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Greater sensitivity of the cortical face processing system to perceptually-equated face detection

S. Maher, T. Ekstrom, Y. Tong, L.D. Nickerson, B. Frederick, and Y. Chen* McLean Hospital, Department of Psychiatry, Harvard Medical School

Abstract

Face detection, the perceptual capacity to identify a visual stimulus as a face before probing deeper into specific attributes (such as its identity or emotion), is essential for social functioning. Despite the importance of this functional capacity, face detection and its underlying brain mechanisms are not well understood. This study evaluated the roles that the cortical face processing system, which is identified largely through studying other aspects of face perception, play in face detection. Specifically, we used functional magnetic resonance imaging (fMRI) to examine the activations of the fusifom face area (FFA), occipital face area (OFA) and superior temporal sulcus (STS) when face detection was isolated from other aspects of face perception and when face detection was perceptually-equated across individual human participants (n=20). During face detection, FFA and OFA were significantly activated, even for stimuli presented at perceptual-threshold levels, whereas STS was not. During tree detection, however, FFA and OFA were responsive only for highly salient (i.e., high contrast) stimuli. Moreover, activation of FFA during face detection predicted a significant portion of the perceptual performance levels that were determined psychophysically for each participant. This pattern of result indicates that FFA and OFA have a greater sensitivity to face detection signals and selectively support the initial process of face vs. non-face object perception.

Keywords

facial; visual; perception; vision; cognition; FMRI

1. Introduction

Face detection plays a crucial role in the survival and success of the social world. Although face detection is considered a critical initial stage in the face perception process (Ellis, 1981), its underlying brain mechanisms remain poorly understood. Unlike other aspects of face perception, face detection allows identification of a visual stimulus as a face.

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^{*} Correspondence: MS 303, 115 Mill St., Belmont, MA 02478, ychen@mclean.harvard.edu.

Presumably this identification of the presence of a face needs to occur before a more detailed analysis of specific facial attributes (such as type of emotion expression and personal identity). Studies of patients with prosopagnosia bolsters this division, as these patients can identify face from non-face but cannot tell the identity of faces (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2003; Behrmann & Avidan, 2005). Further evidence comes from demonstration of face detection without awareness (Morris, Pelphrey, & McCarthy, 2007). It is not entirely clear whether this initial process of face perception is mediated by the same face processing system that is responsible for other aspects of face perception, though involvement of fusiform gyrus has been shown in a previous study (Morris et al., 2007).

Due to its ecological and functional importance, an efficient and sophisticated brain system has developed for face perception (Bodamer, 1947; Kanwisher, McDermott, & Chun, 1997). This system, which is identified largely by finer grain aspects of face perception, includes fusiform face area (FFA) (Kanwisher et al., 1997), occipital face area (OFA) (Gauthier et al., 2000) and superior-temporal sulcus (STS) (Haxby, Hoffman, & Gobbini, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Mechanistically, in order to trigger and activate such a face processing system, a face stimulus ought to be first identified as a face and it is reasonable to hypothesize that the detection aspect of face perception involves the face processing system in the brain. Previous work showed FFA activation when detecting photographs of real faces vs. other object types (Grill-Spector, Knouf, & Kanwisher, 2004). In a more recent study requiring detection of faces or cars from a noisy background, FFA activity was found to precede that of OFA (Jiang et al., 2011). Note that OFA was conventionally thought to process face information earlier than FFA in feed-forward models of the ventral visual stream (Ishai, 2008; Pitcher, Walsh, & Duchaine, 2011). This suggests a possible role for FFA in early stages of face perception such as face detection. Despite these results, however, the roles of the cortical areas in face detection remain unresolved.

Face detection is a fast and holistic visual process that relies upon primitive configuration signals (Cauchoix, Barragan-Jason, Serre, & Barbeau, 2014; Garrido, Duchaine, & Nakayama, 2008; Lewis & Edmonds, 2003). To probe its underlying brain mechanisms, it is imperative that face detection is disassociated from other aspects of face perception. It is therefore crucial to limit the perceptual features of face stimuli used for recognition of individualized and detailed attributes (such as identity and emotion) and present only configuration signals from the face stimuli. To meet this requirement, face images rendered like line drawings are more appropriate because this type of face stimulus, unlike photo face images, contains minimal information about facial identity or facial emotion. Applying such face stimuli allows for isolation and evaluation of the brain responses specific to face detection.

Detection of visual objects also depends upon stimulus contrast (Kelly, 1979; Regan, 1988; Solomon & Pelli, 1994) and brain responses during visual detection have been shown to vary systematically with stimulus contrast level (Boynton, Engel, Glover, & Heeger, 1996). When assessing face perception, a recent study showed that lower level features including contrast strongly influenced the response of FFA (Yue, Cassidy, Devaney, Holt, & Tootell,

2011). This suggests that the responses of the face processing areas to face detection signals may vary with stimulus contrast.

In addition, face perception capacities vary across individuals (McBain, Norton, & Chen, 2009; Wilmer et al., 2012). To probe the brain mechanisms underlying face detection, another key issue is to associate an individual's brain responses during face detection with his/her own perceptual sensitivities. This issue is particularly important for face detection when visual signals are not optimal or are weak (such as at low contrast levels). Availability of only weak visual signals may make a face detectable for one individual but not for another, likely leading to different types of brain responses. Thus, it is critical to take into account differences in perceptual ability when evaluating the corresponding brain responses by using stimuli that are based upon each individual's perceptual ability rather than applying a one-size-fits-all stimulus across participants.

