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Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex

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People are extremely proficient at recognizing faces that are familiar to them, but are poor at identifying unfamiliar faces. We used fMR-adaptation to ask whether this difference in recognition might be reflected in the relative viewpoint-dependence of face-selective regions in the brain. A reduced response (adaptation) to repeated images of unfamiliar or familiar faces was found in the fusiform face area (FFA), but not in the superior temporal sulcus (STS) face-selective region. To establish if the neural representation of faces was invariant to changes in viewpoint, we parametrically varied the viewing angle of successive images using 3-dimensional models of unfamiliar and familiar faces. We found adaptation to familiar faces across all changes in viewpoint in the FFA. In contrast, a release from adaptation was apparent in the FFA when unfamiliar faces were viewed at increasing viewing angles. These results provide a neural basis for differences in the recognition of familiar and unfamiliar faces.

Keywords: Visual cortex; View-dependent; View-independent; Object-centred; FFA; OFA; STS

Introduction

Recognising faces is a simple and effortless process for most human observers. However, the face of any individual can generate countless different retinal images depending on the viewing position. To discriminate and recognize faces, the visual system must discount sources of variation caused by changes in view. Models of face processing propose a dual route for processing information about identity and changeable aspects of faces. The initial processing of facial identity involves computation of a view-dependent representation. Information from this early stage of processing is then compared with view-independent representations that are integral in the recognition of familiar faces (Bruce and Young 1986; Burton et al., 1999).

Behavioural studies suggest that both view-dependent and view-independent representations can be used to recognize faces. For example, while people are very good at identifying familiar faces (even from very low quality images), performance in recognition or matching of unfamiliar faces across different views is poor (O'Toole et al., 1998; Hill et al., 1997; Hancock et al., 2000; Lee et al., 2006). This difference in the ability to recognise familiar and unfamiliar faces has led to the suggestion that familiar faces are represented by a view-invariant representation, whereas unfamiliar faces are represented in a view-dependent manner (Bruce and Young, 1986; Burton et al., 1999). However, psychophysical studies using adaptation have shown that view-dependent after-effects can occur for both familiar and unfamiliar faces (Fang and He, 2005; Ryu and Chaudhuri, 2006; Jiang et al., 2007). Further evidence for viewpoint dependence can be found in studies of repetition priming using familiar faces in which a reduced priming effect is apparent as the difference between prime and the test faces is increased (Ellis et al., 1987; Bruce et al., 1994).

Physiological investigations also provide support for both view-independent and view-dependent mechanisms underlying face recognition. Neurons in the temporal lobe of non-human primates are known to respond to complex objects such as faces. Although the majority of these neurons respond to a particular view of a face (view-dependent), a subpopulation of neurons has been shown that respond in a view-independent fashion (Perrett et al., 1985; Perrett

Table 1
Mean change in intensity between successive images in each condition of the adaptation scan (SEM)

	Identity	0°	2°	4°	8°
Unfamiliar	Same	0 (0)	10 (1.0)	10 (0.7)	12 (1.2)
	Different	28 (1.5)	30 (2.3)	28 (2.5)	27 (1.6)
Familiar	Same	0 (0)	12 (1.1)	15 (2.3)	17 (0.9)
	Different	31 (4.5)	32 (4.7)	35 (1.5)	33 (3.1)

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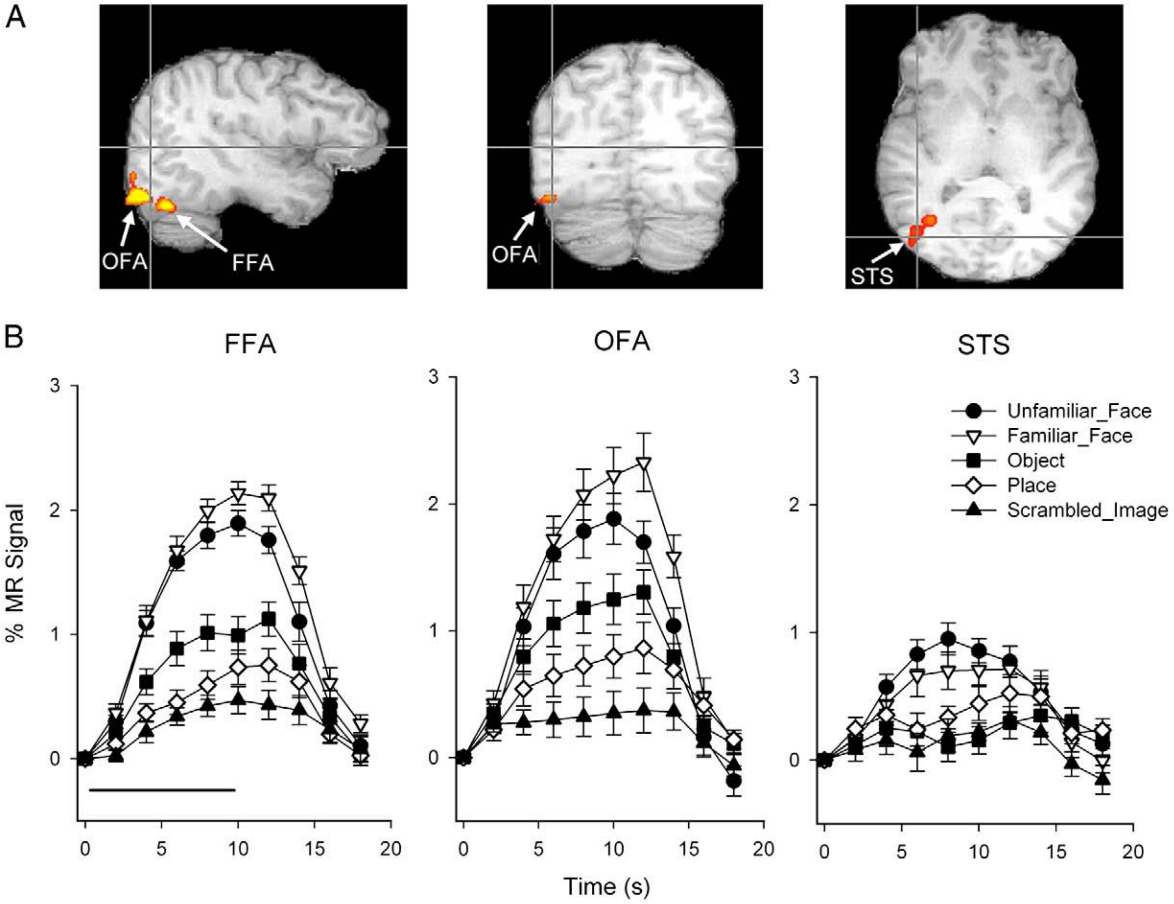
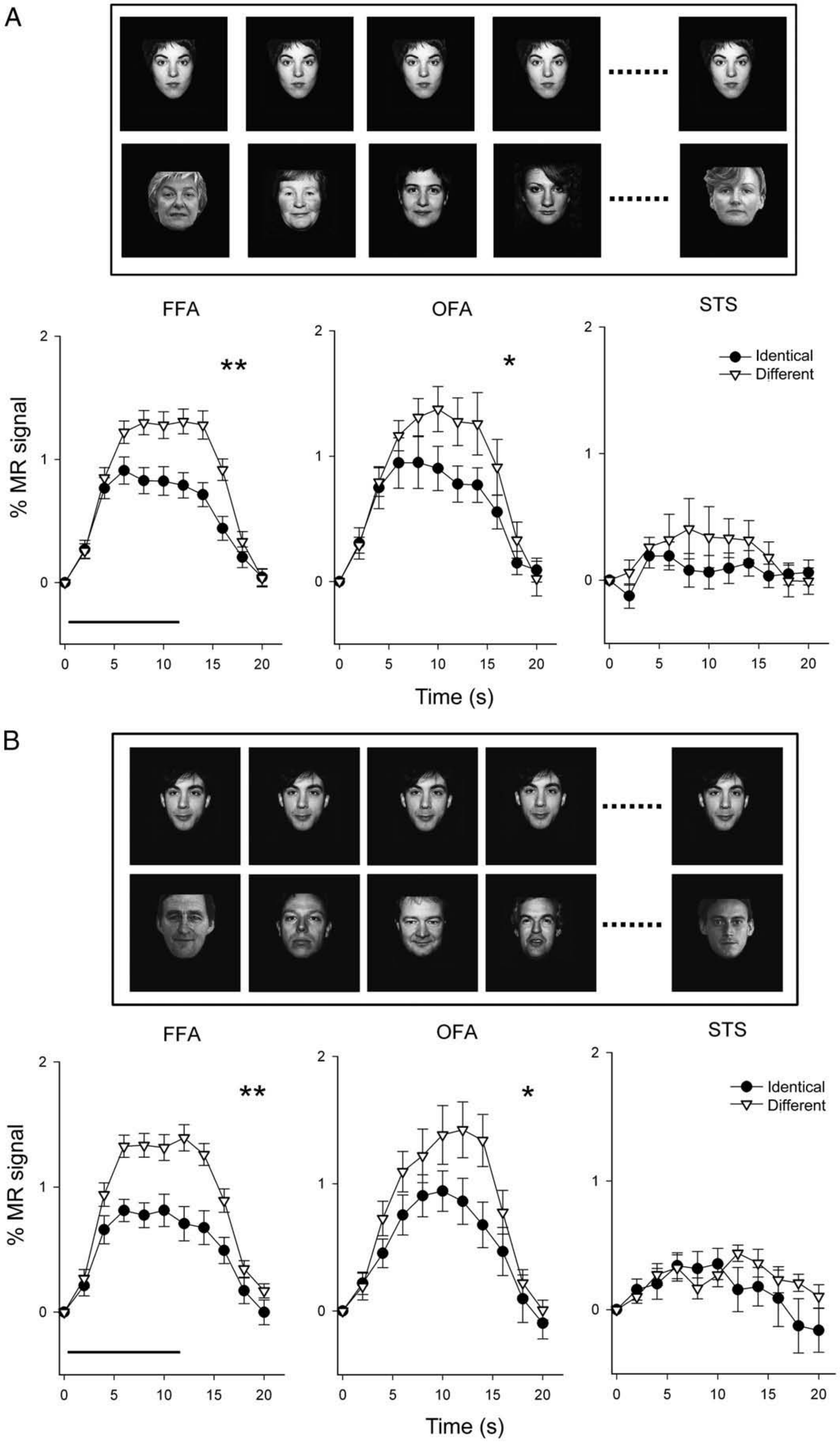


