Why is the Meaning of a Sentence Better Remembered Than its Form?  
An fMRI Study on the Role of Novelty-Encoding Processes

J. Poppenk, G. Walia, A.R. McIntosh, M.F. Joanisse, D. Klein, and S. Köhler

ABSTRACT: Episodic memory is based primarily on meaning. This is behaviorally well documented in studies on memory for prose, in which the meaning of novel sentences is typically well remembered but information pertaining to exact wording and syntax is not. The neural basis of this ‘verbatim effect’ is poorly understood. In the current fMRI study, we manipulated the novelty of sentences at different levels to test whether medial temporal lobe (MTL) regions that are known to play a critical role in verbal episodic encoding would respond preferentially to the novelty of sentence meaning. Fifteen participants were pre-familiarized with auditory sentences describing unique episodes. During scanning, they encountered sentences that were old, that contained a change in (i.e., were novel in terms of) syntactic relationships, that contained a change in semantic relationships, or that described an entirely novel episode. Subsequently, participants performed a recognition memory test for the different types of novel information encountered. Behavioral data confirmed the typical verbatim effect. Analyses of fMRI data revealed differential MTL activation in the left hippocampus and entorhinal cortex with a response profile across conditions that paralleled the behavioral results; the identified region responded selectively to those conditions that contained semantic novelty. Other regions, by contrast, showed a novelty response that did not share this selectivity. Our findings suggest that the verbatim effect can be linked to hippocampally-based novelty-assessment processes that operate based on semantic relationships. © 2008 Wiley-Liss, Inc.

KEY WORDS: episodic memory; verbatim; novelty; hippocampus; medial temporal lobe

INTRODUCTION

What distinguishes those aspects of our daily experiences we remember from those we do not? One important cause of not remembering is failing to initially encode the relevant information, i.e., failing to create a corresponding record in the first place. Tulving and Kroll (1995) proposed that successful encoding of episodes depends on the presence of novel information. Support for this notion comes from functional neuroimaging research showing that novel stimuli activate brain regions that are known to play a role in episodic memory encoding. For example, numerous studies, involving various materials (e.g., scenes, faces, words) and tasks, have been reported in which the presentation of novel as compared with previously encountered stimuli was associated with increased activity in the medial temporal lobe (MTL; Stern et al., 1996; Tulving et al., 1996; Strange et al., 1999; Constable et al., 2000; Hunkin et al., 2002; Köhler et al., 2002; Düzel et al., 2003; Habib et al., 2003; Henson et al., 2003; Schott et al., 2004; Kumanar and Maguire, 2006). Importantly, a direct link between such novelty effects and encoding processes has also been demonstrated. Kirchhoff et al. (2000) found that the functional magnetic resonance (fMRI) signal in the very same MTL regions that are sensitive to the novelty of pictures of scenes predicted which scenes would subsequently be remembered successfully and which ones would not. Although such research has clearly established a role for novelty in triggering the cascade of cognitive and neural processes that lead to successful encoding of information in episodic memory (Ranganath and Rainer, 2003; Bunzeck and Düzel, 2006), it also raises many new questions. One of the most important ones is: what is the type of novel information that elicits a response from the MTL regions that support episodic encoding (e.g., Köhler et al., 2005; Nyberg, 2005; O’Kane et al., 2005)?

A substantial body of evidence from cognitive psychology indicates that episodic memory is primarily meaning-based. For example, research on memory for word lists has consistently demonstrated that words are better remembered when they are processed in terms of their semantic characteristics at the time of encoding than in terms of their phonological features (i.e., the levels of processing effect; Craik and Lockhart, 1972). With more complex verbal structures, it has been shown in the psycholinguistic literature that humans typically remember the meaning of sentences and prose well, but not their specific wording or syntax (this phenomenon is referred to here as the verbatim effect to make reference to poor memory for verbatim information in discourse; Sachs, 1967, 1974). Viewed in relation to the role of novelty at encoding, both lines of evidence suggest that it may be at the level of semantics that novelty triggers episodic encoding processes. Moreover, given that the content of new sentences and prose is typically novel at the level of...
relationships between their elements, rather than at the level of individual words, the available evidence also points to a critical role of relational processes in the verbatim effect.

