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Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe

Timothy J. Andrews[*] and Michael P. Ewbank

Department of Psychology, Wolfson Research Institute, University of Durham, UK

The neural system underlying face perception must represent the unchanging features of a face that specify identity, as well as the changeable aspects of a face that facilitate social communication. However, the way information about faces is represented in the brain remains controversial. In this study, we used fMR adaptation (the reduction in fMRI activity that follows the repeated presentation of identical images) to ask how different face- and object-selective regions of visual cortex contribute to specific aspects of face perception. We report that activity in the face-selective region of the fusiform gyrus (FG) was reduced following repeated presentations of the same face. Adaptation in this area was not sensitive to changes in image size, but was sensitive to changes in viewpoint. In contrast, face-selective regions in the superior temporal lobe failed to adapt to identical presentations of the same face, but showed an increased response when the same face was shown from different viewpoints and with different expressions. These results reveal a largely size-invariant neural representation in the inferior temporal lobe that could be involved in the recognition of facial identity, and a separate face-selective region in the superior temporal lobe that could be used to detect changeable aspects of faces. The absence of fMR-adaptation in object-selective regions of visual cortex challenges the idea that a more distributed network of areas is used to represent information about faces.
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Introduction

Recognising complex objects, such as faces, is a simple and effortless process for most human observers. However, the apparent ease with which recognition takes place belies its inherent complexities and ambiguities. For example, as we move about or as gaze or expression change, the size and shape of a face image on the retina also changes. To be useful, the visual system must take into account these sources of variation to facilitate recognition, but at the same time be able to detect changeable aspects of faces that are important in social communication. Although models of face processing have proposed ways to deal with these different tasks, it remains unclear how these mechanisms might be implemented in visual cortex.

One model of human face processing proposes that information is processed in specialised modules (Breen et al., 2002; Bruce and Young, 1986; Haxby et al., 2000). This conception is supported by several physiological studies that show specific regions of the temporal lobe are more responsive to faces than to other complex objects (Allison et al., 1994; Kanwisher et al., 1997; Kreiman et al., 2000). These findings are consistent with brain lesion studies that report specific deficits in recognising, identifying and naming faces following damage to the inferior temporal lobe (Damasio et al., 1982; McNeil and Warrington, 1993). Interestingly, such individuals have a largely preserved ability to recognise other objects (McNeil and Warrington, 1993). In contrast, lesions to other areas of the temporal lobe can leave face recognition intact, but impair an individual's ability to identify other objects (Moscovitch et al., 1997).

An alternative model of face processing appeals to a more distributed representation across a large network of visual cortex. In this theory, the representation of a face is not restricted to those areas that respond maximally to this object category. This is because non-face, object-selective regions such as the lateral occipital complex (LOC) and the parahippocampal place area (PPA) also respond to the presentation of a face-albeit less than to non-face objects (Andrews and Schluppeck, in press; Ishai et al., 1999). Indeed, a recent study has shown that our perception of faces could be based on a distributed pattern of response across the whole temporal lobe rather than on the activity of a few specialised modules (Haxby et al., 2001). Moreover, because of the spatial limitations of fMRI, it is possible that a weak response

* Corresponding author. Department of Psychology, Wolfson Research Institute, Parks Road Stockton Campus TS17, University of Durham, UK. Fax: +44 191 3340006.
E-mail address: tim.andrews@durham.ac.uk (T.J. Andrews).
Available online on ScienceDirect (www.sciencedirect.com.)

to a face in a particular brain region does not reflect a sub-optimal activation, but reveals the activation of a small proportion of face-selective neurons (Avidan et al., 2002).

