Selectivity for low-level features of objects in the human ventral stream

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ABSTRACT

Category selective regions in the ventral visual stream are considered to support higher-level representations of objects. The aim of this study was to determine the extent to which category selectivity in face and place regions can be explained by selectivity for low-level features of these complex objects. First, we compared the relative responses to intact and Fourier-scrambled images of faces and places. Next, we compared the magnitude of fMR adaptation to both intact and scrambled faces and places. The results revealed that global differences in the amplitude spectrum of face and place images can explain a small proportion of the category selectivity that is found in regions such as the fusiform face area (FFA) and parahippocampal place area (PPA). However, a whole-brain analysis revealed selectivity to scrambled images in more posterior regions of the ventral stream. Consistent with the pattern evident for intact images, more lateral regions responded selectively to scrambled faces, whereas more medial regions responded more strongly to scrambled places. These findings suggest that selectivity for object categories emerges from the differential processing of low-level features that are typical of different object categories in early visual areas.

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Introduction

Visual areas involved in object recognition form a ventral processing stream that projects toward the temporal lobe (Ungerleider and Mishkin, 1982; Milner and Goodale, 1995). Lesions to this region of the brain often result in difficulties in recognizing, identifying, and naming different categories of objects (Habib and Sirigu, 1987; McNeil and Warrington, 1993; Moscovitch et al., 1997). Evidence from neuroimaging supports the concept that distinct areas of the human temporal lobe are specialized for certain categories of objects. The fusiform face area (FFA) is typically defined by a higher response to faces compared to a variety of non-face objects (Kanwisher et al., 1997; Allison et al., 1999), whereas the para-hippocampal place area (PPA) responds more to images of buildings and scenes than to faces and other objects (Epstein and Kanwisher, 1998). Similar category specific visual responses have been found for inanimate objects (Malach et al., 1995), human body parts (Downing et al., 2001), and letter strings (Allison et al., 1999).

While these data clearly indicate regional specialization for object categories within the ventral temporal lobe, single neuron studies in non-human primates suggest that these regions need not be discrete or uniquely sensitive to the high-level cues that define category membership. For example, although many neurons in the temporal lobe have response properties that are important for object recognition, such as selectivity for form, texture, or colour, they do not appear to respond to particular classes of object (Desimone et al., 1984; Tanaka, 1996). This suggests that object perception is based on the distributed response from neurons coding different aspects of an object. One apparent exception to this view is the neural response to faces. A number of studies have found clusters of neurons in the temporal lobe that are highly selective for faces (Gross et al., 1972; Hasselmo et al., 1989; Perrett et al., 1992; Tsao et al., 2006).

The aim of this study was to use fMRI to determine whether the responses of category-selective regions in the ventral visual stream can be explained by higher-level object representations or by selectivity for the distinct patterns of low-level spectral features that are typical of particular categories of object (Torralba and Oliva, 2003). To address this question, we compared the response to Fourier-scrambled and intact images of faces and houses in the FFA and PPA. Previous studies have found that, in category-selective regions, responses to intact versions of an object are significantly greater than the response to scrambled images of the same object (Malach et al., 1995; Kanwisher et al., 1997; Epstein and Kanwisher, 1998). However, responses to scrambled images from different categories have not been explicitly compared. Our prediction was that, if these areas are sensitive to low-level spectral features, a category-selective response would also be apparent with scrambled versions of the stimulus which preserve the key spectral characteristics. On the other hand, if these regions contained a higher-level representation of objects, then there would be no selectivity for the scrambled images in which their distinctive shapes and edges are removed. We also asked whether these regions would show fMR adaptation to repeated images of scrambled images. Although previous studies have reported adaptation to faces and houses in the FFA and PPA, respectively (Grill-Spector et al., 1999;

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Avidan et al., 2002; Epstein et al., 2003; Andrews and Ewbank, 2004; Ewbank et al., 2005), the extent to which this adaptation could be explained by the response to the low-level features of the image has not been explicitly tested.

Methods

Subjects

Ten subjects took part in the fMRI study (7 females; mean age, 27.7 years). All observers were right-handed and had normal or corrected-to-normal vision. Written consent was obtained for all subjects and the study was approved by the York Neuroimaging Centre Ethics Committee. Visual stimuli (approx. 8° × 8°) were back-projected onto a screen located inside the bore of the scanner at an apparent distance of approximately 57 cm when viewed through a mirror immediately in front of the subjects' eyes.

Imaging Parameters

All experiments were carried out using a GE 3 T HD Excite MRI scanner at the York Neuroimaging centre (YNiC) at the University of York. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage, radiofrequency coil tuned to 127.4 MHz. A gradient-echo EPI sequence was used to collect data from 38 contiguous axial slices (TR = 3 s, TE = 25 ms, FOV = 28 × 28 cm, matrix size = 128 × 128, slice thickness = 3 mm).

Stimuli

Face images were taken from the Psychological Image Collection at Stirling (PICS; http://www.pics.psych.stir.ac.uk) and from a variety of Internet sources. Only faces with a frontal pose and neutral expression were used. Body images were taken from a body image collection at Bangor (http://www.bangor.ac.uk/~pss811/), and place images were from the Caltech house collection (www.vision.caltech.edu/archive.html). Images of other categories were taken from a variety of Web-based sources. Images were presented in grey scale and were adjusted to a constant average brightness level. Fourier-scrambled images were created by randomising the phase of each two-dimensional frequency component in the original image, while keeping the power of the components constant (Suppl. Fig. 1).

fMRI procedure

To identify face-selective and place-selective regions, a localizer scan was carried out for each subject. Subjects viewed 20 blocks of 10 images. Each block contained images taken from one of five different categories: faces, bodies, objects, places, or Fourier-scrambled images derived from the corresponding categories. Each image was presented for 700 ms followed by a 200 ms fixation cross. Stimulus blocks were interleaved with a fixation cross superimposed on a grey screen. The interval between blocks was 9 s. Each condition was repeated four times and arranged in a counterbalanced block design.

The main experimental scan used two techniques (category selectivity and fMR adaptation) to determine whether the selectivity of response in the face- and place-selective regions could be explained by the responses to low-level features of objects. There were 8 conditions: (1) face (same, intact), (2) face (different, intact), (3) face (same, scrambled), (4) face (different, scrambled), (5) place (same, intact), (6) place (different, intact), (7) place (same, scrambled), and (8) place (different, scrambled). Stimuli from each condition were presented in blocks. Each stimulus block consisted of 10 images, which were shown for 700 ms followed by a 200 ms fixation cross. In the same conditions, the same image was repeated, whereas in the different conditions, different images were presented.

