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Research report

An image-invariant neural response to familiar faces in the human medial temporal lobe

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ABSTRACT

The ability to recognise familiar faces with ease across different viewing conditions contrasts with the inherent difficulty in the perception of unfamiliar faces across similar image manipulations. Models of face processing suggest that this difference is based on the neural representation for familiar faces being more invariant to changes in the image, than it is for unfamiliar faces. Here, we used an fMR-adaptation paradigm to investigate neural correlates of image-invariant face recognition in face-selective regions of the human brain. Participants viewed faces presented in a blocked design. Each block contained different images of the same identity or different images from different identities. Faces in each block were either familiar or unfamiliar to the participants. First, we defined face-selective regions by comparing the response to faces with the response to scenes and scrambled faces. Next, we asked whether any of these face-selective regions showed image-invariant adaptation to the identity of a face. The core face-selective regions showed image-invariant adaptation to familiar and unfamiliar faces. However, there was no difference in the adaptation to familiar compared to unfamiliar faces. In contrast, image-invariant adaptation for familiar faces, but not for unfamiliar faces, was found in face-selective regions of the medial temporal lobe (MTL). Taken together, our results suggest that the marked differences in the perception of familiar and unfamiliar faces may depend critically on neural processes in the medial temporal lobe.

1. Introduction

As members of a highly social primate species, our everyday lives depend critically on being able to recognise people we know, so that we can interact with them appropriately based on our knowledge of their characteristics and personal histories. Recognising the faces of familiar individuals is often central to this process, and this has led to a great deal of interest in the neural underpinnings of face recognition.

The distinction between often seen familiar faces and unfamiliar faces that have not been previously encountered is central to understanding face recognition. While photographs of unfamiliar faces can be remembered and later recognised

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remarkably well, recognition performance with unfamiliar faces breaks down as soon as any changes are made between studied and test images (Bruce, 1982; Longmore, Liu, & Young, 2008). Remarkably, the same problems arise in perceiving unfamiliar faces, where the perceptual matching of unfamiliar faces is severely hampered by image changes (Hancock, Bruce, & Burton, 2000; Kemp, Towell, & Pike, 1997). In striking contrast, the behavioural hallmark of familiar face recognition is that it is remarkably successful across substantial changes in expression, viewing angle, and lighting conditions (Bruce, 1994; Bruce & Young, 2012; Burton, 2013).

These findings have been incorporated into cognitive models of face processing which propose that familiar faces are represented differently from unfamiliar faces (Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999). These models propose that all faces are initially encoded in an image-dependent representation, which is sufficient to recognise identical images of faces. However, our ability to recognise familiar faces across changes relies on representations that are relatively invariant to changes in the image, which are often referred to as face recognition units (FRUs) in models of face processing (Bruce & Young, 1986). These FRUs interact with person identity nodes (PINs), which are involved in the retrieval of names, and other semantic information associated with the face (Bruce & Young, 1986).

In terms of how faces are represented in the brain, many studies have followed Kanwisher et al. (1997) procedure of localising face-selective regions by contrasting neural responses to faces and other visual stimuli. These have revealed a network of posterior regions now usually designated the occipital face area (OFA), the fusiform face area (FFA) and the posterior superior temporal sulcus (STS) which form a core system for the visual analysis of faces in the widely used neural model proposed by Haxby, Hoffman, and Gobbini (2000). Within this core system of face-selective regions, the FFA is thought to be particularly important to the representation of invariant facial characteristics necessary for face recognition (Grill-Spector, Knouf, & Kanwisher, 2004; Haxby et al., 2000; Ishai, 2008). The Haxby et al. model explicitly acknowledges that other brain regions will contribute to the recognition of faces. One of these regions is the anterior temporal lobe which is suggested to represent biographical semantic knowledge associated with a face, e.g., the name of the person (Collins & Olson, 2014).

Although functional localisers can be used to identify face-selective brain regions, this in itself gives only limited information about what such regions do. A powerful complementary method for understanding the functional properties of a region is fMR-adaptation, as it offers insight into the underlying neural mechanisms (Grill-Spector, Henson, & Martin, 2006). Consistent with Haxby et al.'s (2000) idea of FFA involvement in processing invariant aspects of faces (such as identity), fMRI studies have shown a reduced response (adaptation) to repeated images of the same face in the FFA (Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Harris, Rice, Young, & Andrews, 2015; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2004; Yovel & Kanwisher, 2005). Such findings imply that the identity of the face is represented at some level in the FFA and it is being adapted by repeated presentations. However, given our discussion of the behavioural evidence, a much stronger test for a link between neural activity and the recognition of facial identity is needed to determine whether this adaptation is still evident when different images of the same identity are shown (i.e., image-invariant adaptation). It turns out that fMR-adaptation studies that have used different images of the same identity have shown mixed results. Some studies show a complete absence of adaptation to different images in the FFA (Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a; Xu, Yue, Lescroart, Biederman, & Kim, 2009), whereas other studies show continued adaptation (Loffler et al., 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004).