In this study, we examined brain activations of face processing areas during detection of face and control tree stimuli that contain only configuration signals. Contrast levels of the stimuli were set based on individuals' perceptual thresholds to provide a range of perceptually-equated signal strengths for the two visual detection tasks. By measuring and comparing fMRI responses during face detection and tree detection, this study aimed to provide a more clear answer to the question of whether and how the conventionally defined face processing areas mediate visual detection of face presence. Specifically, we tested the following hypotheses that: 1. face processing areas - FFA, OFA, and STS - selectively respond to face detection signals (i.e., greater activation for faces than trees) and 2. face-selective cortical responses are associated with perceptual sensitivity during face detection.

2. Results

2.1. Behavioral responses

For off-line (prior to fMRI) accuracy, stimulus type and contrast level did not interact. Accuracy was higher for trees than faces (F[1,19] = 61, p < .023), and accuracy improved as contrast level increased (F[5,95] = 65.6, p < .001).

On-line (during fMRI) accuracy showed no interaction or effect of stimulus type, but did show a significant effect of contrast level (F[1,18] = 24.6, p < .0001) (Figure 1).

2.2. OI BOLD responses

To establish that the three ROIs were active for face detection, ANOVA of BOLD response (0% vs. average of TH, TH2 and 100%) was conducted first. The analysis showed a significant main effect in FFA (F[1,19] = 71.7), p < .0001) and OFA (F[1,19] = 37.5, p < .0001), but not in STS (F[1,19] = 3.8, p = .064) (Figure 2). This result indicates that STS was not significantly activated by this particular type of face stimulus and, as such, the subsequent analyses focused on FFA and OFA.

ANOVA of BOLD contrasts (Th vs. 0%, Th2 vs. 0% and 100% vs. 0% contrast levels) were conducted next. For FFA, significant interactions were found for stimulus type by contrast level (F[2,36] = 10.97, p < .001), and stimulus type by contrast level by hemisphere (F[2,36])

= 10.97, p < .001). Main effects were found for stimulus type (F[1,18] = 10.24, p = .005) and contrast level (F[1,18] = 4.49, p = .018).

To follow up the significant interactions, pair-wise comparisons of contrast levels for faces and trees were performed for each hemisphere. For trees, all comparisons save for the Th2 vs. 100% in the right hemisphere were significant, F values > 6.13, p values < .05 (Figure 3), where activation increased with contrast level. No significant difference was found for faces. Inspection of Figure 3 shows that FFA was activated by faces at all contrast levels; whereas for trees there was minimal activation at the Th level and increasing levels of activation as the contrast level increased.

In OFA, a significant interaction of stimulus type by contrast level (F[2,36] = 10.97, p <. 001) was found. Follow-up pairwise comparisons of contrast levels showed significant differences for trees only (Figure 3), where Th differed from Th2 (p < .05) and 100% (p < .001), but Th2 did not differ from 100% (p = .22). Figure 3 shows that OFA robustly activated to both faces and trees, with the significant interaction appearing to be driven by activations that were invariant to contrast for faces but not for trees.

For those subjects (n=16) who had enough incorrect trials (8 or more out of 37), BOLD responses did not differ between correct and incorrect trials, in either FFA or OFA and at any stimulus contrast levels.

2.3. BOLD Timecourse

For timecourses of BOLD responses, all comparisons showed a significant effect of time-point. For face detection, ANOVAs of BOLD signal change in either FFA or OFA showed no significant main effects of contrast level or significant interactions of contrast level by time-point.

For tree detection, however, all regions save for right OFA showed a significant interaction of contrast level \times time-point (p < .05). Significant effects of contrast level were also found for all regions (ps < .01).

Pair-wise comparisons of contrast level at each time-point were performed to follow up the significant interactions. At the 2 sec time-point, significant differences were found for Th vs. 100% at left FFA (p < .05) and Th vs. Th2 at left OFA (p < .05). For the remaining timepoints, significant differences were found for the Th vs. Th2 (ps < .05) and the Th vs. 100% (ps < .002) at left FFA, right FFA and left OFA. A significant difference was also found for the Th2 vs. 100% conditions at the timepoint 5 sec for left FFA (Figure 4).

2.4. rrelation between perceptual responses and BOLD

For off-line perceptual thresholds, a single significant correlation was found for the BOLD response of the right FFA to the face images presented at the perceptual threshold level (r(18) = .47, p < .05) (Figure 5). For online performance accuracies, significant correlations with BOLD responses to the face images presented at the two times perceptual threshold level were found at left FFA (r[18] = -.48, p < .05) and left OFA (r[18] = -.45, p < .05).

3. Discussion

This study found that two face-processing areas, FFA and OFA, were significantly activated during the detection of low and high contrast face images, but these same regions were activated primarily during the detection of high contrast tree images. Another face processing area, STS, remained virtually inactive during both face detection and tree detection, regardless of stimuli contrast level. The activation of FFA during face detection was associated with perceptual performance levels as determined separately using a psychophysical procedure.

