Perceptual Priming Versus Explicit Memory: Dissociable Neural Correlates at Encoding

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Abstract

■ We addressed the hypothesis that perceptual priming and explicit memory have distinct neural correlates at encoding. Event-related potentials (ERPs) were recorded while participants studied visually presented words at deep versus shallow levels of processing (LOPs). The ERPs were sorted by whether or not participants later used studied words as completions to three-letter word stems in an intentional memory test, and by whether or not they indicated that these completions were remembered from the study list. Study trials from which words were later used and not remembered (primed trials) and study trials from which words were later used and remembered (remembered trials) were compared to study trials from which words were later not used (forgotten trials), in order to measure the ERP difference associated with later memory (DM effect). Primed trials involved an early (200–450 msec) centro-parietal negative-going DM effect. Remembered trials involved a late (900–1200 msec) right frontal, positive-going DM effect regardless of LOP, as well as an earlier (600–800 msec) central, positive-going DM effect during shallow study processing only. All three DM effects differed topographically, and, in terms of their onset or duration, from the extended (600–1200 msec) fronto-central, positive-going shift for deep compared with shallow study processing. The results provide the first clear evidence that perceptual priming and explicit memory have distinct neural correlates at encoding, consistent with Tulving and Schacter's (1990) distinction between brain systems concerned with perceptual representation versus semantic and episodic memory. They also shed additional light on encoding processes associated with later explicit memory, by suggesting that brain processes influenced by LOP set the stage for other, at least partially separable, brain processes that are more directly related to encoding success. ■

INTRODUCTION

The distinction between explicit and implicit memory (Graf & Schacter, 1985) is fundamental to current memory research. ''Explicit memory'' typically refers to the conscious awareness of prior events that accompanies voluntary retrieval of studied information and has usually been examined using intentional tests of recall and recognition memory. ''Implicit memory'' typically refers to the involuntary retrieval of studied information and has often been examined using incidental tests of perceptual priming, such as word stem and word fragment completion. In these tests, prior study of words enhances the likelihood that these words will be used as completions of the test cues, even though the test does not require any mental reference to the study phase. In an influential article, Tulving & Schacter (1990) (see also Schacter, Wagner, & Buckner, 2000) argued that perceptual priming depends on brain systems concerned with perceptual representation, whose operation is not associated with awareness of memory, whereas explicit memory depends on brain systems concerned with

semantic and episodic memory. According to this theory, the episodic memory system, which is embedded within the semantic memory system, is responsible for awareness of the past in relation to the self—a defining characteristic of explicit memory (e.g., Wheeler, Stuss, & Tulving, 1997; Nyberg & Tulving, 1996; Tulving, 1995).

Much evidence from event-related potential (ERP) and hemodynamic investigations of brain activity now confirms that explicit memory and perceptual priming have different neural bases at retrieval (for reviews, see Friedman & Johnson, 2000; Mecklinger, 2000; Paller, 2000; Rugg & Allan, 2000; Schacter et al., 2000). Tulving and Schacter's (1990) theory—along with double dissociations between explicit memory and perceptual priming caused by brain lesions (for reviews, see Mayes, 2000; Moscovitch, 2000)—can additionally be taken to suggest that encoding into the semantic and episodic memory systems might be distinguishable from encoding into the perceptual representation system. The present experiment addressed this hypothesis using an ERP measure of neural activity at encoding.

A powerful method of examining the neural basis of encoding is to measure neural activity during the study phase of an experiment and then sort these

measurements according to subsequent memory test performance (e.g., Fernández et al., 1999; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998; Paller, Kutas, & Mayes, 1987). ERP experiments employing intentional tests have typically shown positive deflections of waveforms recorded during study of items that are subsequently recalled or recognized compared with waveforms recorded during study of items that are subsequently unrecalled or unrecognized (e.g., Friedman & Trott, 2000; Fernández et al., 1998, 1999; Weyerts, Tendolkar, Smid, & Heinze, 1997; Friedman, Ritter, & Snodgrass, 1996; Van Petten & Senkfor, 1996; Besson & Kutas, 1993; Paller, Kutas, & Mayes, 1987; Paller, Kutas, Shimamura, & Squire, 1987; Paller, McCarthy, & Wood, 1988; Paller, 1990; Paller & Kutas, 1992; Fabiani, Karis, & Donchin, 1986, 1990; Fabiani & Donchin, 1995; Neville, Kutas, Chesney, & Schmidt, 1986; Johnson, Pfefferbaum, & Kopell, 1985; Karis, Fabiani, & Donchin, 1984; for discussion of exceptions, see Rugg & Allan, 2000). Paller, Kutas, and Mayes (1987) dubbed this association between test performance and study ERPs the "difference due to later memory effect" (DM effect). However, ERP experiments have not yielded clear evidence for a distinct DM effect for later perceptual priming: DM effects for priming in incidental tests have not been consistently observed, and where they have been observed, they have resembled those for later intentional test performance (Friedman et al., 1996; Paller, Kutas, Shimamura, et al., 1987; Paller, 1990).
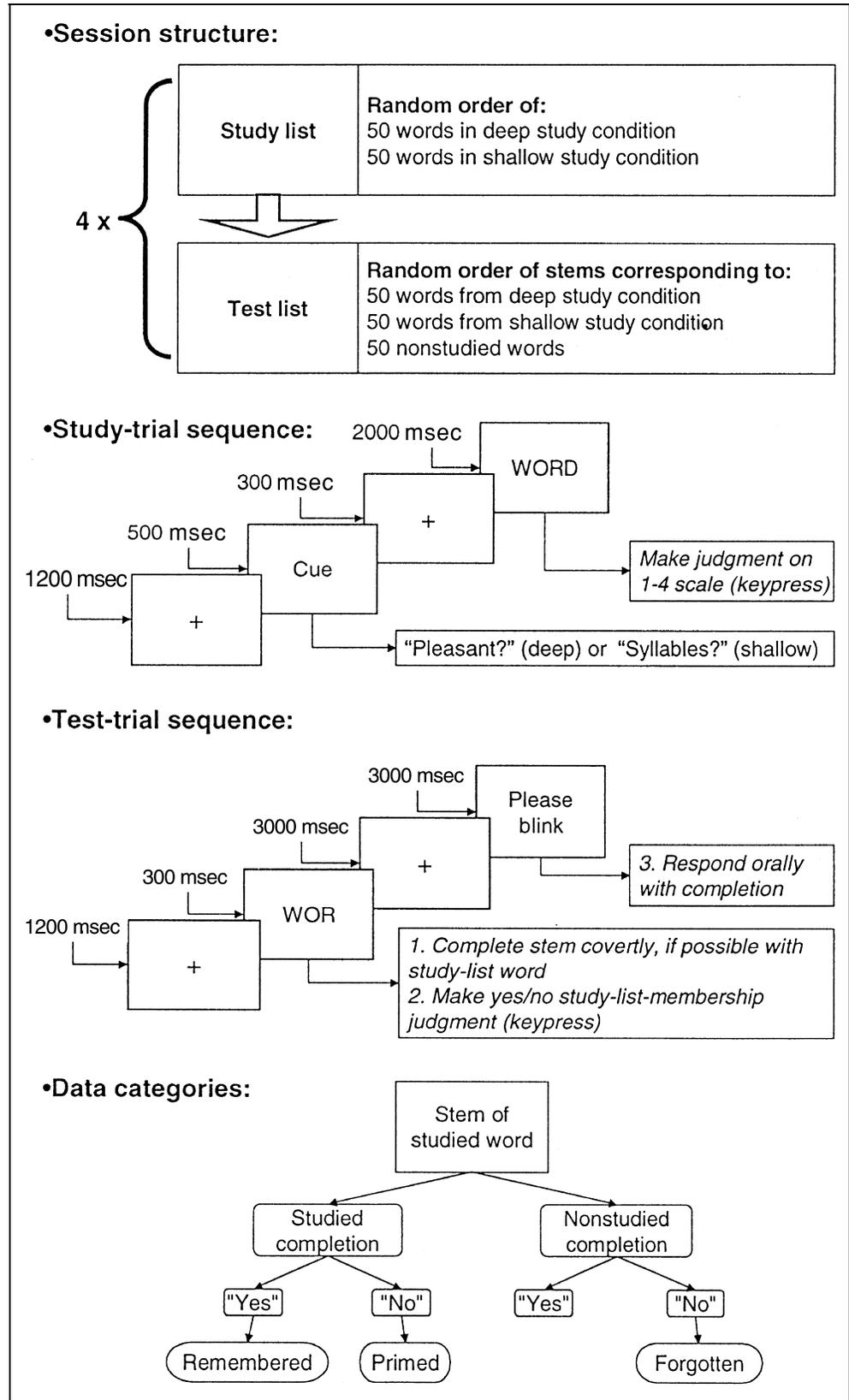
As discussed by Rugg (1995) (see also Curran, 1999), a major reason for this difficulty might be that even when perceptual priming in incidental tests is involuntary—meaning that priming is not contaminated by deliberate attempts to retrieve studied items—participants nevertheless spontaneously become aware that some items in the test phase were previously studied. Schacter (1987) labeled this kind of awareness "involuntary explicit memory." There is considerable evidence, both from behavioral and ERP measures, that involuntary explicit memory occurs frequently during incidental tests of perceptual priming (e.g., Curran, 1999; Richardson-Klavehn, Gardiner, & Java, 1994; Richardson-Klavehn, Lee, Joubran, & Bjork, 1994; Richardson-Klavehn & Gardiner, 1995, 1996; Paller & Kutas, 1992; Paller, Kutas, & McIsaac, 1995; for discussion, see Richardson-Klavehn, Gardiner, & Java, 1996). If involuntary explicit memory occurs at test, encoding activities that support later involuntary explicit memory must have taken place at study. In consequence, if ERPs at study are simply sorted by primed versus unprimed status in a later incidental test, the study ERPs will be contaminated by the encoding activity associated with later involuntary explicit memory—even when priming in this later test does not reflect deliberate attempts to retrieve studied items. Thus, according to Tulving and Schacter's (1990) theory, the study ERPs formed for later priming will reflect encoding into the semantic and episodic systems as well

