

Functional delineation of the human occipito-temporal areas related to face and scene processing

A PET study

K. Nakamura,¹ R. Kawashima,² N. Sato,¹ A. Nakamura,³ M. Sugiura,² T. Kato,³ K. Hatano,³ K. Ito,³ H. Fukuda,² T. Schormann⁴ and K. Zilles^{4,5}

¹Department of Behavioral and Brain Sciences, Primate Research Institute, Kyoto University, Inuyama, ²Department of Nuclear Medicine and Radiology, IDAC, Tohoku University, Sendai, ³National Institute for Longevity Sciences, Obu, Japan, ⁴C. O. Vogt Institute of Brain Research, University of Düsseldorf, Düsseldorf and ⁵Institute of Medicine, Research Center, Jülich, Germany

Correspondence to: Dr Katsuki Nakamura, Department of Behavioral and Brain Sciences, Primate Research Institute, Kyoto University, Kanrin, Inuyama, Aichi 484-8506, Japan
E-mail: knakamur@pri.kyoto-u.ac.jp

Summary

By measuring regional cerebral blood flow using PET, we delineated the roles of the occipito-temporal regions activated by faces and scenes. We asked right-handed normal subjects to perform three tasks using facial images as visual stimuli: in the face familiar/unfamiliar discrimination (FF) task, they discriminated the faces of their friends and associates from unfamiliar ones; in the face direction discrimination (FD) task, they discriminated the direction of each unfamiliar face; in the dot location discrimination (DL) task, they discriminated the location of a red dot on a scrambled face. The activity in each task was compared with that in the control fixation (CF) task, in which they fixated on the centre of a display without visual stimuli. The DL task activated the occipital cortices and posterior fusiform gyri bilaterally. During the FD task, the activation extended anteriorly in the right fusiform gyrus and laterally to the right inferior

temporal cortex. The FF task further activated the right temporal pole. To examine whether the activation due to faces was face-specific, we used a scene familiar/unfamiliar discrimination (SF) task, in which the subjects discriminated familiar scenes from unfamiliar ones. Our results suggest that (i) the occipital cortices and posterior fusiform gyri non-selectively respond to faces, scrambled faces and scenes, and are involved mainly in the extraction of physical features of complex visual images; (ii) the right inferior temporal/fusiform gyrus responds selectively to faces but not to non-face stimuli and is involved in the visual processing related to face perception, whereas the bilateral parahippocampal gyri and parieto-occipital junctions respond selectively to scenes and are involved in processing related to scene perception; and (iii) the right temporal pole is activated during the discrimination of familiar faces and scenes from unfamiliar ones, and is probably involved in the recognition of familiar objects.

Keywords: brain; visual; recognition; temporal pole; familiar

Abbreviations: CF = control fixation task; DL = dot location discrimination task; FD = face direction discrimination task; FF = face familiar/unfamiliar discrimination task; rCBF = regional cerebral blood flow; SF = scene familiar/unfamiliar discrimination task

Introduction

It has been suggested that the human brain contains a specialized system for face recognition, and damage to the system produces the inability to recognize faces (prosopagnosia or face agnosia) despite intact intellectual functioning and apparently intact visual recognition of other stimuli (e.g. Meadows, 1974; Damasio *et al.*, 1982;

Shuttleworth *et al.*, 1982; Damasio *et al.*, 1990; Farah, 1990). The neuropathology of prosopagnosia has received much attention. Focal damage to various regions of the occipito-temporal areas can impair the ability to recognize faces (Damasio *et al.*, 1990; Farah, 1990; De Renzi *et al.*, 1991; Farah *et al.*, 1995). The lesion site and the nature of the

deficit vary from patient to patient. Some patients cannot discriminate faces from non-face objects, but others can do so but may not recognize familiar faces. Recent brain imaging studies have reported that face stimuli can activate the right fusiform gyrus, suggesting its involvement in face perception (Sergent *et al.*, 1992; Haxby *et al.*, 1994; Puce *et al.*, 1995; Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997; Farah and Aguirre, 1999; Haxby *et al.*, 1999). However, in our social lives the visual recognition of familiar faces based on memory, such as the recognition of the faces of our parents and friends, etc., is important. Which brain regions are involved in the visual recognition of familiar faces remains under debate.

The objective of the present study was to determine the brain regions associated with the recognition of familiar faces by measuring regional cerebral blood flow (rCBF) using PET while normal subjects performed visual discrimination tasks. We addressed the following two questions: (i) which brain regions are associated with the recognition of familiar faces and which with the perception of faces; and (ii) is the activity of each brain region face-specific? To answer the first question, we used three face tasks which required different levels of face processing and determined the brain regions activated by the recognition of familiar faces but not by the perception of unfamiliar faces, as well as those activated by faces but not by non-face stimuli. To answer the second question, we used a scene discrimination task and compared the activity between face and scene tasks, as faces and scenes are reportedly processed differently (Aguirre *et al.*, 1996; Aguirre and D'Esposito, 1997; Epstein and Kanwisher, 1998; Maguire *et al.*, 1998; Haxby *et al.*, 1999).

