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Citation for the published paper:

Elfgren, Christina and van Westen, Danielle and Passant, Ulla
and Larsson, Elna Marie and Mannfolk, Peter and Fransson, Peter
"fMRI activity in the medial temporal lobe during famous face processing"
Neuroimage. 2006 Apr 1;30(2):609-16.
<http://dx.doi.org/10.1016/j.neuroimage.2005.09.060>.

Access to the published version may require journal subscription.

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fMRI activity in the medial temporal lobe during famous face processing

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Abstract

The current event-related fMRI study examined the relative involvement of different parts of the medial temporal lobe (MTL), particularly the contribution of hippocampus and perirhinal cortex, in either intentional or incidental recognition of famous faces in contrast to unfamiliar faces. Our intention was to further explore the controversial contribution of MTL in the processing of semantic memory tasks. Subjects viewed a sequence of famous and unfamiliar faces. Two tasks were used encouraging attention to either fame or gender. In the fame task the subjects were requested to identify the person when seeing his/her face and also to try to generate the name of this person. In the gender task the subjects were asked to conduct a judgement of a person's gender when seeing his/her face. The visual processing was hence directed to gender and thereby expected to diminish attention to semantic information leading only to a "passive" registration of famous and non-familiar faces.

Recognition of famous faces, in both contrasts, produced significant activations in the MTL. First, during the intentional recognition (the person identification task) increased activity was observed in the anterolateral part of left hippocampus, in proximity to amygdala. Second, during the incidental recognition of famous faces (the gender classification task) there was increased activity in the left posterior MTL with focus in the perirhinal cortex. Our results suggest that the hippocampus may be centrally involved in the intentional retrieval of semantic memories while the perirhinal cortex is associated with the incidental recognition of semantic information.

Keywords: Famous faces; un-familiar faces; semantic memory; hippocampal region; perirhinal region; medial temporal lobe

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Introduction

Psychological studies of face processing have suggested a series of steps, involving familiarity discrimination, retrieval of semantic information and finally access to name generation for complete identification of a familiar face (Bruce and Young, 1986). The ability to recognize and identify a familiar person is a fundamental skill of our social interactions. For example, when meeting a person in the street, you might know that the face is familiar without recollecting further information, such as her or his name. Identification of a known face requires reactivation of pre-existing information from long-term memory. The type of information retrieved from long-term memory might consist of personal experiences of events (episodic memories) or facts about the world (semantic memories).

It is well documented from animal, human lesion and neuroimaging studies that the medial temporal lobe (MTL) which includes the hippocampal formation, entorhinal, perirhinal and parahippocampal cortices support long-term memory functions (Squire and Alvarez, 1995, Petersson et al., 1997). However, there are different views on whether parts of the medial temporal lobe play a role in both episodic and semantic memory or only a selective role in episodic memory (Squire and Zola, 1998, Tulving and Markowitsch, 1998, Eichenbaum, 2003). Furthermore, there is an enduring debate regarding the relative involvement of hippocampus, parahippocampal and perirhinal cortices in recognition memory (Duzel et al., 2003). Lesion studies and electrophysiological recordings in non-human primates studies have lead to a proposal that the hippocampal formation is needed if recognition memory requires the retrieval of associative information while the perirhinal cortex seems to be critical in recognition memory to assess the relative familiarity of an object (Brown and Aggleton, 2001). Consistent with this suggestion, Henson et al., using event-related fMRI, reported findings that the anterior MTL (corresponding to perirhinal cortex) was sensitive to whether a visual stimulus was presented in an experimental condition for the first or the second time (New-Old effect) (Henson et al., 2003). Different views have been proposed on whether perirhinal cortex might primarily support memory functions, specifically object memory, or if it might be important for visual discriminations which have a high degree of feature ambiguity (Bussey et al., 2003, Squire et al., 2004). In a recent study on patients with semantic dementia (temporal variant of frontotemporal dementia) it has been suggested that the perirhinal cortex has an important role for semantic memory processing (Davies et al., 2004). This study demonstrated that performance on tests of semantic memory correlated with perirhinal volume.

