Sensitivity to Faces with Typical and Atypical Part Configurations within Regions of the Face-processing Network: An fMRI Study

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Abstract
Perception of faces has been shown to engage a domain-specific set of brain regions, including the occipital face area (OFA) and the fusiform face area (FFA). It is commonly held that the OFA is responsible for the detection of faces in the environment, whereas the FFA is responsible for processing the identity of the face. However, an alternative model posits that the FFA is responsible for face detection and subsequently recruits the OFA to analyze the face parts in the service of identification. An essential prediction of the former model is that the OFA is not sensitive to the arrangement of internal face parts. In the current fMRI study, we test the sensitivity of the OFA and FFA to the configuration of face parts. Participants were shown faces in which the internal parts were presented in a typical configuration (two eyes above a nose above a mouth) or in an atypical configuration (the locations of individual parts were shuffled within the face outline). Perception of the atypical faces evoked a significantly larger response than typical faces in the OFA and in a wide swath of the surrounding posterior occipitotemporal cortices. Surprisingly, typical faces did not evoke a significantly larger response than atypical faces anywhere in the brain, including the FFA (although some subthreshold differences were observed). We propose that face processing in the FFA results in inhibitory sculpting of activation in the OFA, which accounts for this region’s weaker response to typical than to atypical configurations.

INTRODUCTION
Face perception is perhaps our most remarkable visual ability and has therefore been the topic of intense study for several decades. This research has identified many brain regions that are central to the processing of faces. Principal among them is a region of the fusiform gyrus (Puce, Allison, Gore, & McCarthy, 1995; Allison, McCarthy, Nobre, Puce, & Belger, 1994; Haxby et al., 1994; Sergent, Ohta, & MacDonald, 1992), often referred to as the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997), and a region of the posterior occipitotemporal sulcus/inferior occipital gyrus, often referred to as the occipital face area (OFA; Gauthier et al., 2000). However, the functional role for each of these regions is still uncertain.

Cognitive models of face perception (e.g., Bruce & Young, 1986) include a node tasked with the initial structural encoding of faces that supports face detection and a separate node tasked with a detailed analysis of the relationship of the inner face features that supports face identification. Popular neural models (e.g., Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000) have ascribed these processes to the OFA and the FFA, respectively. The models posit a feed-forward and hierarchical architecture such that information flows from the posterior OFA to the relatively anterior FFA (Zhen, Fang, & Liu, 2013; Liu, Harris, & Kanwisher, 2010; Caldara & Seghier, 2009; Haxby et al., 2000). Consistent with this, Liu and colleagues (2010) found that the OFA response is not modulated by the first-order configuration of face parts (i.e., the arrangement of internal features), whereas the FFA responds more strongly to faces with a typical configuration (two eyes above a nose above a mouth).

However, this intuitively appealing hierarchical model is challenged by studies of patients with unilateral or bilateral lesions in the OFA region. Despite the absence of an intact OFA, fMRI of these individuals shows near typical activation of the FFA during face viewing (Weiner et al., 2016; Rossion, Dricot, Goebel, & Busigny, 2011; Schiltz et al., 2006; Steeves et al., 2006; Rossion, Caldara, et al., 2003). Additional challenges come from studies that implicate the OFA in higher-order aspects of face perception, such as identity recognition (Andrews, Davies-Thompson, Kingstone, & Young, 2010; Rossion, Schiltz, & Crommelinck, 2003). Puce, Allison, and McCarthy (1999) reported a patient in whom direct cortical stimulation of the OFA region caused difficulty in naming a face. Similar effects have been reported more recently, which also implicate the OFA in processing the first-order configuration of face parts (Jonas et al., 2012, 2014). Jonas and colleagues (2012) reported that a patient whose descriptions of face
perception during OFA stimulation included “the facial elements were mixed” and “the facial elements were in disarray” (p. 285).

