UNIVERSITY *of* York

This is a repository copy of *The emergence of view-symmetric neural responses to familiar and unfamiliar faces*.

White Rose Research Online URL for this paper:
https://eprints.whiterose.ac.uk/188141/

Version: Published Version

White Rose
university consortium
Universities of Leeds, Sheffield & York

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/
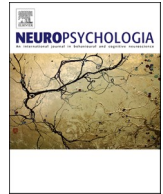
The emergence of view-symmetric neural responses to familiar and unfamiliar faces

Daniel Rogers, Timothy J. Andrews[*]

Department of Psychology, University of York, York, YO10 5DD, United Kingdom

A B S T R A C T

Successful recognition of familiar faces is thought to depend on the ability to integrate view-dependent representations of a face into a view-invariant representation. It has been proposed that a key intermediate step in achieving view invariance is the representation of symmetrical views. However, key unresolved questions remain, such as whether these representations are specific for naturally occurring changes in viewpoint and whether view-symmetric representations exist for familiar faces. To address these issues, we compared behavioural and neural responses to natural (canonical) and unnatural (noncanonical) rotations of the face. Similarity judgements revealed that symmetrical viewpoints were perceived to be more similar than non-symmetrical viewpoints for both canonical and non-canonical rotations. Next, we measured patterns of neural response from early to higher level regions of visual cortex. Early visual areas showed a view-dependent representation for natural or canonical rotations of the face, such that the similarity between patterns of response were related to the difference in rotation. View symmetric patterns of neural response to canonically rotated faces emerged in higher visual areas, particularly in face-selective regions. The emergence of a view-symmetric representation from a view-dependent representation for canonical rotations of the face was also evident for familiar faces, suggesting that view-symmetry is an important intermediate step in generating view-invariant representations. Finally, we measured neural responses to unnatural or non-canonical rotations of the face. View-symmetric patterns of response were also found in face-selective regions. However, in contrast to natural or canonical rotations of the face, these view-symmetric responses did not arise from an initial view-dependent representation in early visual areas. This suggests differences in the way that view-symmetrical representations emerge with canonical or non-canonical rotations. The similarity in the neural response to canonical views of familiar and unfamiliar faces in the core face network suggests that the neural correlates of familiarity emerge at later stages of processing.

1. Introduction

Recognising the identity of a familiar face is a simple and relatively effortless process for most human observers. However, the appearance a face can change dramatically as a person moves their head. The visual system must ignore these sources of variation in order to recognize identity, yet at the same time be able to process these changes because of their role in social communication (Bruce and Young, 1986; Andrews and Ewbank, 2004; Baseler et al., 2014). The challenge of familiar face recognition is demonstrated by the difficulty in the recognition of unfamiliar faces when they are seen from different views (Bruce, 1982; Hancock et al., 2000; Longmore et al., 2008). Cognitive models of face perception suggest that a solution to the problem of familiar facial

recognition is through view-invariant representations (Bruce and Young, 1986; Young and Burton, 2017). The successful generation of view-invariant representations relies on variable input, and experience with multiple facial viewpoints (Bruce, 2017).

How view-invariant representations are generated from view-specific representations is critical to understand how we recognize faces and become familiar with a facial identity. A simple model for how a view-invariant representation could emerge involves the convergence of multiple view-dependent representations in a single step. However, a more recent suggestion is that the process of view-invariance occurs by a two-step process that involves the convergence of view-dependent representations into view-symmetrical representations and then the convergence of these view-symmetric responses into view-invariant

* Corresponding author.
E-mail address: ta505@york.ac.uk (T.J. Andrews).

representations (Freiwald and Tsao, 2010). Behavioural support for the role of view-symmetric representations in face recognition comes from studies that have shown that the perceptual similarity of faces with symmetrical viewpoints (e.g. two profiles) is greater than for non-symmetrical viewpoints (e.g. profile and ¾ view) and also by studies that have shown that recognition judgements are more accurate when the test viewpoint is symmetrical to the learnt viewpoint (Troje and Bulthoff, 1998; Busey and Zaki, 2004; Flack et al., 2019).

Neurophysiological studies provide further support for a model of face recognition that is initially view-specific, with an intermediate view-symmetric representation before view-invariance emerges. For example, different face-selective neurons in the temporal lobe of non-human primates have been shown to be selective for single views, symmetric views and invariant to changes in view (Perrett et al., 1991). Studies using fMRI guided neurophysiological recordings in non-human primates show that face regions at early stages of processing have a more view-specific representation, whereas intermediate face regions show more view-symmetric responses and later face regions show more view-invariance (Friewald and Tsao, 2010). Taken together these results imply that there is a functional hierarchy of facial representation within these regions that could underpin recognition. Interestingly, these symmetrical responses were evident to naturally occurring or canonical rotations of the head (left to right changes in viewpoint), as well as to less common or non-canonical rotations that occur as a result of within-plane rotations of the image that ultimately lead to inversion. The demonstration of view symmetrical responses to non-canonical rotations is intriguing as it suggests that these responses might reflect a more general response to symmetry in the visual brain (Bertamini et al., 2018), rather than something that is directly linked to face recognition.

Neuroimaging studies have also revealed a similar representational hierarchy for viewpoint in face-selective regions. fMRI studies have shown view-selective responses to faces in the OFA (Grill-Spector et al., 1999; Andrews and Ewbank, 2004; Fang et al., 2007; Carlin et al., 2011; Guntupalli et al., 2017; Weibert et al., 2018). However, other studies have also reported view-symmetric representations in regions such as the FFA (Axelrod and Yovel, 2012; Kietzmann et al., 2012; Guntupalli et al., 2017; Flack et al., 2019). Interestingly, these view-symmetric neural responses are predicted by the perceptual similarity of faces from different viewpoints, suggesting that they might play an important role in face recognition (Flack et al., 2019).

There are two important limitations of previous neuroimaging studies in humans. The first is that these studies have only used naturally occurring viewpoint changes. So, it remains unknown whether view-symmetric neural responses are also evident to more unnatural, non-canonical rotations of the face (such as in plane rotation), as has been reported in neurophysiological studies (see Friewald and Tsao, 2010). If view-symmetrical responses to faces were found for these rotations, it could be argued that they reflect a general property of visual cortex, rather being directly linked generating view-invariant representations for face recognition. The second limitation is that all previous neuroimaging studies have used unfamiliar faces (Axelrod and Yovel, 2012; Kietzmann et al., 2012; Guntupalli et al., 2017; Flack et al., 2019). It is not clear therefore whether view-symmetric responses are also evident for familiar faces. Demonstrating view-symmetric responses to familiar faces would provide further evidence for the role of these representations as an intermediate step toward view-invariant representations.

