As such, our findings cannot be attributed solely to the level of similarity in the visual input. It is more likely that our nonface category effects were driven by a combination of the high within-category similarity of the chair exemplars and the featural/configural processing strategies used by the participants.

Another interesting aspect of our findings is that they predict nonface object perception impairments in patients with acquired prosopagnosia, especially those patients with lesions of OFA and FFA. Previous literature on this topic is controversial. Although it is assumed that prosopagnosia is a face-specific recognition deficit (e.g., Busigny et al., 2010), there are several reports indicating that prosopagnosic patients are also impaired on recognizing nonface object categories. For example, Gauthier, Behrmann, and Tarr (1999) showed that their prosopagnosic patients (patients SM and CR) were impaired on both face and nonface object categories, and Barton (2008) demonstrated that 9 of their 10 patients had significant difficulty in identifying fruit and/or vegetables, including one patient who was a professional chef (Barton, 2008). In short, whether or not prosopagnosia is a face-specific impairment is still an open question. Our findings are compatible with the view that damage to the face-processing areas of VOTC leads to more general object discrimination impairments, but probably only in situations similar to the narrowly controlled conditions of our same–different object task session.

In conclusion, we have demonstrated that it is possible for the face-selective regions of VOTC to behave in a domain-general manner, under certain, narrowly constrained conditions even in the absence of expertise on the nonface category. As such, face-selective regions of VOTC cannot be completely domain-specific neural substrates. We have also demonstrated that within-category similarity and cognitive processing strategy play an important role in whether the face-selective regions of VOTC behave in a domain-general or domain-specific manner.

Acknowledgments

Reprint requests should be sent to Valentinos Zachariou, Laboratory of Brain and Cognition, National Institutes of Health, Building 10, RM 4C209, 10 Center Drive, Bethesda, MD 20814, or via e-mail: zachariouv@mail.nih.gov.

Notes

1. *SEM* of the fMRI activity for faces in the localizer session: 0.06%; *SEM* of the fMRI activity for faces in the same–different object task session: 0.08%.

2. *SEM* of the fMRI activity for chairs in the localizer session: 0.04%; *SEM* of the fMRI activity for chairs in the same–different object task session: 0.07%.

3. It should be noted that our findings are applicable to FFA-1 but not necessarily to FFA-2. We were unable to localize FFA-2 at the group level or consistently across participants at the individual level, and as such, it is uncertain whether the findings we report generalize to FFA-2.

4. It should be noted that some studies have demonstrated that extensive training does not necessarily increase activity in right FFA for the nonface object category (e.g., Yue et al., 2006).

REFERENCES

Barton, J. J. (2008). Structure and function in acquired prosopagnosia: Lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology, 2,* 197–225.

Biederman, I., & Shiffrar, M. M. (1987). Sexing day-old chicks: A case study and expert systems analysis of a difficult perceptual-learning task. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 13,* 640.

Busigny, T., Graf, M., Mayer, E., & Rossion, B. (2010). Acquired prosopagnosia as a face-specific disorder: Ruling out the general visual similarity account. *Neuropsychologia, 48,* 2051–2067.

Chen, G., Saad, Z. S., Britton, J. C., Pine, D. S., & Cox, R. W. (2013). Linear mixed-effects modeling approach to fMRI group analysis. *Neuroimage, 73,* 176–190.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research, 29,* 162–173.

Cox, R. W., Chen, G., Glen, D. R., Reynolds, R. C., & Taylor, P. A. (2017). fMRI clustering in AFNI: False-positive rates redux. *Brain Connectivity, 7,* 152–171.

Della Sala, S., & Young, A. W. (2003). Quaglino's 1867 case of prosopagnosia. *Cortex, 39,* 533–540.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General, 115,* 107.

Domagalik, A., Beldzik, E., Oginska, H., Marek, T., & Fafrowicz, M. (2014). Inconvenient correlation–RT–BOLD relationship for homogeneous and fast reactions. *Neuroscience, 278,* 211–221.

Duchaine, B. C., Yovel, G., Butterworth, E. J., & Nakayama, K. (2006). Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology, 23,* 714–747.

Eklund, A., Nichols, T. E., & Knutsson, H. (2016). Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. *Proceedings of the National Academy of Sciences, U.S.A., 113,* 7900–7905.

Feinberg, T. E., Schindler, R. J., Ochoa, E., Kwan, P. C., & Farah, M. J. (1994). Associative visual agnosia and alexia without prosopagnosia. *Cortex, 30,* 395–411.

Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience, 11,* 349–370.

Gauthier, I., Curran, T., Curby, K. M., & Collins, D. (2003). Perceptual interference supports a non-modular account of face processing. *Nature Neuroscience, 6,* 428–432.

Gauthier, I., & Nelson, C. A. (2001). The development of face expertise. *Current Opinion in Neurobiology, 11,* 219–224.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. *Nature Neuroscience, 2,* 568–573.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience, 12,* 495–504.