A limitation of previous studies using fMR-adaptation to probe the neural correlates of face recognition is that they often fail to provide a direct comparison of familiar and unfamiliar faces (Johnston & Edmonds, 2009; Natu & O'Toole, 2011). This is a key limitation since, as we have noted, cognitive models only propose an image-invariant representation for familiar and not for unfamiliar faces (Bruce & Young, 1986; Burton et al., 1999). However, studies that have compared familiar and unfamiliar faces also report mixed results. Some studies have found image-invariant identity adaptation in the FFA for familiar but not unfamiliar faces (Eger, Schweinberger, Dolan, & Henson, 2005; Ewbank & Andrews, 2008), whereas other studies fail to find any difference in adaptation to familiar and unfamiliar faces (Davies-Thompson, Gouws, & Andrews, 2009; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b). Together, these findings show at best limited evidence that the marked behavioural differences in the perception of familiar and unfamiliar faces are linked to differences in the way faces are represented in core face-selective regions of the human brain. One problem with identifying image-invariant responses to faces is that the representation of identity may involve a sparse code (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005) involving only a limited number of neurons and thus require substantial power to be detected in fMRI. To address this issue, we performed an fMR-adaptation experiment with a large sample of participants ($N = 80$). Our aim was to use the combination of the sensitive adaptation method and the statistical power of a large participant sample to reveal regions in either the core or extended face processing network that show an image-invariant response to familiar faces.

2. Methods

2.1. *Participants*

Eighty right-handed participants with normal or corrected to normal vision participated in the experiment (45 females; mean age: 23.8 years, SD: 4.24 years). All participants gave their written informed consent. The study was approved by the York Neuroimaging Centre Ethics Committee.

2.2. *fMRI experiment*

Face stimuli were taken from previous studies (Davies-Thompson, Newling, & Andrews, 2013; Weibert & Andrews, 2015) and included male and female identities. All images showed frontal views and neutral facial expressions, but varied in other aspects of appearance such as hairstyle and viewpoint. Our aim was to capture naturally occurring variation in images. Faces were either familiar or unfamiliar. Our familiar face stimuli depicted famous identities. An advantage of using famous faces was that it allowed us to use the same stimuli for each participant. This contrasts with the use of personally familiar faces in which different stimuli are used for each participant. To ensure familiarity with our familiar faces, prior to taking part in the experiment, participants were tested on their recognition of the familiar faces. Participants could name over 85% of the identities used (M = 85.5%, SD = 10.0%). Crucially, they could name all (100%) of the identities from the familiar same condition. This way we ensured that they could recognise when the same famous identity was repeated across different images. We also measured low-level image properties of the familiar and unfamiliar faces. The mean change in image intensity 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 the mean intensity change was similar across all face conditions [$F(3,108) = .488$, $p > .5$].

There were 6 stimulus conditions in a block design fMRI experiment:

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

The different condition blocks included face images from different identities. The same condition blocks involved sequences of different images from the same identity (Fig. 1). Scene stimuli were taken from the LabelMe scene database (Oliva & Torralba, 2001). Scrambled face images were created by scrambling the phase of the face images.

All images were presented in grey scale. Stimuli from each condition were presented in a blocked design. Each stimulus block lasted for 9 sec and contained 8 images. Within each stimulus block each image was presented for 950 msec followed by a 200 msec blank screen. Each of the six stimulus conditions was repeated 4 times. This gave a total of 24 blocks, which were presented in a counterbalanced order. Blocks were separated by a 9 sec fixation screen (a white fixation cross on a black background). To maintain attention during the scan, participants performed a one-back task in which they responded with a button press every time an identical image was directly repeated (one target per block). This allowed us to use a common behavioural task across all conditions and minimised the influence of task on the neural response.

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

	Same identity	Different identity
Familiar	16.1 (7.6)	17.2 (8.0)
Unfamiliar	18.0 (8.7)	18.7 (8.7)

Data from the fMRI experiment were collected using a GE 3 T HD Excite MRI scanner at the York Neuroimaging Centre at the University of York. A T1-weighted structural MRI (1 × 1 × 1 mm voxel) and a gradient-echo EPI were acquired for each participant. Functional data was collected using a gradient-echo EPI sequence with a radio-frequency coil tuned to 127.4 MHz was used to acquire 38 axial slices (TR = 3 sec, TE = 33 msec, flip angle = 90°, FOV = 260 mm, matrix size = 128 × 128, slice thickness = 3 mm, voxel size: 2.25 × 2.25 × 3 mm).

Statistical analysis of the fMRI data was carried out using FEAT version 4.1 in the FSL toolbox (http://www.fmrib.ox.ac.uk/fsl). The first 3 volumes (9 sec) of each scan were removed to minimise the effects of magnetic saturation, and slice-timing correction was applied. Motion correction was followed by spatial smoothing (Gaussian, full width at half maximum 6 mm) and temporal high-pass filtering (cut-off, .01 Hz). Regressors for each condition in the general linear model (GLM) were convolved with a gamma hemodynamic response function. Individual participant data of all subjects were then aligned into MNI 152 space and combined using a higher-level mixed effects group analysis of the whole-brain to generate statistical maps across participants (FLAME, http://www.fmrib.ox.ac.uk/fsl).

Face-selective regions were defined by contrasting each face condition with scenes and scrambled faces and then computing the average of these contrasts. This average contrast was used as a mask for all further analyses. Next, we determined voxels that responded more to familiar than unfamiliar faces (familiar different & familiar same > unfamiliar different & unfamiliar same). Finally, we measured adaptation to familiar and unfamiliar faces. Adaptation was defined by the contrast different > same. This was done separately for familiar and unfamiliar faces. To correct for multiple comparisons in all analyses, the resulting statistical maps were thresholded at $z > 3.5$, corresponding to $p < .05$ (voxel-wise corrected).