The aim of this study is to determine if view-symmetric representations are evident for both canonical or non-canonical rotations of the face. If mirror-symmetric representations are an important process that precedes the generation of a view-invariant, then it might be expected that the view-symmetric responses would only be evident for naturally occurring rotations of the face. To address this question, we compared the response to faces that rotated canonically (left/right rotations of the head) with faces that rotated noncanonically within the plane of the image (within plane rotation). As a further test of whether view-symmetry is important for recognition, we compared the response to

familiar faces for which view-invariant representations are thought to exist. Finally, to determine how patterns of viewpoint selectivity response emerge in visual cortex, we measured the pattern of response in early visual areas and in face-selective regions. Our hypothesis was that face images will initially be represented by a view-dependent (image-based) representation in early visual areas, but that a view-symmetric representations will emerge in higher-level face regions.

2. Methods

2.1. Participants

Participants were recruited separately for the behavioural (n = 38, female = 26, mean age = 23.6 years, SD = 5.58) and fMRI experiments (n = 25, female = 14, mean age = 23.5 years, SD = 6.87). All participants had normal or corrected to normal vision and were drawn from an opportunity sample of students and staff at the University of York. All participants gave their written informed consent. The study was approved by the Psychology department Ethics Committee and the York Neuroimaging Centre Ethics Committee.

2.2. Stimuli

The stimuli were either familiar (well-known celebrities) or unfamiliar faces. There were three conditions: (1) canonical-familiar, (2) canonical-unfamiliar and (3) noncanonical-unfamiliar. The unfamiliar faces were taken from the Radbound Faces Database (Langner et al., 2010). The familiar images were taken from five celebrities popular to a UK student demographic (Angelina Jolie, Brad Pitt, George Clooney, Jennifer Aniston, Taylor Swift). Naturally occurring changes in view for the familiar and unfamiliar faces are shown in Figs. 1 and 2. These images show canonical, left/right rotations of the head at approximately −90°, −45°, 0°, 45°, 90°. View-symmetric images of familiar faces were created by taking the mirror image of each viewpoint. Otherwise, it would have been impossible to get symmetric views with similar appearance. The symmetric views for the unfamiliar faces were created by different cameras being set up at precise angles and all photos being taken simultaneously (Langner et al., 2010). Non-canonical views were generated by taking the frontal view of each unfamiliar face and rotating it in the frontal plane by 45° and 90° to the left and right (Fig. 3). All face images were superimposed on a 1/f amplitude mask and scaled to 500 × 500 pixels, to ensure that all images stimulated the same amount of the visual field despite changes in viewpoint and rotation.

2.3. Behavioural experiment

To determine whether symmetrical viewpoints were perceived as being more similar than non-symmetrical viewpoints, participants were asked to rate the perceptual similarity of pairs of faces that differed in view (canonical-familiar, canonical-unfamiliar; non-canonical-unfamiliar). Participants completed this experiment online using the Pavlovia platform (PSYCHOJS, Version 202.2). Each trial began with a white fixation cross superimposed on a grey background for 0.5 s. This was followed by a pair of faces (from the same identity) that were presented for 3 s. Each view was presented with every other view (10 combinations), there were 5 identities for each of the 3 image sets giving a total of 150 trials. Images subtended approximately 8° of visual angle. The order of trials was randomised for each individual participant. Participants were required to respond with a button press indicating how similar they perceived the images to be, on a scale of 1–7 (1 being less similar and 7 being more similar). Participants had an unlimited time to respond.

2.4. fMRI experiment

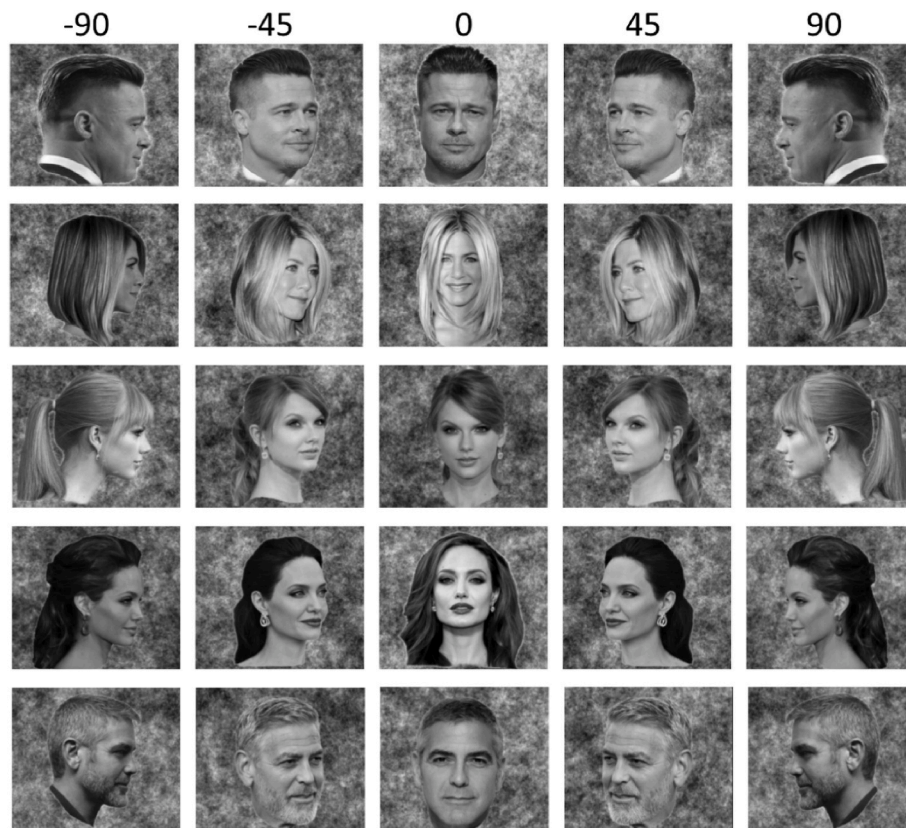The main fMRI experimental scans used a block design with 5

Fig. 1. Exemplars from the canonical-familiar condition. Images from 5 different viewpoints are show in columns. Images from 5 familiar identities are shown in rows.

different stimulus conditions each depicting a different rotation (−90°, −45°, 0°, 45°, 90°). Images from the different conditions (canonical-familiar, canonical-unfamiliar; non-canonical-unfamiliar) were shown in separate scans. In each scan, the 5 images corresponding to each viewpoint (columns in Figs. 1–3) were shown in 6 s blocks. Within each block, each image was presented for 1 s followed by a 200 ms grey screen. A 9 s fixation screen was presented between each block. There were 5 views and each was shown 6 times during the scan, giving a total of 30 blocks. The order of the blocks was pseudorandomised across the scan. Images subtended a retinal angle of approximately 15° and were viewed on a screen at the rear of the scanner via a mirror placed immediately above the participant's head. Participants maintained attention during the scans by fixating on a cross in the centre of the images and indicating using a response box when they saw a green cross. Accuracy on this task was very high (Familiar: 98.3% SD 2.46, Unfamiliar: 97.7% SD 4.35, Orientation: 98.3% SD 2.74).