3.1. reater sensitivity of FFA and OFA to visual signals during face detection

Previous studies have identified three brain areas - FFA, OFA and STS - for the processing of various aspects of face information (Haxby et al., 2000; Haxby, Hoffman, & Gobbini, 2002). By primarily examining brain responses only while salient face information was present, these studies left open the question of whether the identified face processing system also mediates the detection of the presence of a face, which often occurs while only weak signal (such as that from low contrast face images) is available. In weak signal situations, an adequate level of neural sensitivity is crucial for supporting the processing of face information. The result that FFA and OFA, but not STS, were significantly activated even when face detection signals were presented at perceptual threshold levels (Figure 3) indicates that the first two face processing areas possess the neural capacity to mediate visual detection of faces. Moreover, contrast-independent activations of FFA and OFA occurred during face detection but not during tree detection, highlighting the selective role of these two face processing areas in the initial process of face perception, but not in nonface object perception. This result is consistent with previous results that showed a greater degree of contrast-invariance for other aspects of face processing than for non-face visual object processing (Avidan et al., 2002; Grill-Spector et al., 2004). This property is important when considering the face-specificity of these cortical regions as it allows for greater sensitivity for detecting faces in noisy environments, giving this class of stimulus priority.

The contrast-independent FFA and OFA activations seem to be at odds with the result of a recent study which showed that lower level features of face images such as contrast strongly influenced the activation of FFA (Yue et al., 2011). This apparent discrepancy may be related to the different aspects of face processing tapped in the two studies. First, the stimulus used in the prior study was a 3-D face model that contained detailed face information whereas the stimuli used in the present study were faces rendered to resemble line drawings that contained only facial configuration information. In the visual system, neural analysis of global and coarse visual information is typically less dependent on stimulus contrast than that of detailed visual information (Kaplan & Shapley, 1986; Sclar, Maunsell, & Lennie, 1990), and this basic visual processing provides inputs to the face processing system. If contrast-dependence for less coarse input continues through higher levels of the face processing system, the different types of face stimuli used in the two studies may be a contributing factor to the different patterns of FFA responses observed.

Second, in the present study, contrast levels of face stimuli were equated according to the perceptual sensitivities of individual participants. The use of the individualized stimuli in the

present study may methodologically reduce the variability of online perceptual performance and brain activations. Low contrast faces lying below an individual subjects' perceptual threshold in the prior study may have been missed by that subject's face detection processes. This "below vs. above perceptual threshold" scenario would drive contrast dependent FFA activation, as we found here for tree detection. Third, the change of FFA response with stimulus contrast, found in the prior study, occurred mainly between the two lowest contrast levels (2% to 5%, Figure 3c in (Yue et al., 2011)). Such a change was noticeably reduced for other contrast levels. The present study employed stimulus contrasts at perceptual threshold levels (6.6% on average) and above. Therefore, when excluding very low contrast conditions, the relationships between FFA response and stimulus contrast were not substantially different between the two studies. One likely scenario is that stimulus contrast is critical in determining if a face is detectable and once the detection threshold is reached, contrast is no longer as critical.

Neural selectivity to faces has been well established for FFA and OFA (Kanwisher et al., 1997; Tsao, Freiwald, Tootell, & Livingstone, 2006). The result of this study further shows that the selectivity to face signals in the two brain areas begins at an initial stage of face processing – the detection of the presence of a face. Although the two face processing areas also responded during tree detection, such response was not generated until salient visual signals were present. This result suggests that during the detection of visual objects, saliency of visual signals plays an important role in determining the response selectivity of the two face processing areas.

3.2. elationship between perceptual performance and activation of FFA

In addition to assessment of brain activations, another way to understand the role of the face processing system in face detection is to evaluate the extent to which this perceptual capacity can be defined through associated brain activations within the same individuals. The significant correlation between participants' off-line perceptual thresholds and their FFA activations during face detection, measured with MRI, (Figure 5) indicates that this face processing area was activated to a greater extent in those who had lower perceptual sensitivities (higher perceptual thresholds). This relationship suggests that in response to face detection signals, this face-selective area operates like an efficiency mechanism; that is, high perceptual performance levels only require support from low-level brain activations during face detection. Note that this significant correlation was driven largely by one subject's data, and thus needs to be replicated in future studies.

The significant inverse correlations between online MRI performance accuracy and FFA activations (Table 1) provides additional evidence for the notion that this face processing area operates as an efficiency mechanism. The negative correlations indicate that this face processing area was activated to a lesser extent in those who had higher performance accuracies on the face detection task. The relationships between FFA activations and both online and off-line perceptual responses converge to suggest that this face processing area plays a significant role in defining perceptual capacity for face detection. Note that the relationship between perceptual performance and brain responses was established when signal strengths (contrast levels) for face detection were individually adjusted according to

the perceptual abilities of participants. The positive finding of such a relationship highlights the importance of using a personalized fMRI strategy for linking face perception to its underlying brain mechanisms.

3.3. FFA as neural substrate for initial stage of face-specific processing

A recent fMRI study argued that the FFA plays an important role in face detection by showing the precedence of FFA response over that of other brain areas such as OFA in detecting the appearance of a face from a noisy background (Jiang et al., 2011). The present study lends support to this argument. While not finding different temporal dynamics of FFA and OFA, the result of the present study (Figure 4) did show different patterns of fMRI time-courses for face and tree detection. Significant interactions between stimulus contrast and time after stimulus onset were found for tree detection but not for face detection, indicating that FFA and OFA response to low contrast tree images had lower amplitude and delayed time course (Figure 4). Neither lower amplitude nor slower time course were present for low contrast face images, indicating that rapid and robust face detection response from FFA and OFA was present even to sub-salient visual signals.