Functional neuroimaging studies have demonstrated that the recognition of famous faces (actors, media celebrities and politicians), presented without associated semantic information, as compared to unfamiliar faces activates extensive frontal and temporal regions (Sergent et al., 1992, Kapur et al., 1995, Gorno-Tempini et al., 1998, Leveroni et al., 2000, Bernard et al., 2004). The results have, however, been divergent whether recognition of famous faces activates MTL or not. Furthermore, there are inconsistencies across the studies concerning laterality of MTL involvement. In a PET-study, when subjects were asked to match famous faces, widespread activation in the left frontotemporal regions was found, but no increased activity in any part of the MTL (Gorno-Tempini et al., 1998). However, an event-related fMRI study demonstrated that the recognition of famous faces compared to recognition of unfamiliar faces was associated with increased activity in the right hippocampus (Leveroni et al., 2000). Recently Bernard and co-workers demonstrated that the successful recognition of famous faces was associated with activation in the anterior as well as the posterior parts of the left hippocampus (Bernard et al., 2004). They concluded that the hippocampus was involved in mediating effective access to conscious recollection of semantic information. During the

recognition of famous faces increased activity of multiple brain regions including the left prefrontal cortex, right cerebellum, posterior cingulate, precuneus, caudate and the temporo-parietal junction was also shown in addition to the hippocampal activation. Sergent et al. (Sergent et al., 1992), using a categorization task in a PET study, found activation in a right parahippocampal area while Kapur et al. (Kapur et al., 1995) found a left hippocampal activity when comparing an explicit task requiring recognition of famous politicians' faces with a control task involving gender classification of unfamiliar faces (PET study). The contradictory results regarding MTL activity may be explained by task differences during face perception as well as differences in baseline condition (rest vs gender classification).

The objective of the present event-related fMRI study was to examine the relative involvement of different parts of MTL, particularly the contribution of hippocampus and perirhinal cortex, in either intentional or incidental recognition of famous faces in contrast to unfamiliar faces. Thus, our intention was to further explore the controversial contribution of MTL in the processing of semantic memory tasks. Subjects viewed a sequence of famous and unfamiliar faces. Two tasks were used encouraging attention to either fame or gender. In the fame task the subjects were requested to identify the person when seeing his/her face and also to try to generate the name of this person. Bernard and co-authors (2004) have previously demonstrated that the hippocampus is involved in the successful recognition of famous faces (intentional recognition but with no name generation). We expected activation in the hippocampus when recognition memory requires identification, thus mediating access to pre-existing semantic representations stored in the long-term memory. In the gender task the subjects were asked to conduct a judgement of a person's gender when seeing his/her face. The visual processing was hence directed to gender and thereby expected to diminish attention to semantic information leading only to a "passive" registration of famous and non-familiar faces.

Material and Methods

Subjects

The participants were 15 healthy subjects (7 male and 8 female) with a mean age of 23.3 years (range 19-32 years). Personal medical history was reviewed using a semi-structured interview. None of the subjects had any past or present history of a major psychiatric or neurological disorder. Structural MRI scans, read by an experienced neuroradiologist, were normal. The study was approved by the Lund University Ethics committee and written informed consent was obtained from all subjects.

Experimental task

The study used an event-related fMRI design. Stimuli were colour photographs of the faces of 64 famous and 64 unfamiliar persons. The set of famous faces were selected from a larger pool of well-known faces; all were celebrities known from the mass media (e.g. actors, royalties, politicians). In a pilot experiment, the famous faces had been rated as famous and highly familiar by a separate group of subjects who did not participate in the fMRI study. The set of unfamiliar faces were photographs of unfamiliar persons collected especially for this study. These faces were selected to match the famous faces regarding age, race, gender and visual appearance. The photographs were digitally edited using Adobe Photoshop; a white background was applied and all photographs were of the same size.

The photographs were back-projected to a mirror mounted on the head coil (visual angle approximately 30°). All 128 face stimuli were presented centrally in a pseudo-randomized order and were preceded by a fixation cross. Each face stimulus was shown for 3,5 – 4 s. The

face stimulus was preceded by a fixation cross shown for 4 – 4, 5 s, serving as an interstimulus interval. Thus, the total trial duration was randomly jittered between 7,5 and 8,5 s to allow for sampling of the hemodynamic signal over successive time points (mean trial duration 8 s). The baseline task consisted of viewing scrambled photographs of faces.