All imaging data was collected using a GE 3 T HD Excite MRI system with an eight-channel phased array head coil tuned to 127.4 MHz, at the York Neuroimaging Centre (YNiC), University of York. A T1-weighted structural MRI image (1 × 1.13 × 1.13 mm voxel) was collected and a gradient-echo EPI was used to collect the functional images. A gradient-echo EPI sequence with a radio-frequency coil tuned to 127.4 MHz was used to acquire 38 contiguous axial slices (TR = 3 s, TE = 25 ms, flip angle = 90°, FOV = 260 mm, matrix size = 128 × 128, slice thickness = 3 mm, voxel size: 2.25 × 2.25 × 3 mm) in a bottom-up interleaved acquisition.

Data were analysed with FEAT version 5.0.9 (http://www.fmrib.ox.ac.uk/fsl). The first 9 s (3 vol) 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.

To understand how the representation of facial viewpoint might change from early to higher levels of the visual system, we used ROIs based on probabilistic visual-field maps (Wang et al., 2015). Overall, we investigated 16 ROIs in each hemisphere giving a total of 32 independent regions. The analysis extracted mean percentage signal changes within the given ROI for each cope (condition) for each of the functional scans. We also used the core face-selective regions (FFA, STS, OFA). Face specific regions were defined at the same size (500 voxels), to allow the MVPA analyses to have comparable potential power to detect underlying patterns of response in each region. A group analysis was performed across participants comparing the response to unfamiliar faces compared to baseline. Using masks from a previous study (Flack et al., 2019), we identified the most face-selective voxel for each ROI from the group analysis. ROIs were then created using a flood fill algorithm that progressively selected voxels with the highest face-selectivity until the mask reached 500 voxels in size (Weibert et al., 2018; Flack et al., 2019).

Pattern analyses were performed using the PyMVPA toolbox (http://www.pymvpa.org/; Hanke et al., 2009). Parameter estimates from a univariate analysis of the main experiment were first normalized by subtracting the average response across the five viewpoint conditions (−90°, −45°, 0°, 45°, 90°). The reliabilities of the neural patterns of response were then determined using a modified form of the correlation-based MVPA method devised by Haxby et al. (2001), in which patterns of response from each participant were compared with the patterns resulting from the group analysis with that participant left out. This leave one participant out (LOPO) method allowed us to determine the consistency of the patterns of response across participants by measuring how similar each participant's responses were to those for the rest of the group (Rice et al., 2014; Watson et al., 2014; Coggan et al., 2016; Weibert et al., 2018). The group pattern was derived by entering all but one of the participants' data into a higher-level group analysis (mixed effects; FLAME, http://www.fmrib.ox.ac.uk/fsl). This group
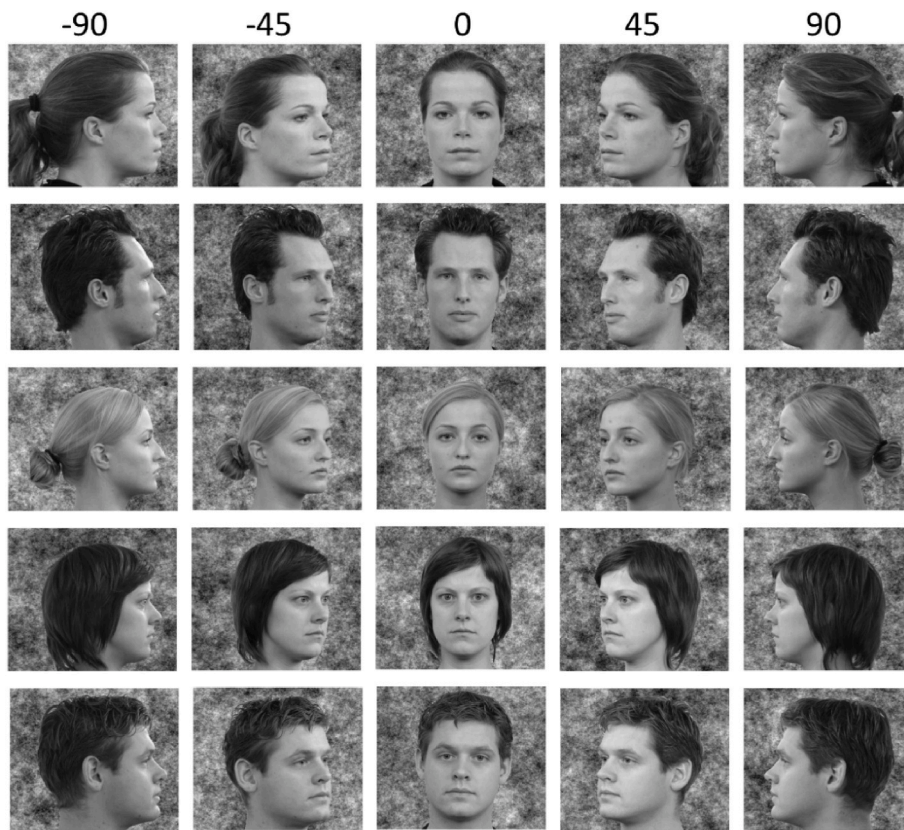
Fig. 2. Exemplars from the canonical-unfamiliar condition. Images from 5 different viewpoints are show in columns. Images from 5 unfamiliar identities are shown in rows.

pattern of response for each condition was then correlated with the pattern from the participant who was omitted from the group. For each unique pair of conditions, the LOPO method was repeated 25 times, with a different participant being omitted from the rest of the group each time. A Fisher's Z-transformation was then applied to the correlations before statistical analysis. To assess whether there were reliable responses to each view we compared the within-condition and between-condition correlations.

Next, a representational similarity analysis (Kriegeskorte et al., 2008; Flack et al., 2019) was performed to determine how information regarding facial viewpoint was represented across the ROIs using a viewpoint and a symmetry model. In the Viewpoint model the value of each cell was proportional to the degree of difference in rotation between views. In the Symmetry model, cells showing symmetrical viewpoints were given a value of 1 (e.g. −90; 90) and nonsymmetrical viewpoints were given a value 0. To prevent differences in the overall magnitude of within-condition and between-condition correlations artificially inflating differences in correlations between matrices, our analysis was only performed on the between-cluster comparisons. All models were normalized using a Z-transform (mean 0, SD 1) which was then inputted into a linear regression analysis, with the outcomes defined as the correlation matrices obtained from the MVPA concatenated across LOPO iterations. For each model, elements within the matrix were extracted and flattened to a vector. These vectors were then repeated and tiled to match the number of participants. For each participant, correlation matrices were extracted and flattened to a vector. These vectors were then concatenated and entered into the model as the outcome variable. This analysis yielded a regression coefficient and an error that reflected variance across participants. All regression analyses included a constant term. From this analysis, it was possible to determine the relative fit to each model in each ROI. To determine how the representations emerged throughout visual cortex, we compared the

regression coefficients for each model across different ROIs. Statistical values were corrected for multiple comparisons using Bonferroni-Holm.