With regard to the neural mechanisms underlying this effect, there is considerable evidence to implicate the MTL, and specifically the hippocampus, in the processing of those flexible relationships that characterize episodes (see Cohen et al., 1999; Eichenbaum, 2004; Davachi, 2006; Eichenbaum et al., 2007; Mayes et al., 2007 for reviews). For example, several neuropsychological studies have been reported in which hippocampal lesions were linked to disproportionate deficits in associative recognition compared with item recognition (Vargha-Khadem et al., 1997; Mayes et al., 2002; Giovanello et al., 2003; Turriziani et al., 2004; Holdstock et al., 2005). It has also been known for some time that large MTL lesions that include the hippocampus produce deficits in memory for prose (Frisk and Milner, 1990; Isaac and Mayes, 1999). Frisk and Milner observed this deficit in patients who underwent left-sided resection of the anterior temporal lobe for treatment of intractable epilepsy. In their study, the extent of removal from the hippocampal region was related to the severity of the deficit in prose learning and retention. Returning to the issue of novelty, although neuroimaging studies have shown novelty signals in the hippocampus that are specific to relationships (e.g., Pihlaja­mäki et al., 2004; Köhler et al., 2005), no systematic investigation has been conducted in the domain of prose processing. Given the behavioral literature on the verbatim effect, one might predict that the hippocampal response to novel sentences is specific to the semantic relationships they express. In the present fMRI study, we tested this hypothesis using sentences that describe unique episodes.

In a typical verbatim-effect paradigm, participants first listen to or read passages of text or a series of unconnected sentences. Subsequently, they are asked to distinguish previously presented sentences from semantically changed or paraphrased versions. In such an experimental setup, participants readily recognize semantic changes during the recognition test, but regularly fail to distinguish paraphrased versions from the original sentences. Cognitive research building on this paradigm supports the view that the verbatim effect is indeed an encoding and not a storage phenomenon. For instance, Begg and Wickelgren (1974) observed a verbatim effect immediately after learning of the original sentences but showed that the differentially acquired semantic and syntactic information followed the same retention function.

For the current neuroimaging study, we developed a variant of the typical verbatim-effect paradigm that allowed for an fMRI investigation of the sensitivity of the hippocampus to different types of novelty in sentences at the time of encoding. The paradigm involved three phases (see Fig. 1): (1) a pre-scanning familiarization phase, in which participants listened to auditory sentence stimuli, each describing a unique episode; (2) a novelty-encoding phase, in which participants were scanned while listening to sentences that were either identical to the originals, changed in terms of their syntax, changed in terms of a specific semantic relationship in the episode, or that were entirely new in terms of the episode described; and (3) a post-scanning recognition memory test for the sentences encountered during scanning in Phase II. Phase I served to provide a set of familiar stimuli from which novel derivatives could be created. Phase II allowed us to examine differential fMRI activation for the various types of novelty. To assess any potential role of attentional focus on this novelty response, we also manipulated incidental encoding instructions (syntactic vs. semantic focus) in this phase. Finally, Phase III allowed us to determine the effectiveness of encoding processes for the different types of novel information encountered in Phase II, and thus to verify that the verbatim effect was indeed present.

**FIGURE 1.** Schematic of the three-phase protocol used in the current experiment. Different sentence types are shown in boldface (see Table 1).

![Diagram](https://via.placeholder.com/150)

**METHOD**

**Participants**

Fifteen neurologically healthy students and researchers at the University of Western Ontario, all English native-speakers with normal or corrected to normal vision and hearing, participated in the experiment (7 female; age range 22–37 years, mean age 28.0). They were screened for the absence of neurological and psychiatric conditions and compensated for participation. Fourteen of the participants were right-handed and one was ambidextrous. One additional participant was excluded due to overall near-chance performance on the behavioral task and another was excluded due to severe scanner artifacts. The protocol for this study was approved by the Health Sciences Research Ethics Board at The University of Western Ontario.

