

Activity in the right fusiform face area predicts the behavioural advantage for the perception of familiar faces



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ABSTRACT

People are extremely proficient at discriminating the identity of familiar faces, but are significantly worse with unfamiliar faces. Despite this clear behavioural difference in perception, the neural correlates of the advantage for familiar faces remain unclear. Here, we use an individual differences approach to explore the link between neural responses in face-selective regions and the behavioural advantage for the perception of familiar faces. First, we compared performance on an identity matching task with either familiar or unfamiliar faces. We found that participants were significantly better at matching the identity of familiar compared to unfamiliar faces. Next, we used fMRI to measure the response to familiar and unfamiliar faces. Consistent with the behavioural data, there was a significant difference in the neural response to familiar and unfamiliar faces in face-selective regions. Finally, we asked whether inter-individual variation in behavioural performance could be predicted by corresponding variation in fMRI response. We found a significant correlation in the right fusiform face area (rFFA) between the difference in response to familiar and unfamiliar faces and corresponding differences on the face-matching task. That is, participants who showed a larger response to familiar compared to unfamiliar faces in the rFFA also matched familiar faces much more accurately than unfamiliar faces. No other face-selective region showed a correlation between neural and matching accuracy. These results provide a link between activity in the rFFA and the perception of familiar faces.

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1. Introduction

The ability to recognise 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 (Bruce et al., 1987; Davies-Thompson et al., 2009; Hancock et al., 2000; Jenkins et al., 2011; Megreya and Burton, 2006; Johnston and Edmonds, 2009). This difference in perception has been incorporated into cognitive models of face processing, which propose that familiar and unfamiliar faces are represented differently in the human visual system (Bruce and Young, 1986; Burton et al., 1999). These models propose that faces are initially encoded in a pictorial or image-dependent representation. This image-dependent representation can be used for the perception and matching of unfamiliar faces. In contrast, the identification of a familiar face requires an image-invariant representation that can be used to recognise familiar identity across different images.

Despite the clear behavioural difference in the perception of

familiar and unfamiliar faces, the neural correlates of these differences are much less clear (Natu and O'Toole, 2011). Functional imaging studies have consistently found regions in the occipital and temporal lobes that respond selectively to faces (Kanwisher et al., 1997; McCarthy et al., 1997). Models of face processing suggest that one region within this core network—the fusiform face area (FFA)—is important for the representation of invariant facial characteristics that are necessary for familiar face recognition (Grill-Spector et al., 2004; Haxby et al., 2000; Ishai, 2008). Consistent with these predictions, neuropsychological studies show that lesions in the approximate location of the FFA can lead to selective impairments in face recognition (Barton et al., 2002; Damasio et al., 1982). In contrast to evidence from brain lesions, neuroimaging studies that have directly compared the response in the FFA to familiar and unfamiliar faces have shown mixed results. Some studies report stronger FFA activity for familiar compared to unfamiliar faces (Elfgren et al., 2006; Gobbini et al., 2004; Pierce et al., 2004; Sergent et al., 1992), while others find no difference in response (Gorno-Tempini and Price, 2001; Leveroni et al., 2000).

Support for the role of the FFA in familiar face recognition comes from studies that directly correlate neural responses with behavioural measures of face processing. For example, Grill-Spector et al. (2004) showed that the activation in the FFA was

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higher in trials when participants successfully detected and identified a familiar face than when they did not. Other studies have used an individual differences approach in which neural responses are correlated with behavioural performance in face recognition (Yovel and Kanwisher, 2005; Furl et al., 2011; Huang et al., 2014). For example, Furl and colleagues showed that performance across tasks that measure face matching and recognition correlated with face-selectivity in the FFA. However, this study included both normal and prosopagnosic participants, so it is not clear whether this relationship was primarily based on the difference between these two participant groups. A more recent study, using a large population of normal participants found that differences in a memory task for faces compared to non-face objects was correlated with the selectivity of the FFA (Huang et al., 2014). However, this study only used unfamiliar faces and only tested recognition performance with identical images. So, it is unclear whether this relationship reflects image-based rather than identity-based face processing. A stronger test for a link between neural activity and the recognition of facial identity is to determine whether this correlation is still evident when different images from the same identity are shown (i.e. image-invariant perception).

The aim of this study was (1) to determine whether there is a difference in the response to familiar and unfamiliar faces in face-selective regions and (2) to determine if individual differences in the response to familiar and unfamiliar faces can predict the behavioural advantage for familiar faces. To address these questions, we first measured the difference in neural response to familiar and unfamiliar faces in face-selective regions using fMRI. Next, participants performed a matching task that involved discriminating whether two different face images belonged to the same identity or a different identity. Participants performed this task with both familiar and unfamiliar faces. Our hypothesis was that individual differences in the matching task for familiar and unfamiliar faces would be reflected in corresponding differences in the neural response in face-selective regions, such as the FFA. To determine the face-specific nature of any relationship between neural and behavioural measures of face processing, we repeated the experiment with familiar and unfamiliar scenes.

2. Methods

2.1. Participants

40 right-handed participants with normal or corrected to normal vision participated in the experiment. Data from two participants had to be excluded: one participant showed uncorrectable motion artefacts, while data from another participant was withdrawn for routine screening. Data sets from 38 participants were therefore analysed (19 females; mean age: 24.3 years). All participants gave their written informed consent. The study was approved by the York Neuroimaging Centre Ethics Committee.

