

An image-dependent representation of familiar and unfamiliar faces in the human ventral stream

Jodie Davies-Thompson, André Gouws, Timothy J. Andrews*

Department of Psychology and York Neuroimaging Centre, University of York, UK

ARTICLE INFO

Article history:

Received 3 July 2008

Received in revised form

28 November 2008

Accepted 11 January 2009

Available online 19 January 2009

Keywords:

Visual cortex

FFA

OFA

STS

Adaptation

ABSTRACT

People are extremely proficient at recognizing faces that are familiar to them, but are much worse at matching unfamiliar faces. We used fMR-adaptation to ask whether this difference in recognition might be reflected by an image-invariant representation for familiar faces in face-selective regions of the human ventral visual processing stream. Consistent with models of face processing, we found adaptation to repeated images of the same face image in the fusiform face area (FFA), but not in the superior-temporal face region (STS). To establish if the neural representation in the FFA was invariant to changes in view, we presented different images of the same face. Contrary to our hypothesis, we found that the response in the FFA to different images of the same person was the same as the response to images of different people. A group analysis showed a distributed pattern of adaptation to the same image of a face, which extended beyond the face-selective areas, including other regions of the ventral visual stream. However, this analysis failed to reveal any regions showing significant image-invariant adaptation. These results suggest that information about faces is represented in a distributed network using an image-dependent neural code.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The ability to easily recognize familiar faces across a variety of changes in illumination, expression, viewing angle and appearance contrasts with the inherent difficulty found in the perception and matching of unfamiliar faces across similar image manipulations (Hancock, Bruce, & Burton, 2000). This difference in perception has been integrated into cognitive models of face processing, which propose that familiar and unfamiliar faces are represented differently in the human visual system (Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999). These models propose that the initial processing of all faces involves computation of a view-dependent representation. The information from this early processing stage is compared with image-invariant representations that are specific to familiar faces. Visual areas involved in processing faces form a ventral processing stream that projects toward the temporal lobe (Kanwisher, McDermott, & Chun, 1997; Milner & Goodale, 1995). These findings have been incorporated into a model of face processing which proposes that processing of facial identity is associated with an image-invariant representation in the inferior temporal lobe (FFA), whereas changeable aspects of faces important for social communication are pro-

cessed by the superior-temporal lobe (Haxby, Hoffman, & Gobbini, 2000).

The aim of this study is to determine whether face-selective regions in the human ventral stream use an image-invariant neural code to represent familiar faces. fMR-adaptation (the reduction in response to repeated presentations of a stimulus) has been used by a number of studies to probe how faces are represented in the human visual system (Grill-Spector, Henson, & Martin, 2006; Krekelberg, Boynton, & van Wezel, 2006). These studies have found that the neural representation underlying face perception is invariant to changes in the size (Andrews & Ewbank, 2004; Grill-Spector et al., 1999), position (Grill-Spector et al., 1999), emotional expression (Winston, Henson, Fine-Goulden, & Dolan, 2004) and spatial frequency composition (Eger, Schyns, & Kleinschmidt, 2004) of the image. In contrast, a release from adaptation occurs with changes in illumination (Grill-Spector et al., 1999) and viewing angle (Andrews & Ewbank, 2004; Eger, Schweinberger, Dolan, & Henson, 2005; Fang, Murray, & He, 2006; Grill-Spector et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b).

It is not clear why changes in viewing angle and illumination should result in a release from adaptation in regions such as the FFA that have been implicated in face recognition (Haxby et al., 2000). One possibility is that most neuroimaging studies have used unfamiliar faces and an invariant representation is only predicted for familiar faces (Bruce & Young, 1986; Burton et al., 1999; Hancock et al., 2000; Haxby et al., 2000). However, even when familiar faces

* Corresponding author at: Department of Psychology, University of York, York, YO10 5DD, UK. Tel.: +44 1904 434356; fax: +44 1904 433181.

E-mail address: t.andrews@psych.york.ac.uk (T.J. Andrews).

were used, a release from adaptation has been reported (Eger et al., 2005; Pourtois et al., 2005b). One explanation for these findings is that changes in viewpoint were often confounded with changes in illumination and appearance. It is also conceivable that the event-related designs used in these studies may have lacked the sensitivity to detect view-invariant responses in face-selective regions. More recently, we used a blocked-design fMR-adaptation paradigm in which we parametrically varied the viewpoint of familiar and unfamiliar faces. In contrast to previous studies (Eger et al., 2005; Pourtois et al., 2005b), we found that adaptation to the same identity was still evident in the FFA when we varied the viewing angle of a familiar face (Ewbank & Andrews, 2008). In contrast, a release from adaptation was found with increasing viewing angles with unfamiliar faces.

Here, we extend these findings by asking whether adaptation occurs to images of the same unfamiliar or familiar face that vary in appearance, but are taken from the same viewpoint. We compared the response to images from the following conditions: (1) *same identity, same image*; (2) *same identity, different images*; (3) *different identities, different images*. Our prediction was that the response to familiar faces with the same identity would be significantly lower than the response to images from different identities. In contrast, the response to unfamiliar faces would only be lower when the same image is presented. This will provide a direct test of the view-invariant face recognition units proposed in cognitive and neurological models of face processing. The clear prediction from these models is that image-independent adaptation should occur for familiar, but not unfamiliar faces.

2. Methods

2.1. Subjects

Nineteen subjects took part in the fMRI study (10 females; mean age, 26). All observers were right-handed, and had normal to 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 (approximately $8^\circ \times 8^\circ$) were back-projected onto a screen located inside the magnetic bore, approximately 57 cm from subjects' eyes.

2.2. Localizer scan

To identify regions responding selectively to faces in the visual cortex, a localizer scan was carried out for each subject. Subjects viewed 20 blocks of 10 images. Each block contained images from one of the five different categories: faces, bodies, objects, places, or Fourier scrambled images of the former categories. Face images were taken from the Psychological Image Collection at Stirling (PICS; <http://www.pics.psych.stir.ac.uk>) and body images were taken from a body image collection at Bangor (Downing et al., 2001; <http://www.bangor.ac.uk/~pss811/page7/page7.html>). Images of other categories were taken from a variety of web-based sources. Each image was presented for 700 ms followed by a 200 ms fixation cross. Stimulus blocks were separated by a 9 s fixation grey screen. Each condition was repeated four times, and arranged in a counterbalanced block design.