Fig. 1. Localiser scan. (A) Location of face-selective regions in the brain of one observer (FFA: fusiform face area, OFA: occipital face area, STS: superior temporal sulcus). These scan images follow radiological convention, with the left hemisphere shown on the right. (B) MR time-course during localiser scans, showing activity averaged across hemispheres and subjects for each stimulus category in face-selective areas. The horizontal bar represents the duration of each stimulus block. Error bars represent ±1 standard error.

et al., 1991; Rolls, 2000). Neuroimaging studies have also revealed a core network of face-selective regions in the occipital and temporal lobe that are involved in face processing (Haxby et al., 2000). Processing of facial identity is associated with view-invariant representations in the inferior temporal lobe regions, such as the fusiform face area (FFA), whereas changeable aspects of faces are processed in the superior temporal lobe (Hoffman and Haxby, 2000; Andrews and Ewbank, 2004). Using fMR-adaptation, a number of studies have found that the response to faces in face-selective regions, such as the FFA, is viewpoint-dependent (Grill-Spector et al., 1999; Andrews and Ewbank, 2004; Fang et al., 2007). However, the changes in viewpoint used in these studies were quite large (>30°) and they only used unfamiliar faces. It is possible, therefore, that viewpoint-invariant responses may be found when presenting smaller changes in viewing angle, or when showing faces that are familiar to the observer. Support for the influence of familiarity in view-invariance can be found in the responses of brain regions outside the core face-selective regions. For example, viewpoint-invariant responses to familiar faces are found in the anterior and lateral regions of the temporal lobe and in inferior frontal lobe regions (Pourtois et al., 2005; Eger et al., 2005). Further evidence for the effect of familiarity on view-independence is evident in the hippocampus of human patients undergoing surgery, where neurons can respond to strikingly different images of well-known individuals (Quiroga et al., 2005).

The aim of this study was to determine whether there is a difference in the view-dependency for familiar and unfamiliar faces in face-selective regions of the human brain. Using an fMR-adaptation paradigm, we parametrically varied the viewpoint of successive images using three-dimensional models of unfamiliar and familiar faces. If the representation of faces in a region is view invariant, we would predict a reduced response to repeated images of the same face when shown from different viewpoints. In contrast, any recovery from adaptation when images of the same

Fig. 2. Unfamiliar face adaptation experiment. Examples of images in the same-identity and different-identity conditions at (A) 0°, (B) 2°, (C) 4° and (D) 8° change. 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 horizontal bar represents the duration of stimulus presentation. Error bars represent ±1 standard error. $^{**}P<0.01$, $^{*}P<0.05$.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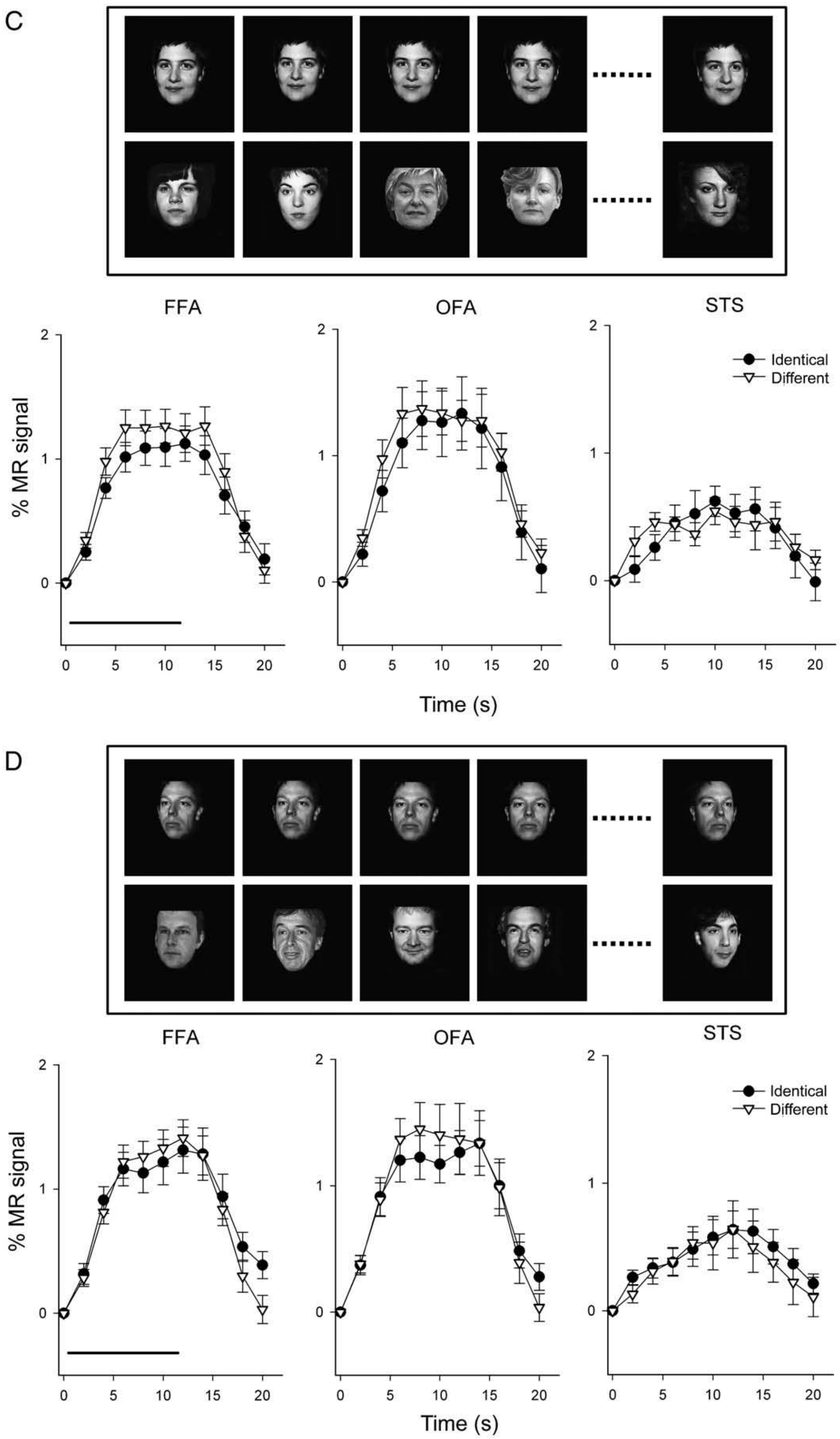


