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Brain potentials associated with perceptual priming vs explicit remembering during the repetition of visual word-form

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Abstract—Priming of visual word-form was studied using a reading manipulation in which some words appeared in a backward format (e.g., d-r-o-w) instead of the usual forward format. In Experiment 1, subjects discriminated occasional targets (common first names) from other words with a speeded response. Reaction time was faster for words that had also appeared earlier in the forward format compared to the backward format. Event-related potentials (ERPs) recorded in response to word presentations showed a corresponding difference, a positive offset present during the time interval beginning about 300 ms after word onset from electrodes over occipital and parietal cortex. In Experiment 2, the task was changed to a recognition test, and a later and more widespread ERP response was observed, thus confirming the association between the ERP difference in Experiment 1 and priming rather than explicit remembering. ERP measures were presumably sensitive to neural events underlying the specific influence of recent reading experiences on the processing of visual word-form, thus providing real-time evidence on the neural mechanisms of priming. © 1998 Elsevier Science Ltd. All rights reserved

Key Words: implicit memory; repetition priming; event-related potentials; ERPs.

Introduction

Reading a passage, a sentence, or a word for the second time is easier than reading it for the first time. This phenomenon, repetition priming, has been studied in a variety of different experimental situations, most commonly involving repeated presentations of isolated words on a video monitor. Altered responses to the second presentation have been attributed to various theoretical constructs, such as automatic activation with respect to word identification units or logogens [1–5] or to biasing of perceptual or response processing [6, 7]. Indeed, it is likely that priming effects are mediated by changes in more than a single aspect of information processing. Although it has generally not been possible to measure these various information processing changes directly, measures of brain function may be able to achieve this end and thus provide new information useful for understanding repetition priming and how it is mediated in the brain.

Here we focus on one effect of repetition restricted to neural representations of the visual image of the word as a unit, or *visual word-form*. Three lines of evidence suggest that the brain makes use of representations of this sort. First, analyses of the acquired neurological disorder of pure alexia, a specific reading impairment first described by Déjerine [8], have provided many insights about neocortical regions dedicated to processing visual word-form, although many questions are currently still under debate. Conventional neurological explanations for pure alexia postulated a disconnection between early visual processing and phonological or semantic processing [8, 9]. In contrast, Warrington and Shallice [10] suggested that a *visual word-form system* is operative following early visual processing and prior to phonological and semantic processing, that it parses letter strings into familiar units, and that pure alexia results from damage to cortical areas that function as the visual word-form system. Second, intracranial recordings of event-related potentials (ERPs) in epileptic patients have revealed word-specific responses from electrodes adjacent to the area of the fusiform gyrus in the inferior temporal region [11]. Third, functional neuroimaging studies using positron emission tomography (PET) have demonstrated activations in medial

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areas of the occipital lobe that appear to be word-specific [12].

Evidence from neuroimaging and neuropsychology also suggests that processing in posterior neocortical regions is responsible for behavioral changes observed in certain priming tests. PET studies have demonstrated decreases in blood flow to regions of the occipital lobe as a function of word repetition [13, 14]. Moreover, studies of two patients with posterior neocortical damage have revealed deficits on perceptual priming tests that occur without parallel deficits on recognition tests [15, 16]. In addition, studies of patients with Alzheimer's disease have demonstrated the opposite pattern, with impaired recognition and intact perceptual priming [17].

These neuropsychological results provide a useful framework for studies of brain mechanisms underlying perceptual priming in normal subjects. One way to specifically monitor the activity of brain regions that process visual word-form is to take advantage of the effects of word repetition. The reasoning behind this approach is that visual word-form areas will be activated less by the second presentation of a word than by the first. The change in an ERP from first to second presentation of an item, often referred to as an *ERP repetition effect* (for reviews see [18–21]) may provide a useful measure of a subset of the relevant processing. However, a complication for this approach is that word repetition not only influences subsequent activation of visual word-form representations, but it can also lead to an abundance of other effects, including episodic recognition. Indeed, prior results suggest that ERPs are sensitive to recollective processing of this sort [22–25].

