On the Processing of Semantic Aspects of Experience in the Anterior Medial Temporal Lobe: An Event-related fMRI Study

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Abstract

■ Recognition memory based on familiarity judgments is a form of declarative memory that has been repeatedly associated with the anterior medial temporal lobe. It has been argued that this region sustains familiarity-based recognition not only by retrieving item-specific information but also by coding for those semantic aspects of an event that support later familiarity-based recognition. Here, we used event-related fMRI to directly examine whether the contribution of anterior medial temporal lobe to declarative memory indeed results from its role in processing semantic aspects of an event. For this purpose, a sentence comprehension task was employed which varied the demands of semantic and syntactic processing of the sentence-final word. By presenting those sentence-final words together with new words in a subsequent incidental recognition memory test, we were able to determine the mnemonic consequences of presenting words in different sentential contexts. Results showed that enhanced semantic processing during comprehension activates regions in medial temporal lobe cortex and leads to response suppression in partly overlapping regions when the word is successfully retrieved. Data from a behavioral follow-up study support the view that enhanced semantic processing at study enhances familiarity-based remembering in a subsequent test phase. ■

INTRODUCTION

Recognition memory describes the mental capacity of becoming aware that a particular event has been encountered before. Recognition memory is widely viewed as consisting of two qualitative different processes, which are associated with two distinct phenomenal experiences: recollection and familiarity (Rugg & Yonelinas, 2003; Yonelinas, 2002; Brown & Aggleton, 2001). Via recollection, unique details of an episode such as its spatio-temporal context can be retrieved. Familiarity-based recognition reflects the awareness that an event has been experienced before. It leads to a subjective feeling of knowing, without one being able to recall any further details of the prior episode. Some dual-process models assume that familiarity reflects the assessment of memory strength information, whereas recollection rather reflects a threshold retrieval process (Yonelinas, 2002).

Concerning the functional characteristics of both processes, familiarity is supposed to be an automatic, fast-acting process restricted to single or unitized items detached from additional contextual information. Thus, familiarity-supporting representations share important characteristics with semantic long-term memory. Recollection, on the other hand, is a slower process requiring effort or elaboration. As recollection allows the retrieval of associations between arbitrary events, it is a core feature of episodic memory (e.g., Brown & Aggleton, 2001).

Several techniques have been developed to examine the relative contribution of familiarity and recollection to recognition memory, such as the remember/know (R/K) procedure (Tulving, 1985), the process dissociation procedure (PDP; Jacoby, 1991), or the receiver operator characteristics (ROC) method (Yonelinas, 1997). Also, a considerable number of electrophysiological, neuroimaging, animal, and neuropsychological case studies support the distinction between familiarity and recollection (see Aggleton & Brown, 2006, for a review; but see Squire, Wixted, & Clark, 2007, for a different view). Although recollection is assumed to rely critically on the hippocampus proper, familiarity-based recognition is supposed to be instantiated by computations in medial temporal lobe (MTL) cortex comprising entorhinal, parahippocampal, and perirhinal cortices. In support of the latter view, a recent study showed that a circumscribed lesion to perirhinal cortex selectively impairs familiarity-based remembering and does not affect recollection (Bowles et al., 2007).

From a neurocomputational point of view, familiarity is assumed to arise from a sharpening mechanism mediated by anterior MTL structures (Norman & O'Reilly, 2003). This process allows stimulus representations to become sharper over repeated exposures, with fewer neurons distinctively tuned to represent a particular item, while other

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neurons are inhibited. As a consequence, the total activity of anterior MTL cortices in response to a familiar relative to a novel item is decreased. Additionally, by assigning overlapping representations to similar stimuli, the binding characteristics of anterior MTL cortices allow for the representation of the shared structure of events and therefore make it possible to generalize to novel stimuli as a function of their similarity to previously encountered items. From this view, it follows that the anterior MTL cannot support recall of specific event details owing to its inability to sufficiently differentiate the representations of different events. This sharpening model is supported by a number of recent findings. Intracranial recordings in monkeys performing visual recognition tasks indicate that up to 25% of neurons in perirhinal cortex react strongly to items that are new, but only weakly when the items have been seen before. Moreover, these neurons show single-exposure learning, that is, responses to the even second appearance of a stimulus already show some attenuation. Such response reductions are found even after extended delays involving the presentation of many other stimuli (Aggleton & Brown, 2006; Brown & Aggleton, 2001). A recent study with intracranial recordings in humans also demonstrated a dramatic decrease in the number of cells in the anterior MTL responding to repeated as compared to novel stimuli (Viskontas, Knowlton, Steinmetz, & Fried, 2006). By showing that item recognition (i.e., familiarity) in humans is related to decreased activation in the anterior MTL, recent fMRI studies are consistent with those intracranial recording data (Fernández & Tendolkar, 2006; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Weis et al., 2004; Henson, Cansino, Herron, Robb, & Rugg, 2003). Lately, a parametric analysis of familiarity-based responses showed that activity in perirhinal cortex linearly declined with the amount of perceived familiarity (Daselaar, Fleck, & Cabeza, 2006; Montaldi, Spencer, Roberts, & Mayes, 2006).

