Retention of identity versus expression of emotional faces differs in the recruitment of limbic areas

Christian H. Röder [a,*], Harald Mohr [b,c], David E.J. Linden [d]

[a] Dept. of Psychiatry, Erasmus MC, Erasmus University Rotterdam, PO 2040, NL-3000 CA Rotterdam, The Netherlands
[b] Dept. of Biological Psychology, Institute of Psychology, Johann-Wolfgang-Goethe-University, Frankfurt, Germany
[c] Brain Imaging Center, Frankfurt, Germany
[d] Bangor Imaging Unit, Wolfson Centre for Clinical and Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, UK

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ABSTRACT

Faces are multidimensional stimuli that convey information for complex social and emotional functions. Separate neural systems have been implicated in the recognition of facial identity (mainly extrastriate visual cortex) and emotional expression (limbic areas and the superior temporal sulcus). Working-memory (WM) studies with faces have shown different but partly overlapping activation patterns in comparison to spatial WM in parietal and prefrontal areas. However, little is known about the neural representations of the different facial dimensions during WM. In the present study 22 subjects performed a face-identity or face-emotion WM task at different load levels during functional magnetic resonance imaging. We found a fronto-parietal-visual WM-network for both tasks during maintenance, including fusiform gyrus. Limbic areas in the amygdala and parahippocampal gyrus demonstrated a stronger activation for the identity than the emotion condition. One explanation for this finding is that the repetitive presentation of faces with different identities but the same emotional expression during the identity-task is responsible for the stronger increase in BOLD signal in the amygdala. These results raise the question how different emotional expressions are coded in WM. Our findings suggest that emotional expressions are re-coded in an abstract representation that is supported at the neural level by the canonical fronto-parietal WM network.

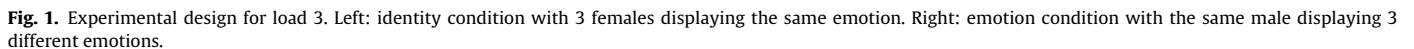© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Functional imaging studies of visual working memory have focused on the maintenance and manipulation of visual objects, features and spatial information (Linden, 2007; Wager & Smith, 2003). Important areas involved in visual working memory processes are the prefrontal cortex, intraparietal sulcus and higher visual areas. Each of these regions is supposed to subserve a special function in this network. It has been suggested that some areas in the prefrontal cortex are specialised regarding the material type (object, spatial, verbal) (Jennings, Van der Veen, & Meltzer, 2006; McIntosh, Grady, Haxby, Ungerleider, & Horwitz, 1996; Ventre-Dominey et al., 2005), while others suggest that differences are mainly based on processes such as maintenance, manipulation, or inhibition, which are necessary to perform the WM task (Petrides, 2005; Petrides, Alivisatos, & Frey, 2002) or by an interaction between material type and processes (Mohr, Goebel, & Linden, 2006).

Faces are multidimensional stimuli and convey many important features simultaneously. They represent a special category in the field of visual objects, probably based on their importance for the recognition of relevant others (identity) and for nonverbal communication (emotional expression). The identity of a person can be recognised by his/her individual physiognomy, which is based on the spatial composition of facial features (nose, eyes, mouth, etc.). Emotional expression is then derived from subtle changes in the spatial composition of facial features (Bruce & Young, 1986). Neuroimaging has elucidated the brain structures involved in the processing of faces (Haxby et al., 2001; Kanwisher, Stanley, & Harris, 1999) and their emotional expression (Gur, Schroeder, et al., 2002; Phillips et al., 2001; Vuilleumier & Pourtois, 2007). These studies converge to suggest that structures involved in the recognition of the identity of faces (structural and static properties of faces) are mainly located in the extrastriate visual cortex (Adolphs, 2002; Haxby, Hoffman, & Gobbini, 2000). More changeable configurational features of faces (emotional expression) are processed in the superior temporal lobe (Adolphs, 2002; Haxby, Hoffman, et al., 2000; Haxby, Petit, Ungerleider, & Courtney, 2000b). Further support for the role of the superior temporal cortex comes from animal studies with single cell recordings (Hasselmo, Rolls, &

* Corresponding author. Tel.: +31 10 7035864; fax: +31 10 7033217.
E-mail address: c.roder@erasmusmc.nl (C.H. Röder).

Fig. 1. Experimental design for load 3. Left: identity condition with 3 females displaying the same emotion. Right: emotion condition with the same male displaying 3 different emotions.

Baylis, 1989; Jellema & Perrett, 2003) Many functional neuroimaging studies have investigated the impact of emotional expression of human faces on brain activity (Gläscher, Tuscher, Weiller, & Buchel, 2004; Gur, Schroeder, et al., 2002; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002; Pegna, Khateb, Lazeyras, & Seghier, 2005; Phillips et al., 2001). The amygdala is the structure mostly associated with the recognition of emotional expressions (Gur, Schroeder, et al., 2002; Hariri et al., 2002; Morris et al., 1998; Wright, Martis, Shin, Fischer, & Rauch, 2002; Yang et al., 2002), although the debate is ongoing as to whether the amygdala primarily is active to negative facial expressions as fear and sadness or relevant in recognizing all human emotional expressions. Breiter et al. (1996) found that the repeated presentation of faces with emotional expressions causes a reduction of amygdala activity, but Gläscher et al. (2004) found increased amygdala activity for the repeated presentation of fearful faces of different subjects compared to conditions where either identity was constant or emotion was varied.

In working memory, faces show partly overlapping activation patterns in comparison to spatial WM (Haxby, Petit, et al., 2000; Sala, Rama, & Courtney, 2003) with a dorso-ventral gradient for spatial versus facial stimuli (Haxby, Hoffman, et al., 2000; Haxby, Petit, et al., 2000).