2.2. Behavioural experiment

There were two behavioural experiments: a face matching experiment and a scene matching experiment. A matching task was employed since it is commonly used to assess differences in recognition ability between familiar and unfamiliar stimuli (Bruce et al., 2001; Davies-Thompson et al., 2009; Epstein et al., 2007; Young et al., 1986). There were 4 trial types in the face matching task (Fig. 1A):

- (i) familiar face same (two different images with the same identity)

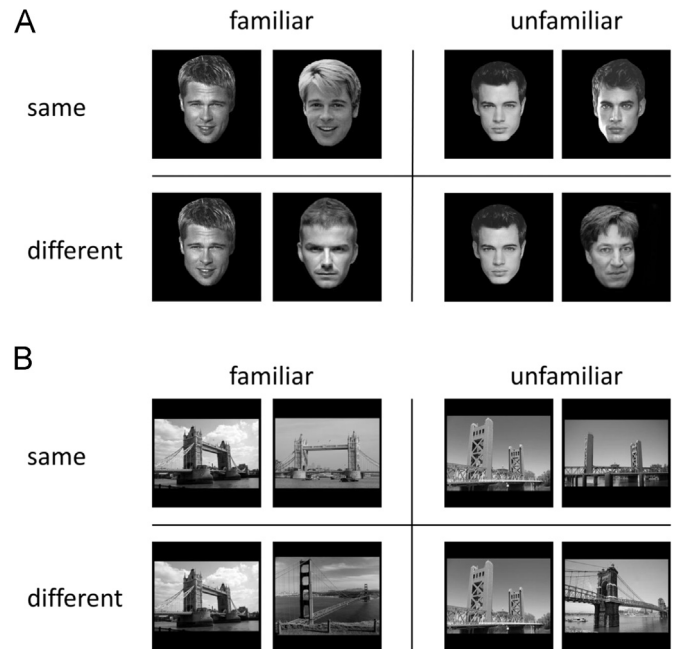


Fig. 1. Example of trials from the matching task. Participants had to judge (A) whether two successive face images had the same identity or (B) whether two successive scenes depicted the same landmark. Images were either familiar or unfamiliar to the participants.

- (ii) familiar face different (two different images with different identities)
- (iii) unfamiliar face same (two different images with the same identity)
- (iv) unfamiliar face different (two different images with different identities).

Face stimuli were taken from a previous study (Davies-Thompson et al., 2013) and included male and female identities. Familiar faces consisted of pictures depicting famous UK/US celebrities. Unfamiliar faces depicted celebrities from other countries and were unknown to the participants.

Participants had to judge whether the two images depicted the same identity or different identities with a button press. On each trial, a fixation cross on a black screen was presented for 1.5 s. This was followed by a face image for 800 ms, a black screen for 200 ms and then a second face image for 800 ms. The gender was always the same in each trial. 8 images of 36 identities (288 images) were used to create 144 trials. Half the trials used familiar faces and half the trials used unfamiliar faces. Moreover, half the trials included faces from the same identity and half the trials used faces from different identities. Accuracy and reaction time were measured for each trial. Response accuracy was converted to d' [z -score(hits) – z -score(false alarms)].

The scene matching task had an identical design (Fig. 1B). Scene stimuli were taken from public sources on the world-wide web and consisted of buildings from the following architectural styles: bridges, domed structures, classical architecture, neoclassical architecture, skyscrapers (art deco), and skyscrapers (high-tech). Pairs of images in each trial were taken from the same subcategory of scene to minimise visual differences between the images.

After the behavioural tasks, participants were given a recognition test. Recognition ability was measured with a questionnaire depicting one image of each of the familiar stimuli used (18 familiar faces, 18 familiar scenes). Participants were asked to name or provide some information of the images. Participants correctly recognised 91.5% (SD = 13.7%) of the familiar faces and 56.1% (SD=17.1%) of the familiar scenes.

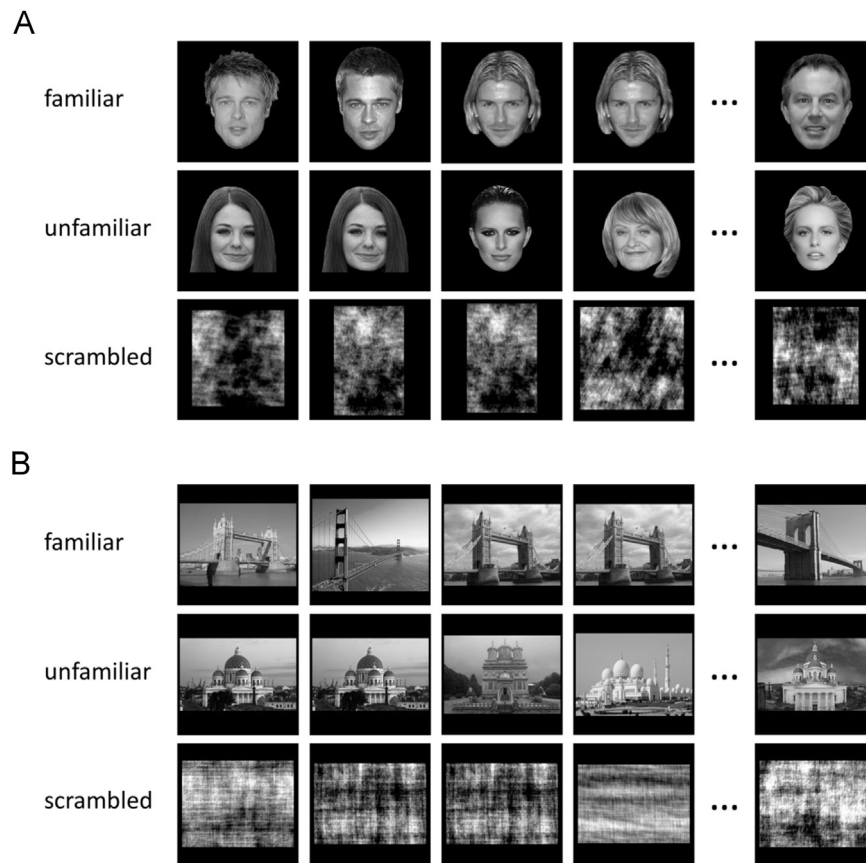


Fig. 2. Examples of image sequences in blocked presentations from the different stimulus conditions in the fMRI experiment: (A) face stimuli and (B) scene stimuli.

