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Content-dependence of the electrophysiological correlates of recollection

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Abstract

The neural correlates of episodic retrieval ('recollection') have been shown to differ according to the content of retrieved episodes. It has been hypothesized that these content-dependent differences reflect the 'reinstatement' of encoding-related processes or representations at the time of recollection. It remains unclear, however, whether these effects directly reflect the recollection of differential episodic content, as would be predicted by the reinstatement hypothesis, or whether they are instead associated with processes that are contingent on successful recollection. To address this issue, the present study employed event-related potentials (ERPs), permitting the investigation of the temporal dynamics of content-dependent neural effects during retrieval, and in particular, their onset with respect to well-established ERP correlates of recollection, such as the left parietal old-new effect. Subjects studied a series of words that were each presented in the context of one of two encoding tasks. One task required the covert generation of a sentence incorporating each word, whereas the other required imagining the object corresponding to each word within a superimposed scenic picture. Memory for the words was subsequently tested with the 'remember/know' procedure. ERPs elicited by recollected words differed according to the prior encoding history of the word, beginning at approximately 300 ms following word onset. These content-dependent ERP differences were maximal over the anterior scalp and, importantly, onset as early as the left parietal old-new effect. The findings demonstrate that content-dependent neural activity during retrieval can occur in a time-frame that is compatible with a direct role in the recollection and representation of episodic information.

Episodic memory retrieval ('recollection') is widely held to involve the reactivation, or 'reinstatement', of processes that were engaged when the episode was encoded (Damasio, 1989; James, 1890). This idea has been incorporated into several neurally-inspired models of memory retrieval (e.g., Alvarez & Squire, 1994; McClelland et al., 1995; Norman & O'Reilly, 2003; Rolls, 2000; Shastri, 2002), which posit that recollection occurs when a pattern of cortical activity corresponding to an episode is reinstated via activation of a hippocampally-stored representation of that pattern. By such an account, it follows that the retrieval of two different episodes that are associated with distinct content—i.e., different sensory information or records of cognitive operations—will be associated with distinct, 'content-dependent' patterns of neural activity.

Empirical evidence for the content-dependency of neural correlates of recollection has been obtained in several studies that employed event-related functional magnetic resonance imaging (fMRI; Gottfried et al., 2004; Johnson & Rugg, in press; Kahn et al., 2004; Khader et al.,

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2005; Wheeler & Buckner, 2003, 2004; Wheeler et al., 2000, 2006; Woodruff et al., 2005). The most compelling findings from these studies involve the demonstration of regionally-specific double dissociations of cortical activity associated with the recollection of one of two different classes of trial-unique episodes (see Johnson & Rugg, in press; Kahn et al., 2004; Woodruff et al., 2005). For instance, Kahn et al. (2004) presented subjects with words to be encoded with a task requiring either visual imagery or phonological processing. On a later source memory test, words recollected from the visual imagery condition elicited greater activity relative to words from the phonological condition in left parahippocampal cortex, whereas the reverse pattern of activity was evident in left posterior frontal (premotor) cortex. In a similar vein, Woodruff et al. (2005) identified two distinct regions within left fusiform cortex that exhibited a material-dependent double dissociation of activity according to whether words or pictures were recollected.

Johnson and Rugg (in press) extended the aforementioned findings by directly linking recollection to the reinstatement of encoding-related neural activity. Subjects were presented with a series of words and required either to generate a sentence incorporating the word (hereafter, the 'sentence' condition) or to imagine the referent of the word within a superimposed scenic picture (the 'scene' condition). Memory for the words was subsequently tested using the 'remember/know' procedure (Tulving, 1985). Dissociable patterns of cortical activity were observed when words belonging to the two encoding conditions were recollected, in that words from the sentence condition elicited greater activity in ventromedial prefrontal cortex, whereas words from the scene condition elicited greater activity in occipital and fusiform cortex. Importantly, the regions demonstrating content-dependent retrieval effects were a subset of those exhibiting differential activity when the words from the two conditions were encoded. This finding is consistent with the idea that encoding-related processes are reinstated during recollection. Other regions, notably in left lateral parietal, entorhinal, and retrosplenial cortex, exhibited 'generic' (or 'content-independent') recollection-related activity that was invariant with respect to the prior encoding task completed for the words (also see Kahn et al., 2004). The generality of these latter effects, particularly in left inferior parietal cortex, is consistent with the findings of previous studies in which similar recollection effects have been demonstrated across a variety of materials and tasks (Cansino et al., 2002; Eldridge et al., 2000; Henson et al., 1999; Wheeler & Buckner, 2004; Woodruff et al., 2005; Yonelinas et al., 2005).

An unresolved issue that bears heavily on the significance of these findings to the reinstatement hypothesis of episodic retrieval centers on the time course of the content-dependent effects. Because of the limited temporal resolution of the hemodynamic measure obtained with fMRI, the relative timing of these effects in comparison to the timing of more general neural correlates of recollection is unknown. If content-dependent effects are a manifestation of the reinstatement of processing that is necessary for recollection, then they should emerge relatively soon after the presentation of a retrieval cue and at least as early as (and possibly preceding) the emergence of generic recollection-related activity. Conversely, if the effects reflect processes that are contingent on successful recollection, as for example, in the case of processes involved in evaluating retrieved content, then the effects should emerge after the onset of generic recollection effects. To adjudicate between these two accounts of content-dependent effects, it is necessary to employ neural measures, such as event-related potentials (ERPs), that have substantially higher temporal resolution than fMRI.

ERPs have been employed to study the neural correlates of successful retrieval since the early 1990s. These studies have consistently identified a retrieval-related effect that takes the form of more positive-going ERPs for correctly-classified old recognition test items relative to new items. This effect, often referred to as the 'left parietal old-new effect', is maximal over the left posterior scalp between approximately 500 and 800 ms following stimulus onset and, on

a variety of grounds, is widely held to be a neural correlate of recollection (for reviews, see Friedman & Johnson, 2000; Rugg & Allan, 2000; Rugg and Curran, 2007). The left parietal effect is elicited by a variety of different stimuli, including pictures and visually- and auditorily-presented words (e.g., Curran & Dien, 2003; Schloerscheidt & Rugg, 1997; Wilding et al., 1995), and there is little evidence to suggest that its scalp topography varies according to these or other stimulus variables. Together, these findings suggest that the effect is a reflection of ‘generic’ recollection-related processes that are engaged regardless of the content of the retrieved information (cf. Johnson & Rugg, in press).

In contrast to the sizeable literature on the left parietal effect, there is a paucity of studies demonstrating content-sensitive ERP recollection effects. Arguably the strongest evidence for such effects comes from a study by Fabiani and colleagues (Fabiani et al., 2000). At study, subjects were presented with a series of words displayed either to the left or right visual field. Recognition memory for the words was subsequently tested using centrally-presented items. ERPs elicited by correctly recognized items exhibited lateralized differences that varied with study location, suggesting that the ERPs carried a ‘signature’ of where the words were presented at study. These location-dependent retrieval effects were evident by approximately 200 ms post-stimulus onset—somewhat earlier than the onset of the left parietal old-new effects that were also elicited by correctly recognized items. The findings clearly demonstrate that retrieval-related neural activity can discriminate two different classes of study episode, with the timing of the effects occurring sufficiently early to sustain the claim that they might reflect the reinstatement of the content of those episodes. However, since the authors did not employ a memory test that permitted the segregation of recollection- and familiarity-based recognition judgments, it is unclear whether these content-dependent ERP effects were associated with successful recollection rather than with familiarity-based recognition.

In the present study, we investigated the time course of content-dependent neural activity during episodic retrieval by employing ERPs in an experimental procedure very similar to that adopted in our previous fMRI study (Johnson & Rugg, in press). Subjects were presented with a series of words that were encoded with one of two distinct tasks (the aforementioned sentence and scene conditions). Memory for the words was later tested with the remember/know procedure, permitting the identification of test items for which recognition was accompanied by recollection of details about the study episode. ERP data acquired during the memory test were used to identify both content-dependent and content-independent (generic) effects that were associated with recollection. For the reasons noted above, if content-dependent effects reflect processes that support recollection, then these effects should have onset latencies similar to, and perhaps even earlier than, the left parietal old-new effect. By contrast, if content-dependency is contingent on successful recollection, the effects should not emerge until after the onset of generic recollection effects.