3. Results

3.1. Behavioural experiment

Participants made perceptual similarity judgements between pairs of faces with different viewpoints. Fig. 4 shows the average ratings for symmetrical (e.g. −90° & 90°) and asymmetrical (e.g. −90° & −45°) face pairs for each condition (canonical-familiar, canonical-unfamiliar & noncanonical-orientation). An ANOVA with Symmetry (symmetrical, non-symmetrical) and Condition (canonical-familiar; canonical-unfamiliar, noncanonical-unfamiliar) showed a main effect of symmetry (F(1,37) = 260.52, $p < .001$) and condition (F(1.31, 48.48) = 12.99, $p < .001$) as well as an interaction between symmetry and condition (F (2,74) = 18.83, $p < .001$). The effect of symmetry was a result of symmetrical views being more similar than non-symmetrical views for both canonical (familiar t(37) = 14.10, $p < .001$); unfamiliar: (t(37) = 6.78, $p < .001$) and non-canonical (t(37) = 8.88, $p < .001$) rotations of the face. The interaction between symmetry and condition was due to a greater difference between symmetrical and asymmetrical viewpoints in the canonical-familiar condition compared to both the canonical-unfamiliar (t(37) = 4.67, $p < .001$, d = 0.76) and the non-canonical-unfamiliar (t (37) = 5.30, $p < .001$, d = 0.86). These findings show a perceptual similarity advantage for symmetrical views is evident for both canonical and non-canonical rotations and is also evident for familiar faces.

3.2. fMRI experiment

Next, we measured the effect of viewpoint on the neural response to faces. We measured patterns of response to each viewpoint using LOPO
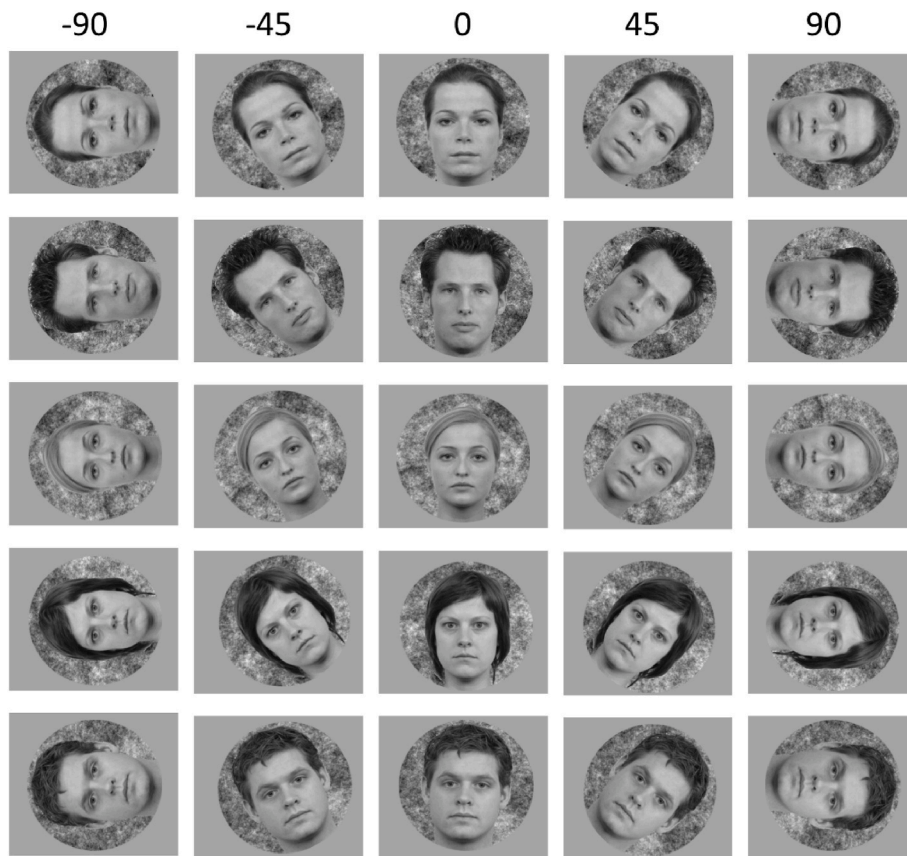
Fig. 3. Exemplars from the non-canonical-unfamiliar condition. Images from 5 different viewpoints are show in columns. Images from 5 unfamiliar identities are shown in rows.
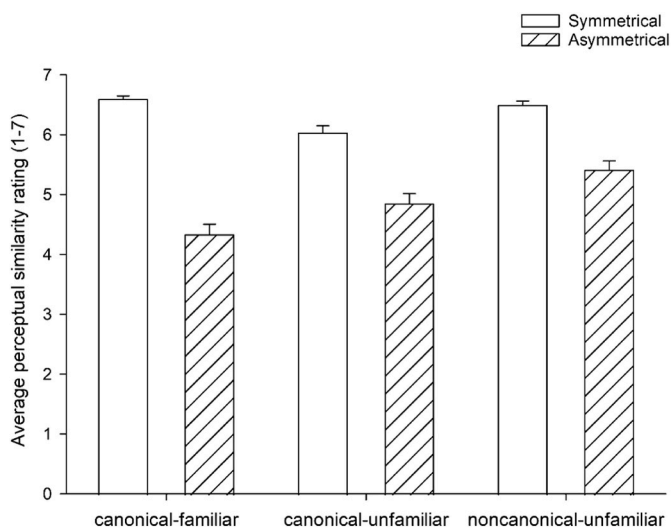

Fig. 4. Average perceptual similarity ratings of symmetrical and asymmetrical viewpoints for each condition. For each condition, symmetrical viewpoints were rated as being more similar than asymmetrical viewpoints. Error bars indicate SEM.

MVPA. To determine the reliability of the patterns of response to different viewpoints, we first compared same-viewpoint similarity with between-viewpoint similarity. Higher same-view compared to different-view correlations shows that the patterns of response were reliable. Reliable patterns of response were evident across most regions of interest (Table 1). This demonstrates consistency in the patterns of response across participants to different viewpoints of faces (see also Weibert et al., 2018; Flack et al., 2019).

Next, we asked whether the patterns of response in each region were better explained by a view-dependent model (in which the similarity in the patterns of response to different viewpoints is explained by the difference in rotation) or by a view-symmetric model (in which symmetric viewpoints elicit more similar patterns of response compared to asymmetric viewpoints).