as into the perceptual representation system. To test hypotheses concerning the perceptual representation system with ERPs, therefore, it is necessary to obtain a purer measure of perceptual priming—one that indexes priming that is both involuntary and unassociated with awareness of prior study (see also Rugg et al., 1998).

Richardson-Klavehn, Gardiner, et al. (1994) and Richardson-Klavehn and Gardiner (1995, 1996) developed a behavioral testing method that provides such a measure and we adapted it for the current experiment. In its current manifestation, this method employed intentional, rather than incidental, test instructions. On each test trial, participants attempted to complete a word stem (i.e., the first three letters of a word) with a word from a previous study list, but if they could not, they used the first word coming to mind. Stem completion was covert, but participants indicated on each trial whether or not they had used a word remembered from the study list to complete the stem. During a pause to blink after each trial, participants responded overtly with the word they had used as a completion, and these completions were scored (see also Allan, Doyle, & Rugg, 1996; Allan & Rugg, 1997; Allan, Robb, & Rugg, 2000, for a similar approach to word stem completion). Some of the test stems could not be completed with studied words. However, for current purposes, the three critical trial types all involved stems that could be completed with studied words. We assumed (1) that completion of these stems with studied words that were judged not to be from the study list reflected perceptual priming that was both involuntary and unassociated with explicit memory; (2) that completion of these stems with studied words that were judged to be from the study list reflected both voluntary and involuntary explicit memory; and (3) that completion of these stems with nonstudied words that were judged not to be from the study list reflected forgetting of study list words, thus forming a suitable baseline. These three kinds of test trials are henceforth termed "primed," "remembered," and "forgotten" trials, respectively, and we used them to sort ERPs recorded during the previous study phase. The DM effect for priming was evaluated by contrasting study ERPs corresponding to primed and forgotten test trials, and the DM effect for explicit remembering was evaluated by contrasting study ERPs corresponding to remembered and forgotten test trials.

The assumption that primed trials reflect perceptual priming in the absence of explicit memory follows from two findings. First, under appropriate study conditions, there can be robust facilitatory priming of word stem completion, even when participants attempt not to complete stems with studied words and even when they are given an opportunity to reexamine their responses and edit out studied words (Richardson-Klavehn, Gardiner, et al., 1994; Richardson-Klavehn & Gardiner, 1995). Second, the level of this priming in the absence of explicit memory is accurately predicted by performance

Figure 1. Summary of the experimental design and procedure and the resulting data categories. ERPs reported here were recorded during the study trials.

•Session structure:

4 x

Study list	**Random order of:** 50 words in deep study condition 50 words in shallow study condition

Test list	**Random order of stems corresponding to:** 50 words from deep study condition 50 words from shallow study condition 50 nonstudied words

•Study-trial sequence:

2000 msec — WORD

300 msec — +

500 msec — Cue

1200 msec — +

Make judgment on 1-4 scale (keypress)

"Pleasant?" (deep) or "Syllables?" (shallow)

•Test-trial sequence:

3000 msec — Please blink

3000 msec — +

300 msec — WOR

1200 msec — +

3. Respond orally with completion

1. Complete stem covertly, if possible with study-list word
2. Make yes/no study-list-membership judgment (keypress)

•Data categories:

Stem of studied word

Studied completion — Nonstudied completion

"Yes" — "No" — "Yes" — "No"

Remembered — Primed — Forgotten

in an intentional test with on-line study list membership judgments, as used here, the relevant measure being the level of stem completion with studied words judged not to be from the study list (Richardson-Klavehn & Gardiner, 1995). The primed trials in the current experiment correspond to this measure. The assumption that

remembered trials reflect both voluntary and involuntary explicit memory follows from findings that awareness of study list membership in intentional word stem completion tests reflects not only voluntary but also involuntary retrieval. For example, match (in contrast to mismatch) in perceptual modality between study and test confers an involuntary benefit on intentional word stem completion performance that is accompanied by increased awareness of study list membership (Richardson-Klavehn & Gardiner, 1996; Richardson-Klavehn, Clarke, & Gardiner, 1999; Craik, Moscovitch, & McDowd, 1994). This involuntary benefit also boosts the late positive ERP effect at retrieval that indexes awareness of study list membership in intentional word stem completion tests (Allan et al., 2000).

The use of intentional, rather than incidental, test instructions was designed to maximize the proportion of studied words classified as remembered, so that the primed trials should give the purest possible measure of priming in the absence of explicit memory. Along with the use of a very large number of study and test trials, and the use of normative stem completion data to select the stimulus words, both of which should minimize noise in the data, the purity of this priming measure should permit greater sensitivity to detect a DM effect for priming than was previously available. We expected the DM effect for primed trials to be topographically and temporally different from the DM effect for remembered trials, because these DM effects should reflect encoding into the perceptual representation system and into the semantic and episodic memory systems, respectively, and because these systems are thought to have different neuroanatomical bases (e.g., Schacter et al., 2000), and to be responsible for different levels in the hierarchy of encoding processes (e.g., Tulving, 1995).

