Contents lists available at ScienceDirect

Vision Research

The roles of shape and texture in the recognition of familiar faces

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A B S T R A C T

The surface texture of the face is proposed to be the dominant cue in face recognition. In this study, we investigated the role of shape information in face recognition. We compared the roles of shape and surface texture in the recognition of face identity using familiar and unfamiliar hybrid faces in which the average shape from one facial identity was combined with the average texture of a different identity. In the first experiment (n = 53), participants had to match the name of a familiar person to one of eight hybrid face images. In texture trials, all images had the correct shape, but only one image had the correct texture. In shape trials, all images had the correct texture, but only one image had the correct shape. Importantly, neither task could be performed by perceptual matching. Although performance was lower for the shape trials (81%) compared to texture trials (99%), both were significantly above chance (12.5%). In the second experiment (n = 110), participants had to name hybrid faces. There were two potentially correct answers for each face image: one based on the texture and one based on the shape. Participants reported the correct name based on the texture on 61% of trials and the correct name based on the shape on 12% of trials. In the third experiment (n = 19), fMR-adaptation was used to measure the neural sensitivity to changes in the shape or texture. The core face-selective regions showed a similar sensitivity to shape and texture. These findings confirm that texture is the dominant cue for face recognition, but also show that shape plays an important role in the recognition and neural response to familiar faces.

1. Introduction

Recognising the identity of a person from their face is fundamental for appropriate social interactions. Processing the visual information that is used to recognise faces is central to understanding this behaviour. In face perception, a distinction can be made between the texture (or surface) properties of the face and its shape properties (Bruce and Young, 1998, 2012). Shape properties arise from the geometry of the facial features, and how they are projected onto a 2D image (Maurer, Le Grand, & Mondloch, 2002), whereas texture results from changes in reflectance, due to the combination of ambient illumination, facial pigmentation and shape from shading cues (Bruce & Young, 2012).

Texture plays a critical role in the perception of a face identity (Burton, 2013). For example, familiar face recognition is still possible when surface properties are projected onto a standardised shape (Burton, Jenkins, Hancock, & White, 2005) or when linearly stretching or morphing a face image in a way that dramatically alters the shape of the face (Hole, George, Eaves, & Rasek, 2002; Sandford & Burton, 2014; Baseler, Young, Jenkins, Burton, & Andrews, 2016; Itz, Schweinberger, Schulz, & Kaufmann, 2014; Itz, Golle, Luttmann, Schweinberger, & Kaufmann, 2017). Changes to the texture of the face, on the other hand,

caused by contrast negation or spatial blurring have a dramatic effect on recognition, even when the shape of the face is unchanged (Bruce & Langton, 1994; Kemp, Pike, White, & Musselman, 1996; Hole et al., 2002). It is also difficult to recognize line drawings of a familiar face that have the correct shape, but limited texture information (Leder, 1999) and perceptual matching of facial identity has been shown to be more accurate when based on texture compared to shape (Andrews, Baseler, Jenkins, Burton, & Young, 2016).

Although these studies imply that texture information provides the dominant cue for face recognition, manipulations of shape can have a significant effect on the judgements of recognition. For example, non-linear manipulations of shape can have a significant effect on the ability to recognise identity (Hole et al., 2002). Further support for the role of shape in face recognition comes from studies that show shape information can be used to discriminate unfamiliar face images (O'Toole et al., 1999; Jiang, Blanz & O'Toole, 2006; Russell, Biederman, Nederhouser, & Sinha, 2007; Russell & Sinha, 2007, Caharel et al., 2009; Jiang, Blanz, & Rossion, 2011; Lai, Oruç, & Barton, 2013; Itz, Schweinberger, & Kaufmann, 2016). Although judgements based on texture are more accurate than judgements based on shape, it is still possible to make some use of shape information in matching tasks

involving familiar faces (Andrews et al., 2016). However, in all these studies it is possible that these tasks involving shape could be performed by lower-level perceptual matching of features rather than higher-level processes critical to the recognition of identity in natural viewing conditions (Burton et al., 2015). Indeed, a challenge for a central role of shape in face recognition is that shape cues (particularly those involving the internal features of the face) can vary quite dramatically across different images of the same person (Burton, 2013; Burton et al., 2015). For example, the spatial distances between features can often vary as much within-person as between-person.

The behavioural sensitivity to the shape and texture of faces should be mirrored by the neural responses of face-selective regions involved in recognition. Neuroimaging studies have revealed a core network of face-selective regions in the occipital and temporal lobes that are involved in the perception and recognition of faces (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997). Within this network, the fusiform face area (FFA) is held to be important for representing invariant facial characteristics that play an important role in the recognition of facial identity (Haxby et al., 2000; Grill-Spector, Knouf, & Kanwisher, 2004; Rotshtein, Henson, Treves, Driver, & Dolan, 2004). Support for the importance of the FFA in processing facial identity is found in neuroimaging studies that have shown adaptation to repeated images of faces in this region (Andrews & Ewbank, 2004; Grill-Spector et al., 1999). This suggests that the neural response in the FFA represents the identity of the face and that this representation is being adapted by repeated images.

A more robust link between activity in the FFA and face recognition would be a demonstration that adaptation is still found when the images vary along a dimension that is not important for face recognition (i.e., changes in shape). For example, Jiang and colleagues (Jiang, Dricot, Blanz, Goebel, & Rossion, 2009; see also; Caharel, Jiang, Blanz, & Rossion, 2009; Itz et al., 2016) found an equal release from adaptation to identity in the FFA with changes in either the shape or texture. This suggests that both properties are represented in this region, which differs from behavioural studies of familiar faces that show a greater sensitivity to changes in texture. Although these findings might be explained by their use of unfamiliar faces, we also found a similar release from adaptation to shape and texture with familiar faces (Andrews et al., 2016). Although this provides further support for a dissociation between the behavioural and neural response to faces, it is possible that a more sensitive adaptation paradigm could show a difference in the neural response to shape and texture.