First, we measured patterns of response to different viewpoints in the canonical familiar condition. Fig. 5A shows how the view-dependent model predicts patterns of response across different regions. The data shows that regression coefficients for the view-dependent model were highest in early visual areas, but then decreased in higher visual areas. Fig. 5B shows how the view-symmetric model predicts patterns of response across different regions. In contrast to the view-dependent model, regression coefficients for the view-symmetric model were lowest in early visual areas, but increased in higher visual areas, particularly the face-selective regions. These findings suggest the emergence of a view-symmetric representations from an initial view-dependent representation. To quantify the transition from a view-dependent to a view-symmetric representation, the regression coefficients were correlated across the different models. There was a significant negative correlation in both the left (r = 0.72, p = .003) and right (r = 0.91, p < .001) hemisphere.

Next, we measured patterns of response in the canonical unfamiliar condition. Similar to the pattern for familiar faces, there were high regression coefficients for the view-dependent model in early visual areas, but lower values in higher visual areas (Fig. 6A). Regression coefficients in the view-symmetric model (Fig. 6B) were lowest in early visual areas, but increased in higher visual areas, particularly the face-selective regions. Again, these findings show the emergence of a view-

Table 1
Same-view versus different-view comparisons for each condition across all ROIs. Distinct patterns of response were demonstrated by higher within-viewpoint correlations compared with between-viewpoint correlations. ***p < .001, **p < .01, *p < .05.

		Canonical familiar		Canonical unfamiliar		Noncanonical unfamiliar	
		t	p	t	p	t	p
V1	Left	5.21	***	6.07	***	6.70	***
	Right	6.78	***	6.82	***	4.68	***
V2	Left	3.58	**	7.13	***	5.33	***
	Right	3.71	**	4.03	***	2.56	*
V3	Left	4.09	***	5.63	***	4.92	***
	Right	7.52	***	5.51	***	6.46	***
V3a	Left	2.46	*	1.11	0.298	2.78	*
	Right	3.89	***	3.63	**	5.42	***
V3b	Left	1.63	0.116	1.19	0.247	3.57	**
	Right	2.17	*	2.46	*	2.17	*
V4	Left	3.82	***	4.76	***	5.02	***
	Right	3.44	**	3.87	***	4.65	***
VO1	Left	1.48	0.152	1.99	0.058	4.74	***
	Right	3.21	**	2.69	*	1.33	0.198
VO2	Left	2.44	*	2.48	*	2.30	*
	Right	3.45	**	3.31	**	2.06	*
PH1	Left	0.55	0.589	2.14	*	1.32	0.200
	Right	3.53	**	1.57	0.130	0.22	0.831
PH2	Left	3.80	***	1.36	0.187	3.62	**
	Right	3.69	**	4.05	***	1.66	0.110
LO1	Left	2.35	*	3.21	**	5.82	***
	Right	4.85	***	3.97	***	4.60	***
LO2	Left	5.34	***	3.50	**	5.25	***
	Right	3.39	**	2.06	*	5.05	***
OFA	Left	6.10	***	9.26	***	5.09	***
	Right	7.54	***	8.58	***	7.59	***
FFA	Left	3.61	***	5.88	***	9.73	***
	Right	4.97	***	8.33	***	8.01	***
STS	Left	5.81	***	5.99	***	9.56	***
	Right	4.88	***	6.14	***	5.77	***

symmetric   representations   from   an   initial   view-dependent

representation of faces. To quantify this change from view-dependent to view-symmetric patterns of response, the regression coefficients were correlated across the two models. Similar to the familiar faces, there was a significant negative correlation in both the left (r = 0.63, p = .012) and right (r = 0.68, p = .005) hemispheres.

Finally, we measured patterns of response to viewpoints in the non-canonical-unfamiliar condition (Fig. 7). In contrast to canonical rotations of the face, regression coefficients for the view-dependent model were low, with only V1 (left hemisphere) having a significant positive regression coefficient and there was no obvious change in the magnitude of regression coefficients from early to higher visual areas. The regression coefficients for the Symmetry model were, however, significant in many of the higher visual areas. Although these findings demonstrate the existence of view-symmetric representations for non-canonical rotations, this does not appear to emerge from an initial view-dependent representation. This is also shown by the lack of correlation between regression coefficients across the two models in either the left (r = 0.15, p = .589) or right (r = 0.35, p = .205) hemispheres.

4. Discussion

The aim of this study was to investigate whether view-symmetric representations are an important intermediate step in the generation of view-invariant representations that are used for face recognition. The main findings from this study are: (1) The emergence of view-symmetric responses is different for canonical and non-canonical rotations and (2) view-symmetric representations are evident for familiar faces. Together these findings argue that view-symmetric representations play an important role in the perception and recognition of faces.

First, we investigated the emergence of view-symmetric patterns of response in unfamiliar faces following naturally occurring (canonical) rotations of the head. We found that patterns of neural responses to canonical rotations were view-dependent in early visual areas. That is, the neural response was predicted by degree of rotation between different viewpoints. These findings are consistent with other neuro-physiological (Perrett et al., 1991, 1998; Freiwald and Tsao, 2010;
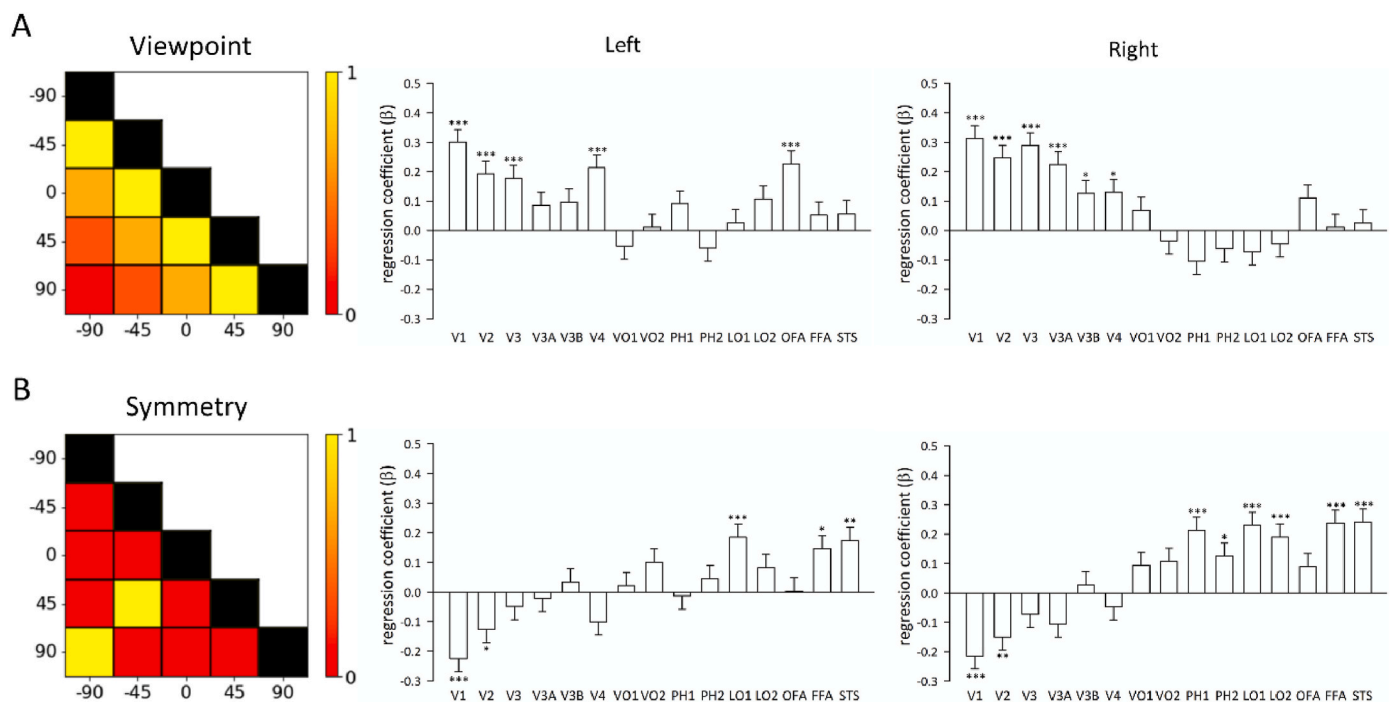