Furthermore, two recent brain imaging studies demonstrated that encoding in anterior MTL selectively predicts familiarity-based recognition (Davachi, Mitchell, & Wagner, 2003; Ranganath et al., 2003). Referring to these studies, Diana, Yonelinas, and Ranganath (2007) argued that during encoding the anterior MTL should be more active for items that are subsequently judged as more familiar, because increased processing at study leads to strengthened and more efficient item representations, resulting in anterior MTL deactivation during retrieval to the extent that the item is familiar. Thus, anterior MTL regions seem to subserve familiarity-based recognition not only by retrieving item-specific information but also by coding for the semantic aspects of an event that can support later familiarity.

Furthermore, activity modulations in the anterior MTL can also be induced at the sentential level, that is, by semantically incongruent sentence endings such as "I ordered a ham and cheese *scissors*." ERP studies with intracranial electrodes revealed that semantic incongruencies and violations elicit a negativity at around 400 msec in anterior MTL of the collateral sulcus (the AMTL N400; Meyer et al., 2005; McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995). Similarly, in scalp-recorded ERPs, the so-called N400 has also been shown to respond to semantic violations. The N400 is thought to reflect the access of conceptual information in semantic long-term memory. It varies systematically with the processing of potentially meaningful stimuli and it is reduced by a variety of factors that increase these items' predictability in the local context at the word or sentence level (Kutas & Federmeier, 2000), be it due to a match with the preceding sentential context (McCarthy et al., 1995) or to semantic expectedness in the context in which they appear (Kutas & Hillyard, 1984).

Interestingly, no N400 is observed in sentence contexts containing grammatical violations, that is, in sentences whose terminal verb is incongruent with the preceding context due to a double (semantic *and* syntactic) violation (Hahne & Friederici, 2002). The absence of an N400 in such sentence contexts suggests that words that are not syntactically licensed are not semantically integrated during on-line language comprehension. In support of this view, a recent study with intracranial recordings revealed that syntactic integration problems do not elicit an AMTL N400 (Meyer et al., 2005).

Preliminary evidence from ERP studies suggests a functional relationship between the N400 at encoding and familiarity-based remembering in a later memory test (Meyer, Mecklinger, & Friederici, 2007; Mangels, Picton, & Craik, 2001). These studies revealed that items eliciting a large negative deflection around 400 msec after item onset at encoding later tend to be retrieved on the basis of familiarity, irrespective of whether familiarity was operationally defined with behavioral (Mangels et al., 2001) or ERP variables (Meyer et al., 2007).

The present event-related fMRI study aimed at investigating the effect of enhanced semantic and syntactic processing at encoding on subsequent recognition memory qualities. Previous fMRI studies investigating the correlation between MTL activity and later familiarity-based versus recollection-based recognition compared brain activity at encoding on the basis of subsequent item or source memory performance (Davachi et al., 2003; Ranganath et al., 2003). Using a similar approach, in the present study, we directly manipulated encoding processes by introducing semantic and syntactic violations in sentence-final words of the study phase. For this purpose, we used a sentence comprehension task, which was composed of sentences that were either correct or contained a semantic or a syntactic violation. In contrast to correct and easily interpretable sentence endings, semantically incongruent sentence endings require enhanced semantic processing to integrate the word into the sentence context. Syntactically incongruent sentences—containing a word category error—instead trigger enhanced syntactic processing and prevent semantic integration processes (Friederici, 2002).

In a subsequent incidental recognition memory test, the critical sentence-final words were presented again together with new words not presented in the preceding sentence comprehension task. To prevent strategic encoding processes in the study phase, participants were not informed about the following recognition memory test. Additionally, to control for perceptual fluency in the test phase, a cross-modal task procedure was used (spoken sentences at study and visually presented words at test).

The extent to which semantic processing at study modulates retrieval-related brain activation should be reflected in the contrasts between correctly recognized words from the semantic violation condition and the correctly recognized words from the remaining sentence conditions. If enhanced semantic processing at encoding contributes to the formation of familiarity-supporting memory representations in anterior MTL regions, then those items violating a sentence primarily semantic at study should be those to display the neural marking of familiarity-based recognition at test, that is, a neural deactivation in the anterior MTL (Daselaar, Fleck, & Cabeza, 2006; Fernández & Tendolkar, 2006; Montaldi et al., 2006; Gonsalves et al., 2005; Weis et al., 2004; Henson et al., 2003).

Based on earlier studies, we additionally expect activity in neocortical brain regions being involved in sentence comprehension and recognition memory processes. Semantically and syntactically anomalous sentences as the ones used in the present study have been used in several fMRI studies. These studies have consistently shown greater activation for sentences with semantic or syntactic anomalies in a variety of regions in the left inferior frontal (BA 44, 45, and 47) and left superior temporal lobes (BA 41 and 22) (Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Friederici, 2002; Newman, Pancheva, Ozawa, Neville, & Ullman, 2001; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Friederici, Meyer, & von Cramon, 2000; Kuperberg et al., 2000; Ni et al., 2000; Caplan, Alpert, & Waters, 1998; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996).

In the test phase, contrasting correctly recognized old words with correctly rejected new words should reveal activity of the hippocampus proper, fronto-polar cortex, the precuneus, and some parietal lobe regions including retrosplenial cortex and regions in the neighborhood to the intraparietal sulcus as suggested by previous findings (Kahn, Davachi, & Wagner, 2004; Maril, Simons, Mitchell, Schwartz, & Schacter, 2003; Konishi, Wheeler, Donaldson, & Buckner, 2000; McDermott, Jones, Petersen, Lageman, & Roediger, 2000; Nolde, Johnson, & D'Esposito, 1998).