Accordingly, a new method is required to specifically isolate brain activity associated with priming of visual word-form. We have developed such a method by virtue of the literature demonstrating that various factors differentially influence performance on implicit and explicit memory tests (for review see [26]). Central to this method is a manipulation of physical stimulus parameters at the encoding stage that leads to differential effects on priming and recognition. Specifically, words were either read backwards, beginning with the right-most letter and continuing to the left, or they were read in the normal manner from left to right. Encoding and retrieval stages were embedded in a continuous sequence such that the mean delay between first and second presentations was about 22 s. We predicted that reading backwards would lead to smaller priming effects based on previous experiments using similar manipulations [2, 27–29]. Furthermost, we reasoned that effects of repetition would be identical between normal and reversed conditions except for priming of visual word-form. Word repetition and corresponding ERPs elicited at the retrieval stage were thus compared with respect to whether the forward or backward format was used in the encoding stage.

Effects of this word repetition manipulation were investigated in two task conditions: an implicit memory test in Experiment 1 and an explicit memory test in Experiment 2. We reasoned that ERPs related to explicit remembering would be enhanced in Experiment 2. Comparisons between the two experiments could thus provide additional evidence linking ERPs to priming versus explicit remembering. Indeed, we propose that an ERP isolated in Experiment 1 can be taken as a measure specific to the repetition of visual word-form, and as such can provide an estimate of the time-course of visual word-form priming.

Method

Subjects

Eight subjects participated in each experiment. Subjects were right-handed, native English-speaking men and women, aged 18–23 years old, who gave informed consent and received course credit for their participation. One additional subject in Experiment 1 was excluded due to excessive electroocular artifacts.

Stimuli

For the two critical conditions, 240 words were selected according to three criteria: (1) common nouns or verbs; (2) three or four letters in length; (3) frequency of usage [30] between 16 and 65 occurrences per million (mean frequency = 36.3). Words were coded according to high or low frequency on the basis of a median split on frequency of usage norms. Filler words were selected to blend in with the critical words, although length varied from three to six letters. There were 180 fillers, 60 of which were used only in Experiment 2. Additionally, for Experiment 1 only, a set of 48 words were used as recognition foils and a set of 87 common first names were used as targets.

Procedure

Experiment 1: Semantic task. The subjects' task was to read each word and determine whether or not it was a name. Subjects were instructed to press a button in their left hand following the presentation of a word that was a name and to press a button in their right hand following the presentation of a word that was not a name. Instructions stressed that responses should be made accurately and, with secondary priority, as quickly as possible. Then, subjects completed a practice phase during which two short sequences of words were presented and the experimenter verified that instructions were understood.

Following the practice phase, words were presented in 12 experimental runs. Words were never repeated across runs, but within runs each critical word was presented on two occasions, separated by 5–9 other words (mean = 6.5). The presentation format for the first word of each pair was manipulated such that there were two types of word pair. The two presentation formats were *forward* and *backward*. For the backward format, letters were presented in reverse order and separated by hyphens (e.g., "dark" in the forward format and "k-r-a-d" in the backward format). The two types of word pair were termed *F-pairs* and *B-pairs*. For F-pairs, words were presented in the forward format on both first and second occasions; for B-pairs, words were presented in backward format on the first occasion and forward format on the second occasion. The two members of an F-pair were termed *F1* and *F2*, whereas the two members of a

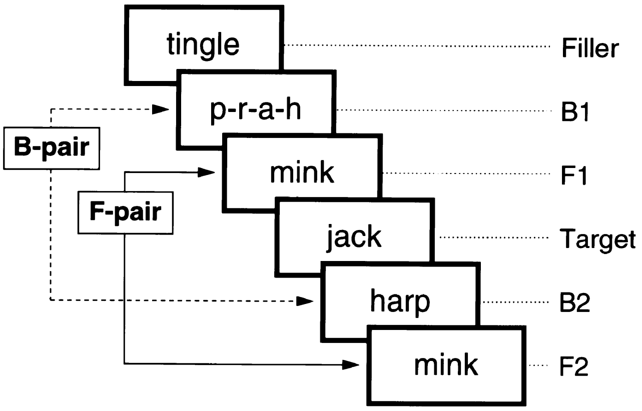

Fig. 1. Schematic representation of the trial structure in Experiment 1. Two types of word pairs were embedded in word lists such that repetitions occurred after a variable number of items. Second presentations were always in the forward format, but first presentations were either in the backward format (B-pairs) or in the forward format (F-pairs).

