Report

Processing of configural and componential information in face-selective cortical areas

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We investigated how face-selective cortical areas process configural and componential face information and how race of faces may influence these processes. Participants saw blurred (preserving configural information), scrambled (preserving componential information), and whole faces during fMRI scan, and performed a post-scan face recognition task using blurred or scrambled faces. The fusiform face area (FFA) showed stronger activation to blurred than to scrambled faces, and equivalent responses to blurred and whole faces. The occipital face area (OFA) showed stronger activation to whole than to blurred faces, which elicited similar responses to scrambled faces. Therefore, the FFA may be more tuned to process configural than componential information, whereas the OFA similarly participates in perception of both. Differences in recognizing own- and other-race blurred faces were correlated with differences in FFA activation to those faces, suggesting that configural processing within the FFA may underlie the other-race effect in face recognition.

\textbf{Keywords:} Face perception; FFA; OFA; Configural processing; Other-race effect.

Faces pose a challenge to the visual system in that they are highly similar and, for our social species, highly important for correct identification. The underlying neural substrates and the cognitive mechanisms involved in face perception seem to be specialized for this particular class of visual stimuli (Haxby, Hoffman, & Gobbini, 2000; Maurer, Le Grand, & Mondloch, 2002). In the brain, face perception activates a network of brain areas that preferentially respond to faces rather than to other objects, such as the fusiform face area (FFA, Kanwisher, McDermott, & Chun, 1997) and the occipital face area (OFA, Gauthier et al., 2000). At the behavioral level, compared to processing of non-face objects, face perception shows stronger reliance on configural information (i.e., information about the relative positions of facial components in a face; Maurer et al., 2002).

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Many studies have investigated the association between brain and behavior in face processing, however, the precise manner in which different face-selective areas contribute to processing of configural and componential information remains elusive. Some studies demonstrate that the FFA is more tuned to processing first-order configural information (i.e., the T-shape arrangements of face components) and the OFA is selectively tuned to analyze componential information (Liu, Harris, & Kanwisher, 2010; Pitcher, Walsh, & Duchaine, 2011), whereas others show that the FFA and the OFA are sensitive to both second-order configural information (i.e., spacing between face components) and componential information (Harris & Aguirre, 2008; Rhodes, Michie, Hughes, & Byatt, 2009). However, these studies often presented componential information in conjunction with first-order configural information and/or holistic face template (Harris & Aguirre, 2008; Liu et al., 2010; Maurer et al., 2007). It is therefore hard to tease apart brain activations for face components and those for accompanying first-order configural information or holistic face template (Betts & Wilson, 2010; James, Arcurio, & Gold, 2013; Liu et al., 2010).

Responses in face-selective areas are more prominent for faces with which people have extensive experiences (e.g., own-race faces) compared with faces of little contact (e.g., other-race faces). In comparison to other-race faces, own-race faces tend to elicit higher brain activity in the FFA (Golby, Gabrieli, Chiao, & Eberhardt, 2001; Natu, Raboy, & O’Toole, 2011), better performance in recognition (Meissner & Brigham, 2001), and stronger configural processing (Hayward, Rhodes, & Schwaninger, 2008; Tanaka, Kiefer, & Bukach, 2004). These neural and behavioral other-race effects (OREs) are correlated (Golby et al., 2001), suggesting that higher FFA activity to own-race faces might underpin superior recognition performance for these faces. Nonetheless, as all these studies tested intact faces, it remains unclear whether the association between the neural and behavioral OREs is based on configural or componential information, or both.

We investigated whether face-selective areas are more sensitive to one type of information than another (configural vs. componential), and how race of face may influence configural and componential processing in the brain. We used blurred/scrambled faces to dissociate configural and componential information (Hayward et al., 2008; Lobmaier, Klaver, Loenneker, Martin, & Mast, 2008). Scrambled faces contained key face components such as eyes, eyebrows, nose, and mouth, and were rearranged to remove configural information embedded in normal upright faces. Blurred faces were used to preserve configural information. They preserve low spatial frequency information supporting configural processing while removing much of the high spatial frequency information supporting componential processing (Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux et al., 2011; Lobmaier et al., 2008). Moreover, we blurred faces to the extent that the residual componential information leads to chance-level face recognition (Hayward et al., 2008), therefore removing componential information that can be used to effectively identify a face.