Methods

Subjects

Seven right-handed normal male volunteers (aged 23–29 years) participated in this study. Written informed consent was obtained from each subject in accordance with guidelines approved by the ethics committee of National Institute for Longevity Sciences and the Declaration of Helsinki (1991). All of the subjects were healthy, with no history of psychiatric or neurological illness, and were not on any medication.

Behavioural tasks

The stimuli were digitized coloured images of faces presented at various orientations and scrambled images of the faces with a red dot near one of the four corners, and coloured images of a scene (Fig. 1). To delineate the roles of the regions activated by faces, we used three face tasks which required different levels of processing of facial images. In the face familiar/unfamiliar discrimination (FF) task, the subjects were required to discriminate the faces of their friends and associates from unfamiliar faces. All of the familiar and unfamiliar faces were presented at various orientations. Each subject was instructed to click a computer

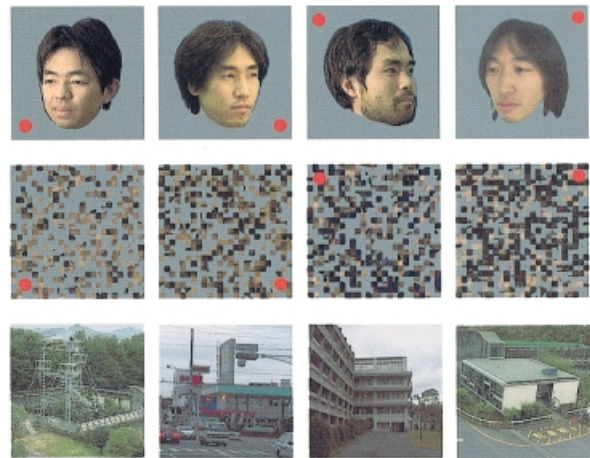


Fig. 1 Examples of stimuli. The stimuli were digitized coloured images of a face presented at various orientations (*top*), scrambled images of the same face (*middle*) with a red dot near one of the four corners, and coloured images of a scene (*bottom*).

mouse during visual stimulation when the face was familiar to him in the FF task. In the face direction discrimination (FD) task, the subjects were asked to discriminate the direction of each face and to click the mouse when the face was facing right (or left). All of the faces were unfamiliar to the subjects. In the dot location discrimination (DL) task, they discriminated the location of a red dot on a scrambled face image and clicked the mouse when the red dot was located to the right (or left). We used scrambled images of the same faces to control for luminance, colour and local features (Allison *et al.*, 1994a, b). The red dot had no significance in the FF and FD tasks. We assumed the following cognitive processes: complex visual stimulation in all three tasks; perception of unfamiliar faces in the FD and FF tasks; recognition of familiar faces and their discrimination from unfamiliar ones only in the FF task. In the FF, FD and DL tasks, 89% (75–98%), 91% (78–100%) and 99% (98–100%) of the responses were correct, respectively. The DL test tended to be easier than the FF test (Wilcoxon matched-pairs signed-ranks test, $P = 0.03$). There were no significant differences between the FF and FD tests or between the FD and DL tests. To examine whether the activation due to familiar faces was face-specific, we used an analogous task in which the subjects viewed familiar and unfamiliar scenes. In this scene familiar/unfamiliar discrimination (SF) task, the subjects discriminated familiar scenes, e.g. their university or town railway station, from unfamiliar scenes. In the SF task, 70% (56–90%) of the responses were correct, and there were no significant differences between the percentages correct in the SF and FF tasks (Wilcoxon test, $P > 0.05$). In all tasks, images were presented for 1.0 s on a face-mounted display at 1.0 s intervals. Each image had 200×200 pixels and subtended horizontal and vertical visual angles of 10° . The activity in each task was compared with that in the control fixation (CF) task, in which the subjects were instructed to fixate on the centre of a display without visual stimuli. Each