B-pair were termed *B1* and *B2*. These conditions are represented schematically in Fig. 1.

Each run included a pseudorandomized list of 10 F-pairs, 10 B-pairs, 10 targets, and 10 fillers. Slightly less than half of the targets were names that were presented once per run and the others were names presented on two occasions within a run. Furthermore, half of the fillers and half of the targets were presented in the backward format. Thus, the target-nontarget discrimination could not be done accurately on the basis of format or repetition.

Each word appeared horizontally, centered beneath a fixation point that was visible continuously in the center of the screen. Word presentation was preceded by a cue that indicated whether the forward or backward format would be used ("*" = forward format; "B" = backward format). Cues were presented for a 100-ms duration, followed by a 900-ms blank interstimulus interval (ISI), at which time a word was presented for a 150-ms duration. The blank ISI following forwards words was 2350 ms. For backwards words, a longer response period was occasionally required, so the ISI was set to end 1 sec after the subject's response instead of after a fixed interval, which resulted in an average blank ISI of about 2 sec.

The assignment of words to conditions was counterbalanced across subjects such that each critical word appeared in the F condition for four subjects and in the B condition for the other four subjects. Similarly, the words in the first and second halves of the study were counterbalanced such that each critical word appeared in one of the first six runs for four subjects and in one of the last six runs for the other four subjects. Given that each F1 word must occur prior to the corresponding F2 word, this comparison is confounded with serial position within each run. However, the vast majority of the words did not occur at the very beginning of a run, so the contribution of any serial position effects on ERPs would be minimal. Furthermore, the critical comparisons were between F2 and B2 conditions, for which serial position was matched.

Recognition was tested at the end of the last run by providing the subject with a randomized list of 96 words and instructions to circle words they remembered having seen earlier in the experiment. The list included 24 words from F-pairs, 24 words from B-pairs, and 48 recognition foils. Testing for F and B words was for an equal number of words from each run.

Experiment 2: *Recognition test*. Critical items were presented in a manner identical to that in Experiment 1. However, targets were excluded and new filler words were inserted in their place. Five new filler words were used in each run, and each was presented twice, first in the forward format and then in the backward format. Thus, words presented in the backward format were not necessarily first presentations, so presentation format per se provided no information regarding whether or not the word had been presented previously.

The only other procedural difference between the two experiments was that subjects in Experiment 2 were given the task of detecting word repetitions instead of targets. Subjects were instructed to press a button in their left hand following the presentation of an old word (a word that had also been presented earlier in that run) and to press a button in their right hand following the presentation of a new word.

ERP recordings

Electroencephalographic recordings were made from 21 scalp electrodes embedded in an elastic cap (Fpz, Fz, Cz, Pz, Oz, Fp1, Fp2, F3, F4, F7, F8, C3, C4, P3, P4, O1, O2, T3, T4, T5, T6). A left mastoid reference electrode was used on-line, but the reference was changed off-line to the average of left and right mastoid recordings. In addition, two channels were used for monitoring horizontal and vertical eye movements, and trials contaminated by electroocular artifacts were excluded from the analyses (16.4% on average). The band pass was 0.1–100 Hz. Recordings were sampled at a rate of 250 Hz and ERPs were computed for 1000-ms epochs beginning 100 ms prior to stimulus onset. ERP measurements were evaluated using analysis of variance (ANOVA). In analyses involving electrode as a factor, ANOVA results were evaluated using critical F ratios based on degrees of freedom adjusted according to the Geisser–Greenhouse procedure to control for Type I errors in repeated-measures designs. To compare scalp distributions of ERPs, amplitude measurements were normalized by scaling by the square root of the sum of squared voltages over all electrode locations, because in the absence of scaling, amplitude differences between conditions can masquerade as topographic differences [31].