We measured fMRI activations in the FFA and the OFA to blurred, scrambled, and whole faces of Chinese and Caucasian people. Unlike prior studies that focus on configural and componential processing in identity processing (Golby et al., 2001; Lobmaier et al., 2008), we investigated how face-selective brain areas respond automatically to configural and componential information in own- and other-race faces. To minimize possible attention bias to configural information in face identity processing, we had participants perform a location-repetition detection task during scanning (Figure 1b). To examine whether differences in neural responses to own- and other-race facial information are associated with behavioral differences in recognition of these faces, we employed a post-scan face recognition task to test participants’ performance on recognizing blurred and scrambled faces.

METHODS

Participants

Twelve Chinese students participated in the experiment (six females; age 22–31, mean age, 23.7). All had lived most of their lives in Hong Kong or Mainland China. One participant failed to follow the instructions and was excluded from data analysis. The procedure was approved by IRB of the University of Hong Kong, and a signed consent form was obtained from each participant before the experiment.

fMRI acquisition

MR scanning was performed on a Philips™ Achieva 3.0T system. Functional images were obtained using a T2*-weighted single-shot gradient echo-planar imaging (EPI) sequence (TR: 2000 ms, TE: 24 ms, 90° flip angle, FOV: 230 mm × 230 mm, voxel size: 1.8 × 1.8 × 2 mm³). Each volume contained 35 oblique axial slices (parallel to the temporal cortex) covering the occipitotemporal regions (thickness 2 mm, no gap, interleaved order). A high-resolution T1-weighted
MPRAGE 3D MRI sequence was obtained from each participant (FOV = 240 mm × 256 mm; 1 mm³ isotropic voxels, FA = 8°; TR = 7 ms; TE = 3.1 ms; 156 continuous sagittal slices). Participants viewed the display through a head-coil-mounted mirror.

fMRI experiment

Each participant had six experiment scans, two localizer scans, and one anatomical structure scan in a single session.

Experiment scan

Whole, blurred, and scrambled face stimuli were created based on photographs of 72 (36 female) Chinese and 72 (36 female) Caucasian faces (Figure 1a). Whole faces were converted into 8-bit grayscale (subtended 6.5° × 8°) images. Blurred faces were created by applying a Gaussian filter (radius: 3 pixels; SD = 3 pixels) four times to whole faces, resulting in the removal of spatial frequencies above 3.5 cycles/degree at a viewing distance of 45 cm. Hayward et al. (2008) showed that face recognition based on independent components of these blurred faces (i.e., scrambled blurred faces) was at chance-level, suggesting that identity-discriminative componential information was disrupted. Scrambled faces consisted of six face components (two eyes, two eyebrows, nose, and mouth) that were arranged into a non-facelike configuration. Faces were placed at one of the four corner locations within a 10° × 10° square frame (Figure 1b).

Each experiment scan had 12 blocks of trials (3 face types × 2 races × 2 examples), each followed by 10-s fixation. In each trial, six faces were displayed for 1 s each, with an inter-stimulus interval (ISI) of 400 ms (Figure 1b). The race and types of faces were blocked, and the order of blocks was counterbalanced across scans. Participants pressed a button whenever they saw two successive faces displayed in the same corner location of the square frame (10% of trials).

Localizer scan

Stimuli consisted of images of 36 Chinese faces (18 female, all different from those used in experiment scan,) and 36 everyday objects (e.g., chair, car, etc.). All images were grayscale and subtended 10° × 10° visual angle. Each localizer scan had 11 alternate blocks of face and object trials, each followed by 10-s fixation. In each trial, 10 faces or 10 objects were displayed sequentially for 750 ms each, with an ISI of 250 ms. Participants pressed a button whenever they saw two identical stimuli displayed successively (10% of trials).

fMRI analysis

Data were preprocessed and analyzed using the BrainVoyager QX (Version 1.9, Brain Innovation, Maastricht, The Netherlands). Preprocessing of functional images included 3D motion correction, slice scan time correction (using sine interpolation), high-pass temporal filtering (3 cycles/scan), and spatial smoothing (with a Gaussian kernel of 6-mm FWHM). General linear model (GLM) analysis was then applied to preprocessed data. Six predictors (3 face types × 2 races) were created for the GLM,
and were convolved with canonical hemodynamic response function. Both structural and functional images were transformed to the standard Talairach space and were aligned.