In the present study, we have used the technique of fMR-adaptation (the decreased activity that occurs following repeated presentation of the same image) to determine how different aspects of face processing are represented in visual cortex (Grill-Spector and Malach, 2001). In two previous studies, adaptation to faces was reported in the lateral occipital complex (LOC) (Avidan et al., 2002; Grill-Spector et al., 1999). Because this region of the brain has been characterised as an object-selective area (Malach et al., 1995), these findings could be taken as support for a distributed representation underlying face perception. However, in these studies, the analysis was restricted to face-selective areas of the LOC. Indeed, it is possible that the regions studied may have included the face-selective region in the fusiform gyrus (Kanwisher et al., 1997). In the present study, we have defined face- and object-selective areas in the occipital and temporal lobe in terms of their anatomical location and functional responses and have asked how they are involved in specific aspects of face perception. Our hypothesis was that those regions of the brain that are involved in the recognition of identity would show a reduction in response to repeated presentations of the same face, and that this reduction in response would be invariant to changes in image size
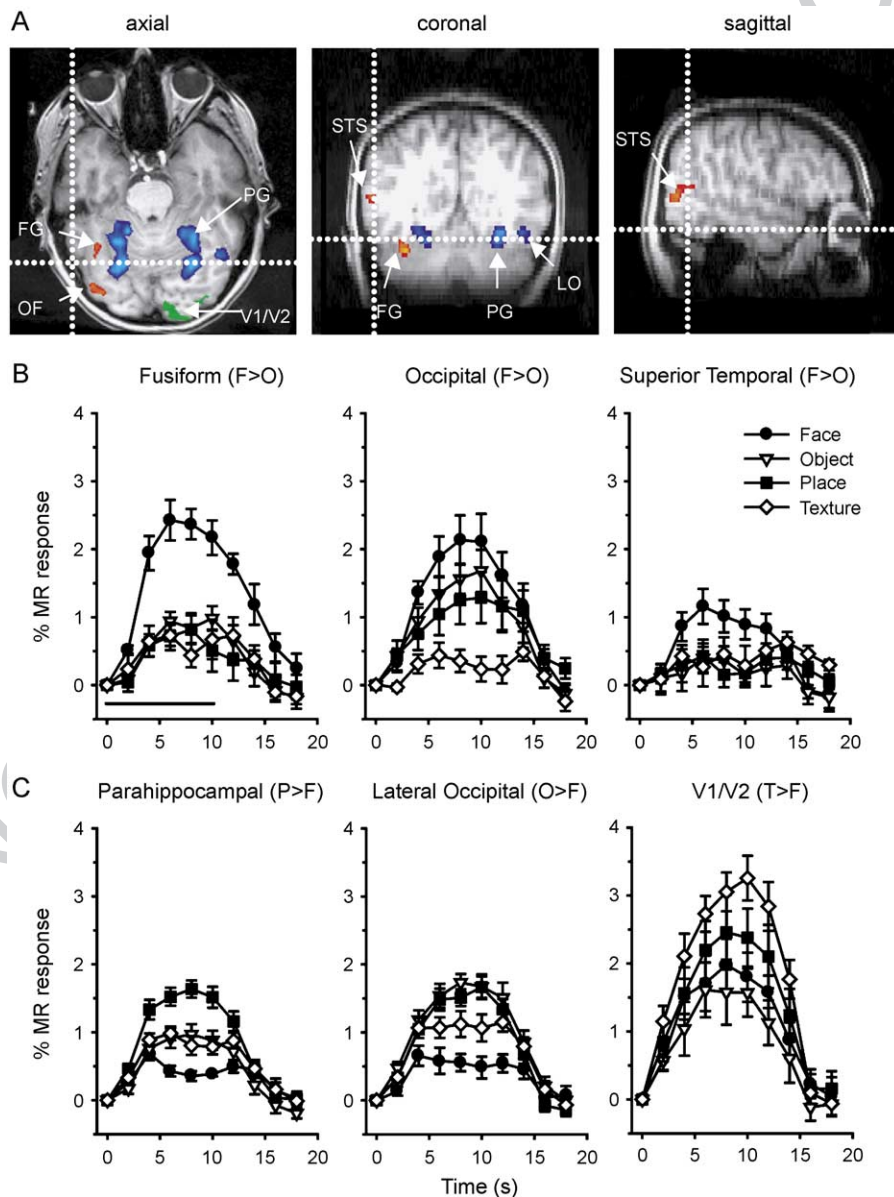

Fig. 1. Localiser scan. Regions of interest were defined by their anatomical location and their functional responses to different object categories. (A) Location of areas in visual cortex that showed selective responses to faces (red), objects (blue) or textures (green) in one subject (FG = fusiform gyrus, OF = occipital face; LO = lateral occipital, STS = superior temporal sulcus, PG = parahippocampal gyrus). These scan images follow radiological convention, with the left hemisphere shown on the right. The dashed lines in each image show the spatial relation of the three slices. MR time-course during localiser scans, showing the activity averaged across subjects in face-selective (B) and non-face selective (C) areas to faces (F), objects (O), places (P) and textures (T). The horizontal bar represents the duration of each block. Error bars represent ± 1 standard error.

100 or viewpoint. In contrast, if an area was involved in representing
101 changeable aspects of faces, we would not expect to find
102 adaptation to repeated images of the same face identity, but rather
103 we would expect responses to be sensitive to changes in viewpoint
104 that are important in social communication.

Methods
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Subjects
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107   All eight observers had normal or corrected to normal visual
108 acuity. Informed consent was obtained from all subjects and the
109 study was approved by the Central Oxford Research Ethics
110 Committee (COREC 98.161). Stimuli (approximately $9° \times 9°$)
111 were back-projected (Focus LP1000, Unicol Engineering, Oxford
112 UK) on to a screen placed at a distance of 280 cm from the
113 subject's eyes. Subjects lay supine in the magnet bore and viewed
114 the back-projection screen outside the bore through prism glasses.

Imaging parameters
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116   All experiments were carried out using the Siemens-Varian 3 T
117 MRI scanner at the FMRIB centre in Oxford. A Magnex head-
118 dedicated gradient insert coil was used in conjunction with a
119 birdcage, head, radio-frequency coil tuned to 127.4 MHz. A
120 gradient-echo EPI sequence was used to collect data from 16
121 contiguous axial slices (TR 2 s, TE 30 ms, FOV 256×256 mm, in-
122 plane resolution 4×4 mm, slice thickness 7 mm). T1 weighted
123 structural images were acquired with a 3D Turbo Flash Sequence at
124 a resolution of 1×1 mm within slice and 3 mm between slices. The
125 statistical maps were registered onto a standard image in Talairach
126 space using FLIRT (www.fmrib.ox.ac.uk/fsl).