Results

Experiment 1: *Semantic task*

Behavioral data. Subjects were nearly perfect at detecting nontarget words. The mean percentage correct was 98% (S.E. = 0.5), whereas for targets it was 84% (S.E. = 1.5). A two-way ANOVA (target/nontarget by format) showed that accuracy was significantly lower for targets than for nontargets [$F(1,28) = 99.16$, $P = 0.0001$], but did not differ between backward and forward formats [$F(1,28) = 0.1$], nor was the interaction significant [$F(1,28) = 0.64$].

Given that our chief hypotheses regard responses to words presented in the forward format, subsequent analyses focus on these trials. Reaction Time (RT) was compared across three conditions: F1, F2, and B2 (i.e., first presentations, second presentations for words previously presented in the forward format, and second presentations for words previously presented in the backward format, respectively). Two RT effects were hypothesized *a priori.* The first was the typical effect of repetition (F2–F1). The second was an effect of the format of the first presentation on RTs to second presentations (F2–B2). We will refer to these two effects as the *priming effect* and the *format effect*, respectively.

Mean RTs are shown in Table 1 along with statistical results. RTs did not differ significantly between F1 and F2 conditions but were reliably slower for B2 than for F2. The absence of a significant priming effect was unexpected. However, when results from Experiment 1 were combined with results from 8 additional subjects treated identically except for the absence of ERP recordings, the priming effect was significant (see Table 1), suggesting that the absence of a priming effect in Experiment 1 is related to the small number of subjects. The format effect reflected the fact that test RTs were slower for words seen previously in the backward format than for words seen previously in the forward format. This result confirmed our prediction that RTs would be slower for B2 than for F2, but we did not predict that RTs would be slower for B2 than for F1. It is possible that priming was partially counteracted by recognition processing that slowed RTs for both F2 and B2 conditions, but this possibility deserves further study.

Recognition results showed a trend towards poorer recognition for F words than for B words [$F(1,14) = 4.3$, $P = 0.057$]. The mean percentage of responses that were correct was 54% for F words, 68% for B words, and 86% for recognition foils. This result parallels earlier work showing better memory for transformed text [16]. A subsequent analysis taking word frequency into account showed a trend for better recognition for low- than for high-frequency words [66% vs 56%, $F(1,14) = 2.85$, $P = 0.1136$], significantly poorer recognition for F words than for B words [$F(1,14) = 6.19$, $P = 0.026$], and a non-significant interaction [$F(1,14) = 0.04$].

ERP data. ERP analyses focused on differences between the same three conditions (F1, F2, and B2). ERPs associated with these conditions are shown in Fig. 2A for midline electrode locations. Two effects were hypothesized *a priori*, paralleling the priming and format effects on RT. ERPs were quantified in several ways. Given the results from a prior experiment in which analogous effects were found over the occipital lobe [32], we first describe ERPs from the midline occipital electrode, Oz.

Recordings from Oz during the first 300 ms after word onset showed typical early ERP componentry, after which ERPs appeared to differ between conditions (Fig. 2A). Effects of repetition—differences between F2 and F1 wave forms—were apparent between 300 and 750 ms. We analyzed these effects by measuring mean amplitudes over consecutive 100-ms latency ranges, as listed in Table 2. These measurements showed that the repetition effect was present at Oz between 300–600 ms, with a marginal effect for the 600–700 ms interval. We will henceforth refer to this F2–F1 ERP difference as the overall repetition effect or *ERP priming effect*.

Repetition effects were also analyzed as a function of whether the first presentation occurred with the forward or backward format. ERPs for the F2 and B2 conditions differed reliably over the interval from 400–500 ms, with a marginal effect for the 300–400 ms interval. We will refer to this differential ERP repetition effect as the *ERP format effect*. Note that these ERPs were elicited by words presented in the forward format; the ERP format effect pertains to the format of corresponding first presentations. As shown in Fig. 2A, ERP format effects at these latencies were evident at Oz, Pz, and Cz, but not at Fz and Fpz. These effects are also shown in Fig. 2B as difference waves formed by subtracting conditions.