Our participants encoded words at two different levels of processing (LOPs) in the study phase: phonemic (shallow study condition) and semantic (deep study condition). Phonemic and semantic study processing produce equivalent priming of word stem completion, but explicit memory—whether voluntary or involuntary—is less likely following phonemic than following semantic processing (Richardson-Klavehn & Gardiner, 1996, 1998; Richardson-Klavehn et al., 1999; Craik et al., 1994). This manipulation, therefore, ensured that both primed and remembered trials occurred frequently enough for effective ERP measurements. Moreover, it enabled a further prediction of the systems theory to be tested, because the perceptual representation system is held to operate at perceptual and lexical LOPs that precede the conceptual LOP typically involved in encoding into the semantic and episodic memory systems. Richardson-Klavehn and Gardiner (1998) showed that phonemic and semantic study tasks involve the same degree of perceptual and lexical processing, and differed only in the degree of conceptual processing. Thus the DM effect for primed trials should reflect differential

activity in neural structures responsible for perceptual and lexical processing, whereas the LOP effect should reflect differential activity in neural structures responsible for conceptual processing. These neural differences should be reflected in temporal and topographic differences between the two ERP effects. Current evidence (e.g., Wagner et al., 1998; Van Petten & Senkfor, 1996) did not allow a clear prediction as to whether the DM effect for remembered trials should also be temporally and/or topographically distinct from the LOP effect. However, we expected the current experiment to yield new information about the relationship between these effects. Figure 1 summarizes the experimental design and procedure, and the resulting data categories.

RESULTS

Behavior

Mean reaction time (RT) at study was longer, $t(9) = 5.9$, $p < .001$, for pleasantness judgments (deep study condition: $M = 1605$ msec, $SEM = 53$) than for syllable judgments (shallow study condition: $M = 1347$ msec, $SEM = 65$), consistent with the effect of LOP on study RTs in previous experiments (e.g., Craik & Tulving, 1975). Table 1 shows the mean percentages of remembered, primed, and forgotten trials at test as a function of study condition, together with the mean RT at test for each trial type. It should be noted that RT at test included the time taken to covertly complete a stem with a word as well as to indicate study list membership. There was a greater mean percentage of remembered trials in the deep than in the shallow study condition, $t(9) = 7.5$, $p < .001$, whereas there were greater mean

Table 1. Completion Performance at Test for Word Stems Corresponding to Studied Words: Mean Percentages of Remembered, Primed, and Forgotten Trials, and Mean RT (in msec) for Each Trial Type, with Standard Errors of the Mean

	Trial Type at Test					
	Remembered		Primed		Forgotten	
Study Condition	M	SEM	M	SEM	M	SEM
Deep						
%	61.5	3.2	9.5	1.6	18.0	1.7
RT	1549	80	2671	192	2893	175
Shallow						
%	34.5	2.8	30.9	2.6	23.3	1.6
RT	1841	127	2684	204	2872	187

For each study condition, percentages for the three trial types do not sum to 100 because of small percentages of uncompleted stems, ambiguous responses, and falsely remembered nonstudied completions.

percentages of both primed trials and forgotten trials in the shallow than in the deep study condition, $t(9) = 8.4$, $p < .001$, and $t(9) = 3.1$, $p = .012$, respectively. These differences reflected the usual effect of LOP on explicit memory. Consistent with this effect, the mean RT for remembered trials was faster in the deep than in the shallow study condition, $t(9) = 5.2$, $p = .001$. The RTs for primed and forgotten trials, however, revealed a different pattern. An analysis of variance (ANOVA) on RTs at test with trial type (primed vs. forgotten) and study condition (deep vs. shallow) as factors revealed that mean RT was faster for primed trials than forgotten trials [main effect of trial type: $F(1,9) = 11.9$, $p = .007$], but that this advantage did not vary with LOP [interaction: $F(1,9) = 0.3$, $p = .614$].[1] Both of these trial types involved completions that were judged as nonstudied, the difference being that a studied word was used as a completion on primed trials and not on forgotten trials. Thus, the RT advantage for primed over forgotten trials at test reflected priming of word stem completion, and this priming did not vary with LOP at study, consistent with previous results from semantic and phonemic study conditions (Richardson-Klavehn & Gardiner, 1996, 1998; Richardson-Klavehn et al., 1999; Craik et al., 1994).

Because there is typically more perceptual priming for low- than for high-frequency words (e.g., Jacoby, 1983; Hall, 1954), an important question is whether any ERP differences between primed and forgotten trials at study could simply reflect differences in normative word frequency between study words that were later primed and later forgotten (i.e., not later used as completions). We

therefore obtained, for each participant, the normative word frequency per million words of text (CELEX; Baayen, Piepenbrock, & von Rijn, 1993) for each studied word that was later remembered, primed, or forgotten. We calculated the individual participant's median word frequencies for each trial type in view of positively skewed individual participant distributions within trial types. An ANOVA of the individual participant medians with trial type (remembered vs. primed vs. forgotten) and study condition (deep vs. shallow) as factors revealed only a marginally significant main effect of trial type, $F(2,18) = 2.9$, $p = .084$. The marginal effect arose because study words that were later remembered (overall $M = 6.6$, $SEM = 0.4$) were of somewhat lower normative frequency than were study words that were later primed (overall $M = 9.2$, $SEM = 1.0$) or later forgotten (overall $M = 9.3$, $SEM = 0.8$). Critically, there was no difference in normative frequency between study words later primed and later forgotten.

ERPs at Study

ERP waveforms elicited during study trials displayed a P100 (110 msec) and an N180 potential, both over parieto-occipital electrodes, a widespread positive deflection peaking around 250 msec, a widespread negative deflection between 300 and 500 msec, and a sustained positive shift from 500 msec onwards. Waveforms started to differ at about 200 msec as a function of the variables of interest. For analyses comparing primed and forgotten trials, the trial-type factor is labeled DMP (i.e., DM for later perceptual priming), and for analyses

Figure 2. The ERP level-of-processing effect. (A) Grand average (10 participants) ERP waveforms elicited by words presented during deep (bold lines) and shallow (thin lines) study conditions for the frontal (Fz), central (Cz), and parietal (Pz) midline electrodes. (B) Spline-interpolated topographic voltage maps of the difference between the deep and shallow study conditions, calculated from mean amplitudes in three time windows (400–600, 600–800, and 1000–1200 msec). The maps are superimposed on a schematic head as viewed from above (top = anterior; bottom = posterior). The deep study condition (compared with the shallow study condition) is associated with more positive-going ERPs over frontal electrodes from approximately 600 msec until after 1500 msec.
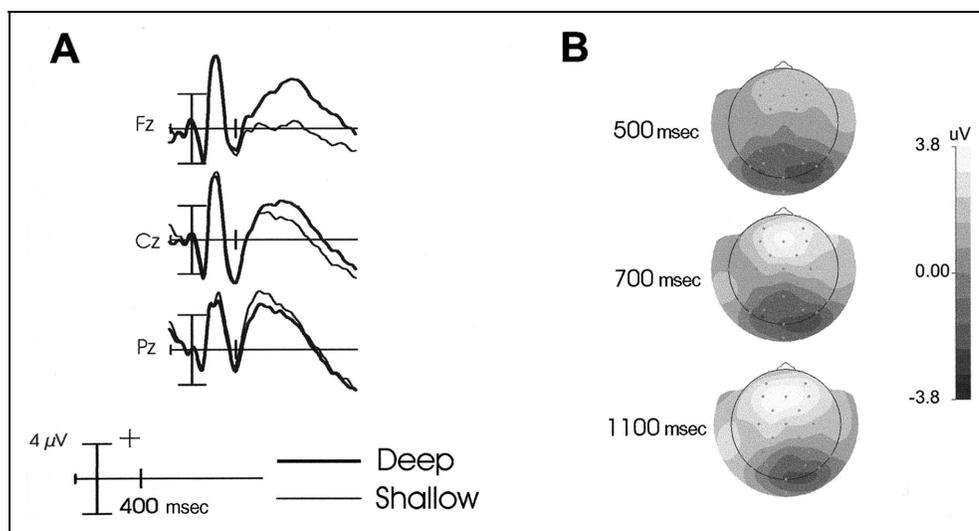
comparing remembered and forgotten trials, this factor is labeled DMR (i.e., DM for later remembering).