2.3. Adaptation scan

There were three image conditions: (i) *same identity, same image*; (ii) *same identity, different images*; (iii) *different identities, different images*. The faces were either familiar or unfamiliar. Images of familiar and unfamiliar faces were obtained from a variety of internet sources using Google Images. Only faces with a frontal pose were used. Emotional expressions did not differ within blocks. Familiar identities were chosen on the basis of familiarity ratings obtained from a separate group of subjects. The familiarity of the faces was confirmed by a post-scan test in which subject were asked whether the faces were familiar and whether they could report the name and occupation. Unfamiliar faces were famous in other countries, but were unknown to the subjects, and were chosen to match familiar faces for their variation in age and appearance. Images were presented in grey scale and were adjusted to an average brightness level. The mean change in image intensity across images was calculated by taking the average of the absolute differences in grey value at each pixel for successive pairs of images within a block. Table 1 shows that there was a similar mean intensity change in the corresponding familiar and unfamiliar conditions.

A blocked design was used to present the stimuli. Each stimulus block consisted of 10 images from one of the conditions. In each block, images were shown for

Table 1

Mean change in intensity between successive images in each condition of the adaptation scan (S.E.M.).

	Same, same	Same, different	Different, different
Familiar	0 (0)	16.7 (1.3)	19.6 (1.4)
Unfamiliar	0 (0)	18.1 (1.4)	18.3 (1.3)

700 ms followed by a 200 ms fixation cross. Stimulus blocks were separated by a 9 s fixation grey screen. Each condition was repeated eight times giving a total of 48 (24 unfamiliar, 24 familiar) blocks. Different images were used in each block. To monitor attentional load across stimulus conditions, a red dot was superimposed on one or two images in each block. Subjects were required to respond, with a button press, as soon as they saw the image containing the target. The target could appear in any location between the eyes and the mouth, and was counterbalanced across conditions.

2.4. Imaging parameters

All experiments were carried out using a GE 3 Tesla 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, radio-frequency 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 cm \times 28 cm, matrix size = 128 \times 128, slice thickness 3 mm). These were coregistered onto a T1-weighted anatomical image (1 mm \times 1 mm \times 1 mm) from each subject. To help with registration, a T1-weighted image was taken in the same plane as the EPI slices.

2.5. fMRI analysis

Statistical analysis of the fMRI data was carried out using FEAT (<http://www.fmrib.ox.ac.uk/fsl>; Smith et al., 2004). The initial 9 s of data from each scan were removed to minimize the effects of magnetic saturation. Motion correction was followed by spatial smoothing (Gaussian, FWHM 6 mm) and temporal high-pass filtering (cut off, 0.01 Hz). For the localizer scan, face-selective regions of interest (ROI) were determined by the contrast *face > place* or *face > object* thresholded at $P < 0.001$ (uncorrected). The time series of the resulting 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 in a given ROI were then averaged to give a single time series in each ROI for each subject. Individual stimulus blocks were normalized by subtracting every time point by the zero point for that stimulus block. The normalized data were then averaged to obtain the mean time course for each stimulus condition. The peak response was calculated as the mean of the response at 9 and 12 s. Repeated-measures ANOVA were used to determine significant differences in the peak response to each stimulus condition.

To determine whether there were adaptation effects occurring outside the regions of interest, the individual subject data was entered into a higher level group analysis using a mixed effects design (FLAME, <http://www.fmrib.ox.ac.uk/fsl>). First, the functional data was 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 adaptation and localizer scans. Specifically, we asked whether the spatial extent of face adaptation was restricted to regions showing face-selectivity (*face > place*) in the localizer scan. Statistical images were thresholded at $P < 0.001$ uncorrected or resel corrected for multiple comparisons at $P < 0.05$ corrected (<http://www.fmrib.ox.ac.uk/fsl>).

2.6. Independent behavioural task

To determine how subjects perceived the identity of the familiar and unfamiliar faces, we performed an independent behavioural study outside the scanner. 18 subjects (11 from the fMRI study) viewed images of faces from the adaptation study on a computer monitor at a distance of 57 cm. Pairs of images were presented in succession and subjects were asked to indicate by a button press whether the two faces were the same person. Each face was presented for 700 ms and separated by an interval of 200 ms. There were three possible conditions: same (identical face images), different (different images of the same person) and unprimed (different images of different people). Each subject viewed a total of 192 trials.

3. Results

3.1. Localizer scan

Fig. 1A shows three different regions in the occipital and temporal lobe that showed face-selective activity (*face > places*): fusiform face area (FFA, Kanwisher et al., 1997); occipital face area (OFA, Gauthier et al., 2000); and superior temporal sulcus (STS, Hoffman & Haxby, 2000) (Table 2). Each region was defined separately for each