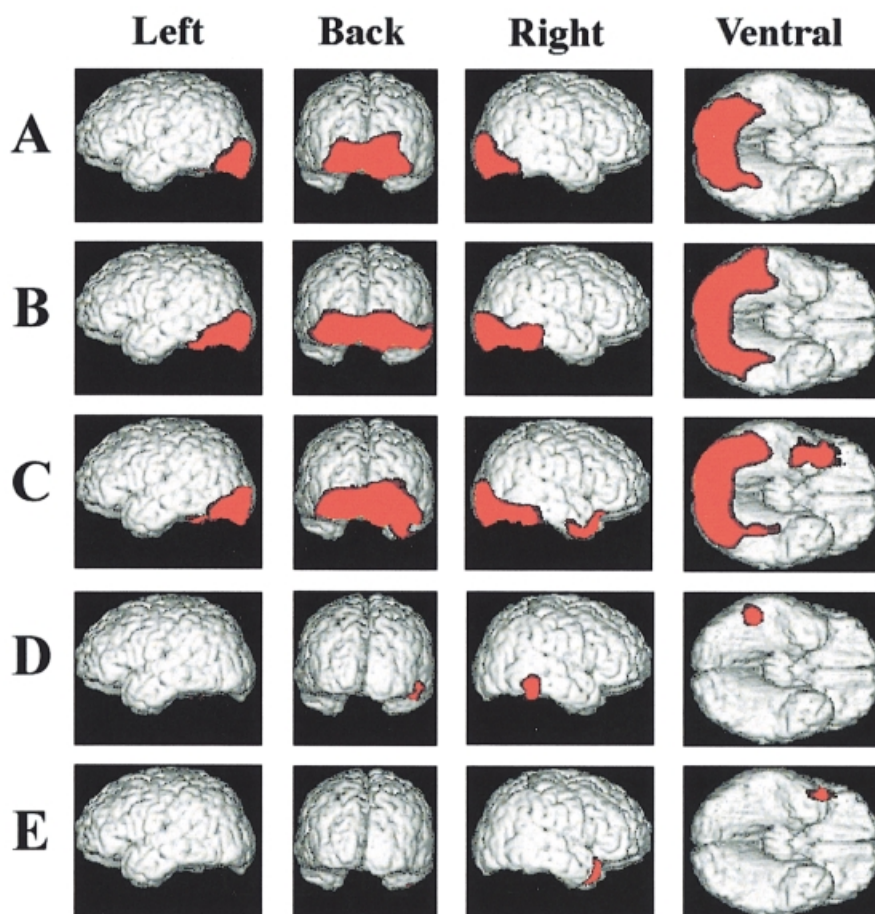


Fig. 2 Regions of increased rCBF in the face tasks on 3D-reconstructed standard brains. Only regions of significantly increased rCBF after correction for multiple comparisons are shown (red). Regions activated during the dot location discrimination (DL, **A**), face direction discrimination (FD, **B**) and face familiar/unfamiliar discrimination (FF, **C**) compared with the control fixation (CF) task, and those revealed by conjunction of (FD–DL) with (FD–CF) (**D**) and by conjunction of (FF–CF) with (FF–FD) (**E**). Back = back view; Left = left view; Right = right view; Ventral = ventral view.

task lasted 1.5 min. Only the CF task was administered twice, i.e. at the beginning and at the end of the experiment for each subject. The order of performing the three face tasks varied, and the responses to the right and left in the FD and DL tasks were counterbalanced among subjects. The SF task was introduced randomly into the task sequence. Each face or scene was presented only once, to avoid the effect of repetition of the same image on neural activity. The subjects were instructed to focus at the centre of the display throughout the experiments. During PET scans, horizontal and vertical monopolar electro-oculograms were recorded. The signals from the surface electrodes, placed in the vicinity of the outer and infraorbital parts of each eye, were fed into an amplifier. There were no significant differences in the numbers of saccadic eye movements among the tasks.

Data acquisition and analysis

Each subject was positioned in a PET scanner (Siemens/CTI ECAT EXACT HR) (Wienhard *et al.*, 1994). The emission

scan was started immediately after the administration of bolus injection of approximately 15 mCi (555 MBq) $H_2^{15}O$, using the three dimensional (3D) collection mode. All injections were performed in a single scanning session for each subject. Each PET image was anatomically normalized using Automated Image Registration (Woods *et al.*, 1998) and Elastic Transformation (Schormann *et al.*, 1996); each subject's MRI was normalized to the standard brain MRI of the Human Brain Atlas (Roland *et al.*, 1994) by affine transformation of Automated Image Registration followed by application of the 3D-deformation field of elastic transformation. These parameters were used subsequently to transform each subject's PET image and MRI into the standard brain anatomy.

Statistical parametric mapping software (SPM96, Wellcome Department of Cognitive Neurology, London) (Friston *et al.*, 1995) was used for smoothing and statistical analysis. A 3D 16 mm Gaussian filter was used. Significant thresholds were set at $P < 0.05$, corrected for multiple comparisons for both the height and extent of activation. The

Table 1 Brain regions showing statistically significant activation in the face tasks

Region	Cluster	DL-CF	FD-CF	FF-CF	(FD-CF) with (FD-DL)	(FF-CF) with (FF-FD)
R LG	A (C)	12, -77, -13 (6.81)	14, -81, -14 (5.88)	12, -78, -14 (6.59)		
L LG	A	(5.13)	-8, -78, -11 (5.75)	-12, -78, -18		
R LOC	A (A)	15, -94, 1 (6.77)	13, -94, -1 (5.91)	15, -92, 0 (6.51)		
R FG	A (D)	28, -65, -16 (6.75)	30, -64, -16 (7.07)	34, -62, -19 (6.67)		
L FG	A (F)		-36, -43, -18 (4.36)			
L OCT	A		-36, -79, -20 (5.28)	-37, -81, -19 (6.13)		
R IT/FG	D (E)		47, -49, -21 (6.42)		45, -49, -19 (6.37)	
L IT/FG	A		-41, -66, -15 (5.44)			
R PR	D (I)			29, -6, -29 (4.36)	28, -7, -29 (4.31)	
R TP	C (J)			34, 23, -27 (5.15)		37, 23, -27 (4.52)