METHODS

Participants

Sixteen native speakers of German (7 men, aged 22–33 years, mean age = 25.2 years) participated in the study after giving informed consent. All participants had normal or corrected-to-normal vision and were right-handed as determined by self-report. No participant had any history of neurological or psychiatric disorders.

fMRI Data Acquisition

Twenty axial slices (4 mm thickness, 1 mm interslice distance, in-plane resolution of 3.5 × 3.5 mm) were acquired every 1750 msec during functional MR measurements (BOLD sensitive gradient-echo EPI pulse sequence: TR = 1750 msec, TE = 50 msec, flip angle = 85°, FoV = 224 mm^2) with a 1.5-T Siemens Sonata system. The first four volumes were discarded to allow for T1 equilibration. Prior to functional imaging, T1-weighted images (TR = 600 msec, TE = 13 msec, flip angle = 80°, slice thickness = 4 mm, interslice gap = 1 mm, in-plane resolution = 1 × 1 mm, 20 axial slices parallel to AC–PC plane) were obtained, which were used to coregister functional scans with previously obtained high-resolution whole-head 3-D brain scans (3-D MP-RAGE).

Materials

The sentence material of the study phase consisted of 96 spoken German sentences, which were either correct, contained a selectional restriction violation (i.e., a semantic violation by a word that is not an instance of the possible set of words restricted by the preceding context), or a syntactic phrase structure violation. All sentences ended with transitive verbs in the imperfect passive form. In semantically incongruous sentences (e.g., *Das Gewitter wurde gebügelt–The thunderstorm was ironed*), the meaning of the verb "ironed" could not be incorporated into the preceding sentence context. In the syntactically incorrect sentences (e.g., *Das Hemd wurde am gebügelt–The shirt was on ironed*), the participle immediately followed a preposition (*am–on*), thus yielding a phrase structure error. In addition to correct sentences (e.g., *Das Hemd wurde gebügelt–The shirt was ironed*), we presented correct filler sentences (e.g., *Das Hemd wurde am Samstag gebügelt–The shirt was on saturday ironed*), which contained a completed prepositional phrase as well as the participle construction and were included to ensure that participants could not predict a syntactic violation based purely on the presence of a preposition. These filler sentences were not included in the fMRI analysis. The sentences were spoken by a trained female native speaker, recorded and digitized, and presented auditorily to the participants via headphones. The same set of sentences has been repeatedly used in previous studies (e.g., Hahne & Friederici, 2002). Sentence duration was about 1700 msec on average. No repetitions of particular sentence-final target words occurred in the study phase and all target words were matched in frequency and length across the experimental conditions.

The test phase included 288 words (144 nouns and 144 verbs). Both the 72 old nouns (serving as control items) and the 72 old verbs where chosen from the three critical types of study sentences (correct, syntactically incorrect, and semantically incorrect). The items were presented visually and old and new words were matched in terms of word frequency and length. Nouns and verbs from the same study sentence were separated by at least ten intervening test items. A maximum of three words from the same word type were presented in succession.

Experimental Procedure

An experimental session consisted of one study and one test block; the whole session was run in the scanner. Subjects were not informed beforehand that there would be a memory test. Inside the scanner, they were equipped with earphones and their gaze was directed to a screen. Each study trial was initiated by presentation of a fixation asterisk in the center of the screen 400 msec before onset of the auditory presentation of the sentence. At 3000 msec after the end of the sentence, question marks cued participants to judge the correctness of the sentence. The type of error (i.e., semantic or syntactic) was irrelevant to their task. Incorrect responses and unanswered trials were not included in the data analysis. In the test block, which started 10 min after the termination of the study block, single words were presented centrally on the screen for 1000 msec each. Subjects were asked to judge whether each word was old (i.e., previously heard) or new; they were given a maximum of 2000 msec to respond. Unanswered trials were not included in the data analysis. All study and test responses were made by pressing one of two buttons of a response box with the index fingers of their hands. The assignment of the left and right index fingers to the "old" and "new" response buttons was counterbalanced across subjects.

Data Analysis

On the behavioral level, analyses involved one-way repeated-measure ANOVAs with a three-level condition factor (formally correct, semantically violated, and syntactically violated). We analyzed the proportion of correct responses in the classification task of the study phase and, to examine recognition memory performance for the verbs from the critical conditions, mean *Pr* values of the test phase. *Pr* values are measures that estimate the accuracy of memory judgments by subtracting the false alarm rate (taken as an estimate of guess responses) from the hit rate (Snodgrass & Corwin, 1988). Therefore, a *Pr* value of 1 indicates perfect recognition performance, whereas a *Pr* value of 0 indicates chance performance. Reaction time was defined as the interval between the appearance of the test item and the participant's keypress.