It should be noted that the face stimuli used in the present study contained primarily configuration information that mostly evokes global processing. Global visual information is typically processed more rapidly than local visual information (Navon, 1977). Thus, the robust responses of FFA and OFA to facial configuration information suggest that these brain areas provide neural substrates for initial processing of global facial signals, in addition to later analysis of local and detailed facial features. Significant activation differences were not found for correct vs. incorrect responses in either region, consistent with the notion that these structures responded automatically to the presence of face regardless of awareness (Morris et al., 2007), a property one may expect of a system tuned to be sensitive to a particular stimulus type.

While both FFA and OFA respond robustly to face detection signals, some functional differences may exist. It has been shown that OFA is responsive to face parts such as mouths (Pitcher, Walsh et al., 2011). In the present study, the correlations between perceptual thresholds for face detection and OFA activations were either reduced or absent (Table 1). These results suggest that although OFA was significantly activated during face detection, its exact functional roles remain to be defined.

Also noticeable is the lack of activations of STS during face detection (Figures 1 and 2). While regarded as a face processing area, STS is primarily responsible for analyzing changeable facial features such eye and mouth movements (Puce et al., 1998), gaze direction (Hoffman & Haxby, 2000), expression (Winston, Henson, Fine-Goulden, & Dolan, 2004) and dynamic faces (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011). As face detection requires only static and configuration information, negligible STS activation during face detection is consistent with the notion that this initial stage of face processing does not entail the analysis of more detailed face information.

3.4. Implications on abnormal face detection

Abnormality in face detection has been shown in social functioning disorders such as schizophrenia (Chen, Norton, McBain, Ongur, & Heckers, 2009; Chen, Norton, Ongur, & Heckers, 2008). The brain mechanisms associated with this face detection problem are still unknown however. The involvement of FFA and OFA in face detection suggests that these two face-processing areas should be focused on when searching for the brain mechanisms responsible for abnormal face detection. Increased knowledge about these mechanisms may help to extend our understanding of social functioning problems associated with brain disorders.

Anatomical locations of functional activation during face perception may slightly vary among individuals (Rossion, Hanseeuw, & Dricot, 2012). This study evaluated multiple face-sensitive regions using established anatomical locations while taking into account individual differences in perceptual response to faces. In future studies, the results from this approach should be compared with those from a functional localizer based approach (Kanwisher et al., 1997) to further elucidate this issue.

3.5 Conclusions

In summary, this study found that FFA and OFA, but not STS, were highly sensitive to the face detection signals at perceptual threshold levels, as compared to the tree detection signals. The response of FFA during face detection can predict a significant portion of perceptual performance. The high sensitivity of these two brain areas to face detection signals may serve as a basis for initiating and gating the analysis of face-specific information.

4. Methods and materials

4.1. Participants

Twenty adults (ten women) participated in this study. Participants ranged from 21 to 73 years of age (mean = 40.9, SD = 15.6), and had no diagnosed organic brain disease and no history of substance abuse or dependence during the past two years. All but two participants were right-handed, and had normal or corrected-to-normal visual acuity (assessed by the Rosenbaum Pocket Vision Screener). This study was reviewed and approved by the McLean Hospital Institutional Review Board, and it was conducted in accord with the Declaration of Helsinki. All volunteers provided verbal and written informed consent and they were compensated for their participation.

4.2. Visual detection tasks

Two visual detection tasks were used, one to assess face detection and one to assess the responses to control stimuli (trees). In a face detection trial, participants judged on which side of a displayed image (left or right) a face was presented. Each face image included a face rendered like a line-drawing in one-half of the image and scrambled line segments in the other half of the image. In tree detection trials, each tree image included a tree rendered like a line-drawing in one-half of the image and scrambled line segments in the other half of the image and participants judged on which side of the presented image a tree was located.

Contrast was manipulated by changing the foreground luminance of the images. In both tasks, each image was displayed within a square window $(10^{\circ} \times 10^{\circ})$ for 300 msec. For fMRI, visual stimuli were delivered using an event-related design over 4 runs, two for each of the two visual detection tasks. Presentation sequences were created using optseq2 (Dale, Fischl, & Sereno, 1999) to efficiently de-convolve overlapping hemodynamic responses by condition. Each trial consisted of an image presented for 300 ms and an average interstimulus interval of 2058 ms (from 1700 to 11700 ms),. Each run consisted of 192 trials, corresponding to face detection or tree detection at the four pre-determined contrast levels (see below). The task conditions (face detection and tree detection) were presented in a counterbalanced order across participants. Each participant's behavioral responses (i.e., perceptual judgments) during fMRI were made with a key press on an MR compatible button response device. Participants were instructed to fixate on a small central target between trials.

4.3. Equating visual detection based on individuals' perceptual sensitivities

Prior to the MRI experiment, off-line testing determined each participant's perceptual threshold for face detection and tree detection, defined as the minimal contrast level under which visual detection performance reached an 80% correct minimum. To obtain perceptual thresholds, performance accuracy (% correct) to faces and trees was assessed at varying contrast levels of 0, 1, 2, 4, and 16% contrast. The accuracy data for each subject were fit to a psychometric function, from which a threshold is derived (Chen, Grossman et al., 2008; Chen et al., 2009).