Stimulus blocks were separated by a 9 s fixation grey screen. Each condition was repeated six times giving a total of 48 blocks. To maintain attention across stimulus conditions, a red dot was super-imposed on one or two images in each block. The location of the red dot could appear in any location within 5° of the centre of the screen. Subjects were required to respond with a button press as soon as they saw the image containing the target.

fMRI analysis

Statistical analysis of the fMRI data was carried out using FEAT (http://www.fmrib.ox.ac.uk/fsl). The initial 9 s of data from each scan was removed to minimize the effects of magnetic saturation. Motion correction (McFlirt, FSL) was followed by spatial smoothing (Gaussian, FWHM 6 mm) and temporal high-pass filtering (cutoff, 0.01 Hz). Functionally-defined regions of interest (ROIs) were determined in the localizer scan by identifying voxels in each individual's ventral temporal cortex where the contrast between face and place conditions indicated a greater response to faces or places when thresholded at $Z > 4$.

In the main experimental scan, the time series of the filtered MR data at each voxel was converted from units of image intensity to percentage signal change by subtracting and then normalizing the mean response of each scan ($[x - \text{mean}] / \text{mean} \times 100$). All voxels from the ROI defined in the localizer scan were averaged to give a single time series in each ROI for each subject. The onset of the response from individual stimulus blocks was then normalized by subtracting every time point by the response at the onset of the stimulus block. The resulting data were then averaged to obtain the mean time course for each stimulus condition on a scan. The peak response calculated as an average of the response at 9 and 12 s after the onset of a block. The peak responses from the face- and place-selective regions in each subject were entered into a $2 \times 2 \times 2$ repeated-measures ANOVA to determine significant differences in the response to each stimulus condition. The main factors in the ANOVA were category (face, place), identity (same, different), and image scrambling (intact, scrambled). Category selectivity was determined by the contrast between face and place images. fMR adaptation was determined by contrasting the response to the same and different conditions.

Finally, to determine whether there were adaptation effects occurring outside the regions of interest, the individual subject data were entered into a higher-level group analysis using a mixed-effects design (FLAME, http://www.fmrib.ox.ac.uk/fsl). First, the functional data were transformed onto a high-resolution T1-anatomical image before being coregistered onto the standard brain MNI brain (ICBM152). We then compared the relative response to different conditions in the experimental scan to determine whether there was selectivity to scrambled images of face and places in other regions of the visual cortex.

Results

Localizer scan

Table 1 and Suppl. Fig. 2 show the average location of face- (FFA, OFA, STS) and place-selective (PPA) regions across subjects. Fig. 1 and Suppl. Fig. 3 show the average time courses of activation to faces, places, objects, and bodies in each ROI. Each region was defined separately for each individual, and all further analyses were performed on the peak responses in these regions.

Category selectivity

To determine category selectivity, the relative response to images of faces and places was compared. There was no difference in the

Table 1

MNI coordinates for face-selective (FFA, OFA, STS) and place-selective regions of interest.

	x	y	z	Size (cm³)
FFA	−40 (0.8)	−61 (2.2)	−21 (1.1)	0.8 (0.2)
	40 (1.1)	−60 (2.1)	−20 (1.1)	1.6 (0.3)
PPA	−25 (1.2)	−71 (1.9)	−15 (1.0)	4.8 (0.4)
	25 (1.4)	−70 (1.7)	−12 (1.1)	5.3 (0.5)
OFA	−39 (2.5)	−89 (3.0)	−11 (2.1)	1.9 (0.6)
	47 (3.0)	−74 (2.3)	−9 (1.7)	2.8 (0.5)
STS	50 (2.1)	−63 (2.4)	9 (1.0)	1.9 (0.4)

FFA: fusiform face area, OFA: occipital face area, STS: superior temporal sulcus, PPA: parahippocampal place area.

pattern of response between the right and left hemispheres. Accordingly, all subsequent analyses were based on a pooled analysis in which ROIs from the right and left hemispheres were combined. The response to intact and scrambled images of faces and places in the different ROI is shown in Fig. 2 and Suppl. Figs. 4 and 5.