**Stimulus Materials**

Forty-eight sentence sets were created, each based upon a unique and vivid episode. Each set consisted of seven distinct sentences (see Table 1): one base sentence, two semantic and syntactic derivatives of this base sentence and two sentences that were entirely novel. Sentences were syntactically altered by shifting a clause within the base sentence to a new position.

**TABLE 1**

<table>
<thead>
<tr>
<th>Description</th>
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<tr>
<td><strong>Familiarization task</strong></td>
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<td><em>Base</em></td>
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<td><strong>Incidental novelty-encoding task</strong></td>
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<td><em>Base</em></td>
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<td><strong>Semantic focus</strong></td>
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<td><strong>Syntactic focus</strong></td>
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<td><strong>New</strong></td>
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<td><em>New 1</em></td>
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*FIGURE 1. Schematic of the three-phase protocol used in the current experiment. Different sentence types are shown in boldface (see Table 1).*
such that the surface sentence structure, but not the meaning, was changed. Semantic alterations were introduced by replacing a pivotal verb or noun of the base sentence while maintaining the original word order. To ensure that semantic novelty was relational in nature (i.e., included new relationships among concepts) rather than stimulus-based (see Nyberg, 2005), semantic substitutions were obtained from other base sentences. The sentences describing entirely novel episodes were designed to be similar in complexity to the base sentences in each set (based on mean number of independent and dependent clauses), but described other distinct episodes. The base sentences were presented for familiarization in Phase I. Subsequently, they served as old sentences during scanning in Phase II, along with one semantic derivative, one syntactic derivative and one of the entirely novel sentences from the set. All three types of novel sentences from Phase II were used as target items in the forced-choice recognition-memory test in Phase III. The remaining novel sentences from the sentence sets were used as lures in Phase III (again one of each novelty type; see Fig. 1). Assignment of the two versions of each novel sentence type was counterbalanced across participants for Phases II and III. For recording purposes, all sentences were read aloud by the same female speaker at a similar volume and duration (sentence length range 5.0–6.9 s, mean length 6.4 s) and were digitized at a sample rate of 22,000 Hz, 16-bit quantization. While inside the magnet bore, participants listened to these auditory stimuli using a pneumatic headphone set.

**Experimental Tasks**

Participants were informed that the study consisted of three parts in which they would be asked to make subjective judgments about a series of sentences. To ensure that incidental rather than intentional novelty encoding took place, no reference was made to the fact that their memory for these sentences would be tested (Kormi-Nouri et al., 2005). All experimental tasks were preceded by practice trials. Two different types of incidental orienting tasks were employed, both utilizing four-point rating scales for the subjective judgments required. The ‘positiveness’ scale required participants to judge the emotional valence of the episodes described. The ‘well-formedness’ scale required participants to judge the quality of the sentence form. Participants provided responses with an MR-compatible four-button keypad. Written task instructions and fixation crosses were projected onto a screen for viewing via an overhead mirror in the scanner.

During familiarization in Phase I, participants encountered four blocks of twelve sentences. Instructions for the type of incidental encoding judgment required preceded each of the four blocks. During playback of each sentence, a fixation cross was displayed. Subsequently, a scale appeared for 2 s and participants were instructed to make their response while the scale was on the screen. A 1 s fixation cross followed each trial. The familiarization task was administered inside the fMRI scanner (with no scanner activity) to maintain a constant environment between Phases I and II.