LOP Effect

Figure 2 shows that over frontal electrodes, the deep study condition was associated with a sustained positive shift in ERPs compared with the shallow study condition (collapsed over trial types), from approximately 600 msec until the end of the recording epoch. This shift reversed in polarity over posterior electrodes. LOP × Electrode ANOVAs were conducted. In the 600–800-msec time window there was an LOP × Midline Electrode interaction, $F(2,18) = 12.8$, $\varepsilon = 0.687$, $p = .002$, and a main effect of LOP over frontal electrodes, $F(1,9) = 13.8$, $p = .005$. The same pattern occurred in the 900–1200-msec time window [LOP × Midline Electrode interaction: $F(2,18) = 8.4$, $\varepsilon = 0.657$, $p = .009$; main effect of LOP over frontal electrodes: $F(1,9) = 11.5$, $p = .008$]. The polarity reversal over posterior electrodes was not significant. After normalization, topographic analysis confirmed that the LOP effect was most prominent over frontal electrodes in both the 600–800-msec [LOP × Anterior/Posterior interaction: $F(1,9) = 9.1$, $p = .015$] and the 900–1200-msec [LOP × Anterior/Posterior interaction: $F(1,9) = 7.3$, $p = .024$] time windows. The effect was not significantly lateralized.

DMP Effect

Figure 3 shows that primed test trials were associated with more negative ERPs than were forgotten test trials at study over the central and parietal electrodes in a time window ranging from 200 to 450 msec. LOP × DMP × Electrode ANOVAs were conducted. In the early portion (200–300 msec) of this time window, there was a main effect of DMP over parietal electrodes only,

$F(1,9) = 7.71$, $p = .021$. In the later portion (350–450 msec) of this time window, there was a main effect of DMP over midline electrodes, $F(1,9) = 9.2$, $p = .014$, and over parietal electrodes, $F(1,9) = 11.4$, $p = .008$. Although there was a tendency for this DMP effect to persist after 450 msec, this tendency was only significant in the 900–1200-msec time window over frontal electrodes [main effect of DMP: $F(1,9) = 7.6$, $p = .022$]. Because four participants did not have a sufficient number (16 or more) of primed trials in the deep study condition, we do not report a test of the interaction between the DMP and LOP effects.[2] However, it should be noted that effects of LOP in the 200–300- and 350–450-msec time windows did not approach significance (for LOP main effects, all $ps > .802$; for LOP × Electrode interactions, all $ps > .396$), demonstrating that LOP did not affect ERPs in these time windows, even when only primed and forgotten trials—rather than all trials—were considered. Topographically, the earlier (200–300 msec) portion of the DMP effect was most prominent over parietal electrodes, as revealed by a DMP × Anterior/Posterior interaction after normalization, $F(1,9) = 6.2$, $p = .034$, whereas the later (350–450 msec) portion of the effect was more widespread and most prominent over central electrodes, as reflected in the absence of an interaction with electrode position after normalization.
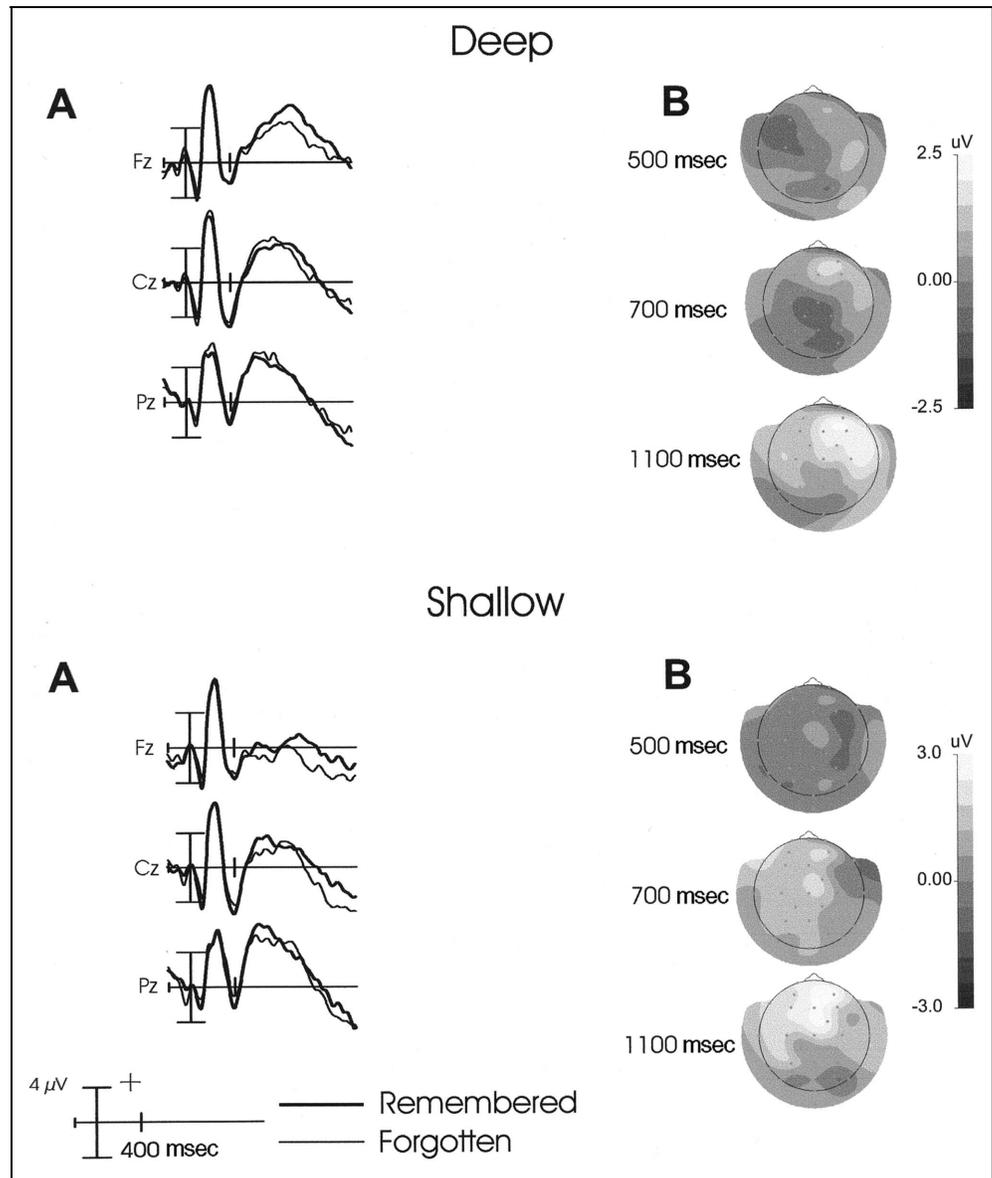
DMR Effect