The scalp topography of these two effects was first analyzed by grouping nearby electrodes to form seven regions: fronto-polar, frontal, central, parietal, occipital, left-lateral, and right-lateral (Fp1/Fp2/Fpz, F3/F4/Fz, C3/C4/Cz, P3/P4/Pz, O1/O2/Oz, F7/T3/T5, and F8/T4/T6, respectively). A repeated-measures ANOVA was run for each region comparing conditions in a pairwise manner to test for ERP priming and ERP format effects. Statistical results for the ERP priming effect are shown in Table 3. For the interval from 300–400 ms, the ERP priming effect was apparent at central, parietal, and occipital regions. In the interval from 400–500 ms, the ERP priming effect was apparent for all regions except the fronto-polar region. At left lateral regions, the ERP priming effect was significant beginning in the interval from 200–300 ms. In all cases of significant ERP priming effects, ERPs were more positive for the F2 condition than for the F1 condition.

Statistical results for the ERP format effect (see Table 3) showed that differences were significant for parietal and occipital regions at 400–500 ms. At these locations,

Table 1. Reaction times for F1, F2, and B2 conditions, with corresponding statistical results. Standard error given in parentheses

	Mean reaction time (ms)			*P* value from *t*-test	
Experiment	F1 (S.E.)	F2 (S.E.)	B2 (S.E.)	F1 vs F2 (priming effect)	F2 vs B2 (format effect)
Experiment 1: Semantic Task	533 (21)	524 (20)	553 (21)	0.44	0.016*
Experiment 1 with 8 additional subjects	536 (18)	523 (18)	549 (18)	0.041*	0.0001*
Experiment 2: Recognition Task	771 (47)	700 (27)	712 (29)	0.13	0.12

* Significant *P* values.

the F2 response was more positive than the B2 response. There was also a significant difference at the left lateral region from 600–700 ms in which the B2 response was more positive than the F2 response. The scalp topography of the format effect can also be displayed as a voltage map, as shown in Fig. 2C. This map reflects a spherical spline interpolation based on ERP amplitude difference measurements between F2 and B2 conditions from 400–500 ms from all 21 electrodes.

The interpretation of the ERP format effect is complicated somewhat by reaction-time differences between F2 and B2 conditions. Mean RTs differed by 25 ms, although RT distributions overlapped to a large extent. Even though these RT differences were predicted, they may have produced a latency shift in some ERP components that could masquerade as an effect related to visual word-form priming. To address this issue, additional analyses were conducted that took into account the RT measure on each trial, so as to negate this RT confound. ERPs were formed across subjects for trials in which RTs fell into discrete time intervals, selected arbitrarily. These intervals spanned the range from 300–1000 ms, using contiguous 25-ms intervals from 300–600 ms and 50-ms intervals from 600–1000 ms, although the first two and the last three intervals were not used because fewer than 20 trials per interval were available. Within the remaining 15 intervals, there were no consistent RT differences between conditions. Accordingly, ERPs were computed using data from all subjects together and giving equal weight to each time interval, rather than to each trial, thus forming new ERPs for the F2 and B2 conditions, as shown in Fig. 3A. This procedure for generating ERPs resulted in a comparison between F2 and B2 conditions such that RT was no longer a confounded variable. The ERP format effect was still apparent, particularly at occipital scalp locations. Fig. 3C shows the scalp topography of this difference over the latency range from 400–500 ms.

In another analysis, the same RT intervals were used to derive a comparison between ERPs differing in RT but mixing F2 and B2 trials together. ERPs for odd intervals were compared to ERPs for even intervals, because these two conditions had a corresponding RT difference of 32 ms. As shown in Fig. 3B, this small RT difference gave rise to a late ERP effect, but this effect was maximal over central electrodes. The scalp topography of this RT-related ERP difference is shown in Fig. 3D. These results suggest that the RT confound may have made a contribution to the F2–B2 ERP difference at some recording electrodes. However, the decidedly posterior scalp maximum of the ERP format effect suggests that it cannot simply be attributed to RT differences. Topographic comparisons between the RT-related ERP difference (Fig. 3D) and the ERP format effect (Fig. 2C) using the Geisser–Greenhouse correction revealed significant differences using either the five midline electrode locations [$F(4,28) = 4.63$, $P = 0.03$] or all electrode locations [$F(20,140) = 3.50$, $P = 0.041$]. Furthermore,