To accommodate these results, several nonhierarchical models have been proposed that do not posit the OFA as the critical “gate-keeper” into the face processing network (Duchaine & Yovel, 2015; Pitcher, Duchaine, & Walsh, 2014; Atkinson & Adolphs, 2011; Rossion, 2008; but see Yang, Susilo, & Duchaine, 2012). For instance, Rossion (2008) has put forward a model in which the FFA receives input directly from early visual cortex. Thus, the OFA is not necessary for the detection of a face but is subsequently engaged by the FFA for “fine-grained” analysis of the face.

An essential feature of the hierarchical model is that the OFA is not sensitive to first-order configuration, consistent with its proposed role as the first node in the network tasked solely with detecting and processing face parts. However, there is surprisingly little evidence to support first-order configuration invariance in the OFA (but see Zhang, Li, Song, & Liu, 2012; Liu et al., 2010) and there are some reports that directly contradict this notion (Jonas et al., 2012, 2014). Given these contradictions, we sought to reexamine the relative sensitivities of the OFA and the FFA to the first-order configuration of face parts in a larger sample than used in the imaging studies cited above. In this fMRI study, participants viewed faces in which the internal parts either had a typical or atypical first-order configuration. Of particular importance is the response of the OFA, as the hierarchical model predicts that this response should not be modulated as a function of these conditions. The results will thus inform and constrain neural models of face perception.

METHODS
Participants
Twenty-one healthy adults (10 women, mean age = 24.0 years, 20 right-handed) with normal vision and no history of neurological or psychiatric illness participated in the study. Twenty participants identified as “white” and one identified as “Asian.” All participants provided written and informed consent. The protocol was approved by the Yale University institutional review board.

Stimuli
Sixty frontal-view neutral faces were created using FaceGen software (Singular Inversions, Toronto, Ontario, Canada). An equal number of Black and White faces were included. All faces were male, hairless, and wore no accessories. Faces were sized to a common height and converted to line-drawn images using GIMP software’s edge detection filter (www.gimp.org). The luminance and contrast of all faces were equalized to make low-level features as similar as possible. The main task consisted of two stimulus categories: faces with a typical first-order configuration (two eyes above a nose above a mouth) and faces with an atypical first-order configuration (internal features were shuffled within the face; Figure 1). We used seven different configurations of the left eye (L), right eye (R), mouth (M), and nose (N) to create the atypical faces. The arrangements, starting at the upper left and moving clockwise to the upper right, lower right, and lower left, were as follows: N-R-L-M, M-R-N-L, R-N-M-L, N-R-M-L, R-M-N-L, M-R-L-N. In repeated versions of the same configuration, the distance between parts could vary. For instance, two faces that shared the R-M-N-L configuration might differ in that the mouth was further offset from the right eye in one of the faces. With regard to placement of the eyes, there were two rules that all configurations adhered to. First, the two eyes never appeared next to each other in the upper or lower half of the face. Second, an eye in the upper half of the face was always placed on the wrong side (e.g., a right eye would be placed in the upper left position).

Experimental Procedure
In each of four runs, participants passively viewed 120 face images (30 from each of the four stimulus categories). Images were presented for 300 msec with a 2000-msec intertrial interval. The event-related design was jittered by including 25 “null” trials in which no image appeared during the 300-msec presentation window. A unique randomized presentation order of images and nulls was created for each of the four runs. The order of runs was counterbalanced across participants.

At the conclusion of the main task, participants completed four runs of a face localizer task. The localizer task followed the same procedure as used in Kim, Lee, Erlendsdottir, and McCarthy (2014). Briefly, participants viewed 12-sec stimulus blocks interleaved with 12-sec fixation blocks. Each stimulus block included eight exemplar images from one of three possible categories: faces, bodies, or houses. Participants were instructed to count the number of times they saw the same picture twice in a row. The localizer data collected for the current study.
were among the data used for the creation of the Atlas of Social Agent Perception (ASAP; Engell & McCarthy, 2013).