Low values of perceptual threshold indicate the better sensitivity to detect faces/trees (i.e., requiring lower levels of contrast). Stimuli used for the fMRI study were faces and trees at four contrast levels: 0%, perceptual threshold, two times perceptual threshold, and 100% contrast (Figure 6). In the perceptual threshold condition (Th), the contrast of the images was set at each individual participant's offline perceptual threshold. In the two times perceptual threshold condition (Th2), the contrast of the images was set at twice each individual participant's off-line perceptual thresholds. In the 100% contrast conditions, an identical stimulus contrast (100%) was used for all participants.

4.4. MRI Acquisition

All MRI data were acquired on a 3.0 Tesla Siemens TIM Trio scanner (Siemens AG, Erlangen, Germany) with a 32-channel head coil, at the McLean Imaging Center (Belmont, MA). High-resolution structural images were acquired for registration of subjects' imaging data to a standard space (TR = 2.1 s, TE 3.3 ms, slices = 128, matrix = 256×256 , flip angle 7° , resolution = 1.0 mm×1.0 mm×1.33 mm). Structural imaging data were read and interpreted by a clinical neuroradiologist to ensure that participants were free of neurological abnormalities.

All fMRI data were acquired using a state-of-the-art multiband imaging technique to achieve high temporal resolution while maintaining adequate spatial resolution. This multiband technique provided better sampling of the event-related responses acquired. In each functional run, 32 3.5 mm axial slices were collected with TR/TE = 400 ms/30 ms, flip angle

 30° , matrix = 64×64 on a 220 mm×220 mm FOV, in plane resolution = 3.44 mm × 3.44 mm, multiband factor = 8 (Feinberg et al., 2010; Tong & Frederick, 2014).

4.5. MRI Data Pre-processing

FMRI data analysis was performed with FMRI Expert Analysis Tool (FEAT) version 5.0.6 (FMRIB's Software Library, http://www. FMRIb.ox.ac.uk/fsl) (Smith et al., 2004). Preprocessing of FMRI data consisted of motion correction (Smith et al., 2004), spatial smoothing with a Gaussian kernel of full-width-at-half-maximum 5.0 mm, and high-pass temporal filtering (high-pass filter cutoff: 100 sec). Non-brain tissue was removed from T1-weighted structural images using BET (Smith, 2002) and each subjects' functional scans were subsequently registered to the structural images using FLIRT (Jenkinson & Smith, 2001; Jenkinson et al., 2002). The structural images were registered to the MNI standard space using FNIRT (Smith et al., 2004) and functional images were then registered to MNI standard space using these two transformations.

4.6. Statistical Analysis of fMRI Data

Standard general linear modeling (GLM) was performed at both a single subject level and at the group level. Functional imaging data were analyzed using a three-level hierarchical modeling strategy: standard first-level analysis for each individual run, the second level combined like-stimulus type runs (i.e., combined two runs for each of face and tree stimuli) in a fixed effects analysis, and third level analyses of variance (ANOVA) to combine second-level parameter estimates averaged over regions-of-interest (FFA, OFA, STS) across subjects. We also conducted a third-level whole brain exploratory analysis that used a GLM to combine subjects in a mixed effects (Flame 1) analysis.

First-level modeling was implemented using a massively univariate GLM with voxel-wise pre-processed BOLD timeseries as the dependent variable and regressors that modelled the event-related response as independent variables (impulse functions convolved with a standard hemodynamic response function). A gamma model (phase = 0; SD =3 sec; mean lag = 6 sec) of the hemodynamic response function (HRF) was used. First-level maps of the following contrasts were estimated for use in the second-level model: 100% vs. 0%, Th2 vs. 0% and Th vs. 0%. Second-level modeling was implemented using a GLM to average these signal changes across like-stimulus runs.

Primary hypotheses were tested by extracting mean percent signal change values for each region-of-interest (FFA, OFA and STS) from the resulting spatial maps of regression coefficients using Featquery in FSL during performance of the face detection and the tree detection tasks. MNI standard space coordinates for ROIs (depicted in Figure 2) were based on previous studies probing face-selective processing (Harris, Young, & Andrews, 2012). This approach, unlike using a localizer scan, takes advantage of the established coordinates for the ROIs. They were as follows: left FFA (x = -40, y = -59, z = -23); right FFA (x = -42, y = -51, z = -24); left OFA (x = -41, y = -84, z = -17); right OFA (x = 44, y = -78, z = -17); left STS (x = -55, y = -50, z = 3); right STS (x = -55, y = -50, z = 3). ROIs were constructed by placing a 10 mm sphere around these coordinates. Anatomically, the FFA

was bound to the occipital fusiform gyrus and the OFA to V4, based on the Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006).

For FFA and OFA, ANOVAs were performed on percent signal change with factors of stimulus Type (face vs. tree) by contrast Level by hemisphere. For this analysis, the average signal change for each ROI, for left and right hemispheres, was extracted from parameter estimate contrasts of the 0% level versus each of the other three levels by stimulus type (e.g., ANOVA contrast levels were: Th vs. 0%, Th2 vs. 0%, 100% vs. 0%).