Echo planar MR images were acquired while the subjects were viewing sequences of famous, unfamiliar and scrambled faces. The subjects were instructed to perform one of the following tasks upon viewing a face (familiar or unfamiliar); either to identify the person presented (explicit task) or to categorize the gender (incidental task). The participants were asked to respond by pressing one of two buttons on a mouse to indicate whether a face was famous or not or whether a face was female or male. Each face stimulus was labelled with a text denoting either “*famous – index finger/unfamiliar – middle finger*” or “*man – index finger/woman – middle finger*”. Thus, in the explicit task the participants were requested to identify the person presented and also to try to generate the name of this person. In the gender classification task there was no explicit instruction to give attention to fame. This resulted in five experimental conditions: familiar (FFN) and unfamiliar faces identification (UFN), familiar (FF) and unfamiliar faces (UF) during gender classification and viewing of scrambled faces (BASE). In each scanning session there were 8 trials per condition (8 FFN, 8 UFN, 8 FF, 8 UF and 8 BASE). There were four scanning sessions, totally resulting in 32 trials of each condition.

The face stimuli were randomly assigned to belong to either the gender task or to the identification task. Different stimuli lists were created for each participant. The presentation order of all five conditions were randomized in each subject. The participants were asked to respond to the baseline task (scrambled faces) by pressing the left button on a mouse; “*scrambled face – index finger*”. The baseline task was used as an index that the processing of faces relative to scrambled faces yield activity in the critical fusiform areas in individual subjects. However, since the focus of this paper was to examine the role of the MTL in face recognition/identification, investigations involving a direct comparison with baseline condition were not pursued any further. Before scanning, all subjects practiced the different tasks (5 incidental, 5 explicit and 5 baseline tasks).

After scanning, all subjects were shortly interviewed with two questions; 1) Were you able to maintain focus on the two tasks, face identification and gender discrimination, throughout the scanning procedure? 2) Did you notice that there were famous/unfamiliar faces presented also during the gender tasks?

Imaging

MRI was performed using a 3 T head scanner (Siemens Allegra) with a quadrature birdcage coil. Morphological T1-weighted images with a resolution of $1 \times 1 \times 1 \text{ mm}^3$ were acquired using a magnetisation prepared gradient echo sequence (MPRAGE). Functional echo-planar image volumes of the whole brain (number of slices = 36, thickness = 3 mm, interslice gap 0.9 mm, matrix size = 64×64 , FOV = 192 mm, voxel size = $3 \times 3 \times 3 \text{ mm}^3$) sensitised to the Blood Oxygenation Level Dependent (BOLD)-effect (echo time = 30 ms) were acquired. Four scanning sessions were performed, each including 107 functional volumes with a temporal resolution of 3 seconds. The first two volumes in each session were discarded from further analysis to allow for initial T1-equilibrium effects.

Postprocessing and data analysis

Image processing and analysis were carried out using the SPM99 software package (Friston et al., 1995) [<http://www.fil.ion.ucl.ac.uk>]. Differences in slice time acquisition times were corrected for using sinc-interpolation. Each subjects' images were realigned independently

and motion-corrected. A mean functional image was constructed for each subject and used to derive parameters for spatial normalisation into the modified Talairach (Talairach and Tournoux, 1988) stereotaxic space implemented in SPM99. The normalization parameters for each mean image were then applied to the corresponding functional images for each session and the images resampled into isotropic 2-mm voxels. The normalized images were subsequently smoothed with a 10-mm full-width at half-maximum (FWHM) Gaussian kernel. A high-pass filter (cut off frequency 0.008 Hz) was applied to eliminate low frequency signal fluctuations. Statistical analysis was performed using the General Linear Model implemented in SPM99. Event-related responses were modelled using the canonical hemodynamic response function with a peak latency of 6 s. Images of parameter estimates contrasting the fitted response for FFN relative to UFN trials and for FF versus UF trials were computed for each subject. These were then entered into a second level one-sample t-test. The resultant SPM(t) was thresholded with a p value corresponding to 5 % false discovery rate (FDR) to control for multiple comparisons. Only activations involving contiguous clusters of at least 15 voxels were accepted. The use of an implicit task does not allow for pooling of successful intentional encoding and we therefore refrained from such pooling also as regards the explicit task. Analysis involved the use of all trials. Coordinates are reported and displayed in the modified Talairach stereotaxic space implemented in SPM99. A transformation algorithm was applied to localize activations within standard Talairach space [Talairach and Tournoux, [1988]; see <http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html> for the transformation algorithm]. In 3 T EPI volumes signal loss in the inferior temporal lobes occurs, possibly leading to misregistration and subsequent slight displacement of the basal parts of the temporal lobes in the z-direction. Reported coordinates are therefore approximate in that direction.