Methods

Subjects

Twenty-five volunteers between 18 and 23 years of age were recruited from the University of California, Irvine (UCI) community and paid for their participation (\$15/hr). All subjects reported that they were right-handed, learned English as their first language, and had normal or corrected-to-normal vision. Informed consent was obtained in accordance with UCI Institutional Review Board guidelines.

The data from five subjects were excluded from all analyses because they contributed fewer than 16 trials to at least one critical experimental condition. Four of the excluded subjects exhibited excessive horizontal eye-movement artifact in their EOG, and the other excluded

subject had an insufficient number of trials due to inadequate memory performance. The remaining 20 subjects (12 males) had a mean age of 20 years.

Stimuli

Stimuli were drawn from a pool of 284 words (mean length = 6 letters; mean written frequency = 21/million; Kucera & Francis, 1967) and a pool of 93 color pictures. The words were names of single objects from several categories, including tools, furniture, animals, and food. The pictures were of natural scenes that had no obvious depictions of buildings, animals, or people, and were selected to minimize inter-stimulus overlap in content. For each subject, 240 words from the pool were randomly assigned to three groups of 80 words. The words from two of the groups were presented in the study phase and subsequently served as old test items, while the words from the remaining group served as new test items. For the study phase, each word from one group was randomly paired with a picture of a scene. Ten words and five pictures from the original pools were used as study buffers (two at the beginning and two at the end of the study list, along with two following each of three breaks), and eight words were used as test buffers (two at the beginning and two following each of three breaks). The remaining words and pictures were used in practice study and test phases.

Stimuli were displayed on the black background of a 19-inch LCD monitor that was placed at a viewing distance of 1 m. All words were presented in black uppercase 30-point Helvetica font (subtending a vertical visual angle of $.5^\circ$ and a maximum horizontal visual angle of 4°) on a solid yellow rectangle ($1^\circ \times 4.5^\circ$). Words in the study phase were presented near one of the four corners (each occurring equally often) of a centrally-presented background stimulus ($7^\circ \times 7^\circ$), which consisted of either a scenic picture or a solid gray background. During the test phase, words were presented centrally on a nonsense background ($7^\circ \times 7^\circ$) that was constructed by heavily blurring and pixelating an unused landscape picture, so as to be of roughly equal similarity to the scene and gray backgrounds used at study. A fixation character (+; $.5^\circ \times .5^\circ$) was presented centrally during the inter-stimulus intervals.

Procedure

Prior to the experiment, instructions were administered, and a short practice version of the study and test phases was completed. The subject was then fitted with an electrode cap and seated in a darkened, sound-attenuated room, facing a computer monitor. The experiment proper consisted of a study phase, followed by a break of around three minutes, and a test phase.

For the study phase, subjects were informed that they would see a series of words superimposed near the corners of either scenic pictures or a gray background. They were further informed that the presentation location was random and irrelevant both to their task and the later memory test. For words superimposed on pictures, instructions were to imagine the object corresponding to the word at any location within the scene (the 'scene' condition). For words presented against the gray background, subjects were instructed to generate a meaningful sentence that incorporated the word (the 'sentence' condition). To ensure comprehension of the task instructions, during an initial practice phase subjects were required to point to the location on the screen at which they were imagining the object for the scene condition, and to vocalize their sentences for the sentence condition. During the study trials for the experiment proper, however, the tasks were carried out covertly, and each trial was terminated by a single button press. The instructions emphasized that subjects were to complete the two tasks to the best of their abilities throughout the study phase, while proceeding at their own pace. Subjects were instructed to begin the task for each trial immediately after the stimulus appeared and to press a button with their right index finger as soon as they had finished.

Each study trial began with the presentation of a red fixation character for 500 ms, followed by a word and its background, which were displayed until the response button was pressed. After the response, a white fixation character was displayed for 1 s, and the next trial followed. The order of study trials was chosen randomly for each subject, with a limit of three consecutive trials for a given task. The study phase was divided into four blocks (40 critical trials per block) by 20 s rest periods.

Instructions for the test phase informed subjects that they would see a series of words, each of which had either been presented in the previous study phase ('old') or was not studied ('new'). Each test word was presented on a common nonsense background (see Stimuli). Subjects were informed that the background was irrelevant to their task and provided no indication as to whether or not the word had appeared at study. Instructions for the test phase followed standard instructions for the remember/know procedure (e.g., Rajaram, 1993), and examples of the types of subjective judgments to be made were provided during the practice phase. Subjects were instructed to make one of three responses to each test word, according to whether (i) any details about the word's study presentation could be recollected ("remember", R), (ii) the word was judged to have appeared in the study phase but no details could be recollected ("know", K), or (iii) the word was judged not to have been presented in the study phase ("new", N). To minimize the likelihood that R and K responses were made in circumstances when subjects were guessing whether the word was studied or not, subjects were further instructed to use these two responses only when they were highly confident that a test word was studied, and to use the N response in the event that they were unsure of a word's study status (cf. Gardiner et al., 1998). The R, K, and N responses were made with the right index, middle, and ring fingers, respectively. Accuracy and speed of responding were given equal emphasis in the test instructions.

Test phase trials consisted of the presentation of a red fixation character for 500 ms, followed by a test word for 500 ms, and a white fixation character for 2000 ms. The order of test trials was chosen randomly for each subject, with a limit of three consecutive trials of a given type (sentence, scene, and new). The test phase was divided into four blocks (60 critical trials each) by 20 s rest periods.

ERP recording and analysis

EEG data were recorded continuously from 29 Ag/AgCl sintered ring electrodes embedded in an elastic cap (EASYCAP, Herrsching-Breitbrunn, Germany; www.easycap.de). The locations of the cap electrodes were based on the International 10–20 system (American Electroencephalographic Society, 1994) and corresponded to three midline sites (Fz, Cz, Pz) and 13 homotopic pairs of sites (Fp1/Fp2, AF7/AF8, F3/F4, F5/F6, F7/F8, C3/C4, C5/C6, T7/T8, P3/P4, P5/P6, P7/P8, PO7/PO8, and O1/O2). Additionally, two electrodes were adhered to the left and right mastoid processes, and a ground electrode was embedded in the cap at the location corresponding to FCz. Vertical and horizontal EOG were recorded from bipolar electrode pairs situated above and below the left eye and on each outer canthus, respectively.

EEG data were acquired with a Contact Precision Instruments system (London, UK; www.psylab.com). The data were recorded with reference to the Cz electrode at a sampling rate of 256 Hz and an amplifier bandwidth of 0.01 to 40 Hz (–3 dB). Prior to the start of the experiment, each electrode was adjusted until its impedance was < 5k Ω . Off-line, the data were epoched (2048-ms duration) with respect to the onset of each test item, and baseline corrected according to a 102-msec pre-stimulus interval. The epoched data were down-sampled to 125 Hz (resulting in 256 time points per epoch) and algebraically re-referenced to linked mastoids, allowing for recovery of the data from Cz. Trials containing movement artifact, horizontal EOG artifact, vertical EOG artifact other than blinks, or excessive baseline drift were manually rejected. The remaining trials were averaged to form ERPs, which were then smoothed with a

five-point moving-window filter (-3 dB at 19.4 Hz). Blink artifacts were corrected for each subject using a previously described linear regression method (see Henson et al., 2004).

Results

For all analyses of variance (ANOVAs) described below, the degrees of freedom associated with effects involving factors with more than two levels were corrected for nonsphericity (Greenhouse & Geisser, 1959).

Behavioral results

In the study phase, response times (RTs) were reliably shorter to words presented in the sentence condition ($M = 5305$ ms, $SD = 2369$) than in the scene condition [$M = 5925$ ms, $SD = 2950$; $t(19) = 2.41$, $p < .05$].