fMRI Acquisition and Preprocessing

Brain images were acquired at the Magnetic Resonance Research Center at Yale University using a Siemens 3.0-T TIM Trio scanner with a 12-channel head coil. Functional images were acquired using an echo-planar pulse sequence (repetition time [TR] = 2 sec, echo time [TE] = 25 msec, flip angle = 90°, matrix = 64², field of view [FOV] = 224 mm, slice thickness = 3.5 mm, 37 slices). Two sets of structural images were acquired for registration: coplanar images, acquired using a T₁ Flash sequence (TR = 300 msec, TE ≥ 2.3. A Gaussian random field theory-based cluster correction (p < .05) was then applied to correct for multiple comparisons. Voxels were first thresholded at a level of z ≥ 2.3. A Gaussian random field theory-based cluster correction (p < .05) was then applied to correct for multiple comparisons.

Data preprocessing and modeling were performed using the FMRIB Software Library (FSL; www.fmrib.ox.ac.uk/fsl). ROI and cluster analyses were performed using AFNI (Analysis of Functional Neuroimages; Cox, 1996). All images were skull-stripped using FSL’s brain extraction tool. The first three volumes (6 sec) of each functional data set were discarded to diminish MR equilibration effects. Data were spatially realigned to correct for head motion using FSL’s MCFLIRT realignment tool and spatially smoothed with a 5-mm FWHM isotropic Gaussian kernel. Each time series was high-pass filtered (0.02 Hz cutoff) to eliminate low-frequency drift. Functional images were registered to structural images using FSL’s linear registration tool (FLIRT). Functional images were first registered to coplanar anatomical images (6 DOF), which were then registered to high-resolution anatomical images (6 DOF), and then normalized to the Montreal Neurological Institute’s MNI 152 template (12 DOF).

Univariate Analysis

Whole-brain voxel-wise regression analyses were performed using FSL’s fMRI expert analysis tool. Within each preprocessed run, the typical and atypical conditions were modeled with a boxcar function convolved within a single-gamma hemodynamic response function. Participant-level analyses (i.e., across runs) were performed using a fixed-effects model.

Group analysis was performed using a mixed-effects model with the random effects component of variance estimated using FSL’s FLAME Stage 1 + 2 procedure. For both the regression and group analyses, clusters of active voxels were identified using FSL’s two-stage procedure to correct for multiple comparisons. Voxels were first thresholded at a level of z ≥ 2.3. A Gaussian random field theory-based cluster correction (p < .05) was then applied to correct for multiple comparisons.

We identified all local maxima with a separation distance of 20 mm using AFNI’s 3dExtrema program.

ROI Analyses

Several ROI analyses further investigated localized differences between the response to typical and atypical faces.

The first ROI analysis most directly addressed our primary aim by evaluating the responses evoked within the OFA and the FFA. These regions were defined using the ASAP (Engell & McCarthy, 2013) and data from an independent localizer task that was run at the conclusion of the main experiment. Spheres (r = 17 mm) were created around the OFA (48, −76, −6) and FFA (44, −48, −22) voxel with highest probability of being face sensitive as indicated by the ASAP. For each participant, we identified all clusters within each sphere at which the face > house contrast yielded a z score of ≥1.65. Of these voxels, the largest cluster was selected for the analysis. One participant was excluded because the face localizer did not yield any significant voxels within either of the ROIs. The voxels within this cluster for each participant were averaged within each ROI: OFA and FFA. These mean ROI responses from each participant were then analyzed as described below. This approach allowed the ROI sizes to vary across participants, thus resulting in the possibility that the accuracy of the estimate of the mean also varied accordingly. However, this should not meaningfully affect the current results because this is a repeated-measures design, which means the quality of the estimates would be homogenous across conditions within each participant.