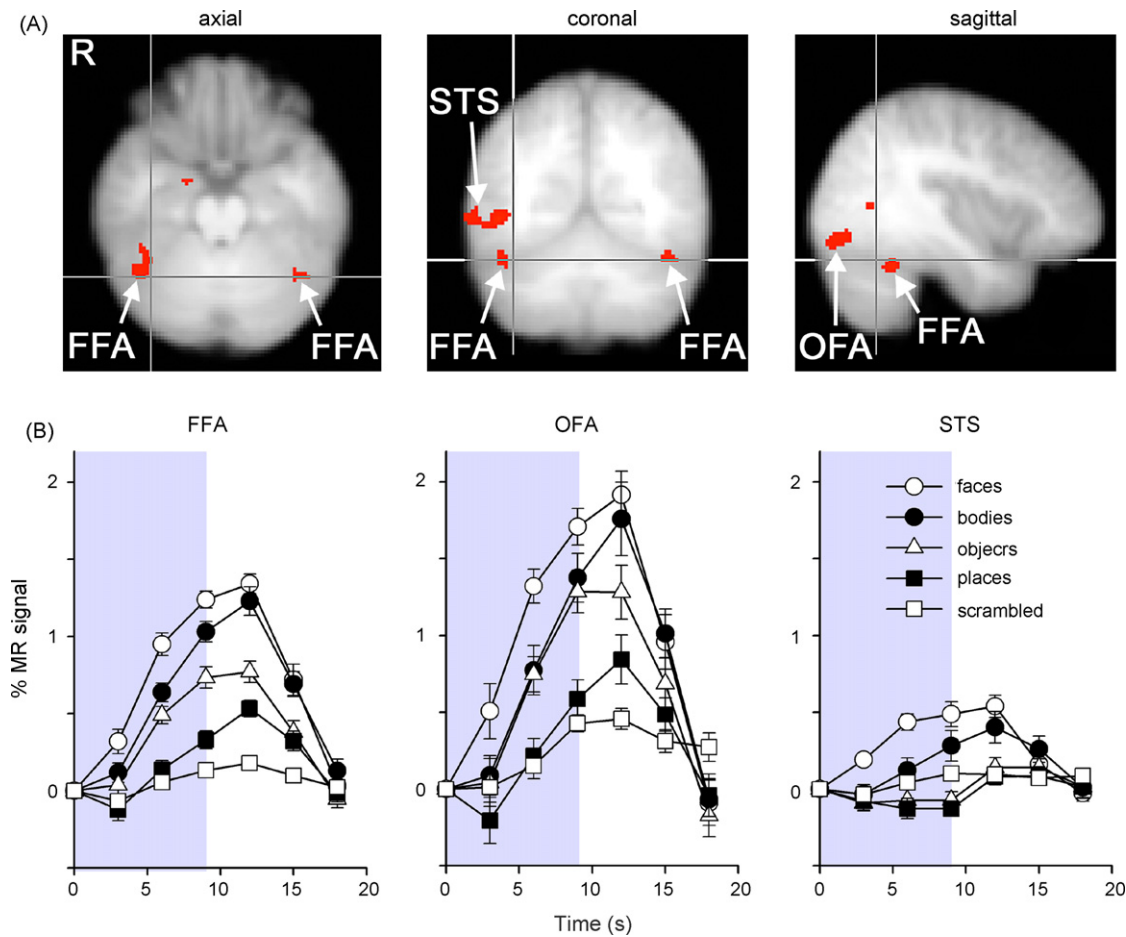


Fig. 1. Localizer scan. (A) Location of face-selective regions from the group analysis (FFA: fusiform face area, OFA: occipital face area, STS: superior temporal sulcus). These scan images follow radiological convention, with the left hemisphere shown on the right. (B) MR time-course during localizer scans, showing activity averaged across hemispheres and subjects for each stimulus category in face-selective areas. The shaded represent the duration of each stimulus block. Error bars represent \pm S.E.

individual and all further analyses were performed on the mean time courses of voxels in these ROI. The average time-courses of activation in the face-selective regions are shown in Fig. 1B. An ANOVA revealed a main effect of stimulus condition in the FFA ($F(4,68) = 55.16, P < 0.001$), OFA ($F(4,64) = 16.99, P < 0.001$), and STS ($F(4,56) = 9.45, P < 0.001$). The FFA was significantly more activated by images of faces than objects ($F(1,17) = 24.36, P < 0.001$), places ($F(1,17) = 109.06, P < 0.001$) and scrambled images ($F(1,17) = 126.89, P < 0.001$), but not to bodies ($F(1,17) = 4.22, P = 0.06$). The OFA also showed a significantly greater response to faces than to objects ($F(1,16) = 5.59, P < 0.05$), places ($F(1,16) = 46.47, P < 0.001$), and scrambled images ($F(1,16) = 73.90, P < 0.001$), but not to bodies ($F(1,16) = 1.04, P = 0.32$). Finally, STS showed significantly greater activation to faces than objects ($F(1,14) = 13.63, P < 0.01$), places

($F(1,14) = 30.28, P < 0.001$), and scrambled images ($F(1,14) = 12.43, P < 0.01$), but not to bodies ($F(1,14) = 2.66, P = 0.13$). The roughly equivalent response to faces and bodies in face-selective regions such as the FFA is consistent with previous studies that reported an overlapping response to faces and bodies with a voxel size similar to that used in this study (Peelen and Downing, 2005; Schwarzlose et al., 2005). However, it is possible to differentiate face- and body-selective regions in the fusiform gyrus using high-resolution fMRI (Schwarzlose et al., 2005).

3.2. Adaptation scan

Figs. 2 and 3 show the response to unfamiliar and familiar faces across all image conditions. The analyses showed no difference in the pattern of response between the right and left hemispheres (FFA: $F = 0.0001, P = 0.99$; OFA: $F = 0.006, P = 0.81$; STS: $F = 0.09, P = 0.78$). Accordingly, all subsequent analyses were based on a pooled analysis in which the right and left hemisphere voxels are combined in each ROI. A $2 \times 3 \times 3$ ANOVA (image condition, familiarity, region) showed a significant main effect for image condition ($F(2,18) = 16.02, P < 0.001$), familiarity ($F(1,9) = 5.44, P < 0.05$) and region ($F(2,18) = 9.05, P < 0.005$). We also found a significant interaction between image condition \times region ($F(4,36) = 11.43, P < 0.001$) suggesting the different regions responded differently to the conditions. However there also no significant interaction between familiarity \times region ($F(2,18) = 0.61, P = 0.55$), or familiarity \times viewpoint ($F(2,18) = 0.74, P = 0.49$), suggesting that the pattern of responses to familiar and unfamiliar faces was similar across regions.

Table 2
Mean MNI coordinates of face-selective regions-of-interest.

Region	n	Co-ordinates			
		x	y	z	
FFA	L	17	-41	-53	-22
	R	18	37	-55	-22
OFA	L	15	-41	-83	-15
	R	16	42	-80	-11
STS	R	15	50	-58	2