The mean proportions of “remember” (R), “know” (K), and “new” responses for each type of test item are listed in Table 1. These proportions were used to calculate two measures of memory performance, based on the assumption that R and K responses are indices of independent recollection and familiarity processes, respectively (Yonelinas & Jacoby, 1995). Recollection-based memory performance, taken as the difference in probability of making an R response to old and new words ($pR_{old} - pR_{new}$), was higher for words from the sentence condition (.68) than from the scene condition [.57; $t(19) = 3.69$, $p < .005$]. Familiarity-based memory performance was calculated as the probability difference of making a K response to old and new words, after adjusting for the proportions of R responses to those items: $[pK_{old} / (1 - pR_{old})] - [pK_{new} / (1 - pR_{new})]$. Because there were ten subjects who made fewer than eight K responses to old words from either the sentence condition or the scene condition, the familiarity measure was derived from the data of the ten remaining subjects. This measure did not significantly differ for the sentence (.67) and scene (.58) conditions ($p > .14$). The familiarity measures for both conditions were, however, reliably greater than zero (scene: $t[9] = 9.17$, $p < .001$; sentence: $t[9] = 11.61$, $p < .001$), confirming that K responses were not merely guesses of old/new status.

Analysis of the test phase RTs indicated that R responses to test words from the sentence condition ($M = 1269$ ms, $SD = 308$) were faster than those from the scene condition [$M = 1313$ ms, $SD = 306$; $t(19) = 2.27$, $p < .05$]. The RTs from neither of these conditions differed significantly from those to correctly-classified new items ($M = 1301$ ms, $SD = 196$). As before, subjects who made fewer than eight K responses in at least one old condition were excluded from the analysis of RTs for those items. The resulting RTs for the scene ($M = 1601$ ms, $SD = 234$) and sentence ($M = 1619$ ms, $SD = 231$) conditions did not differ.

ERP results

The ERP analyses were conducted in four parts. In the first part, the ERPs associated with words given R responses from the two encoding conditions (hereafter, $R_{sentence}$ and R_{scene}), along with the ERPs corresponding to correctly-rejected new items, were contrasted. These analyses were initially conducted on the mean amplitudes from consecutive 100-ms latency intervals to determine the onset latencies of any effects, and were then carried out on the amplitudes from longer latency intervals more typical of those analyzed in prior ERP studies of retrieval (e.g., Allan et al., 1998; Wilding, 2000; Woodruff et al., 2006). A second analysis focused specifically on the left parietal old-new effect, directly contrasting the amplitude of the effect according to the encoding history of the recollected test items. The third part of the analyses investigated the scalp topographies of the differences between the $R_{sentence}$, R_{scene} , and new-item ERPs. Finally, in an effort to determine whether content-dependency was

selective to recollection, the content-dependent ERP effects based on R responses were compared to analogous effects corresponding to K responses.

Grand average ERPs corresponding to the R_{sentence} , R_{scene} , and new items are shown in Figure 1. Figure 2 illustrates these data from the electrode sites where ERP effects were most apparent. The across-subjects mean numbers of trials (and ranges) forming the R_{sentence} , R_{scene} , and new ERPs were 38 (24–63), 32 (18–54), and 43 (18–76), respectively. Inspection of the figures reveals several differences among these ERPs. From around 300 ms post-stimulus onset, R_{sentence} ERPs over the anterior scalp appear more positive-going than the ERPs for other item types. By 500 ms, R_{sentence} and R_{scene} ERPs over the left posterior scalp are more positive-going than new-item ERPs. From about 800 ms post-stimulus, R_{scene} ERPs over the posterior scalp appear more positive-going than the ERPs for the other categories. Finally, there are late-onsetting differences over the right anterior scalp, where ERPs for R responses appear to be more positive-going than for new items.

100-ms latency intervals—To investigate the onset latencies of ERP effects among the three item types of interest, the mean amplitudes of the ERPs (with respect to the pre-stimulus baseline) were segregated into consecutive 100-ms latency intervals, beginning at stimulus onset. The electrode montage used for these and all subsequent analyses is depicted in Figure 1. The electrodes within the montage were factored according to hemisphere (left and right), chain (anterior and posterior), and site (five electrodes within each quadrant). Separate ANOVAs of these data were conducted for each pairwise combination of the item types (R_{sentence} versus R_{scene} , R_{sentence} versus new, and R_{scene} versus new). For significant interactions involving the item type factor, subsidiary ANOVAs were used to probe for simple effects of item type at the different levels of electrode factors. Because the primary interest of the present analyses was with the onsets of any ERP effects, only the results from the earliest intervals in which the item type effects were significant are described here. (The complete results of the 100-ms ANOVAs are available on request from the corresponding author.)

For the R_{sentence} - R_{scene} comparison, ANOVAs gave rise to a reliable item type effect, in the form of an item type \times hemisphere interaction, beginning in the 300–400 ms latency interval [$F(1, 19) = 5.72, p < .05$]. Subsidiary ANOVAs of the data from each hemisphere revealed a reliable item type main effect for the left hemisphere only [$F(1, 19) = 6.42, p < .025$], indicating that the R_{sentence} ERPs were more positive-going than the R_{scene} ERPs. ANOVAs of the R_{sentence} -new comparison also gave rise to significant effects in the 300–400 ms latency interval [item type main effect: $F(1, 19) = 5.51, p < .05$; item type \times chain \times site interaction: $F(1.5, 29.1) = 4.67, p < .05$], indicating that the R_{sentence} ERPs were more positive-going than the new-item ERPs, especially at superior sites over the anterior scalp. Finally, beginning in the 600–700 ms latency interval, the R_{scene} -new ANOVA resulted in significant interactions of item type \times chain [$F(1, 19) = 4.43, p < .05$] and item type \times hemisphere \times chain [$F(1, 19) = 4.53, p < .05$], reflecting the greater positivity of R_{scene} ERPs compared to new-item ERPs that was maximal over the left posterior scalp.¹

Based on the results of the foregoing analyses, and to facilitate comparison with previous ERP studies of retrieval, the data were next collapsed into five longer latency intervals (300–500, 500–800, 800–1100, 1100–1400, and 1400–1900 ms). ANOVAs of the data from these intervals employed the same electrode montage (see Figure 1) and factors used in the previous

¹Given the extensive prior evidence for left parietal old-new effects (see Friedman & Johnson, 2000; Rugg & Allan, 2000), additional 100-ms ANOVAs of the R_{sentence} -new and R_{scene} -new comparisons were conducted on the ERPs restricted to the left posterior quadrant of electrodes (see Figure 1). For the R_{sentence} -new comparison, statistical significance of the effects did not emerge until the 400–500 ms latency interval [item type main effect: $F(1, 19) = 7.96, p < .025$; item type \times site interaction: $F(1.8, 34.7) = 5.43, p < .025$]. For the R_{scene} -new comparison, the effects were reliable beginning in the 500–600 ms interval [item type main effect: $F(1, 19) = 5.42, p < .05$]. Thus, the left parietal old-new effects onset later than the earliest indication of content-dependency.

analyses. The results of these ANOVAs are described below and listed in Table 2. Because our primary interest was in the content-dependency of the ERPs elicited by recollected items (i.e., endorsed with R responses), the following report is focused on the results of the ANOVAs of the $R_{\text{sentence}}-R_{\text{scene}}$ comparison. Subsidiary ANOVAs were conducted as necessary to elucidate interactions between the item type and electrode location factors. Effects not involving the item type factor are of no interest in the present context and not reported.

300–500 ms latency interval—ANOVAs of the data from the 300–500 ms latency interval gave rise to item type effects for both the $R_{\text{sentence}}-R_{\text{scene}}$ and $R_{\text{sentence}}-\text{new}$ comparisons. For the former, ANOVA revealed significant item type \times chain, item type \times hemisphere, and item type \times hemisphere \times site interactions. Subsidiary chain-wise ANOVAs gave rise to an item type main effect for only the anterior chain [$F(1, 19) = 5.43, p < .05$], indicating that the R_{sentence} ERPs were more positive-going than the R_{scene} ERPs. The item type differences were also left-lateralized, as confirmed by an item type main effect for only the left hemisphere [$F(1, 19) = 4.60, p < .05$]. For the $R_{\text{sentence}}-\text{new}$ comparison, ANOVA gave rise solely to an item type main effect, indicating that the R_{sentence} ERPs were also more positive-going than the new-item ERPs in this interval.