Additionally, we performed a Region of Interest (ROI) analysis. ROIs were individually defined in each participant as in Weibert and Andrews (2015). First, an individual's statistical map was divided into individual face-selective clusters corresponding to core face-selective regions FFA, OFA, and STS by increasing the z-score threshold. Next, the peak voxel within each face-selective cluster was identified using the cluster function in FSL. Then, a flood-fill algorithm was used to grow a ROI from each peak voxel of a fixed size (50 voxels, based on Weibert & Andrews, 2015). This was accomplished by increasing the z-score threshold until only 50 voxels lay above threshold. This resulted in ROIs with the same number of voxels across individuals. Only ROIs where all voxels were above a minimum threshold of $Z = 2.3$ were included in the analysis. Using this criterion it was not possible to reliably identify a face-selective region in the left STS at an individual level, so this region was not included in further analysis.

3. Results

3.1. *Face-selective regions*

Using a whole-brain group analysis, we localised face-selective voxels across the 80 participants. Significant face-

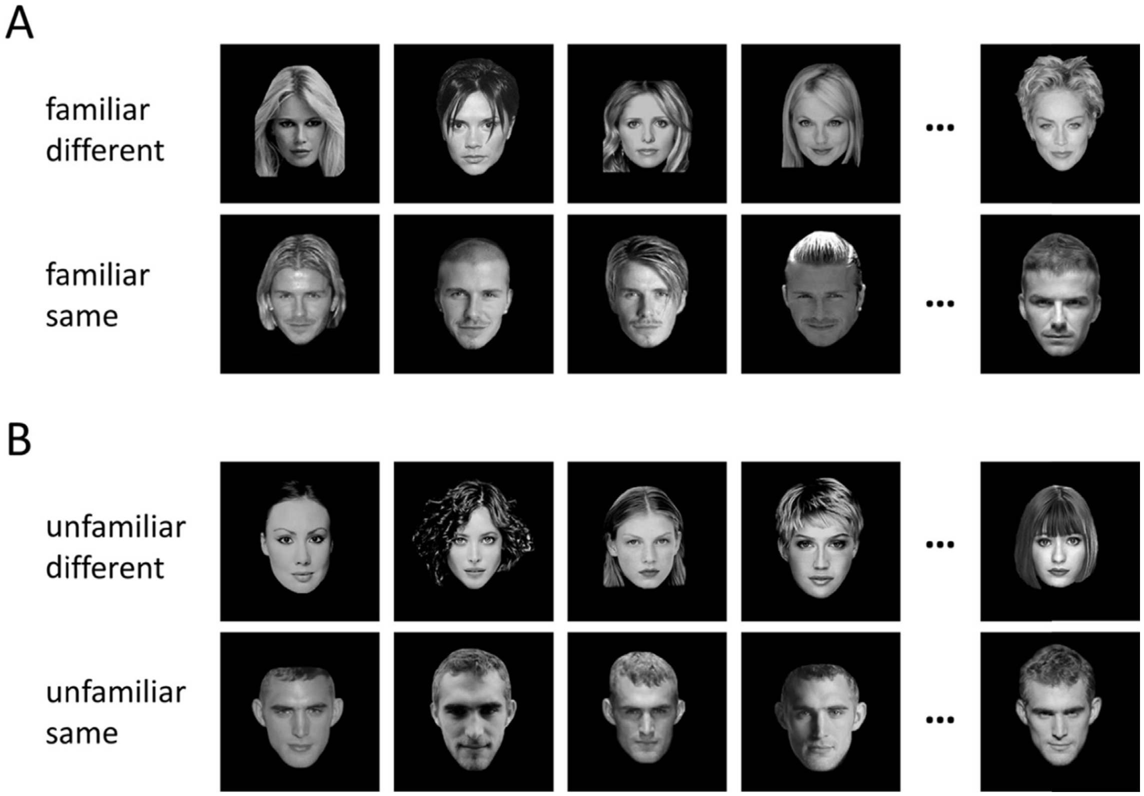

Fig. 1 – Examples of stimuli. During each face condition different face images were shown of either different identities or the same identity of (A) familiar faces and (B) unfamiliar faces.

selectivity was evident in the core face-selective regions: FFA, OFA, and posterior STS (Fig. 2A). We also found significant face-selective responses with the whole-brain group analysis in the right inferior frontal gyrus (rIFG) and in the medial temporal lobes (MTL) of both hemispheres (Fig. 2B). The MTL region overlapped with hippocampus and amygdala (http://www.cma.mgh.harvard.edu/fsl_atlas.html). The peak co-ordinates of these regions were also comparable to previous studies (Table 2; Davies-Thompson & Andrews, 2012; Kanwisher, McDermott, & Chun, 1997; Weibert & Andrews, 2015).

3.2. *Selectivity for familiarity*

Next, we performed a voxel-wise analysis within the face-selective regions to locate voxels that were more selective to familiar compared to unfamiliar faces. We found that 19.5% of voxels within core face-selective regions responded more to familiar faces than to unfamiliar faces. These voxels were located in the FFA, but not in the OFA or STS (Fig. 2A, Table 2). This familiarity effect was more pronounced in the left hemisphere (LH: 57.1%, RH: 42.9%). There were no voxels that responded more to unfamiliar than familiar faces. We then asked whether voxels in extended face-selective regions responded more to familiar than to unfamiliar faces. We found that 31.7% of voxels within extended face-selective regions responded more to familiar faces than to unfamiliar faces. These voxels overlapped with both the rIFG (30.8%) and MTL (69.2%) regions (Fig. 2B, Table 2). In the MTL, this familiarity effect was more pronounced in the left hemisphere (LH: 88.3%, RH: 11.7%). Again, there were no voxels that responded more to unfamiliar than familiar faces.