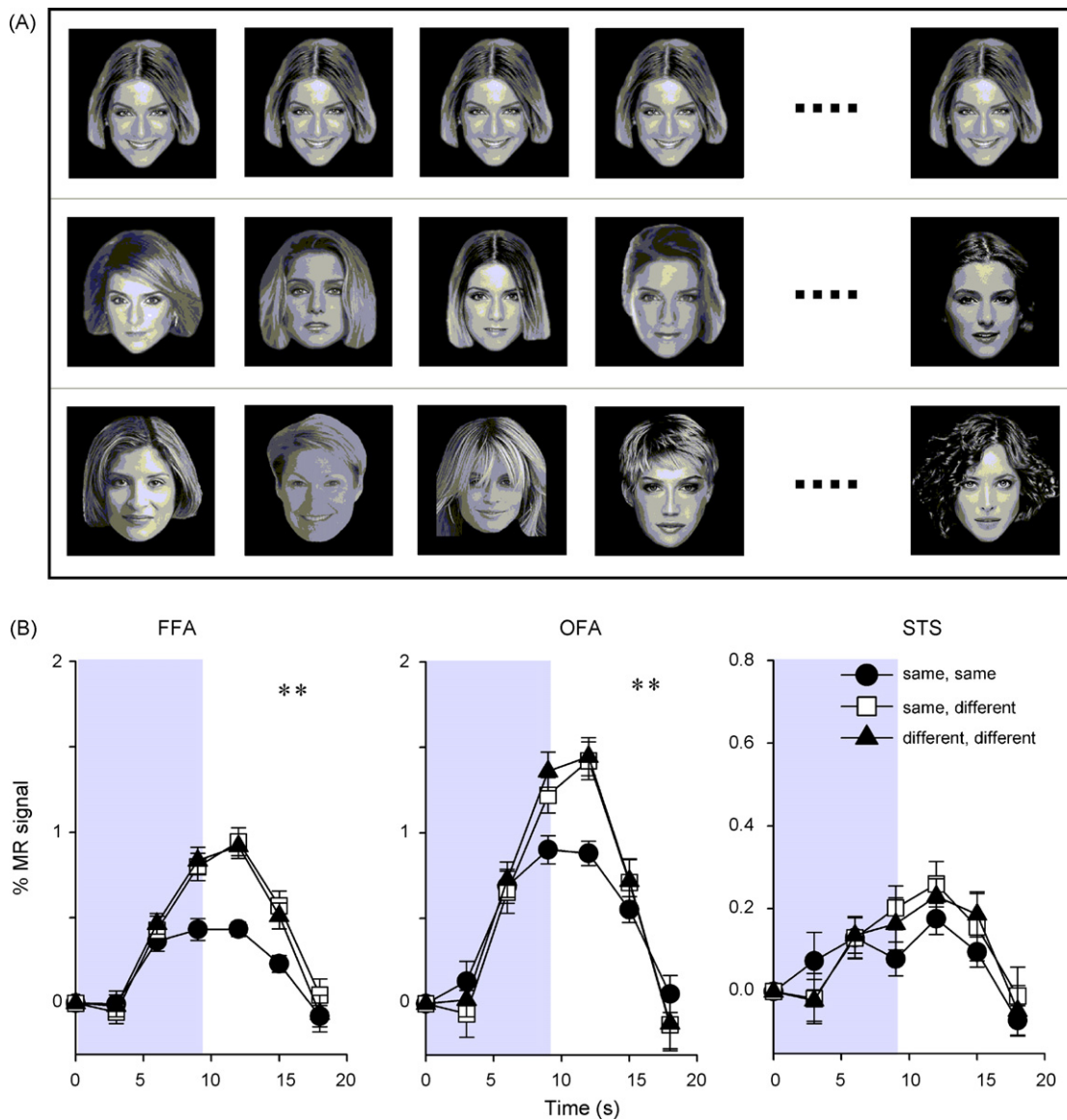


Fig. 2. Adaptation to unfamiliar faces. (A) Examples of images used in the *same-identity, same-image* (top), *same-identity, different-images* (middle), and *different-identities, different-images* (bottom) conditions. (B) The average response across subjects is shown in the fusiform face area (FFA), the occipital face area (OFA), and the superior temporal sulcus (STS). MR time-courses were averaged across hemispheres and subjects. The shaded regions represent the duration of stimulus presentation. Error bars represent \pm S.E. ****** $P < 0.01$, ***** $P < 0.05$.

3.2.1. FFA

The responses in the FFA to images of the same and different faces at different viewpoints in the unfamiliar and familiar face conditions was analyzed using a 2-way ANOVA. This revealed a main effect of image condition ($F(2,34)=69.80$, $P < 0.001$). This was due to a reduced response (adaptation) to the *same identity, same image* compared to the *different identities, different images* conditions in both unfamiliar ($t(17)=-6.53$, $P < 0.001$) and familiar ($t(17)=-5.67$, $P < 0.001$) faces. However, we found no difference in response between the *same identity, different image*, and *different identities, different image*, conditions for unfamiliar ($t(17)=0.66$, $P=0.52$) or familiar ($t(17)=0.48$, $P=0.64$) faces. We also found an effect of familiarity ($F(1,17)=7.84$, $P < 0.05$), which was due to a larger response to familiar compared to unfamiliar faces. However, there was no interaction between familiarity \times image condition ($F(2,34)=0.03$, $P=0.97$), suggesting that patterns of adaptation did not differ across familiarity.

3.2.2. OFA

A 2-way ANOVA revealed a main effect of image condition ($F(2,32)=23.45$, $P < 0.001$), but no effect of familiarity ($F(1,16)=1.64$, $P=0.22$). The main effect of image condition was due to a reduction in response amplitude to the *same identity, same image* condition compared to the *different identities, different images* condition for both unfamiliar ($t(16)=-3.58$, $P < 0.005$) and familiar ($t(16)=-3.16$, $P < 0.01$) faces. Similar to the FFA, there was no difference between the *same identity, different image*, and the *different identities, different image*, conditions for either unfamiliar ($t(16)=-0.46$, $P=0.66$) or familiar ($t(16)=1.74$, $P=0.10$) faces. There was also no interaction between familiarity \times viewpoint ($F(2,32)=0.79$, $P=0.46$).

3.2.3. STS

There was no main effect of image condition ($F(2,28)=5.38$, $P < 0.05$). The response to the *same identity, same image* condition was not significantly different from the response to *different identi-*

