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Neural responses to Mooney images reveal a modular representation of faces in human visual cortex

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The way in which information about objects is represented in visual cortex remains controversial. One model of human object recognition poses that information is processed in modules, highly specialised for different categories of objects; an opposing model appeals to a distributed representation across a large network of visual areas. We addressed this debate by monitoring activity in face- and object-selective areas while human subjects viewed ambiguous face stimuli (Mooney faces). The measured neural response in the face-selective region of the fusiform gyrus was greater when subjects reported seeing a face than when they perceived the image as a collection of blobs. In contrast, there was no difference in magnetic resonance response between face and no-face perceived events in either the face-selective voxels of the superior temporal sulcus or the object-selective voxels of the parahippocampal gyrus and lateral occipital complex. These results challenge the concept that neural representation of faces is distributed and overlapping and suggest that the fusiform gyrus is tightly linked to the awareness of faces.

Keywords: Perception; Awareness; Object recognition; Temporal lobe; Ventral pathway; FMRI

Introduction

Recognising an object in a visual scene is a simple and effortless process for most human observers. However, the apparent ease with which object recognition takes place belies its inherent complexities and ambiguities (Marr, 1982). For example, any given two-dimensional retinal image could be the projection of countless object configurations in the three-dimensional world. Conversely, the same object can give rise to markedly different retinal images, depending on the viewing conditions. The visual system must take into account sources of variation caused by changes in viewpoint, but at the same time be able to detect differences between objects. Although computational models of object recognition have proposed ways to deal with the ambiguity inherent in the retinal image (Ullman, 1996; Edelman, 1997), it remains unclear how these mechanisms might be implemented in visual cortex.

Visual areas involved in object recognition form a ventral processing stream that projects toward the temporal lobe (Milner and Goodale, 1995; Ungerleider and Mishkin, 1982). Neurons in the ventral stream have properties that are important for object recognition, such as selectivity for form, texture, and colour (Komatsu and Ideura, 1993). In the temporal lobe, some neurons display even greater selectivity, responding preferentially to faces and objects (Fried et al., 1997; Gross et al., 1972; Tanaka, 1997). Lesions to this region of visual cortex often result in difficulties in recognising, identifying, and naming different categories of objects (Farah, 1992). One of the most thoroughly studied deficits of recognition is prosopagnosia, where patients are often unable to identify familiar individuals by their facial characteristics, and in some cases cannot recognise a face at all. Nonetheless, 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 leave face recognition intact, but impair an individual's ability to identify other objects (Moscovitch et al., 1997).

The concept that discrete areas of the temporal lobe are specialised for different categories of objects is supported by a number of physiological studies. For example, a region in the fusiform gyrus has been shown to be more responsive to faces than to other complex objects (Allison et al., 1994; Kanwisher et al., 1997). Similar category-specific visual responses have been found for buildings (Epstein and Kanwisher, 1998), human body parts (Downing et al., 2001), and letters (Allison et al., 1994; Polk and Farah, 1998). These results are consistent with single-neuron recordings in humans that have also revealed category-specific responses for faces, natural scenes, houses, famous people, and animals on the medial surface of the temporal lobe (Fried et al., 1997; Kreiman et al., 2000). However, this selectivity of neural response does not mean that the perception of different categories of objects is specific to particular regions of visual cortex. This is because the neural response to any object is not restricted to the area that responds maximally to that particular category of

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object (Ishai et al., 1999). Thus, it is possible that our perception of objects is based on the entire pattern of response across the temporal lobe (Cohen and Tong, 2001; Haxby et al., 2001).

In the present study, we have used ambiguous Mooney images to determine how one category of object is represented in visual cortex (Fig. 1). The Mooney images were thresholded photographs of faces that were either perceived as a face or a collection of unrelated blobs (Mooney, 1957). Our aim was to compare neural responses in pre-defined face- and object-selective areas for events when the Mooney images were perceived as a face and events when a face was not perceived. The advantage of using ambiguous stimuli, such as Mooney images, is that the stimulus remains unchanged, and thus controls for lower level changes in the stimulus that may confound the interpretation of previous studies. So, any changes in activity that accompany a difference in perception are likely to be specific to that particular aspect of sensory perception (Andrews, 2001).

In a previous study, Dolan et al. (1997) examined activity resulting from ambiguous Mooney faces and objects using PET. They reported that perception of faces or objects enhanced the activity of inferior temporal regions that are involved in face and object perception. However, the spatial resolution of PET did not allow the discrimination of different face- and object-selective areas. More recently, Kanwisher et al. (1998) asked whether Mooney faces activated face-selective areas in the fusiform gyrus. They reported that the neural response was greater for Mooney faces compared to photographs of objects. However, they did not compare responses to Mooney images in other face- or object-selective areas, nor did they directly compare events when a Mooney image was perceived as a face to events when it was not.