Face-selective regions of interest (ROIs) were defined individually with the ‘face>object’ contrast using a lax threshold of \( t = 2 \). A similar liberal threshold was frequently used in prior studies to localize face-selective ROIs (e.g., Gauthier et al., 2000; Golby et al., 2001; Maurer et al., 2007; Rhodes et al., 2009). An object-selective area within the posterior fusiform gyrus (pFG) was also identified with the ‘objects>faces’ contrast, serving as a control area.

### Post-scan face recognition task

Participants performed four blocks of a face recognition task, resulting from a combination of face race (Chinese vs. Caucasian) and face types (blurred vs. scrambled). In each block, participants learned 10 normal upright faces twice (each displayed for 10 s), and were tested immediately with an old-new recognition task for 20 faces (10 old/10 new). Block order was counterbalanced across participants. Whole, blurred, and scrambled faces were created similarly to those in the fMRI experiment except that scrambled faces also included cheeks, chin, and forehead parts. Thus, all componential information presented during learning was also available at recognition.

### RESULTS

#### Behavioral results

**In-scan location-repetition detection task**

Mean accuracies (+ SE) for blurred, scrambled, and whole faces were 89 ± 6%, 94 ± 4%, and 88 ± 7% for Chinese faces, and 90 ± 6%, 97 ± 2%, and 95 ± 4% for Caucasian faces. A repeated-measures ANOVA revealed neither significant main effect nor significant interaction (\( F_s < 2.97, \eta > .05 \)). So there was no difference in task difficulty across face races and face types.

**Post-scan face recognition task**

Table 1 summarizes mean response sensitivity (\( d' \)) and response bias (\( C \)). Blurred faces showed better recognition than scrambled faces (\( F_{1, 10} = 25.72, \eta < .001 \)). Neither the race effect nor its interaction with face-type was significant (\( F_s < 1 \)), though own-race faces produced numerically better performance than other-race faces. This result is probably due to our small sample of participants, as a significant ORE was shown using identical procedures with a larger number of participants (Hayward et al., 2008). Participants showed equivalent response biases between races and across face-types (both \( F < 1 \)). However, they tended to be more conservative in recognizing own- than other-race blurred faces, but not in recognizing scrambled faces (race by face-type interaction, \( F_{1, 10} = 3.36, \eta = .1 \)).

#### fMRI results

As in prior studies (Pitcher et al., 2011; Rhodes et al., 2009), we identified the FFA in all 11 participants but only identified the OFA in seven participants (Table 2, Figure 2a). A hemisphere × race × face type ANOVA revealed no significant interaction involving hemisphere for the FFA (\( F_s < 1.34, \eta > .27 \)), the OFA (\( F_s < 0.61, \eta > .55 \)), or the object-selective pFG (\( F_s < 1.30, \eta > .28 \)). These results are consistent with Liu et al. (2010), which also used a task that required no face processing. Left and right ROIs were combined and BOLD signal change were then extracted and submitted to a face race × face type repeated-measures ANOVA.

Responses of FFA were consistent with the hypothesis that the FFA is preferentially engaged in configural processing (Figure 2b). The main effect of face type was significant (\( F_{2, 20} = 18.54, \eta < .0001 \)), whereas the main effect of face race and its interaction with face type were not (all \( F_s < 0.17, \eta > .84 \)). The FFA showed significantly lower activity to scrambled faces than blurred faces (\( t_{10} = 5.54, \eta = .0001 \)).

