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

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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.

Keywords: Fusiform; Perception; Awareness; Object recognition; Ventral pathway; FMRI

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). Despite this deficit in face perception, 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, 2004; 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

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the spatial limitations of fMRI, it is possible that a weak response 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

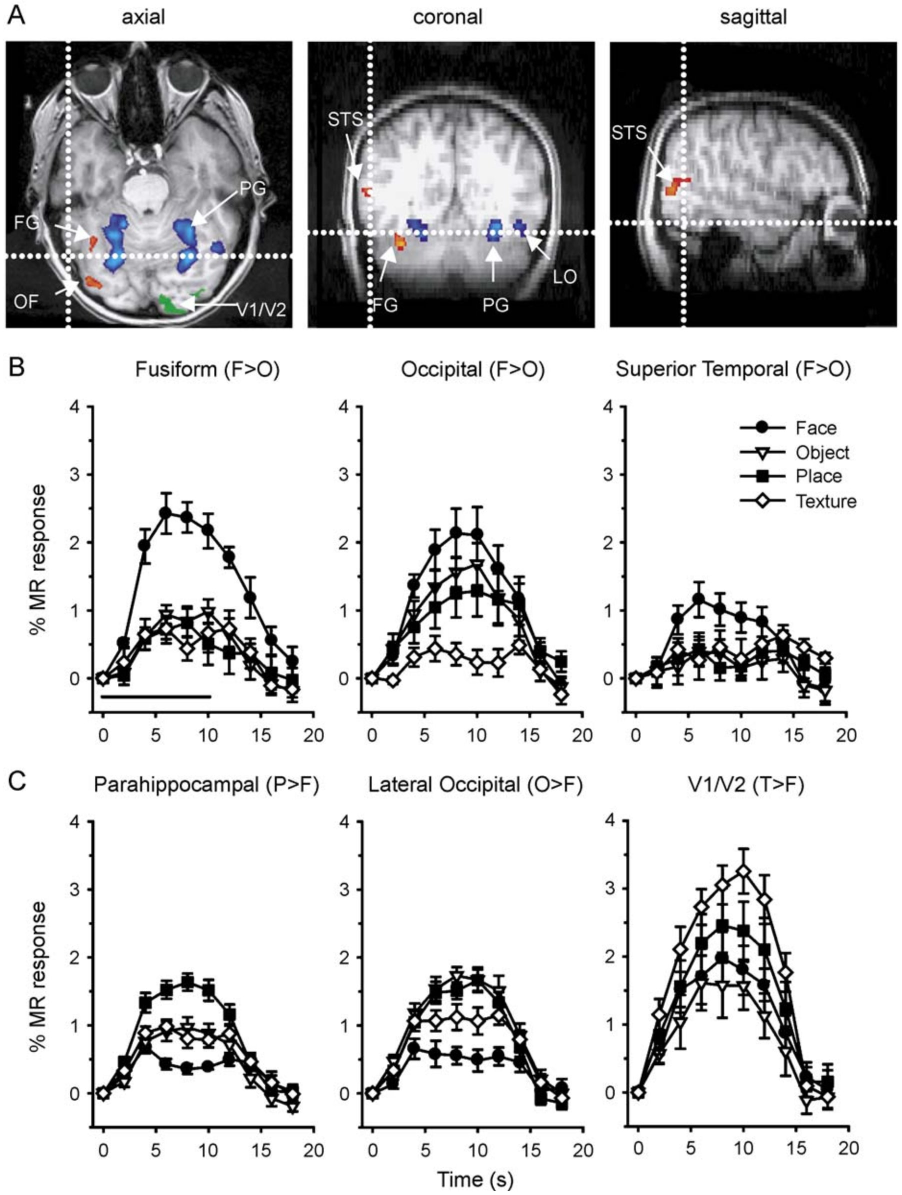

Fig. 1. Localiser scan. Regions of interest were defined by their anatomical location and their functional responses to different object categories. (A) Location of areas in visual cortex that showed selective responses to faces (red), objects (blue) or textures (green) in one subject (FG = fusiform 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.