3.3. *Selectivity for identity*

Next, we investigated image-invariant adaptation to identity within core face-selective regions. This analysis was performed separately for familiar and unfamiliar faces by contrasting different identities > same identity. First, we investigated the core face-selective regions. There were no voxels in the core face-selective regions that showed significant adaptation to familiar or unfamiliar faces. There were also no voxels that showed a significantly higher response to the inverse contrast (same identity > different identities) (Table 2).

It is possible that, although there were no significant differences in the independent voxels across the core face-selective regions, there was a difference in the mean response of a region. To address this possibility, we performed a ROI analysis in which the responses to each condition were averaged across voxels in each core face-selective ROI. The results of this analysis are shown in Fig. 3. To analyse these results a 2 × 2 ANOVA was performed with familiarity and identity as factors. There was a significant effect of familiarity in the FFA [$F(1,73) = 33.17$, $p < .001$] and STS [$F(1,46) = 30.41$, $p < .001$] but not in the OFA [$F(1,57) = .43$, $p = .516$]. This was due to a higher response to familiar faces compared to unfamiliar faces. There was a significant effect of identity in all

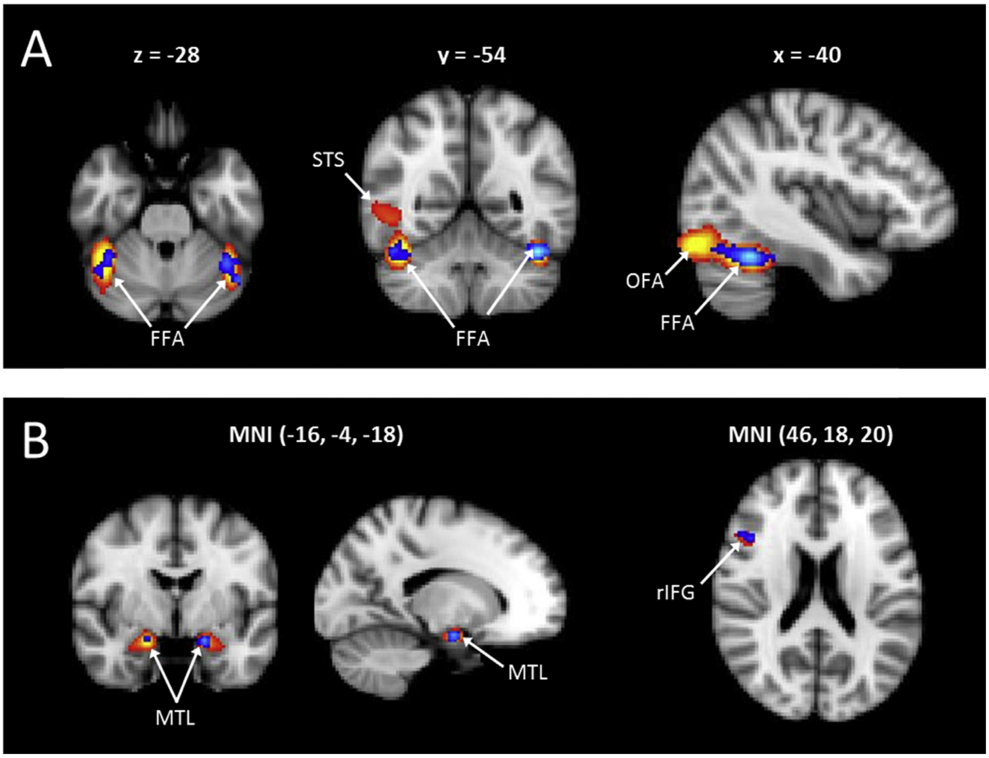

Fig. 2 – Face-selective regions (red) in the (A) core face-selective regions (FFA: fusiform face area, OFA: occipital face area, posterior STS: superior temporal sulcus) and (B) extended face-selective regions (MTL: medial temporal lobe, rIFG: right inferior frontal gyrus). Voxels showing selectivity for familiarity (familiar > unfamiliar) are shown in blue and were found in the FFA, rIFG and MTL. Images are shown in radiological convention reporting MNI coordinates.

regions [FFA: F(1,73) = 35.89, $p < .001$; OFA: F(1,57) = 20.05, $p < .001$; STS: F(1,46) = 26.18, $p < .001$]. This was due to higher responses to different identity compared to same identity faces. Critically, however, none of the ROIs showed a significant interaction between familiarity and identity: FFA: F(1,73) = 2.64, $p = .109$; OFA: F(1,57) = .81, $p = .372$; STS: F(1,46) = 2.76, $p = .104$. The absence of any difference in adaptation to familiar and unfamiliar faces suggests that the core face regions do not explain the behavioural advantage for familiar face recognition.

Next, we investigated image-invariant adaptation in the extended face-selective regions separately for familiar and unfamiliar faces. Within the extended face-selective regions, 16.6% of voxels showed an image-invariant adaptation to familiar faces. These voxels showed a smaller response (adaptation) to different images of the same familiar identity compared to images of different familiar identities (Table 2). Voxels showing image-invariant adaptation to familiar faces were found bilaterally in the MTL (Fig. 4A, Table 2). These voxels overlapped with the anatomical location of the hippocampus (59.8%) and the amygdala (40.2%) regions (Fig. 4B). No voxels showed image-invariant adaptation to unfamiliar faces. This analysis suggests that these voxels show image-invariant adaptation to familiar but not unfamiliar faces.