500–800 ms latency interval—For the 500–800 ms latency interval, ANOVAs revealed significant effects for each pair of response categories. ANOVA of the $R_{\text{sentence}}-R_{\text{scene}}$ comparison gave rise to an item type \times chain interaction. As in the previous latency interval, chain-wise ANOVAs revealed a significant item type main effect for only the anterior chain [$F(1, 19) = 10.83, p < .005$]. The $R_{\text{sentence}}-\text{new}$ ANOVA revealed an item type main effect and interactions of item type \times hemisphere, item type \times site, and all four factors. These effects reflected the fact that the R_{sentence} ERPs were more positive-going than the new-item ERPs—a difference that was most pronounced over the superior anterior and left posterior scalp. Turning to the $R_{\text{scene}}-\text{new}$ comparison for this interval, ANOVA gave rise solely to an item type \times site interaction, indicating the positivity of the R_{scene} ERPs in relation to the new ERPs, especially at superior sites.

800–1100 ms latency interval—Similar to the results from the previous interval, ANOVAs of the data from 800–1100 ms also gave rise to significant differences between each pair of response categories. The $R_{\text{sentence}}-R_{\text{scene}}$ ANOVA revealed interactions of item type \times chain and item type \times chain \times site. As before, ANOVA restricted to the anterior chain gave rise to an item type main effect [$F(1, 19) = 18.70, p < .001$], reflecting the more positive-going R_{sentence} ERPs. ANOVA restricted to the posterior chain gave rise to an item type \times site interaction [$F(1.8, 34.1) = 3.53, p < .05$]. By contrast with the anteriorly-distributed item type differences observed in this and the preceding intervals, the posterior differences took the form of more negative-going R_{sentence} compared to R_{scene} ERPs, and were reliable at the posterior-most electrodes [PO7/PO8: $F(1, 19) = 5.90, p < .05$; O1/O2: $F(1, 19) = 7.28, p < .025$].

ANOVA of the $R_{\text{sentence}}-\text{new}$ comparison for this latency interval gave rise to an item type main effect along with four interactions involving this factor (see Table 2). For the $R_{\text{scene}}-\text{new}$ comparison, ANOVA gave rise to item type \times hemisphere, item type \times chain, and item type \times site interactions. As in the previous interval, the $R_{\text{sentence}}-\text{new}$ effects were prominent over the anterior and left posterior scalp, whereas the $R_{\text{scene}}-\text{new}$ effects exhibited a left posterior maximum.

1100–1400 ms latency interval—ANOVAs of the data from the 1100–1400 ms latency interval also revealed reliable item type effects for each comparison. The $R_{\text{sentence}}-R_{\text{scene}}$ ANOVA gave rise solely to an item type \times chain interaction, and subsidiary ANOVAs revealed item type main effects for both the anterior and posterior chains [$F(1, 19) = 8.55, p < .01$, and $F(1, 19) = 4.40, p < .05$, respectively]. As in the previous interval, the R_{sentence} ERPs were

more positive-going than the R_{scene} ERPs over the anterior scalp, whereas the posterior effects were in the opposite direction. The $R_{\text{sentence-new}}$ ANOVA for this interval revealed an item type main effect, along with item type \times site and item type \times hemisphere \times chain interactions, indicating that the item type effects were largest across the anterior chain of the right hemisphere. ANOVA of the $R_{\text{scene-new}}$ comparison for this latency interval gave rise to an item type main effect and an item type \times site interaction.

1400–1900 ms latency interval—ANOVAs of the data from the 1400–1900 ms latency interval gave rise to reliable effects for all three item type comparisons. The $R_{\text{sentence-}R_{\text{scene}}}$ ANOVA revealed an item type \times chain interaction, with subsidiary chain-wise ANOVAs giving rise to an item type main effect for only the posterior chain [$F(1, 19) = 6.62, p < .025$]. Whereas there were no longer any reliable effects for the anterior chain, the posterior effect reflected the greater negativity of the R_{sentence} ERPs in relation to the R_{scene} ERPs. ANOVAs of the $R_{\text{sentence-new}}$ and $R_{\text{scene-new}}$ comparisons revealed item type main effects and several interactions with this factor (see Table 2). As in the previous latency interval, the $R_{\text{sentence-new}}$ differences were maximal over the right anterior scalp and were joined by similar effects for the $R_{\text{scene-new}}$ comparison.

Insensitivity of the left parietal old-new effect to encoding condition—The previous analyses of data from the 500–800 ms latency interval revealed reliable old-new (i.e., $R_{\text{sentence-new}}$ and $R_{\text{scene-new}}$) effects. As can be seen in Figure 3, the old-new effect for words from the sentence condition was maximal over the anterior scalp but extended to left posterior sites, whereas the effect for words from the scene condition was maximal over the left posterior scalp. To confirm that these old-new effects were reliable over the left posterior scalp, separate ANOVAs employing the factors of item type (remember and new) and site (five electrodes within the left posterior quadrant) were conducted for the items from the sentence and scene conditions. For both classes of items, these ANOVAs gave rise to significant item type main effects [sentence: $F(1, 19) = 20.46, p < .001$; scene: $F(1, 19) = 9.33, p < .01$] and item type \times site interactions [sentence: $F(1.8, 34.6) = 11.46, p < .001$; scene: $F(2, 38.3) = 4.70, p < .025$]. To further assess whether there were any differences between the two encoding conditions, an additional ANOVA of the old-new differences employed the factors of encoding condition (sentence versus scene) and site (five electrodes within the quadrant). This ANOVA gave rise to no effects involving the encoding condition factor ($F_s < 1.83, p_s > .18$). These null findings concur with the impression gained from Figures 1 and 2, in which the left parietal ERPs elicited by the two classes of recollected items appear almost identical until around 800 ms post-stimulus.

Topographic analyses—The scalp topographies of differences between the ERPs associated with the R_{sentence} , R_{scene} , and new-item response categories are shown in Figure 3. These topographies are plotted only for the latency intervals in which the item type effects were reliable, as determined by the foregoing amplitude analyses. As can be seen in the figure, the $R_{\text{sentence-}R_{\text{scene}}}$ differences appear to have a maximum over mid-frontal scalp from about 300 to 1400 ms post-stimulus onset, as well as a polarity-reversed posterior maximum beginning at around 800 ms. The $R_{\text{sentence-new}}$ differences exhibit a similar anterior positivity that begins early in the recording epoch and subsequently extends to the left posterior scalp. A similar posterior effect, albeit more bilateral, is evident for the $R_{\text{scene-new}}$ differences. Finally, near the end of the recording epoch, both the $R_{\text{sentence-new}}$ and $R_{\text{scene-new}}$ differences are maximal over the right anterior scalp.

The scalp topographies of the ERP differences were analyzed in two parts. First, the topographies of the $R_{\text{sentence-}R_{\text{scene}}}$ differences were contrasted across the latency intervals in which they were significant (i.e., across the top row of Figure 3) to determine whether the differences changed in topography over the recording epoch. Second, the $R_{\text{sentence-new}}$ and

R_{scene} -new differences were compared within the latency intervals in which the differences were separately reliable in the foregoing amplitude analyses, allowing for investigation of whether the old-new effects differed in topography according to encoding condition. All topographic analyses were based on the data from the same 20 electrodes used in the foregoing amplitude analyses (see Figure 1). Prior to analysis, the ERP data were range-normalized to minimize the influence of any between-interval or between-condition amplitude differences that could potentially confound the results (McCarthy & Wood, 1985).