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

Methods

Subjects

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

Imaging parameters

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

Localiser scan

To discriminate regions of visual cortex that are selectively activated by faces and non-face objects, a localiser scan was carried out for each subject. Each scan contained 16 stimulus blocks. The stimuli in each block were grey-scale photographs of either (1) faces, (2) inanimate objects, (3) places (buildings, indoor scenes & natural landscapes) or (4) textures. Images of faces were taken from a database of the Psychological Image Collection at Stirling (PICS: http://www.pics.psych.stir.ac.uk/) and were not familiar to any of the subjects. Photographs of inanimate objects, places and textures were obtained from various sources including CorelDraw and Microsoft clip-art. Each stimulus block contained 10 images with each image being presented for 800 ms followed by a 200-ms blank screen. Subjects were instructed to perform a one-back matching task using a response box. Each stimulus condition was repeated four times in a counterbalanced block design. Blocks were separated by periods of fixation when a grey screen, of the same average luminance was viewed for 10 s.

Analysis of the localiser scans was carried out using FEAT (www.fmrib.ox.ac.uk/fsl). The initial 8 s of data from each scan was discarded to minimise the effects of magnetic saturation. Motion correction was carried out using MCFLIRT (www.fmrib.ox.ac.uk/fsl), followed by a spatial smoothing algorithm (FWHM 5.0 mm). Z statistic images were generated using resel (corrected Bonferroni) thresholding ($P < 0.05$). Areas defined as face-selective included voxels that responded significantly more to faces than to objects or textures, whereas non-face selective areas responded more to inanimate objects, scenes or textures than to faces at this level of significance (Friston et al., 1995).

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

Face adaptation experiment

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

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

Region	Hemisphere	*n*	x	y	z
Fusiform gyrus	right	8	44	−58	−22
(F>O)	left	3	−46	−61	−27
Occipital face	right	6	43	−83	−10
(F>O)	left	1	−45	−82	−5
Superior temporal	right	6	54	−66	8
(F>O)	left	–	–	–	–
Parahippocampal gyrus	right	8	30	−61	−14
(P>F)	left	8	−32	−63	−15
Lateral occipital	right	6	42	−77	−3
(O>F)	left	6	−47	−74	−3
V1/V2	right	6	13	−98	−2
(T>F)	left	6	−14	−99	−2

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 (STS) (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