The percent signal change (PSC) of the hemodynamic response to Black and White typical and atypical faces was averaged across all voxels within the peak cluster within each ROI for each participant. Visual inspection of the time courses (PSC at each TR from −4 sec pre-stimulus to 12 sec post-stimulus) revealed that the maximal (or near maximal) response was, with few exceptions, at 4 sec post-stimulus across all conditions. We therefore performed all subsequent ROI analyses on data from this time point. Thus, there were 160 data points for this analysis: Each of the 20 participants contributed an average response from within both ROIs for each face type and race. These data were analyzed with a three-way repeated-measures ANOVA with within-subject factors of ROI (OFA, FFA), Face configuration (typical, atypical), and Face race (black, white).

Spatial Distribution of Response

In a final analysis, we investigated the anterior–posterior and medial–lateral spatial distributions of first-order configuration-effects within the right ventral occipitotemporal cortices (VOTC). For this analysis, we defined two additional ROIs in which the average peak response was calculated within voxels of individual slices along the anterior–posterior
or medial–lateral axes. The difference between atypical and typical was calculated at each slice for each participant. The group differences at each slice were evaluated with a nonparametric $t_{\text{max}}$ permutation test that avoids inflation of the family-wise error rate due to multiple comparisons. $t$ tests were run on 10,000 random permutations of the participant difference values and slice positions. A null distribution of $t$ values was created that included the maximum $t$ value from each permutation. A new critical $t$ value was then determined by selecting the smallest value of the most extreme 5% of the distribution. At each slice, Cohen’s $d$ was used to evaluate effect size.

The first of the spatial distribution ROIs focused on the response within face-selective voxels of the right VOTC. We created an anatomical mask of VOTC by combining the “temporal occipital fusiform cortex” (TOFC) and “occipital fusiform gyrus” areas as delineated by the Harvard–Oxford Structural Atlas, then further restricted the ROI to include only those voxels within the VOTC that were likely to be face selective using a probabilistic atlas for face perception, which is included in the ASAP (Engell & McCarthy, 2013). Voxels within the anatomically defined VOTC that had a face-selective probability of $p > .25$ were included in the ROI analysis. The mean PSC from each participant was calculated at 26 equidistant slices along the anterior–posterior axis (MNI $y = 38$ to $-88$). $t_{\text{max}}$ Permutation tests (see above) indicated that $p < .05$ required $t_{\text{critical}} = ±3.05$.

The second of the spatial distribution ROIs was designed to be less conservative and thus to explore any broader effect of first-order configuration in regions such as the collateral sulcus that neighbor typical “face-selective” regions. This ROI consisted of the anatomically defined right TOFC without any additional functional constraints (i.e., no minimum probability of face selectivity). The TOFC mask includes the collateral sulcus and inferior temporal gyrus medial and lateral to the mid-fusiform gyrus, respectively. The ROI was subdivided into anterior (MNI $y = 38$ to $-48$) and posterior (MNI $y = -48$ to $-58$) sections. The MNI $y$ coordinate of $-48$ was chosen as the demarcation point between the anterior and posterior ROIs as this is the coordinate of peak probability for face selectivity in the ASAP. The mean PSC from each participant was calculated at 16 equidistant slices along the medial–lateral axis (MNI $22$–$52$). $t_{\text{max}}$ Permutation tests indicated that $p < .05$ required $t_{\text{critical}} = ±3.01$ and $t_{\text{critical}} = ±2.83$ for the anterior and posterior segments, respectively.

RESULTS

Univariate Analyses

Perception of faces with an atypical arrangement of internal features evoked significantly greater activation than faces with a typical arrangement throughout a large swath of bilateral occipitotemporal cortex (Figure 2). Large clusters that extended from ventral temporal to lateral occipital to superior parietal cortices were observed in both the right (64,544 mm$^3$) and left (59,144 mm$^3$) hemispheres. A third cluster (4264 mm$^3$) was observed in the right frontal pole. Within these clusters we identified, nine, five, and two local maxima, respectively (see Table 1 and Figure 2).

Using a threshold of $p < .05$ (corrected), no significant activation was observed for the contrast of typical greater than atypical.