During fMRI scanning in Phase II, participants encountered four runs of 10 blocks, with each block corresponding to a single experimental condition with three sentences. Every run consisted of four blocks of old sentences and two blocks of sentences of each novelty type. Half of the blocks for each experimental condition required the ‘positiveness’ judgments, while the other half required the ‘well-formedness’ judgments. Task and experimental conditions were presented in a pseudorandom order with the constraint that each condition appeared on average in the same position as all other conditions during each run. Order was also counterbalanced across participants. Each trial in Phase II started with a 1 s presentation of instructions for the incidental encoding judgment. Following the playback of a sentence, participants expressed their judgment using the same type of scales employed in Phase I within a 2 s period. A fixation cross was then displayed during a 1 s intertrial interval. Since the length of each sentence varied to some extent, block duration was standardized to 33 s by presenting a fixation period at the end of the block for up to 5 s.
Fifteen minutes after the end of the scanning session, a forced-choice recognition memory test was administered in Phase III. The test consisted of 60 pairs of sentences, each pair including one of the sentences encountered as new in Phase II and a lure sentence from the same set and type (see Table 1) that had not previously been encountered by the participants. In 20 of the 60 pairs, the sentences differed from each other in terms of syntax. In another 20 pairs, they differed in terms of a semantic relationship. In the remaining pairs, targets and lures described completely distinct episodes. In each trial of the forced-choice recognition task, a pair of target and lure sentences was auditorily presented in random sequence, followed by a prompt to provide a response as to which had been heard previously in Phase II. Participants were instructed that the sentences would always differ in some way and to listen carefully for such differences. A repeat option was available for each sentence pair. Timing of responses was self-paced.

Functional Data Acquisition and Image Analysis

All imaging was performed on a 4 Tesla whole body magnetic resonance imaging (MRI) system (Varian, Palo Alto, CA; Siemens, Erlangen, Germany). To minimize artifacts and increase the signal-to-noise ratio in the MTL, a semiautomated, localized second-order shimming algorithm (Klassen and Menon, 2004) was used and combined with a multishot, short echo-time imaging sequence. The plane of image acquisition was positioned perpendicular to the longitudinal axis of the hippocampus (determined based on initial scout images). For each participant, 25 contiguous 5-mm thick oblique coronal slices were obtained covering the brain from the anterior extent of the temporal lobe to the occipital pole. The field of view was 19.2 by 19.2 cm (64 × 64 matrix) providing an in-plane resolution of 3 mm. T2-weighted spiral image acquisition was used for all functional scans (TE = 10 ms; TR = 750 ms i.e., volume acquisition time of 3.0 s with 4-shot sequence). Each run involved the acquisition of 110 image volumes (11 volumes per block with 10 blocks. An additional T1-weighted high-resolution MRI volume was obtained for the display of neuroanatomy in the same experimental session using a 3D MDEFT pulse sequence in the same plane orientation as the functional scans but covering the entire brain (96 slices; 2.50 mm thick; 256 × 256 matrix; 0.75 mm in-plane resolution).

Image postprocessing was performed using FSL (FMRIB Software Library version 3.3; see Smith et al., 2004). Following motion correction of the T2*-weighted functional images, probabilistic Independent Component Analysis (ICA) was conducted on a run-by-run basis to identify and remove high-amplitude time course spikes as well as residual motion artifacts, high-frequency scanner noise and artifacts from gradient timing errors. This step was performed upon the data using a semiautomated procedure involving MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components version 2; see Beckman and Smith, 2004) and detailed inspection of ICA components. Functional data were then resampled into isotropic voxels (4 × 4 × 4 mm), coregistered with the anatomical images, transformed into standardized MNI space (Cocosco et al., 1997) and overlaid on an MNI T1 template image. Following transformation, images were smoothed using a 3D Gaussian kernel with a full-width at half maximum (FWHM) value of 6 mm.