Fig. 2 (*continued*).

face are presented over different viewpoints would suggest that the underlying neuronal representation is view-dependent. Our hypothesis was that the neural representation underlying familiar faces should be less view-dependent than for unfamiliar faces.

Methods

Subjects

Fourteen subjects participated in the fMRI study, (eight females; mean age, 25). All observers had normal or corrected to normal visual acuity. Written consent was obtained from all subjects and the study was approved by the York Neuroimaging Centre Ethics Committee. Subjects lay supine in the magnet bore and viewed stimuli (approx. 8°×8°) back-projected onto a screen located inside the bore of the scanner, approximately 57 cm from their eyes.

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 20 contiguous axial slices. (TR 2s, TE = 30 ms, FOV 240 mm^2, in plane resolution 1.875 × 1.875 mm, slice thickness 4 mm).

Localizer scan

To discriminate regions of visual cortex that are selectively activated by faces, a localizer scan was carried out for each subject. Each scan contained 20 stimulus blocks. Each block contained images from one of five different object categories: (i) unfamiliar faces, (ii) familiar faces, (iii) inanimate objects, (iv) places (buildings, indoor and outdoor scenes) or (v) phase scrambled images of faces, inanimate objects and places. Photographs of unfamiliar faces were taken from a database of the Psychological Image Collection at Stirling (PICS: http://pics.psych.stir.ac.uk), images of familiar faces were taken from the World Wide Web and differed to those used in the adaptation scan. Images of inanimate objects and places were obtained from various sources including commercial clip-art collections (CorelDraw, Microsoft). Phase scrambled images were Fourier randomized images from each of the other four categories. Each stimulus block contained 10 images with each image being presented for 800 ms followed by a 200-ms blank screen. Each stimulus condition was repeated four times in a counterbalanced block design. Stimulus blocks were separated by periods of fixation when a white cross on a grey screen was viewed for 10 s.

Statistical analysis of the localizer scans was carried out using FEAT (http://www.fmrib.ox.ac.uk/fsl). The initial 8 s of data from each scan were removed to minimize the effects of magnetic saturation. Motion correction was carried out using MCFLIRT (http://www.fmrib.ox.ac.uk/fsl), followed by spatial smoothing (Gaussian, FWHM 5.0 mm) and temporal high-pass filtering (cutoff, 0.01 Hz). Z-statistic images based on the contrast between different events were generated using resel thresholding ($P<0.05$). Face selective regions of interest (ROI) were determined by the contrast unfamiliar face > object. 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 by the mean response of each scan ([x – mean] / mean * 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. Repeated-measures ANOVA was used to determine significant differences in the response to each stimulus condition.

Adaptation Scan

Next, we determined whether the previously defined face-selective ROIs showed adaptation to facial identity. There were two adaptation scans, one consisting of unfamiliar faces and another containing familiar faces. The order of scans was counterbalanced across subjects. The experimental procedure was identical for both scans. In each scan, stimulus blocks contained either 12 images of the same face (same-identity) or 12 images of different faces (different-identity). Each image was presented for 800 ms followed by a 200-ms blank screen. Stimulus blocks also varied in the degree of viewpoint change about the vertical axis between images. Four different viewpoint change conditions were used: (1) 0° same viewpoint; (2) 2° change; (3) 4° change; (4) 8° change. Thus, there were 8 different stimulus conditions in each scan. Each condition was repeated four times giving 32 blocks. A different identity was used for each repetition of the same identity conditions. Images in the same viewpoint condition were shown from a frontal viewpoint throughout the block. In the viewpoint change conditions, the first face image in each block was always a frontal view; this was followed by subsequent images rotation to the left or right of the preceding image. Faces were rotated 3 increments to the left and the right. For example, in the 2° change condition faces were shown over a range of 12° (0°, 2°, 4°, 6°, 4°, 2°, 0°, −2°, −4°, −6°, −4°, −2°).

To generate the images of unfamiliar and familiar faces at different viewpoints, we recovered a 3-dimensional model of each face from a single, frontal view using shape-from-shading technique that exploits the statistical properties of facial shape (Smith and Hancock, 2006). By restricting the algorithm to a certain class of objects (namely faces); the model provides a sufficiently powerful constraint to allow accurate reconstructions from a single image. The estimated 3-dimensional models can be rotated to yield realistic images of each face from different viewpoints. 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 two successive images. Table 1 shows that there was a similar mean intensity change in the corresponding familiar and unfamiliar conditions. The identities of the familiar faces used are listed in Supplementary Table 1.

Each stimulus condition was repeated four times in a counterbalanced block design giving a total of 32 blocks for each scan (familiar or unfamiliar). Blocks of images were separated by a grey screen, containing a white fixation cross, shown for a period of 10 s. During each stimulus block, subjects were instructed to perform a target detection task, with one or two images in each block containing a red dot. 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 on the face. Although the position of the red dot was varied within a condition, identical locations were used across all conditions.

The time series of the resulting filtered MR data at each ROI was converted from units of image intensity to units of percentage signal change. The average peak response was calculated from each ROI in each condition for each subject using the mean signal change during the period of 6 to 12 s after stimulus onset. Activity was averaged across hemispheres for bilaterally activated regions following a 2-way ANOVA to determine effects of hemisphere. A multi-factorial ANOVA was used to determine the main effects of Identity (same, different), and viewpoint (0, 2, 4, 8) in each ROI. To assess whether the reduction in response was significant for particular viewpoints we performed a two-sample *t*-test on the peak MR response across subjects. We also calculated an adaptation index to quantify the reduction in the MR response during the same image blocks compared to different image blocks: Response[same]/Response [different]. Finally, we performed a series of simple regressions to examine the relationship between the adaptation index and changes in viewpoint.