Figure 4 shows that remembered trials at test were associated with more positive waveforms at study than were forgotten trials, starting at 600 msec in the shallow study condition and at 900 msec in the deep study condition. LOP × DMR × Electrode ANOVAs were conducted. In the 600–800-msec time window, there were no main effects of DMR, but there was an LOP × DMR × Electrode interaction over parietal electrodes,

Figure 3. The DMP effect (difference in study ERPs associated with later perceptual priming). As in Figure 2, grand average ERPs over the midline electrodes and topographic maps of mean amplitude differences in three time windows (200–300, 350–450, and 450–550 msec) are presented. (A) Primed trials (compared with forgotten trials) elicit more negative-going ERP waveforms between 200 and 450 msec. (B) Topographically, the difference between primed and forgotten trials is most prominent over parietal electrodes from 200 to 300 msec and central electrodes from 350 to 450 msec.
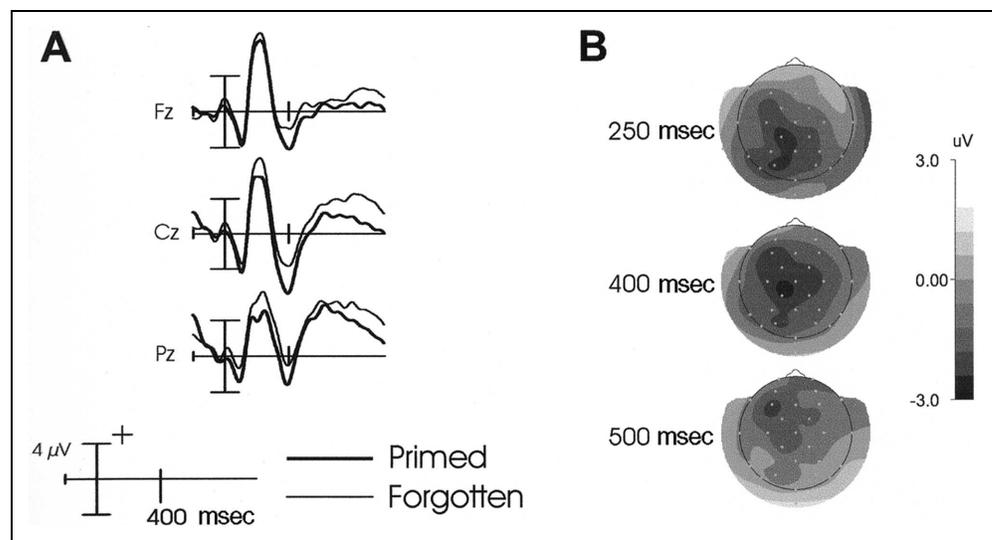
Figure 4. The DMR effect (difference in study ERPs associated with later remembering) for the deep (upper panel) and shallow (lower panel) study conditions. As in Figure 2, the grand average ERPs over the midline electrodes and topographic maps of mean amplitude differences in three time windows (400–600, 600–800, and 1000–1200 msec) are presented. Upper panel: (A) Remembered trials (bold lines) are associated with more positive-going ERPs than forgotten trials (thin lines) from 900 msec until after 1500 msec. (B) Topographically, this DMR effect is most prominent over the right frontal electrodes. Lower panel: (A) As in the deep study condition, remembered trials in the shallow study condition (bold lines) are associated with more positive-going ERPs than forgotten trials (thin lines), but in this case both from 600 to 800 msec and from 900 msec until after 1500 msec. (B) Topographically, the DMR effect in the shallow study condition is widespread from 600 to 800 msec and has a similar right frontal distribution to the DMR effect in the deep study condition from 1000 to 1200 msec.

$F(1,9) = 18.5$, $p = .002$. In the 900–1200-msec time window, there was a main effect of DMR over frontal electrodes, $F(1,9) = 5.9$, $p = .037$, as well as DMR × Electrode interactions over midline, $F(2,18) = 6.5$, $\varepsilon = 0.684$, $p = .021$, and frontal electrodes, $F(1,9) = 8.0$, $p = .020$. As in the 600–800-msec time window, there was an LOP × DMR × Electrode interaction, $F(1,9) = 14.8$, $p = .004$, over parietal electrodes. The three-way interactions indicate that, in both the 600–800- and 900–1200-msec time windows, a DMR effect occurred over left posterior scalp areas only in the shallow study condition. Topographically, the DMR effect was widespread in the 600–800-msec time window, whereas it was localized over the right frontal electrodes in the 900–1200-msec time window. After normalization, no DMR × Electrode interaction emerged in the 600–800-msec time window. By contrast, the right frontal distribution between 900

and 1200 msec was confirmed by DMR × Anterior/Posterior, $F(1,9) = 5.2$, $p = .048$, and DMR × Anterior/Posterior × Laterality, $F(1,9) = 16.9$, $p = .003$, interactions. The topography of the DMR effect did not interact with LOP in either of these time windows.

In view of the distinguishable early and late DMR effects in the shallow study condition, we examined the correlation between these effects at the electrodes where they were maximally apparent (i.e., P3 in the 600–800-msec time window and AF4 in the 900–1200-msec time window). The effects were negatively correlated across participants (Spearman's $\rho = -0.69$, $p = .029$).

DISCUSSION

Our ERP results provide the first clear evidence that perceptual priming and explicit memory have distinct

neural correlates at encoding. Also, by providing additional information about the time course and topography of study ERPs associated with later explicit memory, they assist in understanding the relationship between study processing and encoding success.

Study ERPs Associated with Later Perceptual Priming: The DMP Effect

Disentangling the neural correlates of perceptual priming from those of explicit memory initially proved difficult in research on ERPs recorded at test (Rugg & Allan, 2000), and thus far has not been possible in research on ERPs recorded at study (Friedman et al., 1996; Paller, Kutas, Shimamura, et al., 1987; Paller, 1990; for discussion, see Rugg, 1995). The current behavioral method (Richardson-Klavehn, Gardiner, et al., 1994; Richardson-Klavehn & Gardiner, 1995, 1996) permitted a clear separation among explicit memory, whether voluntary or involuntary (remembered trials), perceptual priming unaccompanied by explicit memory (primed trials), and trials in which no memory at all occurred (forgotten trials). It thus allowed study ERPs associated with later perceptual priming to be clearly revealed (see also Rugg et al., 1998, for a similar approach to retrieval ERPs).