In the FFA, there was a significant effect of category (face>place, $F(1,9) = 104$, p<0.0001) and image scrambling (intact>scrambled, $F(1,9) = 215$, p<0.0001). There was also an interaction between the category and image scrambling ($F(1,9) = 190$, p<0.0001). This interaction is explained by the larger difference in response between intact faces and places (diff. $= 1.06 \pm 0.08\%$; $t(9) = 13.4$, p<0.0001) compared with scrambled faces and places (diff. $= 0.11 \pm 0.05\%$; $t(9) = 2.3$, p<0.05). A similar pattern of activation was apparent when we analyzed the peak FFA voxel (Suppl. Fig. 4).
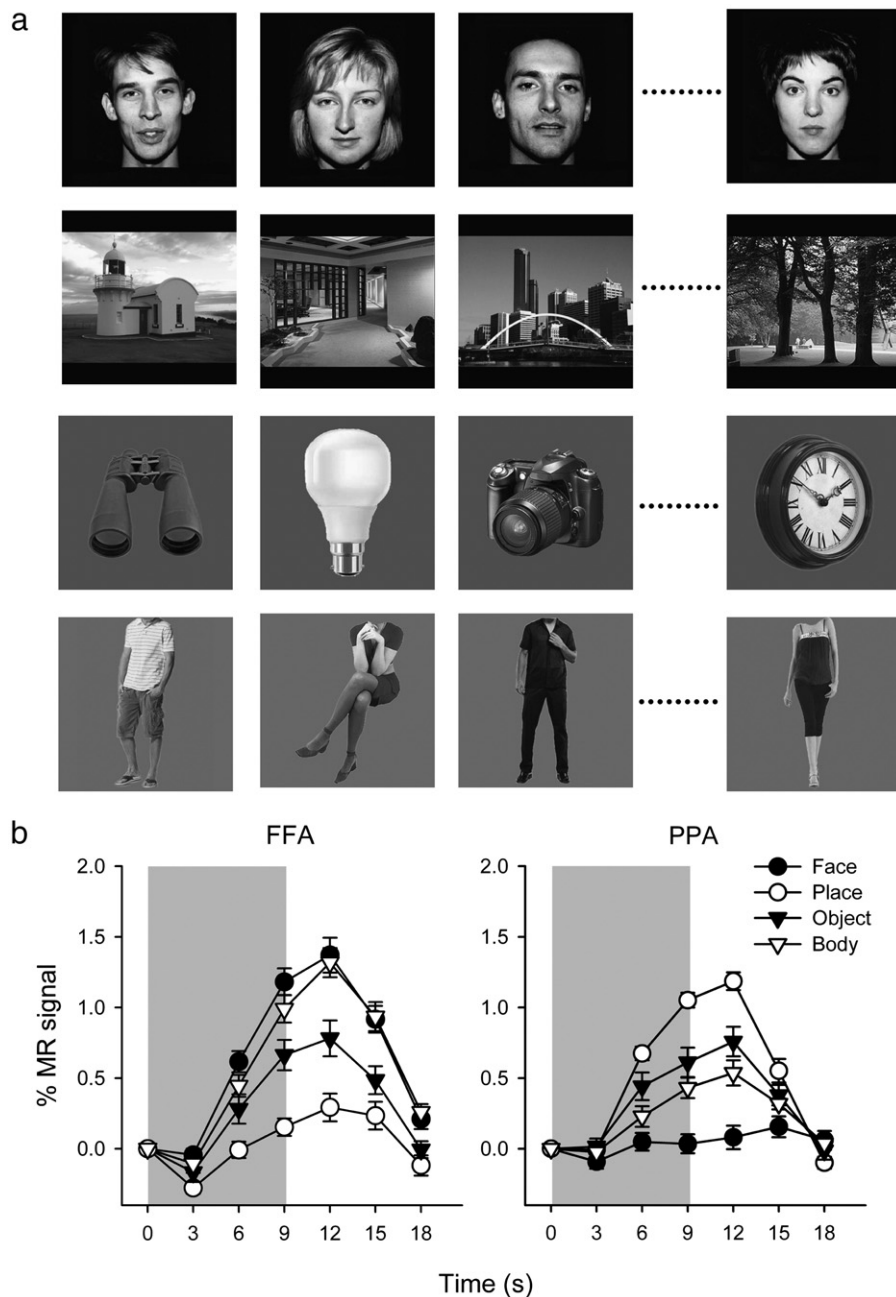

Fig. 1. Localizer scan. (a) Examples of faces, places, objects, and body images used in the localizer scan. (b) Average MR response in the fusiform face area (FFA) and parahippocampal place area (PPA) across all subjects. The shaded area represents the duration of each stimulus block. Error bars are SEM.
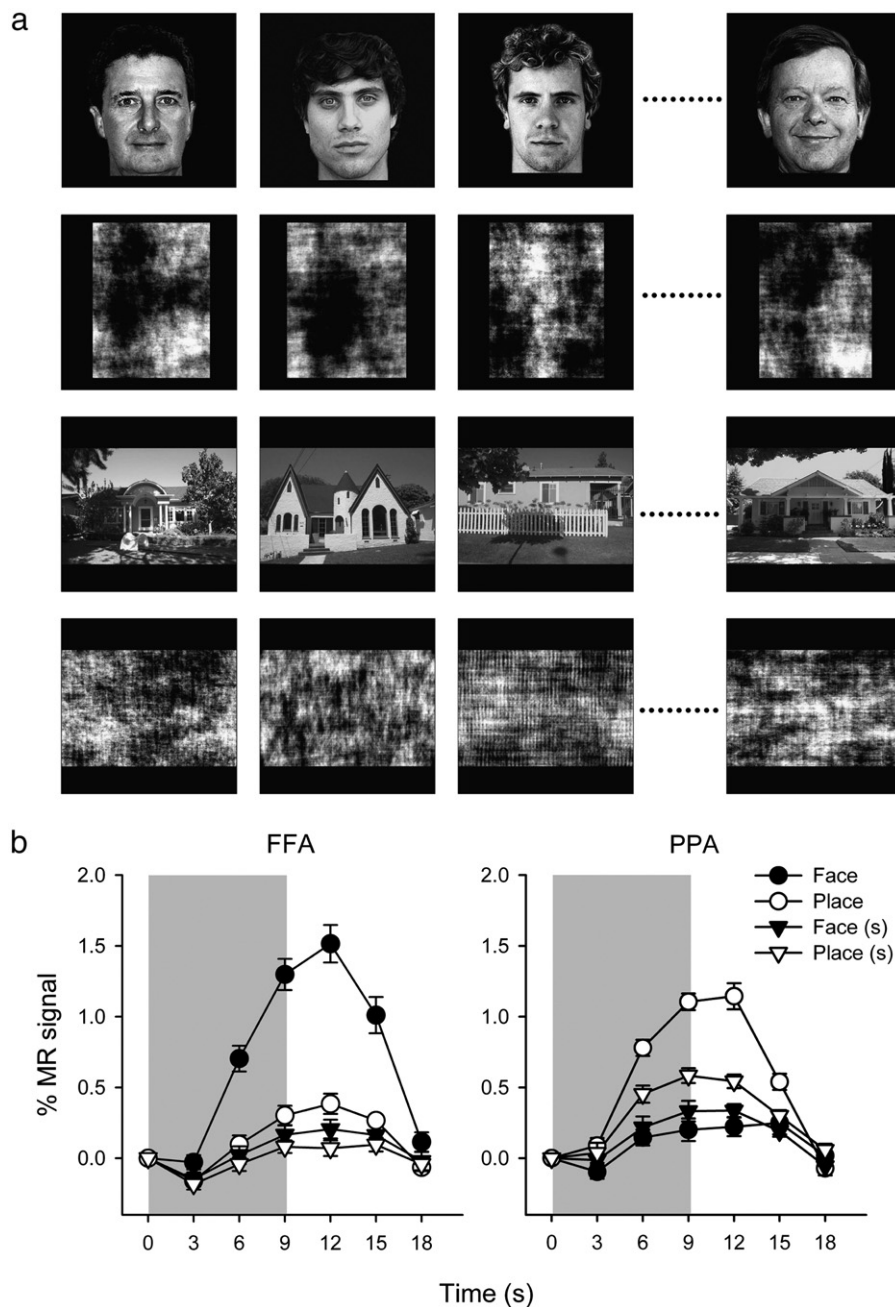
Fig. 2. Category selectivity to intact and Fourier-scrambled images of faces and places. (a) Examples of faces, scrambled faces, places, and scrambled places, respectively. (b) Average MR response in the FFA and PPA across all subjects. The shaded area represents the duration of each stimulus block. Error bars are SEM.