Behavioural Experiment

To determine whether there were any differences in the ability to discriminate changes in viewpoint for familiar and unfamiliar faces, we performed a behavioural experiment outside the scanner using 20 subjects who had not been involved in the fMRI experiment. The behavioural experiment used the same stimulus parameters and images that were employed in the fMRI experiment. Subjects viewed a central fixation cross throughout each trial. During each trial a face image oriented at 0° was presented for 400 ms. This was followed by an interval of 500 ms before a second face image was presented for 400 ms. The second face image had the same identity, but could vary in viewpoint (0, 2, 4, 8°). The task was to report the direction of rotation.

Results

Localizer scan

Fig. 1A shows three different regions in the occipital and temporal lobe that showed face-selective activity: (1) fusiform face area (FFA, Kanwisher et al., 1997); (2) occipital face area (OFA, Gauthier et al., 2000); superior temporal sulcus (STS, Hoffman and Haxby, 2000). Face-selective responses were found in the right FFA of all 14 subjects, the left FFA of 12 subjects, the right OFA of 12 subjects and right posterior STS of 8 subjects. Each region was defined separately for each 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. There was a significantly larger response to images of familiar faces than unfamiliar faces in FFA ($F(1,13) = 5.0$, $P < 0.05$) and OFA ($F(1,11) = 19.0$, $P < 0.05$), but not in STS ($F(1,7) = 0.72$, $P = 0.48$). Consistent with the FEAT analysis, an ANOVA showed that the FFA was significantly more activated by images of unfamiliar faces than inanimate objects ($F(1,13) = 41.6$, $P < 10\text{e-}5$), places ($F(1,13) = 156.4$, $P < 10\text{e-}8$) and phase scrambled images ($F(1,13) = 190.34$, $P < 10\text{e-}8$). The FFA also showed a significantly greater response to images of familiar faces compared to inanimate objects ($F(1,13) = 76.9$, $P < 10\text{e-}6$), places ($F(1,13) = 176.5$, $P < 10\text{e-}8$) and phase scrambled images ($F(1,13) = 262.1$, $P < 10\text{e-}9$). The OFA also showed a significantly greater response to unfamiliar faces than to inanimate objects ($F(1,11) = 44.4$, $P < 10\text{e-}5$), places ($F(1,11) = 67.8$, $P < 10\text{e-}6$), and phase scrambled images ($F(1,11) = 50.9$, $P < 10\text{e-}5$), and also to familiar faces compared to inanimate objects ($F(1,11) = 50.4$, $P < 10\text{-}5$), places ($F(1,11) = 88.4$, $P < 10\text{e-}6$), and phase scrambled images ($F(1,11) = 57.8$, $P < 10\text{e-}5$). Finally, STS showed significantly greater activation to unfamiliar faces than inanimate objects ($F(1,7) = 45.5$, $P < 0.01$), places ($F(1,7) = 57.6$, $P < 0.0002$), and phase scrambled images ($F(1,7) = 26.1$, $P < 0.01$), and to familiar faces compared to inanimate objects ($F(1,7) = 10.2$, $P < 0.05$), places ($F(1,7) = 21.3$, $P < 0.01$) and scrambled images ($F(1,7) = 7.8$, $P < 0.05$).

Adaptation Scan

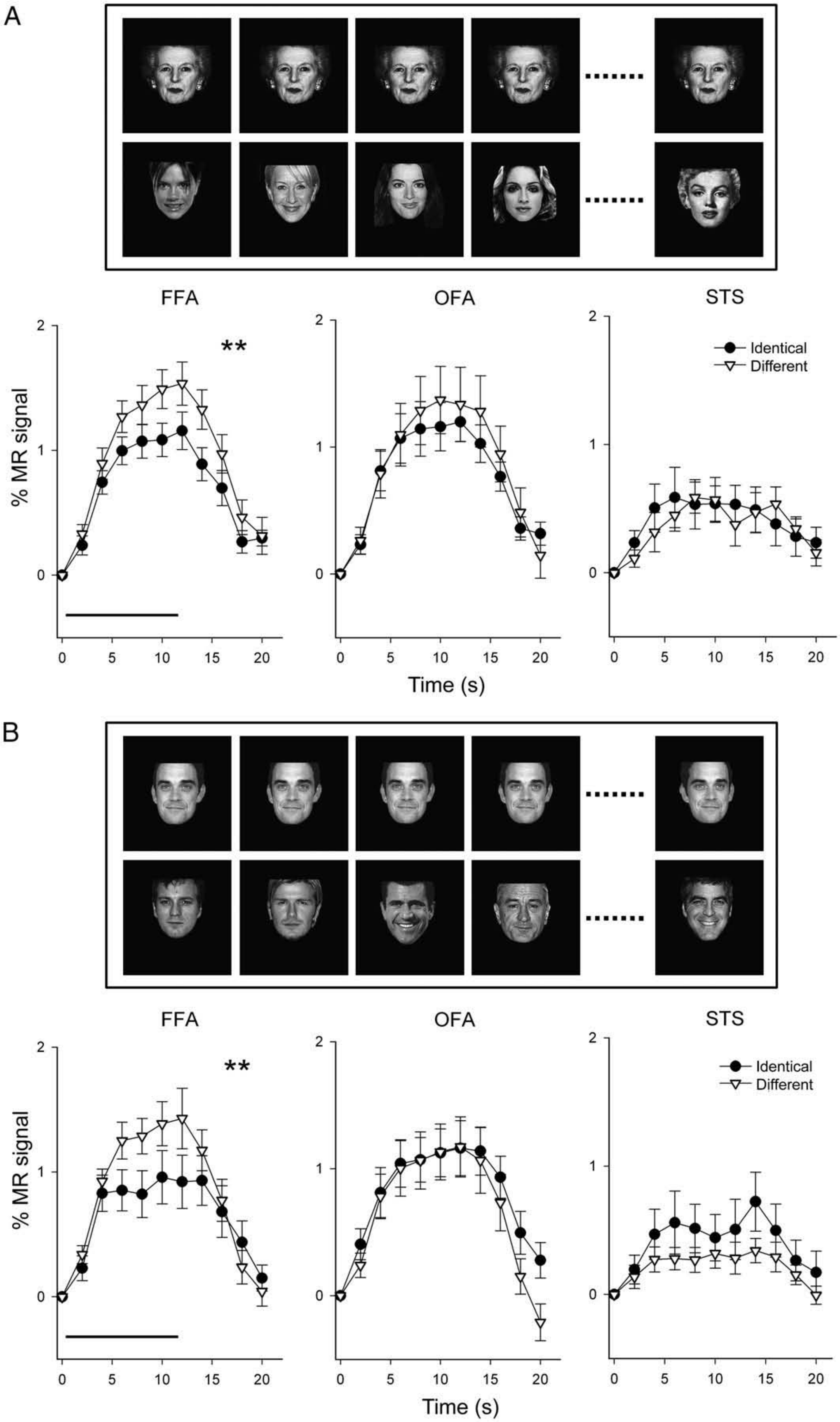
First, we examined the average response to unfamiliar (Fig. 2) and familiar (Fig. 3) faces across all face-selective ROIs and to all changes in identity and viewpoint. For unfamiliar faces, a 3-factor ANOVA 2 × 3 × 4 (Identity, Region, Viewpoint) showed a significant main effect for Identity ($F(1,6) = 8.70$, $P < 0.05$) and Region ($F(2,12) = 4.67$, $P < 0.05$). We also found a trend toward an interaction between Identity × Viewpoint ($F(3,18) = 2.88$, $P = 0.06$) suggesting that the degree of adaptation differed across viewpoint. An ANOVA on familiar faces failed to show a main effect of Identity ($F(1,6) = 1.06$, $P = 0.34$). However, we found a highly significant interaction between Identity × Region ($F(3,18) = 20.02$, $P < 0.001$), suggesting that adaptation to familiar faces was only apparent in some face-selective regions.