Localiser scan
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128   To discriminate regions of visual cortex that are selectively
129 activated by faces and non-face objects, a localiser scan was carried
130 out for each subject. Each scan contained 16 stimulus blocks. The
131 stimuli in each block were either grey-scale photographs of (1)
132 faces, (2) inanimate objects, (3) places (buildings, indoor scenes &
133 natural landscapes) or (4) textures. Images of faces were taken from
134 a database of the Psychological Image Collection at Stirling (PICS:
135 http://www.pics.psych.stir.ac.uk/) and were not familiar to any of
136 the subjects. Photographs of inanimate objects, places and textures
137 were obtained from various sources including CorelDraw and
138 Microsoft clip-art. Each stimulus block contained 10 images with
139 each image being presented for 800 ms followed by a 200-ms blank
140 screen. Subjects were instructed to perform a one-back matching
141 task using a response box. Each stimulus condition was repeated
142 four times in a counterbalanced block design. Blocks were
143 separated by periods of fixation when a grey screen, of the same
144 average luminance was viewed for 10 s.
145   Analysis of the localiser scans was carried out using FEAT
146 (www.fmrib.ox.ac.uk/fsl). The initial 8 s of data from each scan
147 was discarded to minimise the effects of magnetic saturation.
148 Motion correction was carried out using MCFLIRT (www.fmrib.
149 ox.ac.uk/fsl), followed by a spatial smoothing algorithm (FWHM
150 5.0 mm). Z statistic images were generated using resel (corrected
151 Bonferroni) thresholding ($P < 0.05$). Areas defined as face-
152 selective included voxels that responded significantly more to

faces than to objects or textures, whereas non-face selective areas 153
responded more to inanimate objects, scenes or textures than to 154
faces at this level of significance (Friston et al., 1995). 155

To determine the temporal characteristics of the response, the 156
time-series of the resulting filtered MR data at each voxel was 157
converted from units of image intensity to units of fractional signal 158
change (% MR activity). The time-course plots were also 159
normalised to the activity at stimulus onset. Signals in the different 160
regions were then averaged separately for face, inanimate object, 161
place and texture stimulus blocks. A repeated-measures ANOVA 162
was used to determine whether there were significant between- 163
subject changes in activity for each stimulus condition. 164

Face adaptation experiment
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Each experiment contained 24 stimulus blocks. Each stimulus 166
block lasted for 12 s and contained 12 images. Each image was 167
presented for 800 ms followed by a 200-ms blank screen. 168
Stimulus blocks contained 12 repetitions of the same face image 169
(*same identity*) or 12 different face images (*different identity*). To 170
determine whether the response to faces was size-invariant, we 171
varied image size in some stimulus blocks ($3° \times 3°$, $6° \times 6°$ and 172
$9° \times 9°$). We also determined whether the response to faces was 173
view-invariant by varying the direction of gaze and emotional 174
expression in the face images. Changes in gaze direction 175
included frontal, 3/4 and side profiles and the faces could 176
convey a happy emotion or speech. Different combinations of 177
gaze and expression were randomly interleaved in these stimulus 178
blocks, but this did not lead to the perception of apparent 179
motion. Thus, in total, we monitored MR activity for the 180
following 6 stimulus conditions: (1) *same-identity same-size* (2) 181
different-identity same-size (3) *same-identity vary-size* (4) *diffe-* 182
rent-identity vary-size (5) *same-identity vary-viewpoint* (6) *diffe-* 183
rent-identity vary-viewpoint. Each stimulus condition was 184
repeated four times in a counterbalanced block-design within a 185
single scan. Blocks of faces were separated by periods of fixation 186
when an equiluminant grey screen was viewed for 10 s. Subjects 187
were instructed to perform a one-back matching task on the 188
identity of the face during the scan using a response box. The 189
time-series of the resulting filtered MR data at each ROI was 190
converted from units of image intensity to units of fractional 191
signal change (% MR activity). The average peak response was 192
calculated from each ROI in each condition for each subject. A 193

Table 1   t1.1
Mean Talairach coordinates of face-selective and non-face selective regions
of interest (F = face, O = Object, P = place, T = texture)   t1.2

Region	Hemisphere	n	x	y	z	
Fusiform gyrus	right	8	44	−58	−22	t1.4
(F>O)	left	3	−46	−61	−27	t1.5
Occipital face	right	6	43	−83	−10	t1.6
(F>O)	left	1	−45	−82	−5	t1.7
Superior temporal	right	6	54	−66	8	t1.8
(F>O)	left	–	–	–	–	t1.9
Parahippocampal gyrus	right	8	30	−61	−14	t1.10
(P>F)	left	8	−32	−63	−15	t1.11
Lateral occipital	right	6	42	−77	−3	t1.12
(O>F)	left	6	−47	−74	−3	t1.13
Medial occipital	right	6	13	−98	−2	t1.14
(T>F)	left	6	−14	−99	−2	t1.15

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repeated-measures ANOVA was performed on the between subject variation for different stimulus conditions.

Results

Localiser scan

Spatially discrete face- and object-selective areas were localised using a blocked design (Fig. 1A and Table 1). In each subject, a region of the fusiform gyrus showed significant activation for faces versus non-face objects. This activation was predominantly in the right hemisphere. The Talairach coordinates of this area suggest that it is analogous to the FFA (Kanwisher et al., 1997) and area LO-a/pFs (Avidan et al., 2002; Grill-Spector et al., 1999). In addition, a more posterior region on the lateral surface of the occipital lobe

(OF) was routinely found to be more active for faces compared to objects. This region of activation is likely to correspond to regions previously described as the LOC (Avidan et al., 2002; Grill-Spector et al., 1999), the inferior occipital gyrus (Hoffman and Haxby, 2000) or the occipital face area (Gauthier et al., 2000). We also found a reliable activation for faces compared to non-face objects in the superior temporal lobe (ST) (see also Hoffman and Haxby, 2000; Kanwisher et al., 1997).