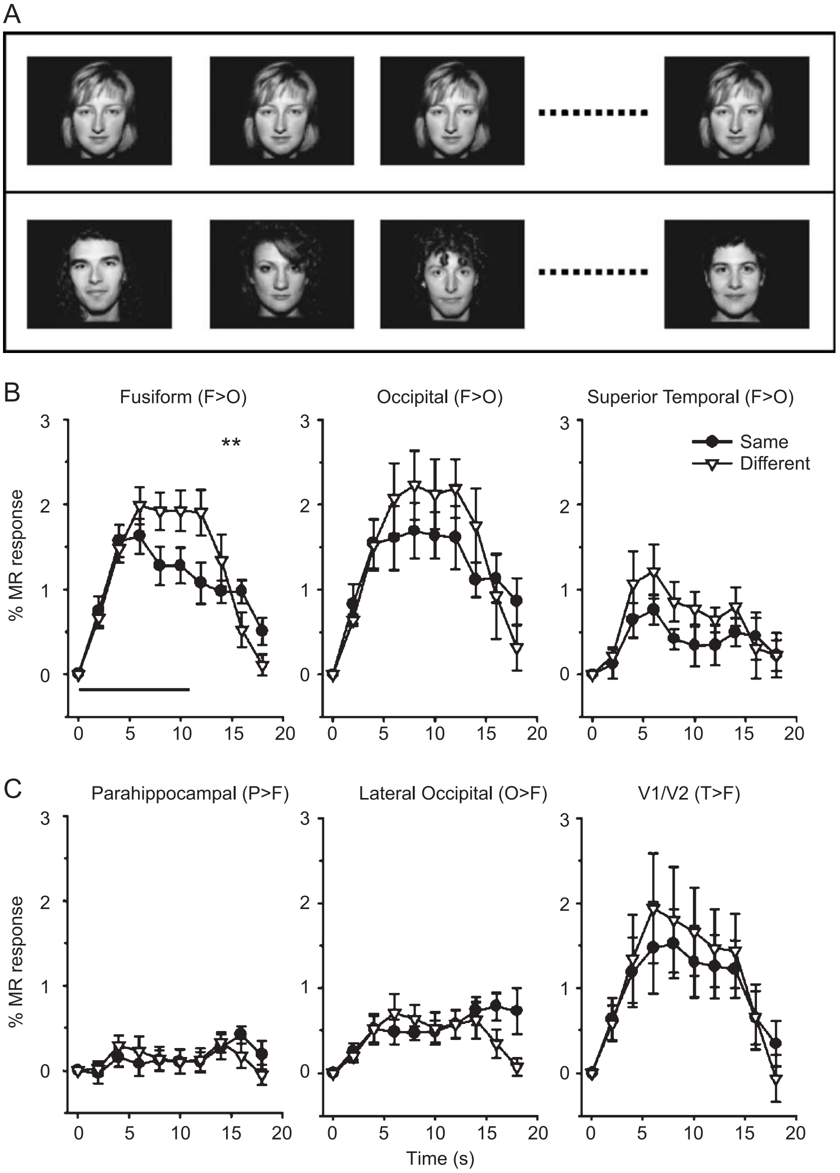

Fig. 2. Face adaptation experiment. (A) Examples of images from the *same-identity same-size* (top) and *different-identity same-size* (bottom) conditions. (B) Time courses taken from face-selective (B) and non-face selective (C) regions were averaged across subjects (F = face, O = object, P = place, 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).

By definition, 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, $P < 0.00001$),

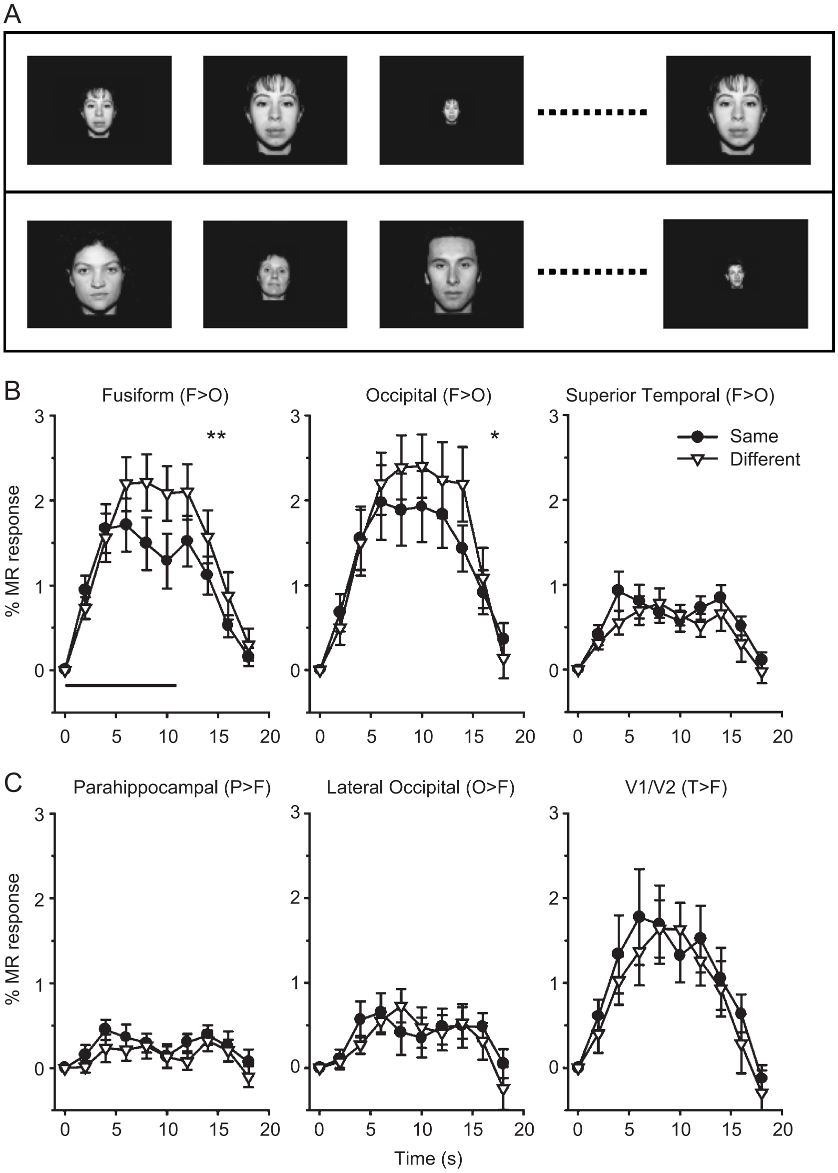

Fig. 3. Vary size experiment. (A) Examples of images from the *same-identity vary-size* (top) and *different-identity vary-size* (bottom) conditions. Time courses taken from face-selective (B) and non-face selective (C) regions were averaged across subjects (F = face, O = object, P = place, T = texture).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

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 ($F = 5.6$, $P < 0.0001$). These regions of interest (ROI) were defined for each individual and used as a mask in subsequent analyses.