Two recently published studies investigated WM of emotional faces. LoPresti et al. (2008) explicitly instructed subjects to match a sample and a test face either for identity or for the emotional expression. In the identity condition, sample and test faces expressed a different emotion, whereas in the emotion condition sample and test faces differed in identity. The authors focused on three structures more active in the delay for faces versus a control stimulus, the left orbitofrontal cortex (OFC), the left amygdala and the left hippocampus. Only the OFC had significantly higher activity for the emotion task during the presentation of the sample face and significantly higher activity for negative faces during the presentation of the test face. The absence of differences between the two conditions during delay came as a surprise. However, it is important to notice that the authors only measured working memory at a load of one, which may have led to a marginal activation of emotion- or identity specific networks. Jackson, Wolf, Johnston, Raymond, and Linden (2008) used a design wherein emotional expression was varied at four load levels. Subjects were only asked to match the faces for identity, so the emotional aspect was studied implic-

itly. Another important difference was the short delay of only 1 s, which did not allow for a separation of the processes of encoding, maintenance and retrieval. This study revealed higher activity for negative emotion (angry faces) in the right hemispheric inferior frontal gyrus, superior temporal gyrus and globus pallidus internus for all conditions.

Load-dependent changes are an inherent characteristic of the brain's working memory networks (Linden, 2007). We therefore regarded the manipulation of the number of faces to be maintained in either the identity or emotion task as crucial. In the present study we focused on neural processes during the maintenance phase for identity or emotional expression of faces at different load levels. Because of its dual role in emotion processing and memory, we hypothesized that the amygdala and connected limbic areas would play an important role in the maintenance of emotional faces.

2. Methods

2.1. Participants

Twenty-two right-handed volunteers (13 females/9 males) (mean age = 27.3, SD = 4.3) with normal or corrected to normal vision participated in the experiment. The subject's physical health was verified in an interview before the study, and those who had a history of neurological diseases, psychiatric diseases, or drug or alcohol abuse were excluded. No subject was taking medication affecting cerebral blood flow at the time of the study. All participants gave informed consent and experimental procedures were approved by the local ethics committee and in accordance with the Declaration of Helsinki 1975.

2.2. Stimuli and experimental procedure

In each trial of the paradigm, participants had to memorize one, two, or three sequentially presented black-and-white exemplars human faces taken from the samples of Ekman (Ekman, Friesen, & Ellsworth, 1972) and Gur, McGrath, et al. (2002) in a forced choice paradigm. Faces displayed the following emotions: anger, disgust, fear, happiness, sadness, surprise or a neutral expression. Trials consisted either of the same subject expressing different emotional expressions (emotion condition) or different subjects with the same emotional expression (identity condition), leaving some ambiguity in the case of only one presented stimuli. Faces were cropped with an individually formed shape in order to avoid that peripheral face features allow easy identification of faces. The term emotion was explicitly not named in the instruction to avoid verbalization of emotional expressions. Stimuli were matched for gender, but not for emotional expressions, due to the fact that there are more negative facial emotional expressions and a limited number of faces. Sample stimuli were presented for 500 ms each. In case of presentation of two or three faces, stimuli were separated by 250 ms blank screens. After a 8 s delay, one

Table 1
Behavioural data of task performance.

	ID LOAD 2	ID LOAD 3	EMO LOAD 2	EMO LOAD 3
Accuracy	0.81 (0.13)[*]	0.72 (0.13)	0.76 (0.11)	0.72 (0.14)
A′ prime	0.88 (0.08)	0.81 (0.14)	0.83 (0.08)	0.78 (0.13)
Hit rate	0.79 (0.12)	0.71 (0.14)	0.75 (0.11)	0.71 (0.14)
False alarms	0.17 (0.1)	0.23 (0.13)	0.21 (0.08)	0.25 (0.12)
Reaction times	1094 (149) ms	1162 (163) ms	1096 (173) ms	1170 (150) ms

[*] Mean values, standard deviation in brackets.

exemplar from the same category was presented as test stimulus, and participants had to decide by button press whether it matched one of the sample stimuli (50% matches) (Fig. 1).

Dependent on the number of presented stimuli, trials were separated by an inter-trial interval of 8000, 8750 or 9500 ms. Ninety trials (45 per category) were presented in 3 runs, each containing 30 trials in randomized order. Stimulus presentation was controlled by a personal computer running the Experimental Run Time Software (Berisoft GmbH, Germany). Images were backprojected on the centre of a screen, subtending 5° of visual angle, and viewed by participants through an angled mirror mounted on the head coil. Before the main experiment participants were given a short practice session inside the scanner.

2.3. Image acquisition parameters

Anatomical three-dimensional T1-weighted images and functional images were acquired on a 3 T Magnetom Trio scanner (Siemens Medical Systems, Erlangen, Germany) equipped with a standard head coil. A T1 weighted 3D MPRage scan (magnetization-prepared rapid acquisition gradient echo, $T_R = 9.7$ ms, $T_E = 4$ ms, FA 12°, Matrix 256×256, FOV 256 mm $\times 256$ mm, voxel size 1.0 mm $\times 1.0$ mm $\times 1.0$ mm) was recorded in every session for anatomical coregistration.

Functional images were collected using 30 slices (3 mm thickness with 3.45 mm $\times$ 3.45 mm in-plane resolution) covering the whole brain with a BOLD-sensitive EPI sequence ($T_R = 2$ s, $T_E = 30$ ms, FA = 90°; FOV = 220 mm, matrix = 64 × 64; duration of each run = 618 s). To minimize head movements the head was fixed with foam pads that were attached to the holding fixture of the head coil.

2.4. Analysis of behavioural data

Behavioural data were analyzed with SPSS 15 (SPSS, Inc.). Signal detection models were used to analyze the data.

Accuracy was calculated as percent correct answers per category. Reaction times were calculated for correct answers only. In addition, A-prime (A′) scores were calculated as measure of signal detection sensitivity (Grier, 1971) to detect an interference effect. A-prime increases from 0.5 for chance performance to 1 for perfect performance. A-prime was used instead of d-prime because A-prime is more robust against violations of the assumption that the variances of the hypothetical distributions are equal (Donaldson, 1993) and A-prime does not suffer from the indeterminacy of d-prime that occurs in the absence of false alarms. A-prime estimates the area under the receiver operating curve and was calculated for each participant following the formula by Grier (1971):

$$A' = 0.5 + \frac{[(H - FA) \times (1 + H - FA)]}{[4 \times H \times (1 - FA)]},$$

where H (hit) is the correct detection of matching trial and FA (false alarm) is the nonmatching trial identified as matching trial.