Non-face selective responses were evident in the parahippocampal gyrus and other regions of the occipital lobe. The parahippocampal gyrus (PG) was more active when subjects viewed images of places compared to faces. The coordinates of this area suggest that it is analogous to an area previously called the PPA (Epstein and Kanwisher, 1998), CoS (Avidan et al., 2002) or medial fusiform gyrus (Ishai et al., 1999). An object-selective area that responded more to inanimate objects than to faces was located
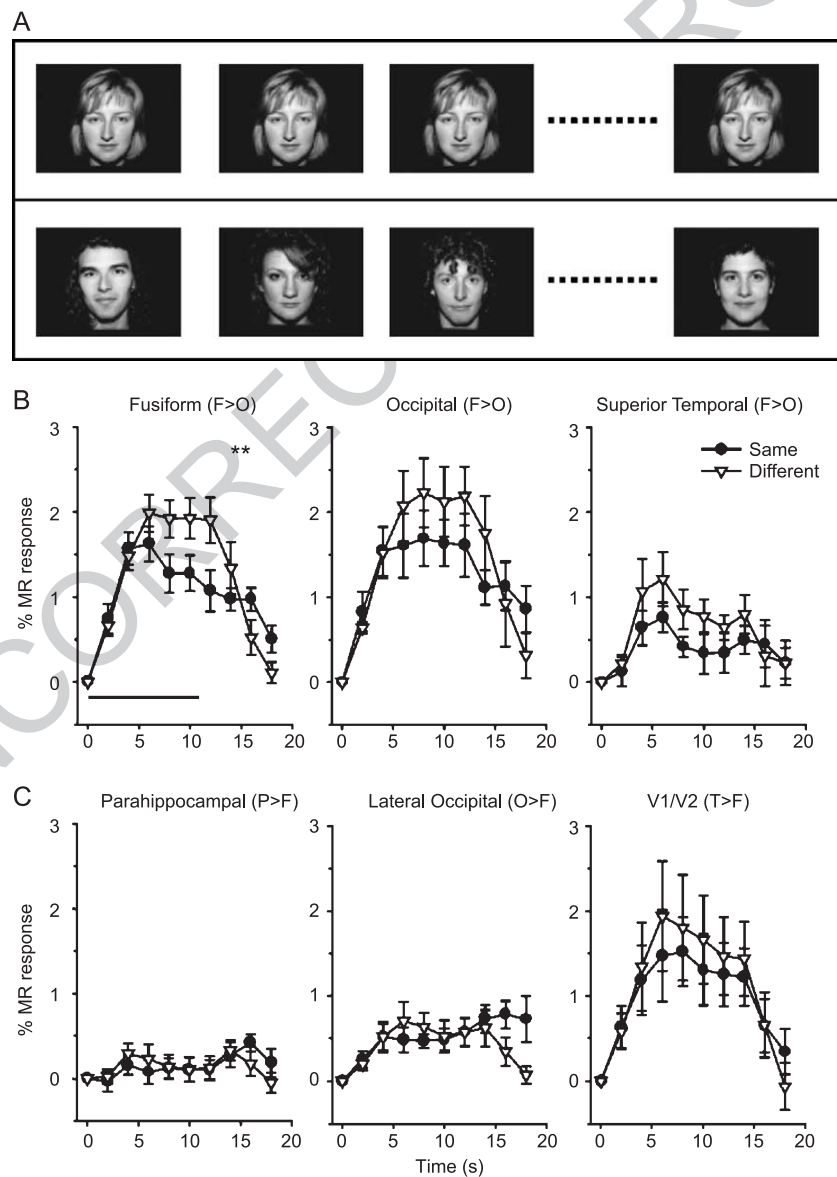

Fig. 2. Face adaptation experiment. (A) Examples of images from the *same-identity same-size* (top) and *different-face same-size* (bottom) conditions. (B) Time courses taken from face-selective (B) and non-face selective (C) regions were averaged across subjects (F = face, O = object, P = place, T = texture). The horizontal bar represents the duration of the presentation. Error bars represent ± 1 standard error. **$P < 0.01$.

on the lateral aspect of the occipital lobe (LO) and corresponds to a different region of the lateral occipital complex (Malach et al., 1995). Finally, we located a region of the medial occipital lobe that responded more to textures than to faces. Similar contrasts have previously been used to reveal primary visual areas (Grill-Spector et al., 1999). Indeed, we found the location of this region overlapped with the calcarine sulcus and is, therefore, likely to contain V1 and V2 (Andrews et al., 1997).

The average time-courses of activation in the face-selective regions are shown in Fig. 1B. Consistent with the FEAT analysis, an ANOVA showed images of faces resulted in a significant activation of the FG ($F = 18.3$, $P < 0.00001$), OF ($F = 8.4$, $P < 0.00001$) and the STS ($F = 6.37$, $P < 0.00001$). However, activation to faces was not restricted to face-selective regions of visual cortex. For example, images of faces also caused significant increases in MR activity in the PG ($F = 6.7$, $P <$

0.00001), LO ($F = 3.1$, $P = 0.01$) and V1/V2 ($F = 7.6$, $P < 0.00001$) regions (Fig. 1C).

