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Conscious recollection and illusory recognition: an event-related fMRI study

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Abstract

In this event-related functional magnetic resonance imaging (fMRI) study we examined the neuronal correlates of the subprocesses underlying recognition memory. In an explicit memory task, participants had to discriminate studied ('old') words from semantically related and unrelated 'new' (unstudied) words. We examined whether the correct rejection of semantically related words which were similar to old words, which had elicited correct responses, was based on conscious recollection of study phase information. In this task, false-positive responses to semantically related new words can be assumed to result from the assessment of the semantic similarity between test words and studied words with minimal recollection. For correct identification of old words and correct rejection of new related words we found common activation in a variety of brain areas that have been shown to be involved in conscious recollection, among them the left middle frontal gyrus, the precuneus, the retrosplenial cortex, the left parahippocampal gyrus and the thalamus. For correct responses to old words, the frontomedian wall, the posterior cingulate cortex and the nucleus accumbens were additionally activated, suggesting an emotional contribution to these judgements. Correct rejections of related new words were associated with additional activation of the right middle frontal gyrus, suggesting higher monitoring demands for these more difficult recognition judgements. False-positive responses to semantically related new words were associated with enhanced activation in the frontomedian wall. The results point to an important role of the prefrontal cortex as well as medial temporal and medial parietal regions of the brain in successful memory retrieval and conscious recollection.

Introduction

Memory enables us to re-experience the past. Recollection, the conscious retrieval of information from memory, is a complex process that entails the reactivation of a particular event as well as other information units such as contextual information and other source information from the study episode (Mandler, 1980; Curran, 2000). This form of retrieval can be contrasted with retrieval that is free of contextual information and that is accompanied by a feeling of familiarity (Hintzmann & Curran, 1994; Jacoby, 1991). Familiarity is assumed to result from the assessment of the similarity between a test item and a study item. It entails the experience that a particular event 'reminds one of something'; however, the spatial and temporal context in which the event was initially experienced, i.e. the full recollection experience, is not achieved.

One way to dissociate conscious recollection from other forms of remembering is to investigate the subjective experience accompanying memory retrieval. Tulving (1985) introduced the "Remember/Know" procedure, in which participants responded with an 'R' (remember) response when they explicitly remembered an item and with a 'K' (know) response when they only experienced a feeling of familiarity with an item. A variety of brain imaging studies support the distinction between the two forms of subjective experience during recognition memory judgements: using the event-related potential (ERP) technique, Smith (1993) found enhanced positive potentials between 500 and 700 ms over parietal recording sites for 'Remember' responses relative to 'Know' responses. A similar but topographically more widespread ERP effect for 'Remember' responses was also reported by Düzel *et al*., 1997). Using functional magnetic resonance imaging (fMRI), Henson *et al*. (2000) found that lateral and medial prefrontal brain regions showed differential responses for 'R' and 'K' judgements, confirming the view that the two forms of subjective experience accompanying retrieval have different neuronal substrates.

Another way to dissociate conscious recollection from other forms of episodic retrieval is to use tests of source memory (Wilding & Rugg, 1996; Trott *et al*., 1999). In these tests participants study items in various contexts and at test they have to discriminate studied from unstudied items and must indicate the context (source) in which a particular item was presented. Successful retrieval of item and source information is assumed to involve recollection. In support of this view several ERP studies found enhanced positive potentials over prefrontal areas (Wilding & Rugg, 1996; Senkfor & Van Petten, 1998; Trott *et al*., 1999) and over parietal recording sites (Wilding & Rugg, 1996) in correlation with correct source judgements.

Whilst conscious recollection of an item's prior occurrence in recognition memory tasks in most cases is examined when participants responded 'old' to a particular event, it has recently been proposed that conscious recollection of studied items can also contribute to correct 'new' responses, i.e. in testing conditions in which old and new words are difficult to discriminate. One

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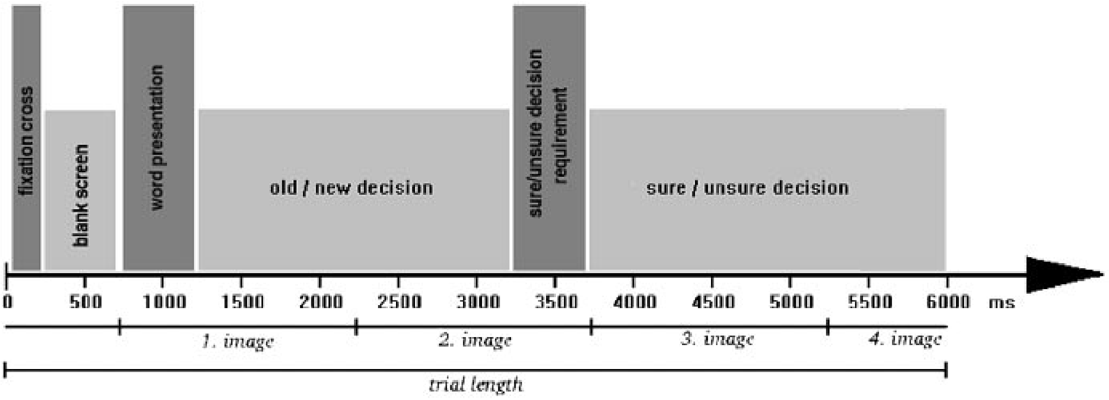

FIG. 1. Temporal sequence of events occurring during one trial in the test phase. Dark grey boxes indicate the appearance of stimuli/orders on the screen. Light grey boxes represent the decision times during which the screen was blank. The first image was acquired time-locked to the presentation of a word, i.e. after 700 ms.

assumption on how participants correctly reject new words that are highly related to old words is that they adopt a recall-to-reject approach (Clark, 1992). To discriminate new and related words from old words, the old words from a study list are recollected and guide the rejection of the related words. Empirical evidence for this approach has been provided by Hintzmann & Curran (1994). Using the response signal technique, in which participants make recognition judgements at various delay after a test stimulus, the authors showed that the likelihood of an erroneous 'old' response to words that share features with the study words declines the more time is allowed to respond. Curran (2000) reported electrophysiological evidence supporting the view that recollection of study phase information supports the rejection of similar test items.