2.3. fMRI experiment

There were 6 stimulus conditions in the fMRI experiment (Fig. 2):

- (i) familiar faces
- (ii) unfamiliar faces
- (iii) scrambled faces
- (iv) familiar scenes
- (v) unfamiliar scenes
- (vi) scrambled scenes

Face and scene stimuli showed the same identities and landmarks that were used in the behavioural experiment. However, different images were used. Scrambled images were created by scrambling the phase of the face and scene images. All images were presented in grey scale. Stimuli from each condition were presented in a blocked design. Faces in each block always had the same gender. Scenes in each block were taken from the same subcategory of scene. Each stimulus block lasted for 9 s and contained 9 images. Within each stimulus block each image was presented for 800 ms followed by a 200 ms blank screen. Each of the six stimulus conditions was repeated 6 times. This gave a total of 36 blocks. The blocks were presented in a counterbalanced order. Blocks were separated by a 9 s fixation screen (a white fixation cross on a black background). To maintain attention, participants performed a one-back task in which participants responded with a button press every time an identical image was directly repeated. This allowed us to use a common behavioural task across all conditions and minimised the influence of task on neural response (Kanwisher et al., 1997; Davies-Thompson et al., 2009).

Data was collected using a GE 3 Tesla HD Excite MRI scanner at

the York Neuroimaging Centre at the University of York. For each participant, a T1-weighted structural MRI ($2.25 \times 2.25 \times 3$ mm voxel) and a gradient-echo EPI were acquired. The EPI sequence was recorded with a radio-frequency coil tuned to 127.4 MHz and was used to acquire 38 axial slices ($TR=3$ s, $TE = 33$ ms, flip angle = 90° , $FOV = 260$ mm, matrix size = 128×128 , slice thickness = 3 mm, voxel size: $2.25 \times 2.25 \times 3$ mm). Data was analysed with FEAT version 4.1 (<http://www.fmrib.ox.ac.uk/fsl>). The first 9 s (3 volumes) from each scan were discarded, and MCFLIRT motion correction, spatial smoothing (Gaussian, FWHM 5 mm), and temporal high-pass filtering (cutoff 0.0093 Hz) were applied.

The BOLD response for each condition was modelled with a boxcar function convolved with a standard haemodynamic response function. Face-selective regions were defined by the average statistical maps created by familiar faces > scrambled faces and unfamiliar faces > scrambled faces. Scene-selective regions were defined by the average statistical maps created by familiar scenes > scrambled scenes and unfamiliar scenes > scrambled scenes. Face-selective ROIs were defined independently for each participant. First, the threshold of the face-selective statistical map was adjusted until it divided into individual clusters that corresponded with the core face-selective regions (FFA, OFA, STS). The cluster function in FSL was used to identify the peak voxel within each cluster. Next, a flood-fill algorithm was used to increase the size of the region incrementally based on the z-scores of individual voxels. This allowed us an objective method to generate ROIs with the same number of voxels across individuals. Our initial analysis was based on a ROI size of 50 most-selective voxels, but we also varied the size of the ROIs from 25 to 100 voxels. Only ROIs where all voxels lied above the minimum threshold of $Z=2.3$ were included in the analysis.

To measure the neural response to faces and scenes, the response of each voxel was averaged within a ROI. The units were