The response to intact and scrambled face and place images in the OFA and STS face regions is shown in Suppl. Fig. 5. There was a significant effect of category (face>place, $F(1,9) = 24.3$, $p<0.001$) and image scrambling (intact>scrambled, $F(1,9) = 44.0$, p<0.0001) in the OFA. There was also an interaction between category and image scrambling ($F(1,9) = 12.3$, $p<0.01$). This interaction is explained by the larger difference in response between intact faces and places (diff. $= 0.88 \pm 0.20\%$; $t(9) = 4.65$, p<0.001) compared with scrambled faces and places (diff. $= 0.11 \pm 0.08\%$; $t(9) = 1.37$, p>0.2). The STS also showed a significant effect of category (face>place, $F(1,9) = 7.0$, p<0.05) and image scrambling (intact>scrambled, $F(1,9) = 8.9$, p<0.05) and an interaction between the category and image scrambling ($F(1,9) = 6.6$, p<0.05). Again, this interaction is explained by the larger difference in response between intact faces and places (diff. $= 0.40 \pm 0.13\%$; $t(9) = 3.10$, p<0.01) compared with scrambled faces and places (diff. $= -0.001 \pm 0.12\%$; $t(9) = 0.01$, p>0.9).

Next, we investigated category selectivity to intact and scrambled images in the place-selective PPA (Fig. 2). There was a significant effect of category (place>face, $F(1,9) = 186$, p<0.0001), and image scrambling (intact>scrambled, $F(1,9) = 13.8$, p<0.005) in the PPA. There was also a significant interaction between category and image scrambling ($F(1,9) = 198.6$, p<0.0001). This interaction was based on a larger difference in response between intact places and faces (diff. $= 0.91 \pm 0.07\%$; $t(9) = 14.0$, p<0.0001) compared to scrambled place and face images (diff. $= 0.23 \pm 0.03\%$; $t(9) = 8.1$, p<0.0005). A similar pattern of activation was apparent when we analyzed the peak PPA voxel (Suppl. Fig. 4).

Finally, we performed a whole-brain analysis to determine whether selectivity to low-level features common in different object categories can be found in other parts of the ventral stream (Fig. 3). Fig. 3a shows selectivity for intact faces (>places, red/yellow) and places (>faces, blue/light blue). This shows the face-selective OFA and
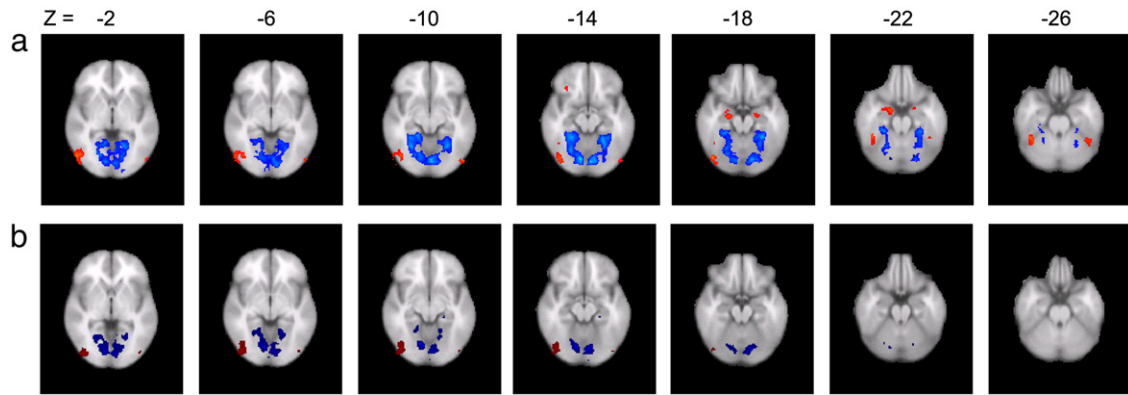
Fig. 3. Category selectivity to intact and scrambled images in the ventral stream. (a) Face-selective (face>place, red/yellow) and place-selective (place>face, blue/light blue) activations to intact images. Lateral regions show selectivity for faces, whereas medial regions are selective for places. (b) Selective activations to Fourier-scrambled images of faces (face>place, red) and places (place>face, blue). Statistical images are superimposed on a standard brain MNI brain and thresholded at p<0.001 (uncorrected).

FFA and the place-selective PPA. Fig. 3b shows the activation to scrambled images of faces (>places, red) and places (>faces, blue). This reveals posterior activations in early visual areas that were selective for scrambled faces and places. Interestingly, these activations show the same medial to lateral organization for place and face selectivity that is apparent with intact images.

Adaptation

The adaptation responses to intact or Fourier-scrambled faces and places in the face- and place-selective regions are shown in Figs. 4 and 5 and Suppl. Figs. 6 to 9. There was no significant main effect of identity (different>same) in the FFA ($F(1,9)=3.8$, p>0.05). However, there was a significant interaction between identity, category, and image in the FFA ($F(1,9)=104.2$, p<0.0001). This was due to significant adaptation (different>same) to intact faces (diff.$=0.41\pm$ 0.07%; $t(9)=5.9$, p<0.0005) but no adaptation to scrambled faces (diff.$=-0.08\pm0.08$%; $t(9)=-1.0$, p>0.3). There was no significant adaptation to intact (diff.$=-0.01\pm0.05$%; $t(9)=-0.25$, p>0.8) or scrambled places (diff.$=0.02\pm0.06$%; $t(9)=0.36$, p>0.7) in the FFA. A similar pattern of response was found in the peak FFA voxel (Suppl. Figs. 6 and 8).