As expected, the non-face selective areas responded maximally to inanimate objects, places and textures. The PG was maximally activated by images of places ($F = 37.2$, $P < 0.00001$), but also responded significantly to inanimate objects ($F = 14.7$, $P < 0.00001$) and textures ($F = 10.9$, $P < 0.00001$). The LO area showed a similar response to images of objects ($F = 19.2$, $P < 0.00001$) and places ($F = 31.2$, $P < 0.00001$), but also responded to textures ($F = 11.4$, $P = 0.00001$). V1/V2 responded significantly to textures ($F = 10.4$, $P < 0.00001$), places ($F = 6.9$, $P < 0.00001$) and objects ($F = 4.8$, $P < 0.0001$). Significant responses to objects and places were also apparent in face-selective regions. For example, the FG responded significantly to objects ($F = 8.5$, $P < 0.00001$), places ($F = 2.1$, $P < 0.05$) and textures ($F = 3.6$, $P < 0.005$), and the OF region showed a significant activation to objects ($F = 5.6$, $P <$
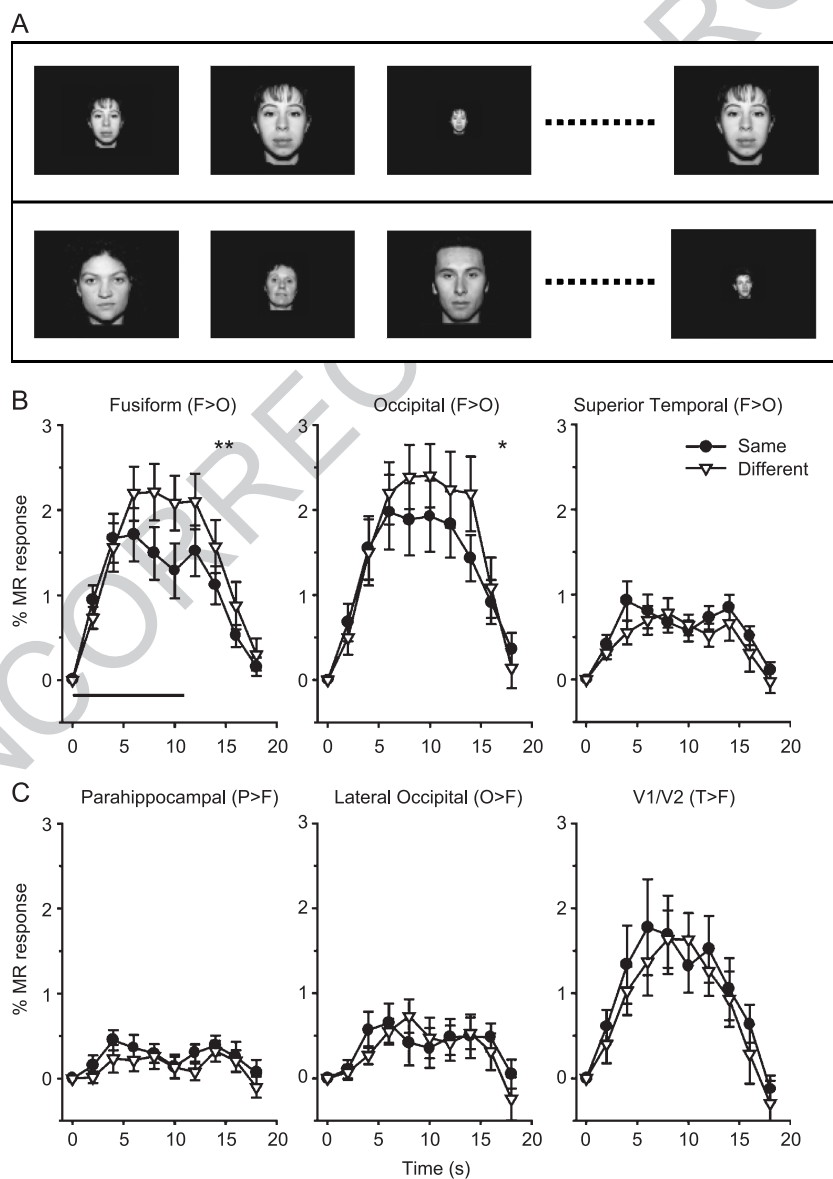

Fig. 3. Vary size experiment. (A) Examples of images from the *same-identity vary-size* (top) and *different-identity vary-size* (bottom) conditions. Time courses taken from face-selective (B) and non-face selective (C) regions were averaged across subjects (F = face, O = object, P = place, T = texture). The horizontal bar represents the duration of the presentation. Error bars represent ± 1 standard error. *$P < 0.05$, **$P < 0.001$.

254 0.0001). These regions of interest (ROI) were defined for each
255 individual and used as a mask in subsequent analyses.