### Table 1

| Race          | Condition  | \( d' \) | SE | \( C \) | M | SE |
|---------------|------------|---------|----|--------|---|----|
| Chinese faces | Blurred    | 1.64    | 0.24 | 0.18   | 0.10 |     |
|               | Scrambled  | 0.81    | 0.24 | 0.21   | 0.11 |     |
| Caucasian faces | Blurred  | 1.55    | 0.26 | 0.06   | 0.08 |     |
|                | Scrambled | 0.61    | 0.14 | 0.18   | 0.13 |     |

Table 2

| ROIs | N  | Voxel Coordinates |
|------|----|-------------------|
| RFFA | 10 | 1061 ± 673        |
|      |    | x = 43 ± 5        |
|      |    | y = −44 ± 7       |
|      |    | z = −19 ± 3       |
| LFFA | 6  | 814 ± 601         |
|      |    | x = −42 ± 5       |
|      |    | y = −47 ± 8       |
|      |    | z = −18 ± 4       |
| ROFA | 6  | 740 ± 1039        |
|      |    | x = 34 ± 5        |
|      |    | y = −73 ± 7       |
|      |    | z = −12 ± 5       |
| LOFA | 6  | 581 ± 415         |
|      |    | x = −37 ± 6       |
|      |    | y = −77 ± 7       |
|      |    | z = −11 ± 2       |

Notes: data are shown as \( M ± SD \); voxel size = 1.8 × 1.8 × 2 mm³.
p = .0002) and whole faces (t_{10} = 7.23, p < .0001), and responded similarly to blurred and whole faces (t_{10} = 1.69, p = .12). Therefore, the FFA was more tuned to process configural information in a face. Whole faces, which had both component and configural information, did not produce significantly higher brain activity than blurred faces, suggesting that the FFA is insensitive to the disruption of componential information.

The OFA responded similarly to blurred, scrambled, and whole faces (Figure 2c). The main effects of face type (F_{2, 12} = 2.51, p = .12) and face race (F_{1, 6} = 0.19, p = .68), and their interaction (F_{2, 12} = 0.68, p = .53) were not significant. Planned contrasts showed that blurred and scrambled faces produced similar OFA activity (t_6 = 0.67, p = .53), and whole faces showed relatively higher activation than either blurred faces (t_6 = 2.57, p = .04) or scrambled faces (t_6 = 1.90, p = .11). Thus, the OFA showed no clear differential sensitivity to configural versus componentual information, consistent with the hypothesis that the OFA is similarly involved in processing of configural and componential information.

To statistically test whether the FFA and the OFA responded differently to different types of faces, we performed an ROIs (FFA vs. OFA) × race (Chinese vs. Caucasian) × face types (blurred vs. scrambled vs. whole faces) repeated-measures ANOVA. We found a main effect of face type (F_{2, 12} = 8.66, p = .005), and more importantly, a significant interaction between face type and ROI (F_{2, 12} = 4.53, p = .03), indicating that the FFA and the OFA showed qualitatively different patterns of response to blurred, scrambled, and whole faces.

Object-selective area in the pFG (Figure 2d) showed different patterns of response from that of face-selective areas (Figure 2e). The main effect of face type was significant (F_{2, 20} = 72.45, p < .0001), whereas the main effect of face race and its interaction with face type were not (F_s < 0.10, p_s > .90). Scrambled faces produced higher neural responses than blurred faces (t_{10} = 11.17, p < .0001) and whole faces (t_{10} = 5.16, p = .0004), whereas whole faces showed higher neural activity than blurred faces (t_{10} = 6.00, p = .0001). Higher activation to scrambled faces in the pFG suggests that perception of independent face components involves neural resources supporting general object processing.

Correlations between behavioral and neural OREs

To investigate whether recognition of own- and other-race blurred and scrambled faces is associated with the neural responses to these faces, we correlated the
neural ORE (BOLD signal change: Chinese–Caucasian) with the behavioral ORE (d’: Chinese–Caucasian). As illustrated in Figure 3, the correlation between neural and behavioral OREs for blurred faces was significant in the FFA (r_{11} = .66, p = .03, 95% confidence interval (CI) estimated using bootstrap procedure with 1000 iterations, [0.08, 0.93]), but not in the OFA (r_{7} = −.002, p = .997, CI = [−0.66, 0.99]), suggesting that FFA responses might underlie the ORE in configural processing. Behavioral and neural OREs for scrambled faces were negatively correlated in both the FFA (r_{11} = −.66, p = .03, CI = [−0.84, −0.08]) and the OFA (r_{6} = −.75, p = .05, CI = [−0.93, 0.36]), implying an interference between component-based processing and holistic face recognition ability (particularly in the FFA).