Face adaptation

First, we measured the response to repeated presentations of the same face compared to images of different faces in different face-selective regions (Fig. 2). Our prediction was that areas involved in face recognition would be less active during the *same-identity same-size* condition compared to the *different-identity same-size* condition. We found that the response to the same face was significantly lower than the response to different faces in the FG ($F = 17.2$; $P < 0.005$). However, we failed to find any difference between the conditions (i.e., adaptation) in the face-selective region of the OF ($F = 2.9$; $P = 0.15$) or the STS ($F = 1.5$; $P = 0.27$). Despite the fact that non-face selective areas showed significant responses to faces, we did not detect any significant reduction in activity when the same face was shown repeatedly.

Next, we compared the FMR-adaptation for repeated presentations of images of the same face that varied in size (*same-identity vary-size*) compared to images of different faces that also varied in size (*different-identity vary-size*) (Fig. 3). If adaptation to faces is not affected by changes in image size, we would expect a relatively lower response to the same face. A significantly reduced response to images of the same face compared to different faces was apparent in the FG ($F = 32.8$, $P < 0.001$) and OF ($F = 9.2$, $P < 0.05$), but was not evident in the STS ($F = 0.02$, $P = 0.96$). Size-invariant fMR-adaptation was not evident in any of the non-face selective ROI.

To determine the degree to which the responses in the FG were size invariant, we performed a 2-way ANOVA (*same-identity same-size*, *different-identity same-size* × *same-identity vary-size*, *different-identity vary-size)*. The results shown in Fig. 4 reveal a significant effect for identity ($P < 0.0005$), but not for size ($P = 0.08$); there was also no interaction between size and identity ($P = 0.96$). Individual comparisons of *same-identity same-size* versus *same-identity vary-size* ($F = 2.0$, $P = 0.19$) and *different-identity same-size* versus *different-identity vary-size* ($F = 2.65$, $P = 0.15$) also failed to show an effect of size.

Finally, we asked whether adaptation to faces would occur, if we changed the viewpoint of the face. We compared the MR response to repeated presentations of images of the same face that varied in viewpoint (*same-identity vary-viewpoint*) compared to images of different faces that also varied in viewpoint (*different-identity vary-viewpoint*) (Fig. 5). We expected that, if the representation of faces in a particular region was invariant to viewpoint, a reduced response should be apparent for the same face. On the other hand, if an area represented changeable aspects of facial processing, we would expect a maximal response for changes in viewpoint of the same face. The results show that there were no differences between these *same-identity vary-viewpoint* and *different-identity vary-viewpoint* conditions in the FG ($F = 0.45$, $P = 0.52$) or OF ($F = 0.1$, $P = 0.78$). One possible explanation for these data is that subjects were unable to distinguish whether consecutive presentations represented a different face or a different view of the same face. However, our behavioural results show that subjects were able to perform this task reliably (>95% correct).

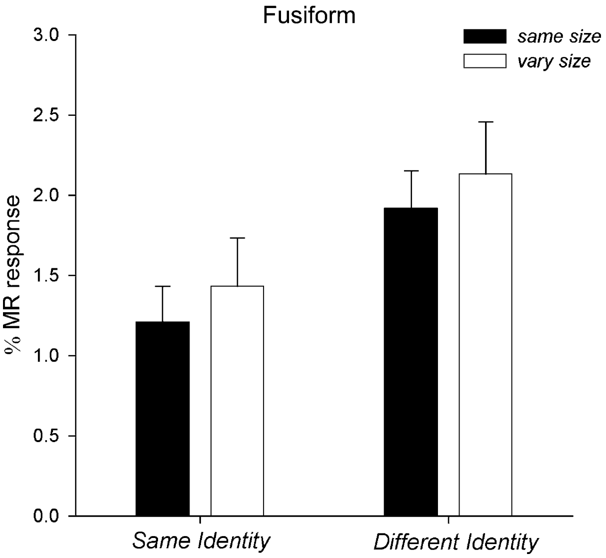

Fig. 4. Graph showing that responses to faces in the face-selective region of the fusiform gyrus were invariant to manipulations in the size of the image. Columns represent the peak response in the different conditions averaged across all subjects and the error bars represent ± 1 standard error.