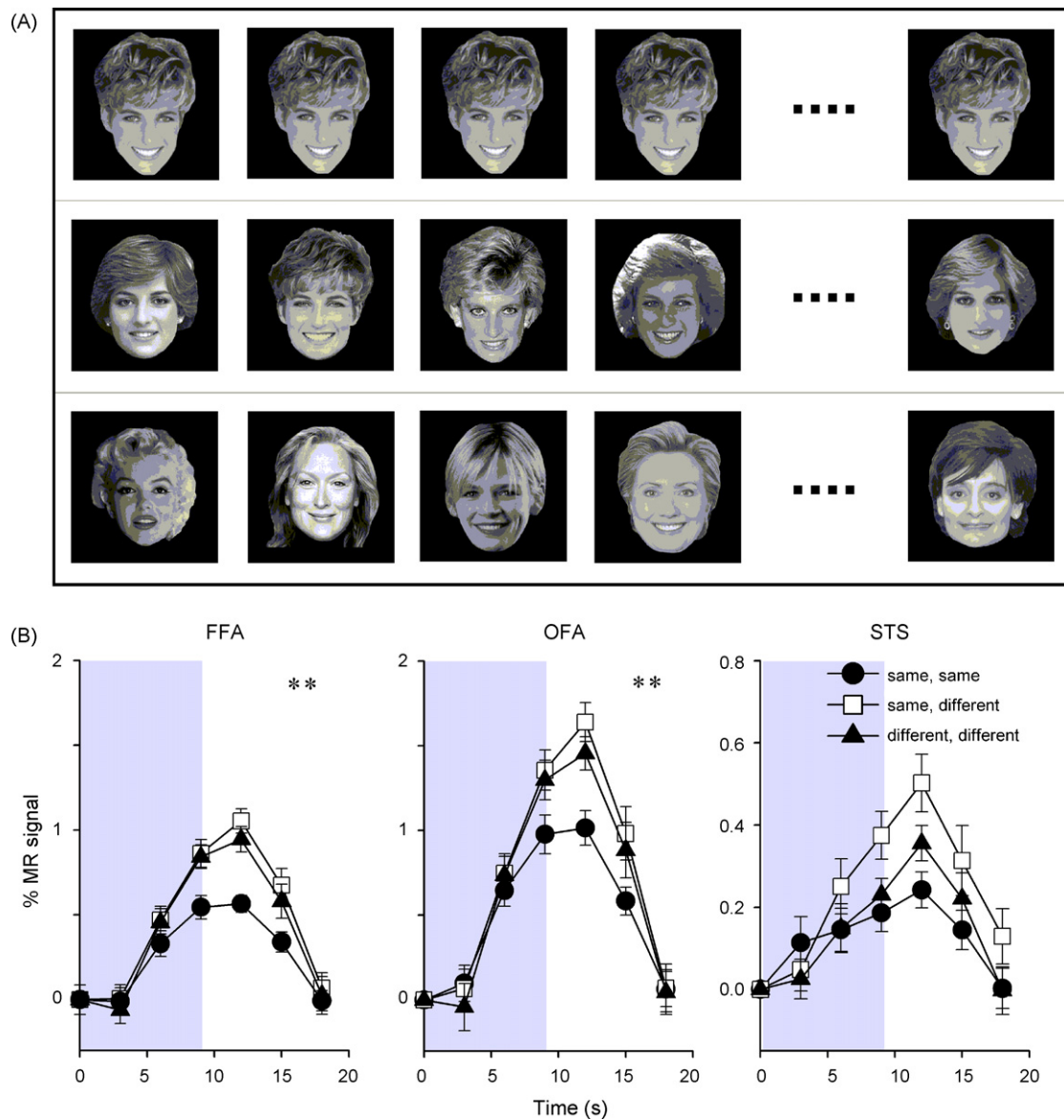


Fig. 3. Adaptation to familiar faces. (A) Examples of images used in the *same-identity, same-image* (top), *same-identity, different-images* (middle), and *different-identities, different-images* (bottom) conditions. (B) The average response across subjects is shown in the fusiform face area (FFA), the occipital face area (OFA), and the superior temporal sulcus (STS). MR time-courses were averaged across hemispheres and subjects. The shaded regions represent the duration of stimulus presentation. Error bars represent \pm S.E. ** $P < 0.01$, * $P < 0.05$.

ties, *different images* condition (unfamiliar: $t(14) = -1.21$, $P = 0.25$; familiar: $t(14) = -1.16$, $P = 0.27$). Interestingly, there was a trend toward a difference between the *same identity, different images* and *different identities, different images* conditions with familiar faces ($t(14) = 2.01$, $P = 0.06$). However, this was not in the direction predicted by fMR-adaptation (see also, Andrews & Ewbank, 2004—Fig. 5). A similar effect was not apparent for unfamiliar faces ($t(14) = 0.57$, $P = 0.58$). Finally, there was a main effect of familiarity ($F(1,14) = 19.66$, $P < 0.001$), which reflected a greater response to familiar compared to unfamiliar faces.

3.2.4. Whole-brain analysis

A whole-brain group analysis was performed to determine whether brain regions outside the regions of interest might show adaptation to faces. Table 3 and Fig. 4 show bilateral regions of the occipital and temporal lobe that showed a smaller response to the *same identity, same image* condition compared to the *different identity, different images* condition. A similar pattern of adaptation was found for familiar and unfamiliar faces. Interestingly, the adap-

tation extended beyond the core face-selective regions shown in Fig. 1A. Time series were obtained from these regions by transforming the group statistical maps back to each participants' brain. Although voxels from the face-selective regions were excluded from this new analysis, a similar pattern of response was found with a lower response to the *same identity, same image* condition.

Several regions showed a reduced response to the *same identity, different images* condition compared to the *different identity, different images* condition at the uncorrected level ($P < 0.001$). However, none of these regions were significant when corrected for multiple comparisons (Table 4). It is also important to note the markedly smaller cluster sizes in Table 4 (image-invariant adaptation) compared to Table 3 (image-dependent adaptation). Supplementary Table 1 shows the contrast *same identity, different images* > *different identity, different images*. Although this shows a more extensive pattern of response for familiar compared to unfamiliar faces at an uncorrected threshold, no voxels were significant when corrected for multiple comparisons.

Table 3
Voxels showing image-dependent adaptation to faces (*different identity, different images > same identity, same images*).

Region	Coordinates			Z-score	Cluster size (cm ³)	
	x	y	z		<i>P</i> < 0.001 (uncorrected)	<i>P</i> < 0.05 (corrected)
Familiar						
Anterior temporal						
L	-22	-6	-22	4.49	2.66	-
R	20	-10	-20	4.49	2.91	-
Occipital temporal						
L	-40	-52	-22	5.9	29.78	3.96
R	40	-52	-24	6.08	35.88	6.58
Unfamiliar						
Anterior temporal						
R	20	-12	-20	3.9	0.70	-
Occipital temporal						
L	-34	-72	-20	5.03	29.76	0.71
R	34	-64	-22	5.3	25.62	1.70

3.2.5. Behavioural task during scan

During the adaptation scans, subjects were instructed to perform a target detection task. Table 5 shows the average response times across all conditions. There was no significant

effect of familiarity ($F(1,18)=0.11, P=0.75$) or image condition ($F(2,36)=3.85, P=0.06$) on the response time. There was also no interaction between familiarity and condition for response times ($F(2,36)=1.25, P=0.33$).