Compared to forgotten test trials, primed test trials were associated with more negative waveforms at study over the central and parietal electrodes starting as early as 200 msec after word onset, but most strongly in the 350–450-msec time window (Figure 3). This DMP effect (difference in study ERPs associated with later perceptual priming) was distinct from the effect of LOP at study (Figure 2) by virtue of its polarity, its earlier onset, and its topography, consistent with the current behavioral priming results, as well as previous behavioral results regarding word stem completion priming from phonemic and semantic study conditions (Richardson-Klavehn & Gardiner, 1996, 1998; Richardson-Klavehn et al., 1999; Craik et al., 1994). By the same criteria, the DMP effect was also distinguishable from the DMR effect (difference in study ERPs associated with later remembering; Figure 4). The distinct DMP effect thus confirms the hypothesis that perceptual priming and explicit memory have distinct neural correlates at encoding. It is consistent with the theory that perceptual priming depends on brain systems concerned with perceptual representation, which can operate in the absence of awareness of memory, and are distinguishable from the semantic and episodic brain systems that are concerned with explicit memory (e.g., Tulving & Schacter, 1990). This finding goes beyond previous findings of double dissociations between perceptual priming and explicit memory caused by brain lesions (Mayes, 2000; Moscovitch, 2000) and of distinct brain activity correlates of perceptual priming and explicit memory at retrieval in both ERP and hemodynamic experiments (e.g., Rugg & Allan, 2000; Schacter et al., 2000).

Our ability to detect the DMP effect probably partly reflects the use of very large numbers of study and test trials, and of normative word stem completion data to select target words, thus minimizing noise in the data. However, it probably mainly reflects our use of on-line study list membership judgments at test, which permitted a measure of priming for words judged not to have been studied (primed trials), thereby selectively isolating priming in the absence of explicit memory. Evidence for this assertion comes from the study ERPs for remembered compared with forgotten trials (Figure 4). These trials showed some evidence of an early negative deflection over parietal and central electrodes similar to the DMP effect, but this effect was apparently cancelled by positive-going effects related to later explicit memory. Such cancellation effects may have been responsible for the absence of significant negative-going DMP effects in previous experiments, because study ERPs in those experiments were simply averaged according to primed versus unprimed status in incidental tests, without the use of on-line study list membership judgments to selectively isolate ERPs for priming in the absence of explicit memory (Friedman et al., 1996; Paller, Kutas, Shimamura, et al., 1987; Paller, 1990). Even though the incidental test participants in those experiments may not have contaminated the test by deliberately retrieving studied words (i.e., voluntary explicit memory), they nevertheless most probably experienced involuntary explicit memory for studied words during test performance (Curran, 1999; Paller & Kutas, 1992; Paller et al., 1995; Richardson-Klavehn, Gardiner, et al., 1994; Richardson-Klavehn, Lee, et al., 1994; Richardson-Klavehn & Gardiner, 1995, 1996; Richardson-Klavehn et al., 1996; Schacter, 1987). Thus, positive-going study ERPs for later involuntary explicit memory may have been averaged together with negative-going study ERPs for priming. Consistent with this reasoning, in the only previous experiment to reveal significant study ERPs for priming (Paller, Kutas, Shimamura, et al., 1987), these ERPs were positive-going rather than negative-going, suggesting that they may have reflected encoding for explicit memory rather than priming (Rugg, 1995). In the Friedman et al. (1996) experiment, another reason for the absence of a negative-going DMP effect might have been that words were always presented twice at study, with the study ERPs being averaged across the first and second presentations. Thus, positive-going effects relating to repetition during the study phase may have weakened negative-going effects relating to later priming.

Our use of intentional test instructions, in contrast to the incidental test instructions used in previous experiments, also probably assisted in detecting the DMP effect, by maximizing the proportion of studied words judged as remembered, so that primed trials gave the purest possible measure of priming in the absence of explicit memory. Consistent with this argument, results from another session of the current

experiment employing incidental test instructions, coupled with on-line study list membership judgments, also showed some evidence of the DMP effect in study ERPs for primed trials, but the signal-to-noise ratio was not sufficiently good to yield reportable results. Until incidental test results with a better signal-to-noise ratio are available, it will not be possible to resolve conclusively whether the DMP effect reflects a general implicit memory encoding process, or whether it is specific to the intentional test instructions used here. This question is an important one for future research.

Whereas the DMP effect consisted of an increased negativity at study, perceptual priming at test is associated with reduced negativity in a similar (300–500 msec) time range (e.g., Curran, 1999; Joyce, Paller, Schwartz, & Kutas, 1999; Paller & Kutas, 1992; Paller & Gross, 1998; Paller, Kutas, & McIsaac, 1998; Rugg & Nagy, 1987; Rugg, 1990; Rugg, Doyle, & Wells, 1995; Rugg et al., 1998; Rugg & Nieto-Vegas, 1999; for reviews, see Friedman & Johnson, 2000; Mecklinger, 2000; Paller, 2000; Rugg & Allan, 2000). We have also observed such reduced negativity for primed trials in the ERPs recorded during the test phase of the current experiment (Richardson-Klavehn et al., 2000). We propose that modulations of this negative-going waveform may be related to the efficiency with which words are perceptually and lexically processed. Behavioral data show that those words that are less efficiently processed at study show the most perceptual priming at test (for review, and analysis, see Kirsner, Speelman, & Schofield, 1993). For example, in the absence of prior study, low-frequency words are harder to identify than high-frequency words, but they show more perceptual priming as a result of prior study than do high-frequency words (e.g., Jacoby, 1983; Hall, 1954). Low-frequency words also show a greater ERP negativity in this time range on initial exposure than do high-frequency words, but a greater reduction in negativity with repetition than do high-frequency words (e.g., Rugg, 1990; Smith & Halgren, 1987). It thus makes good sense that words associated with more negative ERPs in this time range at study would tend to be those that subsequently show perceptual priming, and that this priming would be associated with less negative ERPs at test compared to unprimed words. However, the DMP effect reported here is apparently not a word-frequency effect on study ERPs, because there was no evidence of a difference in normative frequency between study words later primed and study words later forgotten. Future research needs to explore the precise aspects of processing efficiency that differentiate ERPs for primed and forgotten items.

The DMP effect peaked in the time window traditionally associated with the N400 waveform (e.g., Kutas & Hillyard, 1980). Modulations of the N400 waveform elicited by initial as well as repeated presentation of verbal material have been related to semantic integration processes (for reviews, see Münte, Urbach, Düzel, &

Kutas, 2000; Olichney et al., 2000; Kutas & Van Petten, 1994). Our findings suggest that ERP deflections in this time window may sometimes reflect perceptual and lexical processing of individual words in addition to these semantic-associative processes. This conclusion follows from the current behavioral finding of no LOP effect on priming (as indicated by the test RTs), as well as from a variety of previous behavioral findings demonstrating that the basis of priming in word stem completion is perceptual and lexical and not semantic-associative (e.g., Richardson-Klavehn & Gardiner, 1996, 1998; Richardson-Klavehn et al., 1999; Craik et al., 1994). This view also appears consistent with the finding that the DMP effect began in an earlier (200–300 msec) time window than the N400 time window, and that the effect in the earlier time window was topographically more posterior, probably reflecting the more perceptual aspects of processing involved in the effect. It would be of interest to investigate whether the earlier and later portions of the DMP effect can be systematically dissociated, given reports of behavioral and neuropsychological dissociations between perceptual and lexical aspects of priming (e.g., Postle & Corkin, 1998, 1999; Gabrieli et al., 1994).

Study ERPs Associated With Later Explicit Memory: LOP and DMR Effects

An important question is whether DM effects for later explicit memory (here termed ''DMR effects,'' for difference in study ERPs associated with later remembering) reflect the modulation of the same neural processes by which LOP influences later explicit memory. The current findings provide more detailed temporal and topographical information about the relationship between these effects than was previously available.