The response of the OFA and STS in the adaptation contrasts is shown in Suppl. Figs. 7 and 9. There was no significant main effect of identity (different>same) in the OFA ($F(1,9)=0.21$, p>0.05). However, there was a significant interaction between identity, category, and image in the OFA ($F(1,9)=13.7$, p<0.005). This was due to significant adaptation (different>same) to intact faces (diff.$=0.31\pm$ 0.22%; $t(9)=2.5$, p<0.05) but no adaptation to scrambled faces (diff. $=-0.18\pm0.13$%; $t(9)=-1.35$, p>0.2). There was no adaptation to intact places, but rather there was a larger response to the same place (diff.$=-0.22\pm0.06$%; $t(9)=-3.51$, p<0.001). There was no adaptation to scrambled places (diff.$=0.16\pm0.10$%; $t(9)=1.$ 60, p>0.1) in the OFA. Although there was a main effect of identity in the STS ($F(1,9)=5.4$, p<0.05), there was no significant adaptation (different>same) to intact (diff.$=0.06\pm0.08$%; $t(9)=0.68$, p>0.5) or scrambled faces (diff.$=-0.08\pm0.09$%; $t(9)=0.01$, p>0.4). The main effect of identity was due to a larger response to the same compared to different places (diff.$=-0.16\pm0.04$%; $t(9)=-4.29$, p<0.005). There was no difference between the same and different scrambled places (diff.$=-0.04\pm0.14$%; $t(9)=-0.26$, p>0.7).

Fig. 5 shows the adaptation response to intact and Fourier-scrambled places in the PPA. There was a significant effect of identity ($F(1,9)=30.5$; p<0.001; different>same). There was also a significant interaction between identity and image ($F(1,9)=6.6$, p<0.05). This was due to greater adaptation to intact (diff.$=0.33\pm0.04$%; $t(9)=7.6$, p<0.0001) relative to scrambled images of places (diff.$=0.14\pm$

0.04%; $t(9)=3.2$, p<0.05). There was also no significant adaptation to intact (diff.$=0.13\pm0.06$%; $t(9)=2.2$, p>0.05) or scrambled faces (diff.$=0.09\pm0.05$%; $t(9)=1.9$, p>0.05) in the PPA. A similar pattern of response was found in the peak PPA voxel (Suppl. Figs. 6 and 8).

Finally, we performed a whole-brain analysis to determine whether there was adaptation to intact or scrambled images in other regions (Fig. 6). Fig. 6a shows adaptation (different>same) for faces (red/yellow) and places (blue/light blue), with the adaptation to places occurring in more medial regions and adaptation to faces occurring more laterally. In contrast, Fig. 6b reveals no consistent pattern of adaptation to scrambled faces (red) or places (blue).

Discussion

The aim of this study was to investigate whether category-selective regions in the ventral stream only reflect higher-level representations of objects or whether selectivity can also be explained by the response to low-level spectral features characteristic of particular object categories (Torralba and Oliva, 2003). To test this, we compared responses to intact and scrambled images of faces and places in face-selective and place-selective regions of the ventral stream. We found that the response to scrambled places was significantly greater than the response to scrambled faces in the PPA. Consistent with this, there was a significantly reduced response (adaptation) to repeated images of scrambled places. These findings are consistent with Rajimehr et al. (2008) who reported that some of the selectivity in the PPA can be explained by a low-level preference for high spatial frequencies, which are more evident in natural scenes. The FFA also showed a statistically significant difference in the response between scrambled faces and scrambled places. However, there was no adaptation to scrambled faces.

Although some of the selectivity for faces and places can be explained by the responses to low-level features, the overall response to scrambled images was much weaker than the response to the intact images. This is consistent with previous fMRI studies that reported the responses to intact versions of different objects are significantly greater than the response to scrambled versions of the same images (Malach et al., 1995; Kanwisher et al., 1997; Epstein and Kanwisher, 1998). Our data also show that the magnitude of adaptation was much smaller for scrambled images compared to intact images. This demonstrates that the low-level spectral features, preserved by the Fourier scrambling, can only explain a small amount of the category-selective responses found in higher visual areas such as the PPA and FFA. Although this suggests that these regions contain higher-level representations of objects, it is also possible that selectivity in these regions might be based on other low-level features of the stimulus that are disrupted by scrambling phase information in the Fourier
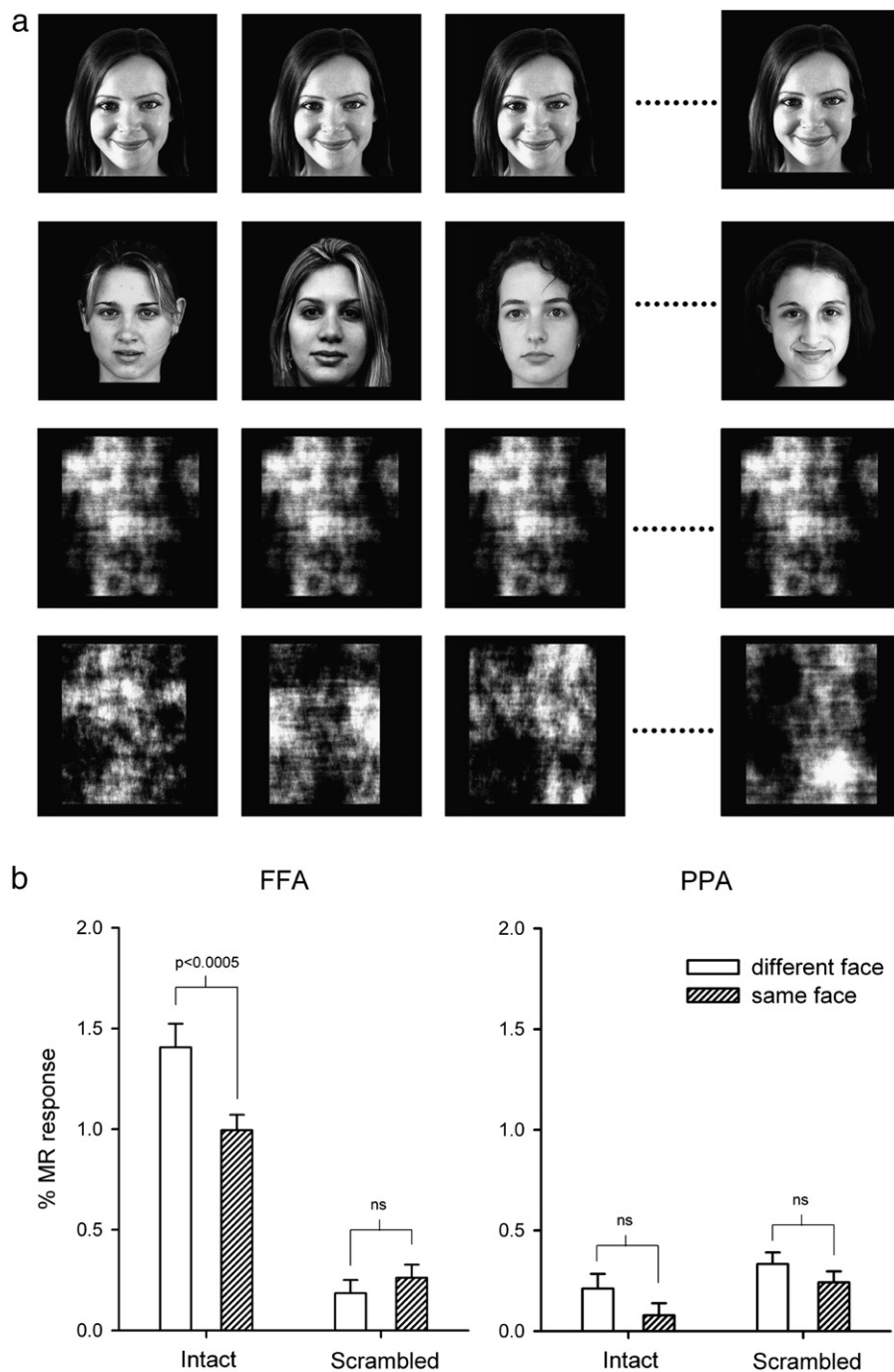
Fig. 4. Adaptation to intact and Fourier-scrambled faces. (a) Examples of intact and scrambled faces. (b) Average MR response in the FFA and PPA across all subjects. Error bars are SEM.