Here, we extend the approach used in these previous studies by determining the activity in specific face- and object-selective areas, when subjects did or did not perceive a Mooney image as a face. If faces are represented by the activity of specific modules, the increased activity associated with perceiving a Mooney face should be specific to face-selective regions in visual cortex. However, if the visual system represents faces in a distributed manner, any object-selective area that shows an activation to photographs of faces should also show an increased response when a Mooney image is perceived as a face.

Methods

Subjects

All nine observers (one author and eight naïve subjects) 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 (approx. 8 deg × 8 deg) 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 (Wardray-Premise, Thames Ditton, UK).

Imaging parameters

All experiments were carried out using the Siemens-Varian 3 T magnetic resonance imaging (MRI) scanner at the Functional Magnetic Resonance Imaging of the Brain (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 for image collection. Sixteen contiguous axial slices were employed to cover the brain (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 mm × 1 mm within slice and 3.5 mm between slices. Image segmentation to extract brain was carried out using BET, FMRIB's Brain Extract Tool (Smith, 2000; www.fmrib.ox.ac.uk/fsl). To facilitate anatomical localisation of the foci of activation, statistical maps from the echo-planar imaging were registered to high-resolution structural images of the subjects. Additionally, the statistical maps were registered on to a standard image in Talairach space (Montreal Neurological

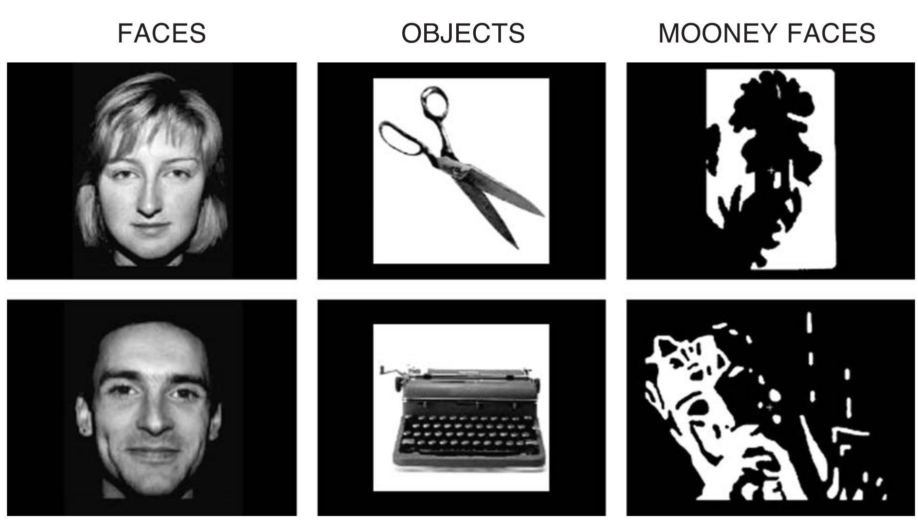

Fig. 1. Examples of faces, objects, and Mooney images.

Institute, MNI average 152 T1 brain). Registration was carried out using FLIRT (www.fmrib.ox.ac.uk/fsl).

Localiser scan

To discriminate which regions of visual cortex are selectively activated by faces and which are selectively responsive for objects, a localiser scan was carried out in each session. The stimuli were grey-scale photographs of actual faces and objects. Images of faces were taken from a database of the Psychological Image Collection at Stirling (PICS: http://pics.psych.stir.ac.uk/) and were not familiar to any of the subjects. The faces had neutral expressions and an equal number of males and females was used. Photographs of inanimate objects were obtained from various sources including the PICS database and Microsoft clip-art. During each localiser scan, subjects were presented with alternating blocks of faces or non-face objects in rapid sequence (12 images per 14 s block). There were no significant differences in the average luminance of the object and face images. Face and object 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, the FMRIB Easy Analysis Tool (www.fmrib.ox.ac.uk/fsl) integrated into MEDx (Sensor Systems, VA, USA). Statistical analysis was carried out using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction (Woolrich et al., 2000). The initial four TRs (8 s) of data from each scan were discarded to minimise the effects of magnetic saturation. The following pre-statistics processing was applied to all EPI scans: 3D motion correction, using MCFLIRT (Jenkinson et al., 2000); spatial smoothing using a Gaussian kernel of FWHM 5.0 mm; mean-based intensity normalization of all volumes by the same factor; nonlinear high-pass temporal filtering (Gaussian-weighted LSF straight line fitting, with sigma = 7.5 s).

Z (Gaussianised T) statistic images were thresholded using resel (corrected Bonferroni) thresholding with a corrected significance threshold of $P < 0.05$ (Forman et al., 1995; Friston et al., 1995). Areas defined as face-selective included voxels that responded significantly more to faces than to objects, whereas object-selective areas included voxels that responded more to inanimate objects than to faces at this level of significance. To estimate the maximum amplitude of the response to faces and objects, we fitted the data, averaged across subjects, with a three-parameter Gaussian function. To define the face and object voxels for further analysis, the statistical images from the localiser experiments were registered on to the event-related EPI data set using FLIRT for each individual.