The table lists the locations of peak activation in at least one of the face tasks in comparison with the CF task that were significant after correction for multiple comparisons. Coordinates (x, y, z) and Z scores (in parentheses) are shown. In the column headed Region, the first character (R or L) indicates the right or left hemisphere. Brain regions: FG = fusiform gyrus; LG = lingual gyrus; LOC = lateral occipital cortex; IT/FG = inferior temporal gyrus/fusiform gyrus; OCT = occipito-temporal junction; PR = perirhinal cortex; TP = temporal pole. Characters in the column headed Cluster represent the name of the clusters defined by the cluster analysis shown in Fig. 4. Characters in parentheses correspond to the labels of the panels of Fig. 5. CF = control fixation task; DL = dot location discrimination task; FD = face direction discrimination task; FF = face familiar/unfamiliar discrimination task.

activated areas were localized anatomically in relation to the mean reformatted MRI of the seven subjects. To extract the activation concerning each cognitive process and to eliminate the confounding effects of deactivation or suppression, we used conjunction analysis (Friston, 1997). Significant thresholds for the conjunction analysis were set at $P < 0.05$ (corrected). The conjunction analysis was applied by masking, whereby the second subtraction was tested only in pixels that reached significance ($P < 0.01$) in both the first and the second subtraction.

To examine the similarity of the response profiles among the activated foci, we calculated Pearson's correlation coefficient for the adjusted rCBF value in each task among the foci and made a correlation matrix representing the distances among the foci. Then, non-metric multidimensional scaling (Kruskal and Wish, 1978) and cluster analysis were applied to the data. In the multidimensional scaling, configurations in one to four dimensions were produced so that analyses in different dimensions could be compared in a scree test (Cattell, 1966; Kruskal and Wish, 1978). The scree test can reveal the extent to which a two-dimensional solution explains the variability in the data. If there were multiple foci of significant activation in the same anatomical area, data for all of the foci were used in this analysis, so that we could examine whether multiple foci in the same anatomical area showed a similar response profile. In the cluster analysis, we used a complete linkage method using the correlation coefficient.

Results

Regions involved in face discrimination

To delineate the roles of the regions activated by faces, we used three tasks using facial images; the FF, FD and DL tasks. The activity in each task was compared with that in the CF task. Compared with the CF task, the DL task activated the occipital cortices bilaterally, including the lingual and lateral occipital gyri, and the posterior fusiform gyri (Fig. 2A). When the FD task was compared with the CF task, the activated regions extended anteriorly in the fusiform gyri and laterally beyond the occipito-temporal sulcus to the posterior portion of the inferior temporal gyri, in addition to the occipital cortices and posterior fusiform gyri (Fig. 2B). The response was more prominent on the right side than on the left. The FF task further activated the right temporal pole and perirhinal cortex (Fig. 2C).

To elucidate the functional characteristic of each region, direct comparisons among face tasks were performed (see Data acquisition and analysis). The brain regions more active in the FD task than in the DL or CF task, revealed by conjunction of (FD-DL) with (FD-CF), were the right inferior temporal and fusiform gyri (Fig. 2D). The activation was observed in the right inferior temporal and fusiform gyri, and the peak location was near the occipito-temporal sulcus. We refer to the anatomical region of this activation as the right inferior temporal/fusiform gyri. The brain region more active in the FF task than in either the FD or the CF task,