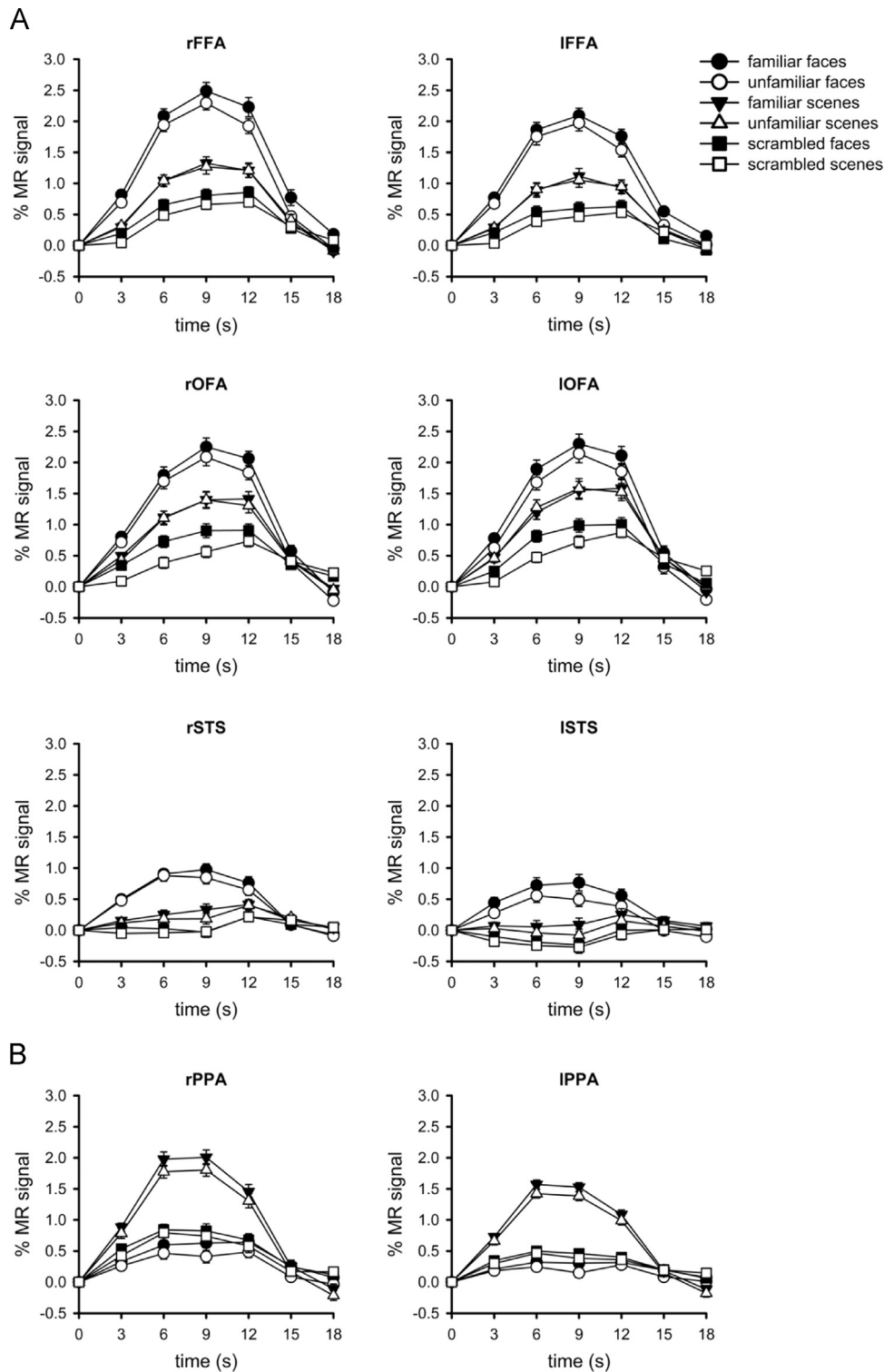


Fig. 3. Average time course of response in (A) face-selective regions and (B) scene-selective regions across participants. Error bars represent SE.

converted from units of image intensity to percentage signal change (% MR signal change) and normalised to the start of each block (Fig. 3). The peak response across the time series was taken at 9 s after the onset of the block for each stimulus condition in each participant. To examine a potential relationship with behaviour, we calculated the difference between peak response to familiar and unfamiliar faces. This normalisation is critical to remove overall differences in the amplitude of response across individuals. The relative difference between the neural response to familiar

and unfamiliar faces was then compared with corresponding difference between familiar and unfamiliar faces in the behavioural task.

Finally, a whole brain analysis was run to test whether effects observed during the ROI analysis could be found in regions outside the defined ROIs. First, the behavioural difference in d' between familiar–unfamiliar face matching was measured for each participant. These values were demeaned across participants and then used as a regressor in the group analysis of the contrast of

familiar > unfamiliar faces. This allowed us to determine if there were any regions in which individual differences in fMRI response between familiar and unfamiliar faces could predict the corresponding difference in matching performance. An analogous analysis was performed for scenes. To account for multiple comparisons, statistical thresholding was carried out using clusters determined by $Z > 2.3$ and a corrected cluster significance of $P = 0.05$.

3. Results

3.1. Face matching task

A matching task was used to determine differences in the perception of familiar and unfamiliar faces. Accuracy (d') in the identification of familiar faces was significantly greater than for unfamiliar faces (familiar: $M = 3.56$, $SD = 0.89$; unfamiliar: $M = 1.99$,