Table 2 – Responses within face-selective clusters to familiarity and image-invariant identity adaptation separately for familiar and unfamiliar faces significant at $p < .05$ (voxel-corrected for multiple comparisons).

	Size (mm^3)	MNI coordinates			Familiarity (mm^3)		Adaptation (mm^3)	
		x	y	z	Familiar > unfamiliar	Unfamiliar > familiar	Familiar different > familiar same	Unfamiliar different > unfamiliar same
OFA	6328	44	−82	−18	–	–	–	–
	3952	−40	−86	−20	–	–	–	–
STS	7096	50	−62	4	–	–	–	–
	1488	−48	−74	4	–	–	–	–
FFA	7016	42	−52	−24	2544	–	–	–
	4536	−40	−56	−24	3384	–	–	–
IFG	688	48	20	18	456	–	–	–
MTL	2088	20	−6	−18	120	–	456	–
	1888	−18	−6	−18	904	–	320	–

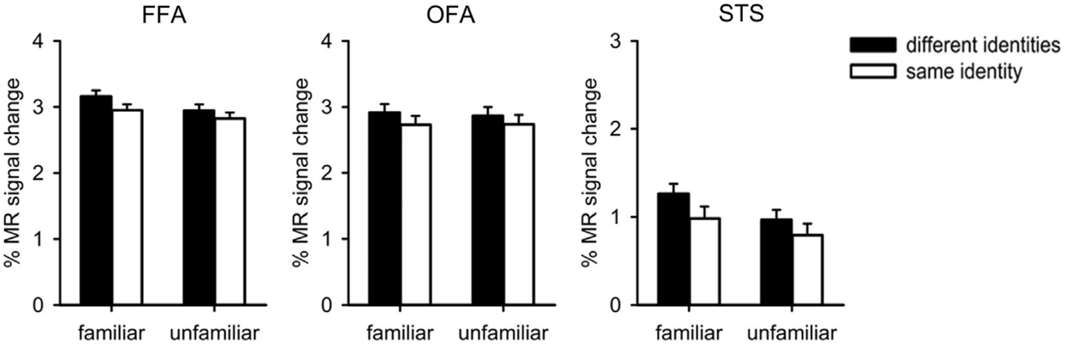

Fig. 3 – ROI analysis of core face-selective regions. A significantly larger response to familiar compared to unfamiliar faces was evident in the FFA (N = 74) and STS (N = 47), but not in the OFA (N = 58). All regions showed adaptation to facial identity. However, there was no interaction between familiarity and identity.

However, although adaptation was evident to familiar faces but not to unfamiliar faces, this does not necessarily show that adaptation was greater to familiar than unfamiliar faces. To directly compare image-invariant adaptation to familiar and unfamiliar faces, we performed a 2 × 2 repeated measures ANOVA with familiarity and identity as factors. There was a significant effect of familiarity with higher response to familiar than unfamiliar faces [$F(1,79) = 19.09$, $p < .001$]. There was also a significant effect of identity with higher response to different identity conditions than same identity conditions [$F(1,79) = 8.76$, $p < .01$]. These effects were driven by a significant interaction between familiarity and identity [$F(1,79) = 9.24$, $p < .01$]. Pairwise *t*-test revealed that there was no difference between the different identity and same identity conditions with unfamiliar faces [$t(79) = .60$, $p = .548$]. However, brain response significantly decreased for the same familiar identity compared to different familiar identities [$t(79) = 3.83$, $p < .001$]. The adaptation to familiar faces was significantly larger than to unfamiliar faces [$t(79) = 3.04$, $p < .01$; Fig. 4C].

Finally, we asked whether there was any adaptation to faces in non face-selective regions. Supplementary Table 1 shows the location of adaptation to faces outside the core and extended face-selective regions using a whole-brain analysis. We found significant adaptation to familiar and unfamiliar faces in the precuneus. Adaptation to familiar faces was found in the middle temporal lobe and the insula. Adaptation to unfamiliar faces was found in the frontal pole.

4. Discussion

The aim of this study was to determine the neural correlates for an image-invariant representation of familiar faces, analogous to FRUs (Bruce & Young, 1986). Using an fMR-adaptation paradigm, we found some evidence for an image-invariant representation of facial identity in the core face-selective regions. However, this adaptation did not differ between familiar and unfamiliar faces. In contrast to the core face-selective regions, image-invariant adaptation was found for familiar, but not unfamiliar faces in face-selective regions of the medial temporal lobe (MTL) potentially underlying the behavioural familiar face recognition advantage.

Consistent with previous studies that have shown a bias towards familiar faces in face-selective regions, familiar faces generated a higher response compared to unfamiliar faces in the FFA, rSTS and MTL (Eger et al., 2005; Elfgren et al., 2006; Leveroni et al., 2000; Sergent, Ohta, & MacDonald, 1992). Overall, the familiarity effect was more pronounced in the left than right hemisphere, which is also consistent with previous studies