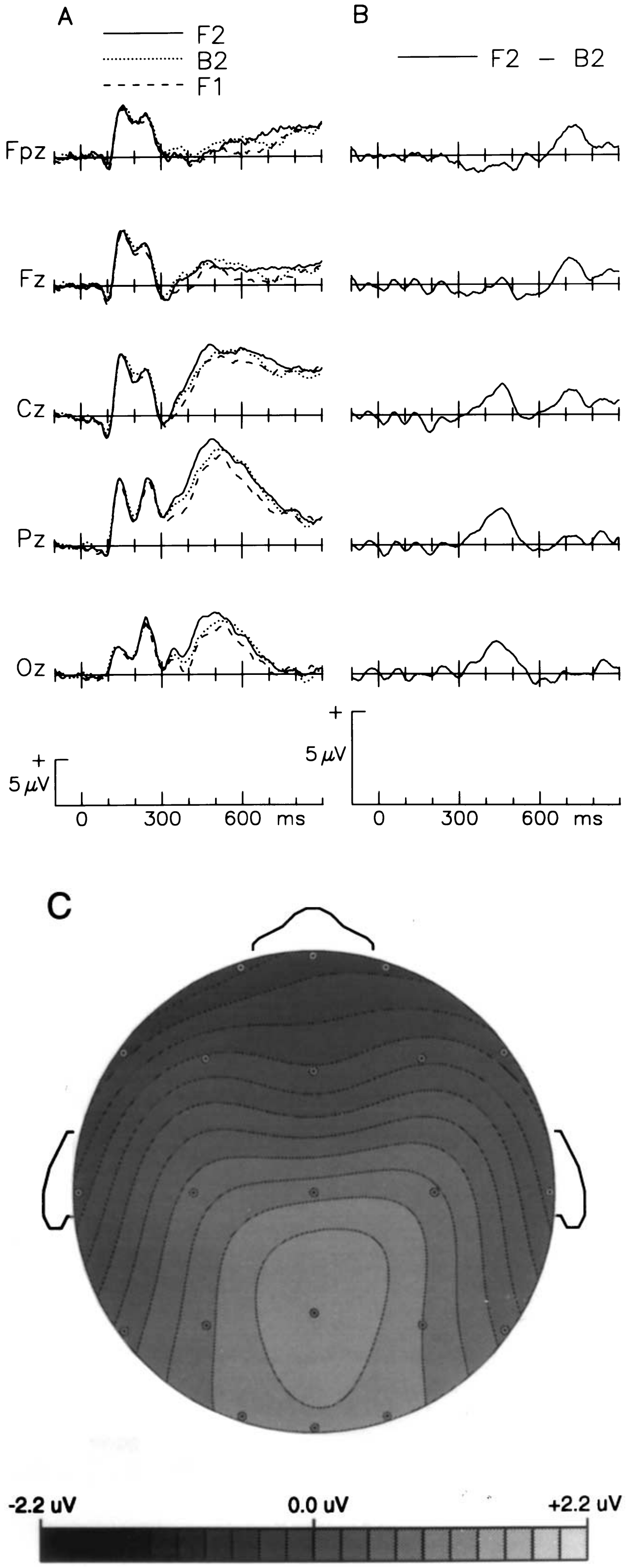

Fig. 2. (A) ERPs from Experiment 1, for electrodes positioned equidistantly along the midline (Fpz = fronto-polar, Fz = frontal, Cz = central, Pz = parietal, and Oz = occipital). (B) Difference waves for the ERP format effect, plotted at double the scale. (C) Topographic map of the mean amplitude of the ERP format effect measured from 400–500 ms. Each electrode location is indicated by a circle.