The aim of this study is therefore to achieve a more detailed understanding of the relative roles of shape and texture in the recognition and neural response to familiar and unfamiliar faces. We used hybrid face images in which the surface texture from one identity is combined with the shape from another identity (Andrews et al., 2016). Our aim in this study was to test recognition directly using tasks that had no component of perceptual matching and instead relied on previously learnt representations for recognition. In all experiments, we compared familiar and unfamiliar faces as previous research has shown differences in how shape and texture information are used when making judgments of familiar and unfamiliar faces (Itz et al., 2014, 2017; Zhou et al., 2021). In the first experiment, a name was shown and participants had to match that name to one of 8 images. The images shown varied in either shape or texture. In the second experiment, participants viewed individual hybrid images and were asked to name the person. There were two potentially correct answers for each familiar face: one based on texture and one based on shape. This directly compared the relative role of shape and texture in the representation of familiar faces. In the final experiment, we measured the relative sensitivity to shape and texture in face-selective regions of the human brain, using an fMR-adaptation paradigm that has previously been used to reveal invariant responses to faces in face-selective regions such as the FFA (Davies-Thompson, Newling, & Andrews, 2013).

2. Methods

2.1. Participants

Participants were recruited separately for the behavioural and fMRI experiments (Experiment 1: n = 53, female = 38, mean age = 26.9 years, SD = 9.8; Experiment 2: n = 110, female = 62, mean age = 22.7 years, SD = 6.8; Experiment 3: n = 19, female = 10, mean age = 25.4 years, SD = 1.39). A priori power analyses (0.9, 1-β err prob) were conducted for Experiment 1 (suggested N = 55) and Experiment 2 (suggested N = 110). Sample size for Experiment 3 was based on previous studies using similar paradigms (Andrews et al., 2016; Baseler et al., 2016). Participants were drawn from an opportunity sample of staff and students from the University of York. They all had normal or corrected to normal vision and 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 faces used were either familiar (UK celebrities) or unfamiliar (Australian celebrities) in the UK (Fig. 1). The familiar images were based on grayscale average images that were generated by combining 12 different images from each of 8 celebrities who are generally familiar to UK participants (Alan Sugar, Chris Moyles, Derren Brown, Gary Lineker, Jeremy Paxman, Jeremy Kyle, Louis Walsh). The unfamiliar images were also based on average images generated by combining 12 different images from each of 8 Australian celebrities who are likely to be unknown to our participants (Brendan Nelson, Don Burke, Grant Hackett, Guy Sebastian, Kyle Sandilands, Mark Holden, Morris Iemma, Shannon Noll). The averaging procedure was performed using graphics software in which key fiducial points on the face were defined in each image, and then connected to form a grid showing the shape or the second-order configural properties of the image (for details see Burton et al., 2005; Burton, Schweinberger, Jenkins, & Kaufmann, 2015). Average shapes could then be generated through averaging the spatial location of corresponding points on the grid across all images with the same identity. Average textures for each identity were created by morphing each image to a standard shape and averaging across all images with the same identity. The photos were selected using an internet image search on the celebrities' names. The only selection criteria were that the full face was visible in high resolution. Selecting images in this way has been shown to provide robust averages (Jenkins, White, Van Montfort, & Burton, 2011; Burton, Kramer, Ritchie, & Jenkins, 2016; Jenkins, Burton, & White, 2006). The images on the diagonal (top left to bottom right) in each panel of Fig. 1 show shape and surface properties from the same identity. Because the shape and surface information are generated separately, it is also possible to combine them across different identities to generate hybrid images. Hybrid faces are shown in the off-diagonal images. Images in each column have the same shape, whereas images in each row have the same surface properties.