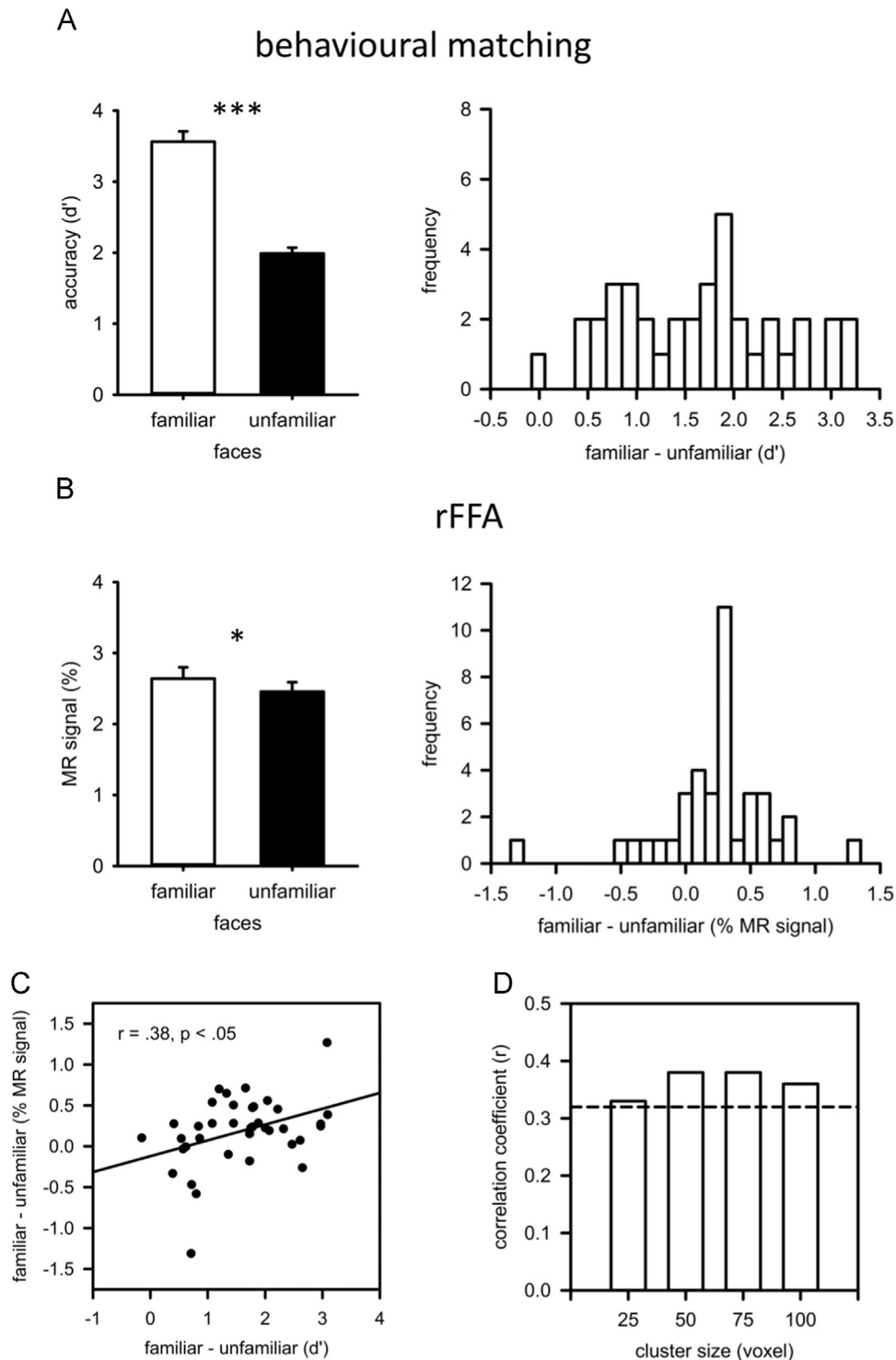


Fig. 4. Behaviour and neural responses to familiar and unfamiliar faces and their correlation. (A) Behavioural matching performance and (B) rFFA response. Left graphs show group average with SE bars, right graphs show individual variation in the difference between familiar and unfamiliar faces. (C) Correlation between the rFFA response and matching performance. (D) The correlation remained significant when ROI size was varied from 25–100 voxels. This shows a link between responses in the rFFA and behavioural matching advantage for familiar faces.

SD=0.51; $t(37)=11.61$, $p < .001$). Although most participants showed an advantage for familiar faces, there was individual variation in the magnitude of the effect. Fig. 4A shows the range of performance across participants (range: -0.15 to 3.24). Response times also revealed a familiar face advantage: familiar faces were matched significantly faster than unfamiliar faces (familiar: $M=0.77$ s, $SD = 0.16$ s; unfamiliar: $M=0.84$ s, $SD = 0.18$ s; $t(37) = -6.60$, $p < .001$). There was also individual variation in the difference in response time to familiar and unfamiliar faces (range: $-.26$ s to $.04$ s).

3.2. fMRI response in face-selective regions

The localiser scan revealed a number of face-selective regions: the fusiform face area (FFA), occipital face area (OFA) and superior temporal sulcus (STS). The peak coordinates of these regions and the number of ROIs that could be localised in each participant are shown in Table 1. The location of these ROIs correspond closely to those found in previous studies (Davies-Thompson and Andrews, 2012; Grill-Spector et al., 2004; Kanwisher et al., 1997).

Next, a repeated-measures ANOVA was performed separately for each ROI with the factors Category (faces and scenes) and Familiarity (familiar and unfamiliar). Table 2 shows the effect of Category and Familiarity for each ROI. There was a significant main effect of Category for each ROI. This was due to higher responses to faces compared to scenes in face-selective regions and higher responses to scenes compared to faces in scene-selective regions. There was also a significant main effect of Familiarity in each ROI. This was due to higher responses to familiar compared to unfamiliar stimuli. There was no interaction between Category and Familiarity in all ROIs except the rOFA. This interaction was due to a higher response to familiar compared to unfamiliar faces, but no difference in the response to familiar and unfamiliar scenes.

3.3. Correlation between fMRI and behavioural responses to faces

To determine whether there was a link between responses in face-selective regions and the perception of familiar faces, we compared individual differences in fMRI response with corresponding differences on the face matching task. Table 3 shows the correlation between neural response (familiar–unfamiliar) and behavioural accuracy (familiar–unfamiliar) across individuals in all ROIs. The rFFA showed a significant correlation ($r(36)=0.38$, $p < 0.05$, confidence interval: 0.07 – 0.69) with accuracy on the face matching task (Fig. 4C). Fig. 4D shows that the correlation was not dependent on the size of the ROI. In contrast to the rFFA, no other face ROIs showed a correlation with behavioural accuracy on the face-matching experiment. The rOFA showed a marginal trend towards a correlation, which did not reach significance ($r(35)=0.29$, $p=0.08$, confidence interval: -0.04 – 0.62). In contrast to accuracy, response times on the face matching task and neural

response of any ROI did not correlate significantly (Table 4).

To test whether a relationship between fMRI activity and the behavioural matching advantage could be found in brain regions outside the core face-selective regions, we performed a whole brain analysis. Consistent with the ROI analysis, a region in the right fusiform gyrus showed a significant correlation (Fig. 5 and Table 5). Only one other region in the ventral striatum showed a significant correlation between neural and behavioural responses.