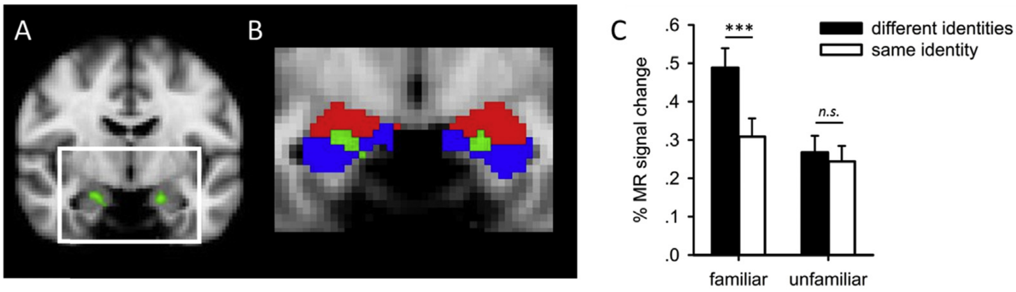

Fig. 4 – Adaptation to familiar face identity in the medial temporal lobe (MTL). Images are shown in radiological convention. (A) Voxels within the MTL that showed adaptation to familiar faces. This adaptation was only evident for familiar faces, but not unfamiliar faces (familiar different identities > familiar same identity, depicted in green). (B) Region of image-invariance to familiar faces superimposed onto Harvard Oxford structural masks (red: amygdala, blue: hippocampus). (C) Mean % MR signal change within this region averaged across participants. Error bars depict ±1 SE. ***$p < .01$.

(Elfgren et al., 2006; Gobbini & Haxby, 2007; Pierce, Haist, Sedaghat, & Courchesne, 2004). However, we did not find any selectivity for unfamiliar compared to familiar faces. This contrasts with previous studies that have found higher responses to unfamiliar faces in regions of the occipital and temporal lobes (Dubois et al., 1999; Gobbini, Leibenluft, Santiago, & Haxby, 2004; Mur, Ruff, Bodurka, Bandettini, & Kriegeskorte, 2010). It is not clear why we did not find selectivity for unfamiliar faces in these regions, but is should be noted that this selectivity was not consistent across these studies.

Next, we investigated how face-selective regions represent identity information. Here, we found some image-invariant adaptation to facial identity in the core face-selective regions. This result is consistent with previous studies, which have shown adaptation to facial identity across different images (Rotshtein et al., 2004; Eger et al., 2005; Pourtois et al., 2005a; Ewbank & Andrews, 2008). This contrasts with other studies that have reported no adaptation to facial identity across different images within these regions (Davies-Thompson et al., 2009; Pourtois et al., 2005b). The ability to detect image-invariant adaptation in this study may reflect the increased power in our design. Although we found image-invariant identity adaptation, we found no interaction between identity processing and familiarity. The observed adaptation was equally pronounced for familiar compared to unfamiliar faces. This is in line with a recent study, where the amount of image variation was systematically varied within a block and a similar release from adaptation was found for familiar as well as unfamiliar faces (Davies-Thompson et al., 2013). Together, it seems that the pattern of response in face-selective regions such as the FFA does not reflect the familiar face bias in face recognition.

In contrast to the core face-selective regions, image-invariant adaptation was found in the MTL. Consistently with Bruce and Young's model (1986), MTL adaptation was observed only for familiar but not unfamiliar faces. The MTL has previously been reported to respond more to familiar than to unfamiliar faces (Bar, Aminoff, & Ishai, 2008; Barense, Henson, & Graham, 2011; Eger et al., 2005; Elfgren et al., 2006; Ishai, Haxby, & Ungerleider, 2002; Leveroni et al., 2000; Nielson et al., 2010; Pierce et al., 2004; Sergent et al., 1992). Additionally, it has been suggested to process semantic information associated with a face rather than the image itself (Haxby et al., 2000; Ranganath, Cohen, Dam, & D'Esposito, 2004; Todorov, Gobbini, Evans, & Haxby, 2007). Our findings suggest that the involvement of MTL in familiar face recognition might reflect the activation of an image-invariant representation of person identity information (Burton et al., 1999).

The reduction in response evident in fMR-adaptation can be explained by a variety of different neural mechanisms (Grill-Spector et al., 2006; Krekelberg, Boynton, & van Wezel, 2006; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Models differ in terms of whether adaptation reflects a change in bottom-up processing (for example, neuronal fatigue or sharpening of the representation) or whether it reflects top-down control (for example, predictive processing or expectation). It is not possible to discriminate between these possibilities in the present data. However, the role of the MTL in the recognition of familiar identity is consistent with studies that have recorded neural responses in the MTL. These electrophysiological studies have revealed that neurons in the MTL respond to familiar identities across different stimuli such as different face images or even across modalities using face images and corresponding names (Nielson et al., 2010; Quiroga, Kraskov, Koch, & Fried, 2009; Quiroga et al., 2005). For example, Quiroga et al. (2005) investigated responses in the MTL in patients who had been implanted with depth electrodes. Subsets of neurons within the MTL seemed to respond selectively to a familiar identity across different stimuli, e.g., the actress Halle Berry. These neurons increased their firing rate for different photos of Halle Berry, her name, line drawings of her and even images depicting her masked as cat woman, a character she played. Such findings suggest that the MTL might play a role in linking perception of a familiar face image with the knowledge associated with it (Ranganath et al., 2004; Todorov et al., 2007). Activity in the MTL might therefore reflect automatic retrieval of person identity information from long-term memory (cf. Bruce & Young, 1986).