For the analysis of R_{sentence} - R_{scene} differences across latency intervals, ANOVA employed an interval factor (300–500, 500–800, 800–1100, 1100–1400, and 1400–1900 ms), along with the electrode factors corresponding to hemisphere, chain, and site. Only the reliable effects involving the interval factor are of interest and reported here. The ANOVA gave rise to a latency interval \times hemisphere interaction [$F(3, 56.1) = 4.82, p < .01$] and a latency interval \times site interaction [$F(3.7, 70) = 2.67, p < .05$]. To further elucidate these interactions, subsidiary ANOVAs were used to compare each pair of latency intervals. Contrasting the first interval with each other interval resulted in a latency interval \times hemisphere interaction in every case [$F_s(1, 19) > 6.27, p_s < .025$], as did the comparison of the 500–800 and 1100–1400 ms intervals [$F(1, 19) = 4.62, p < .05$]. These effects reflect the transition from left-lateralized R_{sentence} - R_{scene} differences early in the recording epoch to more right-lateralized differences in the subsequent intervals. In addition, contrasting the 300–500 and 500–800 ms intervals with the final interval gave rise to interval \times site interactions [$F(1.8, 34.1) = 3.61, p < .05$, and $F(2.2, 41.9) = 5.78, p < .01$, respectively], indicating the more superior distributions of the earlier effects compared to the inferior distribution of the later effects.

The second part of the topographic analyses involved directly contrasting the R_{sentence} -new and the R_{scene} -new differences in each of the 500–800, 800–1100, 1100–1400, and 1400–1900 ms latency intervals. ANOVAs employing the item type factor (sentence versus scene), along with the three electrode factors, gave rise to significant item type \times chain interactions for all intervals [$F_s(1, 19) > 6.88, p_s < .025$]. These effects presumably reflect how the anteriorly-distributed R_{sentence} -new effects contrast with the posterior R_{scene} -new effects. In addition, there was an item type \times chain \times site interaction for the 800–1100 ms interval [$F(2.6, 49) = 4.63, p < .01$], likely resulting from the fact that the R_{sentence} -new effects were maximal at superior sites whereas the R_{scene} -new effects were more prominent at lateral sites.

Selectivity of the content-dependent effects to recollection—As can be seen in Figure 3, content-dependent retrieval effects in the 300–500 ms latency interval were maximal over mid-frontal electrodes. The topographical and temporal characteristics of these effects resemble the ‘mid-frontal’ ERP old-new effects that have frequently been associated with familiarity-based memory judgments (e.g., Curran, 2000; Rugg et al., 1998; for review, see Rugg & Curran, 2007). This resemblance raises the question of whether the present findings are a reflection not of differential recollection-related activity, but rather differential modulation of the familiarity-sensitive mid-frontal effect. Whereas this account would be supported by content-dependent effects that are equivalent in magnitude for items that are recollected and for those items that are correctly recognized in the absence of recollection (i.e., endorsed with a K response), evidence that the content-dependent effects are larger in magnitude when based on R responses only would strongly suggest that the differences are selective for recollection.

As noted earlier, few subjects made at least 16 K responses to each class of studied test item. Thus, to contrast the ERPs elicited by test items endorsed with R and K responses, the minimum trial requirement was eliminated, and four subjects who had no K responses in one or both conditions were excluded. The mean numbers of trials (and ranges) contributing to the resulting ERPs were 35 (24–53) and 30 (18–45) for R responses in the sentence and scene conditions,

respectively, and 11 (1–32) and 14 (1–32) for the corresponding K responses. Figure 4 illustrates the ERPs from a representative left anterior electrode site.

To test whether the content-dependent effects varied according to the nature of response given, an ANOVA of the data from the 300–500 ms latency interval was conducted for the left anterior quadrant, where the $R_{\text{sentence}} - R_{\text{scene}}$ differences were maximal according to the foregoing analyses (also see Figure 3). The ANOVA employed the factors of response type (R versus K), item type (sentence versus scene), and site, and gave rise to a significant response type \times item type \times site interaction [$F(3, 44.4) = 4.04, p < .025$]. Subsidiary ANOVAs restricted to each level of the site factor revealed reliable item type main effects for R responses at two of the sites [$F7: F(1, 15) = 4.60, p < .05$; $F3: F(1, 15) = 4.60, p < .05$], but no significant effects for K responses at any site (all $F_s < 1$). These findings demonstrate that the ERP differences between the sentence and scene conditions are confined to items associated with recollection, and significantly greater than those recognized on the basis of familiarity alone.

Discussion

The reinstatement hypothesis of episodic memory posits that recollection involves the reactivation of processes that were engaged during the encoding of an episode. A key prediction of this hypothesis is that the neural correlates of recollection will differ according to the content of the retrieved episodes. The present study employed ERPs to investigate the time course of content-dependent differences in retrieval-related activity, particularly in relation to the timing of seemingly ‘generic’ (content-independent) recollection effects. The principal finding is that content-dependent ERP effects were evident as early as any generic effects.

Analyses of ERPs elicited by test words that were associated with recollection (i.e., endorsed with a “remember” response) revealed several effects according to the words’ prior encoding history. The earliest of these effects, in which the ERPs corresponding to test words encoded in the sentence condition were more positive-going than the ERPs to words studied in the scene condition, was evident over the anterior scalp by 300 ms following stimulus onset. This anterior effect persisted for approximately a second, and was joined at around 800 ms post-stimulus onset by a second effect that was of opposite polarity and distributed bilaterally over the posterior scalp. Under the assumption that words from each encoding condition were associated with distinct types of informational content, the ERP effects are interpreted as reflecting content-dependent recollective processes. Thus, these findings parallel the results of prior functional neuroimaging studies in demonstrating that the neural correlates of recollection are content-sensitive (Gottfried et al., 2004; Johnson & Rugg, in press; Kahn et al., 2004; Khader et al., 2005; Wheeler & Buckner, 2003, 2004; Wheeler et al., 2000, 2006; Woodruff et al., 2005).

In addition to contributing to the mounting evidence for the content-dependency of recollection-related neural activity, the present findings represent a significant extension to prior functional neuroimaging results. As noted in the introduction, a major difficulty in interpreting the content-dependent effects obtained with fMRI is that the time course of these effects is unknown (for similar criticisms, see Johnson & Rugg, in press; Kahn et al., 2004; Maratos et al., 2001; Woodruff et al., 2005). The timing of the effects, particularly in relation to the timing of content-independent neural correlates of recollection, has important implications for their functional interpretation. The content-dependent ERP effects reported here were evident slightly earlier than the left parietal old-new effects elicited by recollected words from the sentence and scene conditions. Thus, the present ERP findings rule out the possibility that content-dependent retrieval effects are confined to processes engaged as a consequence of recollection, such as those involved in the evaluation of retrieved information or its maintenance in working memory. Instead, the time course of these effects suggests that

the differential patterns of underlying cortical activity are direct reflections of recollected (and possibly reinstated) episodic information.

The present study employed experimental procedures very similar to those we used previously with fMRI (Johnson and Rugg, in press). In that study, brain regions exhibiting content-dependent neural activity during recollection were a subset of the regions where encoding-related activity also differed: Greater recollection-related activity was observed in ventromedial prefrontal cortex for test words from the sentence study condition, whereas regions of occipital and fusiform cortex exhibited greater activity for recollected words from the scene condition. The content-dependent ERP effects demonstrated here might reflect, at least in part, scalp projections of the regionally-specific differences in neural activity identified by the fMRI study. However, it is important to note that whereas the present ERP findings are indicative of content-dependent retrieval processing, there is no evidence that they reflect the reinstatement of neural activity engaged during encoding. Evidence for reinstatement would necessitate findings of overlap between encoding- and retrieval-related ERP effects, which currently presents serious methodological challenges (but see Newman & Norman, 2006, for recent advances).

A notable aspect of the present findings is the insensitivity of the left parietal old-new ERP effect to the encoding manipulation. For the reasons outlined in the introduction, this effect is often regarded as a generic correlate of successful recollection, and the present findings are consistent with that interpretation. In addition, prior findings have indicated that the magnitude of the left parietal effect varies with the amount of information recollected (Vilberg et al., 2006; Wilding, 2000). Importantly, the strong similarity of the left parietal effects elicited by the two classes of recollected items in the present study argues against the possibility that items studied in the sentence condition elicited retrieval of more information than did items from the scene condition, despite their differential probabilities of recollection. Thus, the differences in the ERPs elicited by these items over the anterior scalp are taken as a reflection of qualitative differences in the nature of the episodic content that was recollected, rather than quantitative differences in amount of recollected information.