3.4. Behavioural and neural scene measures

To test whether the patterns of response were specific to face perception, an identical analysis was performed using behavioural and neural responses to scenes. In contrast to faces, we did not observe a significant advantage on the perceptual matching task for familiar scenes. In fact, there was a small advantage for matching unfamiliar scenes in accuracy (famous: $M=3.06$, $SD=0.59$; unfamiliar: $M=3.45$, $SD=0.66$; $t(37)=3.93$, $p < .001$) and response time (famous: $M=0.79$ s, $SD=0.18$ s; unfamiliar: $M=0.77$ s, $SD=0.18$ s; $t(37)=3.60$, $p < .001$). This finding was unexpected, since a matching advantage for familiar scenes has previously been shown (Epstein et al., 2007). Nevertheless, there was individual variation in the difference between familiar and unfamiliar scene matching (d' range: -1.94 to 0.96).

Next, we tested whether individual variation in the perceptual matching of scenes could be predicted by activity in the rFFA. The rFFA did not show a correlation between neural responses and either accuracy (Table 6) or response time (Table 7) to scenes. None of the other face-selective ROIs showed a correlation between neural responses and either accuracy or response time for scenes, except for the rSTS which showed a negative correlation with response time for scenes ($r(36) = -33$, $p < .05$, confidence interval: -0.64 to -0.01).

Then we analysed the response in scene-selective regions using a repeated-measures ANOVA with the factors Category (faces and scenes) and Familiarity (familiar and unfamiliar). The rPPA and lPPA responded significantly more to scenes than faces and to familiar compared to unfamiliar stimuli. There was no significant interaction between Category and Familiarity (Table 2).

Finally, there was no correlation between neural and behavioural responses to scenes in the scene-selective PPA. A whole-brain analysis was used to determine if there were any regions outside the ROIs that were defined that showed a correlation between neural and behavioural responses to scenes. However, we did not find any regions that showed a significant relationship.

Discussion

The aim of this study was to use an individual differences approach to determine the link between activity in face-selective regions and the perception of familiar faces. In a behavioural experiment, we found that participants were significantly more accurate when matching familiar faces compared to unfamiliar faces. Similarly, we found that the response in the rFFA was significantly higher to familiar faces compared to unfamiliar faces. Next, we determined whether there was a link between these neural and behavioural measures. Our results show a correlation between neural processing in the rFFA and the behavioural advantage for the perception of familiar faces.

Our results are consistent with previous studies that have shown familiar faces are easily recognised across changes in viewpoint and illumination, whereas unfamiliar faces are more difficult to recognise across similar image manipulations (Bruce et al., 1987; Davies-Thompson et al., 2009; Hancock et al., 2000; Jenkins et al., 2011; Megreya and Burton, 2006). However, we also

Table 1
Peak coordinates of face-selective and scene-selective regions yielded by group-contrast.

	Hemisphere	MNI coordinates			Number of participants
		x	y	z	
FFA	right	40	-52	-26	38
	left	-42	-48	-24	36
OFA	right	48	-76	-8	37
	left	-40	-82	-18	30
STS	right	46	-66	8	37
	left	-56	-60	6	22
PPA	right	26	-46	-18	37
	left	-28	-46	-22	37

Table 2

Neural response within face-selective regions to all stimulus conditions. Descriptives, mean and standard error, and corresponding statistical results.

ROI		Familiar faces	Unfamiliar faces	Familiar scenes	Unfamiliar scenes	Category	Familiarity	category × familiarity
FFA	right	2.64 (0.16)	2.46 (0.13)	1.28 (0.11)	1.24 (0.12)	$F(1,37)=242.47, p < .001$	$F(1,37)=7.35, p < .05$	$F(1,37)=2.34, p = .135$
	left	2.35 (0.15)	2.22 (0.16)	1.20 (0.13)	1.12 (0.13)	$F(1,35)=121.32, p < .001$	$F(1,35)=7.15, p < .05$	$F(1,35)=0.27, p = .604$
OFA	right	2.41 (0.15)	2.22 (0.15)	1.37 (0.14)	1.37 (0.15)	$F(1,36)=151.25, p < .001$	$F(1,36)=4.90, p < .05$	$F(1,36)=5.02, p < .05$
	left	2.46 (0.17)	2.24 (0.16)	1.57 (0.16)	1.57 (0.17)	$F(1,29)=64.69, p < .001$	$F(1,29)=4.31, p < .05$	$F(1,29)=3.59, p = .068$
STS	right	1.05 (0.10)	0.91 (0.11)	0.34 (0.10)	0.18 (0.09)	$F(1,36)=112.08, p < .001$	$F(1,36)=15.41, p < .001$	$F(1,36)=0.09, p = .766$
	left	0.91 (0.16)	0.55 (0.14)	0.11 (0.13)	-0.09 (0.11)	$F(1,21)=58.31, p < .001$	$F(1,21)=21.07, p < .001$	$F(1,21)=2.90, p = .103$
PPA	right	0.52 (0.75)	0.35 (0.68)	2.03 (0.58)	1.89 (0.70)	$F(1,36)=247.74, p < .001$	$F(1,36)=8.46, p < .01$	$F(1,36)=0.05, p = .817$
	left	0.30 (0.56)	0.09 (0.53)	1.62 (0.54)	1.49 (0.53)	$F(1,36)=186.85, p < .001$	$F(1,36)=9.06, p < .01$	$F(1,36)=0.80, p = .377$

Table 3Correlation between the fMRI response in different regions and accuracy (d') on the behavioural matching of familiar and unfamiliar faces with 95% confidence intervals.