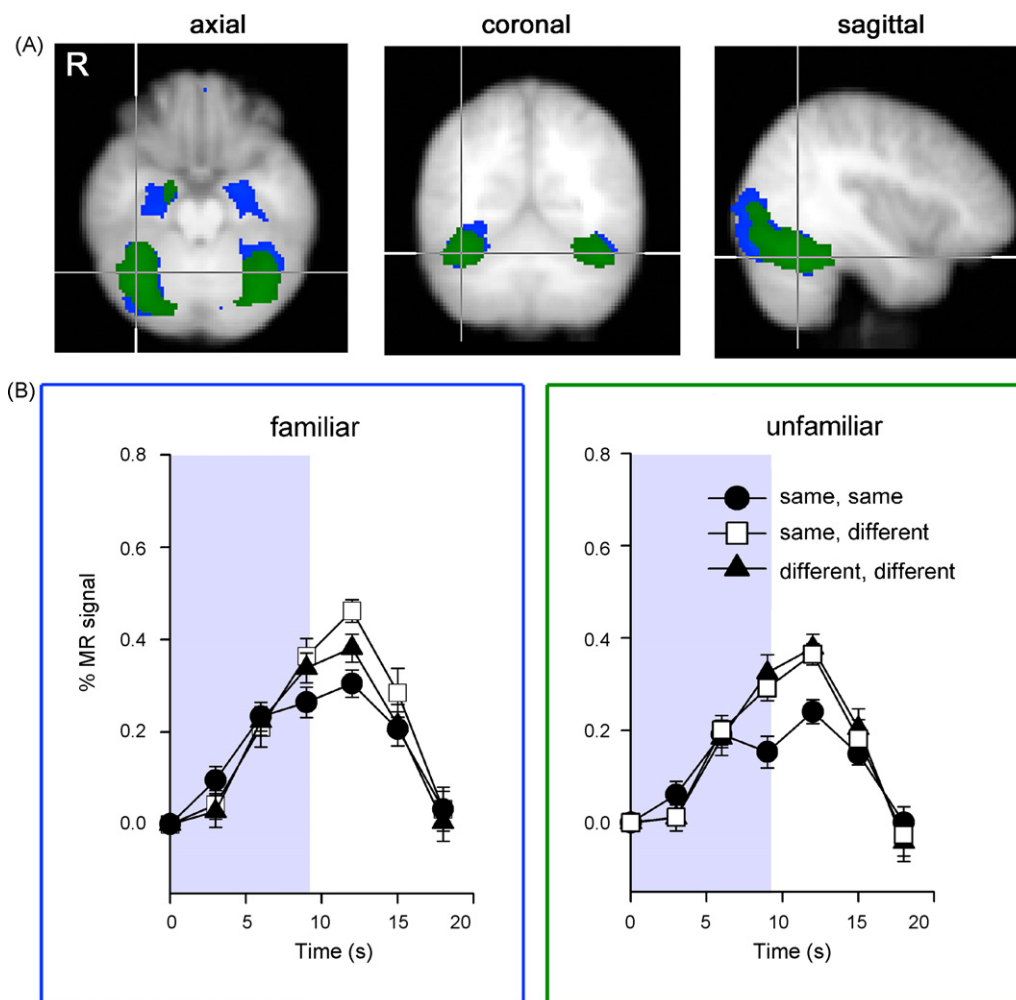


Fig. 4. Adaptation to familiar and unfamiliar faces in whole-brain analysis. (A) Areas showing adaptation to different-identity, different image > same-identity, same-image for familiar (blue) and unfamiliar (green) face conditions. These scan images follow radiological convention, with the left hemisphere shown on the right. The pattern of activation can be compared with face-selective regions shown in Fig. 1. (B) The average response across subjects in the occipital-temporal region. MR time-courses were averaged across hemispheres and subjects. The shaded regions represent the duration of stimulus presentation. Error bars represent \pm S.E. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 4Voxels showing image-invariant adaptation (*different identity, different images > same identity, different images*).

Region	Coordinates			Z-score	Cluster size (cm ³)	
	x	y	z		$P < 0.001$ (uncorrected)	$P < 0.05$ (corrected)
Familiar						
Superior frontal						
R	-26	12	66	3.84	0.16	-
Medial frontal						
R	-4	20	44	3.54	0.44	-
Unfamiliar						
Occipital temporal						
L	-8	-98	6	3.6	0.42	-
Inferior parietal						
L	-42	-36	2	3.58	0.32	-
Occipital						
L	-18	-56	10	3.59	0.26	-
Superior temporal						
L	-32	-54	8	3.43	0.14	-
L	-62	-42	14	3.36	0.14	-
R	70	-30	-18	3.35	0.38	-
Inferior temporal						
R	22	-22	-32	3.82	0.29	-
Cerebellum						
R	14	-48	-38	3.38	0.18	-

Table 5

Mean response times in milliseconds (S.E.M.) across subjects in target detection task performed during adaptation scans.

	Same, same	Same, different	Different, different
Familiar	510 (12.8)	468 (11.9)	491 (12.6)
Unfamiliar	499 (14.1)	482 (23.9)	469 (25.9)

3.2.6. Post-scan test of familiarity

After the scan, each subject was tested to determine their familiarity with the faces presented in the adaptation scan. Subjects reported that on average 88% (± 2.3) of the faces were familiar. In addition, they were able to report the occupation ($87\% \pm 2.3$) and name ($83\% \pm 2.7$) of the majority of the familiar faces. If we restricted our analysis to the same identity images, subjects were able to report that 95% (± 1.7) were familiar.

3.3. Independent behavioural task

The data from the behavioural study (Fig. 5) shows a significant effect of condition on reaction time (RT) and error rate ($F(2,34) = 37.14, P < 0.001$; $F(2,34) = 24.31, P < 0.001$). There was also an interaction between condition and familiarity for reaction times ($F(2,34) = 31.53, P < 0.001$). For familiar faces, the shortest RT occurred in the same condition when the same face was repeated. There was a significant increase in RT in the different condition when different images of the same person were shown compared to the same condition ($t(17) = 3.48, P < 0.01$).