4.7. BOLD Timecourse

The timecourse of the BOLD response for FFA and OFA by stimulus type and contrast level was extracted using Perl Event-related Average Time-course Extraction (www.jonaskaplan.com/peate/peate-tk.html). The time-courses for the Th, Th2 and 100% conditions were subtracted from those for the 0% condition for each stimulus type respectively.

ANOVAs were performed separately for each hemisphere of ROI and stimulus type. Each analysis had factors of contrast level (Th, Th2, 100%) by time-point (2 sec, 3 sec, 4 sec, 5 sec, 6 sec). These time-points represent the ascending phase of response to the respective tasks, which are considered as a reliable reflection of neural activity (Buckner, 1998). All results were reported at a significance level of p<0.05.

4.8. Correlations with BOLD Responses

Average BOLD signals by respective condition were correlated with off-line perceptual thresholds, and online performance accuracy recorded from each participant.

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References

- Avidan G, Harel M, Hendler T, Ben-Bashat D, Zohary E, Malach R. Contrast sensitivity in human visual areas and its relationship to object recognition. J Neurophysiol. 2002; 87(6):3102–3116. [PubMed: 12037211]
- Barton JJ, Cherkasova MV, Press DZ, Intriligator JM, O'Connor M. Developmental prosopagnosia: a study of three patients. Brain Cogn. 2003; 51(1):12–30. [PubMed: 12633587]
- Behrmann M, Avidan G. Congenital prosopagnosia: face-blind from birth. Trends Cogn Sci. 2005; 9(4):180–187. [PubMed: 15808500]
- Bodamer J. Die Posopagnosie. Arch Psychiatriatrie Z Neurol. 1947; 179:6–54.
- Boynton GM, Engel SA, Glover GH, Heeger DJ. Linear systems analysis of functional magnetic imaging in human V1. Journal of Neuroscience. 1996; 16:4207–4221. [PubMed: 8753882]
- Buckner RL. Event-related fMRI and the hemodynamic response. Hum Brain Mapp. 1998; 6(5-6): 373–377. [PubMed: 9788075]
- Cauchoix M, Barragan-Jason G, Serre T, Barbeau EJ. The neural dynamics of face detection in the wild revealed by MVPA. J Neurosci. 2014; 34(3):846–854. [PubMed: 24431443]
- Chen Y, Grossman ED, Bidwell LC, Yurgelun-Todd D, Gruber SA, Levy DL, et al. Differential activation patterns of occipital and prefrontal cortices during motion processing: evidence from

- normal and schizophrenic brains. Cogn Affect Behav Neurosci. 2008; 8(3):293–303. [PubMed: 18814466]
- Chen Y, Norton D, McBain R, Ongur D, Heckers S. Visual and cognitive processing of face information in schizophrenia: detection, discrimination and working memory. Schizophr Res. 2009; 107(1):92–98. [PubMed: 18947982]
- Chen Y, Norton D, Ongur D, Heckers S. Inefficient face detection in schizophrenia. Schizophr Bull. 2008; 34(2):367–374. [PubMed: 17631619]
- Dale AM, Fischl B, Sereno MI. Cortical surface-based analysis. I. Segmentation and surface reconstruction. Neuroimage. 1999; 9:179–194. [PubMed: 9931268]
- Desikan RS, Segonne F, Fischl B, Quinn BT, Dickerson BC, Blacker D, et al. An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. Neuroimage. 2006; 31(3):968–980. [PubMed: 16530430]
- Ellis, H. Theoretical aspects of face recognition. In: AW, Y., editor. Functions of the right hemisphere. Academic Press; London: 1981.
- Feinberg DA, Moeller S, Smith SM, Auerbach E, Ramanna S, Gunther M, et al. Multiplexed echo planar imaging for sub-second whole brain FMRI and fast diffusion imaging. PLoS One. 2010; 5(12):e15710. [PubMed: 21187930]
- Garrido L, Duchaine B, Nakayama K. Face detection in normal and prosopagnosic individuals. Journal of Neuropsychology. 2008; 2:119–140. [PubMed: 19334308]
- Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW. The fusiform "face area" is part of a network that processes faces at the individual level. J Cogn Neurosci. 2000; 12(3):495–504. [PubMed: 10931774]
- Grill-Spector K, Knouf N, Kanwisher N. The fusiform face area subserves face perception, not generic within-category identification. Nat Neurosci. 2004; 7(5):555–562. [PubMed: 15077112]
- Harris RJ, Young AW, Andrews TJ. Morphing between expressions dissociates continuous from categorical representations of facial expression in the human brain. Proc Natl Acad Sci U S A. 2012; 109(51):21164–21169. [PubMed: 23213218]
- Haxby JV, Hoffman EA, Gobbini MI. The distributed human neural system for face perception. Trends Cogn Sci. 2000; 4(6):223–233. [PubMed: 10827445]
- Haxby JV, Hoffman EA, Gobbini MI. Human neural systems for face recognition and social communication. Biol Psychiatry. 2002; 51(1):59–67. [PubMed: 11801231]
- Hoffman EA, Haxby JV. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat Neurosci. 2000; 3(1):80–84. [PubMed: 10607399]
- Ishai A. Let's face it: it's a cortical network. Neuroimage. 2008; 40(2):415-419. [PubMed: 18063389]
- Jiang F, Dricot L, Weber J, Righi G, Tarr MJ, Goebel R, et al. Face categorization in visual scenes may start in a higher order area of the right fusiform gyrus: evidence from dynamic visual stimulation in neuroimaging. J Neurophysiol. 2011; 106(5):2720–2736. [PubMed: 21734108]
- Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci. 1997; 17(11):4302–4311. [PubMed: 9151747]
- Kaplan E, Shapley RM. The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. Proceedings of the National Academy of Science of the United States of America. 1986; 83:2755–2757.
- Kelly DH. Motion and vision. II. Stabilized spatio-temporal threshold surface. Journal of the Optical Society of America. 1979; 69(10):1340–1349. [PubMed: 521853]
- Le Grand R, Cooper PA, Mondloch CJ, Lewis TL, Sagiv N, de Gelder B, et al. What aspects of face processing are impaired in developmental prosopagnosia? Brain Cogn. 2006; 61(2):139–158. [PubMed: 16466839]
- Lewis MB, Edmonds AJ. Face detection: mapping human performance. Perception. 2003; 32(8):903–920. [PubMed: 14580138]
- McBain R, Norton D, Chen Y. Females excel at basic face perception. Acta Psychol (Amst). 2009; 130(2):168–173. [PubMed: 19159861]
- Morris JP, Pelphrey KA, McCarthy G. Face processing without awareness in the right fusiform gyrus. Neuropsychologia. 2007; 45(13):3087–3091. [PubMed: 17643452]