The functional imaging data were analyzed with the software package BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands). Functional data were first corrected for slice time acquisition differences, using the first scan time within a volume as a reference for alignment by sinc interpolation and then for motion artifacts by aligning all acquired volumes to the first volume of the first scanning session via rigid-body transformations. Low-frequency signal changes and baseline drifts were removed by applying a temporal high-pass filter. The images acquired during the functional session were coregistered with the high-resolution full-brain scan and were then transformed by linear scaling to a standard size (Talairach & Tournoux, 1988). The transformation parameters obtained from this step were subsequently applied to the preprocessed functional images, yielding a 4-D data representation (3 × space, 1 × time). Finally, the volume time-course representations were spatially smoothed with a Gaussian kernel, full width at half maximum of 6.0 mm.

The statistical evaluation was based on a least-squares estimation using the general linear model (Friston et al., 1995; Friston, 1994). The rapid event-related design matrix was generated by modeling each conditional event using a box-car function of 1-sec duration convolved with a two-gamma function model of the hemodynamic response with the onset of the critical item. This was the sentence-final verb of the three sentence types (correct, semantically incorrect, and syntactically incorrect) for the study phase. For the test phase, accurately recognized old verbs from the three different sentence conditions and correctly rejected new words were defined as predictors. Correctly recognized old nouns, misses, and false alarms were included as predictors of no interest. Additionally, the 3-D motion parameters (as estimated during preprocessing) were added as predictors of no interest in both blocks.

A three-step procedure was used for the statistical analyses. First, for each participant, the following contrast images were generated for the study block: correct sentence endings versus average baseline, syntactically violated sentence endings versus average baseline, and semantically violated sentence endings versus average baseline, representing the main effects of the critical conditions. For the test phase, contrast images for correctly recognized verbs versus correctly rejected new words were generated. In a second step, contrasts were computed at the group level by performing one-tailed t tests on these images, treating subjects as random effects. BOLD responses were considered significant if they consisted of at least 10 contiguous voxels that exceeded an uncorrected threshold of $p < .001$ (Forman et al., 1995). Additionally, given the lower signal-to-noise ratio often observed in MTL regions due to susceptibility signal loss (e.g., Schacter & Wagner, 1999), a more liberal threshold of $p < .005$ (together with the aforementioned spatial extent criterion) was used to identify MTL activity when appropriate.

For archival purposes, results for all local maxima are summarized in Tables 1 and 2. However, we only discuss results obtained in regions in the anterior MTL and the

Table 1. Brain Regions Activated by Correct Sentence Endings and by Syntactic and Semantic Violations ($p < .001$)

Area	*Left/Right*	*BA*	*Number of Voxels*	*x*	*y*	*z*	Z_{max}
(A) Correct Sentence Endings							
Anterior transverse temporal area	L	41	72	−38	−32	13	4.56
	R	41	100	46	−23	11	5.67
Superior temporal gyrus	L	22	1661	−58	−18	3	6.79
	R	22	1562	56	−13	2	7.09
Insula	L	13	273	−29	19	13	5.35
(B) Syntactic Violations							
Anterior transverse temporal area	L	41	120	−37	−33	13	5.35
	R	41	52	51	−20	8	4.61
Superior temporal gyrus	L	22	1735	−57	−21	3	6.90
	R	22	1219	57	−15	2	6.34
Insula	L	13	512	−35	17	10	5.67
Middle frontal gyrus	L	9	485	−50	10	30	5.74
Pars triangularis (IFG)	L	45	351	−48	23	6	6.20
Pars opercularis (IFG)	L	44	104	−44	17	9	4.99
(C) Semantic Violations							
Anterior transverse temporal area	L	41	285	−39	−31	14	5.73
	R	41	386	49	−22	11	6.05
Superior temporal gyrus	L	22	1484	−57	−18	3	6.95
	R	22	1507	56	−14	2	6.66
Insula	L	13	932	−34	14	10	5.76
	R	13	176	43	−19	8	5.61
Middle frontal gyrus	L	9	694	−51	14	28	5.57
Pars triangularis (IFG)	L	45	539	−45	22	7	5.70
Pars opercularis (IFG)	L	44	118	−47	16	14	5.09
Pars orbitalis (IFG)	L	47	183	−46	24	1	5.33
Entorhinal area	R	28/34	14	19	−12	−13	4.35

Table 2. Brain Regions Showing Significantly Greater BOLD Signal ($p < .001$) for Correctly Recognized Words than for Correctly Rejected Words

Area	*Left/Right*	*BA*	*Number of Voxels*	*x*	*y*	*z*	Z_{max}
Middle frontal gyrus	L	10	36	−38	48	12	5.23
Medial frontal gyrus	L	8	11	−3	22	47	4.43
Cingulate cortex	L	32	36	−5	17	36	4.27
Precuneus	L	31	100	−6	−72	27	4.57
Angular gyrus	L	39	101	−51	−64	11	5.30
Middle temporal gyrus	L	21	65	−58	−29	−13	5.12
Hippocampus	R		24	31	−24	−5	5.01

left inferior frontal gyrus (IFG), given that this study was designed to test a priori hypotheses regarding the roles of these regions in language comprehension and recognition memory. In order to restrict the search space for specific contrasts and to further characterize the fMRI results, in a third step hemodynamic responses were assessed both in a priori predicted regions of interest (ROIs; BA 36, BA 44, BA 45, BA 47) defined via the AFNI Talairach–Tournoux Atlas + tlrc dataset (as provided by the NIMH, Bethesda, MD) as well as in voxels that showed an overall experimental effect in the contrast analyses.