If FA > H, the point lies beyond the chance diagonal and the following formula is used:

$$A' = 0.5 + \frac{[(FA - H) \times (1 + FA - H)]}{[4 \times FA \times (1 - H)]}.$$

2.5. Analysis of imaging data

Image analyses were performed with Brainvoyager QX, version 1.10.4 (Brain Innovation, Maastricht, The Netherlands). The first four volumes of each run were automatically discarded due to signal stabilisation. Data pre-processing included slice scan time correction with the first scan time within a volume used as a reference for alignment by sinc interpolation, three-dimensional motion correction, spatial smoothing with an 8 mm Gaussian kernel (full width at half maximum), temporal high pass filtering with a cut-off of 1/206 s to remove low-frequency non-linear drifts of three or fewer cycles per time course, and linear trend removal. Talairach transformation was performed for the complete set of functional data of each subject, yielding a 4D data representation (volume time course: 3 × space, 1 × time). Statistical analysis was performed by multiple linear regression of the BOLD response time course in each voxel at the individual level. Two of the 22 participants had to be excluded completely, and the data from one run from 3 participants were excluded

due to extensive movement artifacts. For each participant, the general linear model included six experimental conditions (identity load 1, 2 and 3; emotion load 1, 2 and 3) and three task phases (encoding, delay and retrieval). The signal values during these phases were considered the effects of interest. The corresponding predictors were obtained by convolution of an ideal box-car response with gamma function model of the hemodynamic response. The encoding phase lasted for 1250 (load 2) to 2000 (load 3) ms and was modeled by a predictor covering the TR after trial onset. Although the delay lasted for 8 s, it was only modeled by its third TR (7–8 s from trial onset). This predictor was thus separated from encoding by 4 s and from the following retrieval predictor (11–12 s) by 2 s. We used this approach following the theoretical framework of Postle (Postle, 2005). Because of the inertia of the BOLD signal, sequential cognitive operations are difficult to disentangle; therefore each phase (encoding, delay, retrieval) is temporally dependent on the previous one. Based on the previous work of Zarahn, Aguirre, and D'Esposito (1997), Postle (2005) proposes that an interval of at least 4 s between two consecutive predictors is necessary to disentangle the effects of a specific predictor without contamination through the previous one. It seems reasonable that carry-over effects from the encoding phase on delay are much stronger, than carry over effects from the delay phase on retrieval, and thus an interval between the delay and retrieval of one TR seemed sufficient. Trials with incorrect answers were modeled with a separate predictor.

This analysis resulted in beta-values for each predictor for each subject ($n = 20$). Beta-values of the three phases (encoding, delay and retrieval) were entered separately into a random effects ANOVA with the factors load (2 and 3), task (emotion and identity) and phase (encoding, delay, retrieval). Main effects (load, task) and interaction between the factors were thresholded at $p < 0.005$ (uncorr.) with a minimal cluster size of 10 contiguous voxels. Only the factor load during the encoding phase was thresholded at $p < 0.001$ (uncorr.), because the visual stimulation led to high changes of the BOLD-signal. Reported t- and p-values represent cluster level analysis. In order to control for any effects of performance differences between tasks we also performed an analysis of covariance (ANCOVA) with the factors task and load, adding the difference of A′ values between tasks for each participant as covariate.

3. Results

3.1. Behavioural results

A first analysis of the behavioural data showed a paradoxical result in the load 1 condition of the emotion task with a performance in load 1 similar to load 3. A high percentage of false positive responses were detected. A more thorough analysis demonstrated a significantly higher number of errors when the target had to be rejected ($t = -2.08$, df = 8.961, $p = 0.04$) than in the opposite case. In all other load conditions no significant differences appeared. Post trial interviews with subjects indicated some ambiguity in the load 1 condition due to the fact that trials were not introduced as "emotion" or "identity". We therefore excluded the load 1 condition from further analysis due to this systematic error in the behavioural data. In a behavioural study with 46 healthy subjects (unpublished data) where the same paradigm was used, but each trial were preceded with "emotion" or "identity", false positive answer in the emotion load 1 condition dramatically decreased, showing a robust load effect from load 1 to load 3.

We compared accuracy and reaction times (RT, correct trials only) for the remaining conditions with a 2×2 repeated-measurement-ANOVA (see Table 1). Significant results were found for the factor load (mean accuracy: $F(1,19) = 7.993$, $p = 0.01$; RT: $F(1,19) = 13.127$, $p = 0.002$), but neither for the factor task (accuracy: $F(1,19) = 1.059$, $p = 0.315$; RT: $F(1,19) = 0.8$, $p = 0.78$) nor the interaction of the two factors (accuracy: $F(1,19) = 1.568$, $p = 0.224$; RT: $F(1,19) = 0.29$, $p = 0.865$).

Table 2

Brain regions exhibiting significant activity of two-way interactions from ANOVA during encoding and retrieval. X, Y and Z represent coordinates in the Talairach space. t- and p- values are derived from region-of-interest analysis.