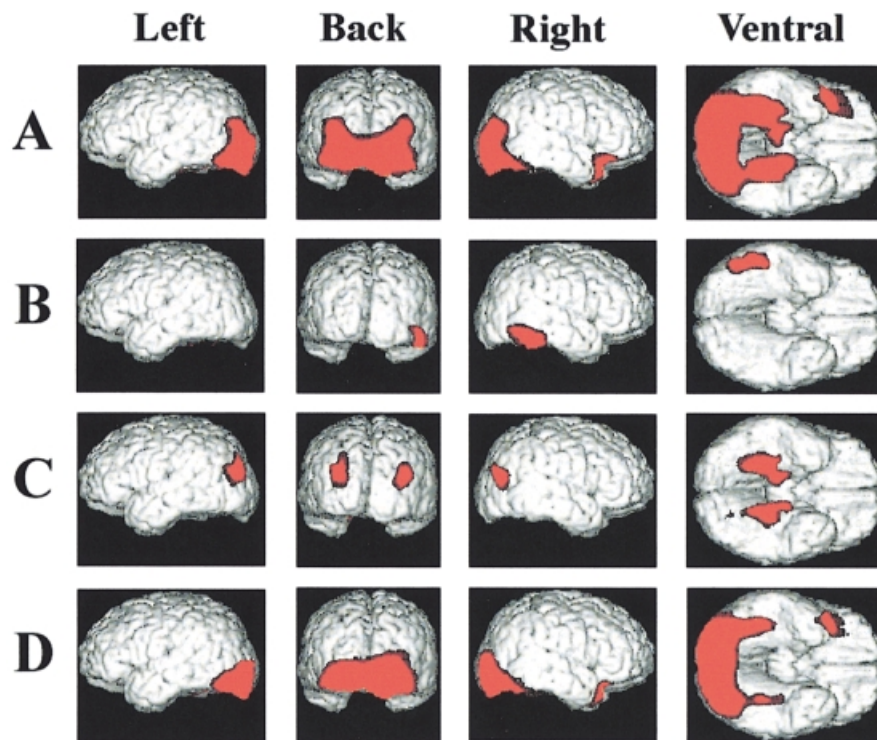


Fig. 3 Regions of increased rCBF in the face and scene tasks on 3D-reconstructed standard brains. Regions activated during the scene familiar/unfamiliar discrimination (SF, **A**) compared with the control fixation (CF) task, and regions more active for faces revealed by conjunction of (FF–SF) with (FF–CF) (**B**), for scenes revealed by conjunction of (SF–FF) with (SF–CF) (**C**), and for both faces and scenes revealed by conjunction of (FF–CF) with (SF–CF) (**D**). For details see legend for Fig. 2.

Table 2 Brain regions showing statistically significant activation in the face and scene tasks

Region	Cluster	SF–CF	(FF–CF) with (FF–SF)	(SF–CF) with (SF–FF)	(FF–CF) with (SF–CF)
R LG	A (C)	12, –79, –14 (6.98)			13, –79, –14 (8.24)
L LG	A	–12, –78, –16 (6.35)			–12, –78, –18 (7.35)
R LOC	A (A)	17, –92, 1 (6.85)			17, –92, 1 (8.11)
R FG	A (D)	29, –62, –15 (6.86)			30, –64, –16 (8.11)
L FG	A (F)				34, –40, –15 (5.05)
R IT/FG	D (E)		43, –52, –19 (5.37)		
R TP	C (J)	32, 30, –22 (5.35)			34, 26, –26 (6.19)
R PHG	A (G)	31, –42, –18 (6.21)		26, –38, –18 (5.48)	
L PHG	B (H)	–23, –40, –11 (5.27)		–22, –39, –9 (5.02)	
L PO	A (B)	–31, –85, 2 (5.43)		–30, –81, 8 (4.66)	

The table lists the locations of peak activation in the scene task in comparison with the CF (control fixation) task or in the conjunction analyses that were significant after correction for multiple comparisons. Brain regions: PHG = parahippocampal gyrus; PO = parieto-occipital junction. CF = control fixation task; SF = scene familiar/unfamiliar discrimination task. For details see legend to Table 1.

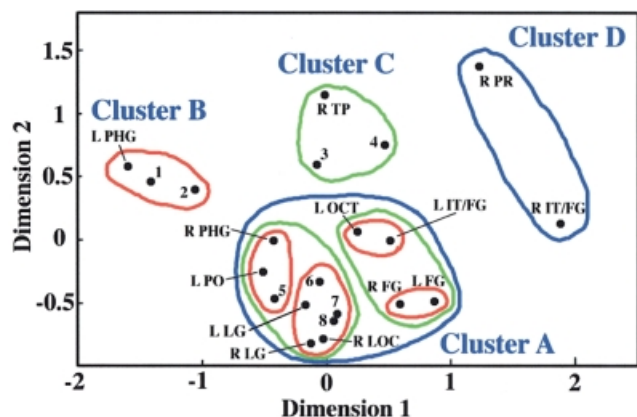


Fig. 4 Diagram of the numerical model of the response profile of all of the activated foci by multidimensional scaling and cluster analysis. Foci showing a similar response pattern are close together. A positive value of Dimension 1 represents greater activation by faces than by scenes and a greater value of Dimension 2 represents greater activation by faces and/or scenes than by scrambled images. This two-dimensional solution explains 98.5% of the variability in the data. Enclosures are clusters identified by the cluster analysis. The colours indicate different significance levels of correlation: red, $P < 0.01$; green, $P < 0.05$; blue, $P < 0.10$. Numbers indicate foci of the second or third peak of anatomical regions. 1, second peak in L PHG; 2, third peak in L PHG; 3, second peak in R TP; 4, second peak in R PR; 5, second peak in L LG; 6, second peak in L OCT; 7, second peak in R LOC; 8, second peak in R LG. For abbreviations see legends to Tables 1 and 2.

revealed by conjunction of (FF–CF) with (FF–FD), was the right temporal pole (Fig. 2E). These results, together with those of the separate comparisons described above, indicate that the right inferior temporal/fusiform gyrus was activated during the processing of faces, whereas the right temporal pole was activated only during the discrimination of familiar from unfamiliar faces. By contrast, the bilateral occipital cortices and posterior fusiform gyri were activated by any complex visual stimuli, either face stimuli or scrambled face stimuli. All of the peaks of the activation during the face tasks are listed in Table 1.