Fig. 5. Regression analysis of fMRI data for canonical-familiar condition showing how different models predict patterns of response across ROIs. (A) The Viewpoint model predicted patterns of response in early visual areas. (B) In contrast, the Symmetry model predicted patterns in higher visual areas, including the face-selective regions. ***p < .001, **p < .01, *p < .05.
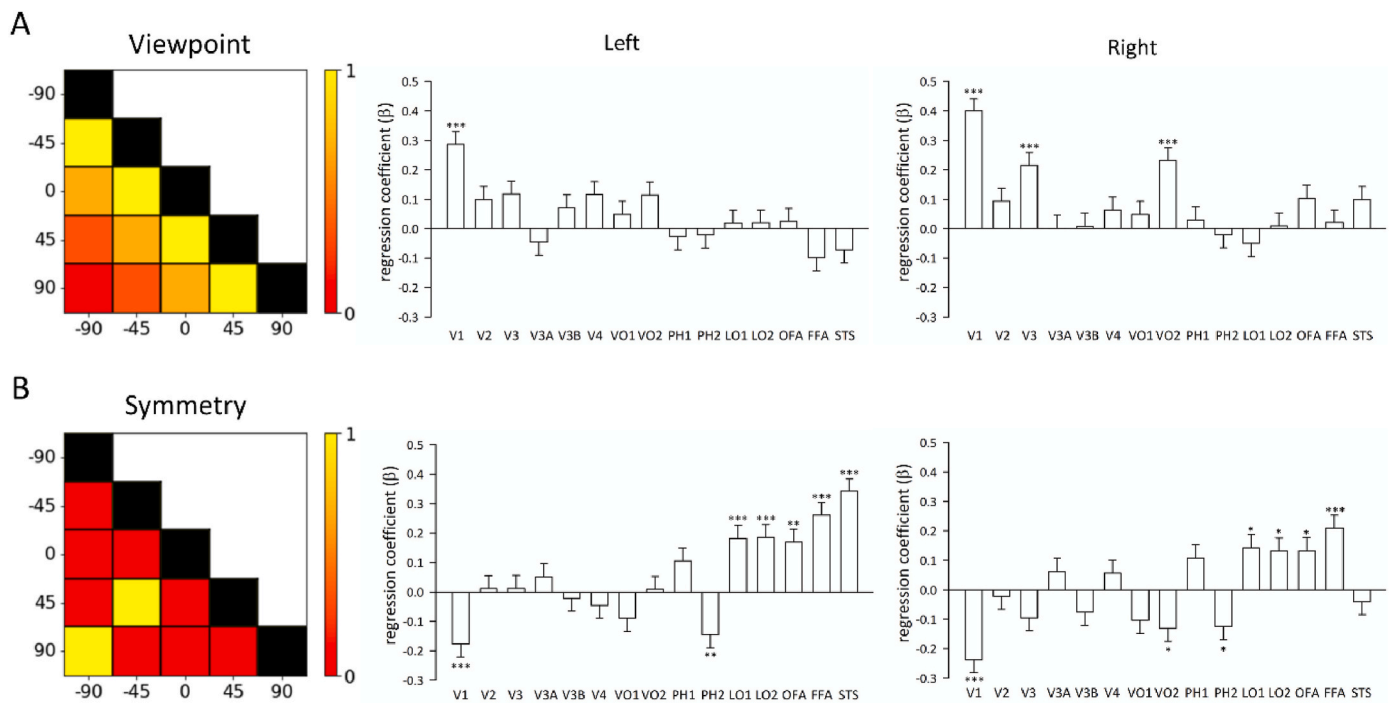
Fig. 6. Regression analysis of fMRI data for canonical-unfamiliar condition showing how different models predict patterns of response across ROIs. (A) The Viewpoint model predicted patterns of response in early visual areas. (B) In contrast, the Symmetry model predicted patterns in higher visual areas, including the face-selective regions. ***p < .001, **p < .01, *p < .05.
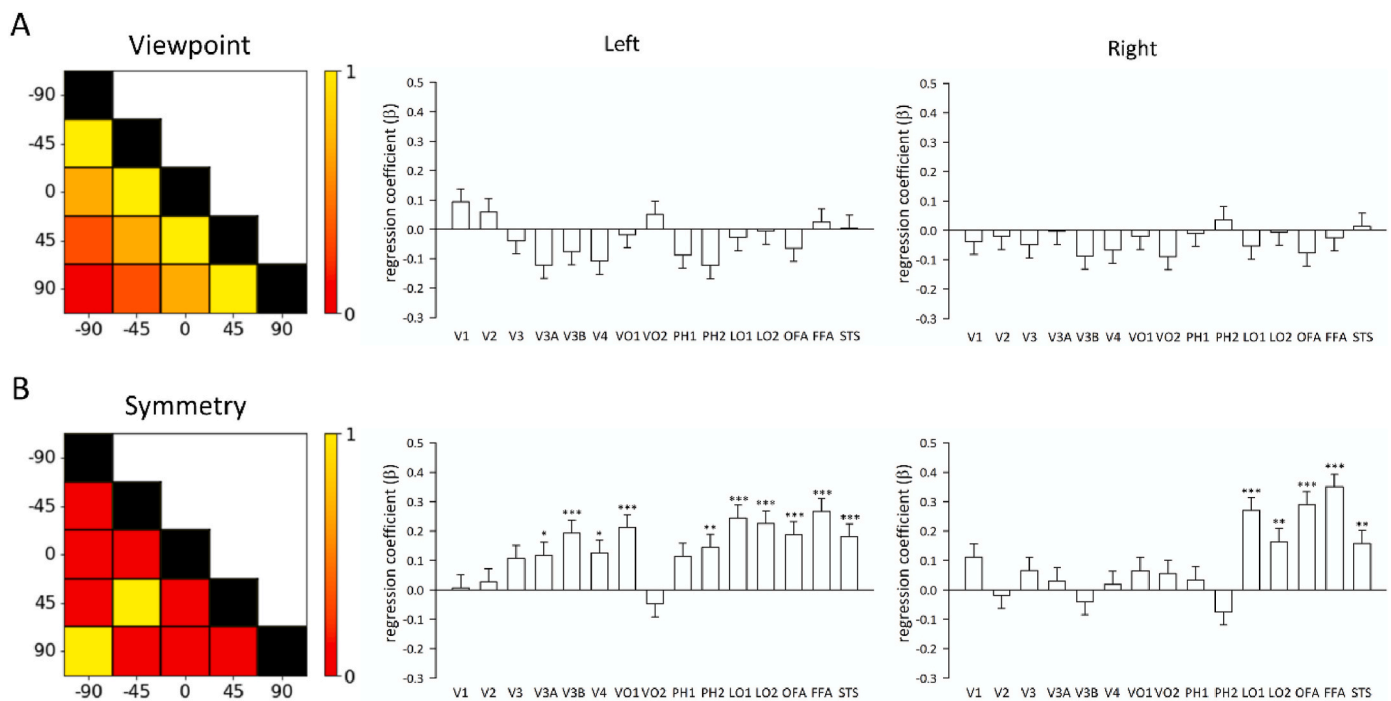