In contrast to the FG and OF, MR-activity in the STS was significantly greater in the *same-identity vary-viewpoint* condition compared to the *different-identity vary-viewpoint* condition ($F = 13.4$, $P < 0.01$). This pattern of activation would be consistent with a brain region that processes changeable aspects of the face. To test this possibility more explicitly, we performed a 2-way ANOVA in which we compared the same and different faces viewed from the same or changing viewpoints (*same-identity same-size*, *different-identity same-size* × *same-identity vary-viewpoint*, *different-identity vary-viewpoint)* in the STS. As expected, the results shown in Fig. 6 show a significant effect for viewpoint ($P < 0.01$), but not effect for identity ($P = 0.87$). Moreover, there was a significant interaction between viewpoint and identity ($P < 0.05$). Further comparisons reveal that the effect of changes in viewpoint was only apparent when the same face is viewed ($P < 0.000001$), but not when different faces were viewed ($P = 0.86$). There were no significant differences between the viewpoint conditions in the non-face selective ROI (Fig. 5C).

Discussion

The aim of this study was to determine how information about faces is represented in visual cortex. Specifically, we were interested in asking which regions of visual cortex are involved in forming an invariant representation of a face that could be used for recognition, and which areas process changeable aspects of faces that are important in social communication.

Consistent with previous studies, regions in the inferior and superior regions of the temporal lobe responded more to photographs of faces than to images of other complex objects (Allison et al., 1994; Grill-Spector et al., 1999; Hoffman and Haxby, 2000; Kanwisher et al., 1997). Our purpose in this study was to determine the nature of the representation in these different regions. For example, as we move about, the size and shape of the retinal image also changes. Thus, a major problem for the neural system