Comparison of activation between face and scene tasks

To examine whether the activation due to face stimuli was face-specific or not, we used the scene familiar/unfamiliar discrimination (SF) task. The SF task activated the bilateral parahippocampal gyri, the regions along the parieto-occipital sulcus of both sides, the bilateral occipital cortices, the right fusiform gyrus, and the right temporal pole, compared with the CF task (Fig. 3A). Unlike in the face tasks, in this task the activations in the bilateral occipital cortices extended dorsally to the parieto-occipital junctions.

We then compared the activations between the FF and SF tasks to determine which regions were activated to a greater extent by faces and which by scenes. The right inferior

temporal/fusiform gyrus was activated to a greater extent during the FF task (Fig. 3B), revealed by conjunction of (FF–SF) with (FF–CF). On the other hand, the bilateral parahippocampal gyri, parieto-occipital sulci and parieto-occipital junctions were activated to a greater extent during the SF task, revealed by conjunction of (SF–CF) with (SF–FF) (Fig. 3C). The brain regions commonly activated by the FF and SF tasks, revealed by conjunction of (FF–CF) with (SF–CF), were the bilateral occipital cortices and posterior fusiform gyri, and the right temporal pole (Fig. 3D). All of the peaks of activation in the scene task compared with the CF task and in these conjunction analyses are listed in Table 2.

Response profiles in each region

How did each of the activated regions respond during each task, and which of the regions can be considered as responding similarly? Based on changes in the adjusted rCBF among the tasks, the similarity of the response profiles among all of the activated foci was examined using multidimensional scaling and cluster analysis (see Data acquisition and analysis). As shown in the two-dimensional configurations that were derived (Fig. 4), all of the activated foci in any task are classified into four clusters. In the two-dimensional configuration, a positive value of Dimension 1 represents greater activation by faces than by scenes, and a greater value of Dimension 2 represents greater activation by faces and scenes than by scrambled images. Foci in Cluster A responded to scrambled images as well as faces and scenes. Foci in Cluster B responded selectively to scenes, while those in Cluster D responded selectively to faces. The right temporal pole (Cluster C) responded to both faces and scenes, but not to scrambled images. This two-dimensional solution explains 98.5% of the variability in the data.

The bilateral occipital cortices and posterior fusiform gyri (Fig. 5A, C, D and F and Cluster A in Fig. 4) were activated equally by all three face tasks and the scene task. These regions showed non-selective responses to any complex visual stimuli. The right inferior temporal/fusiform gyrus and the right perirhinal cortex (Fig. 5E and I and Cluster D in Fig. 4) were activated to a greater extent during the FD and FF tasks, indicating selective responses to faces, but not to scrambled faces or scenes. The left parahippocampal gyrus (Fig. 5H and Cluster B in Fig. 4) were activated to a greater extent during the scene task, indicating a selective response to scenes. The left parieto-occipital junction and the right parahippocampal gyrus (Figs. 5B and G) were classified in Cluster A since they were activated by all tasks, although the rCBF value was highest in the SF task. The right temporal pole (Fig. 5J and Cluster C in Fig. 4) were activated more in the two familiar/unfamiliar discrimination tasks. These results were mostly consistent with and support those of the subtraction and conjunction analyses described above.

Discussion

The face and scene tasks activated various regions in the occipito-temporal areas, from the occipital pole to the