Table 2. ERP measurements from Oz electrode for F1, F2, and B2 conditions in Experiment 1, with corresponding statistical results

	Mean ERP amplitude (μV)			*P* value from *t*-test	
Latency (ms)	F1	F2	B2	F1 vs F2	F2 vs B2
0–100	−0.3	−0.1	−0.1	0.433	0.871
100–200	2.0	2.2	2.4	0.710	0.626
200–300	3.3	3.8	3.7	0.281	0.760
300–400	0.9	2.0	1.5	0.006*	0.070
400–500	3.4	5.6	4.1	0.0001*	0.007*
500–600	4.4	5.6	5.4	0.011*	0.836
600–700	1.8	2.7	2.9	0.062	0.546
700–800	0.3	0.6	0.6	0.656	0.908
800–900	0.5	0.3	−0.2	0.605	0.354

* Significant *P* values.

Table 3. Statistical results from scalp regions analysis of ERP priming effect (F2–F1) and ERP format effect (F2–B2) in Experiment 1, showing *P*-values for the main effect of condition in each ANOVA

		Region						
Latency (ms)	Effect	fronto-polar	frontal	central	parietal	occipital	left-lateral	right-lateral
0–100	F2–F1							
	F2–B2							
100–200	F2–F1							
	F2–B2							
200–300	F2–F1						0.0033	
	F2–B2							
300–400	F2–F1			0.0213	0.003	0.0055	0.0344	
	F2–B2							
400–500	F2–F1		0.0212	0.0084	0.0006	0.0003	0.0104	0.0185
	F2–B2				0.033	0.0079		
500–600	F2–F1		0.036	0.0119	0.0048	0.0263		0.0262
	F2–B2							
600–700	F2–F1	0.0333	0.0201	0.0073	0.0085			0.0064
	F2–B2						0.0489	
700–800	F2–F1							0.0273
	F2–B2							
800–900	F2–F1							
	F2–B2							

Nonsignificant *P* values are omitted.

the ERP format effect endured when the effects of confounding RT differences were removed (Fig. 3C).

There were indications that the ERP format effect tended to decrease over the course of the session (e.g., at Oz, 1.3 μV for the first half vs 0.6 μV for the second), although this effect was not statistically significant. In addition, there was also a nonsignificant trend for larger ERP format effects for low-frequency than for high-frequency words (e.g., at Cz, 1.5 μV vs 0.6 μV, respectively).

Experiment 2: Recognition task

Behavioral data. Recognition scores for second presentations averaged 89% correct and did not differ sig-