The major goal of the present study was to examine the brain activation patterns contributing to conscious recollection. In particular, we were interested in whether the correct rejection of test items that share similarities with study items, as proposed by the recall-to-reject account, is based on the conscious recollection of study phase information. To examine this issue we used an explicit memory task in which participants have to discriminate old (studied) words from unstudied words that either belong to the same semantic category as studied words or to new semantic categories. In this task, the assessment of an item's familiarity, i.e. its categorical relationship with studied items, is not sufficient for correct 'old' responses and correct rejection of semantically related words. Conscious recollection of study phase information can be assumed for correct 'old' responses. If conscious recollection of studied words also contributes to the correct rejection of related words, we hypothesize overlapping activation patterns in brain areas mediating conscious recollection in both conditions. Whilst both conditions may rely on conscious recollection, there may also be processes that are specific to each of the two conditions (e.g. higher familiarity for correct old judgements). To examine the brain activation patterns that are unique for correct 'old' responses and correct rejections of related words, both conditions were also examined separately. Conversely, false-positive responses to semantically related but new words, i.e. illusory recognitions of similar words, may reflect the fact that participants encounter a studied semantic category, presumably by assessing the categorical similarity between study and test words. No (or only minimal) recollection of the studied category members takes place in this condition. For the correct rejection of categorically unrelated new words we assumed that only minimal attempts for conscious recollection would be undertaken and no or only a little information from the prior study episode would be recollected. For this reason correct classification of unrelated new words served as a contrast for the other retrieval conditions.

Materials and methods

Participants

Twelve healthy right-handed volunteers (six male), age 22–32, participated. All of them were right handed and had normal or corrected-to-normal vision. They had given oral or written consent to their participation and were paid 15 DM per hour for their participation.

Stimulus materials

Our stimulus materials consisted of concrete nouns from 30 categories containing 10 words each. The words within each category were ranked by their mean typicality in a separate experiment (cf. Ullsperger *et al*., 2000). Five words out of the seven most typical words per category were used as semantically related new words during the test phase.

Behavioural procedures

Study phase

In the study phase, 90 words from a total of 18 categories (five words per category) were auditorily presented via earphones. Prior to the presentation of the five words of each category, the category name appeared for 2400 ms on a computer screen. Within a category a new word was presented every 2000 ms. There was a break of 4500 ms, then the next category name appeared. The subjects were instructed to carefully attend to the words and were told that their memory for these words (the 'old' words) would be tested later. After the study phase the participants listened to music of their choice for 14 min. In this period anatomical brain images were acquired.

Test phase

To control for perceptual fluency effects for old words, the test phase was conducted in the visual modality. The temporal sequence of events within a trial (see Fig. 1) was as follows. First, a fixation cross appeared for 200 ms, followed by a blank screen (500 ms). Then a word or a string of Xs (baseline trials) equalling the average length of the words appeared for 500 ms. The subjects were instructed to make an old/new decision directly after the appearance of the word and signal that decision by pressing one of two buttons. For the X-strings, participants were asked to press one of the two buttons and stick with this button during the rest of the baseline trials. They were given 2000 ms (during which the screen was blank) for their response. After that a cue for a subsequent certain/uncertain decision (i.e. was the subject certain or uncertain that the old/new decision was correct) was displayed for 500 ms followed by 2300 ms of a blank screen during which the participants had to make this second decision (for the baseline trials the same button as for the old/new decision was to be used). The overall trial length was therefore 6000 ms. The old/new and the certain/uncertain decision were to be given with the index (old and certain) or middle (new and uncertain) finger of the right hand.

Because an unequal proportion of old and new answers can lead to response bias effects and different strategies in solving the task (Wagner *et al*., 1998; Miller & Wolford, 1999) we tried to achieve an approximately even number of old and new responses. Based on behavioural data from previous experiments using the same paradigm (Nessler *et al*., 2001; Mecklinger *et al*., 1999; Mecklinger, 2000) we expected ≈ 30 of the related words to be classified as new and 60 to be incorrectly classified as old. Therefore, we presented a total of 90 old words, 90 related words, 120 categorically unrelated new words and 150 baseline trials in pseudo-randomized order with no more than two repetitions of trials of the same kind in a row. After 150 trials (one block) there was a short break of approximately 30 s during which the subjects could rest and stretch their fingers.