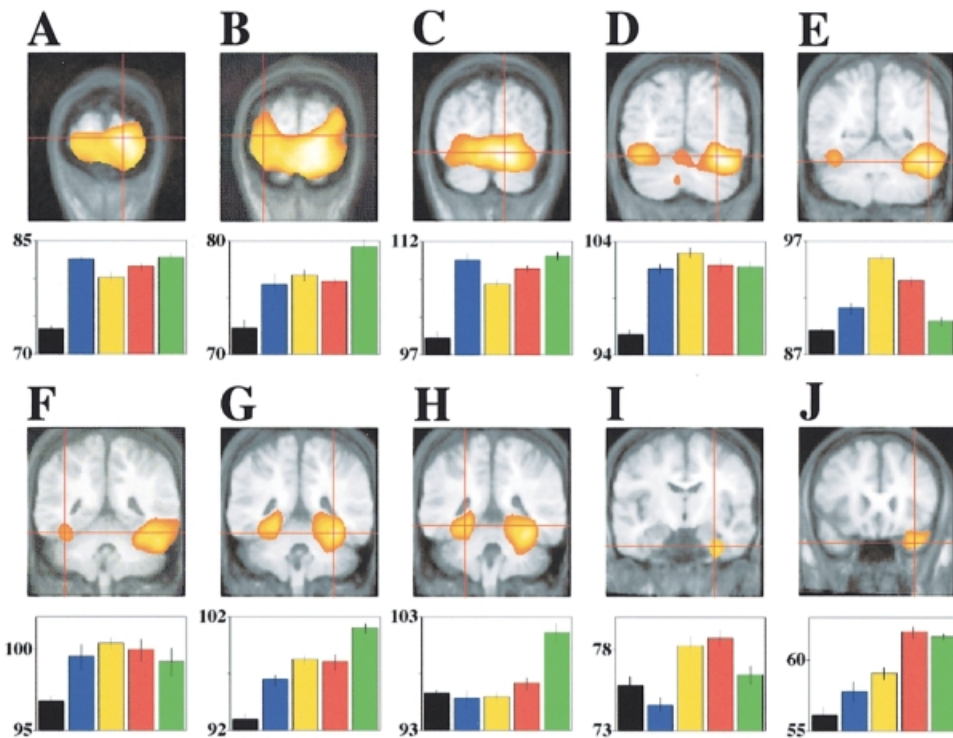


Fig. 5 Examples of regions of increased rCBF and response profiles in each task. Panels are arranged by anatomy (posterior to anterior progression) from **A** to **J**. Activations are shown in the right lateral occipital cortex (**A**), the left parieto-occipital junction (**B**), the right lingual gyrus (**C**), the right posterior fusiform gyrus (**D**), the right inferior temporal/fusiform gyrus (**E**), the left posterior fusiform gyrus (**F**), the right parahippocampal gyrus (**G**), the left parahippocampal gyrus (**H**), the right perirhinal cortex (**I**) and the right temporal pole (**J**). PET images were superimposed on the mean MRI images. Red and yellow indicate regions of significantly increased rCBF after correction for multiple comparisons. The right hemisphere is shown on the right. Each graph shows the adjusted rCBF values (\pm standard error of the mean) in the CF (black), DL (blue), FD (yellow), FF (red) and SF (green) tasks.

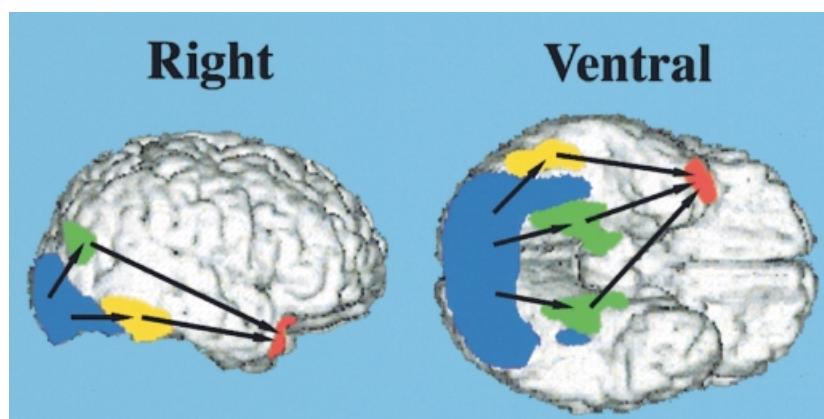


Fig. 6 Schematic diagram of possible information streams in the human brain for the recognition of faces and scenes. Four functionally distinct areas are illustrated on the right and ventral views of 3D brain. The occipital and posterior fusiform regions (blue) extract physical features of complex visual stimuli; the right inferior temporal/fusiform gyri (yellow) process faces; the parahippocampal and parieto-occipital regions (green) process scenes; and the right temporal pole (red) is used for the recognition of familiar faces and scenes. Each arrow represents a stream of information.

temporal pole. The results of our multivariate and comparison analyses indicate that the regions activated by faces and scenes can be placed in four classes. The bilateral occipital cortices and posterior fusiform gyri showed non-selective

responses to complex visual stimuli—faces, scrambled faces or scenes. These areas correspond to the primary and extrastriate visual areas. These regions are considered to be involved mainly in the extraction of the basic physical

features of complex visual stimuli, although some studies have reported selective responses of the occipital areas to faces (e.g. Linkenkaer-Hansen *et al.*, 1998). The right inferior temporal/fusiform gyrus and the right perirhinal cortex were activated to a greater extent by faces, indicating selective responses to faces, but not by scrambled faces or scenes. On the other hand, the bilateral parahippocampal gyri and parieto-occipital regions were activated to a greater extent by scenes. The right temporal pole was active during the discrimination of familiar faces and scenes from unfamiliar ones.