Genovese, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage, 15,* 870–878.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7,* 555–562.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24,* 187–203.

Harel, A. (2016). What is special about expertise? Visual expertise reveals the interactive nature of real-world object recognition. *Neuropsychologia, 83,* 88–99.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4,* 223–233.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17,* 4302–4311.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 361,* 2109–2128.

Liu, J., Harris, A., & Kanwisher, N. (2010). Perception of face parts and face configurations: An fMRI study. *Journal of Cognitive Neuroscience, 22,* 203–211.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6,* 255–260.

Maurer, D., O'Craven, K. M., Le Grand, R., Mondloch, C. J., Springer, M. V., Lewis, T. L., et al. (2007). Neural correlates of processing facial identity based on features versus their spacing. *Neuropsychologia, 45,* 1438–1451.

McGugin, R. W., Gatenby, J. C., Gore, J. C., & Gauthier, I. (2012). High-resolution imaging of expertise reveals reliable object selectivity in the fusiform face area related to perceptual performance. *Proceedings of the National Academy of Sciences, U.S.A., 109,* 17063–17068.

Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience, 9,* 555–604.

Pinsk, M. A., Arcaro, M., Weiner, K. S., Kalkus, J. F., Inati, S. J., Gross, C. G., et al. (2009). Neural representations of faces and body parts in macaque and human cortex: A comparative fMRI study. *Journal of Neurophysiology, 101,* 2581–2600.

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology, 19,* 319–324.

Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS evidence for the involvement of the right occipital face area in early face processing. *Current Biology, 17,* 1568–1573.

Rajimehr, R., Young, J. C., & Tootell, R. B. (2009). An anterior temporal face patch in human cortex, predicted by macaque maps. *Proceedings of the National Academy of Sciences, U.S.A., 106,* 1995–2000.

Rao, N. K., Motes, M. A., & Rypma, B. (2014). Investigating the neural bases for intra-subject cognitive efficiency changes using functional magnetic resonance imaging. *Frontiers in Human Neuroscience, 8,* 840.

Renzi, C., Schiavi, S., Carbon, C. C., Vecchi, T., Silvanto, J., & Cattaneo, Z. (2013). Processing of featural and configural aspects of faces is lateralized in dorsolateral prefrontal cortex: A TMS study. *Neuroimage, 74,* 45–51.

Rhodes, G., Byatt, G., Michie, P. T., & Puce, A. (2004). Is the fusiform face area specialized for faces, individuation, or expert individuation? *Journal of Cognitive Neuroscience, 16,* 189–203.

Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain, 126,* 2381–2395.

Rossion, B., Hanseeuw, B., & Dricot, L. (2012). Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis. *Brain and Cognition, 79,* 138–157.

Saxe, R., Brett, M., & Kanwisher, N. (2006). Divide and conquer: A defense of functional localizers. *Neuroimage, 30,* 1088–1096.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing: A position emission tomography study. *Brain, 115,* 15–36.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain. 3-Dimensional proportional system: An approach to cerebral imaging.* Stuttgart, Germany/New York: Thieme.

Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience, 3,* 764.

Wang, Z., Bovik, A. C., Sheikh, H. R., & Simoncelli, E. P. (2004). Image quality assessment: From error visibility to structural similarity. *IEEE Transactions on Image Processing, 13,* 600–612.

Yarkoni, T., Barch, D. M., Gray, J. R., Conturo, T. E., & Braver, T. S. (2009). BOLD correlates of trial-by-trial reaction time variability in gray and white matter: A multi-study fMRI analysis. *PLoS One, 4,* e4257.

Yovel, G., & Duchaine, B. (2006). Specialized face perception mechanisms extract both part and spacing information: Evidence from developmental prosopagnosia. *Journal of Cognitive Neuroscience, 18,* 580–593.

Yovel, G., & Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron, 44,* 889–898.

Yue, X., Tjan, B. S., & Biederman, I. (2006). What makes faces special? *Vision Research, 46,* 3802–3811.

Zachariou, V., Klatzky, R., & Behrmann, M. (2014). Ventral and dorsal visual stream contributions to the perception of object shape and object location. *Journal of Cognitive Neuroscience, 26,* 189–209.

Zachariou, V., Nikas, C. V., Safiullah, Z. N., Behrmann, M., Klatzky, R., & Ungerleider, L. G. (2015). Common dorsal stream substrates for the mapping of surface texture to object parts and visual spatial processing. *Journal of Cognitive Neuroscience, 27,* 2442–2461.

Zachariou, V., Nikas, C. V., Safiullah, Z. N., Gotts, S. J., & Ungerleider, L. G. (2016). Spatial mechanisms within the dorsal visual pathway contribute to the configural processing of faces. *Cerebral Cortex, 27,* 4124–4138.

Zhang, J., Liu, J., & Xu, Y. (2015). Neural decoding reveals impaired face configural processing in the right fusiform face area of individuals with developmental prosopagnosia. *Journal of Neuroscience, 35,* 1539–1548.