For unfamiliar faces, the fastest RT also occurred when the same image was repeated. There was a significant increase in RT to the unprimed condition ($t(17) = 6.40, P < 0.001$). However, the slowest RT occurred in the different condition, which also had the highest error rate. Indeed, the only difference in RT between the responses

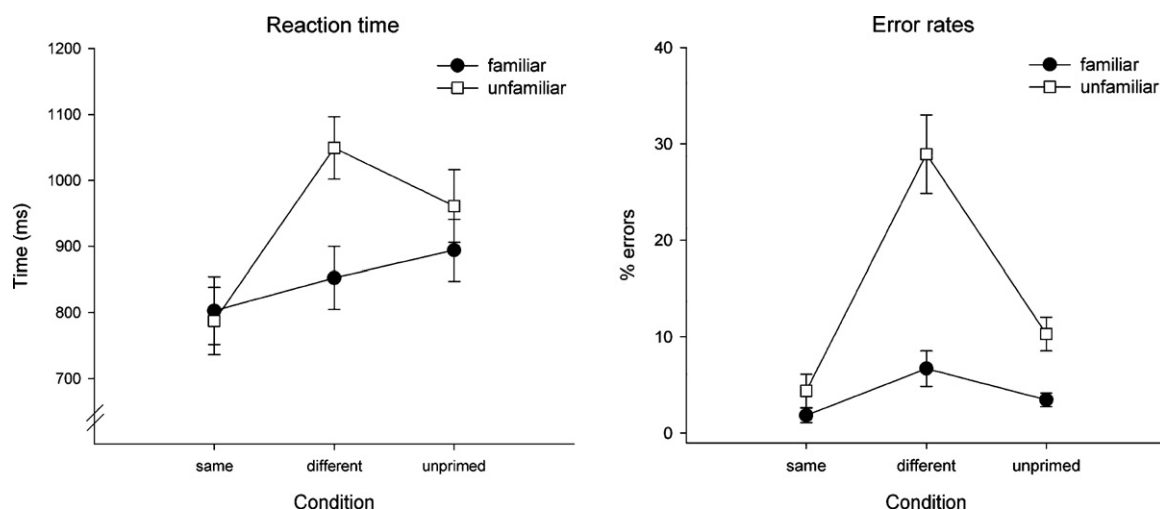


Fig. 5. Reaction time and error rate to images of familiar and unfamiliar faces. Subjects were asked to indicate whether a pair of successively presented images represented the same or a different identity. The images were either identical (same), different images of the same person (different) or different images of different people (unprimed).

to familiar and unfamiliar conditions, was in the different condition ($t(17) = 6.87$, $P < 0.001$), which accounts for the interaction between condition and familiarity.

4. Discussion

The aim of this experiment was to probe the neural representations underlying familiar and unfamiliar faces in the human ventral stream. We found a reduced response (adaptation) to repeated images of the same unfamiliar and familiar faces in the FFA and OFA, but not in the STS. To establish if the neural representation of faces in the FFA was invariant to changes in the image, we presented different images of the same person. Contrary to our prediction, we found a release from adaptation with both familiar and unfamiliar faces in the FFA and OFA. This suggests that an image-dependent representation is used to process familiar and unfamiliar faces in the ventral visual stream.

Models of face processing propose that information about faces is initially encoded in a pictorial or view-dependent representation. This initial encoding leads onto a view-invariant representation that is necessary for recognition (Bruce & Young, 1986; Burton et al., 1999). The difference in the ability to recognize familiar and unfamiliar faces across different image manipulations has led to the suggestion that unfamiliar faces are represented by a pictorial, view-dependent code, whereas familiar faces are represented by a view-invariant representation. We found support for this notion in a previous study, where we varied the viewing angle of successive face images in a fMR-adaptation paradigm (Ewbank & Andrews, 2008). Adaptation in the FFA to familiar faces was found across all changes in viewing angle, but a release from adaptation was found with increasing viewing angles for unfamiliar faces. Although this previous report demonstrates a more view-invariant representation exists for familiar compared to unfamiliar faces, the current study shows that there are limits to the invariance of the neural representation in the core face-selective regions. Indeed, a key difference between these studies is that Ewbank and Andrews (2008) changed the view of the same face image, whereas the images in the current study were from the same view, but varied in appearance.

To monitor attentional load across all conditions, subjects performed a reaction time task in response to a red dot that appeared on some of the images. It is possible that this non-face task may not have engaged the face-selective mechanisms in the brain. However, using a similar design, Andrews and Ewbank (2004) reported that face-selective adaptation was evident in face-selective regions such as the FFA, but not in object- or place-selective regions of the ventral stream. Again using a similar design, Ewbank and Andrews (2008) reported view-invariant fMR-adaptation in the FFA for familiar, but not unfamiliar faces. These results are also supported by event-related studies that did use a face task, but failed to find view-invariant responses in face-selective regions (Eger et al., 2005; Pourtois et al., 2005a, 2005b). Consistent with these findings, Xu, Turk-Browne, and Chun (2007) showed that adaptation in the PPA depends on visual characteristics of the images rather than task difficulty. Together, these results suggest that the absence of a face task may not explain the pattern of response to familiar and unfamiliar faces in this study. Nevertheless, these results cannot exclude the possibility that a view-invariant response may have been apparent, if subjects had to perform a specific face task.

The inability to reveal image-invariant responses in the core face-selective regions need not imply that this pattern of response does not exist in other brain regions. Indeed, previous fMRI studies have reported, viewpoint-invariant adaptation in regions that are not part of the core face-selective network (Eger et al., 2005; Pourtois et al., 2005a, 2005b). Although our group analysis did

reveal some regions that showed a reduced response to different images of the same identity (see Table 4), these were not significant when corrected for multiple comparisons and did not overlap with the patterns reported in previous fMRI studies. These results suggest that the behavioural advantage for the recognition of familiar faces may not depend on an image-invariant representation in the brain. Further support for this conclusion is provided by behavioural studies using repetition priming, which report a reduced priming effect when different images of the same person are used (Bruce, Burton, Carson, Hanna, & Mason, 1994; Ellis, Young, Flude, & Hay, 1987). Using the same stimuli that were employed in the fMRI study, we also found a reduced priming effect when a different image of a previously viewed familiar person was presented compared to when the same image was repeated. However, the behavioural difference in response to different images of the same person compared to the same image of the same person was more apparent for unfamiliar faces with subjects making significantly more errors. Nevertheless, the fMRI responses in the core face-selective regions to familiar and unfamiliar faces were very similar.