Face adaptation

257   First, we measured the response to repeated presentations of
258 the same face (*same-face*) compared to images of different faces
259 (*different-face*) in different face-selective regions (Fig. 2). Our
260 prediction was that areas involved in face recognition would be
261 less active during the *same-identity same-size* condition compared
262 to the *different-identity same-size* condition. We found that the
263 response to the same face was significantly lower than the
264 response to different faces in the FG ($F = 17.2$; $P < 0.005$).
265 However, we failed to find any difference between the conditions
266 (i.e., adaptation) in the face-selective region of the OF ($F = 2.9$;
267 $P = 0.15$) or the STS ($F = 1.5$; $P = 0.27$). Despite the fact that
268 non-face selective areas showed significant responses to faces, we
269 did not detect any significant reduction in activity when the same
270 face was shown repeatedly.
271   Next, we compared the FMR-adaptation for repeated presenta-
272 tions of images of the same face that varied in size (*same-identity
273 vary-size*) compared to images of different faces that also varied in
274 size (*different-identity vary-size*) (Fig. 3). If adaptation to faces is
275 not affected by changes in image size, we would expect a relatively
276 lower response to the same face. A significantly reduced response
277 to images of the same face compared to different faces was
278 apparent in the FG ($F = 32.8$, $P < 0.001$) and OF ($F = 9.2$, $P <
279 0.05$), but was not evident in the STS ($F = 0.02$, $P = 0.96$). Size-
280 invariant fMR-adaptation was not evident in any of the non-face
281 selective ROI.
282   To determine the degree to which the responses in the FG
283 were size invariant, we performed a 2-way ANOVA (*same-
284 identity same-size*, *different-identity same-size* × *same-identity
285 vary-size*, *different-identity vary-size*). The results shown in Fig. 4
286 reveal a significant effect for identity ($P < 0.0005$), but not for
287 size ($P = 0.08$); there was also no interaction between size and
288 identity ($P = 0.96$). Individual comparisons of *same-identity
289 same-size* versus *same-identity vary-size* ($F = 2.0$, $P = 0.19$) and
290 *different-identity same-size* versus *different-identity vary-size* ($F =
291 2.65$, $P = 0.15$) also failed to show an effect of size.
292   Finally, we asked whether adaptation to faces would occur, if
293 we changed the viewpoint of the face. We compared the MR
294 response to repeated presentations of images of the same face that
295 varied in viewpoint (*same-identity vary-viewpoint*) compared to
296 images of different faces that also varied in viewpoint (*different-
297 identity vary-viewpoint*) (Fig. 5). We expected that, if the
298 representation of faces in a particular region was invariant to
299 viewpoint, a reduced response should be apparent for the same
300 face. On the other hand, if an area represented changeable aspects
301 of facial processing, we would expect a maximal response for
302 changes in viewpoint of the same face. The results show that
303 there were no differences between these *same-identity vary-
304 viewpoint* and *different-identity vary-viewpoint* conditions in the
305 FG ($F = 0.45$, $P = 0.52$) or OF ($F = 0.1$, $P = 0.78$). One possible
306 explanation for these data is that subjects were unable to
307 distinguish whether consecutive presentations represented a
308 different face or a different view of the same face. However,
309 our behavioural results show that subjects were able to perform
310 this task reliably (>95% correct).
311   In contrast to the FG and OF, MR-activity in the STS was
312 significantly greater in the *same-identity vary-viewpoint* condition
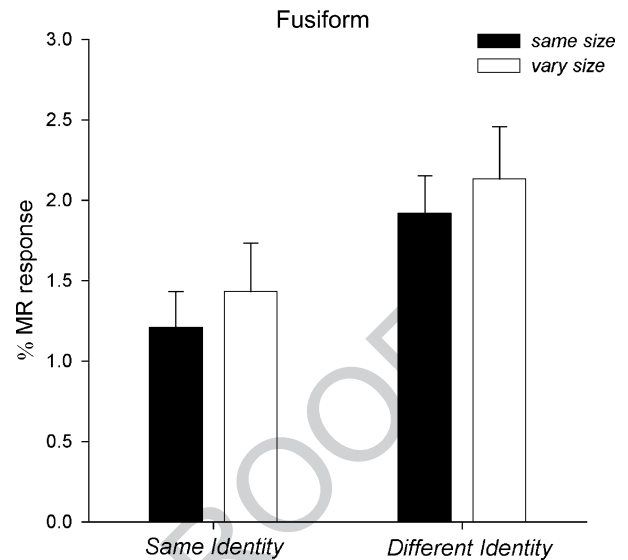

Fig. 4. Graph showing that responses to faces in the face-selective region of the fusiform gyrus were invariant to manipulations in the size of the image. Columns represent the peak response in the different conditions averaged across all subjects and the error bars represent ± 1 standard error.

313 compared to the *different-identity vary-viewpoint* condition ($F =
314 13.4$, $P < 0.01$). This pattern of activation would be consistent with
315 a brain region that processes changeable aspects of the face. To test
316 this possibility more explicitly, we performed a 2-way ANOVA in
317 which compared the same and different faces viewed from the
318 same or changing viewpoints (*same-identity same-size*, *different-
319 identity same-size* × *same-identity vary-viewpoint*, *different-
320 identity vary-viewpoint*) in the STS. As expected, the results
321 shown in Fig. 6 show a significant effect for viewpoint ($P < 0.01$),
322 but not effect for identity ($P = 0.87$). Moreover, there was a
323 significant interaction between viewpoint and identity ($P < 0.05$).
324 Further comparisons reveal that the effect of changes in viewpoint
325 was only apparent when the same face is viewed ($P < 0.000001$),
326 but not when different faces were viewed ($P = 0.86$). There were
327 no significant differences between the viewpoint conditions in the
328 non-face selective ROI (Fig. 4C).