Finally, connectivity analyses based on the general linear model were carried out for each subject by extracting the average time series for a seed region. The time series were entered as covariates of interest in a whole-brain linear regression analysis to find voxels whose time course was correlated with that of the seed region over the whole run. Thereafter, connectivity images for each individual were entered into a random effects analysis as described above (see Waites, Briellmann, Saling, Abbott, & Jackson, 2006, for a similar procedure).

RESULTS

Sentence Comprehension and Recognition Memory Performance

All subjects were highly accurate in classifying the sentences. The proportion of correct responses was 0.92 (*SD* = 0.07) for correct sentences, 0.92 (*SD* = 0.09) for semantically incorrect sentences, and 0.85 (*SD* = 0.12) for syntactically incorrect sentences. Analysis revealed that the classification of the syntactically violated sentences tended to be more difficult than the classification of the other conditions [cor vs. syn: $F(1, 15) = 4.09, p < .07$; sem vs. syn: $F(1, 15) = 3.97, p < .07$].

The analysis of memory performances revealed no reliable differences between the three item types [$F(1, 15) = 0.55, p = .47$; Pr_{cor}: .25 (*SD* = .18); Pr_{syn}: .27 (*SD* = .15); Pr_{sem}: .29 (*SD* = .18)]. In all three cases, recognition accuracy was different from zero, thus chance performance could be ruled out. The statistical analyses for reaction times also showed no reliable differences between the four response categories relevant for the analyses [correct old responses to verbs from the three conditions, RT_{cor}: 1148 msec (*SD* = 437 msec); RT_{syn}: 1340 msec (*SD* = 308 msec); RT_{sem}: 1281 msec (*SD* = 258 msec); and new responses to new verbs, RT_{new}: 1313 msec (*SD* = 492 msec); $F(3, 45) = 2.24, p = .10$].

fMRI Results

The primary question was whether the *processing* of semantic violations is associated with *increased* activation in anterior MTL regions, whereas the correct *recognition* of words from sentences with semantic violations (vs. correct sentences and sentences containing a syntactic violation) is associated with a *decreased* activation in anterior MTL regions.

In order to identify regions involved in semantic processing, we examined regions in which activation was significantly increased for words that violated a sentence semantically. As shown in Figure 1, a region showing semantic integration-related activation was observed in the right entorhinal area (BA 28 and BA 34).

A subsequent assessment of the response pattern in the right entorhinal area confirmed that this region was sensitive to semantic integration. This region was more active in response to semantic violations relative to syntactic violations [sem > syn: $t(15) = 6.81, p < .02$] and also tended to be more active in response to semantic incongruent sentence endings relative to correct endings [sem > cor: $t(15) = 4.43, p < .07$], whereas activity did not differ significantly between syntactic incongruent and correct endings [syn > cor: $t(15) = -1.10, p = .28$]. Additionally, a significant activity increase for the processing of semantic violations in comparison to correct sentence endings and syntactic violations could be found in both rhinal sulci, which were treated as a single ROI [BA 36; sem > cor + syn: $t(15) = 2.38, p < .05$]. Furthermore, we also found a significant activity difference in the rhinal sulci for the processing of semantic violations in comparison to syntactic violations [sem > syn: $t(15) = 3.97, p < .01$] as well as for the processing of syntactic violations in comparison to correct sentence endings [syn > cor: $t(15) = -2.96, p < .01$]. However, a direct contrast of semantic violations and correct sentence endings across both rhinal sulci failed to reach significance.

Along the IFG, semantic and syntactic violations activated comparable regions (BA 44, BA 45) with the exception that the semantic activation in the IFG expanded more into its pars orbitalis (BA 47). For the processing

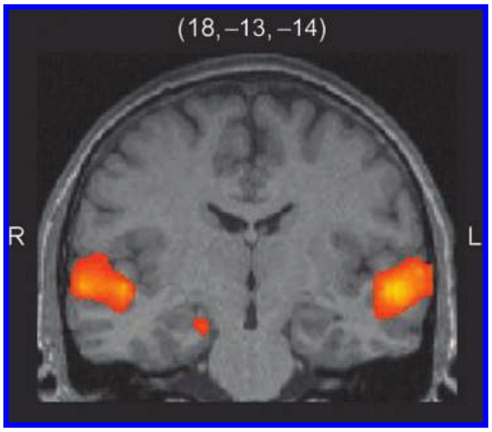
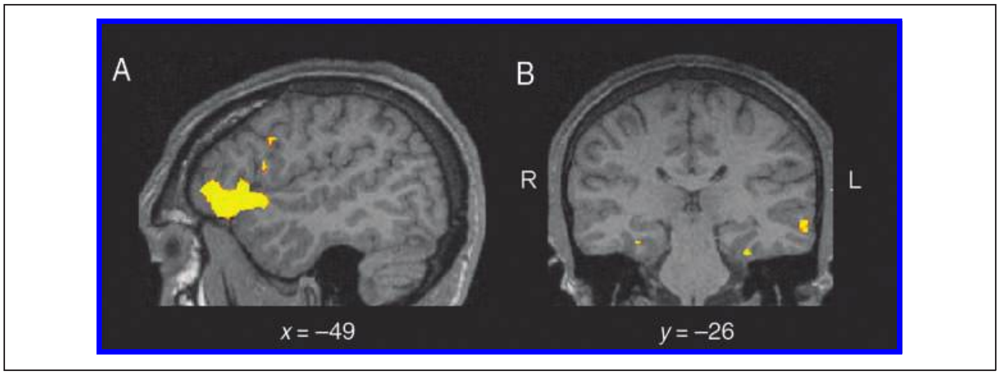


Figure 1. Significant BOLD signals in the superior temporal lobes (STG) and right entorhinal cortex to semantic violations (x, y, z: 18, −13, −14), relative to average baseline (thresholded at $p < .001$, uncorrected for multiple comparisons), superimposed on a Talairach-normalized T1-weighted brain image.