spectrum. Indeed, single neurons in the temporal lobe respond to conjunctions of low-level features that may not in themselves resemble objects, but could provide the building blocks from which their object perception is derived (Desimone et al., 1984; Tanaka, 1996; Op de Beeck et al., 2001).

The FFA and other face-selective regions showed less selectivity and adaptation to the Fourier-scrambled images compared to the PPA. This suggests that the Fourier scrambling may have had more of an effect on the critical features necessary for face perception. It is well established that the spatial configuration of features that comprise a face is critical for face perception and recognition (Yin, 1969; Tanaka and Farah, 1993; Maurer et al., 2002). In scrambled faces, configural cues are abolished, which might explain the more marked effects for scrambled faces in the FFA. In contrast, the

distribution of spatial features in spatial scenes is much less constrained. Consequently, their spectral properties remain distinctive following scrambling. The reduced selectivity for scrambled faces in the face-selective regions fits with single neuron studies that have found strong selectivity for images of faces in the temporal lobe (Gross et al., 1972; Hasselmo et al., 1989; Perrett et al., 1992; Tsao et al., 2006). In these studies, the only non-face objects that elicited significant activity from neurons in this region were objects that had spherical shapes similar to faces. A similar selectivity for non-face objects was reported using fMRI with the face-selective regions being more responsive to concentric patterns compared to radial patterns (Wilkinson et al., 2000) and smooth artificial objects compared to spikey or cubed objects (Op de Beeck et al., 2006, 2008a,b). However, in both the fMRI and single neuron studies, responses to non-face
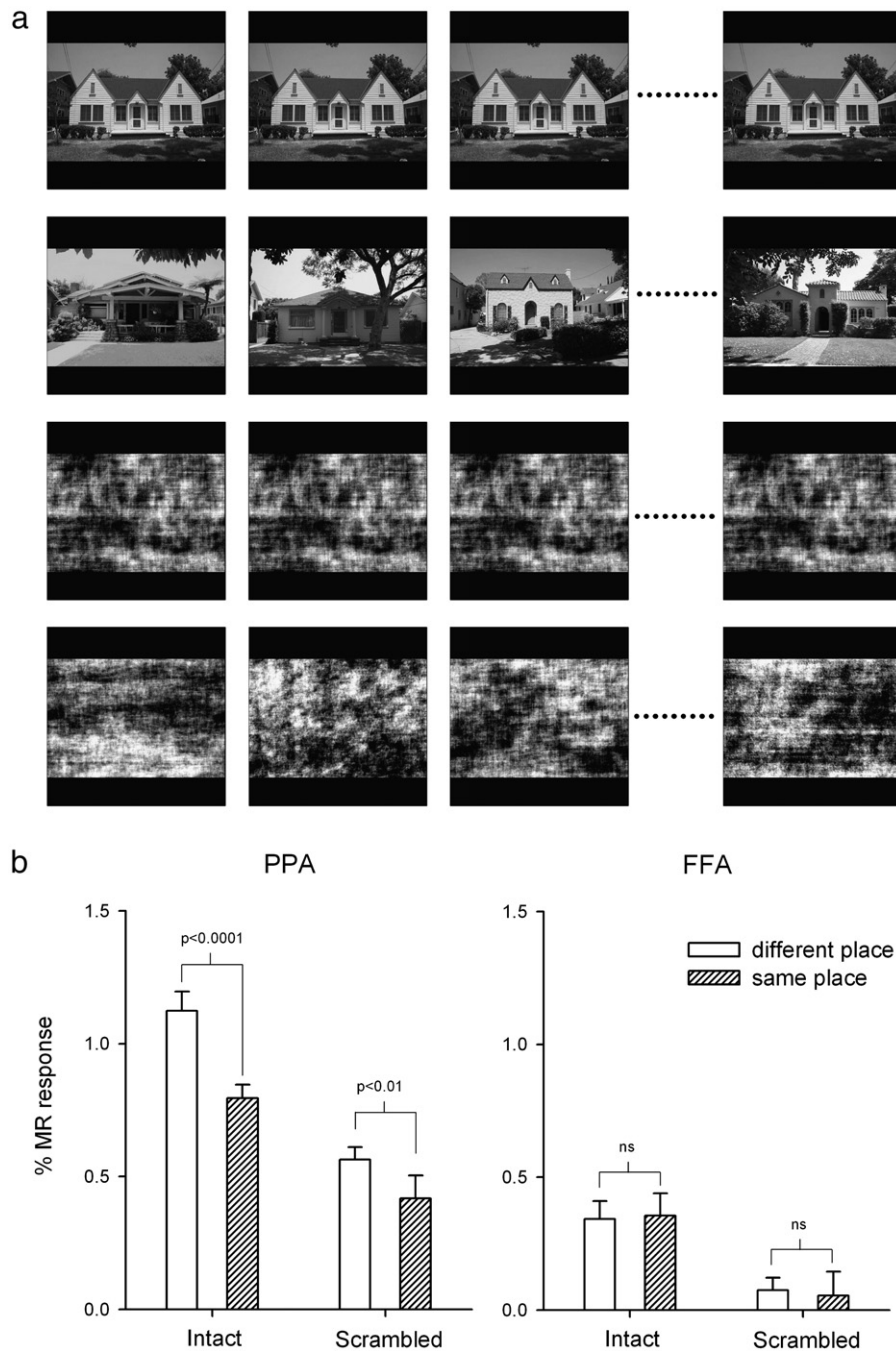
Fig. 5. Adaptation to intact and Fourier-scrambled places. (a) Examples of intact and scrambled places. (b) Average MR response in the PPA and FFA across all subjects. Error bars are SEM.