2.3. Experiment 1

To compare the role of shape and texture in the recognition of familiar faces, participants had to match a name to faces that varied in either shape or texture. Participants first viewed the name of a face. They were then shown 8 hybrid face images (Fig. 2). For a texture trial, all the faces had the shape of the target, but only one also had the correct texture. For a shape trial, all faces had the same texture as the target, but only one also had the correct shape. Participants used a button press to indicate which face corresponded to the target. There were 32 trials (8 familiar and 8 unfamiliar identities, shape/texture). This process was self-paced and no feedback was given. After the task was completed, participants completed a familiarity check to test their ability to recognise the familiar faces. A novel high-resolution image from each
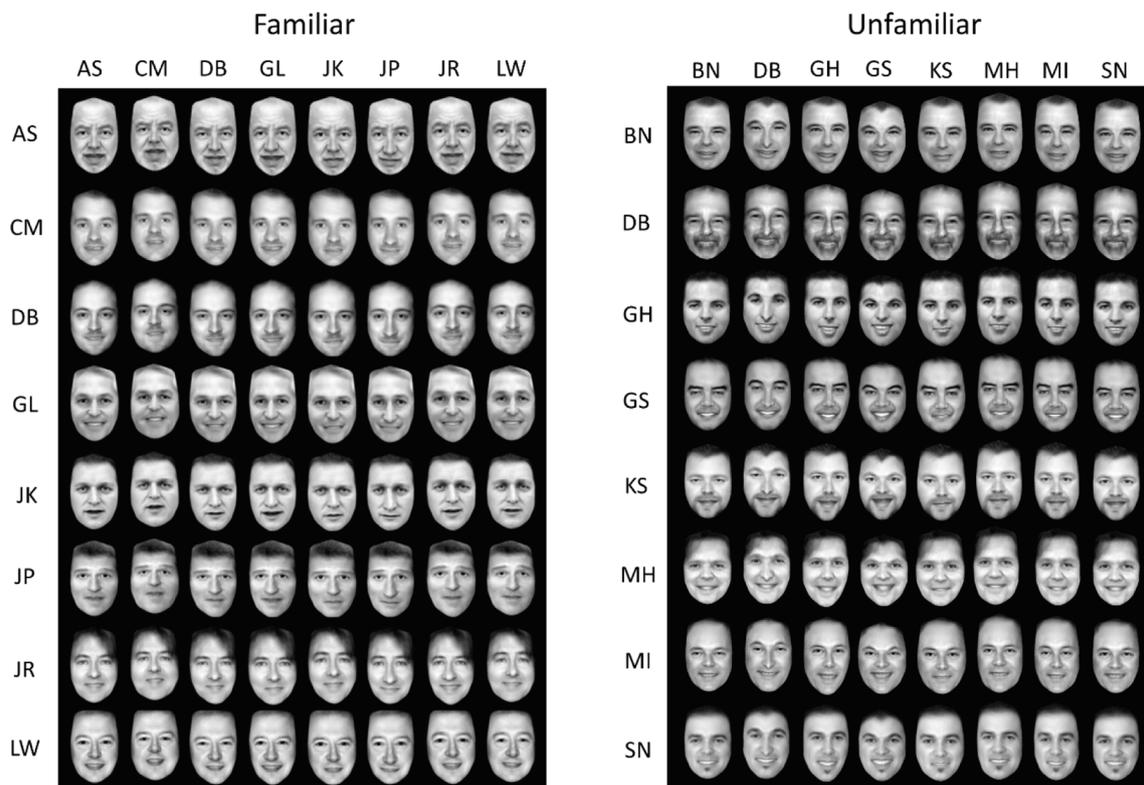
Fig. 1. Familiar and unfamiliar hybrid face images. Hybrid images were created by combining the average shape from one identity with the average texture from another identity. The diagonal images (top left to bottom right) contain the average shape and texture properties of the same identity. Rows depict images containing the average texture of one identity and the average shapes of other identities. Columns depict images containing the average shape of one identity and the average textures of other identities.
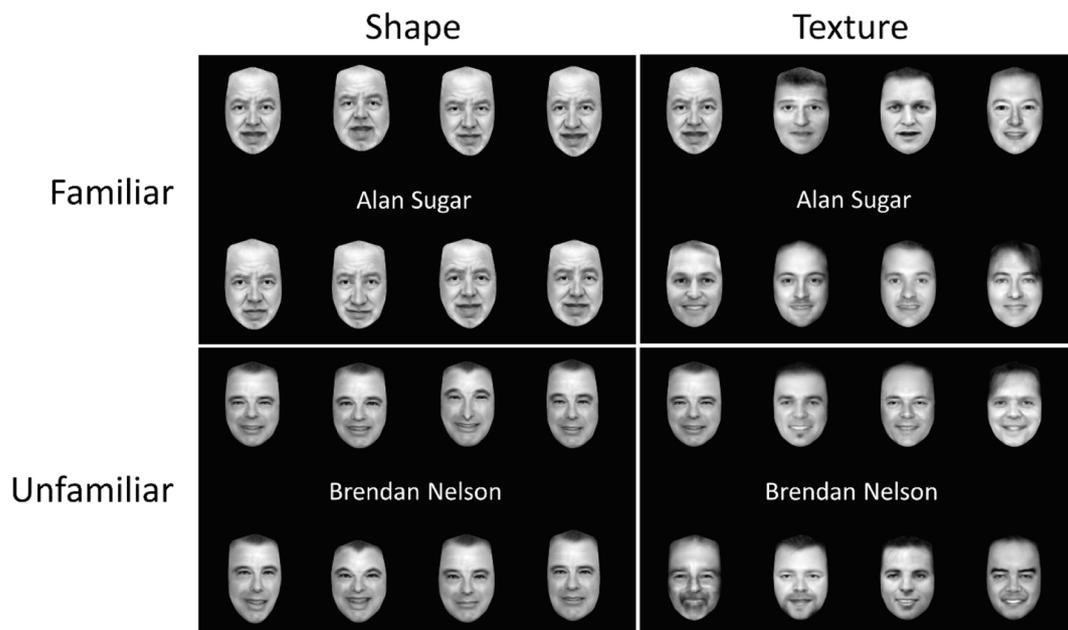
Fig. 2. Experiment 1: Examples of shape and texture trials for familiar and unfamiliar faces. Participants had to match a name to one of 8 hybrid face images. In shape trials, all faces had the same texture, but only one face had the correct shape. In texture trials, all faces had the same shape, but only one shape had the correct texture.

identity was presented to participants and their task was to name the identity depicted in each image. Overall, 88.9% of intended familiar identities were recognised; identities that were not familiar were removed on an individual participant basis. Only 3.3% of the intended unfamiliar identities were recognised; these were also removed on an individual participant basis.

2.4. Experiment 2

In a complementary behavioural experiment, a separate group of participants performed a recognition task on the hybrid images. In this task, participants viewed 16 hybrid faces (8 familiar and 8 unfamiliar). Each image was presented sequentially, and participants were instructed to name the identity depicted in the image with no time constraints. Different participants viewed different combinations of hybrid images, such that the shape and texture from all identities was shown equally across the participants. Moreover, the shape or texture of each identity was contained only once in the images shown to each participant. This prevented any effect of priming that might have occurred (for example, if the texture of a face in one hybrid increased the chance of recognizing the shape of a face in another hybrid or vice versa). To provide a baseline of performance, one group of participants viewed hybrid images in which the shape and texture were from one identity. Following this, participants then completed the same familiarity test used in Experiment 1. Again, identities that were expected to be familiar or unfamiliar but were not, were removed on an individual participant basis.

2.5. Experiment 3

To measure the neural sensitivity to shape and texture, we used a block design fMR-adaptation paradigm with 5 different stimulus conditions (see Fig. 3 for familiar faces): (1) no change (same shape, same surface); (2) shape change (alternating between two shapes, same surface); (3) surface change (alternating between two textures, same shape); (4) shape & surface change-2 (different shape, different texture-alternating between two identities) (5) shape & surface change-8 (different shape, different surface-alternating between eight identities). The shape & surface change-2 condition was included in order to be comparable to the shape change and surface change conditions that alternated between two identities, whilst the shape & surface-8 condition was used in order to increase the sensitivity of the paradigm by showing the maximum release from adaptation. We used this design in a previous experiment to reveal invariant representations of identity in face-selective regions (Davies-Thompson et al., 2013). Data were collected separately using this design for familiar and unfamiliar faces.