The LOP effect was associated with a prominent, long-lasting (600 msec to the end of the recording epoch) fronto-central positive shift in the deep compared to the shallow study condition (Figure 2). An earlier, widespread DMR effect (600–800 msec) occurred only in the shallow study condition, whereas a late, right frontal DMR effect (900–1200 msec) was common to both study conditions (Figure 4). Thus, these three effects differed in terms of a conjunction of onset time, duration, and topography, permitting the conclusion that the neural bases of the three effects were at least partially distinct. The finding of temporal and topographic differences between the LOP and DMR effects extends earlier findings, which raised the possibility of topographic differences between these effects (Fabiani et al., 1990; Paller, Kutas, & Mayes, 1987). These differences make sense if it is noted that the LOP manipulation applied to studied words whether or not those words were later associated with explicit memory. On the other hand, the DMR variable contrasted studied words that were later associated with explicit memory with studied words that

were not, whether those words were in the deep or the shallow study condition. In view of this critical difference between the LOP and DMR variables, it seems reasonable to suggest that the LOP effect reflected variation in the type of study processing performed, whereas the DMR effects reflected encoding success with regard to later explicit memory.

One of the most important insights from the levels-of-processing approach to memory (Craik & Lockhart, 1972) has been that encoding typically involves the retrieval of preexisting knowledge relevant to the to-be-encoded information, which then becomes part of the memory trace for the newly encoded information (for a review, see Brown & Craik, 2000). For example, the current syllable (shallow) study task involved retrieving phonological knowledge about studied words, whereas the current pleasantness (deep) study task involved retrieving semantic and affective knowledge about those words. In Tulving and Schacter's (1990) memory systems approach, this encoding-as-retrieval notion is captured by the hypothesis that encoding into the episodic memory system proceeds via the semantic memory system in which it is embedded (e.g., Tulving, 1995). Therefore, under this theory, the LOP effect on ERPs might be regarded as reflecting differences in the semantic memory subsystems from which retrieval occurs in order to accomplish the study tasks, whereas the DMR effects might be regarded as reflecting encoding into the episodic memory system; that is, the establishment of an episodic memory trace (e.g., Bower, 1967) of sufficient quality to support later explicit memory. This interpretation differs from the one offered by Van Petten and Senkfor (1996), who showed that a DMR effect occurred only for meaningful words, and not for novel, meaningless, visual patterns, and consequently argued that DMR effects themselves reflect retrieval of preexisting semantic information. However, they did not simultaneously examine the LOP and DMR effects. Thus, their DMR effect may have reflected a combination of the separable LOP and DMR effects demonstrated here.

Although the LOP effect on ERPs was distinguishable from the two DMR effects in terms of a combination of onset time, duration, and topography, the LOP manipulation nonetheless modulated DMR, in the sense that the early DMR effect was apparent only in the shallow study condition, whereas the late DMR effect was apparent in both the shallow and deep study conditions. Additionally, there was a negative across-participants correlation between the early and the late DMR effects in the shallow study condition. Taken together with the distinguishable timing and topography of the two DMR effects, this functional dissociation between the DMR effects suggests the existence of two mutually exclusive neural processes of encoding success, an early and a late one. The late one predominates in the deep study condition, whereas both early and late processes occur in the shallow study condition, albeit in different relative proportions for different participants. These two processes might differ as to the informational content of the memory trace that is being successfully formed.

The early DMR effect during shallow study processing may have reflected the formation of memory traces containing distinctive orthographic and/or phonological features. The effect of such distinctiveness on tests designed to tap explicit memory is illustrated by a variety of behavioral results (for a review, see Schmidt, 1991). Most relevant here, Eysenck (1979) found that the usual recognition–memory disadvantage for shallow compared with deep study processing was attenuated or eliminated when phonologically distinctive words were studied, demonstrating that such distinctiveness has special importance for encoding success during shallow study processing. Additionally, Fabiani et al. (1990) and Fabiani and Donchin (1995) showed that perceptually distinctive words elicited more positive ERPs than nondistinctive words over the midline electrodes at study, and were later associated with better recall performance. Furthermore, Fabiani et al. (1990) showed that deep study processing diminished the perceptual distinctiveness effect on study ERPs as well as the memory advantage for perceptually distinctive over nondistinctive words. The latter result is comparable to the absence of the early DMR effect in the current deep study condition, and is consistent with the current finding that the early and late DMR effects were negatively correlated. Our results parallel those of Fabiani et al. (1990) despite the fact that the deep study tasks were quite different (pleasantness judgments vs. formation of sentences with the study words), because the LOP effect in both experiments had a frontal topography.

The late DMR effect may signify the formation of memory traces containing semantic-associative information. Consistent with this possibility, late DMR effects with a right frontal topography have been found during encoding of word pairs (Weyerts et al., 1997), as well as during encoding of high-frequency words, which lend themselves to the formation of interword associations (Fernández et al., 1998). The late DMR effect in the shallow study condition might well have reflected the formation of semantic-associative memory traces that occurred despite the instructions to focus on the syllabic content of the words. The results of Fernández et al. (1998) provide support for this interpretation as well, because the late DMR effect for high-frequency words occurred during a task study requiring rote (shallow) processing. In addition, Fernández et al. (1998) observed an earlier widespread DMR effect for both low- and high-frequency words during this shallow study task. Thus their results parallel both the early and late DMR effects that we found during shallow study processing.

Although our ERP data regarding the relationship between the LOP and the early and late DMR effects make good sense in terms of current cognitive and

neuropsychological perspectives on study processing and encoding (e.g., Tulving, 1995), and although there are parallels in the literature with these ERP data, it must be acknowledged that the picture in the literature regarding the timing and topography of LOP and DMR effects is less than consistent (see, e.g., Rugg, 1995; Rugg & Allan, 2000). For example, whereas a frontal topography for LOP effects has been reported, as observed here (e.g., Fabiani et al., 1990; Karis et al., 1984), different topographies for LOP effects have also been reported (e.g., Friedman et al., 1996; Paller, Kutas, & Mayes, 1987; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). Additionally, DMR effects during deep study processing have varied in timing and magnitude between different deep study tasks (e.g., Paller, Kutas, & Mayes, 1987) and have also had an earlier onset and more widespread topography than the DMR effect that we found during deep study processing (e.g., Friedman et al., 1996; Friedman & Trott, 2000; Paller, Kutas, & Mayes, 1987). Moreover, in the Weyerts et al. (1997) experiment on encoding of word pairs, there was both an early widespread DMR effect and a late, right frontal DMR effect during deep study processing. The apparently disparate findings probably reflect, for the most part, the wide variety of encoding and retrieval tasks that have been employed.[3]

Similar qualifications regarding the generality of the effects reported here apply to the temporal relationship between the DMR and DMP effects. For instance, the timing of the DMR effect for the terminal words of sentences depends on the semantic congruity of those words with the preceding sentence context, and DMR effects are consequently sometimes observed in the 350–450-msec time window in which the current DMP effect peaked (Neville et al., 1986). In summary, therefore, our finding of temporally and topographically separable LOP, DMR, and DMP effects should not be taken as implying that there are neural encoding systems that participate similarly and with a fixed timing in all encoding situations. Additional ERP experiments with higher density electrode placements and with more systematic and comprehensive comparisons of different encoding and retrieval tasks will be necessary to achieve a comprehensive understanding of the complex interplay between study processing and encoding.