	Right hemisphere	Left hemisphere
FFA	$r = .38, p < .05, CI = 0.07-0.69$	$r = .03, p = .88, CI = -0.32-0.38$
OFA	$r = .29, p = .08, CI = -0.04-0.62$	$r = .00, p = .99, CI = -0.39-0.39$
STS	$r = -.08, p = .63, CI = -0.43-0.26$	$r = .12, p = .60, CI = -0.34-0.58$
PPA	$r = -.03, p = .85, CI = -0.38-0.31$	$r = .16, p = .35, CI = -0.18-0.50$

Table 4

Correlation between the fMRI response in different regions and response time on the behavioural matching of familiar and unfamiliar faces with 95% confidence intervals.

	Right hemisphere	Left hemisphere
FFA	$r = .05, p = .79, CI = -0.29-0.38$	$r = .03, p = .85, CI = -0.31-0.38$
OFA	$r = -.02, p = .92, CI = -0.36-0.33$	$r = .04, p = .86, CI = -0.35-0.42$
STS	$r = .00, p = .99, CI = -0.34-0.35$	$r = -.19, p = .41, CI = -0.64-0.27$
PPA	$r = .19, p = .27, CI = -0.15-0.53$	$r = .06, p = .74, CI = -0.29-0.40$

found that the magnitude of the difference on perceptual matching varied across participants (d' range = -0.15 to 3.09). To determine the neural correlates of this individual variation in perceptual matching, we measured the response to familiar and

Table 5

Whole brain regression analysis between behavioural face matching and the contrast of familiar > unfamiliar faces.

	Z_{max}	MNI coordinates			Size (voxel)
		x	y	z	
Fusiform gyrus	3.27	54	-54	-20	593
Ventral Striatum	4.56	-6	12	-4	1849

Table 6Correlation between the fMRI response in different regions and accuracy (d') on the behavioural matching of familiar and unfamiliar scenes with 95% confidence intervals.

	Right hemisphere	Left hemisphere
FFA	$r = -.31, p = .06, CI = -0.63-0.02$	$r = -.24, p = .16, CI = -0.58-0.10$
OFA	$r = -.16, p = .35, CI = -0.50-0.18$	$r = -.15, p = .43, CI = -0.53-0.23$
STS	$r = .04, p = .80, CI = -0.30-0.39$	$r = .03, p = .91, CI = -0.44-0.49$
PPA	$r = -.20, p = .25, CI = -0.53-0.14$	$r = -.26, p = .12, CI = -0.59-0.07$

unfamiliar faces in the FFA. We found that familiar faces elicited a significantly higher response in the FFA compared to unfamiliar faces (see also [Elfgren et al. \(2006\)](#), [Gobbini et al. \(2004\)](#), [Pierce et al. \(2004\)](#), [Sergent et al. \(1992\)](#)). Moreover, the individual variation in neural response in the rFFA was positively correlated with

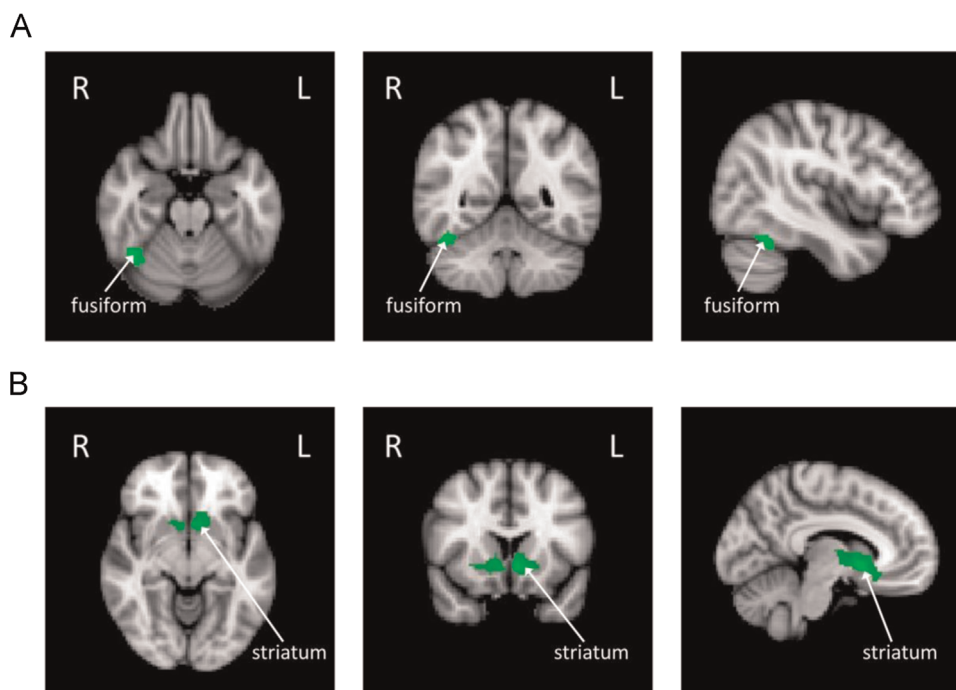


Fig. 5. Whole brain regression analysis between the contrast of familiar > unfamiliar faces and behavioural familiar face advantage. This analysis revealed significant clusters in the (A) right fusiform gyrus (fusiform) and (B) the ventral Striatum (striatum).

Table 7

Correlation between the fMRI response in different regions and response time on the behavioural matching of familiar and unfamiliar scenes with 95% confidence intervals.

	Right hemisphere	Left hemisphere
FFA	$r = -.12, p = .46, CI = -0.46-0.21$	$r = .01, p = .94, CI = -0.34-0.36$
OFA	$r = .05, p = .79, CI = -0.29-0.38$	$r = -.13, p = .50, CI = -0.51-0.26$
STS	$r = -.33, p < .05, CI = -0.64-0.01$	$r = -.18, p = .43, CI = -0.64-0.28$
PPA	$r = -.01, p = .94, CI = -0.35-0.33$	$r = -.08, p = .65, CI = -0.41-0.26$

individual differences in perceptual matching. That is, participants who showed a larger difference in the neural response to familiar and unfamiliar faces showed larger differences in perceptual matching of familiar and unfamiliar faces.