Event-related responses to faces and objects

Next, we determined the temporal characteristics of the response in the face- and object-selective areas to single presentations of faces and objects for six of the nine subjects. An event involved a single presentation of a face or an object for 2 s followed by a grey screen of the same average luminance for 8 s. In each scan, 20 faces and 20 objects were randomly interleaved. 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 (% change in MR activity). The time-course plots were also normalised to the activity at stimulus onset. Signals were then averaged separately for the face and object events in the face- and object-selective areas.

Two strategies were employed to determine activity when subjects viewed single presentations of faces and objects. The first involved analysing the time-series of activity following the presentation of a face or an object. Repeated-measures ANOVA was used to determine whether there were significant changes in activity in the 10 s following the presentation of an image. The second strategy involved a simple average of the integrated MR activity following the initial change in perception. The change in % MR signal was integrated from 0 to 6 s (three TRs) following image onset and a paired t test was used to determine the significance of the difference between the means of the two conditions (*face*, *object*).

Event-related responses to Mooney images

Finally, we determined the response to Mooney images in the previously defined regions of interest in the eight naïve subjects. The Mooney images were thresholded photographs of faces that are sometimes perceived as a collection of black and white blobs (see Fig. 1). However, on other occasions, the relevant blobs can be connected to form the perception of a face. Mooney images were selected on the basis that, on their first presentation, they are seen as a face by about 50% of naïve observers. The subjects who took part in the FMRI experiment were not previously exposed to the Mooney images used in this study.

Mooney images were briefly presented (2 s) and subjects were instructed to fixate a small cross in the centre of the image and indicate by pressing one of two buttons whether they had perceived a face or not. A grey screen with the same average luminance was then presented for 8 s before the next Mooney image was displayed. Twenty upright and 20 inverted Mooney images were randomly interleaved in each scan. The MR signal from each voxel falling within the areas previously defined by the localiser scan was converted into units of fractional signal change and normalised to the level at the time the Mooney image was presented. The difference in MR activity was calculated for events when a face was perceived compared to when no-face was reported. A repeated-measures ANOVA was then performed on this difference signal for the 10 s following the presentation of a Mooney image.

Results

Localiser scan

Spatially discrete face- and object-selective areas were initially localised using a blocked design (Fig. 2a). In each subject, a region in the fusiform gyrus showed significant activation for faces versus non-face objects (Fig. 1). Face-selective responses were also detected in a region of the superior temporal sulcus in five of the nine subjects. Object-selective responses were found bilaterally in the parahippocampal gyrus in all subjects. Another object-selective area was located in the lateral aspect of the occipital lobe in eight of the nine subjects. Regions of interest were defined for each individual and used as a mask in subsequent analyses.

The average time-courses of activation in the face- and object-selective areas during the localiser scan are shown in Fig. 2b.