MR procedures

Acquisition

Magnetic resonance (MR) images were acquired on a 3-Tesla Medspec system by Bruker (Ettlingen, Germany). During the study–test delay period, T1 anatomical, modified driven equilibrium Fourier transform (MDEFT) images (1.5 × 1.5 × 5 mm) were acquired. Echoplanar images (EPI) (3 × 3 mm in plane pixel size; TE = 30 ms) sensitive to blood oxygenation level-dependent (BOLD) changes were recorded during the test phase. Functional images comprised 12 axial slices (5 mm thickness, 2 mm spacing) with the middle of the fifth slice from bottom aligned to the anterior commissure–posterior commissure (AC–PC) line. Images were recorded continuously with a repetition time of 1.5 s synchronized with word presentation, resulting in four images per trial. A total of 1800 volume images was acquired in three runs of 600 images each.

Preprocessing

As successive recordings were made within each image, acquisition times were corrected by applying a temporal Sinc interpolation. Because the first images are usually affected by equilibration effects the first four images of a run were discarded. The three scans were rescaled to the same mean intensity. Low frequency fluctuations in the BOLD signal were removed with a temporal high pass filter using discrete Fourier with a cutoff of 18 s, i.e. three times the trial length. Spatial smoothing was performed with a Gaussian kernel [full width half maximum (FWHM) = 4.935 mm]. Functional data were transposed onto a standard 3D reference brain, and were normalized to average extent values in the space of Talairach & Tournoux (1988) using a linear transformation.

Data analysis

Data were analysed with the software package LIPSIA (Lohmann *et al*., 2000). The statistical evaluation was based on a least-squares estimation using the general linear model (Friston, 1994). Four different word conditions were considered: answers of ‘old’ to old words (old-OLD), answers of ‘old’ to related words (old-REL), answers of ‘new’ to related words (new-REL), and answers of ‘new’ to new (unrelated) words (new-NEW). Two participants showed recognition performance at chance level (< 50% correct new answers) and were therefore excluded from further analyses.

The event-related haemodynamic response to the stimulus onset of each condition was convolved with a Gaussian kernel (FWHM = 6 s.). Group analysis was performed with a random effect model one-sample t-test across all subjects. For the contrasts of interest, t-values were calculated and subsequently transformed into Z-values. For statistical analysis a two-step procedure was used: first, the main effect of word condition vs. baseline was calculated at a threshold of $P < 0.01$, uncorrected. Only those brain regions found active in this contrast were considered for further analysis. Therefore an uncorrected threshold of $P < 0.001$ was applied to the direct contrasts of word conditions (cf. Henson *et al*., 2000b). To assess activation related to conscious recollection we performed an additional analysis of the combined old-OLD and new-REL conditions vs. the new-NEW condition. To analyse unique brain activation for old-OLD and new-REL we further calculated direct contrasts between each of the two conditions and the new-NEW condition.

To precisely localize critical structures found in the group average of the normalized 3D data, activations and corresponding anatomical structures were identified in the individual (functional and anatomical) 2D data of single subjects.

Results

Behavioural data

The hit rate and correct rejection rate were 82.5 ± 3.6 and 90.1 ± 2.4%, respectively. The false-positive response rate to related words was 26.8 ± 2.9% and thus considerably higher than the basic false-positive response rate to new words (9.9%). A one-way repeated-measures ANOVA with the factor answer-type, comprised of the three types of ‘old’ responses (old-OLD, old-REL and old-NEW) revealed a significant main effect ($F_{2,18} = 139.4$, $P < 0.0001$). A *post hoc* comparison confirmed the higher false-positive response rate to related words than to new words ($F_{1,9} = 22.41$, $P < 0.001$). Analysis of the proportion of ‘certain’ and ‘uncertain’ responses revealed a significantly higher proportion of certain than uncertain responses for old-OLD (87.4%, $P < 0.01$) and new-REL (68.2%, $P < 0.03$) responses. For new-NEW and old-REL responses the proportion of ‘certain’ and ‘uncertain’ responses did not differ significantly.

Mean reaction times in the word conditions were as follows: old-OLD, 1137 ± 12.6 ms; old-REL, 1289 ± 27.8 ms; new-REL, 1380 ± 16.7 ms; new-NEW, 1222 ± 11.7 ms. For reaction time data we performed a one-way repeated-measures ANOVA with the four-level factor condition, which comprised those word conditions that were also of relevance for the subsequent analysis of the imaging data (i.e. old-OLD, old-REL, new-REL and new-NEW). This analysis revealed a reliable main effect of the condition factor ($F_{3,27} = 7.37$, $P < 0.001$). *Post hoc* comparisons revealed longer reaction times for correct rejections of related words than for hits ($P < 0.01$) and correct rejections of new words ($P < 0.001$).

Imaging data

Correct answers to old words vs. correct answers to new words

We hypothesized that this contrast would reveal brain activation related to conscious recollection as well as additional activation unique to correct old judgements. We detected a strong BOLD signal at the junction of the inferior frontal sulcus (IFS) and the inferior precentral sulcus [Brodman's area (BA) 8], in the anterior superior insula, the left parietooccipital sulcus, the retrosplenial cortex (RSC) (BA 29/30), the left parahippocampal gyrus and the intraparietal sulcus (IPS) (BA 39).The left thalamus and both nuclei caudati were activated, too. Additionally, we found massive activation in the frontomedian wall (FMW)/anterior cingulate cortex (ACC) (BA 10/32/24). We also found activation of the posterior cingulate cortex (PCC) (BA 23) in the left hemisphere (see Fig. 2).