Conclusion

The present results show for the first time that perceptual priming and explicit memory have distinct neural correlates at encoding, consistent with Tulving and Schacter's (1990) distinction between brain systems concerned with perceptual representation versus semantic and episodic memory. Identification of the neural signature of perceptual priming at encoding was made possible by clearly differentiating explicit memory from priming unaccompanied by explicit memory. The findings revealed that the neural correlates of perceptual

priming (the DMP effect) and explicit memory at encoding were not merely topographically distinct: Encoding processes associated with later perceptual priming occurred in the brain before those associated with explicit memory were measurable. The data also provide additional information about encoding processes associated with later explicit memory, by suggesting that brain processes that are related to LOP merely set the stage for other, at least partially separable, brain processes (DMR effects) that are more directly related to encoding success. They therefore support a brain level distinction between study processing and encoding success.

METHODS

Participants

Ten healthy students (eight women and two men, aged 19–26) attending the Otto von Guericke University, Magdeburg, were paid to participate in the experiment. All were native speakers of German and right-handed according to self-report.

Design

The experimental session was divided into four runs, each consisting of a study phase and a subsequent word stem completion test phase. There were breaks of 2–5 min between study and test phases and between runs. In each study phase, participants made pleasantness judgments on 50 words (deep study condition) and counted the number of syllables in 50 words (shallow study condition). In the corresponding test phase, word stem cues were presented, each stem consisting of the first three letters of a word. Participants attempted to complete each stem with a word from the preceding study list; if they could not, they completed the stem with the first word coming to mind. They also indicated whether or not they had completed each stem with a studied word. Fifty stems could be completed with words studied in the deep condition, 50 could be completed with words studied in the shallow condition, and 50 could only be completed with nonstudied words. The order of judgments in the study phases was random, as was the order of stems in the test phases.

Materials

The materials were selected using normative completion data for 1402 nonoverlapping three-letter German word stems (Mathews et al., in preparation). Six hundred stems and corresponding target words were selected such that the baseline probability of completing the stems with target words in the absence of prior study was about .4. The words were assigned into three sets of 200 each, such that the baseline probabilities for the sets were matched. Each participant was presented with one

of these sets in the deep study condition and another of these sets in the shallow study condition. The stems corresponding to these 400 studied words were used during the test phases, together with the stems corresponding to the set of 200 nonstudied words. Across participants, the sets of words were rotated across the deep study condition, the shallow study condition, and the nonstudied condition.

Procedure

The participants sat in a comfortable position facing a back-projection screen. In the study phases, they were instructed to judge each word appearing on the screen according to a cue that preceded it. If the cue was "Angenehm?" ("Pleasant?"), they judged the pleasantness of the word (deep study condition). They were instructed to base their judgment on the meaning of the word and not on the appearance or sound. Judgments were on a four-point scale (1 = "very unpleasant"; 4 = "very pleasant"). If the cue was "Silben?" ("Syllables?"), they counted the number of syllables in the word (shallow study condition). They were instructed to base their judgment on the sound of the word. Syllable judgments were also on a four-point scale (1 = "one syllable"; 4 = "four or more syllables"). Responses were made via a four-button response box (1 = thumb; 4 = ring finger) and the response hand was counterbalanced across participants. Each study trial consisted of the presentation of a central fixation cross for 1200 msec, a cue for 500 msec, a further fixation cross for 300 msec, and a word for 2000 msec. The fixation cross for the next trial immediately followed the disappearance of the study word. Before each study phase, participants were instructed not to try to memorize the words because doing so would interfere with the task at hand. They were also instructed to avoid blinking as far as possible.

In the test phases, participants were instructed to complete each word stem with a word from the immediately preceding study list whenever possible, but with the first word coming to mind when they could not remember a studied word. Stem completion was covert, but participants indicated via response box whether they had completed each stem with a studied word (yes = index finger; no = middle finger), with response hand counterbalanced across participants. They were discouraged from making false-positive judgments and were instructed not to respond at all if they had been unable to find a completion for the stem. Each test trial consisted of the presentation of a central fixation cross for 1200 msec, a word stem for 300 msec, a further fixation cross for 3000 msec, and the instruction "Bitte blinzeln" ("Please blink") for 3000 msec. The fixation cross for the next trial immediately followed the blink pause. During the blink pause, participants said aloud the word that they had just used to complete the stem or said "Keins" ("None") if they were unable to find a completion.

These overt responses were scored and used to sort the ERP data.

ERP Measurements and Analysis

EEG signals were recorded from 29 electrodes (Ag/AgCl) embedded in an elasticized cap. Electrode locations were Fz, Cz, Pz, Oz, Inz, and Fp1, AF3, F3, F7, C3, P3, T7, FC1, CP1, PO1, PO3, and PO7, together with their right-sided counterparts (American Electroencephalographic Society, 1994; Jasper, 1958). Recordings were referenced on-line to the right mastoid, and were re-referenced offline to a common average. Eye blinks and eye movements were monitored via electrodes located on the infraorbital ridge of the right eye and the outer canthus of the left and right eyes. Signals were amplified with a bandwidth of DC to 100 Hz and digitized at a 254-Hz sampling rate. ERPs were obtained by averaging EEG recordings, time-locked to the onset of the study word, over epochs of 2250 msec, including a 200-msec baseline prior to word onset. Only those study trials that fell into the remembered, primed, and forgotten behavioral categories (see Table 1) were used in averaging. Among these trials, any ($M = 11.2\%$, $SEM = 2.0$) showing contamination of the EEG signals by eye blinks, eye movements, excessive muscle activity, unsystematic slow drifts, or electrode saturation were rejected with a threshold of 112.5 µV—with additional manual artifact rejection where necessary—prior to averaging.

Statistical analysis of the study ERPs involved ANOVAs on mean amplitudes in four separate time windows (200–300, 350–450, 600–800, and 900–1200 msec), and for three separate sets of electrodes (the midline electrodes Fz/Cz/Pz; the frontal electrode pair AF3/AF4; and the parietal electrode pair P3/P4). These time windows and electrode locations were selected on the basis of previous articles reporting ERP indices of study processing and encoding. For brevity, only those effects significant at $\alpha = .05$ are mentioned. The Greenhouse–Geisser correction for nonsphericity was used where appropriate (see Keselman & Rogan, 1980) and the original degrees of freedom, the correction coefficient ε, and the corrected p values are reported. Topographic analyses were conducted after normalization (McCarthy & Wood, 1985), using ANOVAs that included the factors anterior/posterior (AF3/AF4 vs. P3/P4) and laterality (AF3/P3 vs. AF4/P4). Spline-interpolated topographic voltage maps were derived from mean amplitudes of the difference waves for contrasts of interest (Perrin, Pernier, Bertrand, Giard, & Echallier, 1987).

Notes

1. RTs for remembered trials were analyzed separately from RTs for primed and forgotten trials in order to elucidate the data with the fewest statistical comparisons, and because these comparisons were planned in view of prior knowledge about the differential effect of LOP (phonemic vs. semantic) on explicit memory and perceptual priming. A similar confirmatory strategy was adopted for analysis of the stem-completion percentages.

2. For the record, when tested, this interaction did not approach significance.

3. Differences in ERP topography across experiments might also reflect differing practices regarding EEG voltage reference, with a common average reference, as used here, possibly resulting in more focal ERP effects than would be obtained with a single electrode reference. At least with regard to DMR effects, these differences appear to us to be less of a factor than task differences, because focal DMR effects have been observed in experiments using a single electrode (left earlobe) voltage reference (Fernández et al., 1998; Weyerts et al., 1997).

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