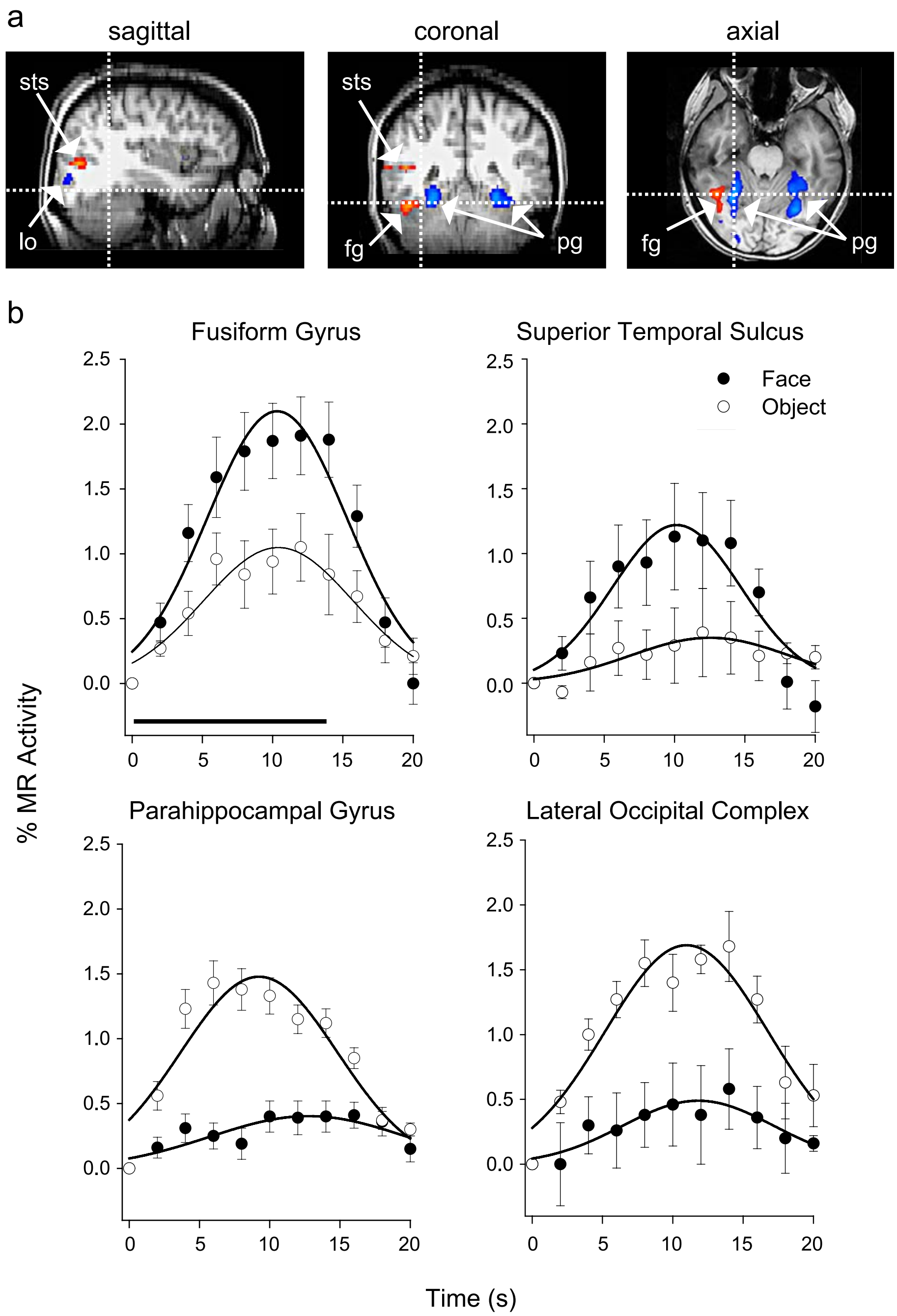

Fig. 2. Localiser scan. (a) Location of areas in visual cortex that showed selective responses to faces (red) or objects (blue) in one subject (fg = fusiform gyrus, sts = superior temporal sulcus, pg = parahippocampal gyrus, and lo = lateral occipital complex). These scan images follow radiological convention, with the left hemisphere shown on the right. The dashed lines in each image show the spatial relation of the three slices. (b) MR time-course during localiser scans, showing the activity averaged across subjects in each face- and object-selective area. The horizontal bar represents the duration of each block. Error bars represent ±1 SE.

Consistent with the FILM analysis, an ANOVA showed that blocks of faces resulted in a significant activation of the fusiform gyrus (mean amplitude ± SEM: 2.1 ± 0.14, $F = 25.8$, $P < 0.00001$) and the superior temporal sulcus (mean amplitude ± SEM: 1.2 ± 0.12, $F = 5.0$, $P < 0.0001$). Blocks of faces also caused a significant increase in MR activity in the object-selective region of the parahippocampal gyrus (mean amplitude ± SEM: 0.40 ± 0.04, $F = 4.4$, $P < 0.0001$), but not in the lateral occipital complex (mean amplitude ± SEM: 0.49 ± 0.05, $F = 1.2$, $P = 0.29$).

The blocked presentation of objects resulted in a significant increase in activity in the object-selective regions of the parahippocampal gyrus (mean amplitude ± SEM: 1.48 ± 0.12, $F = 28.7$, $P < 0.00001$) and lateral occipital complex (mean amplitude ± SEM: 1.69 ± 0.11, $F = 10.7$, $P < 0.00001$). A significant increase in MR activity was also apparent for blocks of objects in the fusiform gyrus (mean amplitude ± SEM: 1.0 ± 0.06, $F = 8.4$, $P < 0.00001$), but not in the superior temporal sulcus (mean amplitude ± SEM: 0.35 ± 0.04, $F = 1.0$, $P = 0.47$).

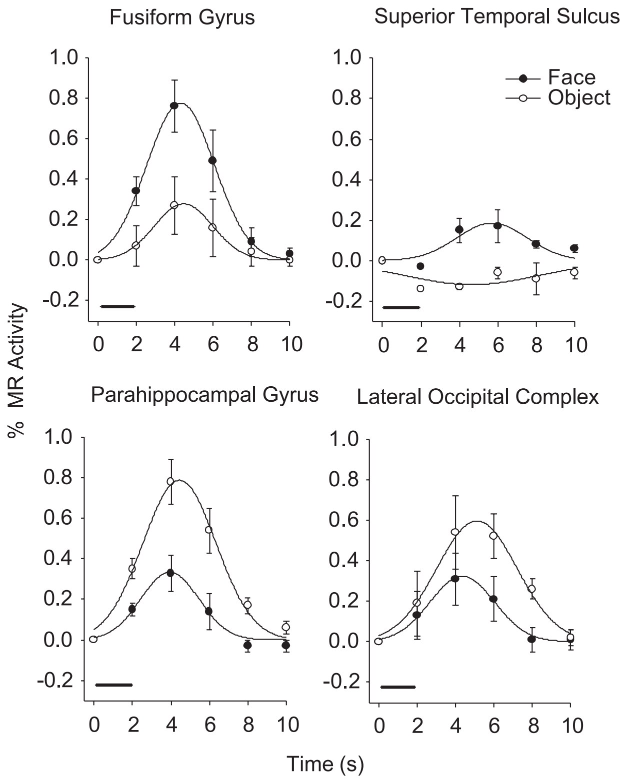

Fig. 3. (a) Face-selective and (b) object-selective areas, defined using the blocked design, also show selective activation in an event-related paradigm. The data represent the MR activity averaged across subjects for single presentations of faces or objects. The horizontal bar represents the duration of the presentation. Error bars represent ±1 SE.