As noted in the Results, the early (300–500 ms) content-dependent effects reported here resemble the ‘mid-frontal old-new effect’ often linked to familiarity-based recognition (for review, see Rugg & Curran, 2007; for an alternative view, see Paller et al., 2007). This similarity raises the concern that these content-dependent effects merely reflect differences in the magnitudes of the mid-frontal old-new effects elicited by items from each encoding condition. In support of this possibility, it has been reported that the mid-frontal old-new effect is sensitive to context change (Ecker et al., 2007; Tsivilis et al., 2001). Applying these findings to the present study, it could be argued that items encoded in the scene condition were subjected to a more pronounced change of context when re-presented at test than those encoded in the sentence condition, and hence elicited a smaller mid-frontal effect. This account is inconsistent, however, with the results obtained by directly contrasting the ERPs associated with items given “remember” and “know” responses. If the anterior content-dependent effects do indeed reflect the modulation of a context-sensitive mid-frontal effect, then they should have been as evident for items judged old on the basis of familiarity as they were for recollected items. Contrary to this prediction, content-dependent ERP differences were significantly attenuated in the ERPs associated with K responses (Figure 4). Thus, our findings extend those of Fabiani et al. (2000; see introduction) by demonstrating that early-onset content-dependent ERP effects are greater for recollected items than for items that are merely familiar. It remains to be established, however, whether items recognized on the basis of familiarity alone elicit any sign of content-dependent retrieval effects.

Whereas the present early-onsetting content-dependent effects are interpreted as reflecting the recollection of different types of episodic information, content-dependent effects occurring later in the recording epoch arguably require a different interpretation. Notably, the effects over the anterior scalp persisted for approximately a second, changing in topography from a left- to a right-lateralized maximum (see Figure 3). This topographic shift likely reflects the summation of the early content-dependent effects with the so-called ‘right frontal old-new effect’, which is held to be a generic correlate of post-retrieval monitoring operations (e.g., Wilding & Rugg, 1996; see Rugg, 2004, for review). A second set of content-dependent effects emerged around 800 ms post-stimulus. These effects had a posterior maximum and were reversed in polarity compared to the anterior effects, such that R_{scene} waveforms were more positive-going than R_{sentence} ERPs. The topography and time course of these latter effects are reminiscent of those frequently reported for tasks requiring the retrieval of contextual information (see Johansson & Mecklinger, 2003, for review), suggesting that the effects may reflect the post-retrieval maintenance or monitoring of such information.

The late-onsetting content-dependent ERP effects reported here serve as an essential caution to the interpretation of content-specific neural activity observed in prior fMRI studies. As noted in the introduction, the reinstatement hypothesis requires that the onset of such differences in retrieval-related neural activity emerge relatively early in the course of retrieval processing and, arguably, no later than the onset of generic recollection-related effects. The present ERP findings clearly indicate, however, that content-dependent retrieval effects can emerge so late as to be associated with post-retrieval processes. Thus, the previous concerns that have been raised about the relevance of analogous fMRI findings to the reinstatement hypothesis should be taken seriously until more is known about the temporal characteristics of the neural events underlying the fMRI findings.

To conclude, the ERP findings reported here strengthen prior neuroimaging evidence that the neural correlates of retrieval are sensitive to episodic content. Crucially, these findings extend those obtained in the prior studies by demonstrating that the content-dependent modulation of retrieval-related neural activity onsets as early as ERP effects that are attributed to generic recollective processes. In addition, the content-dependent effects were enhanced for memory judgments accompanied by recollection as opposed to judgments made on the basis of familiarity alone. Together, the present findings suggest that content-dependent neural activity is, at least in part, an online reflection of the recollection of episodic information.

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References

- Allan K, Wilding EL, Rugg MD. Electrophysiological evidence for dissociable processes contributing to recollection. *Acta Psychologica* 1998;98:231–252. [PubMed: 9621832]
- Alvarez P, Squire LR. Memory consolidation and the medial temporal lobe: a simple network model. *Proceedings of the National Academy of Sciences USA* 1994;91:7041–7045.
- American Electroencephalographic Society. Guidelines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology* 1994;11:111–113. [PubMed: 8195414]
- Cansino S, Maquet P, Dolan RJ, Rugg MD. Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex* 2002;12:1048–1056. [PubMed: 12217968]
- Curran T. Brain potentials of recollection and familiarity. *Memory and Cognition* 2000;28:923–938.
- Curran T, Dien J. Differentiating amodal familiarity from modality-specific memory processes: An ERP study. *Psychophysiology* 2003;40:979–988. [PubMed: 14986851]
- Damasio AR. Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition* 1989;33:25–62. [PubMed: 2691184]

- Ecker UK, Zimmer HD, Groh-Bordin C, Mecklinger A. Context effects on familiarity are familiarity effects on context – an electrophysiological study. *International Journal of Psychophysiology* 2007;64:146–156. [PubMed: 17331603]
- Eldridge LL, Knowlton BJ, Furmanski CS, Bookheimer SY, Engel SA. Remembering episodes: a selective role for the hippocampus during retrieval. *Nature Neuroscience* 2000;3:1149–1152.
- Fabiani M, Stadler MA, Wessels PM. True but not false memories produce a sensory signature in human lateralized brain potentials. *Journal of Cognitive Neuroscience* 2000;12:941–949. [PubMed: 11177415]
- Friedman D, Johnson JR. Event-related potential (ERP) studies of memory encoding and retrieval: a selective review. *Microscopy Research and Technique* 2000;51:6–28. [PubMed: 11002349]
- Gardiner JM, Ramponi C, Richardson-Klavehn A. Experiences of remembering, knowing, and guessing. *Consciousness and Cognition* 1998;7:1–26. [PubMed: 9521829]
- Gottfried JA, Smith APR, Rugg MD, Dolan RJ. Remembrance of odors past: human olfactory cortex in cross-modal recognition memory. *Neuron* 2004;42:687–695. [PubMed: 15157428]
- Greenhouse GW, Geisser S. On methods in the analysis of repeated measures designs. *Psychometrika* 1959;49:95–112.
- Henson RN, Rugg MD, Shallice T, Josephs O, Dolan RJ. Recollection and familiarity in recognition memory: an event-related fMRI study. *Journal of Neuroscience* 1999;19:3962–3972. [PubMed: 10234026]
- Henson RN, Rylands A, Ross E, Vuillemeir P, Rugg MD. The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. *NeuroImage* 2004;21:1674–1689. [PubMed: 15050590]
- James, W. *The principles of psychology*. Henry Holt and Company; New York: 1890.
- Johansson M, Mecklinger A. The late posterior negativity in ERP studies of episodic memory: action monitoring and retrieval of attribute conjunctions. *Biological Psychology* 2003;64:91–117. [PubMed: 14602357]
- Johnson JD, Rugg MD. Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex*. in press
- Kahn I, Davachi L, Wagner AD. Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. *Journal of Neuroscience* 2004;28:4172–4180. [PubMed: 15115812]
- Khader P, Burke M, Bien S, Ranganath C, Rosler F. Content-specific activation during associative long-term memory retrieval. *NeuroImage* 2005;27:805–816. [PubMed: 15964209]
- Kucera, H.; Francis, WN. *Computational analysis of present-day American English*. Brown Univ. Press; Providence, RI: 1967.
- Maratos EJ, Dolan RJ, Morris JS, Henson RNA, Rugg MD. Neural activity associated with episodic memory for emotional context. *Neuropsychologia* 2001;39:910–920. [PubMed: 11516444]
- McCarthy G, Wood CC. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology* 1985;62:203–208. [PubMed: 2581760]
- McClelland JL, McNaughton BL, O'Reilly RC. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychological Review* 1995;102:419–457. [PubMed: 7624455]
- Newman, EL.; Norman, KA. *Society for Neuroscience Abstracts, Program No. 365.2. 2006. Tracking the sub-trial dynamics of cognitive competition*.
- Norman KA, O'Reilly RC. Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychological Review* 2003;110:611–646. [PubMed: 14599236]
- Paller KA, Voss JL, Boehm SG. Validating neural correlates of familiarity. *Trends in Cognitive Sciences* 2007;11:243–250. [PubMed: 17475539]
- Rajaram S. Remembering and knowing: two means of access to the personal past. *Memory and Cognition* 1993;21:89–102.
- Rolls ET. Hippocampo-cortical and cortico-cortical backprojections. *Hippocampus* 2000;10:380–388. [PubMed: 10985277]