ROI Analyses

A three-way repeated-measures ANOVA was conducted that examined the effect of ROI, Face configuration, and Race on the PSC. There was a significant interaction, $F(1, 19) = 11.13, p = .003, \eta_p^2 = .369$, between the effects of ROI and Face configuration on the PSC (Figure 3). Paired samples $t$ tests showed that this interaction is driven by a significantly larger response to atypical than typical faces in the OFA ($t = -2.59, p = .018, d = .91$), but no difference in the FFA ($p = .114$; see Figure 3). However, though not significant, we observe that, in the FFA, the response to typical faces ($M = 0.054, SD = 0.036$) was numerically larger than to atypical faces ($M = 0.033, SD = 0.036$). There was also a marginally significant interaction, $F(1, 19) = 4.32, p = .051, \eta_p^2 = .185$, between the effects of ROI and Race on the PSC. Black faces evoked a larger...
response in the FFA than white faces, whereas black faces evoked a smaller response in the OFA than white faces. This marginal interaction with race is beyond the scope of this report and will not be discussed further.

**Spatial Distribution of Response**

Moving from posterior to anterior within the right VOTC mask, we observed that the response to atypical faces moderately increased until it plateaued across a span from slices \( y = -74 \) to \( y = -64 \) and then monotonically decreased throughout all anterior slices (Figure 4). The response to typical faces did not vary appreciably over much of the ROI but did steadily increase across the last six most anterior slices. A significant difference (\( p < .05 \), corrected) between the response to atypical and typical faces was observed at four adjacent slices, \( y = -72 \) to \( y = -66 \), within the maximum response plateau of the atypical faces (see above). The average effect size across these slices was \( d = 1.07 \) (range 1.03–1.17). The response to typical faces was numerically larger than the response to atypical faces at the four most anterior slices of the ROI. These slices are within the region traditionally found to be the most face selective along the fusiform gyrus. When the responses were contrasted using independent paired samples \( t \) tests (i.e., uncorrected for multiple comparisons), the two most anterior slices, \( y = -40 \) and \( -38 \), were significant with marginally large effect sizes (\( d = 0.76 \) and 0.79, respectively). However, these differences were not significant in the \( t_{\text{max}} \) permutation test that controlled for multiple comparisons.

Moving from lateral to medial within the right anterior TOFC mask, we observed a greater response to typical than atypical faces at \( x = 40 \) (Figure 5). As with the typical > atypical responses found in the ROI described above, despite a relatively large effect size (\( d = 0.70 \)), this difference was only significant when evaluated with the uncorrected paired samples \( t \) test. Four of the five most medial slices showed a larger response to atypical than to typical faces with an average effect size of \( d = 0.87 \) (range 0.69–1.01). But again, this difference was only significant when evaluated without multiple comparisons correction. Within the posterior segment of this mask, the response to atypical faces was significantly larger (average \( d = 1.17 \), range 0.88–1.33) than the response to typical faces at six adjacent medial slices; \( x = 34, 32, 30, 28, 26, 24 \).

**DISCUSSION**

The results of our study show that occipitotemporal cortices (including the OFA, but also extending well beyond this region) show a strong preference for faces with atypical first-order configurations of internal features. However, ostensibly downstream regions of the face-processing network (including the FFA) showed no significant preference to faces with typical first-order configurations of internal features. In the following discussion, we consider the importance of these results and their implications for existing models of face perception.

**Why Does the OFA Prefer Atypical Feature Configurations?**

We found that the OFA is sensitive to the first-order configuration of face parts. Most intriguing is our finding that the OFA responded more strongly to atypically configured faces. We propose that this counterintuitive result

![Figure 3](http://direct.mit.edu/jocn/article-pdf/30/7/963/1787663/jocn_a_01255.pdf)
Figure 4. PSC along the anterior–posterior axis. ROI including probable face-selective voxels of right ventral temporal cortex (see Spatial Distribution of Response section for details.) PSC evoked by the typical (cyan) and atypical (purple) face configurations was extracted from the ROI within successive 2-mm slices moving from posterior (y = −88) to anterior (y = −38). Error bars indicate SEM. Asterisks indicate the locations at which there was a significant difference (orange) between typical and atypical faces. Double asterisks indicate where this difference was significant after correcting for multiple comparisons using a $t_{max}$ permutation approach.