objects were weaker than the response to faces (Op de Beeck et al., 2008a,b).

Although category-selective regions only showed a modest response to scrambled images, we found that more posterior regions of the ventral stream were selective for scrambled images. Lateral regions in the occipital lobe (posterior to OFA) responded more to faces than places and a more medial region (posterior to PPA) responded more to places than faces. This pattern mirrors that observed for intact images in which more lateral regions of the ventral stream are face-selective (FFA, OFA), whereas more medial regions are place-selective (PPA). These findings suggest that selectivity for object categories could emerge from differential processing of low-level features typical of different object categories in early visual areas. The increased selectivity for intact images in anterior regions of

the ventral stream is consistent with a previous study showing a gradual change in selectivity to image scrambling along an anterior–posterior axis in the ventral stream (Lerner et al., 2001). Our results also complement other fMRI studies that have demonstrated that the lateral–medial organization of face and place processing is linked to a weak eccentricity bias, thus extending the mapping of retinal eccentricity seen in early visual areas; face regions were associated with a central visual field bias, whereas places and scenes were associated with a more peripheral visual field bias (Levy et al., 2001; Hasson et al., 2002).

This low-level selectivity for faces and places could provide a physiological explanation for data found in other studies using images that have been manipulated in the Fourier domain. For example, Honey et al. (2008) reported that eye movements to faces are faster
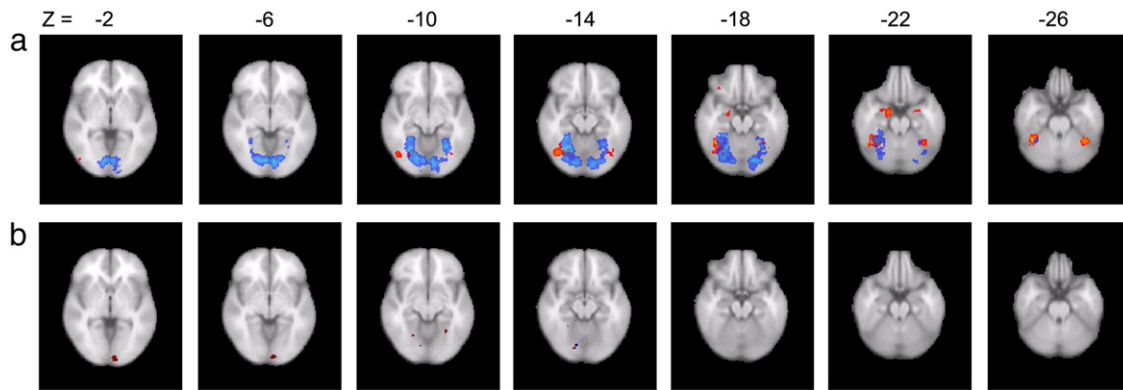
Fig. 6. Adaptation to intact and scrambled images in the ventral stream. (a) Face-selective (different face>same face, red/yellow) and place-selective (different place>same place, blue/light blue) activations to intact images. Lateral regions show adaptation to faces, whereas medial regions show adaptation to places. The statistical map for adaptation to places has been made transparent to show overlap with the adaptation to faces. (b) Adaptation to Fourier-scrambled images of faces (different>same, red) and places (different>same, blue). The pattern of adaptation to scrambled images was less distinct compared to intact images. Statistical images are superimposed on a standard brain MNI brain and thresholded at p<0.001 (uncorrected).

and more accurate compared to eye movements to other objects. Intriguingly, this bias is still evident when the images are scrambled. Yue et al. (2006) filtered face images in the Fourier domain to produce two complementary images that contained different spatial frequency and orientation content. When the two complementary images were presented in sequence, there was a significant reduction in identification compared to when identical images were presented. This manipulation also caused a release from adaptation in the FFA, which led the authors to conclude that face recognition is dependent on a low-level representation in early visual areas (Yue et al., 2006). Finally, Dakin and Watt (2009) reported that observers are substantially better at identifying faces filtered to contain just horizontal information compared to any other orientation band. This corresponds with a bias for horizontal information in the face image.

Patterns of adaptation to faces and places corresponded with the location of category-selective regions such as the FFA and PPA. A whole-brain analysis showed adaptation to intact faces in more lateral parts of the inferior temporal lobe, whereas more medial regions adapted to places. However, this analysis also revealed that adaptation to faces and places was not restricted to the category-selective regions but showed a more distributed and overlapping pattern (see also, Davies-Thompson et al., 2009). These findings are significant in the dispute about whether information in the ventral stream is represented by a modular or distributed neural code (Haxby et al., 2001; Cohen and Tong, 2001; Andrews, 2005; Reddy and Kanwisher, 2006). The overlap in the pattern of fMR adaptation suggests that neural representations underlying the perception and recognition of different categories of objects might be arranged in overlapping maps rather than discrete modules (Op de Beeck et al., 2008a,b). In contrast to the adaptation response to intact images, adaptation to scrambled faces and places failed to show a consistent pattern in the ventral stream. This provides further support for the idea that higher areas in the visual processing stream might adapt more easily than lower areas (Krekelberg et al., 2006).

In conclusion, our results show that low-level spectral statistics of faces and places can explain some of the selectivity found in regions such as the PPA and FFA. However, category selectivity for scrambled images was apparent in more posterior regions of the ventral stream. This implies that category selectivity results from the differential processing of low-level features typical of different object categories in early visual areas.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.08.046.

References

Allison, T, Puce, A, Spencer, D, McCarthy, G., 1999. Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. Cereb. Cortex 9, 415–430.