- Rugg, MD. Retrieval processing in human memory: electrophysiological and fMRI evidence. In: Gazzaniga, MS., editor. *The New Cognitive Neurosciences*. 3. MIT Press; Cambridge, MA: 2004. p. 727-737.
- Rugg, MD.; Allan, K. Event-related potential studies of memory. In: Tulving, E.; Craik, FIM., editors. *The Oxford Handbook of Memory*. Oxford Univ. Press; Oxford: 2000. p. 521-537.
- Rugg MD, Curran T. Event-related potentials and recognition memory. *Trends in Cognitive Sciences* 2007;11:251–257. [PubMed: 17481940]
- Rugg MD, Mark RE, Walla P, Schloerscheidt AM, Birch CS, Allan K. Dissociation of the neural correlates of implicit and explicit memory. *Nature* 1998;9:595–598. [PubMed: 9560154]
- Schloerscheidt AM, Rugg MD. Recognition memory for words and pictures: an event-related potential study. *NeuroReport* 1997;8:3281–3285. [PubMed: 9351657]
- Shastri L. Episodic memory and cortico-hippocampal interactions. *Trends in Cognitive Sciences* 2002;6:162–168. [PubMed: 11912039]
- Tsivilis D, Otten LJ, Rugg MD. Context effects on the neural correlates of recognition memory: an electrophysiological study. *Neuron* 2001;31:497–505. [PubMed: 11516405]
- Tulving E. Memory and consciousness. *Canadian Psychology* 1985;26:1–12.
- Vilberg KL, Moosavi RF, Rugg MD. The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain Research* 2006;1122:161–170. [PubMed: 17027673]
- Wheeler ME, Buckner RL. Functional dissociation among components of remembering: control, perceived oldness, and content. *Journal of Neuroscience* 2003;23:3869–3880. [PubMed: 12736357]
- Wheeler ME, Buckner RL. Functional-anatomic correlates of remembering and knowing. *NeuroImage* 2004;21:1337–1349. [PubMed: 15050559]
- Wheeler ME, Petersen SE, Buckner RL. Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences USA* 2000;97:11125–11129.
- Wheeler ME, Shulman GL, Buckner RL, Miezen FM, Velanova K, Petersen SE. Evidence for separate perceptual reactivation and search processes during remembering. *Cerebral Cortex* 2006;16:949–959. [PubMed: 16162854]
- Wilding EL. In what way does the parietal ERP old/new effect index recollection? *International Journal of Psychophysiology* 2000;35:81–87. [PubMed: 10683669]
- Wilding EL, Doyle MC, Rugg MD. Recognition memory with and without retrieval of context: an event-related potential study. *Neuropsychologia* 1995;33:743–767. [PubMed: 7675165]
- Wilding EL, Rugg MD. An event-related potential study of recognition memory with and without retrieval of source. *Brain* 1996;119:889–905. [PubMed: 8673500]
- Woodruff CC, Hayama HR, Rugg MD. Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research* 2006;1100:125–135. [PubMed: 16774746]
- Woodruff CC, Johnson JD, Uncapher MR, Rugg MD. Content-specificity of the neural correlates of recollection. *Neuropsychologia* 2005;43:1022–1032. [PubMed: 15769488]
- Yonelinas AP, Jacoby LL. The relation between remembering and knowing as bases for recognition: effects of size congruency. *Journal of Memory and Language* 1995;34:622–643.
- Yonelinas AP, Otten LJ, Shaw KN, Rugg MD. Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience* 2005;25:3002–3008. [PubMed: 15772360]

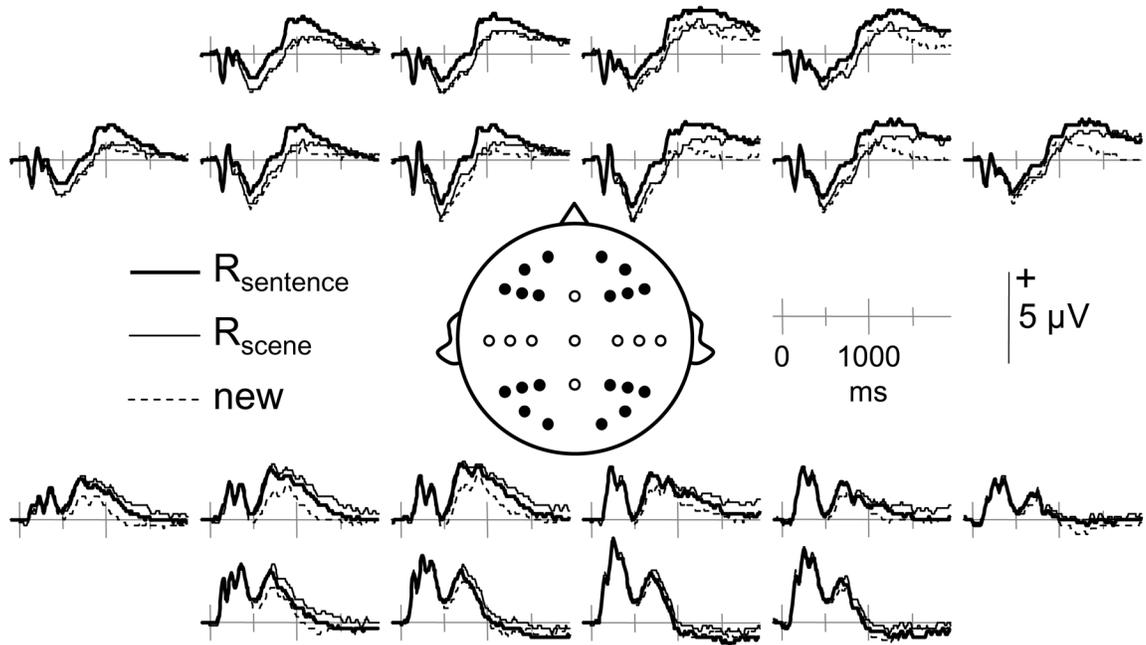


Figure 1. Grand-average ERPs elicited by test words given "remember" (R) responses from the two encoding conditions (R_{sentence} and R_{scene}), along with the ERPs elicited by correctly-rejected new words. The ERPs correspond to electrode locations depicted by filled circles in the headplot.

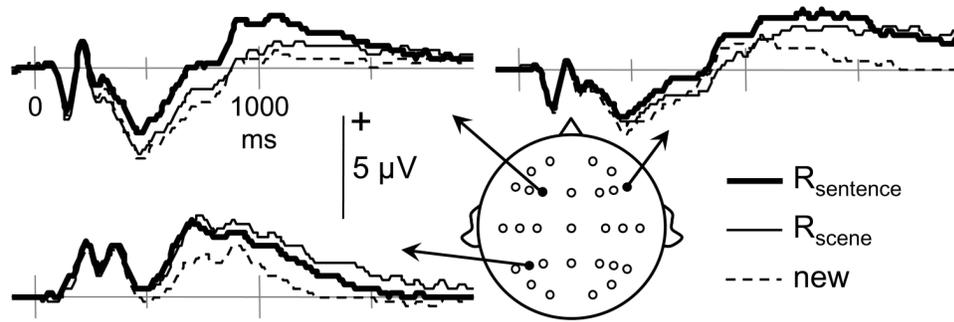


Figure 2. Grand-average ERPs from electrodes where differences among the R_{sentence} , R_{scene} , and new ERPs were most prominent.