Figure 5. PSC along the medial–lateral axis. ROIs including a posterior (y = −58 to y = −48; yellow) and anterior (y = −48 to y = −38; red) segment (see Spatial Distribution of Response section for details). PSC evoked by the typical (cyan) and atypical (purple) face configurations was extracted from each ROI within successive 2-mm slices moving from lateral (x = 52) to medial (x = 22). Error bars indicate SEM. Asterisks indicate the locations at which there was a significant difference (orange) between typical and atypical faces. Double asterisks indicate where this difference was significant after correcting for multiple comparisons using a $t_{max}$ permutation approach.
is possibly due to inhibitory feedback from the FFA during perception of typically configured faces.

Inhibitory feedback from the FFA to the OFA is in agreement with the suggestion that it is the FFA, not the OFA, that is tasked with initially detecting faces in the environment (Rossion, Hanseeuw, & Dricot, 2012; Rossion et al., 2011; Taubert, Apthorp, Aagten-Murphy, & Alais, 2011; Jacques & Rossion, 2006, 2009; Rossion, 2008; Tsao & Livingstone, 2008). In this model, the FFA detects faces based on holistic perception of the typical first-order configuration of face parts. Following detection, the FFA engages the OFA for a more detailed processing of features that facilitates the identification of individual faces. Thus, the FFA essentially focuses the OFA on featural processing. In the absence of such input, as would be expected in the case where atypical part configuration precludes holistic processing in the FFA, activation in the OFA would be unfocused and domain-general and therefore relatively enhanced. In other words, processing of the whole in the FFA might result in inhibitory sculpting of the processing of the parts in posterior occipitotemporal regions, including the OFA. The fact that the observed activation is widely distributed well beyond the OFA might reflect that this inhibitory sculpting input from the FFA extends throughout the visual system. That is, rather than being initiated by face detection in the OFA, it is inhibition from the FFA that directs the visual system from general object processing to face-selective processing.

Recently, Nemrodov, Anderson, Preston, and Itier (2014) introduced the Lateral Inhibition, Face Template and Eye Detector-based (LIFTED) model of holistic and featural processing, which emphasizes lateral inhibition of features in the parafovea onto those at the fovea. They propose that this inhibition prevents overrepresentation of the foveated feature (due to cortical magnification), which would prevent perception of the face as a whole. In their words, “This inhibition mechanism allows features to be perceptually ‘glued’ into a holistic representation.” (Nemrodov et al., 2014, p. 91) Our hypothesis is broadly consistent with the LIFTED model in that we also posit an inhibitory mechanism to account for a weaker response to holistic than part-based processing. The primary difference between the proposals is that the LIFTED model emphasizes inhibition as a function of retinal location, whereas we emphasize sculpting inhibition from the FFA to the OFA. However, these processes need not be mutually exclusive. It should also be noted that the LIFTED model is built on a large body of ERP research, whereas the current study uses fMRI. Although the high temporal resolution of ERPs and the high spatial resolution of fMRI are complimentary, they do not necessarily reflect the same underlying neural activity (cf. Engell, Huettel, & McCarthy, 2012). Additional multimodal studies are necessary to discover how, if at all, these proposed inhibitory mechanisms interact and how the ERP findings integrate with those of fMRI.

We also note that it is possible the significant and widespread preference for atypically configured faces is due to mechanisms that are not face specific. For instance, because of their inherent atypicality, these stimuli might stimulate greater attentional engagement or visual exploration. However, prior studies of face inversion (e.g., Yovel & Kanwisher, 2005) have found no difference between upright and inverted faces within the OFA or an increased response as a function of inversion that was specific to faces (Watson, Huis in’t Veld, & de Gelder, 2016). Therefore, any effect of face inversion is likely due to the disruption of holistic processing of faces and not mere novelty. We would argue the same is likely true of the current results.