Navon D. Forest before trees: the precedence of global features in visual perception. Cogn. Psychology. 1977; 9:353–383.

- Pitcher D, Dilks DD, Saxe RR, Triantafyllou C, Kanwisher N. Differential selectivity for dynamic versus static information in face-selective cortical regions. Neuroimage. 2011; 56(4):2356–2363. [PubMed: 21473921]
- Pitcher D, Walsh V, Duchaine B. The role of the occipital face area in the cortical face perception network. Exp Brain Res. 2011; 209(4):481–493. [PubMed: 21318346]
- Puce A, Allison T, Bentin S, Gore JC, McCarthy G. Temporal cortex activation in humans viewing eye and mouth movements. J Neurosci. 1998; 18(6):2188–2199. [PubMed: 9482803]
- Regan D. Low-contrast visual acuity test for pediatric use. Can J Ophthalmol. 1988; 23(5):224–227. [PubMed: 3179830]
- Rossion B, Hanseeuw B, Dricot L. Defining face perception areas in the human brain: a large-scale factorial fMRI face localizer analysis. Brain Cogn. 2012; 79(2):138–157. [PubMed: 22330606]
- Sclar G, Maunsell JHR, Lennie P. Coding of image contrast in central visual pathways of the macaque monkey. Vision Res. 1990; 30(1):1–10. [PubMed: 2321355]
- Smith SM, Jenkinson M, Woolrich MW, Beckmann CF, Behrens TE, Johansen-Berg H, et al. Advances in functional and structural MR image analysis and implementation as FSL. Neuroimage. 2004; 23(Suppl 1):S208–219. [PubMed: 15501092]
- Solomon JA, Pelli DG. The visual filter mediating letter identification. Nature. 1994; 369(6479):395–397. [PubMed: 8196766]
- Tong Y, Frederick BD. Studying the Spatial Distribution of Physiological Effects on BOLD Signals Using Ultrafast fMRI. Front Hum Neurosci. 2014; 8:196. [PubMed: 24744722]
- Tsao DY, Freiwald WA, Tootell RB, Livingstone MS. A cortical region consisting entirely of face-selective cells. Science. 2006; 311(5761):670–674. [PubMed: 16456083]
- Wilmer JB, Germine L, Chabris CF, Chatterjee G, Gerbasi M, Nakayama K. Capturing specific abilities as a window into human individuality: the example of face recognition. Cogn Neuropsychol. 2012; 29(5-6):360–392. [PubMed: 23428079]
- Winston JS, Henson RN, Fine-Goulden MR, Dolan RJ. fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. J Neurophysiol. 2004; 92(3):1830–1839. [PubMed: 15115795]
- Yue X, Cassidy BS, Devaney KJ, Holt DJ, Tootell RB. Lower-level stimulus features strongly influence responses in the fusiform face area. Cereb Cortex. 2011; 21(1):35–47. [PubMed: 20375074]

Highlights

- \bigcirc Two face processing areas, FFA and OFA, are highly sensitive during face detection.
- FFA and OFA are active even at individualized perceptual threshold levels.
- \bigcirc FFA activity can account for a portion of face detection performance.

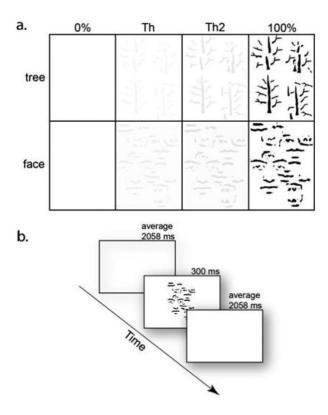


Figure 1.

Off-line perceptual thresholds (prior to MRI) and on-line performance (during MRI) for face detection and tree detection. (a) Individual perceptual thresholds are listed by task type. (b) Group average percent correct (y axis) is plotted as a function of stimulus contrast (x axis). Note that the average on-line performance level at the perceptual threshold was reduced, compared with that measured during off-line psychophysical testing. This may be due to the different visual environment within the MRI scanner. Error bars represent ±1 standard error.