**DISCUSSION**

We investigated whether face-selective cortical areas respond differently to configural and componential information, and whether race of face modulates neural responses to these types of face information. The FFA seems to be more tuned to process configural than component face information. It responded more strongly to configural (blurred faces) than component (scrambled faces) information, and degrading componential information did not reduce FFA responses (i.e., blurred vs. whole faces). By contrast, the OFA showed similar responses to configural and componential information. Moreover, whole faces tended to elicit higher brain activity than configural or componential information alone, again suggesting that the OFA processes both types of information. Finally, an individual difference analysis revealed a strong positive association between neural (FFA) and behavioral OREs in configural processing, although the overall neural response was similar to Caucasian and Chinese faces.

Neural responses in the FFA fit well with earlier studies showing greater FFA responses to whole faces than to isolated face components, and equivalent responses to blurred and whole faces (McCarthy, Puce, Belger, & Allison, 1999). These results are consistent with the hypothesis that the FFA functions as an important neural locus of configural processing (Liu et al., 2010; Schiltz & Rossion, 2006), though it is not the only area underlying this special process (Rhodes et al., 2009). The FFA has been shown to be sensitive to both first-order (Liu et al., 2010; Yovel & Kanwisher, 2005) and second-order configural information (Rhodes et al., 2009) and holistic face template (Betts & Wilson, 2010; James et al., 2013). Our results cannot discern which aspect of configural information the FFA is sensitive to, because they were all disrupted in scrambled faces and preserved in blurred faces. Nevertheless, the similar FFA responses to whole and blurred faces suggest that it is sensitive to configural information embedded in low spatial frequency bands (Goffaux et al., 2005).

Recent studies show that the OFA is involved in processing of componential and second-order configural information (Harris & Aguirre, 2008; Rhodes et al., 2009; Rotshtein, Geng, Driver, & Dolan, 2007). Our results concur with this view. The higher OFA response to whole than blurred faces also echoes the idea that the OFA responds more robustly to high than low spatial frequency facial information (Goffaux et al., 2011). Moreover, Rhodes et al. (2009) showed that even identical face components elicited different OFA responses when their spacing was changed (see also Harris & Aguirre, 2008), indicating that the OFA is not merely sensitive to componential information. These results make it very unlikely that the similar OFA responses to blurred and scrambled faces seen here were due to...
the presence of componential information in both. The OFA may bear the function of face detection, given its earlier locus within the hierarchical face perception network (Fairhall & Ishai, 2007; Haxby et al., 2000). If this is correct, then our results suggest that face detection within the OFA is based on both componential and configurational information.

Unlike Golby et al. (2001), we observed no ORE in the overall brain activity level in face-selective areas (see also Natu et al., 2011). A possible reason for this discrepancy is that neural OREs maybe require some explicit face processing task (e.g., identification). Our location-monitoring task might attenuate the ORE on FFA responses, because information about the faces is task-irrelevant. Alternatively, the effect of race on neural face processing may be relatively weak, and our ROI analysis might not have enough power to detect such an effect.

Nevertheless, the effect of face race still manifested in terms of individual differences. Behavioral and neural OREs in the FFA for blurred faces were significantly correlated. We found no such correlation in the OFA, indicating that the ORE in face recognition may arise from stronger FFA activation to configurational information in own- than other-race faces. In contrast, the correlations between behavioral and neural OREs for scrambled faces were negative. Rotshtein et al. (2007) observed a similar negative correlation between neural and behavioral responses when discriminating faces based on componential information. These results suggest that stronger analytic processing of own-race face components in the face-selective areas might interfere with face recognition, which relies on holistic processing.

In conclusion, face-selective areas responded differently to normal faces and two constituent elements: Configural and componential information. The FFA was more tuned to configural than component face processing, whereas the OFA responded similarly to both types of face information. Therefore, configurational processing in face perception lies within both the fusiform and occipital face-selective cortical areas. However, better recognition of own-race than other-race faces was linked to configurational processing in the FFA only, with a strong positive correlation between behavioral and the neural OREs for blurred faces in the FFA, but not the OFA.

REFERENCES

Bets, L. R., & Wilson, H. R. (2010). Heterogeneous structure in face-selective human occipito-temporal Cortex. Journal of Cognitive Neuroscience, 22, 2276–2288.