In the whole-brain analysis, we found that (image-dependent) adaptation to faces was not restricted to the core face-selective regions, but was evident across a large part of the ventral stream (see Fig. 4). This finding is significant in the dispute about whether information in the ventral stream is represented by a modular or distributed neural code (Andrews, 2005; Cohen & Tong, 2001; Haxby et al., 2001; Reddy & Kanwisher, 2006). Previously, we reported that adaptation to faces was restricted to face-selective regions of the ventral stream and was not found in object- and place-selective regions (Andrews & Ewbank, 2004). However, this study restricted its analysis to functionally defined regions of interest. The current findings would appear to support the idea that information about faces is not restricted to the face-selective regions, but can be found in other regions of the human ventral stream. Indeed, this is consistent with neuropsychological studies that have shown the perception and recognition of faces is not restricted to a single location, but can be impaired by lesions to different parts of the ventral stream (McNeil & Warrington, 1993; Rossion et al., 2003; Steeves et al., 2006). This shows that fMR-adaptation can provide a useful measure of stimulus selectivity in neuroimaging studies of the visual system. As selectivity is typically defined by comparing the relative response to different types of visual stimulus, the choice of control condition is important in determining which brain areas appear 'face-selective'. The key advantage of the adaptation paradigm is that it does not involve the use of a category contrast and is therefore not restricted to circumscribed regions of interest. Adaptation to facial identity was not apparent in all face-selective regions. Consistent with previous studies, we failed to find a reduced response to repeated images of familiar or unfamiliar faces in the superior temporal face regions (Andrews & Ewbank, 2004; Ewbank & Andrews, 2008). This fits with models of face processing that emphasize the difference between inferior temporal processes involved in facial recognition and superior temporal processes involved in understanding dynamic aspects of faces (Andrews & Ewbank, 2004; Haxby et al., 2000; Hoffman & Haxby, 2000). In contrast, we found a trend for a larger response to different images of the same identity compared to different images of different identities with familiar, but not unfamiliar faces in the STS.

In conclusion, we found no evidence of image-invariant adaptation in face-selective regions to either familiar faces or unfamiliar faces. We also report that the pattern of image-dependent adaptation extends beyond the face-selective regions and implies that a distributed neural code is used to represent images of faces. The similarity in response to familiar and unfamiliar faces contrasts with the marked differences in the way these visual stimuli are perceived.

Acknowledgements

We would like to thank Spyroula Spyrou for her help during the initial stages of this project. We would also like to thank Professor Gary Green, Chris Alderson and the other members of the YNiC for their help during the course of this project. JD-T is supported by an ESRC studentship. We are also grateful to the reviewers of this manuscript for their helpful comments.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2009.01.017.

References

- Andrews, T. J. (2005). Visual cortex: How are objects and faces represented? *Current Biology*, 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.
- Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology*, 77, 305–327.
- Bruce, V., Burton, A. M., Carson, D., Hanna, E., & Mason, O. (1994). Repetition priming of face recognition. In C. Umiltà & M. Moskovitch (Eds.), *Attention and performance XV* (pp. 179–210). Cambridge: MIT Press.
- Burton, A. M., Bruce, V., & Hancock, P. J. B. (1999). From pixels to people: A model of familiar face recognition. *Cognitive Science*, 23, 1–31.
- Cohen, J. D., & Tong, F. (2001). The face of controversy. *Science*, 293, 2405–2407.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical areas selective for processing the human body. *Science*, 293, 2470–2473.
- Eger, E., Schyns, P. G., & Kleinschmidt, A. (2004). Scale invariant adaptation in fusiform face-responsive regions. *NeuroImage*, 22(1), 232–242.
- Eger, E., Schweinberger, S. R., Dolan, R. J., & Henson, R. N. (2005). Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *NeuroImage*, 26, 1128–1139.
- Ellis, A. W., Young, A. W., Flude, B. M., & Hay, D. C. (1987). Repetition priming of face recognition. *Quarterly Journal of Experimental Psychology*, 39a, 193–210.
- Ewbank, M. P., & Andrews, T. J. (2008). Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex. *NeuroImage*, 40, 1857–1870.
- Fang, F., Murray, S. O., & He, S. (2006). Duration-dependent fMRI adaptation and distributed viewer-centred face representation in human visual cortex. *Cerebral Cortex*, 17(6), 1402–1411.
- Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, J. W. (2000). The fusiform face area is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, 12, 495–504.
- Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in human lateral occipital complex. *Neuron*, 24, 187–203.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Science*, 10, 14–23.
- Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in Cognitive Sciences*, 4, 330–337.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Science*, 4, 223–233.
- 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.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3, 80–84.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in extrastriate cortex specialised for face perception. *Journal of Neuroscience*, 17, 4302–4311.
- Krekelberg, B., Boynton, G. M., & van Wezel, R. J. A. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neurosciences*, 29(5), 250–256.
- McNeil, J. E., & Warrington, E. K. (1993). Prosopagnosia—a face-specific disorder. *Quarterly Journal of Experimental Psychology*, 46A, 1–10.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford University Press.
- Peelen, M., & Downing, P. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93(1), 603–608.
- Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005a). Portraits or people? Distinct representations of face identity in the human visual cortex. *Journal of Cognitive Neuroscience*, 17, 1043–1057.
- Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005b). View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: An event-related fMRI study. *NeuroImage*, 24, 1214–1224.
- Reddy, L., & Kanwisher, N. (2006). Coding of visual objects in the ventral stream. *Current Opinion in Neurobiology*, 16(4), 408–414.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A.-M., Lazeyras, F., & Mayers, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, 126(11), 2381–2395.
- Schwarzlose, R., Baker, C., & Kanwisher, N. (2005). Separate Face and Body Selectivity on the Fusiform Gyrus. *Journal of Neuroscience*, 25(47), 11055–11059.
- Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., et al. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, 23(S1), 208–219.
- Steeves, J. K. E., Culham, J. C., Duchaine, B. C., Pratesi, C. C., Valyear, K. F., Schindler, I., et al. (2006). The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia*, 44(4), 594–609.
- Winston, J. S., Henson, R. N. A., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-Adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology*, 92, 1830–1839.
- Xu, T., Turk-Browne, N. B., & Chun, M. M. (2007). Dissociating task performance from fMRI repetition attenuation in ventral visual cortex. *Journal of Neuroscience*, 27, 5981–5985.