Discussion

330   The aim of this study was to determine how information about
331 faces is represented in visual cortex. Specifically, we were
332 interested in asking which regions of visual cortex are involved
333 in forming an invariant representation of a face that could be used
334 for recognition, and which areas process changeable aspects of
335 faces that are important in social communication.
336   Consistent with previous studies, regions in the inferior and
337 superior regions of the temporal lobe responded more to photo-
338 graphs of faces than to images of other complex objects (Allison
339 et al., 1994; Grill-Spector et al., 1999; Hoffman and Haxby, 2000;
340 Kanwisher et al., 1997). Our purpose in this study was to determine
341 the nature of the representation in these different regions. For
342 example, as we move about, the size and shape of the retinal image
343 also changes. Thus, a major problem for the neural system
344 involved in face recognition is to generate a representation that
345 does not vary with changes in size and viewpoint. In this study, we
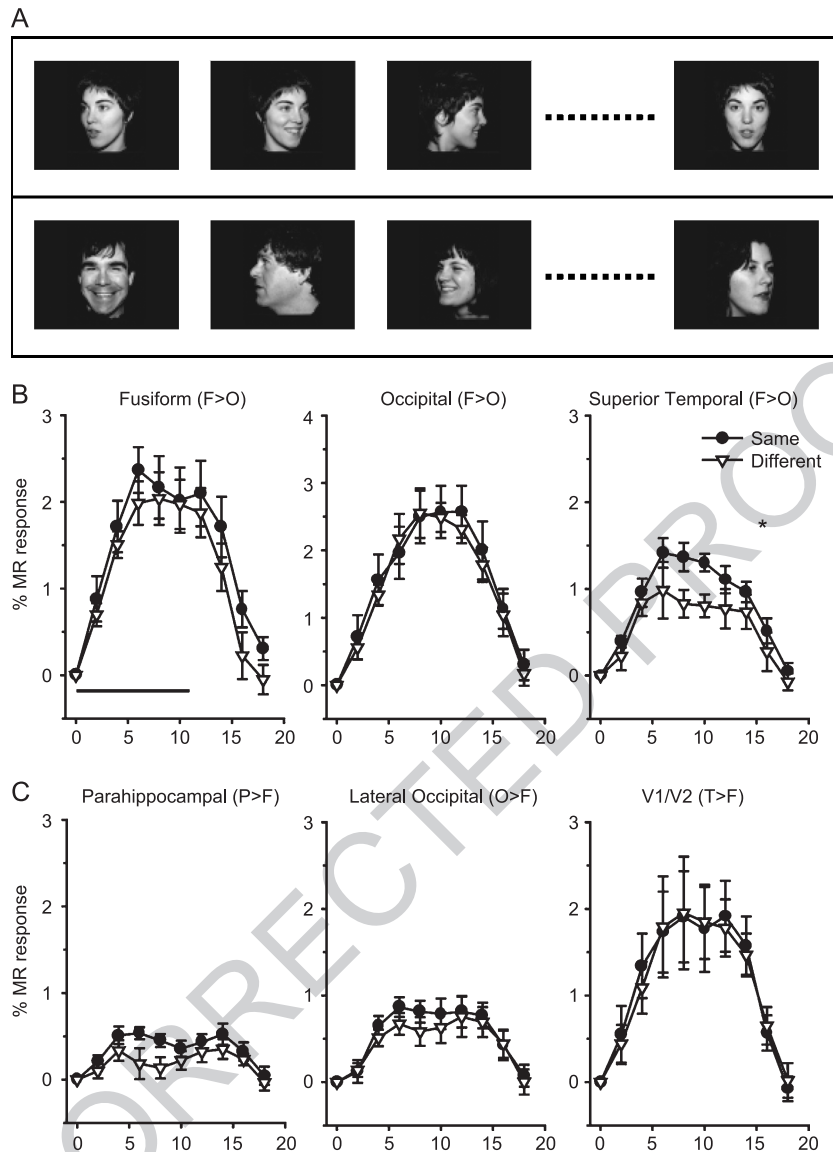346 used fMR-adaptation as a tool to understand the functional

Fig. 5. Vary viewpoint experiment. (A) Examples of images from the *same-identity vary-viewpoint* (top) and *different-identity vary-viewpoint* (bottom) conditions. Time courses taken from face-selective (B) and non-face selective (C) regions were averaged across all subjects (F = face, O = inanimate object, P = place, T = texture). The horizontal bar represents the duration of the presentation. Error bars represent ± 1 standard error. *$P < 0.01$.

properties of neurons in these visual areas (Malach and Grill-Spector, 2001). The principle behind this technique is that neuronal populations that represent particular categories of visual information should show a decrease in response, if the same exemplar of that category is shown repeatedly compared to presentations of different exemplars. Our aim was to determine which areas are adapted by repeated presentations of the same face image and then determine if the adaptation effect is maintained when the size and viewpoint of the face are varied.

We found adaptation to repeated presentations of faces in the face-selective region of the fusiform gyrus (FG). Next, we determined whether the neural representation in this area is invariant to changes in the size of the stimulus. We found that, despite marked changes in retinal image, adaptation to repetitions of the same face image persisted in the FG. To determine whether adaptation in this area was also invariant to viewpoint, we monitored the fMR-adaptation during the presentation of faces with varying head/gaze directions and emotional expressions. However, in this condition we found that the face-selective voxels in the FG were sensitive to this manipulation and failed to show a reduced response to the same identity condition. These findings are consistent with a previous study, in which face-selective regions in the LOC showed size-, but not viewpoint-invariant adaptation to faces (Grill-Spector et al., 1999). A comparison of the activation maps suggests that the LOa/pFs region from this earlier study corresponds to the FG region (FFA; Kanwisher et al., 1997), defined in the present study.

Our finding that face-selective regions in the inferior temporal lobe form a largely size-invariant, but viewpoint-specific representation of faces also fits with other neurophysiological studies. For example, single unit recordings of face-selective neurons have shown responses to faces are maintained over large changes in the size of the image (Gross et al., 1972; Ito et al., 1995; Rolls and Baylis, 1986). On the other hand, most face cells in the inferior
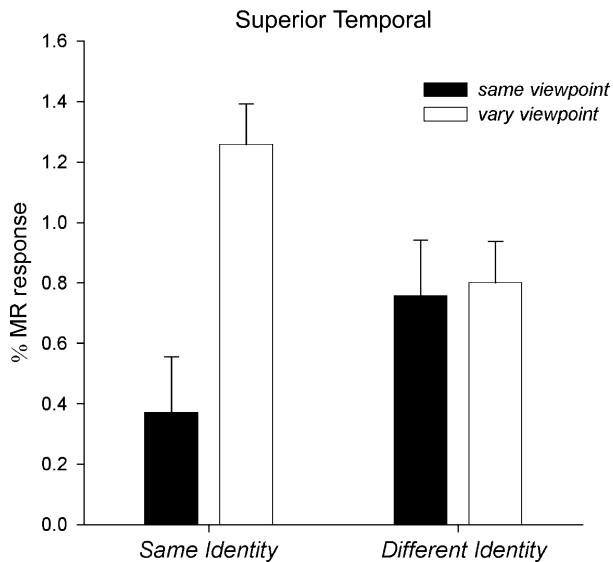
Fig. 6. Graph showing that the averaged MR response in the STS was significantly greater when the same face was viewed from different viewpoints compared to when different faces were viewed from different viewpoints. Columns represent the peak response in the different conditions averaged across all subjects and the error bars represent ± 1 standard error.