In each stimulus block, 8 images were shown for 975 msec followed by a 150 msec blank screen. Blocks were 9 s in duration and were separated by a 9 s fixation screen (a white fixation cross on a mean grey background). Each of the 5 stimulus conditions was repeated 8 times, giving a total of 40 blocks for each scan, which were presented in a counterbalanced order. Participants performed a red dot detection task during the scan in which they were required to press a button when a red dot appeared on any of the images. Mean accuracy was 92% across all familiar conditions (mean response time-494 msec) and 94% across all unfamiliar conditions (mean response time-493 msec).

Data from the fMRI experiment were collected using a GE 3 Tesla HD Excite MRI scanner at the York Neuroimaging Centre at the University of York. A gradient-echo EPI and a T1-weighted structural MRI ($1 \times 1.13 \times 1.13$ mm voxel) were acquired for each participant. The gradient-echo

Fig. 3. FMRI experimental stimuli depicting the familiar faces (British celebrities). Each row portrays an example of images presented during a single 9 s block. A. No change condition; B. Shape change only, alternating between two shapes (AB design); C. Texture change only, alternating between two textures (AB design); D. Shape and texture change, alternating between two identities (AB design); E. Shape and texture change, 8 different identities presented in a block.

EPI sequence used a radio-frequency coil tuned to 127.4 MHz 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). Data were analysed with FEAT version 4.1 (http://www.fmrib.ox.ac.uk/fsl). The first 9 sec (3 volumes) from each scan were discarded, and MCFLIRT motion correction, spatial smoothing (Gaussian, FWHM 6 mm), and temporal high-pass filtering (cutoff 0.0093 Hz) were applied.

A localiser scan was used to identify face-selective regions. The localiser scan images included faces, bodies, inanimate objects, places, and scrambled images. The identity of the faces was different to those used in the main experiment. Images from each category were presented in blocks of 10 images in which images were shown for 700 msec, followed by a 200 msec blank screen. A 9 s grey screen with a central fixation cross was presented between each block. Stimulus blocks were repeated 4 times and were presented in a counterbalanced order. A boxcar function convolved with a standard haemodynamic response function was used to model the BOLD response. Face-selective voxels were defined by contrasting the response to faces with each non-face condition, then averaging the resulting statistical maps and thresholding at $p < .001$ (uncorrected). Neighbouring clusters of voxels located within the occipital and temporal lobes were defined as the FFA, OFA and pSTS in each participant.

The experimental scans were analysed by measuring the time series of response to each condition. Across each scan, the response of each voxel was converted to % signal. A single time series for each ROI was then calculated by averaging across all voxels. Each block was then normalized by subtracting the magnitude of response at the start of the block from the response at each time point in the block. The normalized response to the same stimulus blocks was then averaged to produce a mean time series. The average of the % signal change at 9 and 12 s poststimulus onset was taken as the peak response for each condition within an ROI for each participant. The peak responses were then analysed using repeated measures ANOVAs and post hoc t-tests. Specific contrasts were used to compare each experimental condition to the no-change condition. This allowed us to determine whether there was a release from adaptation (or sensitivity) to each manipulation.

To determine whether any differences in the release from adaptation could reflect differences between the image properties of the familiar and unfamiliar faces, we measured the mean change in image intensity across images. This was calculated by taking the average of the absolute differences in grey value at each pixel for successive pairs of images within a block. A 2 × 5 ANOVA with Familiarity (familiar, unfamiliar) and Condition (No change, Shape change, Texture change, Shape and Texture Change (2), Shape and Texture Change (8)) as the main factors was ran. There was a significant main effect for Condition ($F(4,220) = 194.24, p < .001$), but there was no main effect of Familiarity ($F(1,55) = 0.35, p = .555$) or any interaction between Familiarity * Condition ($F(4,220) = 0.40, p = 0.811$). The largest change in low-level properties was found when both shape and texture changed. However, shape and texture changes for familiar and unfamiliar had a similar effect on this image measure. There was also no difference between the shape change and texture change for familiar faces ($t(55) = -1.85, p = .070$) and unfamiliar faces ($t(55) = -0.16, p = .977$). These findings ensure that any releases in adaptation for shape and texture changes are not due to low-level image properties such as image intensity.

3. Results

3.1. Experiment 1

We measured the ability to recognize faces based on either shape or texture. Fig. 4 shows the recognition accuracy for familiar and unfamiliar faces. To determine whether recognition accuracy differed when using a shape or texture cue, or when faces were familiar or unfamiliar, a 2 × 2 repeated measures ANOVA with Familiarity (familiar, unfamiliar) and Cue (shape, texture) as the main factors. Significant main effects
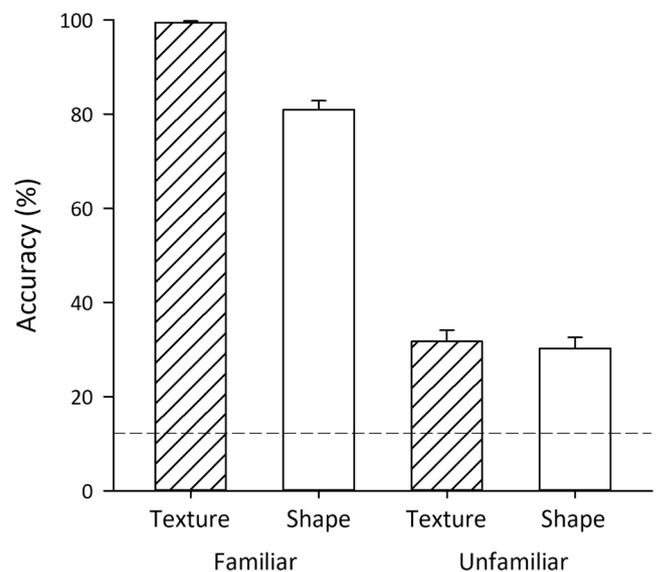
Fig. 4. Accuracy on shape and texture trials in Experiment 1. Accuracy for familiar faces was above chance (12.5%-represented by the dotted line) for both shape and texture. However, accuracy for texture trials was significantly higher than for shape trials. Accuracy for unfamiliar trials was substantially lower but still significantly above chance, despite the fact that participants were not familiar with the identities. However, there was no difference between shape and texture in the unfamiliar trials. Error bars represent SEM.