To characterize the response of MTL structures to the different types of novelty manipulated, we used nonparametric group-based statistical analyses. These analyses involved a direct assessment of our hypothesized experimental effects using pre-specified contrasts in a nonrotated partial least squares (PLS) analysis. They were performed using PLSGUI (Partial Least Squares Graphical User Interface; see McIntosh and Lobaugh, 2004). In all analyses, 500 permutation tests were run to establish the overall significance of contrasts, and 100 bootstrap tests were used to estimate voxel standard error. Latent variables (LVs) were computed that consisted of a singular image, singular profile and singular value (SV). The singular profile described the a priori task contrast of interest that was used to generate a singular image describing the relationship of all voxels to the contrast. Each LV was evaluated for significance as a whole using the SV, an index of the covariance between the singular image and singular profile, as well as an index of the percentage of overall variance in the brain data accounted for by the LV. The threshold for LVs identified in these analyses was set at P < 0.05 (as computations were not done on a voxel-by-voxel basis but on the entire pattern). For the purpose of identifying brain voxels contributing to the pattern expressed in an LV, maps were created to express the ratio of voxel salience over estimated standard error (i.e., bootstrap ratio; BSR) with a threshold set to 3.29 (roughly equal to a z-score with P = 0.001, or a 99.9% confidence interval). The core contrast between entirely new and previously studied sentences was examined at the level of the entire brain with the same conservative threshold typically used in such analysis (P < 0.001, uncorrected) so as to establish a reliability for our MTL responses that is comparable with that typically reported. We specifically inspected these maps for any activated MTL region, defined as a cluster of at least 3 contiguous voxels above threshold that was no closer than 12 mm to another cluster. The specific spacing and minimum cluster size were selected based on the spatial smoothing parameters used (i.e., a FWHM of 6 mm) and voxel size, respectively.

RESULTS

Behavioral Results

To determine whether we observed a verbatim effect for the novel information encountered in Phase II, we examined recognition memory performance in Phase III. All behavioral data from the recognition memory task in Phase III were analyzed using an analysis of variance (ANOVA) and series of pairwise contrasts. In an initial ANOVA of the behavioral data, we
included two factors, type of novelty and orienting task. A main effect was found for novelty type, $F(2,28) = 41.857$, $P < 0.001$. However, there was no main effect of orienting task, $F(1,14) = 1.728$, $P = 0.201$, nor an interaction between orienting task and novelty type, $F(2,28) = 0.458$, $P = 0.510$. Given these results, we collapsed the data across orienting tasks for the behavioral analyses of subsequent memory performance (see Fig. 2). Using a series of pairwise contrasts, we tested whether sentences that contained semantic novelty in Phase II were subsequently recognized more accurately than those containing syntactic novelty. This was the case for sentences with novel semantic relationships, $t(14) = 6.645$, $P < 0.001$, as well as for sentences describing entirely novel episodes, $t(14) = 7.873$, $P < 0.001$. In fact, accuracy for recognition of sentences that contained only novel syntactic information was close to chance level (i.e., 50% accuracy; see Fig. 2). Notably, all participants also showed a verbatim effect numerically in their individual scores.

To rule out that the possibility that the lack of an effect of orienting task reflected an unwillingness or inability of participants to focus their attention on syntactic sentence information, we also performed an item analysis on participants’ responses in Phase I. Participants produced their responses in the syntactic task with high inter-rater agreement (average intraclass correlation = 0.617, $P < 0.001$) for individual sentences, arguing against the notion that participants responded arbitrarily. Participants’ scores were also anchored close to the middle of the scale with comparable variance in both orienting conditions (syntactic orienting, $M = 2.610$, $SD = 0.934$; semantic orienting, $M = 2.554$, $SD = 0.909$). Most important, perhaps, a number of sentences were comparable in the average semantic rating they obtained, but differed in their syntactic rating. For example, the sentence “There was no gleam of triumph, no shade of anger, when the patient opened his eyes from the month-long coma” received a consistently lower score for syntactic well-formedness than the sentence “Jamie appeared confused, disoriented, and somewhat agitated when the senior neurologist talked to him.” This observed difference in ratings is linguistically meaningful as it relates to the presence or absence of potentially confusing syntactic movement in the two sentences. Taken together, this evidence suggests that the syntactic orienting instructions did induce an attentional focus on syntactic information that differed from the one in the semantic orienting task.