Results

Behavioural data

During the explicit task the subjects correctly recognized 85 % of the famous faces and rejected 97 % of the unfamiliar. Paired t-test revealed a significant difference in accuracy between the two conditions ($p < 0.01$). However, there was no difference in reaction time for recognizing a famous face compared to rejecting an unfamiliar face (table 1).

After scanning; two thirds of the subjects reported that they maintained a high level of focused attention on the given tasks; three subjects reported that they kept good concentration during both tasks, while two patients described occasional loss of concentration. Furthermore, all subjects reported that they recognized faces of famous persons among the presented faces also during the gender tasks.

Table 1

Means of proportion correctly recognized famous and unfamiliar faces and means of reaction time during the explicit task

Task	Face type	Proportion correct	Reaction time (ms)
Identification FFN	Famous	85.4 %	1245 (311)
Identification UFN	Unfamiliar	97 %	1268 (310)
Gender decision FF	Famous	Not relevant	1274 (495)
Gender decision UF	Unfamiliar	Not relevant	1272 (468)

Table 2

Brain regions showing significant signal increases for the following comparisons: familiar faces (FFN) vs unfamiliar faces (UFN) during identification; familiar faces (FF) vs unfamiliar faces (UF) during gender classification (UF); main effects of fame FF + FFN > UFN + UF; main effects of task FFN + UFN vs FF + UF.

Cluster size (voxels)	Brain regions	BA	Coordinates			t score	P value FDR-corr
			x	y	z		
<i>familiar faces (FFN) vs unfamiliar faces (UFN) during identification</i>							
19258	L superior frontal gyrus	6	-14	13	60	8.42	0.008
	L inferior frontal gyrus	47	-46	31	4	7.58	0.008
	L inferior frontal gyrus	45	-48	22	10	7.53	0.008
	R nucleus caudate		10	7	16	6.63	0.008
	L anterior cingulate	24	-12	36	15	6.52	0.009
	L superior frontal gyrus	8	-18	39	39	6.46	0.009
377	L fusiform gyrus	37	-44	-49	-13	4.88	0.012
340	R posterior cinguli gyrus	31	2	-35	35	4.62	0.012
	L posterior cinguli gyrus?	31?	-16	-43	35	3.90	0.018
26	R inferior frontal gyrus	45	57	31	8	4.53	0.012
	R superior temporal gyrus	22	59	27	6	3.95	0.017
145	R anterior temporal pole?	38	48	16	-28	4.15	0.015
	R anterior temporal pole?	38	51	15	-18	3.78	0.020
91	L inferior parietal lobe	40	-61	-45	36	4.02	0.016
85	R Middle temporal gyrus	21/22	50	-39	4	4.01	0.016
339	L occipital area	19	-14	-60	-4	3.80	0.020
32	R middle frontal gyrus	10	48	47	5	3.68	0.022
88	L middle temporal gyrus	21	-53	-37	0	3.65	0.023
28	R cerebellum		40	-64	-32	3.51	0.026
41	R fusiform gyrus	37	40	-57	-11	3.45	0.028
15	L hippocampus		-33	-14,7	-21	3.44	0.028
<i>familiar faces (FF) vs unfamiliar faces (UF) during gender classification (UF)</i>							
8852	L middle frontal gyrus	6	-38	5	57	8.01	0.009
	L middle frontal gyrus	6	-30	16	51	7.83	0.009
	L inferior frontal gyrus	47/11	-40	38	-7	7.36	0.009
	L inferior frontal gyrus	47	-38	34	-17	6.49	0.009
	L superior frontal gyrus	10	-20	58	-5	6.24	0.009
	L middle frontal gyrus	9	-38	14	38	5.98	0.010
2260	R cerebellum		10	-83	-23	7.47	0.009
	R cerebellum		36	-62	-39	5.99	0.010
	R cerebellum		34	-58	-40	5.72	0.010
	R cerebellum		38	-70	-27	4.90	0.013
	R fusiform gyrus	37	38	-55	-11	4.56	0.015
	R occipital gyrus	19	46	-76	-8	4.39	0.017
3022	L middle temporal gyrus	21	-57	-35	-7	6.29	0.009
	L middle temporal gyrus	21	-59	-34	-12	6.13	0.010
	L fusiform gyrus	37	-42	-49	-14	5.78	0.010
	L inferior temporal gyrus	20	-51	-26	-19	4.88	0.013
	L fusiform gyrus	37	-51	-55	-14	4.54	0.015
	L perirhinal cortex	35	-19	-29	-7	4.53	0.015
296	L middle temporal gyrus	21	-51	-1	-22	5.71	0.010