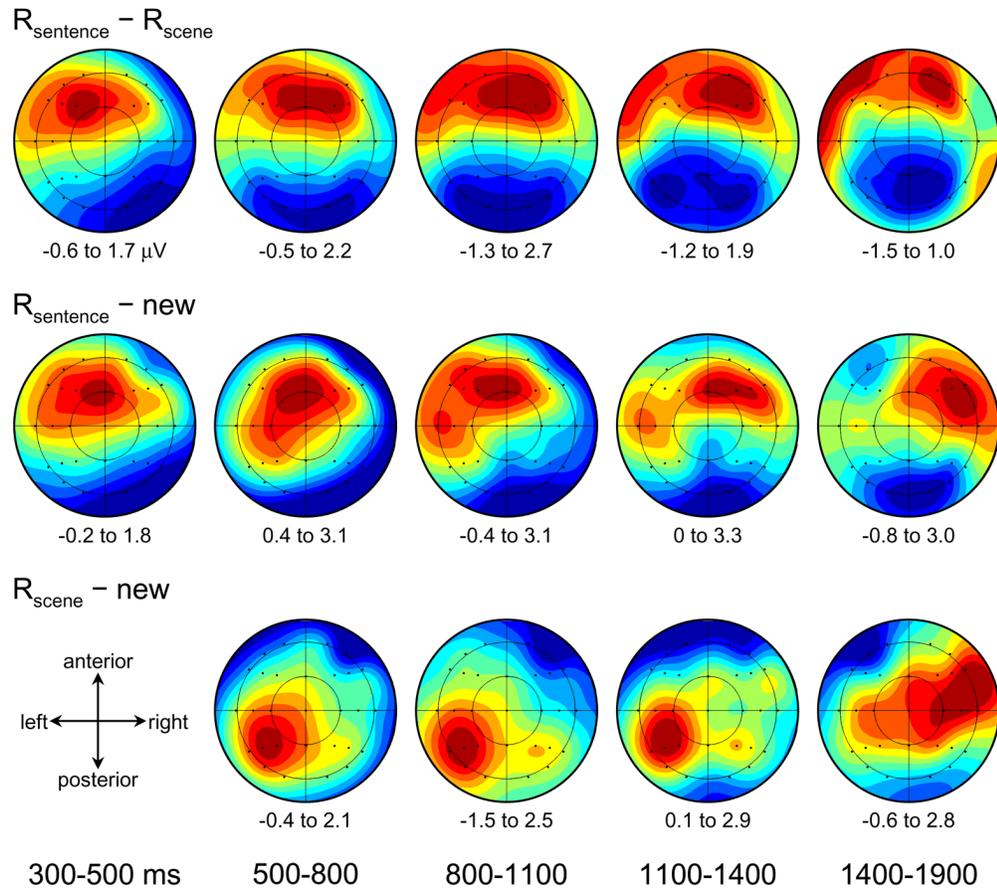


Figure 3. Spherical spline maps of ERP differences among the three item types (R_{sentence} , R_{scene} , and new) for latency intervals in which the amplitude differences were reliable. Each map is proportionally scaled between the minimum (blue) and maximum (red) differences. The range of differences (in microvolts) is provided below each map. The orientation of the plots is shown at the lower left.

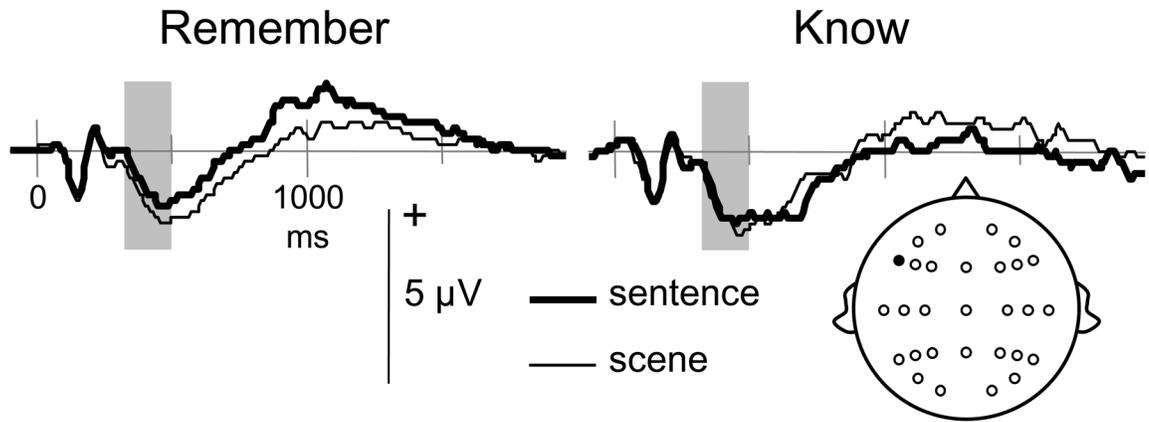


Figure 4. Grand-average ERPs elicited by test words given “remember” and “know” responses, from a representative electrode (F7). The shaded regions highlight the 300–500 ms latency interval.

Table 1
Mean proportions (and SDs) of “remember”, “know”, and “new” responses for each type of test item

	Test item type		
	Scene	Sentence	New
Response			
Remember	.62 (.18)	.72 (.18)	.04 (.06)
Know	.21 (.17)	.18 (.14)	.08 (.09)
New	.17 (.11)	.10 (.10)	.88 (.14)

Table 2

Significant effects ($p < .05$) resulting from ANOVAs of the ERP data in the 300–500, 500–800, 800–1100, 1100–1400, and 1400–1900 ms latency intervals

Latency interval	Comparison	Effect	df	F	p
300–500 ms	$R_{\text{sentence}} - R_{\text{scene}}$	IT×HM	1, 19	5.49	< .05
		IT×CH	1, 19	7.14	< .025
		IT×HM×ST	3, 57.9	3.21	< .05
	$R_{\text{sentence}} - \text{new}$	IT	1, 19	4.78	< .05
500–800 ms	$R_{\text{sentence}} - R_{\text{scene}}$	IT×CH	1, 19	12.33	< .005
	$R_{\text{sentence}} - \text{new}$	IT	1, 19	45.53	< .001
		IT×HM	1, 19	8.20	< .01
		IT×ST	2, 37.1	18.24	< .001
		IT×HM×CH×ST	3, 56.6	3.35	< .025
	$R_{\text{scene}} - \text{new}$	IT×ST	2, 37.6	5.01	< .025
		IT×CH	1, 19	50.67	< .001
800–1100 ms	$R_{\text{sentence}} - R_{\text{scene}}$	IT×CH×ST	2, 6, 49.4	3.87	< .025
	$R_{\text{sentence}} - \text{new}$	IT	1, 19	9.52	< .01
		IT×HM	1, 19	6.38	< .025
		IT×ST	2, 1, 40.8	7.14	< .005
		IT×HM×ST	2, 1, 39.1	3.22	< .05
		IT×CH×ST	2, 3, 43.0	4.58	< .025
	$R_{\text{scene}} - \text{new}$	IT×HM	1, 19	7.75	< .025
		IT×CH	1, 19	8.89	< .01
		IT×ST	2, 6, 48.9	3.07	< .05
		IT×CH	1, 19	25.03	< .001
		IT	1, 19	19.76	< .001
1100–1400 ms	$R_{\text{sentence}} - R_{\text{scene}}$	IT×ST	2, 1, 40.2	11.02	< .001
	$R_{\text{sentence}} - \text{new}$	IT×HM×CH	1, 19	7.84	< .025
		IT	1, 19	10.27	< .005
	$R_{\text{scene}} - \text{new}$	IT×ST	2, 8, 52.5	8.05	< .001
		IT×CH	1, 19	8.00	< .025
1400–1900 ms	$R_{\text{sentence}} - R_{\text{scene}}$	IT	1, 19	6.55	< .025
	$R_{\text{sentence}} - \text{new}$	IT×HM	1, 19	11.46	< .005
		IT×ST	2, 37.3	4.40	< .025
		IT×HM×CH	1, 19	18.07	< .001
	$R_{\text{scene}} - \text{new}$	IT	1, 19	7.42	< .025
		IT×HM	1, 19	6.07	< .025
		IT×ST	2, 2, 40.9	7.61	< .005
		IT×HM×CH	1, 19	10.72	< .005
		IT×HM×CH×ST	2, 9, 55.8	4.59	< .01

R = remember, IT = item type, HM = hemisphere, CH = anterior/posterior chain, ST = sites within each quadrant.