Encoding

Load			Whole brain $p < 0.001$		Load 3 > Load 2	
x	y	z	Voxel	Region	t-Value	p-Value
−1	17	47	150	Medial frontal gyrus, BA6	4.166	0.000524
25	−70	43	301	Superior parietal lobe, BA7	4.394	0.000312
10	−81	40	1537	Precuneus, BA7	2.848	0.010294
−17	−83	35	1121	Cuneus, BA19	2.742	0.012948
46	−39	38	514	Inferior parietal lobe, BA40	5.048	0.000071
43	13	26	1713	Middle frontal gyrus, BA9	4.828	0.000117
43	−74	1	1548	Inferior occipital gyrus, BA19	5.895	0.000011
−14	−67	−8	3258	Lingual gyrus, BA18	5.537	0.000024
−10	−60	−6	2916	Lingual gyrus, BA18	6.557	0.000003
−32	−81	−3	521	Inferior occipital gyrus, BA18	4.684	0.000162
39	−44	−18	495	Fusiform gyrus, BA37	4.451	0.000274

Encoding

Task			Whole brain $p < 0.005$		Identity > emotion	
x	y	z	Voxel	Region	t-Value	p-Value
−1	−54	58	19	Precuneus, BA7	3.374	0.003185
36	−59	51	187	Superior parietal lobule, BA7	3.069	0.006316
7	−67	50	163	Precuneus, BA7	3.521	0.002283
4	−59	40	261	precuneus, BA7	4.013	0.000767
−36	−15	38	670	Precentral gyrus, BA4	3.758	0.001331
6	7	28	97	Cingulate gyrus, BA24	3.591	0.001946
−32	44	24	168	Middle frontal gyrus, BA10	3.320	0.003602
9	−93	4	1208	Cuneus, BA17	4.458	0.000270
40	38	16	131	Middle frontal gyrus, BA46	3.547	0.002155
−13	−94	0	205	Cuneus, BA17	3.742	0.001381

Retrieval

Load			Whole brain $p < 0.005$		Load 3 > Load 2	
x	y	z	Voxel	Region	t-Value	p-Value
−20	58	19	554	Middle frontal gyrus, BA10	3.604	0.001891
21	54	3	498	Superior frontal gyrus	2.358	0.029265
−64	−33	−13	16	Middle temporal gyrus, BA21	3.549	0.002145

Retrieval

Task			Whole brain $p < 0.005$		Identity > emotion	
x	y	z	Voxel	Region	t-Value	p-Value
64	−46	21	52	Superior temporal gyrus, BA22	−2.709	0.013922
−34	−45	−1	281	Parahippocampal gyrus, BA19	−3.652	0.001696
44	−15	1	48	Middle frontal gyrus, BA6	−3.298	0.003783
59	−31	−17	59	Inferior temporal gyrus, BA6	−3.334	0.003490
49	−12	−24	413	Fusiform gyrus, BA20	−4.810	0.000122

Retrieval

Interaction task × load			Whole brain $p < 0.005$		t-Value	p-Value	t-Contrast
x	y	z	Voxel	Region			
−40	−48	55	46	Inferior parietal lobe, BA40	−2.790	0.011676	Ide Load 2 > Ide Load 3
					−2.499	0.024204	Ide Load 2 > Emo Load 2
27	−45	41	97	Precuneus, BA7	−3.079	0.006177	Ide Load 3 > Emo Load 3
−3	61	18	386	Medial frontal gyrus, BA10	3.979	0.000803	Ide Load 2 > Ide Load 3
					−2.566	0.018888	Ide Load 2 > Emo Load 2
					2.349	0.029775	Ide Load 3 > Emo Load 3
23	−27	12	515	Thalamus	−2.400	0.026818	Ide Load 2 > Ide Load 3
					−3.282	0.003919	Ide Load 2 > Emo Load 2
27	−14	−12	134	Parahippocampal gyrus	−3.028	0.006912	Ide Load 2 > Ide Load 3
					4.066	0.000660	Ide Load 2 > Emo Load 2
−5	−14	−17	333	Pons	−3.547	0.002640	Ide Load 2 > Ide Load 3
					−2.839	0.010495	Ide Load 2 > Emo Load 2