Figure 2. Functional connectivity between (A) the left pars orbitalis (BA 47) in the inferior frontal lobe, (B) the left temporal lobe and the perirhinal cortices during sentence comprehension (thresholded at $p < .000001$, uncorrected for multiple comparisons), superimposed on a Talairach-normalized T1-weighted brain image.



of correct sentence endings, activation was found neither in inferior frontal areas nor in the anterior MTL.

The involvement of the pars orbitalis (BA 47) in semantic processing was underpinned by subsequent ROI assessments. Although activity to semantic and syntactic violations was significantly higher than for correct sentences in the left BA 44 [sem > cor: $t(15) = 13.07$, $p < .0008$; syn > cor: $t(15) = 8.94$, $p < .01$] and the left BA 45 [sem > cor: $t(15) = 12.73$, $p < .000002$; syn > cor: $t(15) = 7.87$, $p < .005$], semantic violations, but not syntactic violations, differed from correct sentences endings in left BA 47 [sem > cor: $t(15) = 6.01$, $p < .01$; syn > cor: $t(15) = 1.79$, $p = .65$].

Functional connectivity analysis of the left pars orbitalis (BA 47), which was selectively activated by semantic violations during the sentence comprehension phase, revealed correlated hemodynamic responses in perirhinal cortices and in the left middle temporal gyrus (BA 21) over the whole study block (Figure 2). Neither BA 44 nor BA 45 activity was correlated with any MTL activity.

In the test phase, retrieval-related activity [Hits > Correct Rejections] was observed in prefrontal, medial, and parietal cortices as well as in the lateral and MTLs. In prefrontal cortex, we found increased hemodynamic responses in the anterior part of the left medial frontal gyrus (BA 10). On the medial surface, clusters of differential activation were observed in the medial part of BA 8 in the right hemisphere, in left cingulate cortex (BA 32), and in the left precuneus (BA 31). Moreover, activity in the gyrus angularis (BA 39) was enhanced for hits relative to correct rejections. Finally, retrieval-related activity was also observed within the temporal lobe, including the left medial temporal gyrus (BA 21) and the right hippocampus.

In order to examine the extent to which semantic processing at study was related to episodic retrieval, we directly contrasted correctly recognized words from the semantic violation condition with the two other sentence conditions (sem_hit > cor_hit + syn_hit, $p < .005$). This contrast revealed a selective activity reduction in the left rhinal sulcus (BA 36) in the vicinity of perirhinal cortex for words from the semantically violated sentences (Figure 3). No MTL modulations were obtained by the two complementary contrasts [syn_hit > cor_hit + sem_hit; cor_hit > sem_hit + syn_hit]. A subsequent ROI analysis confirmed the sensitivity of this left perirhinal region for the recognition of words from previously semantically violated sentences [sem_hit < cor_hit: $t(15) = 3.52$, $p < .005$; sem_hit < syn_hit: $t(15) = 2.68$, $p < .02$; syn_hit < cor_hit: $t(15) = 1.54$, $p < .14$].

DISCUSSION

In the present study, fMRI was used to investigate the neural bases of the hypothesized functional relationship between semantic integration processes during language comprehension and familiarity-based recognition memory. For that purpose, we applied a sentence comprehension task, which varied the semantic integration demands for sentence-final words. Presenting those critical sentence-final words again within a recognition memory test enabled us to determine the consequences of presenting words of similar length and frequency in different sentential contexts on recognition memory quality. It was expected

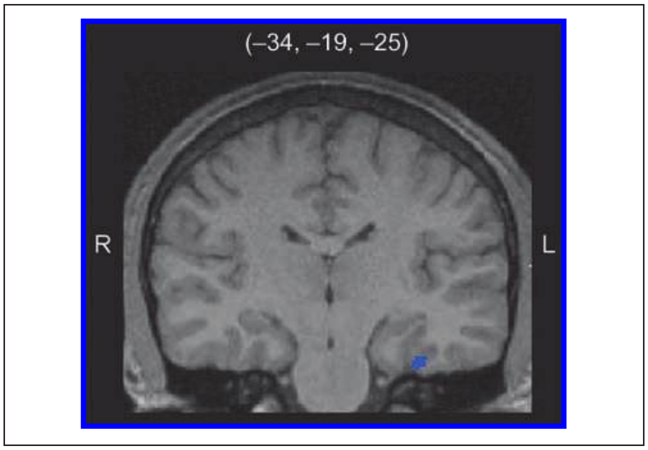


Figure 3. Significant BOLD signals in left perirhinal cortex (BA 36) to correctly recognized words from the semantically violated sentences (x, y, z: −34, −19, −25), relative to correctly recognized words from the two other sentence conditions (thresholded at $p < .005$, uncorrected for multiple comparisons), superimposed on a Talairach-normalized T1-weighted brain image.

that enhanced semantic processing during encoding forms familiarity-supporting memory representations and that this process is reflected by modulations in the anterior MTL.