were found for Familiarity ($F(1, 52) = 1081.86, p < .001, n_p^2 = 0.954$) and Cue ($F(1, 52) = 28.41, p < .001, n_p^2 = 0.353$). There was also a significant interaction between Familiarity and Cue ($F(1, 52) = 17.48, p < .001, n_p^2 = 0.253$). This interaction reflects higher performance for texture compared to shape with familiar, but not unfamiliar faces. For familiar faces, there was a significant difference between accuracy between shape (mean ± SEM = 81.0 ± 13.62) and texture (mean ± SEM = 99.4 ± 2.59) trials for familiar faces ($t(52) = 9.66, p < .001, d = 1.67$). For unfamiliar faces, recognition rates were lower (texture: mean ± SEM = 31.7 ± 17.7; shape: mean ± SEM = 30.2 ± 17.0) and there was no difference between shape and texture trials ($t(52) = 0.46, p = .648, d = 2.10$).

To determine whether recognition accuracy was greater than chance level, one sample t-tests were conducted for all conditions. For familiar faces, recognition accuracy was greater than chance level on shape trials ($t(52) = 36.61, p < .001, d = 5.03$) and texture trials ($t(52) = 244.62, p < .001, d = 33.61$). Recognition accuracy was also greater than chance level for unfamiliar shape trials ($t(52) = 7.59, p < .001, d = 1.04$) and unfamiliar texture trials ($t(52) = 7.89, p < .001, d = 1.08$).

3.2. Experiment 2

In this experiment, participants had to report the identity of hybrid face images that contained the texture from one identity and the shape from another identity. Fig. 5 shows the proportion of trials in which participants were able to recognize the face based on the shape or texture of the image. For familiar faces, participants reported the identity based on the texture (mean ± SEM = 61.2 ± 16.4 %) more often than based on the shape (mean ± SEM = 12.3 ± 11.4 %) of the hybrid image ($t(69) = 19.87, p < .001, d = 2.38$). This shows that texture is a more dominant cue for recognition. Nevertheless, there were trials in which the shape was the dominant cue for recognition. The reported shape ($t(69) = 9.08, p < .001, d = 1.08$) and texture ($t(69) = 31.31, p < .001, d = 3.73$) were both significantly greater than 0. Unsurprisingly, there were no correct identifications based on shape or texture for the unfamiliar faces.

A separate group of participants were shown veridical hybrid images
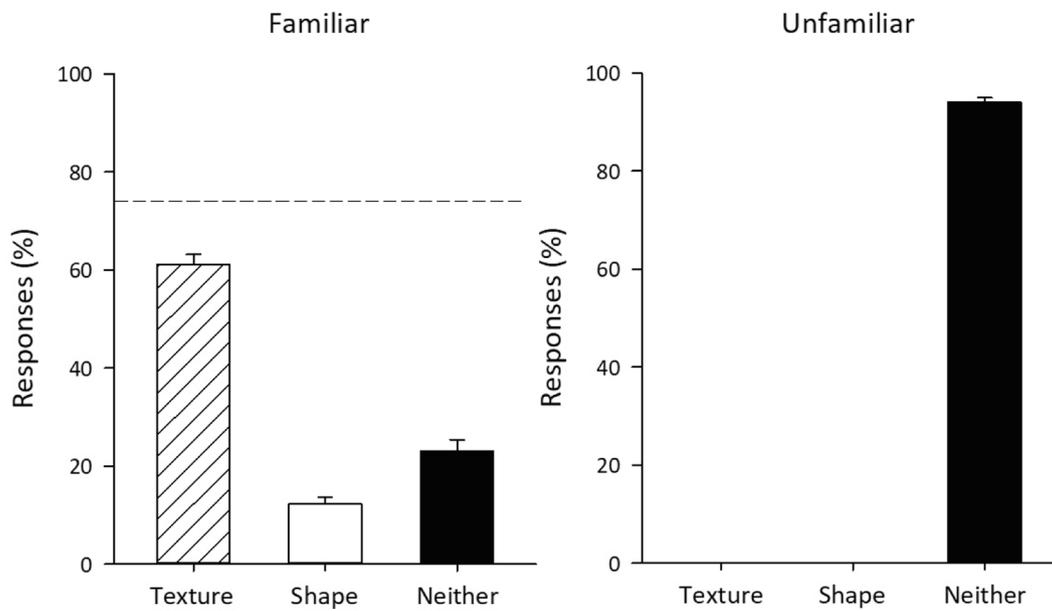
Fig. 5. Distribution of responses for Experiment 2. Participants had to recognise the identity of familiar or unfamiliar hybrid faces. There were two potentially correct responses. For familiar faces, participants reported the identity based on the texture more often than the shape of the face. Nevertheless, there were a significant number of hybrid faces that were recognized from the their shape. Error bars represent 1 SEM. Dotted line shows performance when the shape and texture were from the same identity (74%).

in which the shape and the texture were from the same person. The recognition rate for this group can be seen as the maximum expected recognition rate for the hybrid images. After taking out identities that participants reported not knowing during the familiarity checklist, the accuracy rate of the control group was 74% of faces (Fig. 5 – dotted line). A one-sample *t*-test showed there were significant differences between this maximal rate and the rate based on shape (t(69) = 45.69, p < .001, d = 5.46) and texture (t(69) = 6. 70, p < .001, d = 0.80). This implies that shape and texture properties both carry information regarding identity.

One possible explanation for these findings is that the responses are dominated by faces that have a particularly recognisable texture or shape. To address this issue, we measured the percentage of correct texture or correct shape responses that corresponded to each of the 8 familiar face identities. As can be seen in Table 1, the shape and texture hits were evenly distributed across all identities. This implies that our results do not simply reflect the properties of identities with a particularly dominant shape or texture.