Neuropsychological studies have suggested multiple, distinct neural systems for the processing of different object categories, such as faces (Damasio *et al.*, 1990; De Renzi *et al.*, 1991; Farah *et al.*, 1995), living things (Warrington and Sciallice, 1984; Farah *et al.*, 1991), man-made objects (Warrington and McCarthy, 1994; Moscovitch *et al.*, 1997) and scenes (De Renzi *et al.*, 1977; Whiteley and Warrington, 1978; Hecaen *et al.*, 1980; Habib and Sirigu, 1987; Maguire *et al.*, 1996; McCarthy *et al.*, 1996). Many functional imaging studies (Sergent *et al.*, 1992; Haxby *et al.*, 1994; Puce *et al.*, 1995; Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997; Farah and Aguirre, 1999; Haxby *et al.*, 1999) and recording studies (Allison *et al.*, 1994a, b, 1999) reported that the right inferior temporal/fusiform gyrus responded more to faces than to other complex visual stimuli. We confirmed these results. Our present data demonstrate that the right perirhinal cortex responds selectively to faces. A recent recording study (Allison *et al.*, 1999) also found activation in the right perirhinal cortex by faces. These data suggest that the right perirhinal cortex and the right inferior temporal/fusiform gyri selectively process facial features, leading to the perception of faces. Several neuroimaging studies have reported that the bilateral parahippocampal gyri predominantly process scenes (Aguirre *et al.*, 1996; Aguirre and D'Esposito, 1997; Epstein and Kanwisher, 1998; Maguire *et al.*, 1998; Haxby *et al.*, 1999). The present results further show that the bilateral parieto-occipital junctions and parieto-occipital sulci responded selectively to scenes, suggesting the involvement of temporal and parietal regions in the processing of local environments (Aguirre and D'Esposito, 1997; Maguire *et al.*, 1998; Sato *et al.*, 1999). All of these data confirm the idea that the human brain contains multiple systems for the processing of the different object categories that have been suggested by neuropsychological data.

The major finding of the present study is that the right temporal pole functions in the recognition of familiar faces and their discrimination from unfamiliar faces on the basis of memory. Activation in the temporal pole has been reported in some imaging studies using famous faces as stimuli (Sergent *et al.*, 1992; Damasio *et al.*, 1996; Gorno-Tempini *et al.*, 1998), whereas the right inferior temporal/fusiform gyrus exhibited stable responses to faces (Sergent *et al.*, 1992; Haxby *et al.*, 1994; Puce *et al.*, 1995; Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997; Farah and Aguirre, 1999; Haxby *et al.*, 1999). This inconsistency among previous studies in the observation of activation in the temporal pole

can be explained by the nature of face stimuli, famous (familiar) or unfamiliar. However, the activation of the right temporal pole was not face-specific. The right temporal pole was also activated during the scene task. One explanation is that the right temporal pole is associated with the processing of scenes as well as face recognition. This is unlikely, as no previous studies using scene stimuli have reported activation of the right temporal pole. Another explanation is that the right temporal pole is associated with the recognition of familiar objects regardless of the object categories, at least for faces and scenes. Indeed, damage to the right anterior temporal cortex including the temporal pole can impair the recognition of famous faces, scenes or buildings, suggesting the loss of memory (Ellis *et al.*, 1989; Kapur *et al.*, 1992; Markowitsch *et al.*, 1993; Nakamura and Kubota, 1996; Tranel *et al.*, 1997). The right temporal pole may be the storehouse of personal memory.

The occipito-temporal cortical areas have been implicated in visual processing for object recognition and are well known as the 'ventral visual pathway' (Gross, 1973, 1992; Ungerleider and Mishkin, 1982; Desimone and Ungerleider, 1989; Farah, 1990; Milner and Goodale, 1995). In monkeys, the processing of complex visual stimuli progresses anteriorly along the anterior-posterior axis (Mishkin, 1982; Desimone and Ungerleider, 1989; Gross, 1992; Tanaka, 1996), and the anterior portion of the inferior temporal cortex is more associated with memory functions (Miyashita, 1993; Nakamura and Kubota, 1996; Suzuki, 1996). The present results suggest that visual processing progresses similarly in the human occipito-temporal areas. Figure 6 illustrates the present results schematically. In the human brain, there exists a common neural substrate (the right temporal pole, shown in red) for the visual recognition of familiar objects based on memory, whereas multiple systems, such as the right inferior temporal/fusiform areas and the bilateral parahippocampal and parieto-occipital areas (yellow and green, respectively), are involved in the processing of different object categories, such as faces and scenes. The right temporal pole was also activated during listening to sentences containing information about the subjects' own past (Fink *et al.*, 1996). Thus, the temporal pole seems to function in auditory as well as visual recognition based on memory. The location of peak activation in the right temporal pole of the study of Fink and colleagues (38, 6, -12) (Fink *et al.*, 1996) is dorsal to that of our present study (34, 23, -27). There may be functional subregions in the right temporal pole: its ventral portion for visual processing and its dorsal portion for auditory processing. Further experiments are needed to clarify this issue.

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