381 temporal lobe show selectivity for a specific vantage point and their
382 response decreases as the view of the head is rotated (Tanaka et al.,
383 1991; Perrett et al., 1985). Together, these data support a viewer-
384 centered (Bulthoff and Edelman, 1992), rather than an object-
385 centered (Marr, 1982, Biederman, 1987) representation for faces in
386 the inferior temporal lobe. Behavioural support for this position
387 comes from a report in which recognition of faces falls off with
388 increasing angle of rotation from a familiar view (Hill et al., 1997).
389 Similar viewpoint dependence has been reported for other objects
390 (Tarr and Pinker, 1989).
391   In contrast to the inferior temporal lobe, face-selective regions in
392 superior regions of the temporal lobe failed to show any adaptation
393 to repeated presentations of the same face. In contrast, we found a
394 larger response in the STS to the same face shown from different
395 viewpoints compared to different faces viewed from different
396 viewpoints. A comparable dissociation between face-selective areas
397 has been reported recently, in which the perception of identity
398 engaged inferior temporal regions, whereas perception of eye gaze
399 preferentially activated the superior temporal regions (Hoffman and
400 Haxby, 2000). In this study, we go beyond this earlier finding by
401 showing that changes in head/gaze direction and emotional
402 expression elicit a greater response in the STS when the face
403 images belong to the same identity compared to when these changes
404 occur in different faces with different identities. Because head/gaze
405 direction and expression were randomly interleaved, it was not
406 possible to determine the relative importance of these factors to the
407 response in the STS. However, other neurophysiological evidence
408 reveals that the STS is activated by changes in viewing angle
409 (Hasselmo et al., 1989), facial expression (Perrett and Mistlin,
410 1990) and lip movement (Calvert et al., 1997).
411   One possible explanation for this difference in response across
412 face-selective areas is that the inferior temporal regions are involved
413 in forming a perceptual representation of the face that could be used
414 for recognition of identity, whereas the superior temporal regions are
415 concerned with changeable aspects of face perception that are
416 important in social communication (Allison et al., 2000; Haxby et al.,

417 2000; Langton et al., 2000). This concept of face processing is
418 supported by recent studies in which we reported that the responses
419 of face-selective regions in the FG, but not in the STS, were
420 predictive of whether a face had been perceived when viewing
421 different ambiguous stimuli (Andrews and Schluppeck, in press;
422 Andrews et al., 2000). Further evidence comes from neuropsycho-
423 logical studies that show damage to the inferior temporal lobe results
424 in a selective impairment in face recognition (prosopagnosia),
425 whereas lesions to the superior temporal sulcus affect the emotional
426 associations related to the seeing faces (Capgras and Reboul-
427 Lauchaux, 1923; Ellis and Lewis, 2001; Heywood and Cowey,
428 1992; McNeil and Warrington, 1993).
429   Responses to faces were not restricted to face-selective regions
430 of visual cortex. We found that non-face selective regions of the
431 lateral occipital lobe and parahippocampal gyrus also showed a
432 significant response to faces. It is possible, therefore, that the
433 processing leading to the perception of a face is not restricted to
434 face-selective regions, but is based on a distributed pattern of
435 neural response across a large network of visual cortex that may
436 include 'object-selective' regions (Haxby et al., 2001; Ishai et al.,
437 1999). To test this possibility, we monitored the MR response in
438 these regions to repeated presentations of the same face image.
439 Despite the fact that non-face selective regions of visual cortex
440 responded to photographs of faces, we failed to find any
441 adaptation to repeated presentations of the same face. Based on
442 these data, it would appear that the neural processes that lead to
443 face perception are specific to face-selective regions of visual
444 cortex. This challenges the view that faces are coded by a
445 distributed representation across all regions of the ventral visual
446 pathway. Indeed, a recent study showed that activity in face-
447 selective areas of the fusiform gyrus allowed excellent discrim-
448 ination between faces and non-face objects, but failed to
449 discriminate between pairs of non-face stimuli (Spiridon and
450 Kanwisher, 2002). Consistent with this, we recently reported that
451 object-selective regions in visual cortex were unable to discrim-
452 inate the face percept when subjects viewed ambiguous mooney
453 images (Andrews and Schluppeck, in press). Future studies will
454 be required to determine if there are equipotent regions of visual
455 cortex that may be involved in early stages of both face and
456 object recognition (Grill-Spector et al., 1998; Tanaka, 1996).
457   In conclusion, these results suggest that face-selective regions
458 within the inferior temporal lobe are involved in the perception
459 and recognition of faces, and perhaps other specialised object
460 categories (Tarr and Gauthier, 2000). Whereas the neural
461 processing underlying other aspects of facial processing, partic-
462 ularly those involved in social cognition, embrace superior
463 temporal face-selective regions. The lack of fMR-adaptation in
464 non-face selective regions of visual cortex suggests that not all
465 areas of the ventral occipito-temporal processing stream contri-
466 bute to the processing that leads to face perception.

Uncited reference   467

George et al., 1999   468

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