### Functional Neuroimaging Results

In the first step of our fMRI analyses, we determined whether the pattern of activity that distinguishes between entirely new and old sentences would contain any MTL regions, and more specifically, whether it would include the hippocampus. The corresponding contrast captured a significant source of functional variance in the brain, $SV = 11.68$, $P < 0.05$. The map of this contrast revealed two regions with reliable saliences in the MTL: one in the left MTL extending from the hippocampus into entorhinal cortex (EC), and the other in the right amygdala. A number of other regions in prefrontal cortex (PFC) and parietal cortex also contributed to the pattern (see Table 2). Paralleling our behavioral results, the novelty $\times$ orienting task interaction did not capture any significant source of variance in the brain, $SV = 10.54$, $P = 0.414$; it was thus not investigated further.

<table>
<thead>
<tr>
<th>Region</th>
<th>Peak coordinates</th>
<th>Peak BSR</th>
<th>Cluster size (voxels)</th>
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<tbody>
<tr>
<td>Entirely novel episode old</td>
<td></td>
<td></td>
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<tr>
<td>Frontal lobe</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L cingulate gyrus</td>
<td>$-8$</td>
<td>$-28$</td>
<td>$-8$</td>
</tr>
<tr>
<td>R superior frontal gyrus</td>
<td>$12$</td>
<td>$28$</td>
<td>$60$</td>
</tr>
<tr>
<td>L precentral gyrus</td>
<td>$-8$</td>
<td>$-24$</td>
<td>$64$</td>
</tr>
<tr>
<td>Temporal lobe</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L inferior temporal gyrus</td>
<td>$-40$</td>
<td>$4$</td>
<td>$-36$</td>
</tr>
<tr>
<td>R amygdala</td>
<td>$32$</td>
<td>$-4$</td>
<td>$-28$</td>
</tr>
<tr>
<td>L hippocampus/entorhinal cortex</td>
<td>$-20$</td>
<td>$-16$</td>
<td>$-32$</td>
</tr>
<tr>
<td>Parietal lobe</td>
<td></td>
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<tr>
<td>L precuneus</td>
<td>$-12$</td>
<td>$-36$</td>
<td>$48$</td>
</tr>
<tr>
<td>L posterior cingulate gyrus</td>
<td>$0$</td>
<td>$-40$</td>
<td>$40$</td>
</tr>
<tr>
<td>Old &gt; entirely novel episode</td>
<td></td>
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<tr>
<td>Frontal lobe</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>R posterior dorsolateral PFC</td>
<td>$44$</td>
<td>$8$</td>
<td>$52$</td>
</tr>
</tbody>
</table>

Peak locations are described using MNI standardized space (Cocosco et al., 1997).
In a second stage, we asked whether the MTL regions that showed a response to entirely novel sentences were sensitive to semantic novelty, syntactic novelty, or both. For this purpose, we masked these regions and determined whether they responded to these novelty types relative to the old condition (as reflected in a significant LV in a nonrotated PLS contrast). As predicted, we found that the left hippocampal/entorhinal region responded to semantically novel sentences, $SV = 0.51, P < 0.005$, but not to syntactically novel sentences, $SV = 0.28, P = 0.118$ (see Fig. 3a; note that these $P$-values should be considered more descriptive than exact, given that the regions for these contrasts were selected based on a novelty response in another contrast to begin with). Unlike the hippocampal region, the right amygdala region responded both to sentences with semantic novelty, $SV = 0.32, P < 0.005$ and to those with novel syntax, $SV = 0.29, P < 0.001$ (see Fig. 3b). In line with the pattern for the entirely novel sentences, no interaction with orienting task was observed in either region.

To rule out that the observed insensitivity of the hippocampus to syntactic novelty was due to the subtlety of novelty in that condition, we also explored whether any region would selectively respond to syntactic novelty relative to the old condition. Notably, the LV corresponding to this contrast was significant, $SV = 12.95, P < 0.05$, and the pattern included a region corresponding to Broca’s area in the left inferior PFC (peak coordinates $= (-48, 28, -8)$, BSR $= 5.906$, 50 voxels; see Fig. 3c). When we directly compared the novelty response of this PFC region with that of the hippocampus using region and novelty type as two factors in an ANOVA, we obtained a significant interaction, $F(2,28) = 6.786, P < 0.005$, but no main effect of novelty, $F(2,28) = 0.120, P = n.s.$ (see Fig. 4). This result indicates that the lack of sensitivity to syntactic novelty in the hippocampus is not due to an ineffective manipulation of syntactic novelty, but reflects a functional characteristic that is specific to this structure.