Interestingly, we also observed an increased BOLD response in the ventral striatum with the most likely candidate being the nucleus accumbens (cf. Fig. 3). However, because the nucleus accumbens is a very small structure it is difficult to separate activation there from activation in the head of the caudate nucleus. Even though the activation averaged across subjects seemed to be located outside the caudate nucleus, we nevertheless performed an anatomical analysis of the 2D functional data of individual subjects. The nucleus accumbens was defined as a cell assembly next to the rostroventral edge of the striatum in the coronal level of the anterior commissure (Nieuwenhuys *et al*., 1988). In eight out of 10 subjects the activation was clearly centred in this area. The nucleus accumbens activity was present bilaterally but was more pronounced in the left hemisphere. The results are summarized in Table 1.

Correct answers to related words vs. correct answers to new words

Similar to the old-OLD > new-NEW comparisons we found an increased BOLD signal along the banks of the IFS/middle frontal gyrus (BA8), the insulae, the parietooccipital sulcus, in the RSC (BA 29/30) and in the left parahippocampal gyrus. We also found activation of the thalamus in both hemispheres and in the left caudate nucleus. The insula, the parietooccipital sulcus and the RSC were activated bilaterally whereas thalamic and parahippocampal activity were left-lateralized as in the old-OLD vs. new-NEW comparison. However, in contrast to the conjunction and the old-OLD vs. new-NEW comparison there was also enhanced activation in the right dorsolateral prefrontal frontal cortex (BA 9/46 according to Petrides & Pandya, 1994).The results are summarized in Table 2.

Correct answers to old words and correct rejections of related words vs. correct answers to new words

To further confirm similarities between old-OLD vs. new-NEW and new-REL vs. new-NEW we calculated a conjunction analysis that comprised the latter two conditions. This contrast should reveal brain areas related to conscious recollection because this is the main feature the old-OLD and new-REL conditions have in common. We detected a strong BOLD signal at the junction of the IFS and the inferior precentral sulcus (BA 8), FMW (BA 10/32/24), the ACC (BA 32), in the anterior insula (extending into the frontal operculum) of both hemispheres and the caudate nuclei of both hemispheres. Further, the left RSC (BA 29/30), the left thalamus, the posterior division of the left parahippocampal gyrus, the inferior bank of the IPS (BA 39) and the parietooccipital sulcus/POS (BA 31) of the left hemisphere were activated in this contrast. All regions showing increased event-related activity for this contrast are listed in Table 3**.**

Incorrect answers to related words vs. correct answers to new words

Incorrect answers to semantically related words most probably result from assessing the categorical similarity between study and test words with only minimal recollection of study phase information. For the old-REL vs. new-NEW comparison we found left lateralized prefrontal activity [superior frontal gyrus (SFG) and along the banks of the IFS] and activity in the frontomedian wall (including ACC activity). There was also enhanced activity in both insulae and both nuclei caudati, and increased BOLD responses in the parietooccipital sulcus. Notably, for this contrast no significant activations in medial temporal and medial parietal regions (i.e. the RSC and the PCC) or in the thalamus were obtained even with a low statistical threshold of $Z = 2.4$ ($P < 0.01$, one-tailed); see Fig. 4.

Because the subjects committed fewer false-positive responses to related words than hit responses or correct rejections of related words, it is conceivable that the absence of significant activation patterns in the old-REL vs. new-NEW contrast results from the lower statistical power in detecting such effects as compared to the aforementioned contrasts. We tested this objection indirectly by performing the aforementioned old-OLD vs. new-NEW and new-REL vs. new-NEW comparisons with the same number of trials that also entered the old-REL vs. new-NEW condition. For this *post hoc* analysis for each subject trials were randomly extracted from the old-OLD and the new-REL conditions until the number of trials matched the number of trials in the old-REL condition. For this *post hoc* analysis the alpha level was set to $u = 2.4$ ($P < 0.05$, one-tailed). In this analysis all above-mentioned effects for the old-OLD vs. new-NEW and the new-REL vs. new-NEW comparisons were still present, indicating that the statistical power in the old-REL vs. new-NEW comparison was, in principal, high enough to detect retrieval-related activity. Table 4 shows the results.

Discussion

In this event-related fMRI experiment we tried to identify brain regions involved in conscious recollection during recognition judgements in an explicit memory task. In particular we examined whether conscious recollection of studied words as proposed by the recall-to-reject account contributes to the correct rejection of semantically related words. Our approach was to use a recognition memory paradigm in which subjects had to make old/new judgements for old words, for new words from new semantic categories and for words that belonged to the same semantic category as the studied words. A conjunction analysis of correct 'old' responses and correct rejections of new words was used to increase the chance to exclude processes other than conscious recollection (such as familiarity, response tendencies, retrieval effort) from the analyses. As both conditions also differ in several respects and by this show unique brain activation patterns, they were also analysed separately.

Erroneous 'old' responses to semantically related new words, i.e. illusory recognition, on the other hand should be based to a large extent on assessing the categorical similarity between the test word and the studied words and by this should involve recollection or recollection attempts only to a minimal extent. The conjunction analysis (old-OLD + new-REL vs. new-NEW), the old-OLD vs. new-NEW and the new-REL vs. new-NEW contrasts revealed retrieval-related activation along the banks of the IFS, in medial temporal and medial parietal regions (i.e. the RSC and the parahippocampal gyrus) and in basal structures such as the thalamus and caudate nucleus.