Table 2 (continued)

Cluster size (voxels)	Brain regions	BA	Coordinates			t score	P value FDR-corr
			x	y	z		
<i>familiar faces (FF) vs unfamiliar faces (UF) during gender classification (UF)</i>							
	L middle temporal gyrus	21	-55	-8	-13	3.71	0.027
	L middle/inferior temporal gyrus	21/20	-44	2	-32	3.37	0.037
368	Posterior cingulate gyrus	31	2	-35	29	5.31	0.011
1230	L superior parietal lobe	7	-32	-67	53	5.06	0.012
	L inferior parietal lobe	40	-48	-52	50	4.03	0.021
	L inferior parietal lobe	40	-42	-61	33	3.96	0.022
146	R inferior frontal lobe	44	57	23	28	4.54	0.015
	R middle frontal gyrus	46	55	27	26	4.09	0.020
	R middle frontal gyrus	46	59	23	23	3.95	0.022
26	R uncinata fasciculus		28	11	-12	3.82	0.025
26	R parahippocampus	28	22	-9	-26	3.65	0.028
25	Medial frontal lobe	9	-16	40	24	3.48	0.033
17	R superior temporal gyrus	39	55	-61	28	3.22	0.043
<i>main effects of fame</i>							
<i>FF + FFN > UFN + UF</i>							
3272	L inferior frontal gyrus	11	-24	33	-7	6.87	0.039
	L inferior and middle frontal area	45/46	-30	31	8	5.89	0.039
	L precentral gyrus	6	-46	5	27	5.75	0.039
1422	R nucleus caudate		14	3	18	6.69	0.039
	L nucleus caudate		-14	5	16	5.81	0.039
	L nucleus caudate		-6	12	5	5.73	0.039
1504	L occipital gyrus/occipitotemporal area	19/37	-44	-68	2	6.61	0.039
	L fusiform gyrus	37	-48	-55	-12	5.25	0.039
	L occipital gyrus	19	-42	-83	15	4.53	0.039
167	L temporal area	20	-40	-13	-30	4.95	0.039
	L parahippocampal gyrus/temporal region	28/36	-28	-9	-30	4.04	0.039
	L inferior temporal gyrus	20	-48	-17	-26	3.94	0.040
89	R parahippocampal gyrus	28	26	-7	-27	4.86	0.039
305	L superior parietal lobe	7	-32	-61	53	4.63	0.039
155	L posterior part of hippocampus/perirhinal cortex	(35)	-28	-32	-12	4.49	0.039
69	R inferior temporal gyrus	37	55	-64	3	4.22	0.039
	R inferior temporal gyrus	37/19	51	-70	0	3.81	0.043
61	L precentral gyrus	6	-44	1	53	4.21	0.039
25	L orbital gyrus	11	-10	21	-14	4.17	0.039
239	L medial frontal lobe	8/6	-2	12	49	3.81	0.043
	L superior frontal gyrus	8	-16	22	52	3.78	0.043
	L superior frontal gyrus	8/6	-12	14	47	3.73	0.044
23	L middle frontal gyrus	6	-30	14	49	3.81	0.043
29	L orbital gyrus	10/11	-6	44	-16	3.74	0.044
17	R fusiform gyrus	37	40	-45	-13	3.62	0.046