Fairhall, S. L., & Ishai, A. (2007). Effective connectivity within the distributed cortical network for face perception. Cerebral Cortex, 17, 2400–2406. doi:10.1093/cercor/bhl148

Gauthier, I., Tarr, M. J., Moayan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusim “face area” is part of a network that processes faces at the individual level. Journal of Cognitive Neuroscience, 12, 495–504. doi:10.1162/089892900562165

Goffaux, V., Hault, B., Michel, C. Vuong, Q. C., & Rossion, B. (2005). The respective role of low and high spatial frequencies in supporting configural and featural processing of faces. Perception, 34, 77–86. doi:10.1068/p5370

Goffaux, V., Peters, J., Haxby, J., Schiltz, C., Jansma, B., & Goebel, R. (2011). From coarse to fine? Spatial and temporal dynamics of cortical face processing. Cerebral Cortex, 21, 467–476. doi:10.1093/cercor/bhq112

Golby, A. J., Gabrieli, J. D. E., Chiao, J. Y., & Eberhardt, J. L. (2001). Differential responses in the fusiform region to same-race and other-race faces. Nature Neuroscience, 4, 845–850. doi:10.1038/90565

Harris, A., & Aguirre, G. K. (2008). The representation of parts and wholes in face-selective cortex. Journal of Cognitive Neuroscience, 20, 863–878. doi:10.1162/jocn.2008.20509

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. doi:10.1016/S1364-6613(00)01482-0

Hayward, W. G., Rhodes, G., & Schwaninger, A. (2008). An own-race advantage for components as well as configurations in face recognition. Cognition, 106, 1017–1027. doi:10.1016/j.cognition.2007.04.002

James, T. W., Arcurio, L. R., & Gold, J. M. (2013). Inversion effects in face-selective cortex with combinations of face parts. Journal of Cognitive Neuroscience, 25, 455–464. doi:10.1162/jocn_a_00312

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.

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

Lobmaier, J. S., Klaver, P., Loenneker, T., Martin, E., & Mast, F. W. (2008). Featural and configurual face processing strategies: Evidence from a functional magnetic resonance imaging study. NeuroReport, 19, 287–291. doi:10.1097/0b013e3282f5f6f6

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configurual processing. Trends in Cognitive Sciences, 6, 255–260. doi:10.1016/S1364-6613(02)01903-4

Maurer, D., O’Craven, K. M., Le Grand, R., Mondloch, C. J., Springer, M. V., Lewis, T. L., & Grady, C. L. (2007). Neural correlates of processing facial identity based on features versus their spacing. Neuropsychologia, 45, 1438–1451. doi:10.1016/j.neuropsychologia.2006.11.016

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McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex, 9*, 431–444. doi:10.1093/cercor/9.5.431

Meissner, C. A., & Brigham, J. C. (2001). Thirty years of investigating the own-race bias in memory for faces: A meta-analytic review. *Psychology, Public Policy, and Law, 7*, 3–35. doi:10.1037/1076-8971.7.1.3

Natu, V., Raboy, D., & O’Toole, A. J. (2011). Neural correlates of own- and other-race face perception: Spatial and temporal response differences. *NeuroImage, 54*, 2547–2555. doi:10.1016/j.neuroimage.2010.10.006

Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research, 209*, 481–493. doi:10.1007/s00221-011-2579-1

Rhodes, G., Michie, P. T., Hughes, M. E., & Byatt, G. (2009). The fusiform face area and occipital face area show sensitivity to spatial relations in faces. *European Journal of Neuroscience, 30*, 721–733. doi:10.1111/j.1460-9568.2009.06861.x

Rotshtein, P., Geng, J. J., Driver, J., & Dolan, R. J. (2007). Role of features and second-order spatial relations in face discrimination, face recognition, and individual face skills: Behavioral and functional magnetic resonance imaging data. *Journal of Cognitive Neuroscience, 19*, 1435–1452.

Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage, 32*, 1385–1394. doi:10.1016/j.neuroimage.2006.05.037

Tanaka, J. W., Kiefer, M., & Bukach, C. M. (2004). A holistic account of the own-race effect in face recognition: Evidence from a cross-cultural study. *Cognition, 93*, B1–B9. doi:10.1016/j.cognition.2003.09.011

Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology, 15*, 2256–2262. doi:10.1016/j.cub.2005.10.072