FFA

As FFA activity was found bilaterally in 12 subjects, we compared effects in right and left FFA by including hemisphere as a factor. We found no interaction between Hemisphere × Identity (unfamiliar: $F(1,11) = 2.42$, $P = 0.15$; familiar: $F(1,11) = 1.41$, $P = 0.26$), or Hemisphere × Viewpoint (unfamiliar: $F(3,33) = 0.25$, $P = 0.85$; familiar: $F(3,33) = 1.59$, $P = 0.21$). Accordingly, the responses in subjects showing left and right FFA were combined for the remainder of the analysis. The responses in the FFA to images of the same and different faces at different viewpoints in the unfamiliar and familiar face conditions were analyzed using a 3-way (Familiarity × Identity × Viewpoint) ANOVA. This revealed a main effect of Identity ($F(1,13) = 40.88$, $P < 0.0001$) and Viewpoint ($F(3,39) = 4.06$, $P < 0.05$). There was also an interaction between Identity × Viewpoint ($F(3,39) = 4.17$, $P < 0.05$), suggesting that adaptation differed across changes in view.

Fig. 4A shows the adaptation-index in the FFA plotted against viewpoint change. The results show a significant relationship between adaptation and viewpoint for unfamiliar faces, with the degree of adaptation decreasing as a function of viewpoint change ($r = 0.40$, $P < 0.005$). In contrast, we found no relationship between adaptation and viewpoint change for familiar faces ($r = 0.04$, $P = 0.76$) with the adaptation index remaining unchanged with changes in viewpoint. To determine whether adaptation to faces occurred at each of the different viewpoints, we compared responses to repeated presentations of the same face (same-identity) with responses to images of different faces (different-identity). First, we compared responses to images of the

Fig. 3. Familiar face adaptation experiment. Examples of images in the same-identity and different-identity conditions at (A) 0°, (B) 2°, (C) 4° and (D) 8° change. 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 horizontal bar represents the duration of stimulus presentation. Error bars represent ± 1 standard error. $^{**}P < 0.01$, $^{*}P < 0.05$.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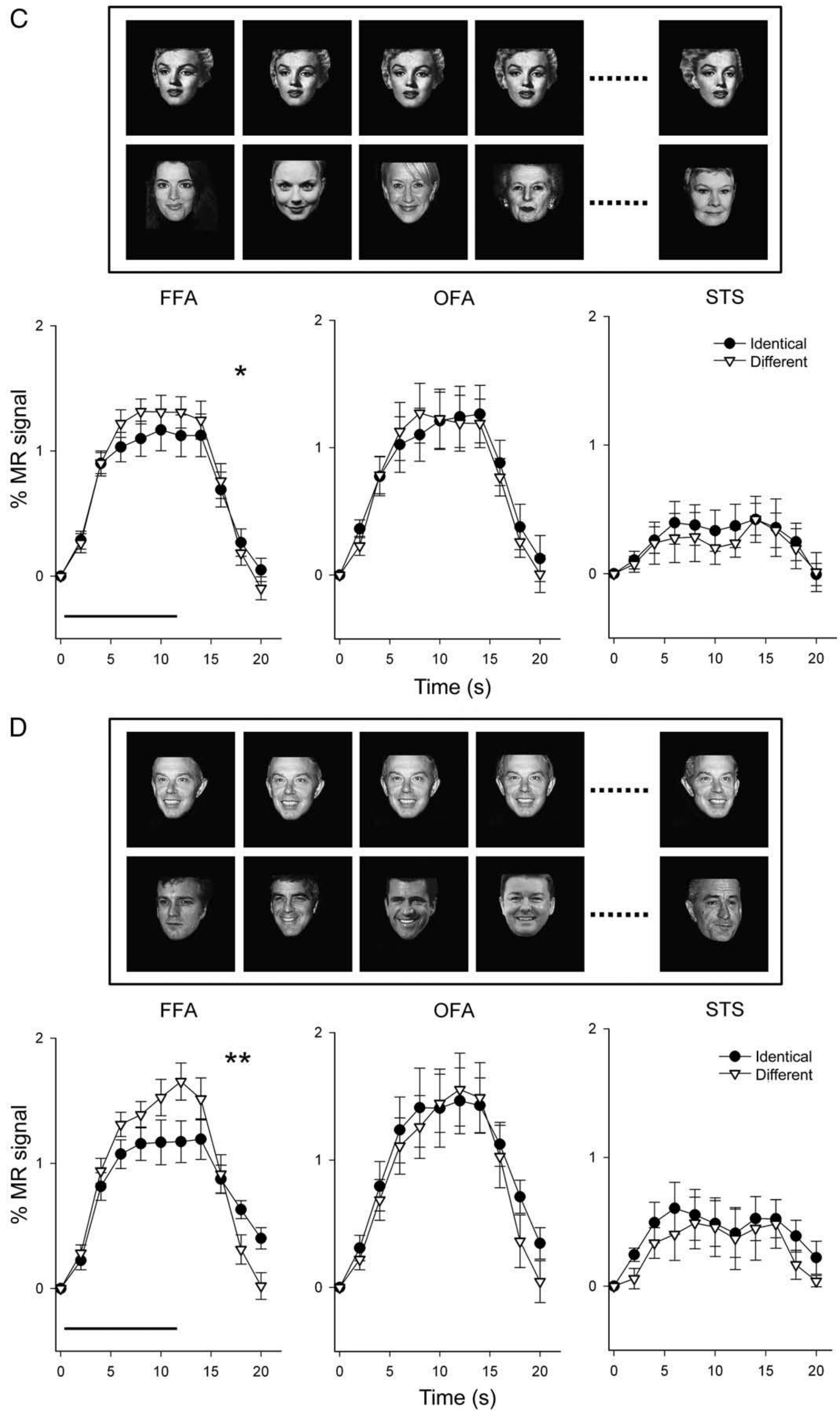