Table 2 (continued)

Cluster size (voxels)	Brain regions	BA	Coordinates			t score	P value FDR-corr
			x	y	z		
<i>main effects of task</i>							
<i>FFN + UFN vs FF + UF</i>							
1330	L postcentral gyrus	2	-63	-10	24	7.91	0.019
	L superior temporal gyrus	22/42	-55	-21	8	6.10	0.024
	L superior temporal gyrus	22	-40	-36	17	5.61	0.024
723	R superior temporal gyrus	42	53	-13	8	7.77	0.019
	R transverse temporal gyri	41	38	-27	12	6.55	0.021
33	L precentral gyrus	4/6	-40	1	13	6.12	0.024
360	R inferior parietal lobe	40	34	-33	38	5.67	0.024
78	R postcentral gyrus	2/3	61	-14	39	4.82	0.028
	R postcentral gyrus	1/3	51	-19	40	4.36	0.038
72	R precentral gyrus	6	38	3	15	4.58	0.033

Imaging data

Effects of fame

The analysis of the contrast between famous faces, naming (FFN) and non-familiar faces, naming (UFN) revealed a significant activation in the left MTL (FDR, $P < 0.05$, corrected), in the anteriolateral part of hippocampus in proximity to amygdala (local maximum at $[-33, -15, -21]$, $t = 3.44$) (fig. 1). No significant MTL activity was observed in the reversed contrast (UFN versus FFN). The incidental task, famous faces (FF) versus non-familiar faces (UF), yielded significant activations in the left MTL. The recognition of famous faces resulted in greater activation in the left perirhinal cortex (local maximum at $[x\ y\ z] = [-20\ -29\ -7]$, $t = 4.53$) (fig. 2). The reverse comparison (UF versus FF) did not reveal any significant activation in MTL.

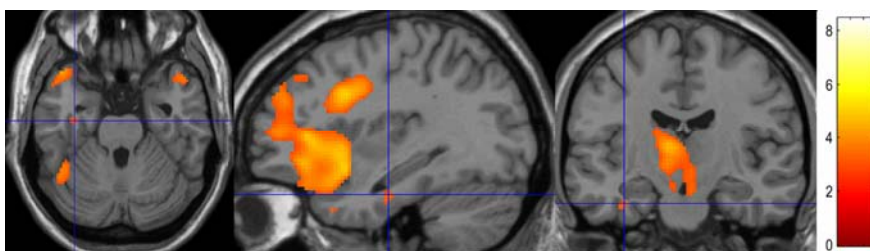


Fig. 1. The comparison famous faces, naming (FFN) versus unfamiliar faces, naming (UFN) during intentional recognition of famous faces (person identification task). Regions of significant activation are superimposed on a T1-weighted anatomical image in standard space, showing increased activity in the left anteriolateral part of hippocampus $[-33, -15, -21]$, $t = 3.44$, (thresholded at $p < 0.05$; FDR corrected, cluster size ≥ 15).

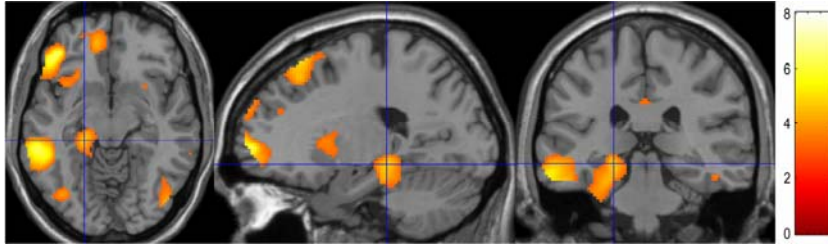


Fig. 2. The comparison famous (FF) versus unfamiliar faces (UF) during incidental recognition of famous faces (gender classification task). Regions of significant activation superimposed on a T1-weighted anatomical image in standard space, showing increased activity the left perirhinal cortex BA 35, $[-20,-29,-7]$, $t=4.53$, (thresholded at $p < 0.05$; FDR corrected, cluster size ≥ 15).