### DISCUSSION

In a replication of the verbatim effect established in previous cognitive investigations (Sachs, 1967; Graesser and Mandler, 1975; Murphy and Shapiro, 1994), we found that sentences containing semantic novelty were better subsequently recognized than sentences that contained only syntactic novelty. This benefit held regardless of whether semantic novelty pertained to the described episode as a whole or to a detail of a previously encountered episode. Consistent with our hypothesis for a neural correlate of this effect in the MTL, we found a region at the border of the left anterior hippocampus and EC that responded differentially whenever semantic but not when syntactic novelty was present at encoding.

Left MTL activity has previously been observed in response to novel verbal stimuli in other fMRI research (Dolan and Fletcher, 1997; Saykin et al., 1999; Strange et al., 1999; Davis and Johnsrude, 2003; O’Kane et al., 2005). The current study extends this past evidence by showing a novelty effect in the MTL that is specific to semantic relationships at the sentence level. O’Kane et al. (2005) observed a semantically-based novelty effect in perirhinal and para-hippocampal cortices that was present for individual words. Its localization in the MTL differed from the semantic novelty effect observed here, which was manifest in the hippocampus and EC. This difference in localization can be explained in the context of theoretical proposals arguing that the hippocampus, and perhaps also EC, support memory processing of relationships between stimuli, while adjacent perirhinal cortex supports memory for individual items (Buckmaster et al., 2004; Eichenbaum, 2004; Davachi, 2006; Mayes et al., 2007). Unlike in the study by O’Kane et al., the novelty condition that revealed the MTL response in the present investigation involved sentences in which novelty was created by recombining previously encountered sentence components. More specifically, it involved replacing a noun or verb from a given sentence with that previously used in another one; this manipulation changed the meaning of the episode described. Given that the word used for replacement had been presented before in our experiment, the corresponding effect cannot be interpreted as pertaining to stimulus or item novelty. In as much as no significant novelty response was observed for the condition that involved a syntactic change, our results also suggest that the response to sentence relationships in the hippocampus is specific to semantic content.

In functional terms, a close link between relational processing and sentence memory is also suggested by evidence from cognitive research. Prior and Bentin (2003) found that pairs of words can be better remembered if embedded in sentences than if presented on their own at encoding; this facilitation effect of sentence context does not hold for memory for individual words. Furthermore, it seems to be specific to situations in which the sentence that includes the word pair is meaningful and can be fully integrated at the semantic level (Prior and Bentin, 2008). In line with the present findings, this cognitive evidence suggests that the memory benefits of relational processing for verbal stimuli are closely tied to the semantic analyses that facilitate sentence comprehension.

Although the design of the present study does not allow us to establish a direct link between the observed semantic novelty responses in the hippocampal/entorhinal region and processes of memory formation, the observation that the fMRI response across conditions at encoding paralleled the pattern of behavioral performance observed in the subsequent recognition memory task is clearly in line with this hypothesis. This interpretation also receives support from past fMRI findings showing that hippocampal activity during semantic processing of verbal relationships predicts subsequent recognition memory for the previously encountered words (Davachi and Wagner, 2002). Importantly, such an encoding interpretation of the present hippocampal data would not be incompatible with the notion that the detection of the novelty of semantic relationships in itself may be the result of a recall-like retrieval process, which may precede or operate in parallel with processes pertaining to memory formation. In support of such an involvement of retrieval processes, Kumaran and Maguire have recently shown
that the hippocampal response to novel relationships can be characterized as the outcome of a match-mismatch process. According to their findings, the hippocampal novelty response reflects a mismatch signal that is generated when predictions that implicate the retrieval of past experiences are violated by current input (Kumaran and Maguire, 2006, 2007).