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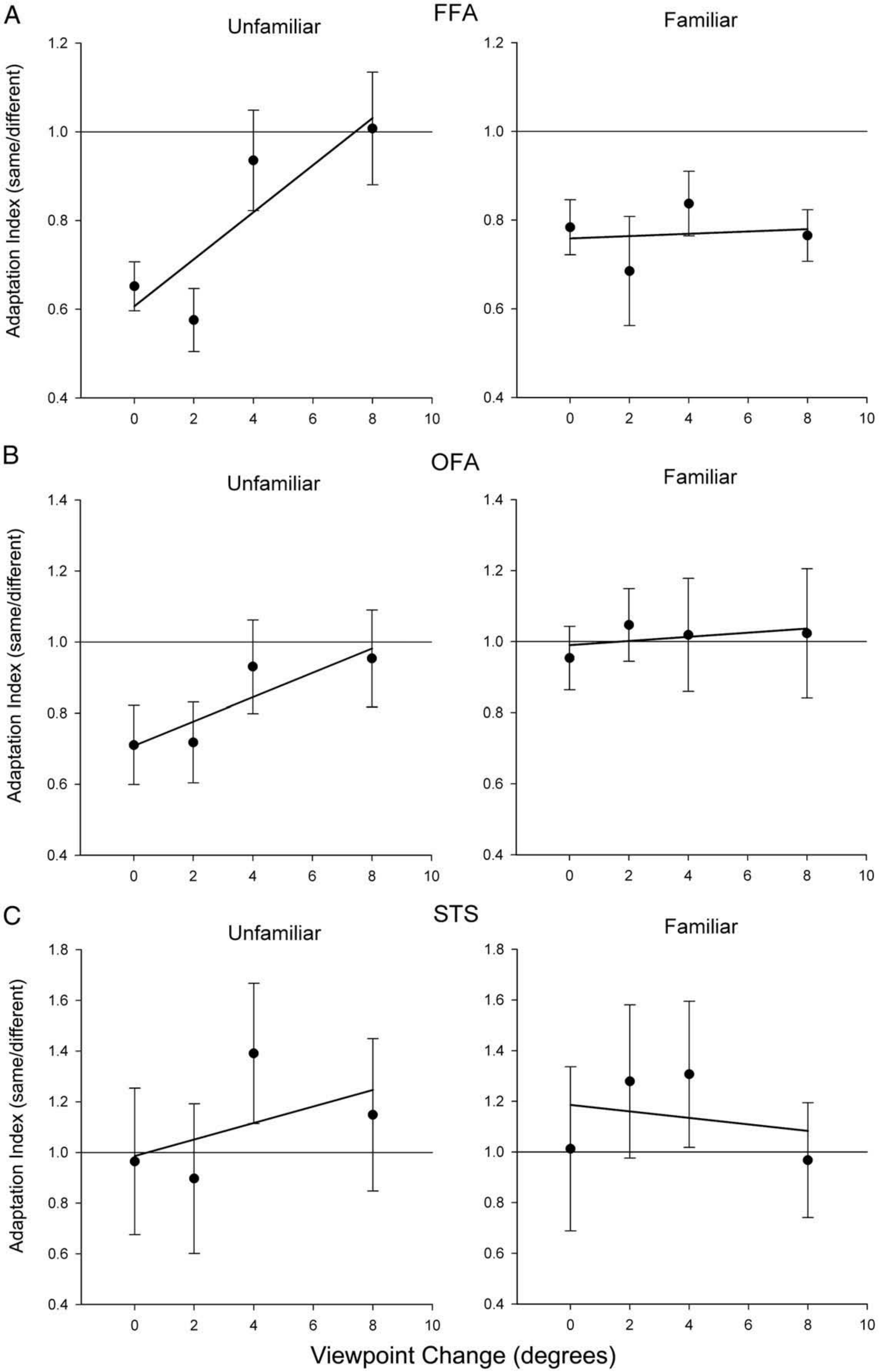

Fig. 4. Adaptation effect in (A) FFA, (B) OFA and (C) STS for unfamiliar (left) and familiar (right) faces. Data points represent adaptation of the MR response (*same identity*/*different identity*) averaged across all subjects plotted against change in viewpoint. An adaptation index = 1 signifies no adaptation effect. Error bars represent ±1 standard error.

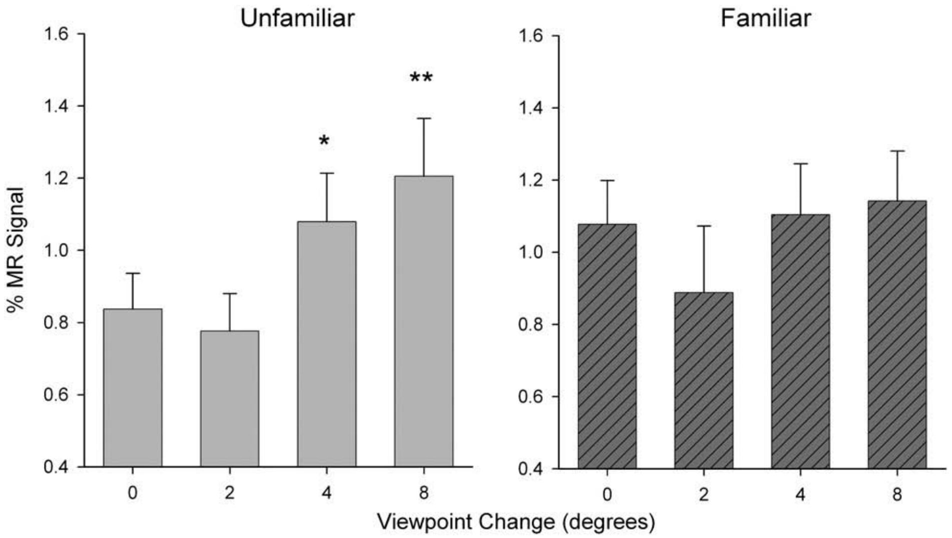

Fig. 5. The response to changes in viewpoint of faces with the same identity in the FFA. There was a significant increase in response (release from adaptation) with viewpoint in the unfamiliar, but not the familiar condition. Error bars represent ±1 standard error. $^{**}P<0.01$, $^{*}P<0.05$.

same face at the same viewpoint (0° change) with images to different faces shown at the same viewpoint. We found a reduction in response amplitude to images of the same face compared to different faces in the unfamiliar ($t(13)=-6.66$, $P<0.0001$) and familiar ($t(13)=-3.79$, $P<0.01$) conditions. We then compared the response to images of the same face shown over 2° changes in viewing angle with different faces also shown over 2° changes in viewing angle. Again, we found a significantly reduced response to images of the same face in the unfamiliar ($t(13)=-3.22$, $P<0.01$) and familiar ($t(13)=-5.61$, $P<0.0001$) conditions. Next, we compared responses to images of the same unfamiliar face shown over 4° changes in viewpoint with images of different faces also shown over 4° changes. Although we found no difference (adaptation) between the response to the same and different faces in the unfamiliar condition ($t(13)=-1.35$, $P=0.19$), significant adaptation was apparent in the familiar condition ($t(13)=-2.47$, $P<0.05$). Finally, we compared response to images of faces that varied by 8° and found a reduced response when the identity was the same compared to when it varied in the familiar ($t(13)=-3.68$, $P<0.01$), but not the unfamiliar ($t(13)=-0.61$, $P=0.54$) condition.

In the previous analyses, we have compared responses of identical faces to different faces. This allows measurement of sensitivity to identity while maintaining the differences in views similar across the same face and different faces. We have complemented this analysis by comparing repetitions of the same face at different rotation levels to repetitions of the same face without rotation. Fig. 5 shows that there is a significant effect of viewpoint for unfamiliar faces in FFA: $F(3,39)=6.10$, $P<0.005$, but not for familiar faces $F(3,39)=1.62$, $P=0.20$).

OFA

Fig. 4B shows the adaptation-index in the OFA for each condition. A 3 factor ANOVA (familiarity, identity, viewpoint) revealed a main effect of identity ($F(1,11)=8.14$, $P<0.05$) and viewpoint ($F(3,33)=4.94$, $P<0.05$). There was also an interaction between familiarity and identity ($F(1,11)=5.99$, $P<0.05$) suggesting adaptation to unfamiliar and familiar faces differed in this region. Paired *t*-tests revealed a significantly reduced response to images of the same face shown at the same viewpoint compared to different faces shown at the same viewpoint ($t(11)=-3.15$, $P<0.01$) in the unfamiliar condition. In contrast, there was no difference between the response to same and different familiar faces shown at the same viewpoint ($t(11)=-0.96$, $P=0.35$) or any other change in viewpoint: 2°: ($t(11)=0.05$, $P=0.952$; 4°: $t(11)$ −0.49, $P=0.62$); 8°: ($t(11)$ 0.93, $P=0.36$). Adaptation to images of the same unfamiliar face was found across 2° changes in viewpoint ($t(11)$ −2.54 =, $P<0.05$), but we found no difference between the response to same and different faces was evident at 4° ($t(11)=-0.46$, $P=0.65$) or 8° ($t(11)=-1.19$, $P=0.25$). A simple regression of adaptation against viewpoint revealed a non-significant trend for unfamiliar faces; with reduced adaptation with increasing viewpoint ($r=0.23$, $P=0.10$). No relationship was found for familiar faces ($r=0.01$, $P=0.90$).