3.3. Experiment 3

A localiser scan was performed to reveal the location of face-selective regions. The average location of the core face-selective regions: fusiform face area (FFA), occipital face area (OFA) and posterior superior temporal sulcus (pSTS), is shown in Fig. 6A and Table 2. We next determined how these regions responded to changes in shape or surface properties of

Table 1
Percentage of responses for each familiar identity relative to the total Shape hits or Texture hits.

Identity	Shape hit	Texture hit
Alan Sugar	11.6	14.0
Chris Moyles	7.3	10.2
Derren Brown	13.0	11.1
Gary Lineker	14.5	13.1
Jeremy Kyle	15.9	13.7
Jeremy Paxman	13.0	12.5
Jonathan Ross	11.6	13.1
Louis Walsh	13.0	12.2

faces. A 3-way ANOVA found no interaction effect of hemisphere * condition (familiar: F(1,14) = 2.09, p = .170; unfamiliar: F(1,15) = 2.06, p = .172), so the responses from each hemisphere were combined.

Fig. 6B and C shows the time course of response to different conditions in the different regions when viewing familiar and unfamiliar faces respectively. The effect of condition was analysed using the peak responses with 1-way ANOVA. There was a significant effect of condition for all face regions with familiar faces (FFA: (F(4,68) = 14.51, p < .001), OFA: (F(4,68) = 7.98, p < .001) , pSTS: (F(4,68) = 6.02, p < .001)). However, for unfamiliar faces, there was only a significant effect of condition for the FFA (F(4, 72) = 8.81, p < .001) and OFA (F(4,72) = 6.41, p < .001). The pSTS showed no significant effect of condition for unfamiliar faces (F(4,72) = 1.25, p = 0.297).

To measure the release from adaptation in each region, the response to each condition was compared to the no change condition. In the FFA, there was a lower response (adaptation) to the no change condition compared to the shape change (familiar: t(17) = 6.41, p < .001, unfamiliar: t(18),= 3.50p = .003), texture change (familiar: t(17) = 4.92, p < .001, unfamiliar: t(18),= 3.49p = .003), shape and texture change with 2 identities (familiar: t(17) = 6.12, p < .001, unfamiliar: t(18),= 2.84p < .011), shape and texture change using 8 identities (familiar: t (17) = 6.25, p < .001, unfamiliar: t(18),= 6.05p < .001). However, there was no difference in the response when comparing a shape change to a texture change for either familiar or unfamiliar faces (familiar- [t(17) = 1.43, p = .170], unfamiliar [t(18),= 0.32p = .754]. This suggests that the FFA is equally sensitive to changes in shape and texture.

The OFA showed a similar pattern of response to the FFA. There was a lower response (adaptation) to the no change condition compared to the shape change (familiar: t(17) = 4.50, p < .001, unfamiliar: t(18),= 2.58, p = .019), texture change (familiar: t(17) = 3.89, p = .001, unfamiliar: t(18) = 3.17, p = .0015), shape and texture change when using 2 identities (familiar: t(17) = 3.03, p = .001, unfamiliar: t(18),= 2.02, p = .058) and shape and texture change using 8 identities (familiar: t(17) = 4.15, p = .001, unfamiliar: t(18) = 4.54, p < .001). Similar to the FFA, there was no difference in the response when comparing a shape change to a texture change for either familiar (t(17) = 1.45, p = .165), or unfamiliar (t(18),= 0.61, p = .555) faces, suggesting the OFA is also equally sensitive to shape and texture changes irrespective of
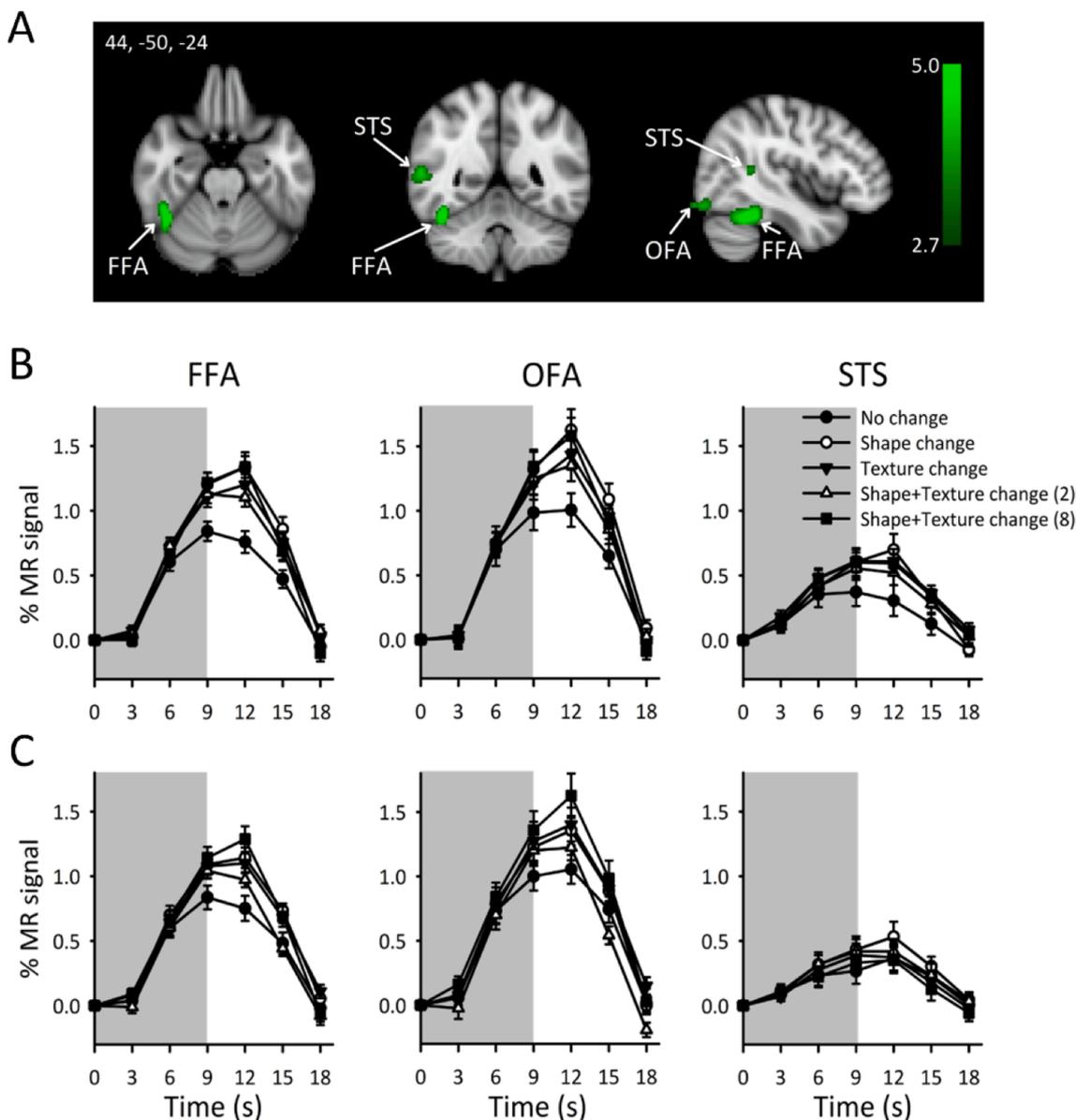
Fig. 6. Experiment 3. (A) Location of face-selective regions-of-interest (FFA: fusiform face area, OFA: occipital face area, STS: superior temporal sulcus). (B) The average timeseries for face-selective regions of interest in response to familiar faces. There was a significant release from adaptation (compared to no change) for familiar faces in all regions for all conditions. There was a similar release from adaptation to texture and shape. (C) There was a similar release from adaptation with unfamiliar faces in the FFA and OFA, but there was no effect in the STS. Time shows the response relative to the onset of the block. Grey shading shows the stimulus duration. Error bars show SEM.