Fig. 7. Regression analysis of fMRI data for non-canonical-unfamiliar condition showing how different models predict patterns of response across ROIs. (A) The Viewpoint model failed to predict patterns of response across early and higher visual areas. (B) In contrast, the Symmetry model predicted patterns in higher level visual areas, including the face-selective regions. ***p < .001, **p < .01, *p < .05.

Dubois et al., 2015) and neuroimaging studies (Carlin et al., 2011; Axelrod and Yovel, 2012; Kietzmann et al., 2012; Ramírez et al., 2014; Dubois et al., 2015; Guntupalli et al., 2017; Flack et al., 2019) that have also found selectivity to specific viewpoints of the face. They also fit with behavioural studies that have shown the importance of view-selective

representations in the perception and recognition of unfamiliar faces (Bruce, 1982; Hill and Bruce, 1996; Fang and He, 2005; Longmore et al., 2008). However, there was a gradual decrease in the view-dependent response from early to higher visual areas and a corresponding increase in view-symmetric responses, particularly in face-selective

regions. The importance of view-symmetrical neural responses is shown by the fact that symmetrical faces are perceived to be more similar than asymmetrical faces (see also, Troje and Bülthoff, 1998; Busey and Zaki, 2004; Flack et al., 2019).

To determine whether view-symmetric responses are specific to naturally occurring rotations of the face, we also measured the behavioural and neural response to non-canonical rotations of the face. We found that there was selectivity to specific viewpoints in early visual areas, but there was limited evidence that the pattern of response was systemically predicted by changes in viewpoint, as was found with canonical rotations. However, we did find view-symmetric neural patterns of response for non-canonical rotations, which matches our behavioural finding that symmetrical viewpoints were more perceived to be more similar that asymmetrical viewpoints. This suggests that the emergence of view-symmetric responses occurs differently for canonical and non-canonical rotations of the face. Nevertheless, our findings are consistent with previous neurophysiological studies that have reported view-symmetric responses to non-canonical rotations that also occur as a result of within-plane rotations of the image that ultimately lead to inversion (Friewald and Tsao, 2010). These findings may be more consistent with a more general preference for bilateral symmetry in the visual system (Corballis and Beale, 2020; Rhodes et al., 2005; Jacobsen et al., 2006; Bertamini et al., 2018; Keefe et al., 2018; Makin et al., 2012).

The recognition of familiar faces requires the ability to integrate information from different viewpoints into an invariant representation (Bruce and Young, 1986; Young and Burton, 2017; Bruce, 2017). One possible mechanism for generating view invariance is the convergence of view-dependent responses (Bruce and Young, 1986; Burton et al., 1999). The discovery of view-symmetric neural responses suggests that they may provide an important intermediate computational step before full invariance is achieved (Freiwald and Tsao, 2010). However, a limitation of previous studies is that they have only used unfamiliar faces, whose representations are more closely linked to the image and do not generalise well to new viewpoints when compared to familiar faces (Bruce, 1982; Hancock et al., 2000; Longmore et al., 2008). Our current findings show that view-symmetric neural responses are also evident for familiar faces in core face regions despite the fact that can be easily recognized across different views. This suggests that the view-invariant representations that are characteristic of familiar faces emerge at later stages of processing (Davies-Thompson et al., 2013; Weibert et al., 2016).

We also found that symmetric views of familiar faces were perceived to be more similar than asymmetric views. This also fits with evidence that symmetrical views may convey an advantage when learning new faces. In a previous study, we found that when participants were tested with novel face images that were symmetrical to learnt viewpoint, recognition rates were higher than when the learnt and test faces had asymmetrical viewpoints (Flack et al., 2019). Moreover, the pattern of recognition performance was predicted by the pattern of neural response in face-selective regions, such as the FFA. Together, this suggests that view-symmetric representations may play an important intermediate step in the recognition of familiar faces.

In conclusion, this study investigated the role of view-symmetric responses in face recognition. Limitations of previous studies are that they have not used familiar faces and that they have not shown whether view-symmetric responses are only found for naturally occurring rotations of the face. We address both issues in the current study. We show that view-symmetrical patterns of response to familiar faces can be found in face-selective regions, such as the FFA. Next, we show distinct differences in the way that view-symmetric responses emerge along the visual hierarchy for canonical and non-canonical rotations of the face. These findings provide important evidence in support of the role of view-symmetry as an important intermediate processing stage in the perception and recognition of faces.

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.

Axelrod, V., Yovel, G., 2012. Hierarchical processing of face viewpoint in human visual cortex. J. Neurosci. 32 (7), 2442–2452.

Baseler, H.A., Harris, R.J., Young, A.W., Andrews, T.J., 2014. Neural responses to expression and gaze in the posterior superior temporal sulcus interact with facial identity. Cerebr. Cortex 24 (3), 737–744.