Superior temporal sulcus

Fig. 4C shows the adaptation-index in STS to images of the same face compared with different faces. A 3 factor ANOVA revealed no main effect of identity ($F(1,7)=0.42$, $P=0.53$) or viewpoint ($F(3,21)=1.4$, $P=0.26$) and no interaction between identity and viewpoint ($F(3,21)=0.81$, $P=0.49$). Consistent with the ANOVA results, paired *t*-tests showed that the response to the same face did not significantly differ from the response to different faces when shown at the same viewpoint (unfamiliar: $t(7)=-1.41$, $P=0.19$; familiar: $t(7)=0.61$, $P=0.55$). Results also revealed no difference between the same and different unfamiliar faces at either 2° (unfamiliar: $t(7)=-0.04$, $P=0.96$; familiar: $t(7)=1.34$, $P=0.22$), 4° (unfamiliar: $t(7)=0.46$, $P=0.65$; familiar: $t(7)=0.84$, $P=0.42$) or 8° (unfamiliar: $t(7)=-0.02$, $P=0.98$; familiar: $t(7)=0.59$, $P=0.57$) viewpoint changes. Finally, a simple regression also revealed no linear relationship between STS adaptation and viewpoint change for both unfamiliar ($r=0.12$, $P=0.49$) and familiar faces ($r=-.05$, $P=0.77$).

Lateral occipital complex

To determine whether adaptation to faces was specific to face-selective regions, we measured the response in an object-selective

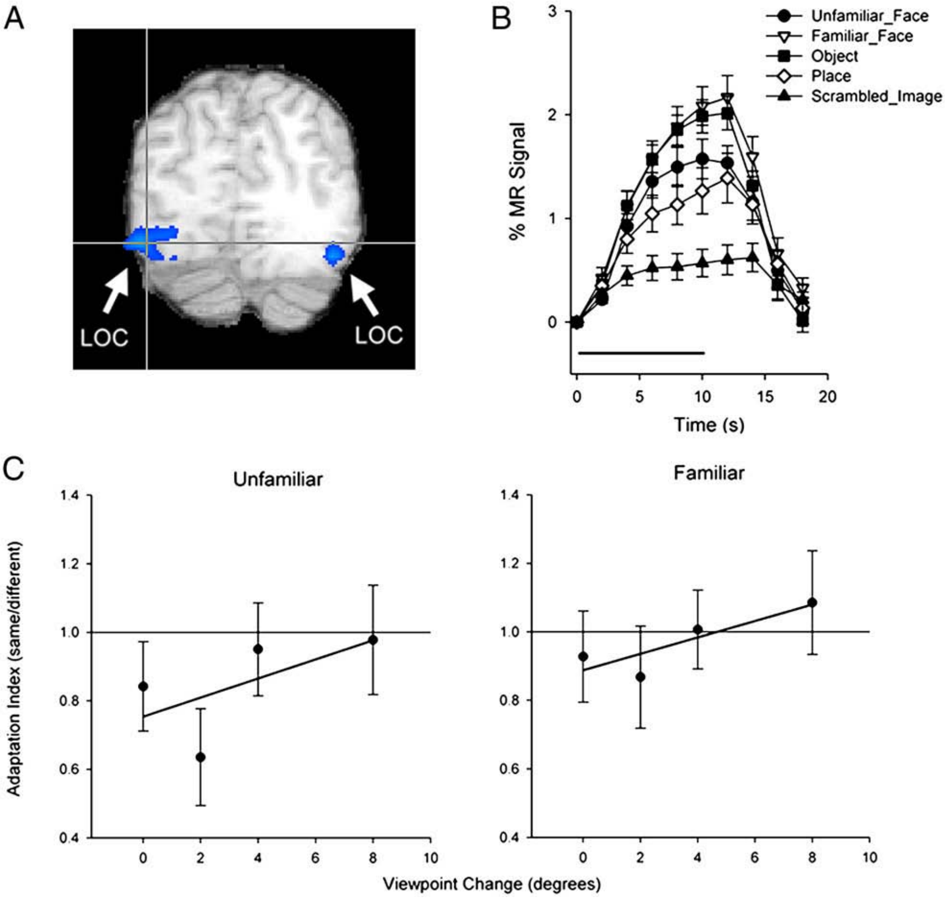

Fig. 6. (A) Location of the object-selective LOC (lateral occipital complex in the brain. (B) MR time-course during localiser scans, showing activity averaged across hemispheres and subjects for each stimulus category. (C) Adaptation effect in the LOC for unfamiliar (left) and familiar (right) faces plotted against change in viewpoint. Error bars represent ±1 standard error.

lateral occipital complex (LOC) that was defined by objects > scrambled images (excluding those voxels overlapping with OFA) in the localizer scan. Fig. 6 shows the location of this area and the response to different object categories. In the unfamiliar face scan, we found a significant effect of identity ($F(1,13)=10.57$, $P<0.01$). Paired t-tests showed that there was a marginally significant reduction in MR response to the same identity compared to different identities at 0° change ($t(13)=-1.97$, $P=0.06$) and a significantly lower response at 2° change ($t(13)=-3.06$, $P<0.01$). However, there was no evidence of adaptation to identity in the 4° ($t(13)=-1.09$, $P=0.29$) or 8 ($t(13)=-0.38$, $P=0.70$) conditions. In contrast to the unfamiliar face condition, we found no significant adaptation to identity in the familiar face condition ($F(1,13)=3.37$, $P=0.09$). Consistent with the ANOVA, paired t-tests failed to show any differences between conditions at each viewpoint (0°: $t(13)=-0.99$, $P=0.33$; 2°: $t(13)=-1.23$, $P=0.23$; 4°: $t(13)=-0.49$, $P=0.62$;8°: t913)$=-0.28$, $P=0.78$).

Behavioural task during scan

During the adaptation scans, subjects were instructed to perform a target detection task. Table 2 shows the average response times and detection rate of the target stimuli across all conditions. There was no significant effect of identity or familiarity on the response time ($F(1,13)=0.75$, $P=0.40$; $F(1,13)=0.45$, $P=0.51$) or target detection ($P=0.87$; $P=0.63$). Importantly, there was also no interaction between familiarity and identity ($F(1,13)=1.56$, $P=0.23$). However, there was a significant effect of viewpoint ($F(3,39)=6.76$, $P<0.01$), with subjects faster to respond in the 0° viewpoint condition.

Behavioural experiment

To determine whether there were any differences in the ability to discriminate changes in viewpoint for familiar and unfamiliar faces, we performed a behavioural experiment outside the scanner. The results in Fig. 7 show that the ability to correctly discriminate the direction of rotation increase with the change in viewpoint ($F(1,19)=$

Table 2
Mean response times in milliseconds (SEM) and mean percentage accuracy (SEM) across subjects in target detection task performed during adaptation scans

	Identity	0°	2°	4°	8°	% correct
Unfamiliar	Same	489 (15)	503 (20)	503 (15)	519 (13)	98.3 (0.4)
	Different	483 (16)	498 (17)	485 (15)	502 (21)	98.8 (0.6)
Familiar	Same	491 (18)	489 (20)	523 (22)	522 (17)	98.1 (0.3)
	Different	498 (23)	488 (20)	518 (21)	538 (23)	97.8 (0.8)

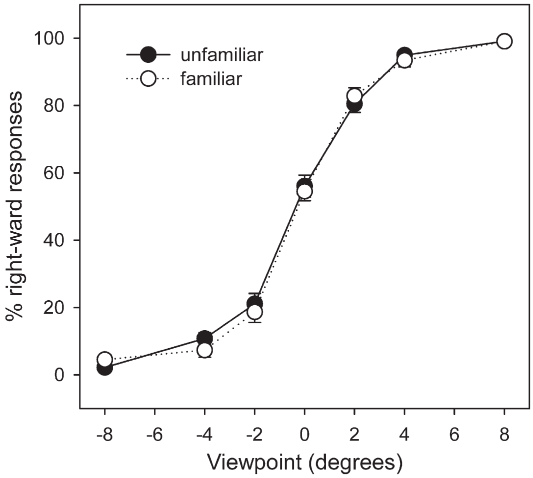

Fig. 7. Behavioural experiment. Percentage of right responses to unfamiliar and familiar faces at different viewpoints. Positive values on the *x*-axis indicate rotations toward the right. There was no difference in performance for unfamiliar and familiar faces. Error bars represent ±1 standard error.