These findings are consistent with neuropsychological studies of prosopagnosia. Lesions to the fusiform gyrus often lead to a selective deficit in the ability to accurately perceive a face (apperceptive prosopagnosia) rather than in the matching of an image with a memory of a facial identity (associative prosopagnosia; Barton, Press, Keenan, & O'Connor, 2002; Barton, 2008). In contrast, lesions to anterior regions of the temporal lobe leave the perception of the face intact but impair recognition and semantic memory of people (Barton, 2008; Collins & Olson, 2014; Ellis, Young, & Critchley, 1989; Gainotti, 2014; Patterson, Nestor, & Rogers, 2007). Similar findings have been reported in people with developmental prosopagnosia. These studies reveal largely intact activity in the core face-selective regions, but reduced activity in anterior regions that may reflect a disruption in the connectivity between the core and extended face regions (Avidan et al., 2014; Thomas et al., 2008). Similar conclusions have been drawn from neuroimaging studies using multivariate analyses that have implicated the ventral anterior temporal lobes in the generation of image-invariant representations of facial identity (Anzellotti, Fairhall, & Caramazza, 2014; Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Nestor, Plaut, & Behrmann, 2011). We did not find face-selective responses in this anterior regions. However, this may reflect signal distortion and drop out in the MRI signal in our data due to the proximity to the sinuses (Axelrod & Yovel, 2013; Visser, Jefferies, & Ralph, 2010).

Finally, we asked whether adaptation was evident outside the face-selective regions. We found adaptation to familiar faces in the precuneus, insula and middle temporal lobe, consistent with a previous study by Pourtois et al. (2005b). We also found adaptation to unfamiliar faces in the precuneus and frontal pole consistent with previous studies (Davies-Thompson et al., 2009; Pourtois et al., 2005b).

In conclusion, we found similar levels of adaptation to facial identity in the core face-selective regions, such as the FFA. In contrast, we only found image-invariant adaptation to familiar faces in the MTL. This suggests that the recognition of familiar faces across different images relies on neural representations in the MTL.

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Supplementary data

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REFERENCES

Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *NeuroImage, 23*(3), 905–913.

Anzellotti, S., Fairhall, S. L., & Caramazza, A. (2014). Decoding representations of face identity that are tolerant to rotation. *Cerebral Cortex, 24*(8), 1988–1995.

Avidan, G., Tanzer, M., Hadj-Bouziane, F., Liu, N., Ungerleider, L. G., & Behrmann, M. (2014). Selective dissociation between core and extended regions of the face processing network in congenital prosopagnosia. *Cerebral Cortex, 24*(6), 1565–1578.

Axelrod, V., & Yovel, G. (2013). The challenge of localizing the anterior temporal face area: A possible solution. *NeuroImage, 81*, 371–380.

Bar, M., Aminoff, E., & Ishai, A. (2008). Famous faces activate contextual associations in the parahippocampal cortex. *Cerebral Cortex, 18*(6), 1233–1238.

Barense, M. D., Henson, R. N., & Graham, K. S. (2011). Perception and conception: Temporal lobe activity during complex discriminations of familiar and novel faces and objects. *Journal of Cognitive Neuroscience, 23*(10), 3052–3067.

Barton, J. J. (2008). Structure and function in acquired prosopagnosia: Lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology, 2*(1), 197–225.

Barton, J. J., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology, 58*(1), 71–78.

Bruce, V. (1982). Changing faces: Visual and non-visual coding processes in face recognition. *British Journal of Psychology, 73*, 105–116.

Bruce, V. (1994). Stability from variation: The case of face recognition. *The Quarterly Journal of Experimental Psychology, 47*, 5–28.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology, 77*(3), 305–327.

Bruce, V., & Young, A. (2012). *Face perception*. Hove, East Sussex: Psychology Press.

Burton, A. M. (2013). Why has research in face recognition progressed so slowly? The importance of variability. *The Quarterly Journal of Experimental Psychology, 66*, 1467–1485.

Burton, A. M., Bruce, V., & Hancock, P. J. (1999). From pixels to people: A model of familiar face recognition. *Cognitive Science, 23*(1), 1–31.

Collins, J. A., & Olson, I. R. (2014). Beyond the FFA: The role of the ventral anterior temporal lobes in face processing. *Neuropsychologia, 61*, 65–79.

Davies-Thompson, J., & Andrews, T. J. (2012). Intra-and interhemispheric connectivity between face-selective regions in the human brain. *Journal of Neurophysiology, 108*(11), 3087–3095.

Davies-Thompson, J., Gouws, A., & Andrews, T. J. (2009). An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia, 47*(6), 1627–1635.

Davies-Thompson, J., Newling, K., & Andrews, T. J. (2013). Image-invariant responses in face-selective regions do not explain the perceptual advantage for familiar face recognition. *Cerebral Cortex, 23*, 370–377.

Dubois, S., Rossion, B., Schiltz, C., Bodart, J.-M., Michel, C., Bruyer, R., et al. (1999). Effect of familiarity on the processing of human faces. *NeuroImage, 9*(3), 278–289.

Eger, E., Schweinberger, S., Dolan, R., & Henson, R. (2005). Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *NeuroImage, 26*(4), 1128–1139.

Elfgren, C., van Westen, D., Passant, U., Larsson, E.-M., Mannfolk, P., & Fransson, P. (2006). fMRI activity in the medial temporal lobe during famous face processing. *NeuroImage, 30*(2), 609–616.

Ellis, A. W., Young, A. W., & Critchley, E. M. (1989). Loss of memory for people following temporal lobe damage. *Brain, 112*(6), 1469–1483.

Ewbank, M. P., & Andrews, T. J. (2008). Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex. *NeuroImage, 40*(4), 1857–1870.