In contrast to the selective hippocampal response to semantic novelty, a left inferior PFC region corresponding to Broca's area (c) that responded to syntactic novelty. The BSR map corresponding to the contrast used to identify each region (BSR > 3.29; \( P < 0.001 \)) is superimposed on coronal and sagittal MR slices from an anatomical template brain. Profiles of novelty responses are based upon regional analyses (+1 SE).
area (Amunts et al., 1999) responded specifically to syntactic novelty in the present study. This finding is fully compatible with past research linking the functional role of this region to syntactic processes in working memory (Fiebach et al., 2005). In the context of the present study, the finding is important in that it indicates that detection of syntactic novelty did occur with the manipulation we employed, and that the lack of a response in the hippocampus is not due to a general insensitivity of the brain to syntactic novelty. This conclusion is also supported by our finding in the right amygdala region, which responded to all forms of novelty tested in the current experiment. Amygdala activity has been observed in association with novelty in previous investigations using a variety of stimulus types (Fried et al., 1997; Kiehl et al., 2001; Rutishauser et al., 2006), and may be related to concomitant emotional responses of surprise (Wild et al., 2001; Kim et al., 2003).

Although our statistical analyses suggest that the response in the hippocampus, unlike that in the amygdala, is selective to semantic relationships, a visual inspection of the hippocampal response profile suggests a numerical increase even for the syntactic condition. It is possible that this increase is related to subtle changes in meaning; while we made every effort to minimize changes in meaning with our syntactic novelty manipulation, syntactic movement of subclauses often does create subtle changes in emphasis. However, we realize that such an interpretation of a nonsignificant response should be considered with caution, and that the tentative interpretation suggested also bears the danger of circularity.

Previous cognitive research has demonstrated that the verbatim effect holds regardless of whether attention is oriented to semantic or syntactic information at encoding (Graesser and Mandler, 1975; Murphy and Shapiro, 1994), and that the effect is modulated only mildly by orienting tasks in samples larger than the one we examined here (more typical for cognitive than neuroimaging investigations). In the present study, we found neither evidence for an effect of orienting task on memory performance nor evidence for an effect on MTL novelty responses. However, this should not be taken as an indication that people treated sentences in the syntactic orienting task in the same manner as in the semantic orienting task. Our item analysis does suggest, for example, that there were sentences that were comparable in the average semantic rating they obtained, but differed in their syntactic rating. This type of evidence suggests that syntactic orienting instructions did induce an attentional focus on syntactic information that differed from the one in the semantic orienting task. In the cognitive literature, the general failure of syntactic orienting tasks to reverse or eliminate the verbatim effect has been taken as evidence that poor memory for syntax is ultimately not due to a lack of attentional focus on syntactic information at encoding, but instead reflects a basic operating principle of verbal long-term memory (e.g., Graesser and Mandler, 1975; Murphy and Shapiro, 1994). In a similar vein, we suggest that the failure of our orienting tasks to significantly modulate MTL activity is also not due to a missing focus of attention on syntactic information. Instead, the current findings hint that the verbatim effect is the result of automatic processes, rather than attentional control, even at the level of MTL functioning. In this respect it may resemble other cognitive phenomena, such as the Stroop effect, that point to automatic access of the meaning of verbal materials (MacLeod, 1991). Future research could help to determine whether the pattern of findings observed with the current set of orienting conditions even holds under circumstances when participants explicitly aim to detect different types of novelty at encoding (syntactic vs. semantic). On the basis of the interpretation put forward, we would expect that this is the case.

To return to the main query of the current investigation: why then is the meaning of sentences better remembered than their form? Insofar as novelty in the environment typically triggers the cascade of MTL processes necessary for the formation of episodic memory representations, our findings for the hippocampus and EC suggest that it is specifically semantic relationships that set this cascade into motion. Novel syntactic information alone cannot play this role.

Acknowledgments

We gratefully acknowledge the assistance of Joy Williams and Kevin Trewartha with data acquisition and of Ken Valyear and Zainab Fatima with imaging analysis.

Hippocampus

REFERENCES


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