The Anterior MTL during Encoding and Retrieval

In the present fMRI study on sentence comprehension, we observed semantic integration processes to be mediated by enhanced activity in the anterior MTL, in particular, in right entorhinal and bilateral perirhinal cortices. This is consistent with previous findings from intracranial ERP depth recordings (Meyer et al., 2005; McCarthy et al., 1995; Nobre & McCarthy, 1995) and fMRI studies (Newman et al., 2001) using other paradigms during study phase. The activation pattern in the sentence comprehension phase partly overlapped with the deactivation pattern in the test phase but extended further into the anterior part of right entorhinal cortex.

The anterior MTLs receive input from multiple sensory areas as well as amodal inputs via connections to the lateral temporal cortices. They likely play a role in object perception and identification by binding the various attributes of an object into a reified representation (Murray & Richmond, 2001). Hence, they may be sufficient for the representation of factual (i.e., semantic) information (Mishkin, Vargha-Khadem, & Gadian, 1998). From a neurocomputational point of view, a mechanism which assigns overlapping representations to similar stimuli (Norman & O'Reilly, 2003) permits the extraction of the shared structures of items. From this perspective, the anterior MTL cortices can be considered as higher order convergence zones, which integrate simple semantic features into a single amodal representation. These regions do not actually store concept representations themselves, but rather are critical for the concerted retrieval of feature information belonging to different concepts. Hence, the observed anterior MTL activation in response to semantic violations is supposedly a sign of increased demands on semantic memory access given the lack of concept preactivation by the preceding sentential context. In the normal case of easily interpretable sentence endings, preactivation has been accounted for by a mechanism of spreading activation (Collins & Loftus, 1975) or conjoint frequency (Wilkins, 1971). According to the former account, activation is spread from one node in semantic memory to neighboring nodes representing related concepts, thereby facilitating responses via preactivation. The latter account is based on the notion of the frequency of co-occurrence of two words or concepts in everyday experience.

A possible explanation for the right lateralization of entorhinal activation in response to semantic violations can be derived from the auditory presentation modality of the study phase. Entorhinal neurons not only receive highly preprocessed major inputs from the perirhinal and parahippocampal cortices but also direct inputs from the ipsilateral auditory association areas, such as BA 22 (in the superior temporal gyrus) and BA 52 (parainsular cortex; Amaral, Insausti, & Cowan, 1983). The observed activation in right entorhinal cortex in the semantic violation condition might be interpretable in the context of those language functions known to reside in the right hemisphere. Spoken language comprehension requires the brain to extract not only semantic and syntactic information but also the intonational form of a sentence. Whereas the former processes are thought to be based on neural networks implemented mainly in the left hemisphere (Friederici, 2002), it has been suggested that the neural extraction of prosodic information is mainly right-lateralized (Meyer, Steinhauer, Alter, Friederici, & von Cramon, 2004; Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002; Pell & Baum, 1997; Behrens, 1985; Blumstein & Cooper, 1974). Hence, the observed activation of right entorhinal cortex in response to semantic violations could, in principle, have resulted from direct inputs from the prosodic sensitive right superior temporal lobe. However, this should hold for all auditorily presented sentences, be they correct or incorrect. As correct sentences and sentences containing syntactic violations did not elicit any MTL activity, this issue could not be verified in the present data.

An objection against this enhanced semantic processing account for right entorhinal activation could be that accuracy during language comprehension tended to be lower for sentences with syntactic violations than the other sentence types and that the activation differences in the right entorhinal could have been contaminated by these performance differences. However, this seems very unlikely for the following reasons: First, a marginally significant enhancement in the right entorhinal area was obtained for semantic violations relative to correct sentences, even though the sentence comprehension level was the same for both conditions. Second, entorhinal activation was indistinguishable for syntactic violations and corrects sentences even though comprehension performance tended to be lower in the former condition. This suggests that the entorhinal activation pattern was not affected by the performance differences in sentence comprehension.

The Fronto-temporal Networks during Sentence Processing

Both semantic and syntactic violations elicited enhanced activation in BA 44 and 45 in the left IFG. Semantic violations, in addition, activated the anterior part of the left IFG (BA 47). These data partly replicate fMRI studies that used the identical sentence structures with the same violation types (Rüschemeyer, Fiebach, Kempe, & Friederici, 2005; Friederici et al., 2003). The activation of BA 47 has been found to be correlated with increased semantic processing demands (Fiez, 1997; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Thus, this region seems to play an important role in strategic semantic processes by providing a top–down influence on posterior regions and by facilitating the retrieval of semantic representations (Badre & Wagner, 2007). This direct influence on activity in the temporally localized conceptual stores was observable in a functional coupling between those areas. During language comprehension, activity in the left BA 47 was correlated with hemodynamic changes in left lateral temporal cortex (BA 22) and the rhinal cortices (BA 36). This was not the case for activity in BA 45.