Although the main focus of the present study was MTL, additional results were obtained showing that the comparison between famous and unfamiliar face processing yielded significant activations in a network of brain regions. The fMRI results are summarized in Table 1. Briefly, the comparison of FFN and UFN revealed an extensive left frontal activation. The activation was dorsal and widespread in the left ventrolateral regions as well as in the left anterior cingulate gyrus and right caudate. Furthermore, there were significant activations in posterior gyrus cinguli, fusiform areas bilaterally, in the left middle temporal gyrus, the left preoccipital area and left inferior parietal lobe. There were also significant but not widespread signal increases in the frontal and temporal regions and in right cerebellum. The reversed contrast, UFN versus FFN, showed restricted activation in small foci in temporal regions. In the comparison of FF versus UF the subjects showed greater activation in a widespread network in the left prefrontal lobe, in frontopolar/dorsal/ventrolateral areas, in the left temporal lobe and in the left inferior. There were also significant activations (as well as in FFN versus UFN) in the posterior cingulate gyrus, fusiform areas bilaterally, in the left temporal regions and inferior parietal lobe, the right cerebellum, smaller areas in the right middle frontal gyrus and in the right cerebellum. No suprathreshold clusters were found in UF versus FF.

The main effects of fame (FF + FFN versus UFN + UF) revealed significant activations in an area encompassing the left posterior part of hippocampus extending into perirhinal cortex and in the parahippocampus bilaterally (Table 1). Furthermore, the comparison yielded significant activations in a network of brain regions including the left frontal cortex, the caudate, the left occipitotemporal area, the inferior temporal and fusiform gyrus bilaterally. The main effect of task (fame decision/gender decision) yielded significant activations in temporal areas bilaterally (table 1). The interaction effects between the effect of fame and decision (FF + FFN versus UF + UFN) revealed no significant activations.

Processing of faces in all conditions (FF, UF, FFN and UFN) relative to scrambled faces resulted in enhanced activity bilaterally in the fusiform gyri.

Discussion

Famous face processing and the medial temporal lobe

The present study assessed the relative involvement of different parts of MTL in the processing of semantic memory tasks, in either intentional or incidental recognition of famous faces versus unfamiliar faces. Recognition of famous faces, in both contrasts, produced significant activations in the MTL. First, during the intentional recognition (the person

identification task) increased activity was observed in the anterolateral part of left hippocampus, in proximity to amygdala. Second, during the incidental recognition of famous faces (the gender classification task) there was increased activity in the left posterior MTL with focus in the perirhinal cortex. In addition, there was increased activity in the right parahippocampus. Third, the main effect of the processing of famous faces (intentional and incidental recognition) yielded activation in left MTL as well as in right parahippocampus. Thus, the current results clearly support the finding that retrieval of information from the long-term semantic memory is related to increased activity in MTL (Squire et al., 2004). Furthermore our results, regarding the intentional recognition of famous faces, resemble the results by Bernard and co-workers (Bernard et al., 2004), who demonstrated increased activity in parts of left hippocampus. Other studies have reported increased MTL activity during recognition of famous faces, although with discrepancies concerning laterality as well as regarding the role of different regions in MTL (Sergent et al., 1992, Kapur et al., 1995, Leveroni et al., 2000, Haist et al., 2001).