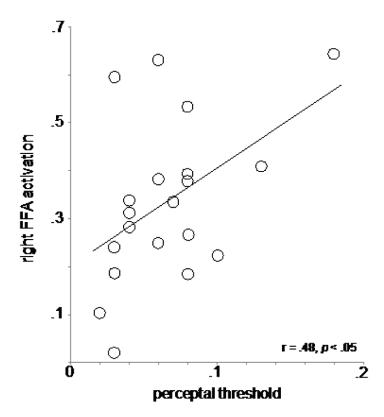


Figure 2. The BOLD signal changes (Z-maps) for face detection and tree detection in MNI space (x = 42, y = -50, z = -18). Each column of panel represents a stimulus contrast level (Th, Th2, and 100%). The three ROIs, FFA, OFA and STS, were shown in each row of panel. The differences in BOLD signal changes between the two tasks are displayed in the bottom panel (c).

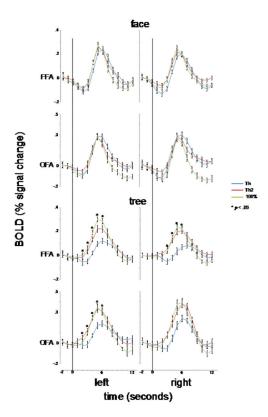


Figure 3. Means of BOLD signal changes for FFA, OFA and STS. The stimulus type (face and tree) and contrast level (Th, Th2, and 100%) are depicted on x axis. Error bars denote within-subject 95% confidence intervals (Cousineau, 2005; Morey, 2008). Significant differences by contrast level were found for tree detection but not for face detection.

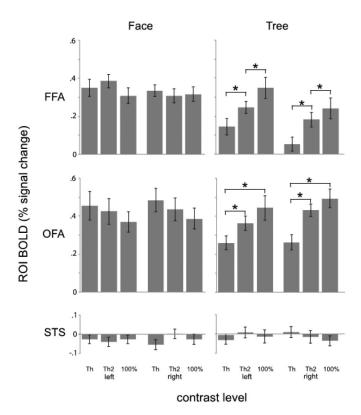


Figure 4.

Timecourse of BOLD response in FFA and OFA. No interaction between timepoint and contrast level was found for face detection whereas significant interactions were found for tree detection (right and left FFA, left OFA). Asterisks denote significant BOLD response differences at respective timepoints (based on pairwise follow-up tests comparing among the three contrast levels).

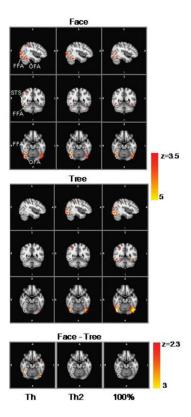
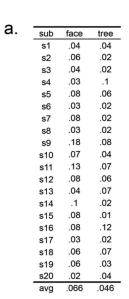


Figure 5.Scatter plot for correlation between BOLD response to the threshold level face images in right FFA and off-line perceptual thresholds for face detection. Each data point represents a subject.



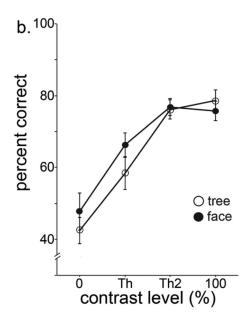


Figure 6. Illustration of face and tree stimuli and task procedure used in fMRI sessions. Top panels include face and tree images at 1) threshold level, 2) 2 times threshold level and 3) 100% level. The task for face and tree detection is to indicate on which side (left or right) of each panel a target image (intact face or tree) is displayed.

Table 1

Correlation coefficients between BOLD and perceptual performance

| | | | | behavior | | | |
|---------------|------|------|------|----------|------|-----|------|
| | | | | 41 | ACC | | |
| | | | | thresh | t | t*2 | 100 |
| BOLD response | face | | Th | .475 | 231 | | _ |
| | | rFFA | Th2 | .279 | | 135 | |
| | | | 100% | .27 | | | .008 |
| | | IFFA | Th | .353 | .134 | | |
| | | | Th2 | .344 | | 482 | |
| | | | 100% | .32 | | | 327 |
| | | rOFA | Th | .261 | 044 | | |
| | | | Th2 | .159 | | 399 | |
| | | | 100% | .309 | | | 145 |
| | | | Th | .43 | 062 | | _ |
| | | IOFA | Th2 | .316 | | 449 | |
| | | | 100% | .414 | | | 252 |
| | tree | | Th | .009 | .158 | | |
| | | rFFA | Th2 | .354 | | 093 | |
| | | | 100% | .176 | | | 402 |
| | | IFFA | Th | .135 | .205 | | |
| | | | Th2 | .251 | | 119 | |
| | | | 100% | .242 | | | 576 |
| | | rOFA | Th | .319 | 054 | | |
| | | | Th2 | .361 | | 123 | |
| | | | 100% | .299 | | | 338 |
| | | IOFA | Th | .11 | 001 | | _ |
| | | | Th2 | .164 | | 164 | |
| | | | 100% | .173 | | | 402 |

Listed in rows are responses of FFA and OFA to images at different contrast levels. Listed in column are offline perceptual threshold and online performance accuracy for images at different contrast levels. Significant correlations were highlighted.