Event-related responses to faces and objects

The average time-courses of MR activity following single presentations of a face or an object are shown in Fig. 3. In the face-selective areas, there was an increase in MR activity following the presentation of a face that reached a maximum after 4–6 s (fusiform gyrus, mean amplitude ± SEM: 0.77 ± 0.03, $F = 1.4$, $P < 0.00001$; superior temporal sulcus, mean amplitude ± SEM: 0.18 ± 0.04, $F = 2.9$, $P = 0.07$). An increase in MR activity was also detected following the presentation of a face in the object-selective region of the parahippocampal gyrus (mean amplitude ± SEM: 0.33 ± 0.03, $F = 7.9$, $P < 0.0005$), but not in the lateral occipital complex (mean amplitude ± SEM: 0.32 ± 0.02, $F = 1.9$, $P = 0.13$).

The presentation of a single object caused a significant increase in MR activity in the object-selective regions of the parahippocampal gyrus (mean amplitude ± SEM: 0.79 ± 0.04, $F = 20.4$, $P < 0.000001$) and the lateral occipital complex (mean amplitude ± SEM: 0.60 ± 0.03, $F = 4.2$, $P < 0.01$). An increase in MR activity also followed the presentation of an object in the face-selective region of the fusiform gyrus (mean amplitude ± SEM: 0.27 ± 0.01, $F = 2.3$, $P = 0.07$), but not in the superior temporal sulcus (mean amplitude ± SEM: −0.12 ± 0.04, $F = 0.95$, $P = 0.49$).

Finally, to determine whether there was a significant difference in activity following the presentation of faces or objects, we performed a paired t test on the integrated MR signal from 0 to 6 s after image onset. A significantly larger response was apparent following the presentation of a face compared to an object in the fusiform gyrus ($t = 8.8$, $P < 0.0001$) and in the superior temporal sulcus ($t = 2.7$, $P < 0.05$). In contrast, both the parahippocampal gyrus ($t = 6.3$, $P < 0.001$) and the lateral occipital complex ($t = 4.4$, $P < 0.01$) were more active for the single presentation of an object compared to a face.

Event-related responses to Mooney images

Next, we monitored activity in the face-selective and object-selective areas when the naïve subjects viewed Mooney images. Consistent with previous studies (George et al., 1999; Tong et al., 1998), subjects perceived upright Mooney images as faces (68.4 ± 9.3%) more often than inverted Mooney images (25.0 ± 9.6%). Fig. 4 shows the difference in MR activity that occurred when a Mooney image was perceived as a face compared to when no-face was reported. In this analysis, Mooney images were grouped according to how they were perceived (*face*, *no-face*) rather than by orientation.

We found that the response of the face-selective region of the fusiform gyrus was significantly greater when a Mooney image was perceived as a face compared to when no-face was reported ($F = 4.5$, $P < 0.005$). However, in the face-selective region of the superior temporal sulcus, there was no difference in MR activity between face and no-face Mooney events ($F = 0.81$, $P = 0.55$). Similarly, there was no difference in MR activity between events when a face was perceived and those when a face was not perceived in object-selective voxels of the parahippocampal gyrus ($F = 0.62$, $P = 0.68$). In the lateral occipital complex, more activity was apparent when no-face was reported, but this difference was not statistically significant ($F = 0.79$, $P = 0.56$).

One possible reason why some regions of interest failed to show a difference in activity for Mooney images perceived as faces could