Furthermore, we compared hit rate (HT) and false alarms (FA) for the remaining conditions with a 2×2 repeated-measurement-ANOVA (see Table 1). Significant results were found for the factor load (mean HT: $F(1,19) = 5.967$, $p = 0.025$; mean FA: $F(1,19) = 7.598$, $p = 0.013$), but neither for the factor task (HT: $F(1,19) = 0.471$, $p = 0.50$; FA: $F(1,19) = 2.573$, $p = 0.125$) nor the interaction of the two factors (HT: $F(1,19) = 1.022$, $p = 0.325$; FA: $F(1,19) = 0.609$, $p = 0.445$).
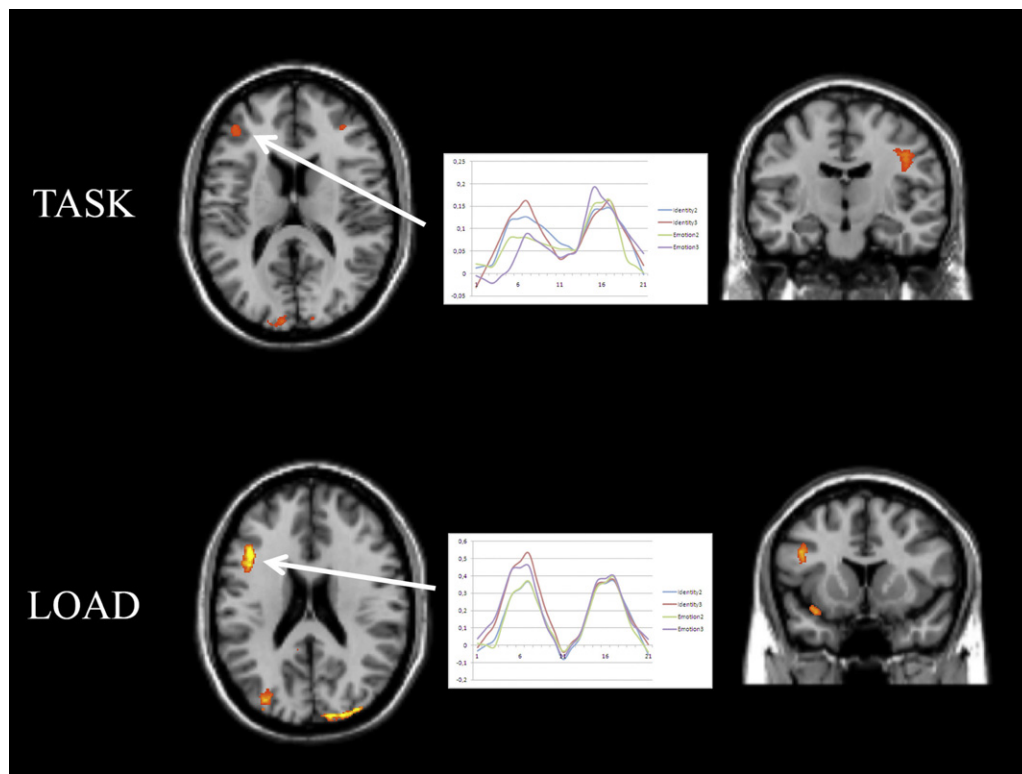
Fig. 2. Axial and coronal slide of the task and load contrast for encoding, whole brain threshold at $p < 0.001$ (uncorr.) for load and $p < 0.005$ (uncor) for task. In the middle time courses of BOLD signal for the designated clusters (time resolution in seconds). For details of clusters with increased BOLD-signal see text and Table 2.
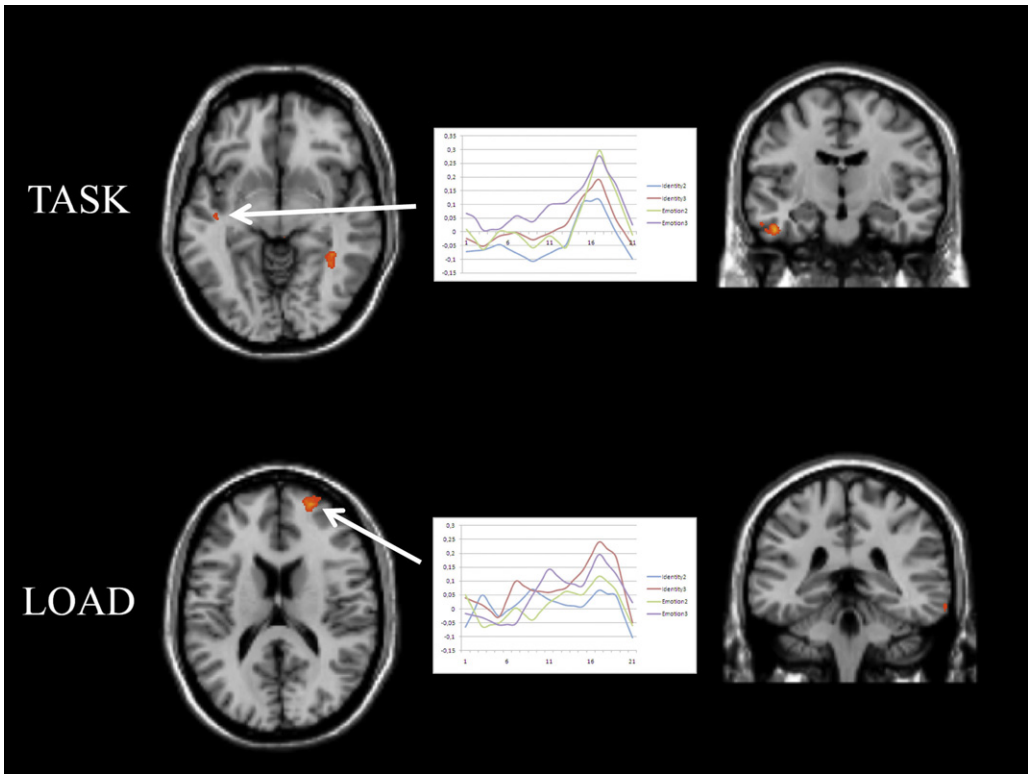
In addition, we contrasted the A'-score for the task-condition (identity vs. emotion) and load (2 and 3) by a 2×2 repeated-measurement-ANOVA. We found a significant load effect ($F(1,19) = 8.356$, $p = 0.009$), reflecting the higher performance for load 2 (mean $A' = 0.86$, $SE = 0.07$) than load 3 (mean $A' = 0.8$, $SE = 0.11$). We found neither a main effect for task (emotion vs. identity) ($F(1,19) = 2.276$, $p = 0.15$) nor an interaction between task and load ($F(1,19) = 0.218$, $p = 0.646$).

We calculated a paired t-test in order to estimate a possible cost of switch between the two tasks. Trials preceded by a trial from the same task (no-switch mean = 0.765, $SD = 0.091$) and trials preceded by a trial from the other task (switch mean = 0.768, $SD = 0.1$), did not differ significantly in accuracy ($t(19) = 0.137$, $p = 0.893$). The same holds true for reaction times (no-switch mean = 1121 ms, $SD = 134$ ms; switch mean = 1137 ms, $SD = 146$ ms; $t(19) = 1.028$, $p = 0.32$).

4. FMRI results

4.1. Encoding

A main effect of load ($F(1,19) = 15.2$, p(uncorr.) < 0.001, cluster size threshold at least 10 voxels), driven by higher activation for load 3, was detected in the medial frontal gyrus, cuneus, inferior occipital gyrus and the lingual gyrus of the left hemisphere and in the superior parietal lobe, precuneus, middle frontal gyrus, inferior occipital gyrus and fusiform gyrus of the right hemisphere (Table 1 and Fig. 2). A main effect of task ($F(1,19) = 10.7$, p(uncorr.) < 0.005, cluster size threshold at least 10 contiguous voxels), driven by higher activation for the identity task, was found in the left middle frontal gyrus, precuneus, cuneus, inferior parietal lobule and precentral gyrus and in the right middle frontal gyrus, superior parietal lobule, precuneus and cingulate gyrus (Table 2 and Fig. 2). No area showed a significant interaction between task and load.

4.2. Delay

A main effect of load ($F(1,19) = 10.7$, p(uncorr.) < 0.005, cluster size threshold at least 10 contiguous voxels), driven by higher activation for load 3, was detected in the left cingulate gyrus, the left thalamus and the right precuneus and medial and middle frontal gyri (Table 3 and Fig. 3). A main effect of task ($F(1,19) = 10.7$, p(uncorr.) < 0.005, cluster size threshold at least 10 contiguous voxels), driven by higher activation for the identity task, was found in the left inferior frontal and the parahippocampal gyri and the right anterior cingulate gyrus, amygdala and cerebellum (Table 3 and Fig. 3). An interaction between load and task ($F(1,19) = 10.7$, p(uncorr.) < 0.005) was found in the right pre- and postcentral gyri, and precuneus (Table 3).