The left parahippocampal gyrus has been reported in correlation with episodic memory retrieval in other studies (Schacter *et al*., 1996a; Petersson *et al*., 1997; Maguire & Mummery, 1999; Stark & Squire, 2000). It is thought to be an important structure for the consolidation of memories in the temporal lobes as well as in cortical association areas (Eichenbaum *et al*., 1999). The present activation of

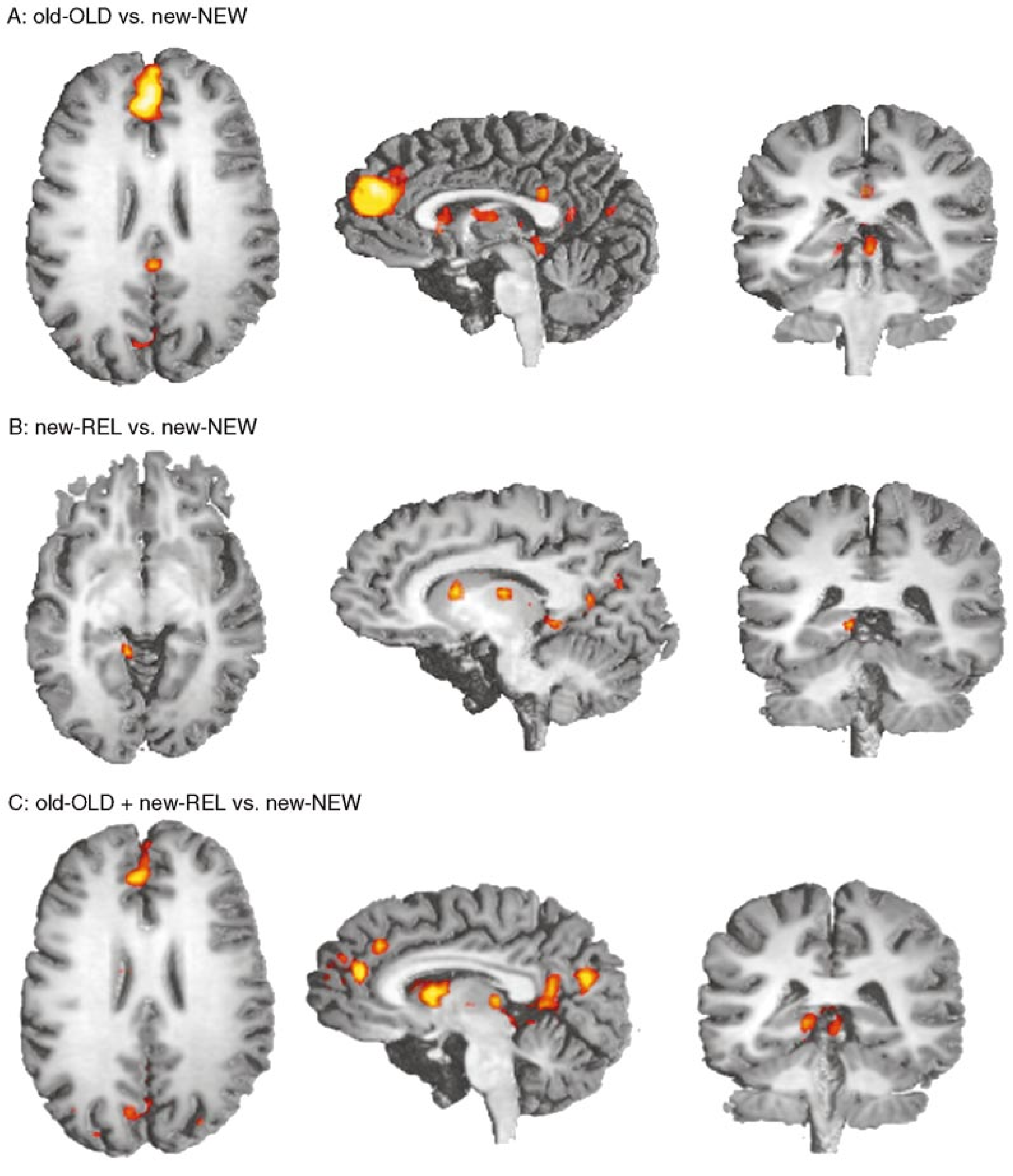

FIG. 2. Images show activations (averaged across subjects) projected on a normalized 3D anatomical reference brain. In the axial and coronal slices the left side corresponds to the left hemisphere of the brain. Sagital views show slices through the left hemisphere. (A) Correct 'old' answers vs. correct rejections of unrelated words (old-OLD > new-NEW). The threshold was set to $Z = 4.4$. The pictures show activity in the FMW/ACC (axial and sagital), in the RSC and POS (sagital). PCC activation is visible in the sagital slice. Parahippocampal activity is visible in the coronal slice. Coordinates and *Z*-scores are listed in Table 1. (B) Correct rejections of related words vs. correct rejections of unrelated words (new-REL > new-NEW). The threshold was set to $Z = 3.4$. Activation in the caudate nucleus, the thalamus, the RSC and the POS are visible in the sagital slice. Activation in the parahippocampal gyrus is visible in all slices. Coordinates and *Z*-scores are listed in Table 2. (C) Correct old answers and correct rejections of related words vs. correct rejections of unrelated words (old-OLD + new-REL > new-NEW). The threshold was set to $Z = 4.1$. Activation in the FMW is visible in the axial and sagital slice. ACC, caudate, RSC and POS activity is visible in the sagital slice; activity in the parahippocampal gyrus is visible in the coronal slice. Stereotaxic coordinates and *Z*-scores can be obtained from Table 3.