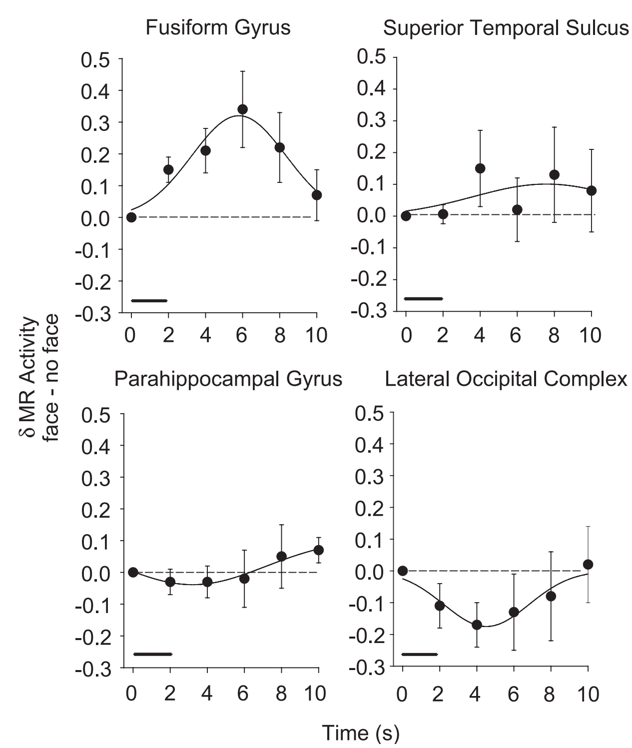

Fig. 4. The difference in activity for events when a Mooney image was perceived as a face compared to when no-face was reported in (a) face-selective and (b) object-selective areas. The data are averaged across subjects for single presentations of Mooney images. The horizontal bar represents the duration of the presentation. Error bars represent ±1 SE.

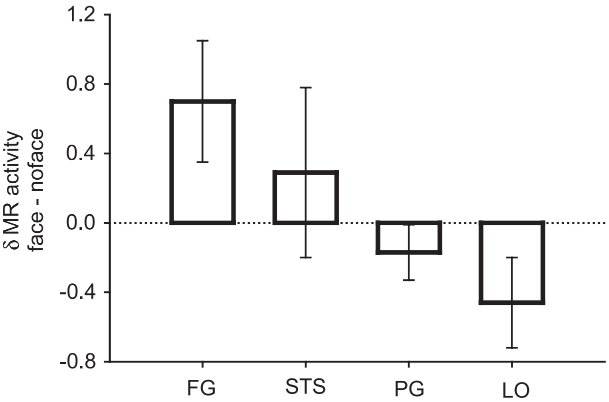

Fig. 5. The difference in integrated MR activity between "face perceived" and "face not perceived" trials in the fusiform gyrus (FG), superior temporal sulcus (STS), parahippocampal gyrus (PG), and the lateral occipital complex (LO). The data are averaged across subjects. Error bars represent ±1 SE.

be that the activation to these impoverished images was too weak to allow a good comparison. To test this possibility, we compared the MR activity following the presentation of a photograph of a face with that caused by the presentation of a Mooney image regardless of whether it was perceived as a face or not. The results show that the integrated MR response to Mooney images (FG: 1.84 ± 0.61, STS: 0.94 ± 0.79, PG: 1.93 ± 0.16, LO: 1.78 ± 0.55) was larger than the response elicited by photographs of faces (FG: 1.84 ± 0.61, STS: 0.30 ± 0.21, PG: 0.67 ± 0.27, LO: 0.65 ± 0.39). Although this difference in MR response only reached significance in the lateral occipital complex ($P < 0.001$), these results demonstrate that the failure to show a difference in activity between Mooney images perceived as faces compared to those that were not perceived as faces does not result from a lower activation to these types of impoverished images.

Although these results appear to show that a face-selective region in the fusiform gyrus is tightly linked to the perception of a face, more Mooney images were perceived as faces in the upright configuration. It is possible, therefore, that the main difference between the two events is the difference in orientation of the images, rather than the difference in perception. To control for this possibility, we reanalysed only those events in which an upright Mooney image was presented. The difference in integrated MR activity between "face perceived" and "face not perceived" trials during these presentations is plotted in Fig. 5. Consistent with the previous analysis, a significant difference in MR response was apparent in the fusiform gyrus ($t = 2.20$, $P < 0.05$), but not in the superior temporal sulcus ($t = 0.58$, $P = 0.60$), parahippocampal gyrus ($t = 1.07$, $P = 0.32$) or lateral occipital complex ($t = 1.78$, $P = 0.12$).

Discussion

We used ambiguous Mooney images to determine neural responses associated with perceiving a face, independent of low-level stimulus features. First, we localised face- and object-selective areas using a blocked design. Consistent with previous studies, we located regions in the fusiform gyrus (Allison et al., 1994; Haxby et al., 1994; Kanwisher et al., 1997; Sergent et al., 1992) and the superior temporal sulcus (Haxby et al., 2000) that were more active for photographs of faces than for other complex objects. Whereas, regions in the parahippocampal gyrus (Epstein and Kanwisher, 1998) and the lateral occipital lobe (Malach et al., 1995) were more active for objects than faces. The blocked design provided a good signal-to-noise ratio and a reliable method to localise face- and object-selective areas. However, for subsequent parts of this study, it was important to determine whether these areas could also be activated by single presentations of faces and objects. Using an event-related design, we confirmed that face-and object-selective areas respond selectively to single presentations of faces and objects (see Fig. 3).

The selectivity for faces and objects does not, in itself, demonstrate that the neural representation associated with the perception of a face or an object is specific to these visual areas. This is because the neural response to a face was not restricted to face-selective areas and the response to an object was not restricted to object-selective areas. Indeed, the response to single presentations of faces was larger in the object-selective region of the parahippocampal gyrus and lateral occipital complex than in the face-selective region of the superior temporal sulcus. Thus, it is possible that an explicit representation of a face is not localised to a particular area in visual cortex, but is based on a distributed and overlapping pattern of neural response across a large network of visual cortex (Haxby et al., 2001; Ishai et al., 1999).