Andrews, T.J., 2005. Visual cortex: how are objects and faces represented? Curr. Biol. 15, 451–453.

Andrews, T.J., Ewbank, M.P., 2004. Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. NeuroImage 23, 905–913.

Avidan, G., Hasson, U., Hendler, T., Zohary, E., Malach, R., 2002. Analysis of the neuronal selectivity underlying low fMRI signals. Curr. Biol. 12, 964–972.

Cohen, J., Tong, F., 2001. The face of controversy. Science 293, 2405–2407.

Dakin, S.C., Watt, R.J., 2009. Biological "bar codes" in human faces. J. Vision 9 (4):2, 1–10.

Davies-Thompson, J., Gouws, A., Andrews, TJ, 2009. An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. Neuropsychologia 47, 1627–1635.

Desimone, R., Albright, TD, Gross, CG, Bruce, C, 1984. Stimulus-selective properties of inferior temporal neurons in the macaque. J. Neurosci. 4, 2051–2062.

Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science 293, 2470–2473.

Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. Nature 392, 598–601.

Epstein, R., Graham, K.S., Downing, P.E., 2003. Viewpoint-specific scene representations in human parahippocampal cortex. Neuron. 37, 865–876.

Ewbank, MP, Schluppeck, D, Andrews, TJ, 2005. FMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. NeuroImage 28, 268–279.

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

Gross, C.G., Rocha-Miranda, C.E., Bender, D.B., 1972. Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol. 35, 96–111.

Habib, M., Sirigu, A., 1987. Pure topographical disorientation: a definition and anatomical basis. Cortex 23, 73–85.

Hasselmo, M.E., Rolls, E.T., Baylis, G.C., 1989. The role of expression and identity in the face-selective responses of neurons in the temporal visual-cortex of the monkey. Behav. Brain Res. 32, 203–218.

Hasson, U., Levy, I., Behrmann, M., Hendler, T., Malach, R., 2002. Eccentricity bias as an organizing principle for human high-order object areas. Neuron 34, 479–490.

Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science 293 (5539), 2425–2430.

Honey, C., Kirchner, H., VanRullen, R., 2008. Faces in the cloud: Fourier power spectrum biases ultra rapid face detection. J. Vision 8 (12), 1–13 9.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in extrastriate cortex specialised for face perception. J. Neurosci. 17, 4302–4311.

Krekelberg, B., Boynton, G.M., vanWezel, R.J.A., 2006. Adaptation: from single cells to BOLD signals. Trends Neurosci. 29 (5), 250–256.

Lerner, Y., Hendler, T., Ben-Bashat, D., Harel, M., Malach, R., 2001. A hierarchical axis of object processing stages in the human visual cortex. Cereb. Cortex 11, 287–297.

Levy, I., Hasson, U., Avidan, G., Hendler, T., Malach, R., 2001. Center–periphery organization of human object areas. Nat. Neurosci. 4, 533–539.

Malach, R., Reppas, J.B., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., Tootell, R.B.H., 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc. Natl. Acad. Sci. U. S. A. 92, 8135–8138.

Maurer, D., Le Grand, R., Mondloch, C.J., 2002. The many faces of configural processing. Trends Cogn. Sci. 6, 255–260.

McNeil, J.E., Warrington, E.K., 1993. Prosopagnosia – a face-specific disorder. Q. J. Exp. Psychol-A 46, 1–10.

Milner, A.D., Goodale, M.A., 1995. The visual brain in action. Oxford Univ. Press.

Moscovitch, M., Winocur, G., Behrmann, M., 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. J. Cogn. Neurosci. 9, 555–604.

Op de Beeck, H., Wagemans, J., Vogels, R., 2001. Inferotemporal neurons represent low-dimensional configurations of parameterized shapes. Nat. Neurosci. 4, 1244–1252.

Op de Beeck, H.P., Baker, C.I., DiCarlo, J.J., Kanwisher, N., 2006. Discrimination training alters object representations in human extrastriate cortex. J. Neurosci. 26, 13025–13036.

Op de Beeck, H.P., Deutsch, J.A., Vanduffel, W., Kanwisher, N., DiCarlo, J.J., 2008a. A stable topography of selectivity for unfamiliar shape classes in monkey inferior temporal cortex. Cereb. Cortex 18, 1676–1694.

Op de Beeck, H., Haushofer, J., Kanwisher, N., 2008b. Interpreting fMRI data: maps, modules, and dimensions. Nat. Rev., Neurosci. 9, 123–135.

Perrett, D.I., Hietanen, J.K., Oram, M.W., Benson, P.J., Rolls, E.T., 1992. Organization and functions of cells responsive to faces in the temporal cortex. Philos. Trans. R. Soc. Lond. B. 335, 23–30.

Rajimehr, R., Devaney, K., Young, J., Postelnicu, G., Tootell, R., 2008. The 'parahippo-campal place area' responds selectively to high spatial frequencies in humans and monkeys [Abstract]. J. Vision 8 (6), 85a, 85.

Reddy, L., Kanwisher, N., 2006. Coding of visual objects in the ventral stream. Curr. Opin. Neurobiol. 16 (4), 408–414.

Tanaka, K, 1996. Inferotemporal cortex and object vision. Annu. Rev. Neurosci. 19, 109–139.

Tanaka, JW, Farah, MJ, 1993. Parts and wholes in face recognition. Q. J. Exp. Psychol. Sect. A 46 (2), 225–245.

Torralba, A., Oliva, A., 2003. Statistics of natural images. Comput. Neural Syst. 14, 391–412.

Tsao, D.Y., Freiwald, W.A., Tootell, R.B.H., Livingstone, M.S., 2006. A cortical region consisting entirely of face-selective cells. Science 311, 670–674.

Ungerleider, L.G., Mishkin, M., 1982. Two cortical visual systems. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J.W. (Eds.), Analysis of Visual Behavior. MIT Press, Cambridge, MA, pp. 549–586.

Wilkinson, F, James, TW, Wilson, HR, Gati, JS, Menon, RS, Goodale, MA, 2000. An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. Curr. Biol. 10, 1455–1458.

Yin, R.K., 1969. Looking at upside-down faces. J. Exp. Psychol. 81, 141–145.

Yue, X., Tjan, B.S., Biederman, I., 2006. What makes faces special? Visi. Res. 46, 3802–3811.