FIG. 3. Bilateral activity in the nucleus accumbens and the caudate nucleus' head for correct 'old' answers vs. correct 'new' answers to new words (old-OLD vs. new-NEW). The threshold was set to $Z = 5.0$.

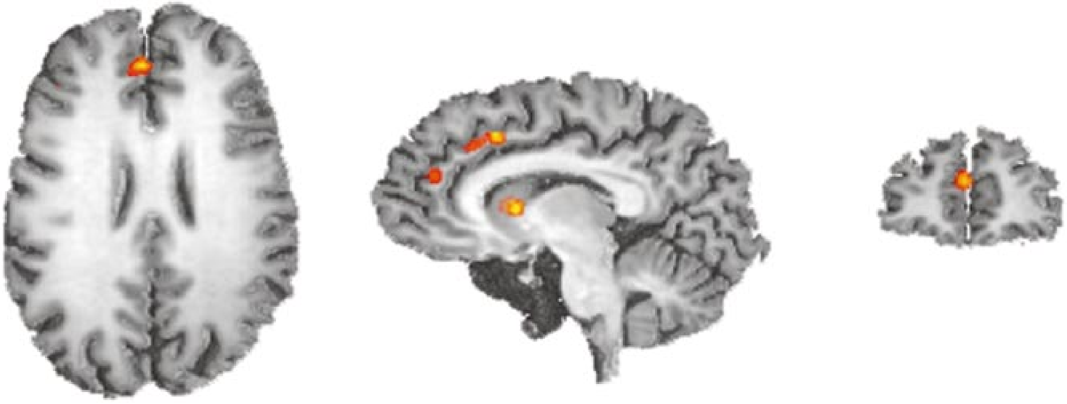

FIG. 4. Activation of the frontomedian wall (all slices), the ACC and the left nucleus caudatus (sagital slice) for incorrect answers to related words vs. correct answers to new words (old-REL vs. new-NEW). The threshold was set to $Z = 3.3$. Z-scores are listed in Table 4.

the parahippocampal gyrus during memory retrieval points to an additional function of this structure in the recovery of explicit memories (cf. Petersson *et al*., 1997; Maguire & Mummery, 1999).

The RSC has been found to be involved in memory retrieval, too. This is indicated by imaging studies (Wiggs *et al*., 1999) and by patients suffering from so-called retrosplenial amnesia (Valenstein *et al*., 1987; Bowers *et al*., 1988; von Cramon & Schuri, 1992). The RSC has strong interconnections with the medial temporal lobes, the PCC and the (anterior) thalamic nuclei (Morris *et al*., 1999; Domesick, 1972). Given its rich interconnectivities, it seems more likely that the RSC serves as a throughput unit with integrating functions rather than as a region in which actual memories themselves are represented (For similar arguments see Wiggs *et al*., 1999).

We also obtained activation in the parietooccipital sulcus extending into the precuneus, a region consistently found during episodic memory retrieval (Fletcher *et al*., 1995a; Reber *et al*., 1998; Henson *et al*., 1999; Krause *et al*., 1999). Contradicting earlier views claiming that the precuneus is responsible for 'imaging' items (Fletcher *et al*., 1995b), Krause *et al*. (1999) showed that the precuneus is activated irrespective of the imagery content of the items that are remembered. The precuneus rather seems to be an amodal representation area with modulating functions for memory retrieval-specific structures. Notably, comparable to old-OLD and new-REL responses, old-REL responses also led to activations in the left precuneus, suggesting that the left precuneus plays a role in both recollection-based and illusory recognition judgements, even though the activation was considerably smaller for erroneous recognition judgements.

The only difference between the two conditions in medial parietal regions was the PCC activation exclusively present in the old-OLD condition. A growing number of imaging studies also report PCC activation in relation to memory retrieval (Henson *et al*., 1999, 2000a; Wiggs *et al*., 1999). Henson *et al*. (1999) reported specific PCC activity in the 'R' condition which is supposed to reflect conscious recollection. Consistent with that finding we obtained PCC activation in the old-OLD condition. Based on single unit recordings during discriminative avoidance learning, Kang & Gabriel (1998) proposed that the posterior cingulate region is forming a circuit especially with the anterior and medial dorsal nuclei of the thalamus and plays an important role for context-specific retrieval, by mediating associative attention. A possible mechanism is that the PCC efferents exert a limiting function in the thalamus (Kang & Gabriel, 1998). Given that the thalamus also participates in other circuits necessary for conscious recollection (e.g. the extended hippocampal diencephalic system as proposed by Aggleton & Brown, 1999), the PCC activation in the old-OLD condition might reflect an associative neuronal pattern that helps to focus on memory contents stored elsewhere in the brain (Gabriel & Smith, 1999). Via its depressing influence on the thalamus the PCC might limit further (unnecessary) activity in other memory circuits. This mechanism may

TABLE 1. Active regions (maxima) for correct old answers (old-OLD) vs. correct new answers (new-NEW)

Region	Talairach coordinates *x*	*y*	*z*	*Z*-value
IFS (L) BA 8	–35	6	33	3.42
FMW (L) BA 9/10/32	–2	52	17	6.70
ACC (L) BA 32	–8	35	30	5.29
Caudate nucleus (L)	–14	9	6	6.02
Caudate nucleus (R)	4	16	8	6.42
Nucleus accumbens (L)	–14	8	1	6.03
Nucleus accumbens (R)	9	8	2	5.31
Insula (L)	–32	15	5	4.73
Insula (R)	25	16	8	4.30
Thalamus (L)	–2	–9	16	4.91
PCC (L) BA 23	–2	–33	33	5.20
RSC (L) BA 29/30	–5	–49	27	4.79
Colliculus sup. (R)	1	–35	7	5.23
Parahippocampal gyrus (L)	–14	–35	7	4.61
POS (L) BA 31	–5	–69	35	5.04
IPS (L) BA 7	–38	–67	43	4.78

L, left hemisphere; R, right hemisphere; BA, Brodman's area; IFS, banks of inferior frontal sulcus; FMW, frontomedian wall; ACC, anterior cingulate cortex; PCC, posterior cingulate cortex; RSC, retrosplenial cortex; POS, parietooccipital sulcus; IPS, interparietal sulcus.