To explore how faces are represented in visual cortex, neural responses were monitored in different face- and object-selective regions while subjects viewed Mooney images. We found that face-selective regions in the fusiform gyrus were more active when a Mooney image was perceived as a face compared to when no-face was reported. This result concurs with previous reports showing an enhanced neural response in the inferior temporal cortex to similar impoverished images when they are perceived as faces (Dolan et al., 1997; George et al., 1999; Jeffreys, 1989; Kanwisher et al., 1998; Perrett et al., 1984; Tovee et al., 1996). Similar evidence for the involvement of the inferior temporal lobe in facial awareness has been shown when viewing ambiguous figures (Andrews et al., 2000; Hasson et al., 2001; Kleinschmidt et al., 1998; Sheinberg and Logothetis, 1997; Tong et al., 1998), during mental imagery (Wojciulik et al., 1998), and following selective attention to faces (O'Craven et al., 1999).

In contrast to the fusiform gyrus, the face-selective region of the superior temporal sulcus did not show a difference in neural response for face versus no-face Mooney events. This finding is similar to a recent report, in which we showed that neural responses in the fusiform gyrus, but not the superior temporal sulcus, were statistically predictive of whether a *vase-to-face* or a *face-to-vase* transition had been perceived when subjects viewed Rubin's vase–face stimulus (Andrews et al., 2000). One possible explanation for this difference in response across different face-selective areas is that the fusiform gyrus is involved in forming a perceptual representation of the face, whereas the superior temporal sulcus is concerned with other aspects of face perception (Allison et al., 2000; Haxby et al., 2000; see also Bruce and Young, 1986). Consistent with this idea, eye gaze (Hoffman and Haxby, 2000; Perrett et al., 1985), facial expression (Hasselmo et al., 1989; Perrett and Mistlin, 1990), and lip movement (Calvert et al., 1997) have all been shown to activate the superior temporal sulcus. Moreover, lesions to the superior temporal sulcus affect the emotional associations related to the seeing faces, but do not impair face recognition (Capgras and Reboul-Lauchaux, 1923; Ellis and Lewis, 2001). These findings may also account for why a selective response to photographs of faces with neutral expressions compared to objects was only apparent in the superior temporal sulcus for only five of the nine subjects in this study.

Object-selective regions in the parahippocampal gyrus and lateral occipital lobe also failed to show an increased activation when Mooney images were perceived as a face compared to when they were perceived as a collection of unconnected shapes. This result was somewhat surprising, given that the object-selective areas did show an increased response to photographs of faces compared to a grey screen with the same average luminance. One reason for the inability to discriminate between the different perceptions elicited by Mooney images could be that there is a lower activation to these impoverished images. However, we show that the response to Mooney images was often larger than to photographs of faces. The implication is that the responses to photographs of faces in object-selective areas result from lower level image features common to faces and objects, but that these responses are not involved in forming an explicit representation of a face (although see Haxby et al., 2001). Rather, a number of studies have reported a direct correlation between the neural responses in these regions and the perception and recognition of non-face objects (Grill-Spector et al., 2000; James et al., 2000; Moore and Engel, 2001; Tong et al., 1998).

In conclusion, these results suggest that a region within the fusiform gyrus is specialised for the perception of faces (see also, Spiridon and Kanwisher, 2002). However, there are a number of caveats: First, the awareness of other aspects of facial processing, particularly those involved in social cognition, is likely to embrace other visual areas (Allison et al., 2000; Haxby et al., 2000). Second, it is possible that this area is not only specific to processing faces, but is also selective for a broader range of specialised object categories (Tarr and Gauthier, 2000). Third, the lack of a distributed representation for the global awareness of faces between visual areas does not imply that such a distributed representation is not implemented within the fusiform gyrus (cf. Young and Yamane, 1992). Finally, our analysis was restricted to areas in visual cortex that respond selectively to photographs of faces compared to photographs of objects. Although other visual areas do not show selective responses to faces or objects, this does not imply that they are not involved in forming a distributed, albeit non-selective, representation of faces.

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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., 2001. Binocular rivalry and visual awareness. Trends Cogn. Sci. 5, 407–409.

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.

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

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.

Cohen, J., Tong, F., 2001. The face of controversy. Science 293, 2405–2407.

Dolan, R.J., Fink, G.R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R.S.J., Friston, K.J., 1997. How the brain learns to see objects and faces in an impoverished context. Nature 389, 596–599.

Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science 293, 2470–2473.

Edelman, S., 1997. Computational theories of object recognition. Trends Cogn. Sci. 1, 296–304.

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.

Farah, M.J., 1992. Agnosia. Curr. Biol. 2, 162–164.

Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved assessment of significant activation in functional magnetic resonance imaging (FMRI): use of a cluster-size threshold. Magn. Reson. Med. 33, 636–647.