According to models of face processing, the recognition of famous faces is proposed to be a match between its encoded representations and different stored structural codes. The recognition of familiar faces can be described in terms of a sequential access of these codes; such as pictorial, identity-specific semantic and visually derived semantic (Bruce and Young, 1986). The two experimental tasks in our study were intended to manipulate attention to different stages of face processing. The recognition of a face as famous was not required for achieving the goal in the gender classification task, hence, this task was supposed to direct attention to visuo-perceptual aspects leading to only a “passive” registration of famous faces. This passive registration might be a visual discrimination between the known and unknown faces probably not resulting in complete retrieval of person identity information. After the fMRI session in the current study, the subjects were asked if they had asked themselves whether famous faces were presented during the gender tasks in the course of the fMRI-experiment. The results of this short interview verified that all subjects had recognised faces of famous persons. Our experiment can not tell if there are any distinct differences between this latter recognition, a type of “computation of familiarity”, and the intentional retrieval of person specific semantic memories. Nonetheless, it appears that both processes were accessible to conscious awareness and that subjects could report on them when asked to do so. Evidence from neuropsychological and neuroimaging studies of episodic memory have led to proposals that recognition memory performances reflect two distinct memory processes referred to as familiarity and recollection. Moreover, these results indicate that the two processes rely on partially distinct neural substrates; that familiarity relies on regions surrounding the hippocampus and that recollection relies on the hippocampus (Yonelinas, 2002). Our findings, regarding retrieval of semantic information, might be considered in the light of the role and contribution of hippocampus and surrounding areas for episodic memory recognition. In the present study we distinguished increased activity in the anterior part of left hippocampus during the explicit recognition and increased activity in posterior parts of MTL, likely a posterior part of the perirhinal cortex, during incidental recognition of famous faces. We propose that this latter finding might parallel the familiarity component of episodic recognition memory.

Although our results regarding the contribution of MTL in the processing of famous faces support the role of this structure in the retrieval of information stored in semantic memory, it is important to take into account the possible influence of specific personal memories associated with the face of a famous person. Westmacott and Moscovitch (Westmacott et al., 2003) have argued “that some knowledge that typically is classified as semantic has a contextual and episodic component”. It has been suggested that there may be a constant interaction between episodic and semantic memory that is automatic and obligatory. During

recall of semantic memories, information that is not semantically related to a specific fact may also be activated automatically. Westmacott et al. (2003) have examined the interaction between autobiographical experience and semantic memory deterioration in patients with Alzheimer's disease, semantic dementia and amnesia. Their findings suggest a critical role for the MTL regions in the interaction between personal experience and semantic memory. It requires further research to explore the possible interaction between these two forms of memory.

Famous face processing and activated regions beyond the MTL

The current study focused its examination on the MTL region, which undoubtedly represents only a part of a more extensive neural network critical for retrieval of information stored in long-term memory (Leveroni et al., 2000). For the completeness we briefly comment some of the activated regions beyond the MTL. Recognition of famous faces during the intentional as well as the incidental condition produced significant activations over widespread areas in the prefrontal and temporal lobe, posterior cingulate gyrus, fusiform areas and cerebellum. In addition, in the intentional recognition of famous faces there was also a pronounced activation in the anterior gyrus cinguli and caudate. A number of neuroimaging studies, using different tasks, implicate the left prefrontal gyrus in the retrieval of semantic knowledge (Thompson-Schill et al, 1997; Leveroni et al., 2000). Furthermore, the activated network in the temporo-parietal regions, have also been associated with semantic processing (Gorno-Tempini et al. 1998). Previous studies have reported that both the left and the right temporal lobes are involved in the retrieval of semantic information (Leveroni et al., 2000). The current study could show a pronounced activation in caudate as has also been reported in the Bernard et al study (2004). Bernard and co-authors put forward one possible explanation for the caudate activation as being the result of high mean age of their subjects (60 years). They proposed that this activation might reflect an age-related compensatory process: "our subjects may possibly have spontaneously or automatically recruited these regions, which are included in fronto-striatal loops, to compensate for inevitable age-related changes and hence to perform the task efficiently". In our study the mean age was 23 years. The caudate activation was encompassing a large volume in the processing of fame (main effect) but was also significant during the intentional recognition of famous faces. Further studies are needed to understand the role of this region in the processing of fameness.

Conclusions

In conclusion, the main focus of this study was to examine the relative involvement of different parts of the MTL in long-term memory retrieval of famous faces. Our results suggest that the hippocampus may be centrally involved in the intentional retrieval of semantic memories while the perirhinal cortex is associated with the incidental recognition of semantic information.

Acknowledgement

The authors thank Daniel Karlsson, Helena Andersson and Fredrik Örtendahl for technical assistance. The study was supported by grants from the Alzheimer Foundation and the Sjöbring Foundation.

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