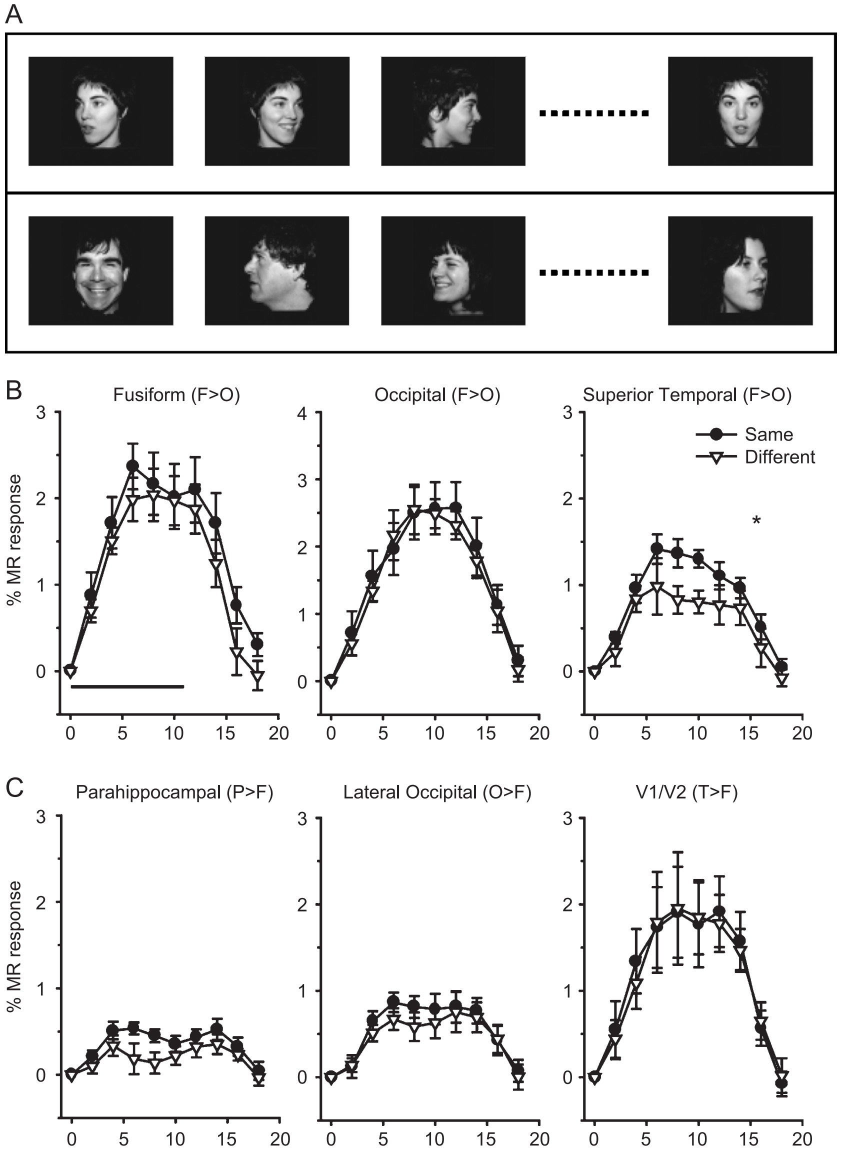

Fig. 5. Vary viewpoint experiment. (A) Examples of images from the *same-identity vary-viewpoint* (top) and *different-identity vary-viewpoint* (bottom) conditions. Time courses taken from face-selective (B) and non-face selective (C) regions were averaged across all subjects (F = face, O = inanimate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

involved in face recognition is to generate a representation that does not vary with changes in size and viewpoint. In this study, we used fMR-adaptation as a tool to understand the functional properties of neurons in these visual areas (Grill-Spector and Malach, 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

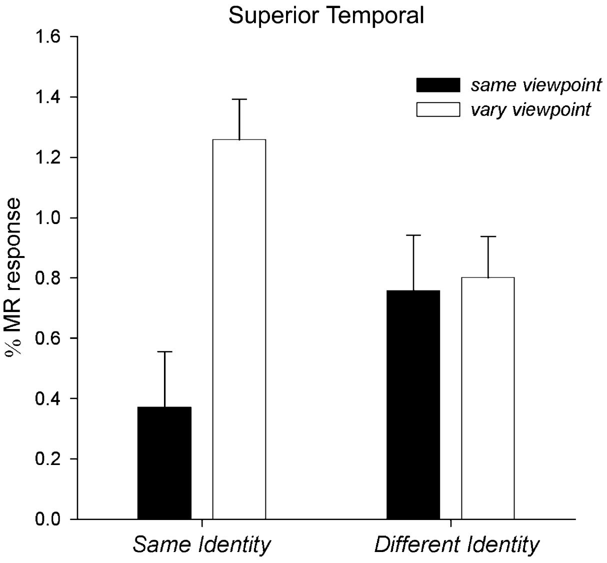

Fig. 6. Graph showing that the averaged MR response in the STS was significantly greater when the same face was viewed from different viewpoints compared to when different faces were viewed from different viewpoints. Columns represent the peak response in the different conditions averaged across all subjects and the error bars represent ± 1 standard error.

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 temporal lobe show selectivity for a specific vantage point and their response decreases as the view of the head is rotated (Tanaka et al., 1991; Perrett et al., 1985). Together, these data support a viewer-centered (Bulthoff and Edelman, 1992), rather than an object-centered (Marr, 1982, Biederman, 1987) representation for faces in the inferior temporal lobe. Behavioural support for this position comes from a report in which recognition of faces falls off with increasing angle of rotation from a familiar view (Hill et al., 1997). Similar viewpoint dependence has been reported for other objects (Tarr and Pinker, 1989).

In contrast to the inferior temporal lobe, face-selective regions in superior regions of the temporal lobe failed to show any adaptation to repeated presentations of the same face. In contrast, we found a larger response in the STS to the same face shown from different viewpoints compared to different faces viewed from different viewpoints. A comparable dissociation between face-selective areas has been reported recently, in which the perception of identity engaged inferior temporal regions, whereas perception of eye gaze preferentially activated the superior temporal regions (Hoffman and Haxby, 2000). In this study, we go beyond this earlier finding by showing that changes in head/gaze direction and emotional expression elicit a greater response in the STS when the face images belong to the same identity compared to when these changes occur in different faces with different identities. Because head/gaze direction and expression were randomly interleaved, it was not possible to determine the relative importance of these factors to the response in the STS. However, other neurophysiological evidence reveals that the STS is activated by changes in viewing angle (Hasselmo et al., 1989), facial expression (Perrett and Mistlin, 1990) and lip movement (Calvert et al., 1997).