36.9, $P<0.001$), but that there was no difference between familiar and unfamiliar faces ($F(1,19)=1.08$, $p>0.05$).

Discussion

The aim of this experiment was to determine the role of face-selective regions in face recognition. We found a reduced response (adaptation) to repeated images of the same unfamiliar and familiar faces in FFA, but not in the STS face-selective region. To establish if the neural representation of faces in the FFA was invariant to changes in viewpoint, we varied the viewing angle of the face between successive presentations. We found that adaptation to familiar faces in the FFA was apparent across all changes in viewpoint. In contrast, there was a progressive release from adaptation when unfamiliar faces were viewed at increasing viewing angles.

Models of face processing (Bruce and Young 1986; Burton et al., 1999) emphasize the distinction between pictorial (an episodic representation such as a photograph) and structural codes (invariant aspects of the stimulus necessary to mediate recognition). fMRI adaptation has previously been used to show that the neural representation in the FFA is invariant to the size (Grill-Spector et al., 1999; Andrews and Ewbank, 2004), position (Grill-Spector et al., 1999), emotional expression (Winston et al., 2004) and spatial frequency composition (Eger et al., 2004) of the face image. The influence of familiarity on viewpoint-invariance provides further support for the idea that this face-selective region in a high-level structural representation of facial identity. This also fits with models of face processing that predict a difference in viewpoint-dependency in the neural representation underlying the recognition of familiar and unfamiliar faces (Bruce and Young, 1986; Burton et al., 1999; Haxby et al., 2000).

Previous event-related fMRI studies have failed to find view-invariant responses to familiar faces in early face processing regions such as the FFA (Eger et al., 2005; Pourtois et al., 2005). The reason for the discrepancy between studies might be related to differences in design. In this study, the viewpoint of faces was changed continuously, and was not confounded by other differences in the image. The maximum change in viewpoint was ±24°. The viewpoint changes used in previous studies were much greater. So, it is not clear whether adaptation to the same identity would occur with larger changes in viewing angle or with other non-rigid changes in the face image. Another difference is the block-design procedure used in this study, which contrasts with previous studies that have used an event-related design. Single neuron and fMRI studies have found that the magnitude of the adaptation effect is dependent on the number of repetitions of a stimulus (Grill-Spector et al., 1999; Sawamura et al., 2006; Grill-Spector et al., 2006). Moreover, it has also been reported that the response selectivity of neurons is predicted more accurately by adaptation in a block design than an event-related design (Sawamura et al., 2006). It is possible therefore that the view-independent adaptation to familiar faces found in this study might reflect the improved signal-to-noise and selectivity of a blocked design.

The relationship between activity in the FFA and the recognition of faces has been shown in other neuroimaging studies. For example, Grill-Spector et al. (2004) showed that the response in FFA correlated on a trial-by-trial basis with both detecting the presence of faces and identifying specific faces. Loffler et al. (2005) provided further support for the role of the FFA in face recognition by showing that adaptation was dependent on the direction (perceived identity) rather than the distance (physical appearance) between images in face space (Leopold et al., 2001). Using an event-related fMR-adaptation, Rotshtein et al. (2005) reported that adaptation to familiar faces in the FFA was more dependent on perceived rather than physical similarity of face images. In contrast, adaptation in the occipital face area (OFA) was dependent on physical differences between faces. We also found a difference in the in the adaptation response between the OFA and FFA. A reduced response (adaptation) to the same face image was found in the FFA for familiar and unfamiliar faces, but adaptation to faces in the OFA was only found for unfamiliar faces. It is not clear why adaptation to identical images of the same familiar face was not found in the OFA. However, we found a similar pattern of results in the object-selective LOC. One explanation for these findings may relate to the different neural mechanisms that could underlie fMR-adaptation: (i) neuronal fatigue or reduced firing rate; (ii) sharpening of the neuronal response (less active neurons); (iii) shorter firing duration (Grill-Spector et al., 2006). It is possible that differences in the adaptation to unfamiliar and familiar faces may reflect differences in the underlying mechanism. Because adaptation to familiar faces was found in the FFA, but not the OFA, it is possible that the reduction in response is not directly dependent on the low-level properties of the image. In contrast, adaptation to unfamiliar faces was evident in the OFA and FFA (and the object-selective LOC), suggesting a bottom-up explanation. Understanding the functional connectivity between these face-selective regions with techniques that have better temporal resolution should help to differentiate between the possible mechanisms underlying the adaptation response.

In contrast to the FFA and OFA, the superior temporal sulcus (STS) face-selective region failed to show adaptation to any face condition. A similar dissociation in response between face-selective regions in the inferior and superior temporal lobe has been found in other neuroimaging (Hoffman and Haxby, 2000; Andrews and Ewbank, 2004; Winston et al., 2004; Grill-Spector et al., 2004) and single neuron (Hasselmo et al., 1989) studies. For example, we reported in an earlier study that adaptation to repeated presentations of a face took place in the FFA, but not in the STS (Andrews and Ewbank, 2004). However, we also found previously that face-selective regions in the STS showed an increased response to faces with different expressions and viewpoints compared to an unchanging face. Together, these findings are consistent with models of face processing that involve a dissociation between the processing of invariant facial information that is used for recognition of identity and the analysis of changeable aspects of faces that is important in social communication (Bruce and Young, 1986; Haxby et al., 2000).

Models of face processing incorporate a core processing system that is involved in the visual analysis of faces as well as an extended system that involves extracting further information that a face can convey (Bruce and Young, 1986; Haxby et al., 2000). It is therefore possible that the adaptation responses in the core face-selective regions could reflect the initial transformation of the facial information into a view-invariant representation or could reflect feed-back signals from regions in the extended network. Indeed, several studies have reported view-independent adaptation in regions of temporal and frontal cortex that are not part of the core face-selective network (Eger et al., 2005; Pourtois et al., 2005). In a recent MEG study, we reported view-dependent adaptation of the face-selective M170 potential to familiar and unfamiliar faces (Ewbank et al., 2008). The source of the M170 is thought to be inferior temporal regions, specifically in the locale of the fusiform gyrus (Halgren et al., 2000; Liu et al., 2002). This suggests that the initial response to faces in the FFA is not view-independent and that the fMRI response that we report to familiar faces could reflect further processing of the stimulus in the FFA or feedback from later stages of processing. Consistent with this possibility, the N170 face-selective potential does not appear to be sensitive to familiarity of a face, whereas later potentials (~250 ms) do show modulation by familiarity (Eimer, 2000; Bentin and Deouell, 2000; Schweinberger et al., 2002).

In conclusion, the aim of this study was to determine whether there is a difference in the view-dependency for familiar and unfamiliar faces in face-selective regions of the human brain. We found adaptation in the FFA to familiar faces that was independent of changes in viewpoint. In contrast, corresponding viewpoint changes to unfamiliar faces resulted in a recovery from adaptation. These findings demonstrate a dissociation between the neural representation underlying familiar and unfamiliar faces that could underlie differences in our ability to recognize faces (Hancock et al., 2000).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2008.01.049.

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