Brain Regions during Recognition Memory

Brain regions associated with global recognition memory processes were identified by contrasting the activity elicited by correctly recognized old items with those of correctly rejected new ones. The results revealed a network of prefrontal, medial, parietal, and temporal cortices including the hippocampus, and thus, are consistent with a large number of previous fMRI studies investigating the neural correlates of recognition memory (see Henson, 2005, for a review).

Notably, only for verbs from semantically violated sentences, which activated the anterior MTL during encoding, did we observe a decrease in left perirhinal cortex activation during retrieval. Anterior MTL deactivation for items judged to be familiar has been quite consistently reported in previous functional neuroimaging, animal, and intracranial recording studies (Daselaar, Fleck, & Cabeza, 2006; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Montaldi et al., 2006; Viskontas et al., 2006; Gonsalves et al., 2005; Weis et al., 2004; Aggleton & Brown, 2005). Accordingly, a recent meta-analysis of several event-related fMRI studies suggested that anterior MTL deactivation is related to familiarity-based remembering (Henson et al., 2003).

The combined findings from the study and test phases suggest that semantic memory access can, in fact, set the stage for later familiarity-based recognition memory. The increased semantic retrieval demands in the case of semantically violated sentences strengthen the memory representation of the item which subsequently supports familiarity. These present results are in line with previous work from our lab showing a correlation between the N400 in the sentence comprehension phase and the frontal old/new effect, that is, the putative electrophysiological correlate of familiarity, in the test phase (Meyer et al., 2007). Although surface-recorded ERPs cannot precisely localize the neural mechanisms underlying both processes, they can provide evidence for a functional relationship between semantic access during encoding and familiarity-based recognition memory at test. The current fMRI data provide more specific information on the brain mechanisms involved and, by this, extend our previous findings in important ways.

However, the design of this experiment (which was hold identical to the aforementioned ERP study due to comparability) in which participants were required to give mere old/new judgments did not allow us to derive direct behavioral estimates of recollection and familiarity. Also, we assumed that the differences in the quality of remembering, that is, enhanced familiarity-based remembering for semantically violated words, as suggested by the anterior MTL deactivations, may have been too subtle to be reflected by changes in hit rates or response speed in the present recognition memory paradigm.

To directly test whether enhanced familiarity-based remembering after semantic processing is also obtained when familiarity and recollection are operationalized using behavioral measures, a follow-up behavioral study with the same sentence materials and target items was conducted. We used the ROC method to derive estimates of recollection and familiarity (Yonelinas, 1997). Rather than giving "old" and "new" judgments, the participants ($n = 10$) in this study were required to judge their decision confidence on a 6-point scale ranging from 1 (*sure old*) to 6 (*sure new*). Responses 1 to 3 reflect "old" responses, whereas Responses 4 to 6 were taken to represent "new" responses. In light of previous studies showing that familiarity is available earlier than recollection (e.g., Diana et al., 2007), we aimed at enhancing the likelihood of familiarity-based responses by decreasing item presentation time and the response window by 500 msec. All other task characteristics were the same as in the fMRI study. In order to obtain behavioral estimates of familiarity and recollection, a formal dual-process model was fitted to the empirically obtained ROC points (i.e., the proportions of hits and false alarms across confidence levels). Consistent with the hypothesis that words violating a sentence semantically during study should be recognized mainly on the basis of familiarity, the results revealed a higher familiarity estimates (d' value) for semantically violated words as compared to words from correct sentence endings and from syntactically violated sentences. To test the statistical significance of these observations, the model was next fit to individual ROCs. These estimates were subjected to a Condition (correct, semantic incorrect, and syntactic incorrect) by Estimate (d', R) ANOVA, which revealed significant main effects of condition [$F(2, 9) = 5.88, p = .01$] and of estimate [$F(1, 9) = 15.52, p < .01$], and a significant Condition × Estimate interaction [$F(2, 18) = 4.26, p < .05$]. Planned comparisons (using one-tailed p values) revealed that familiarity (d') was significantly lower for the correct condition than for the semantic condition [$t(9) = -3.45, p < .01$] and was also lower for the syntactic condition than for the semantic condition [$t(9) = -1.75, p = .05$]. Familiarity estimates of the correct and the syntactic condition did not differ. Moreover, there was a marginally significant difference between the correct and the semantic condition for the estimate of recollection [$t(9) = 1.61, p = .07$], with recollection being higher in the correct condition.

Taken together, in showing that estimates for familiarity-based remembering derived from behavioral data are largest for words from semantically violated sentences, the results from this follow-up study support the view that familiarity-based remembering is, indeed, enhanced after enhanced semantic processing. By this, they provide converging evidence that recognizing words that fostered semantic processing at study is associated with familiarity-based remembering.

Conclusion

The findings of the present study demonstrate that strongly preactivated semantic representations can lead to facilitated access to conceptual information related to a test word. Aspects of semantic retrieval during language comprehension and the familiarity part of recognition memory seem to rely at least in part on analogous brain areas, namely, the rhinal cortices, which in turn might explain their previously detected functional relationship. Given these results, it might be reasonable to leave behind the classical modular view of specific language-related semantic processes and specific memory-related semantic processes and start to think in terms of the representations that brain structures contain and the computations that they perform (Bussey & Saksida, 2007).

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