A number of previous studies have used an individual differences approach to explore the link between activity in the FFA and behavioural performance in face processing (Bi et al., 2014; Furl et al., 2011; Huang et al., 2014; Yovel and Kanwisher, 2005). For example, Yovel and Kanwisher (2005) investigated whether response in any face-selective region could account for the behavioural face inversion effect. They found that individual differences in neural response in the FFA between upright and inverted faces correlated with difference in accuracy when matching upright versus inverted faces. A related finding was reported by Huang et al. (2014) who found that individual differences in a face-memory task correlated with face-selectivity in the FFA (Huang et al., 2014). However, these studies used unfamiliar faces and only tested performance with identical images. Furl et al. (2011) addressed this issue by measuring performance on tests of face perception and recognition that could not be solved by image matching. In their study, they showed that performance across these tasks correlated with face-selectivity in the FFA. However, this study included both normal and prosopagnosic participants, so it is not clear whether this relationship was primarily based on the difference between these two participant groups. The findings from this study demonstrate a clear link between the recognition of familiar faces and neural processing in the rFFA in normal participants.

The responses in other face-selective regions, such as the OFA and STS, were also higher for familiar compared to unfamiliar faces. However, these regions did not correlate with accuracy on the matching task. There was also no correlation between neural and behavioural measures in the lFFA. This finding contrasts with previous studies that have reported a relationship between perception and neural response in both the right and left FFA (Bi et al., 2014; Furl et al., 2011; Huang et al., 2014; Yovel and Kanwisher, 2005). It is possible that the difference in this study reflects the use of familiar faces and an experimental design that could not be performed by image matching. There was also no correlation between activity in the STS and accuracy on the face matching task. This is consistent with the role of this region in the processing of changeable aspects of faces, such as expression and viewpoint (Allison et al., 2000; Baseler et al., 2014; Engell and Haxby, 2007; Harris et al., 2012).

A number of studies have used fMR-adaptation paradigms to probe the neural basis of familiar face perception in the FFA. Evidence that the FFA is important for face recognition has been shown in fMRI studies in which a reduced response (adaptation) is found for repeated images of the same face image (Andrews and Ewbank, 2004; Ewbank and Andrews, 2008; Grill-Spector et al., 1999; Loffler et al., 2005; Rotshtein et al., 2004). However, a stronger test for whether this demonstrates selectivity for the identity of the face is if the adaptation is still evident when different images from the same identity are shown (i.e. image-invariant adaptation). Although a number of studies have shown

image-invariant adaptation to familiar faces in the FFA (Davies-Thompson et al., 2013; Eger et al., 2005; Ewbank and Andrews, 2008; Henson et al., 2000; Loffler et al., 2005; Rotshtein et al., 2004), other studies have failed to find any image-invariant adaptation (Davies-Thompson et al., 2009; Pourtois et al., 2005).

Studies using multivariate analyses have investigated if the pattern of response in the FFA can predict facial identity. Although early studies failed to find identity-selective patterns in the FFA (Kriegeskorte et al., 2007; Natu et al., 2010), more recent reports suggest that it is possible to decode identity in the pattern of response from the FFA (Nestor et al., 2011; Anzellotti et al., 2013; Goesaert and Op de Beeck, 2013; Axelrod and Yovel, 2015).

To investigate whether regions outside the face processing network could predict the behavioural familiar face matching advantage, we performed a whole brain analysis using difference in matching performance between familiar and unfamiliar faces as a regressor. Consistent with the ROI analysis, we found a significant effect in a region of the right fusiform gyrus overlapping with the average rFFA region of the ROI analysis. This analysis also revealed a region in the ventral striatum. The ventral striatum is part of the reward network (Haber and Knutson, 2010; Olds and Milner, 1954). It is not clear why this region was correlated with behavioural performance. However, it has also been shown to be activated by attractive faces which were not associated with any reward outcome (Aharon et al., 2001). Therefore, it is possible that this relationship might reflect other aspects of the images that covary with familiarity.

A number of studies have suggested that the FFA may be selective for within-category discrimination of familiar objects rather than being specifically face-selective (Gauthier et al., 2000; Harley et al., 2009; McGugin et al., 2012). For example, McGugin et al. (2012) reported that individual differences in the behavioural ability of car experts could be predicted by the difference in the selectivity of the FFA for cars. To address this issue, we compared behavioural performance on scenes with the response to scenes in the rFFA. Scenes were chosen since they are visually distinct from faces and, similarly to faces, there is a network of brain regions highly selective for scenes, like the PPA. In contrast to faces, we found no correlation between the difference in rFFA response to famous and unfamiliar scenes and corresponding differences in accuracy on the perceptual matching task. We also did not see any correlation between these neural and behavioural measures in the PPA. One explanation could be that participants were not familiar enough with the famous scenes used in this study. Only about half of the famous scenes were reported as being familiar in the recognition test. Our results contrast with previous studies which have shown a matching advantage for familiar scenes across different views (Epstein et al., 2007). However, in this previous study, they used pictures of personally familiar scenes. Thus our famous scene stimuli might have not been sufficiently familiar, which is in line with the low recognition score for famous scenes.

In conclusion, our results show that individual responses in the rFFA response can predict individual differences in perception of familiar and unfamiliar faces. This relationship seems to be specific to the rFFA as it was not observed for any other face-selective region. Taken together our results demonstrate a link between activity in the rFFA and the perception and recognition of familiar faces.

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