Table 2

Shape/Texture Experiment 3 (AB), N = 19. Mean (SEM) MNI coordinates of regions of interest (centre of gravity). Regions defined by localiser scan (Faces > (Bodies + Objects + Places + Scrambled images).

Region	x	y	z
FFA			
L	−41.94 (0.82)	−55.63 (1.52)	−21.66 (0.96)
R	42.55 (0.63)	−52.04 (1.34)	−21.33 (1.00)
OFA			
L	−39.34 (1.31)	−83.52 (1.01)	−14.97 (1.57)
R	41.00 (0.95)	−79.20 (1.16)	−13.68 (0.97)
STS			
R	52.38 (1.79)	−49.52 (1.91)	4.97 (1.39)

familiarity.

The rSTS was only found to show an effect of condition with familiar faces. Similar to the FFA and OFA, there was a lower response (adaptation) to the no change condition compared to the shape change (t(17) = 3.94, p = .001), texture change (t(17) = 3.61, p = .002), shape and surface change with 2 identities (t(17) = 2.85, p = .011) and shape and texture change using 8 identities (t(17) = 2.74, p = .014). There was no difference in response when comparing a shape change to a texture change (t(17) = 0.68, p = .505), suggesting a similar sensitivity to shape and texture.

4. Discussion

In this study, we investigated the roles of shape and texture in the perceptual and neural representation of familiar (as compared to unfamiliar) faces. The main findings are that: (1) shape can contribute to the

recognition of familiar faces in tasks that cannot be performed by perceptual matching; (2) texture is, however, the dominant source of information for familiar face recognition; (3) face-selective regions are equally sensitive to changes in shape and texture.

In the first experiment, we asked how shape and texture information in face images contribute to the recognition of person identity. To address this issue, we used hybrid images that were created by combining an average shape from one identity with the average texture from a different identity. We then asked whether it was possible to determine whether shape or texture could be used to match a name to a face. In a previous study (Andrews et al., 2016), it was possible to match a previously presented hybrid face that contained the shape and texture from one identity with a subsequent array in which either the shape or the texture varied. Andrews et al. (2016) found that it was possible to do this task for both shape and texture, but performance on texture trials was higher. However, the task used by Andrews et al. (2016) could be performed with perceptual matching between the target and the test array, limiting its relevance to the way in which we recognise faces in natural viewing conditions. To address this issue in the current study, we used a task in which participants had to match a written name to an array of faces that either varied in texture or shape. This gave no opportunity for perceptual matching, as participants were only able to rely on previously stored representations for recognition. Our results clearly show that participants were able to perform this task at well above chance levels when it was based on either shape or texture.

To further explore whether participants were able to use shape or texture for the recognition of identity, we presented hybrid faces and asked them to name the person in Experiment 2. In a previous study (Andrews et al., 2016), we performed a similar experiment in which hybrid faces were presented with a list of possible names. Included in those names was the name associated with the shape of the hybrid and another name that was associated with the texture of the hybrid. We found that the texture was chosen on 90% of trials and the shape on only 5% of trials. However, a possible limitation of this study is that participants were not directly recognising the face, but were rather using a more cognitive strategy to relate the appearance of the hybrid face with one of the names. To address this issue, we simply presented each hybrid face and asked participants to name the person. This task had no component of perceptual matching and could not involve any non-visual cognitive strategy. Nevertheless, we found that both shape and texture information were used in this pure recognition task. More hybrid faces were recognised from their texture compared to their shape, but there were some hybrids in which the shape was more dominant. We also measured performance in participants in which the hybrid faces contained the shape and texture from the same familiar identity. We found that performance with these images was best approximated to the sum of performance on texture or shape alone. The images used in this study were all grayscale because colour is known to have at best a limited role in recognition (Bruce and Young, 2012). An interesting question for further investigations might therefore be the extent to which colour can influence neural responses to surface properties.