One possible explanation for this difference in response across face-selective areas is that the inferior temporal regions are involved in forming a perceptual representation of the face that could be used for recognition of identity, whereas the superior temporal regions are concerned with changeable aspects of face perception that are important in social communication (Allison et al., 2000; Haxby et al., 2000; Langton et al., 2000). This concept of face processing is supported by recent studies in which we reported that the responses of face-selective regions in the FG, but not in the STS, were predictive of whether a face had been perceived when viewing different ambiguous stimuli (Andrews and Schluppeck, 2004; Andrews et al., 2000). Further evidence comes from neuropsychological studies that show damage to the inferior temporal lobe results in a selective impairment in face recognition (prosopagnosia), whereas lesions to the superior temporal sulcus affect the emotional associations related to the seeing faces (Capgras and Reboul-Lauchaux, 1923; Ellis and Lewis, 2001; Heywood and Cowey, 1992; McNeil and Warrington, 1993).

Responses to faces were not restricted to face-selective regions of visual cortex. We found that non-face selective regions of the lateral occipital lobe and parahippocampal gyrus also showed a significant response to faces. It is possible, therefore, that the processing leading to the perception of a face is not restricted to face-selective regions, but is based on a distributed pattern of neural response across a large network of visual cortex that may include 'object-selective' regions (Haxby et al., 2001; Ishai et al., 1999). To test this possibility, we monitored the MR response in these regions to repeated presentations of the same face image. Despite the fact that non-face selective regions of visual cortex responded to photographs of faces, we failed to find any adaptation to repeated presentations of the same face. Based on these data, it would appear that the neural processes that lead to face perception are specific to face-selective regions of visual cortex. This challenges the view that faces are coded by a distributed representation across all regions of the ventral visual pathway. Indeed, a recent study showed that activity in face-selective areas of the fusiform gyrus allowed excellent discrimination between faces and non-face objects, but failed to discriminate between pairs of non-face stimuli (Spiridon and Kanwisher, 2002). Consistent with this, we recently reported that object-selective regions in visual cortex were unable to discriminate the face percept when subjects viewed ambiguous mooney images (Andrews and Schluppeck, 2004). Future studies will be required to determine if there are equipotent regions of visual cortex that may be involved in early stages of both face and object recognition (Grill-Spector et al., 1998; Tanaka, 1996).

In conclusion, these results suggest that face-selective regions within the inferior temporal lobe are involved in the perception and recognition of faces, and perhaps other specialised object categories (Tarr and Gauthier, 2000). Whereas the neural processing underlying other aspects of facial processing, particularly those involved in social cognition, embrace superior temporal face-selective regions. The lack of fMR-adaptation in non-face selective regions of visual cortex suggests that not all areas of the ventral occipito-temporal processing stream contribute to the processing that leads to face perception.

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References

Allison, T., McCarthy, G., Nobre, A., Puce, A., Belger, A., 1994. Human extrastriate visual cortex and the perception of faces, words, numbers and colors. Cereb. Cortex 4, 544–554.

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.

Andrews, T.J., Schluppeck, D., 2004. Neural responses to mooney images reveal a modular representation of faces in human visual cortex. NeuroImage 21, 91–98.

Andrews, T.J., Halpern, S.D., Purves, D., 1997. Correlated size variations in human visual cortex, lateral geniculate nucleus, and optic tract. J. Neurosci. 17, 2859–2868.

Andrews, T.J., Schluppeck, D., Homfray, D., Matthews, P., Blakemore, C., 2000. Activity in the fusiform gyrus predicts perception when viewing Rubin's vase-face stimulus. NeuroImage 17, 890–901.

Avidan, G., Hasson, U., Hendler, T., Zohary, E., Malach, R., 2002. Analysis of the neuronal selectivity underlying low fMRI signals. Curr. Biol. 12, 964–972.

Biederman, I., 1987. Recognition-by-components—A theory of human image understanding. Psychol. Rev. 94, 115–147.

Breen, N., Caine, D., Coltheart, M., 2002. Models of face recognition and delusional misidentification: a critical review. Cogn. Neuropsychiatry 17, 55–71.

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

Bulthoff, H.H., Edelman, S., 1992. Psychophysical support for a 2-dimensional view interpolation theory of object recognition. Proc. Natl. Acad. Sci. U.S.A. 89, 60–64.

Calvert, G.A., Bullmore, E., Brammer, M.J., Campbell, R., Iversen, S.D., Woodruff, P., McGuire, P., Williams, S., David, A.S., 1997. Silent lipreading activates the auditory cortex. Science 276, 593–596.