TABLE 2. Active regions (maxima) for correct answers to related words (new-REL) vs. correct new answers (new-NEW)

Region	Talairach coordinates *x*	*y*	*z*	*Z*-value
IFS (R) BA 9/46	34	31	30	3.24
IFS (L) BA 8	–38	14	33	3.81
Insula (L)	–32	17	7	3.40
Insula (R)	25	22	15	3.13
Caudate nucleus (L)	–11	10	15	4.30
Thalamus (L)	–11	–13	18	3.89
Thalamus (R)	4	–7	18	3.46
RSC (L) BA 29/30	–11	–56	26	4.03
RSC (R) BA 29/30	10	–58	29	4.48
Parahippocampal gyrus (L)	–11	–44	12	4.03
POS (L) BA 31	–8	–64	36	3.71
POS (R) BA 31	1	–67	31	3.61

L, left hemisphere; R, right hemisphere; BA, Brodman's area, IFS, banks of inferior frontal sulcus; RSC, retrosplenial cortex; POS, parietooccipital sulcus.

TABLE 3. Active regions (maxima) for the conjunction of correct old answers (old-OLD) and correct rejections of related words (new-REL) vs. correct new answers (new-NEW)

Region	Talairach coordinates *x*	*y*	*z*	*Z*-value
IFS (L) BA 8	–38	9	27	3.86
FMW (L) BA 9/10/32	–8	44	9	5.21
ACC (L) BA 32	–8	36	22	4.76
Caudate nucleus (L)	–11	7	5	5.61
Caudate nucleus (R)	4	15	3	5.13
Insula (L)	–32	15	1	4.84
Insula (R)	25	19	3	4.30
Thalamus (L)	–5	–13	4	4.40
RSC (L) BA 29/30	–5	–50	18	4.73
Parahippocampal gyrus (L)	–14	–38	4	4.57
POS (L) BA 31	–8	–69	30	4.92
IPS (L) BA 7	–38	–68	36	4.36

L, left hemisphere; R, right hemisphere; BA, Brodman's area; IFS, banks of inferior frontal sulcus; FMW, frontomedian wall; ACC, anterior cingulate cortex; PCC, posterior cingulate cortex; RSC, retrosplenial cortex; POS, parietooccipital sulcus; IPS, interparietal sulcus.

TABLE 4. Active regions (maxima) for incorrect answers to related words (old-REL) vs. correct new answers (new-NEW)

Region	Talairach coordinates *x*	*y*	*z*	*Z*-value
SFG (L) BA 9/10	–23	53	23	3.39
FMW (L) BA 9/10/32	–5	45	16	3.90
ACC (L) BA 32	–8	23	38	4.06
IFS (L) BA 8	–40	3	33	3.37
Insula (L)	–32	22	6	4.57
Insula (R)	31	21	4	4.11
Caudate nucleus (L)	–14	16	8	4.44
Caudate nucleus (R)	7	16	10	3.92
POS (L) BA 31	–8	–68	40	3.23
POS (R)	1	–70	32	3.18

L, left hemisphere; R, right hemisphere; BA, Brodman's area, SFG, superior frontal gyrus; FMW, frontomedian wall; ACC, anterior cingulate cortex; IFS, banks of inferior frontal sulcus; POS, parietooccipital sulcus.

help to keep the focus on what has been retrieved. This function may be of special relevance for the explicit recollection of a word's prior occurrence and only of minor relevance when a variety of old words are recollected in order to reject a new but related word, as in the new-REL condition.

The major differences between old-OLD vs. new-NEW and new-REL vs. new-NEW were obtained in the prefrontal cortex: whilst the superior bank of the left IFS was activated in both conditions, presumably reflecting more general semantic processing requirements imposed by the task (Gabrieli *et al*., 1998), only the correct rejections of related words activated the right BA 9/46. The superior bank of the right IFS/middle frontal gyrus has been associated with post-retrieval processing (Rugg & Wilding, 2000), like monitoring or evaluating the output of the retrieval process. Moreover, recent fMRI studies reported higher activity in a highly similar right prefrontal region for 'Know' responses as compared to 'Remember' responses (Henson *et al*., 1999), for low vs. high confidence ratings (i.e. for a higher degree of uncertainty: Henson *et al*., 2000a), and for correct rejections of related words vs. hits (McDermott *et al*., 2000). In the light of these findings, the present results suggest higher monitoring demands, less decision certainty or more retrieval attempts when a semantically related word has to be rejected as compared to correctly encountering an old word.