4.3. Retrieval

A main effect of load ($F(1,19) = 10.7$, p(uncorr.) < 0.005, cluster size threshold at least 10 contiguous voxels) driven by higher activation for load 3, was detected in the left middle frontal, middle temporal and right superior frontal gyrus (Table 2 and Fig. 4).

A main effect of task ($F(1,19) = 10.7$, p(uncorr.) < 0.005, cluster size threshold at least 10 contiguous voxels) driven by higher activation for the emotion task, was detected in the right inferior and superior temporal, the middle frontal and the fusiform gyrus and the left parahippocampal gyrus (Table 2 and Fig. 4).

An interaction between task and load ($F(1,19) = 10.7$, df = 19, p(uncorr.) < 0.005, cluster size threshold at least 10 contiguous voxels) revealed effects in the left medial frontal gyrus, inferior parietal lobe and pons, and the right precuneus, thalamus and parahippocampal gyrus (Table 2). Posthoc t-test revealed that this interaction was mainly driven by lower BOLD signal in condition identity load 2 compared with the other conditions (all p's < 0.05).

Table 3
Brain regions exhibiting significant activity of two-way interactions from ANOVA during delay. X, Y and Z represent coordinates in the Talairach space. t- and p-values are derived from region-of-interest analysis.

Delay						
Load			Whole brain $p < 0.005$		Load 3 > Load 2	
x	y	z	Voxel	Region	t-Value	p-Value
18	−18	51	57	Medial frontal gyrus, BA6	3.822	0.001151
−18	−27	42	154	Cingulate gyrus, BA 31	4.473	0.000261
21	−39	39	99	Precuneus	3.729	0.001423
−12	−13	4	17	Thalamus	3.488	0.002461
28	48	−8	132	Middle frontal gyrus, BA11	3.036	0.006790

Delay						
Task			Whole brain $p < 0.005$		Identity > emotion	
x	y	z	Voxel	Region	t-Value	p-Value
−34	42	0	635	Inferior frontal gyrus, BA10	3.642	0.001734
2	0	−5	43	Anterior cingulate gyrus, BA25	3.349	0.003372
−34	−32	−8	70	Parahippocampal gyrus, BA36	3.286	0.003888
6	−30	−17	159	Cerebellum, anterior lobe	3.597	0.001921
16	2	−17	112	Amygdala	3.275	0.003983

Delay							
Interaction task × load			Whole brain $p < 0.005$		Cluster analysis		
x	y	z	Voxel	Region	t-Value	p-Value	t-Contrast
22	−11	65	498	Precentral gyrus, BA6	4.176	0.000513	Ide Load 2 > Ide Load 3
					−2.639	0.016166	Ide Load 3 > Emo Load 3
39	−27	58	175	Precentral gyrus, BA4	2.833	0.010637	Ide Load 2 > Ide Load 3
					−2.955	0.008129	Ide Load 3 > Emo Load 3
50	−33	49	511	Postcentral gyrus, BA40	2.623	0.016730	Ide Load 2 > Ide Load 3
					−2.419	0.025751	Ide Load 3 > Emo Load 3
21	−47	43	510	Precuneus	−3.700	0.001520	Ide Load 2 > Emo Load 2
					4.927	0.000094	Emo Load 2 > Emo Load 3

Fig. 3. Axial and coronal slide of the task and load contrast for delay, whole brain threshold at $p < 0.005$ (uncorr.). In the middle column time courses of BOLD signal for the designated clusters (time resolution in seconds). For details of clusters with increased BOLD-signal see text and Table 3.

Fig. 4. Axial and coronal slide of the task and load contrast for retrieval, whole brain threshold at $p < 0.005$ (uncorr.). In the middle column time courses of BOLD signal for the designated clusters (time resolution in seconds). For details of clusters with increased BOLD-signal see text and Table 2.

4.4. Specificity of effects for the delay period

Based on the present design, we cannot completely rule out that task effects during the delay were carried over from the encoding phase. We addressed this issue by adding phase (encoding, delay and retrieval) as a factor to a whole brain 2 (task: identity vs. emotion) × 3 (phase) repeated measurement ANOVA (cluster size threshold at least 10 contiguous voxels). A significant task × phase interaction was observed in the right amygdala: $F(2,38) = 8.3$, $p < 0.001$, the right parahippocampal gyrus: $F(2,38) = 10$, $p = 0.001$, and the left lingual gyrus $F(2,38) = 10$, $p < 0.001$ (Table 4 and Fig. 5).

The significant phase by task interaction in the right amygdala supported our finding that differences between emotion and identity in this area were only present in the delay period (posthoc t-test encoding n.s.; delay $t(19) = 3.4$ $p = 0.002$; retrieval n.s.). In the three-way interaction task × phase × load $F(2,38) = 8.3$, $p < 0.001$ only one significant cluster in the right precuneus was observed. Posthoc t-test revealed a significant difference for load in the delay phase: $t(19) = 3.221$, $p < 0.005$. All other posthoc t-test for load and task were not significant.

4.5. Covariance analysis with behavioural data

For the cluster of the right amygdala with a significant main effect of the factor task during the delay we calculated an ANCOVA with the mean difference in A' values for the two tasks. We found significant task effects ($F = 7.5$, $p = 0.01$), indicating that difference between identity and emotion was not driven by any performance differences.

5. Discussion

Subjects performed better on load 2 than on load 3, but no differences for task and no significant interaction were observed. The main novelty of the present study lies in the differences in brain activation between the maintenance of identity and emotional expression of faces. These task effects were driven by higher activity in the identity condition during encoding in the frontal and parietal lobe and extrastriate visual cortex and during delay in the frontal and medial temporal lobe including the right amygdala and anterior cingulate gyrus. Conversely, activity associated with the emotional expression condition was higher during retrieval in right frontal

Table 4
Brain regions exhibiting significant activity of two-way interaction task by phase from ANOVA during delay. X, Y and Z represent coordinates in the Talairach space. t- and p-values are derived from region-of-interest analysis.