Gainotti, G. (2014). The neuropsychology of familiar person recognition from face and voice. *Psychologica Belgica*, 54(3), 298–309. http://dx.doi.org/10.5334/pb.at.

Gobbini, I. M., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia, 45*(1), 32–41.

Gobbini, I. M., Leibenluft, E., Santiago, N., & Haxby, J. V. (2004). Social and emotional attachment in the neural representation of faces. *NeuroImage, 22*(4), 1628–1635.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences, 10*(1), 14–23.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*(5), 555–562.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24*(1), 187–203.

Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in Cognitive Sciences, 4*(9), 330–337.

Harris, R. J., Rice, G. E., Young, A. W., & Andrews, T. J. (2015). Distinct but overlapping patterns of response to words and faces in the fusiform gyrus. *Cerebral Cortex*, 1–8.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*(6), 223–233.

Ishai, A. (2008). Let's face it: It's a cortical network. *NeuroImage, 40*(2), 415–419.

Ishai, A., Haxby, J. V., & Ungerleider, L. G. (2002). Visual imagery of famous faces: Effects of memory and attention revealed by fMRI. *NeuroImage, 17*(4), 1729–1741.

Johnston, R. A., & Edmonds, A. J. (2009). Familiar and unfamiliar face recognition: A review. *Memory, 17*(5), 577–596.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience, 17*(11), 4302–4311.

Kemp, R., Towell, N., & Pike, G. (1997). When seeing should not be believing: Photographs, credit cards and fraud. *Applied Cognitive Psychology, 11*, 211–222.

Krekelberg, B., Boynton, G. M., & van Wezel, R. J. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neurosciences, 29*(5), 250–256.

Kriegeskorte, N., Formisano, E., Sorger, B., & Goebel, R. (2007). Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proceedings of the National Academy of Sciences, 104*(51), 20600–20605.

Leveroni, C. L., Seidenberg, M., Mayer, A. R., Mead, L. A., Binder, J. R., & Rao, S. M. (2000). Neural systems underlying the recognition of familiar and newly learned faces. *The Journal of Neuroscience, 20*(2), 878–886.

Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience, 8*(10), 1386–1391.

Longmore, C. A., Liu, C. H., & Young, A. W. (2008). Learning faces from photographs. *Journal of Experimental Psychology: Human Perception and Performance, 34*, 77–100.

Mur, M., Ruff, D. A., Bodurka, J., Bandettini, P. A., & Kriegeskorte, N. (2010). Face-identity change activation outside the face system: "release from adaptation" may not always indicate neuronal selectivity. *Cerebral Cortex, 20*, 2027–2042.

Natu, V., & O'Toole, A. J. (2011). The neural processing of familiar and unfamiliar faces: A review and synopsis. *British Journal of Psychology, 102*(4), 726–747.

Nestor, A., Plaut, D. C., & Behrmann, M. (2011). Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. *Proceedings of the National Academy of Sciences, 108*(24), 9998–10003.

Nielson, K. A., Seidenberg, M., Woodard, J. L., Durgerian, S., Zhang, Q., Gross, W. L., et al. (2010). Common neural systems associated with the recognition of famous faces and names: An event-related fMRI study. *Brain and Cognition, 72*(3), 491–498.

Oliva, A., & Torralba, A. (2001). Modeling the shape of the scene: A holistic representation of the spatial envelope. *International Journal of Computer Vision, 42*(3), 145–175.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*(12), 976–987.

Pierce, K., Haist, F., Sedaghat, F., & Courchesne, E. (2004). The brain response to personally familiar faces in autism: Findings of fusiform activity and beyond. *Brain, 127*(12), 2703–2716.

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*(7), 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*(4), 1214–1224.

Quiroga, R. Q., Kraskov, A., Koch, C., & Fried, I. (2009). Explicit encoding of multimodal percepts by single neurons in the human brain. *Current Biology, 19*(15), 1308–1313.

Quiroga, R. Q., Reddy, L., Kreiman, G., Koch, C., & Fried, I. (2005). Invariant visual representation by single neurons in the human brain. *Nature, 435*(7045), 1102–1107.

Ranganath, C., Cohen, M. X., Dam, C., & D'Esposito, M. (2004). Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *The Journal of Neuroscience, 24*(16), 3917–3925.

Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. J. (2004). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience, 8*(1), 107–113.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing: A positron emission tomography study. *Brain, 115*(1), 15–36.

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience, 11*(9), 1004–1006.

Thomas, C., Avidan, G., Humphreys, K., Jung, K. J., Gao, F., & Behrmann, M. (2008). Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. *Nature Neuroscience, 12*(1), 29–31.

Todorov, A., Gobbini, M. I., Evans, K. K., & Haxby, J. V. (2007). Spontaneous retrieval of affective person knowledge in face perception. *Neuropsychologia, 45*(1), 163–173.

Visser, M., Jefferies, E., & Ralph, M. L. (2010). Semantic processing in the anterior temporal lobes: A meta-analysis of the functional neuroimaging literature. *Journal of Cognitive Neuroscience, 22*(6), 1083–1094.

Weibert, K., & Andrews, T. J. (2015). Activity in the right fusiform face area predicts the behavioural advantage for the perception of familiar faces. *Neuropsychologia, 75*, 588–596.

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*(3), 1830–1839.

Xu, X., Yue, X., Lescroart, M. D., Biederman, I., & Kim, J. G. (2009). Adaptation in the fusiform face area (FFA): Image or person? *Vision Research, 49*(23), 2800–2807.

Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology, 15*(24), 2256–2262.