Bertamini, M., Silvanto, J., Norcia, A.M., Makin, A.D., Wagemans, J., 2018. The neural basis of visual symmetry and its role in mid-and high-level visual processing. Ann. N. Y. Acad. Sci. 1426 (1), 111–126.

Bruce, V., 1982. Changing faces: visual and non-visual coding processes in face recognition. Br. J. Psychol. 73 (1), 105–116.

Bruce, V., 2017. Recognising Faces, vol. 3. Routledge.

Bruce, V., Young, A., 1986. Understanding face recognition. Br. J. Psychol. 77 (3), 305–327.

Burton, A.M., Bruce, V., Hancock, P.J., 1999. From pixels to people: a model of familiar face recognition. Cognit. Sci. 23 (1), 1–31.

Busey, T.A., Zaki, S.R., 2004. The contribution of symmetry and motion to the recognition of faces at novel orientations. Mem. Cognit. 32 (6), 916–931.

Carlin, J.D., Calder, A.J., Kriegeskorte, N., Nili, H., Rowe, J.B., 2011. A head view-invariant representation of gaze direction in anterior superior temporal sulcus. Curr. Biol. 21 (21), 1817–1821.

Coggan, D.D., Liu, W., Baker, D.H., Andrews, T.J., 2016. Category-selective patterns of neural response in the ventral visual pathway in the absence of categorical information. Neuroimage 135, 107–114.

Corballis, M.C., Beale, I.L., 2020. The Psychology of Left and Right. Routledge.

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. Cerebr. Cortex 23 (2), 370–377.

Dubois, J., de Berker, A.O., Tsao, D.Y., 2015. Single-unit recordings in the macaque face patch system reveal limitations of fMRI MVPA. J. Neurosci. 35 (6), 2791–2802.

Fang, F., He, S., 2005. Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. Neuron 45 (5), 793–800.

Fang, F., Murray, S.O., He, S., 2007. Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. Cerebr. Cortex 17 (6), 1402–1411.

Flack, T.R., Harris, R.J., Young, A.W., Andrews, T.J., 2019. Symmetrical viewpoint representations in face-selective regions convey an advantage in the perception and recognition of faces. J. Neurosci. 39 (19), 3741–3751.

Freiwald, W.A., Tsao, D.Y., 2010. Functional compartmentalization and viewpoint generalization within the macaque face-processing system. Science 330 (6005), 845–851.

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.

Guntupalli, J.S., Wheeler, K.G., Gobbini, M.I., 2017. Disentangling the representation of identity from head view along the human face processing pathway. Cerebr. Cortex 27 (1), 46–53.

Hancock, P.J., Bruce, V., Burton, A.M., 2000. Recognition of unfamiliar faces. Trends Cognit. Sci. 4 (9), 330–337.

Hanke, M., Halchenko, Y.O., Sederberg, P.B., Hanson, S.J., Haxby, J.V., Pollmann, S., 2009. PyMVPA: a python toolbox for multivariate pattern analysis of fMRI data. Neuroinformatics 7 (1), 37–53.

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

Hill, H., Bruce, V., 1996. The effects of lighting on the perception of facial surfaces. J. Exp. Psychol. Hum. Percept. Perform. 22 (4), 986.

Jacobsen, T., Schubotz, R.I., Höfel, L., Cramon, D.Y.V., 2006. Brain correlates of aesthetic judgment of beauty. Neuroimage 29 (1), 276–285.

Keefe, B.D., Gouws, A.D., Sheldon, A.A., Vernon, R.J., Lawrence, S.J., McKeefry, D.J., Morland, A.B., 2018. Emergence of symmetry selectivity in the visual areas of the human brain: fMRI responses to symmetry presented in both frontoparallel and slanted planes. Hum. Brain Mapp. 39 (10), 3813–3826.

Kietzmann, T.C., Swisher, J.D., König, P., Tong, F., 2012. Prevalence of selectivity for mirror-symmetric views of faces in the ventral and dorsal visual pathways. J. Neurosci. 32 (34), 11763–11772.

Kriegeskorte, N., Mur, M., Bandettini, P.A., 2008. Representational similarity analysis-connecting the branches of systems neuroscience. Front. Syst. Neurosci. 2, 4.

Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D.H., Hawk, S.T., Van Knippenberg, A.D., 2010. Presentation and validation of the radboud faces Database. Cognit. Emot. 24 (8), 1377–1388.

Longmore, C.A., Liu, C.H., Young, A.W., 2008. Learning faces from photographs. J. Exp. Psychol. Hum. Percept. Perform. 34 (1), 77.

Makin, A.D.J., Pecchinenda, A., Bertamini, M., 2012. Implicit affective evaluation of visual symmetry. Emotion 12 (5), 1021.

Perrett, D.I., Oram, M.W., Harries, M.H., Bevan, R., Hietanen, J.K., Benson, P.J., Thomas, S., 1991. Viewer-centred and object-centred coding of heads in the macaque temporal cortex. Exp. Brain Res. 86 (1), 159–173.

Perrett, D.I., Oram, M.W., Ashbridge, E., 1998. Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations. Cognition 67, 111–145.

Ramírez, F.M., Cichy, R.M., Allefeld, C., Haynes, J.D., 2014. The neural code for face orientation in the human fusiform face area. J. Neurosci. 34 (36), 12155–12167.

Rhodes, G., Peters, M., Lee, K., Morrone, M.C., Burr, D., 2005. Higher-level mechanisms detect facial symmetry. Proc. Biol. Sci. 272 (1570), 1379–1384.

Rice, G.E., Watson, D.M., Hartley, T., Andrews, T.J., 2014. Low-level image properties of visual objects predict patterns of neural response across category-selective regions of the ventral visual pathway. J. Neurosci. 34 (26), 8837–8844.

Troje, N.F., Bülthoff, H.H., 1998. How is bilateral symmetry of human faces used for recognition of novel views? Vis. Res. 38 (1), 79–89.

Wang, L., Mruczek, R.E., Arcaro, M.J., Kastner, S., 2015. Probabilistic maps of visual topography in human cortex. Cerebr. Cortex 25 (10), 3911–3931.

Watson, D.M., Hartley, T., Andrews, T.J., 2014. Patterns of response to visual scenes are linked to the low-level properties of the image. Neuroimage 99, 402–410.

Weibert, K., Harris, R.J., Mitchell, A., Byrne, H., Young, A.W., Andrews, T.J., 2016. An image-invariant neural response to familiar faces in the human medial temporal lobe. Cortex 84, 34–42.

Weibert, K., Flack, T.R., Young, A.W., Andrews, T.J., 2018. Patterns of neural response in face regions are predicted by low-level image properties. Cortex 103, 199–210.

Young, A.W., Burton, A.M., 2017. Recognizing faces. Curr. Dir. Psychol. Sci. 26 (3), 212–217.