There also was pronounced FMW activation that extended into the ACC for the old-OLD but not for new-REL condition. Interestingly this activation was also present for erroneous 'old' responses (i.e. in the old-REL condition) indicating that it is not related to successful retrieval but rather to 'old' judgements *per se*. Activation in the FMW is rarely seen in cognitive tasks. Neuropsychological studies suggest that orbital and medial areas of the frontal lobe are of special relevance for the self-monitoring of behaviour and in evaluating its emotional significance (Damasio, Tranel & Damasio, 1990). As all words had a neutral emotional valence we do not assume that the FMW activation reflects the processing of the words' emotional valence but rather a particular emotional significance of giving an 'old' answer.

The assumption of a particular emotional valence of an 'old' response is partly supported by another finding, rarely reported in cognitive tasks, i.e. the activation of the nucleus accumbens in the old-OLD vs. new-NEW condition. This latter activation pattern was present in a previous experiment using the same paradigm (Mecklinger *et al*., 1999). The nucleus accumbens is part of the mesolimbic dopamine-releasing system and plays an important role in reward prediction, motivation and detection of important stimuli during learning (Schwarting, 1997; Hollerman & Schultz, 1998; Tremblay & Schultz, 1999). Because in this experiment the subjects were given no extra reward for good performance nor was there any feedback during the test phase this activity might reflect the subjects' confirmation of the expectancy to be presented with an old word. It is conceivable that under the present testing conditions (i.e. low proportion of old words [0.2] in combination with a rather long test interval) old words in general were evaluated emotionally, as reflected in the FMW activation and, when they lead to a recollection experience, activated a self-initiated reinforcement mechanism, as revealed by the nucleus accumbens activation. This view is supported by the fact that the nucleus accumbens as part of a fronto-striatal circuit receives descending projections from prefrontal cortical areas including the ACC and the FMW and from the limbic system including hippocampal regions (Alexander, 1986; O'Donnel & Grace, 1995; Paus *et al*., 1998).

For false-positive responses to related words a different pattern of results were obtained. The participants indicated that they recognized a word that was never studied and by this claimed a memory for an event that never happened (Schacter & Curran, 2000). In contrast to other brain imaging studies, which compared veridical and illusory memories, the behavioural and neuroanatomical bases of these incorrect recognitions (Schacter *et al*., 1996b, 1997) differ from correct recognitions in several respects. First, the proportion of 'certain' responses was substantially smaller than for correct 'old' responses and correct rejections of related words. Second, incorrect answers to related words did not activate cortical regions such as the PCC and RSC or medial basal temporal lobe structures that have been associated with episodic memory retrieval, and thereby differ significantly from the old-OLD and new-REL conditions. It seems unlikely that the absence of these activations for this condition is only due to the lower number of events obtained for the old-REL condition. This view is supported by the fact that adjusting the trial number in the old-OLD and new-REL conditions to the trial number in the old-REL condition still leads to clear activation patterns in those critical structures. It is conceivable that the assessment of categorical similarity that underlies old-REL judgements entails assessment of links of items with long-term memory information without forming larger representational units that allow recollection to occur. This might be accompanied by only weak activation in structures related to conscious recollection (as indicated by the second-level analysis of the old-OLD and old-REL conditions). The discrepancies between these results and those of other brain imaging studies on illusory recognition that report overlapping brain activity for true and false recognition may be accounted for by the lower proportion of false (incorrect) memories in the present study. Illusory recognition in the present study may be to a large extent based on familiarity assessment (i.e. the assessment of the semantic relationship between study and test words) that did not give rise to recollection experience. Conversely, the high false-positive response rate that equals the hit rates in the above-mentioned studies suggests that conscious recollection may have contributed to the incorrect recognitions.

It has been proposed that the ACC, which showed the strongest activation in the old-REL vs. new-NEW condition, is an important structure for performance monitoring especially under conditions of high task difficulty (Carter *et al*., 1998; Paus *et al*., 1998). It seems unlikely that this activation reflects a process specifically tied to illusory recognition. Rather, it may be associated with a response conflict or enhanced response uncertainty when related words have to be rejected.

In conclusion, the experiment provides insights into the neuronal subprocesses underlying episodic retrieval. In a model recently proposed by Aggleton & Brown (1999), recollection is assumed to rely on the integrity of a so-called Extended Hippocampal Diencephalic System (EHDS) that comprises the hippocampus proper, the fornix, mamillary bodies, anterior nuclei of the thalamus and backprojections to the hippocampus via the cingulum bundle. Even though the present study did not find activation in the hippocampus proper or the mamillary bodies, the present results support the importance of diencephalic, medial temporal and medial parietal structures for explicit memory retrieval. Another unique finding is the activation of the nucleus accumbens in concert with the frontomedian cortex during episodic retrieval under experimental conditions that do not involve direct rewarding.

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Abbreviations

ACC, anterior cingulate cortex; BA, Brodman's area; BOLD, blood oxygenation level-dependent; EPI, echoplanar images; ERP, event-related potentials; fMRI, functional magnetic resonance imaging; FMW, frontomedian wall; FWHM, full width half maximum; IFS, inferior frontal sulcus; IPS, intraparietal sulcus; MDEFT, modified driven equilibrium Fourier transform; MR, magnetic resonance; new-NEW, answers of 'new' to unrelated new words; new-OLD, answers of 'new' to old words; new-REL, answers of 'new' to related new words; old-NEW, answers of 'old' to unrelated new words; old-OLD, answers of 'old' to old words; old-REL, answers of 'old' to related new words; PCC, posterior cingulate cortex; POS, parietooccipital sulcus; RSC, retrosplenial cortex; SFG, superior frontal gyrus.

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