Finally, we note that this finding contradicts the prior report of Liu and colleagues (2010). The reason for this discrepancy is not clear, though there are several differences between the studies. The prior work manipulated two additional factors: the presence or absence of face parts (the latter condition replaced parts with Black ovals) and the presence or absence of the face contour. The authors report that the presence or absence of face parts did not affect the finding of configuration sensitivity in the FFA, or the configuration insensitivity in the OFA. It is unclear, however, whether the same is true of the face contour manipulation. In the current work, the face contour was always present, which makes a direct comparison with the prior results challenging. It is also the case that the current study would be more sensitive to an effect given the larger sample size (ROI analysis in current report, n = 20; prior report, n = 9).

Hierarchical, Nonhierarchical, and Reciprocal Processing

A widely held theory of face processing posits that occipitotemporal regions, including the OFA, serve as the first node in a neural face-processing network (Zhen et al., 2013; Calder & Young, 2005; Haxby et al., 2000). In this model, the OFA detects face parts and routes this visual information to specialized neural systems rather than general object recognition areas. This specialized machinery includes the FFA, which is thought to be sensitive to the first- and second-order configuration of face parts (the distance between each part). This hierarchical model posits that information flows from the OFA to the FFA (Zhen et al., 2013; Liu et al., 2010; Caldara & Seghier, 2009; Haxby et al., 2000).

As noted above, an alternative nonhierarchical model suggests that face information is first processed in the FFA and then (or possibly in parallel) in the OFA (Rossion 2008). In this model, the FFA detects faces in the environment and then passes this information to the OFA for more detailed processing of the individual features to facilitate recognition of individual faces.

The current data do not directly speak to the temporal order of processing within and across the OFA and FFA. However, we can tentatively and speculatively infer the order of processing based on the response properties of each region. The lack of strong preference for typically
configured faces in the FFA suggests that face information reaches this region regardless of the configuration of internal features and thus is not dependent on prior processing in the OFA. This is consistent with typical activation of the FFA despite a lesioned OFA (Weiner et al., 2016; Rossion et al., 2011; Schiltz et al., 2006; Steeves et al., 2006; Rossion, Caldara, et al., 2003) and fMRI evidence that the FFA processes whole faces and face parts (Harris & Aguirre, 2008, 2010; Yovel & Kanwisher, 2004). The latter is in agreement with our recent electrocorticography (ECoG) report of eye-selective regions along the fusiform gyrus (Engell & McCarthy, 2014). Strikingly, these eye-selective sites were more abundant and showed greater selectivity than the face-selective sites.

The notion that the FFA is a “downstream” node in the face-processing network is, in part, based on its anterior location within the ventral visual processing stream relative to the more posterior OFA. It is inferred from these anatomical locations that information would reach the FFA at longer latencies than the OFA. This inference is indirectly supported by behavioral deficits in face processing induced by TMS of the OFA at latencies of 60–100 msec (Pitcher, Walsh, Yovel, & Duchaine, 2007). The relatively early latency of this effect is consistent with the notion that the OFA is an “entry node” and precedes the FFA. But the early disruption of the OFA does not preclude the possibility of parallel—or even earlier—processing in the FFA, a region that is inaccessible to TMS. Yue, Cassidy, Devaney, Holt, and Tootell (2011) cite monkey data that suggest as few as one or two intervening steps as information travels from V1 to FFA (Rajimehr, Young, & Tootell, 2009; Distler, Boussaoud, Desimone, & Ungerleider, 1993; Nakamura,Gattass, Desimone, & Ungerleider, 1993; Van Essen, Anderson, & Felleman, 1992), which allows for the possibility that initial face information reaches the FFA at very short latencies. Indeed, a recent ECoG study found FFA activity as early as 50 msec could be used to discriminate between face and nonface stimuli (Ghuman et al., 2014). Finally, though based on informal and unpublished observations from our laboratories, comparison of face-selective ERPs evoked at electrodes implanted in regions of the FFA and the OFA (cf. Engell & McCarthy, 2011) have not shown systematic latency differences.