Fried, I., MacDonald, K.A., Wilson, C., 1997. Single neuron activity in human hippocampus an amygdala during recognition of faces and objects. Neuron 18, 753–765.

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.

George, N., Dolan, R.J., Fink, G.R., Baylis, G.C., Russell, C., Driver, J., 1999. Contrast polarity and face recognition in the human fusiform gyrus. Nat. Neurosci. 2, 574–580.

Grill-Spector, K., Kushnir, T., Hendler, T., Malach, R., 2000. The dynamics of object-selective activation correlate with recognition performance in humans. Nat. Neurosci. 3, 837–843.

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., 1989. The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of monkey. Behav. Brain Res. 32, 203–208.

Hasson, U., Hendler, T., Bashat, D.B., Malach, R., 2001. Vase or face? A neural correlate of shape-selective grouping processes in the human brain. J. Cogn. Neurosci. 13, 744–753.

Haxby, J.V., Horwitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P., Grady, C.L., 1994. The functional organisation of the human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J. Neurosci. 14, 6336–6353.

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.

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.

James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., Goodale, M.A., 2000. The effects of visual object priming on brain activation before and after recognition. Curr. Biol. 10, 1017–1024.

Jeffreys, D.A., 1989. A face-responsive potential recorded from the human scalp. Exp. Brain Res. 78, 193–202.

Jenkinson, M., Bannister, P., Brady, M., Smith, S.M., 2000. Improved optimisation for the robust and accurate linear registration and motion correction of brain images. NeuroImage 17, 825–841.

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.

Kanwisher, N., Tong, F., Nakayama, K., 1998. The effect of face inversion on the human fusiform face area. Cognition 68, B1–B11.

Kleinschmidt, A., Buchel, C., Zeki, S., Frackowiak, R.S., 1998. Human brain activity during spontaneously reversing perception of ambiguous figures. Proc. R. Soc. Lond., B Biol. Sci. 265, 2427.

Komatsu, H., Ideura, Y., 1993. Relationships between color, shape, and pattern selectivities of neurons in the inferior temporal cortex of the monkey. J. Neurophysiol. 70, 677–694.

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.

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. W.H. Freeman, New York.

McNeil, J.E., Warrington, E.K., 1993. Prosopagnosia: a face-specific disorder. Q. J. Exp. Psychol. 45A, 1–10.

Milner, A.D., Goodale, M.A., 1995. The Visual Brain in Action. OUP, New York.

Mooney, C.M., 1957. Age in the development of closure ability in children. Can. J. Psychol. 11, 219–226.

Moore, C., Engel, S.A., 2001. Neural response to perception of volume in the lateral occipital complex. Neuron 29, 277–286.

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.

O'Craven, K.M., Downing, P.E., Kanwisher, N., 1999. FMRI evidence for objects as the units of attentional selection. Nature 401, 584–587.

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

Perrett, D.I., Smith, P.A., Potter, D.D., Mistlin, A.J., Head, A.S., Milner A.D., Jeeves, M.A., 1984. Neurones responsive to faces in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception. Hum. Neurobiol. 3, 197–208.

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. Proc. R. Soc. Lond., B 223, 293–317.

Polk, T.A., Farah, M.J., 1998. The neural development and organization of letter recognition: evidence from functional neuroimaging, computational modeling and behavioral studies. Proc. Natl. Acad. Sci. U. S. A. 95, 847–852.

Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing: a positron emission tomography study. Brain 115, 15–36.

Sheinberg, D.L., Logothetis, N.K., 1997. The role of temporal cortical areas in perceptual organization. Proc. Natl. Acad. Sci. U. S. A. 94, 3408–3416.

Smith, S., 2000. Robust automated brain extraction. Sixth Int. Conf. on Functional Mapping of the Human Brain, p. 610.

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., 1997. Mechanisms of visual object recognition: monkey and human studies. Curr. Opin. Neurobiol. 7, 523–529.

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

Tong, F., Nakayama, K., Vaughan, J., Kanwisher, N., 1998. Binocular rivalry and visual awareness in human extrastriate cortex. Neuron 21, 753–759.

Tovee, M.J., Rolls, E.T., Ramachandran, V.S., 1996. Visual learning in neurons of the primate temporal visual cortex. NeuroReport 7, 2757–2760.

Ullman, S., 1996. High level vision. MIT Press, Cambridge, MA.

Ungerleider, L.G., Mishkin, M., 1982. Two cortical visual systems. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J. (Eds.), Analysis of Visual Behaviour. MIT, Cambridge, MA, pp. 549–580.

Wojciulik, E., Kanwisher, N., Driver, J., 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: FMRI study. J. Neurophysiol. 79, 1574–1578.

Woolrich, M., Ripley, B., Brady, J., Smith, S., 2000. Nonparametric estimation of temporal autocorrelation in fMRI. Sixth Int. Conf. on Functional Mapping of the Human Brain, p. 610.

Young, M.P., Yamane, S., 1992. Sparse population coding of faces in inferotemporal cortex. Science 256, 1327–1331.