Capgras, J., Reboul-Lauchaux, J., 1923. L'illusion des sosies dan un delire systematise chronique. Bull. Soc. Clin. Med. Ment. 11, 6–16.

Damasio, A.R., Damasio, H., Vanhoesen, G.W., 1982. Prosopagnosia-anatomic basis and behavioral mechanisms. Neurology 32, 331–341.

Ellis, H.D., Lewis, M.B., 2001. Capgras delusion: a window on face recognition. Trends Cogn. Sci. 5, 149–156.

Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. Nature 392, 598–601.

Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.P., Frith, C.D., Frackowiak, R.S.J., 1995. Statistical parametric maps in functional imaging: a general linear approach. Hum. Brain Mapp. 2, 189–210.

Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. The fusiform face area is part of a network that processes faces at the individual level. J. Cogn. Neurosci. 12, 495–504.

Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol. 107, 293–321.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., Malach, R., 1998. A sequence of object-processing stages revealed by fMRI in the human occipital lobe. Hum. Brain Mapp. 6, 316–328.

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, 187–203.

Gross, C.G., Rocham-Miranda, C.E., Bender, D.B., 1972. Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol. 35, 96–111.

Hasselmo, M.E., Rolls, E.T., Baylis, G.C., Nalwa, V., 1989. Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. Exp. Brain Res. 75, 417–429.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cogn. Sci. 4, 223–233.

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, 2425–2430.

Heywood, C.A., Cowey, A., 1992. The role of the 'face-cell' area in the discrimination and recognition of faces by monkeys. Philos. Trans. R. Soc. London, B Biol. Sci. 335, 31–37.

Hill, H., Schyns, P.G., Akamatsu, S., 1997. Information and viewpoint dependence in face recognition. Cognition 62, 201–222.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80–84.

Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., Haxby, J.V., 1999. Distributed representation of objects in the human ventral visual pathway. Proc. Natl. Acad. Sci. U. S. A. 96, 9379–9384.

Ito, M., Tamura, H., Fujita, I., Tanaka, K., 1995. Size and position invariance of neuronal responses in monkey inferotemporal cortex. J. Neurophysiol. 73, 218–226.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in extrastriate cortex specialised for face perception. J. Neurosci. 17, 4302–4311.

Kreiman, G., Koch, C., Fried, I., 2000. Category-specific visual responses of single neurons in the human medial temporal lobe. Nat. Neurosci. 3, 946–953.

Langton, S.R.H., Watt, R.J., Bruce, V., 2000. Do the eyes have it? Cues to the direction of social attention. Trends Cogn. Sci. 4, 50–59.

Malach, R., Reppas, J.B., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., Tootell, R.B.H., 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc. Natl. Acad. Sci. U. S. A. 92, 8135–8138.

Marr, D., 1982. Vision. Freeman.

McNeil, J.E., Warrington, E.K., 1993. Prosopagnosia—A face-specific disorder. Q. J. Exp. Psychol., A 46, 1–10.

Moscovitch, M., Winocur, G., Behrmann, M., 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. J. Cogn. Neurosci. 9, 555–604.

Perrett, D.I., Mistlin, A.J., 1990. Perception of facial characteristics by monkeys. Stebbins, W.C., Berkley, M.A. Comparative Perception, Complex Signals vol. 2. Wiley, New York, pp. 187–215.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., Jeeves, M.A., 1985. Visual cells in the temporal cortex sensitive to face view and gaze direction. P. Roy. Soc. Lond. B Bio. 223, 293–317.

Rolls, E.T., Baylis, G.C., 1986. Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the monkey. Exp. Brain Res. 65, 38–48.

Spiridon, M., Kanwisher, N., 2002. How distributed is visual category information in human occipito-temporal cortex? An fMRI study. Neuron 35, 1157–1165.

Tanaka, K., 1996. Inferotemporal cortex and object vision. Annu. Rev. Neurosci. 19, 109–139.

Tanaka, K., Saito, H., Fukada, Y., Moriya, M., 1991. Coding visual images of objects in the inferotemporal cortex of the macaque monkey. J. Neurophysiol. 66, 170–189.

Tarr, M.J., Pinker, S., 1989. Mental rotation and orientation-dependence in shape-recognition. Cogn. Psychol. 21, 233–282.

Tarr, M.J., Gauthier, I., 2000. FFA: a flexible fusiform area for subordinate visual processing automatized by expertise. Nat. Neurosci. 3, 764–769.