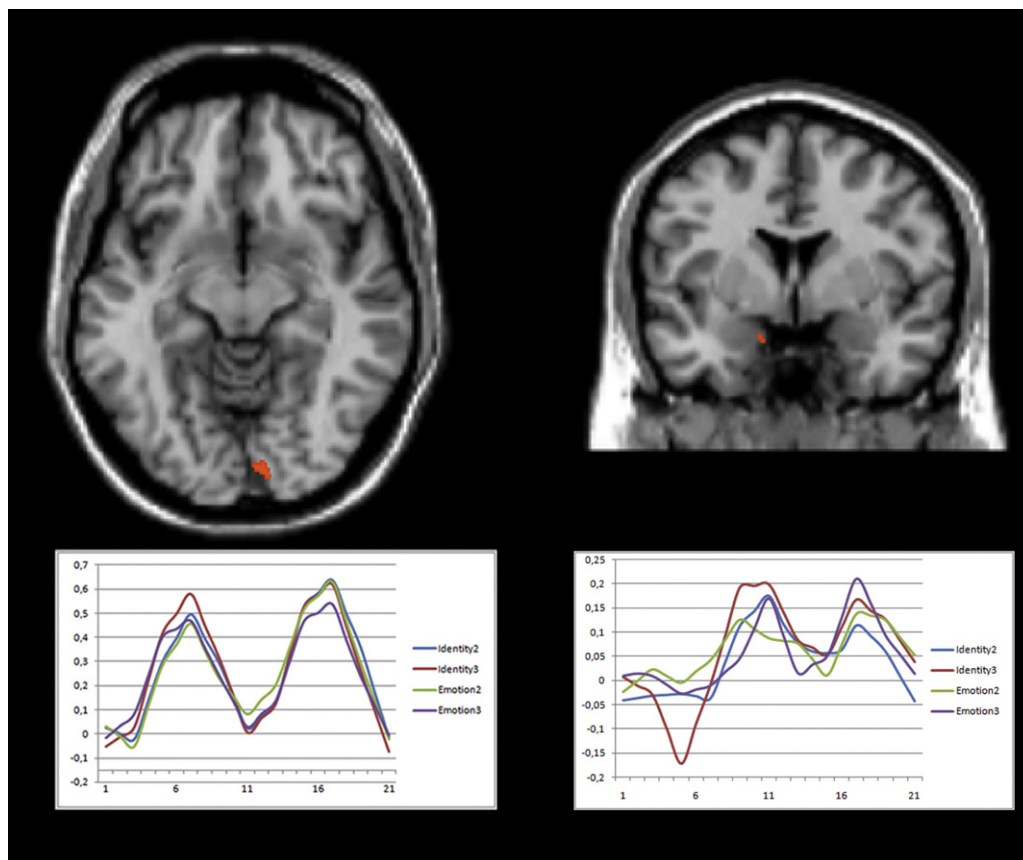| Interaction task × time						
Load			Whole brain $p < 0.001$		Encoding identity > emotion	
x	y	z	Voxel	Region	t-Value	p-Value
18	−10	−19	37	Amygdala	0.060	0.952777
16	2	−17	65	Parahippocampal gyrus	−1.557	0.136041
−7	−85	−4	118	Lingual Gyrus, BA 18	2.880	0.009591

Fig. 5. Axial and coronal slide of the whole brain task by phase interaction, whole brain threshold at $p < 0.001$ (uncorr.). In the upper row two of the three clusters with significant BOLD increase, in the lower row time courses of BOLD signal for the designated clusters (time resolution in seconds). For details of clusters with increased BOLD-signal see text and Table 4.

and temporal areas and fusiform gyrus, and left parahippocampal gyrus.

5.1. Load effects

The behavioural load effect conforms to many studies showing decreasing performance with higher number of faces to be maintained in WM (Jackson et al., 2008). The fMRI load effects correspond to the typical network of visual working memory encoding with BOLD signal enhancement in the frontal, parietal lobe and occipital lobe (Druzgal & D'Esposito, 2003; Jackson et al., 2008). In contrast to Druzgal & D'Esposito (2003) and Jackson et al. (2008) we only find unilateral activation of the fusiform gyrus with increasing load. This may be an effect of comparing only two load conditions. Load effects were additionally seen in the superior parietal lobe, possibly reflecting higher attentional demand with increasing load (Mayer et al., 2007), and in the medial and middle frontal gyrus and occipital lobe (Leung, Oh, Ferri, & Yi, 2007). Several of the prefrontal and occipital regions had shown an increased BOLD-signal during encoding of faces in previous studies as well (Fischer, Sandblom, Nyberg, Herlitz, & Backman, 2007; Hofer et al., 2007; Rama & Courtney, 2005).

The frontal working memory network was also active during the maintenance phase, again conforming to previous work (Munk et al., 2002). In contrast to earlier facial WM studies (Beneventi, Barndon, Ersland, & Hugdahl, 2007; Druzgal & D'Esposito, 2003), we did not find load-dependent activation increases in bilateral fusiform gyrus during the delay. This is in keeping with several studies that did not report significant activation in higher visual areas during delay phases of visual WM tasks (Linden, 2007; Mayer

et al., 2007). No regions of the limbic system, except the left posterior cingulated gyrus showed increased bold signal due to increasing load, probably due to the fact that a variety of different emotions were presented which included faces with neutral expression, similar to Jackson et al. (2008).