The current results and the literature cited above are also in line with a perspective that deemphasizes the order of processing altogether and instead emphasizes reciprocal information flow (e.g., Harris & Aguirre, 2010; Schiltz, Dricot, Goebel, & Rossion, 2010) between the densely connected OFA and FFA (Kim et al., 2006). This framework supports functional roles that evolve over time within a region, rather than strictly independent functional roles across regions. We have recently published a series of ECoG studies (Engell & McCarthy, 2010, 2011, 2014) that report functional differences between the evoked face-N200 and the induced gamma response at the same intracranial electrode sites. The former is ostensibly an obligatory response during face perception, whereas the latter is sensitive to bottom–up (e.g., line-drawn vs. realistic faces) and top–down (e.g., attention) influences. Previously, single-cell recording in the macaque (Sugase, Yamane, Ueno, & Kawano, 1999) showed that, within the same neural population, initial information processing facilitates detection of faces whereas a later wave of information processing facilitates identification of individual faces. Similarly, Ghuman and colleagues (2014) used multivariate pattern classification of intracranial EEG data to investigate the nature of information processing in the FFA. They found that the FFA was involved in face detection at early latencies and face identification at longer latencies. Together, these studies support the notion that the stages of face processing might evolve within a region(s) rather than being properties of independent regions.

**Why Does the FFA Not Prefer Typically Configured Faces?**

In three different analyses—mass univariate, ROI, and spatial distribution—we did not find a significant modulation of the FFA response by first-order configuration. Whole-brain univariate analysis did not find any voxels in which there was a stronger response to typical than to atypical faces. ROI analysis of the functional defined FFA also failed to find a significant difference, though the response to typical faces was numerically larger than to atypical faces (see Figure 3). We were surprised by this null effect and therefore followed up the functional ROI analysis with an exploratory analysis of signal changes throughout the region. This analysis also failed to find a significantly stronger response to typical than to atypical faces. However, at a location in the neighborhood of the FFA, we did find a significant difference of typical > atypical when using a liberal paired samples t test at each slice that did not correct for the family-wise error rate (16 independent t tests were performed within two of the ROIs and 26 independent t tests were performed within the third ROI). We therefore conclude that if the FFA prefers typical to atypically configured faces, the effect is modest.

As is the case with our finding in the OFA, the null effect in the FFA is in contrast to a prior report that used a similar paradigm and found a preference for typical faces in this region (Liu et al., 2010). Insufficient sensitivity to detect such a difference in the current report is possible but not likely, given its larger sample size. It is also possible that the response in the FFA is disproportionately driven by the upright head/neck/chin/ears outline, which was the same for both our typical and atypical faces. Though again, this seem unlikely, given the importance of the internal features of the face (Andrews et al., 2010).

One might argue that the null effect in the FFA does not support our speculative proposal of inhibitory feedback from the FFA to the OFA that the feedback signal would be associated with an increased BOLD signal in the former. Although this is certainly possible, we would note...
that the BOLD response to whole faces and to parts might reflect the activation of functionally independent, but spatially commingled, neurons. Thus, the overall level of activation would not necessarily change, but this will need to be tested by future studies.

An alternative interpretation of the current results is that the presence of a face outline and of face parts, regardless of configuration, is sufficient for the FFA to engage the OFA, thus accounting for the configuration invariance within the FFA. In this account, the increased activation within the OFA and throughout visual cortex is driven by the increased processing demands of the atypically configured faces. That is, our inhibitory sculpting proposal accounts for the net activation difference within the OFA as being driven by an inhibitory signal from the FFA during perception of typical configurations; the alternative “mental sweat” interpretation would account for this same net activation difference as being driven by increased local processing demands within the OFA and visual cortex during perception of atypical configurations.

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