The importance of shape in the recognition of familiar faces has been challenged by well-established behavioural findings that show (1) large changes in shape can leave recognition unimpaired, (2) large changes in texture have a significant effect on recognition, (3) texture dominates shape in judgements of identity (Burton et al., 2015). Although our results confirm the fact that texture is a more dominant cue for recognition, they do show that shape can make a significant contribution to familiar face recognition. Previous studies that have investigated the role of shape have often manipulated the configuration of facial features in unfamiliar faces (Freire, Lee, & Symons, 2000; Le Grand, Mondloch, Maurer, & Brent, 2001; Rossion, 2008). The typical task is to determine whether two faces are the same or different and the extent to which performance is affected by inversion. However, it has not been clear if this has any relevance to judgements of familiar faces in natural viewing in which it is necessary to recognise a face in the absence of any

comparison to other faces. Our results provide the first evidence that shape information plays an important role in recognition, albeit less than for texture.

An interesting finding was that performance on unfamiliar faces in Experiment 1 was above chance for both shape and texture trials. This was unexpected because participants were not familiar with the identities and hence could not have reflected the association between the name and the correct hybrid image. The accuracy on unfamiliar shape trials was similar to the accuracy on unfamiliar texture trials. This suggests that participants were not using a similar mechanism to that used for familiar faces, in which performance on texture trials was significantly higher than for shape trials. Rather, it would appear that participants were able to reject hybrid images (thus, inflating chance-level) for which the combination of shape and texture did not appear naturally face-like. These findings suggest the importance of including unfamiliar faces as a point of comparison in studies of familiar faces. The difference in the use of shape and texture in familiar and unfamiliar faces that we show converges with previous studies that have also found that texture is disproportionately more important than shape for familiar compared to unfamiliar faces (Itz et al., 2014, 2017; Zhou et al., 2021).

In Experiment 3, we investigated the neural sensitivity of face-selective regions to changes in shape and texture. Our aim was to reveal which regions showed a corresponding sensitivity to that shown in the behavioural analysis. Using a fMR-adaptation paradigm, we compared neural responses to changes in texture, shape, or both texture and shape with the response to a 'no change' baseline that would create maximal adaptation. In a previous study, we measured the release from adaptation to shape and texture and found an equal release to both changes (Andrews et al., 2016; see also Jiang et al). However, the lack of any difference in sensitivity to shape and texture may have resulted from a design in which 8 different images were presented in a block. In the current study, we used a more sensitive paradigm in which 2 images alternated. We have previously shown that that this paradigm is able to demonstrate invariant representations in face-selective regions (Davies-Thompson et al., 2013).

We found a lower response (adaptation) in the FFA and OFA to repeated images of the same face compared to faces that differed in both shape and texture (see also Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Weibert et al., 2016). However, the critical conditions were those in which either the shape or the texture changed independently. Given our behavioural results, our predictions were that face-selective regions responsible for the recognition of facial identity should show a release to both shape and texture, but that there should be more sensitivity to changes in texture. We did find a release from adaptation in the FFA and OFA to both shape and texture, but we did not find a difference between shape and texture. The similar sensitivity to shape and texture could not be explained by greater low-level image differences between these changes, as these were similar for both changes. Although our results show a similar release from adaptation to shape and texture in the OFA and FFA, this does not mean that both regions represent information in the same way. Indeed, a recent study using MVPA (Tsantani et al., 2021) showed that the OFA and FFA encode distinct types of face identity information.

There is mixed evidence for whether the FFA has an image-invariant representation of face identity. A number of studies have reported image dependent responses in the FFA (Andrews & Ewbank, 2004; Davies Thompson, Gouws, & Andrews, 2009; Grill-Spector et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Weibert & Andrews, 2015; Xu, Yue, Lescroart, Biederman, & Kim, 2009), whereas others have shown varying degrees of image invariance (Davies-Thompson et al., 2013; Eger, Schweinberger, Dolan, & Henson, 2005; Ewbank & Andrews, 2008; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein et al., 2004). In a large-scale study of 80 participants, we reported image-invariant adaptation to identity in face-selective regions, such as the FFA, but no difference in the magnitude of

adaptation to familiar and unfamiliar faces (Weibert et al., 2016). This fits with our current findings, where we do not find any difference between the pattern of neural response to familiar and unfamiliar faces. Overall, this suggests that the FFA does not process identity to a degree by which full image invariance is achieved. It seems more likely that the FFA is involved in a form of image normalization that contributes to face recognition. This would fit with studies of developmental prosopagnosia in which normal patterns of response in face regions can occur despite impaired face recognition (Avidan & Behrmann, 2014; Furl, Garrido, Dolan, Driver, & Duchaine, 2011; although see Jiahui, Yang, & Duchaine, 2018). This should not, however, undermine the role of regions such as the FFA and OFA in face processing. Other studies have shown that the response in the FFA is linked with individual differences in familiar face recognition (Furl et al., 2011; Weibert & Andrews, 2015) and disruption to these regions is known to affect face recognition (Barton, 2008; Rossion et al., 2003; Jonas et al., 2012; Parvizi et al., 2012). Rather, it seems likely that interactions between the core and extended face processing networks are important for familiar face recognition (Collins & Olson, 2014; Weibert et al., 2016).

Models suggest that a dorsal pathway leading to the posterior superior temporal sulcus (pSTS) plays a key role in processing changeable aspects of faces such as emotional expression and gaze direction (Haxby et al., 2000). We found a different pattern of response in the pSTS compared to the OFA and FFA, in which there was a release from adaptation to familiar faces, but not unfamiliar faces. This increased sensitivity to familiar faces converges with previous studies that have shown that the response of the pSTS is more sensitive to familiar compared to unfamiliar faces (Davies-Thompson, Gouws, & Andrews, 2009). Although it is not clear why the pSTS is more sensitive to familiar faces, we have also shown that connectivity with the FFA may play a role in tracking meaningful changes in the face (Baseler, Harris, Young, & Andrews, 2014).

In conclusion, our results demonstrate that both shape and texture are used in the recognition of facial identity. These findings provide the first direct evidence for the importance of shape in a paradigm that is similar to face recognition in natural viewing. The equal sensitivity to shape and texture in the neural response of core face-selective regions provides evidence that these regions contribute to the early stages of face recognition.

Acknowledgements

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