5.2. Emotion vs. identity

This was the first study directly to examine the contrast between WM for identity and emotion. LoPresti et al. (2008) compared conditions separately with a control condition, and Jackson et al. (2008) only used an identity condition. The higher encoding-related activity in the frontal and parietal lobes in the identity condition may have been an effect of higher attentional demand. We observed a reverse pattern during retrieval, where activity in several areas was higher for the emotion condition. Because these areas included higher visual areas, this may reflect the higher demand on fine-grained visual analysis at the matching stage of the emotion condition. During delay, higher signal was only observed for the identity condition, for example in the right amygdala and the left parahippocampal gyrus. These two regions showed an increased BOLD-response during active maintenance when comparing faces with a control stimulus, but did not show a task effect in the study by LoPresti et al. (2008), which may have been a result of the low load (one face only) used in that study.

The identity task generally resulted in higher BOLD signal than the emotion task during encoding and delay. Interestingly, structures of the limbic system were less active in the emotion condition during the delay period only. The higher amygdala activity in the identity condition may be driven by repetition effects. Gläscher

et al. (2004) found that repetitive presentation of faces with the same emotion induced a stronger increase in BOLD signal in the amygdala compared to varying emotions. It thus seems that the amygdala is more responsive to the repeated presentation of the same emotion than to rapidly changing emotional expressions (van der Gaag, Minderaa, & Keysers, 2007). The role of the amygdala might be to build up automatically a stable representation of the currently relevant and repeatedly presented emotion and to aid its encoding into long-term memory (LaBar & Cabeza, 2006), but not so much to track rapid changes of emotional context. This interpretation seems to conflict with the study by Breiter et al. (1996), who found a habituation of amygdala activity to the repeated presentation of emotional faces displaying the same emotion. However they compared blocks lasting 36 s which were separated by a time span of 108 s. In the present study a maximum of three faces were presented in a time frame of 2 s, and it thus seems unlikely that habituation due to the repeated stimulation of the same emotion could account for our findings.

In addition to its direct activation by sensory stimuli the amygdala plays an important role in the consolidation of memory (Cahill et al., 1996; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Malin & McGaugh, 2006), its attentional modulation (Gallagher & Chiba, 1996; Gallagher & Holland, 1994; Holland, Han, & Gallagher, 2000) and arousal effects (Mickley Steinmetz, Addis, & Kensinger, 2010). The delay-specific task modulation of amygdala activity may thus reflect the more stable emotional representation that was automatically generated in the identity condition and the associated higher arousal.

Additional regions of the paralimbic system in the bilateral parahippocampal gyrus and in the anterior cingulate gyrus, which both receive projections from the amygdala (Young, Scannel, Burns, & Blakemore, 1994), and the cuneus showed an increased BOLD-signal in the identity task as well. These regions have been reported to be more active in response to dynamic compared to static stimuli (Kilts, Egan, Gideon, Ely, & Hoffman, 2003; Trautmann, Fehr, & Herrmann, 2009). The brief presentation of facial stimuli with varying identity may produce the same effect. The cerebellum showed increased BOLD-response in the identity condition during delay as well. Several other studies (Beneventi et al., 2007; Brahmbhatt, McAuley, & Barch, 2008; LoPresti et al., 2008) found activation in the cerebellum during facial working memory tasks, but its functional role has remained unclear. Hautzel, Mottaghy, Specht, Muller, and Krause (2009) suggested that the extensive involvement of the cerebellum during WM tasks is owed to its contribution to executive processes. A recent meta-analysis (Stoodley & Schmahmann, 2009) has suggested a different topography of cerebellar BOLD-signal changes for the phases of WM tasks, but further research seems necessary to elucidate the specific role of the cerebellum.

A limitation of our paradigm was that it did not allow for separation of the influence of specific emotions, as investigated by Jackson et al. (2008). The advantage of our procedure is that we were able to examine the difference between identity and emotion in a WM paradigm.

A further limitation is that our approach does not completely rule out carry-over effects from the encoding into the delay phase. In working memory studies the BOLD signal change for a given trial phase (encoding, delay retrieval) is not independent of the BOLD response from earlier trial phases (colinearity problem and carry over effects, e.g., Dale & Buckner, 1997). This reduces the accuracy in estimating the portions of the BOLD response attributable to each phase separately (Cairo, Liddle, Woodward, & Ngan, 2004; Manoach, Greve, Lindgren, & Dale, 2003; Ollinger, Shulman, & Corbetta, 2001).

Different designs have been used to address this problem in working memory studies. One method has been to jitter the duration of the maintenance interval (Cairo et al., 2004), but this does not eliminate the colinearity problem (Motes & Rypma, 2010) and the variable duration of the delay phase induces several new cognitive processes and task demands which need to be controlled as separate factors. Another option is the use of delay intervals of more than 20 s (Jha & McCarthy, 2000), resulting in long measurement times and potentially consolidation processes that go beyond classical working memory. A third possible way to control this problem is to model only the middle or later parts of the maintenance response (Feredoes & Postle, 2007; Postle, 2005; Rypma & D'Esposito, 1999). All these described methods (jitter; long delay phases; model late parts of the delay) reduce the influence of the encoding-related BOLD responses on maintenance-related effects, but do not entirely eliminate the colinearity problem (Motes & Rypma, 2010). We therefore decided on modelling the late parts of the delay only (similar to Postle, 2005; with a time gap of 4 s between off-set of the encoding and on-set of the delay predictor) because this design is an efficient without extremely long delay phases.

Further research is needed to assess whether there is a specific WM system for emotionally salient stimuli, and whether it is further subdivided according to categorical emotions. A further limitation is that in order to obtain perfect estimates of brain activity for separate task phases we would have had to jitter the duration of the delay. In the present study we did not use this method, because jittering would also introduce a new factor into the cognitive task, which would have to be modeled in the GLM (with sufficient number of trials per jitter), resulting in very long measurement-times.

In conclusion we describe a network of frontoparietal, limbic and cerebellar brain regions that were more active during the maintenance of identity compared to the emotional expression of faces. These areas, which included the right amygdala, responded more strongly to stable than changing emotional facial expression. Repeated presentation of faces with similar expressions may be needed to build up stable representations of emotions in the amygdala, which will then aid memory for emotional stimuli (Hamann, Ely, Grafton, & Kilts, 1999). Ours is the first study to demonstrate such an effect for memory over brief time scales.

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