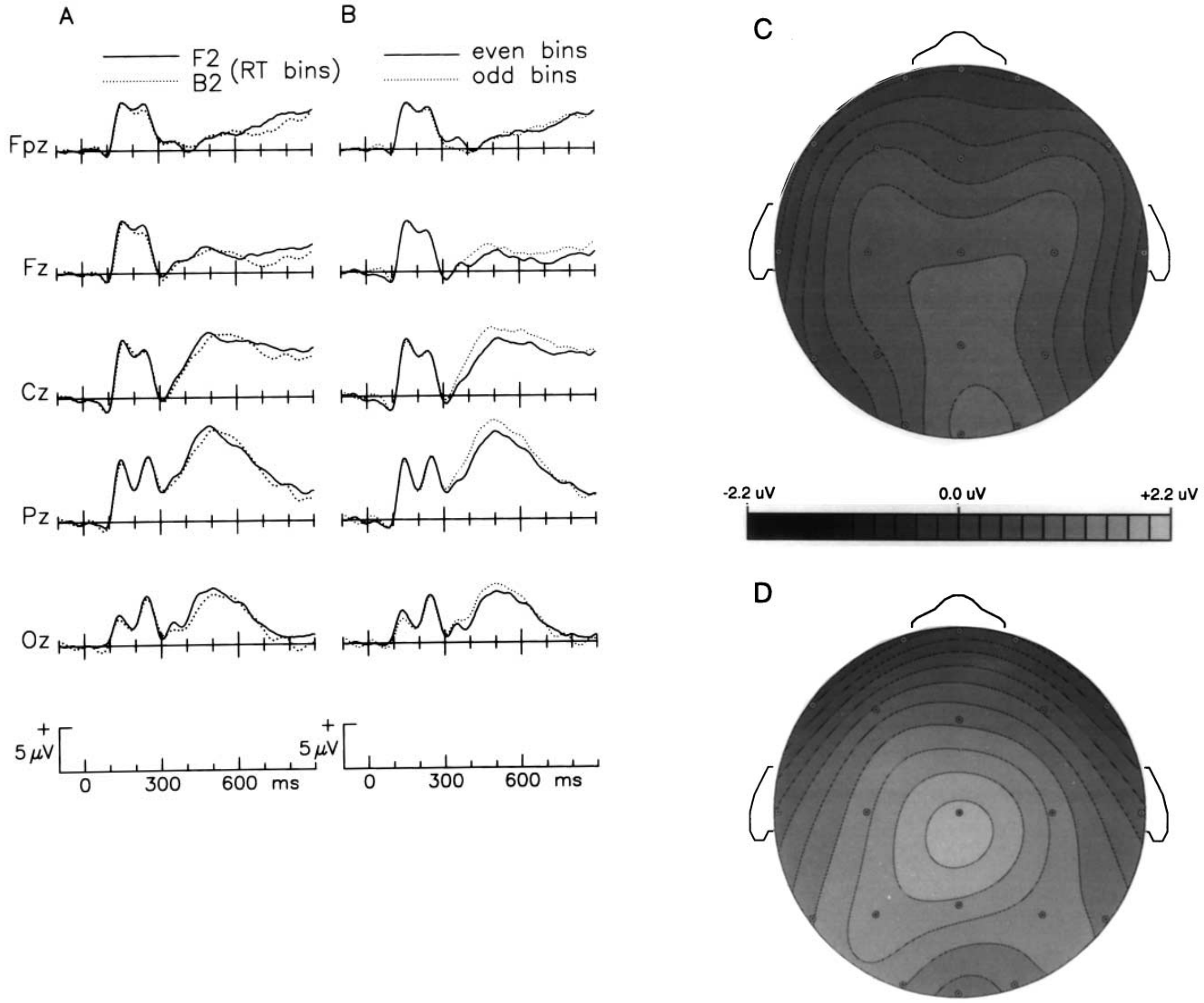

Fig. 3. (A) ERPs from Experiment 1 following procedure to correct for RT differences (electrode locations as in Fig. 2). (B) ERPs obtained by combining alternate bins from the same analysis, yielding a 32-ms difference in mean RT between conditions. (C) Topographic map of the mean amplitude of the corrected F2–B2 difference from (A), measured from 400–500 ms. (D) Topographic map of the mean amplitude of the ERP difference from (B), measured from 400–500 ms.

nificantly as a function of condition (F2 vs B2) or word frequency, nor was the interaction in the 2-way ANOVA of condition by frequency significant. Recognition scores for initial presentations averaged 94% correct and also did not differ significantly as a function of condition (F1 vs B1), word frequency, or the interaction of the two. However, given the high level of recognition accuracy at this short retention delay, the lack of effects on recognition may reflect ceiling effects.

RTs corrected by only including responses less than 2 standard deviations from the mean are shown in Table 1. Pairwise comparisons between conditions showed no statistically significant differences. However, in a between-experiment comparison, RTs from the recognition task were longer than RTs from the semantic task [$F(1,14) = 25.47$, $P = 0.0002$].

ERP data. ERPs recorded during the recognition task are shown in Fig. 4A. A clear effect of word repetition (F2 vs F1) was observed at nearly every electrode location. The amplitude of this ERP difference was larger and its peak latency somewhat later than the F2–F1 ERP difference in Experiment 1.

Mean amplitude measurements of F2–F1 ERP differences were made over consecutive 100-ms windows. Table 4 shows results from a scalp regions analysis (with separate ANOVAs for sets of 3 nearby electrodes, as in Experiment 1). For central, parietal, and occipital regions, differences were statistically significant from 400–600 ms. There were also hints of earlier differences of opposite polarity, including a reliable difference from 100–200 ms at the central region.

Repetition for words presented first in the backward format influenced ERPs in a similar manner, in that ERPs were more positive for the B2 condition than for the

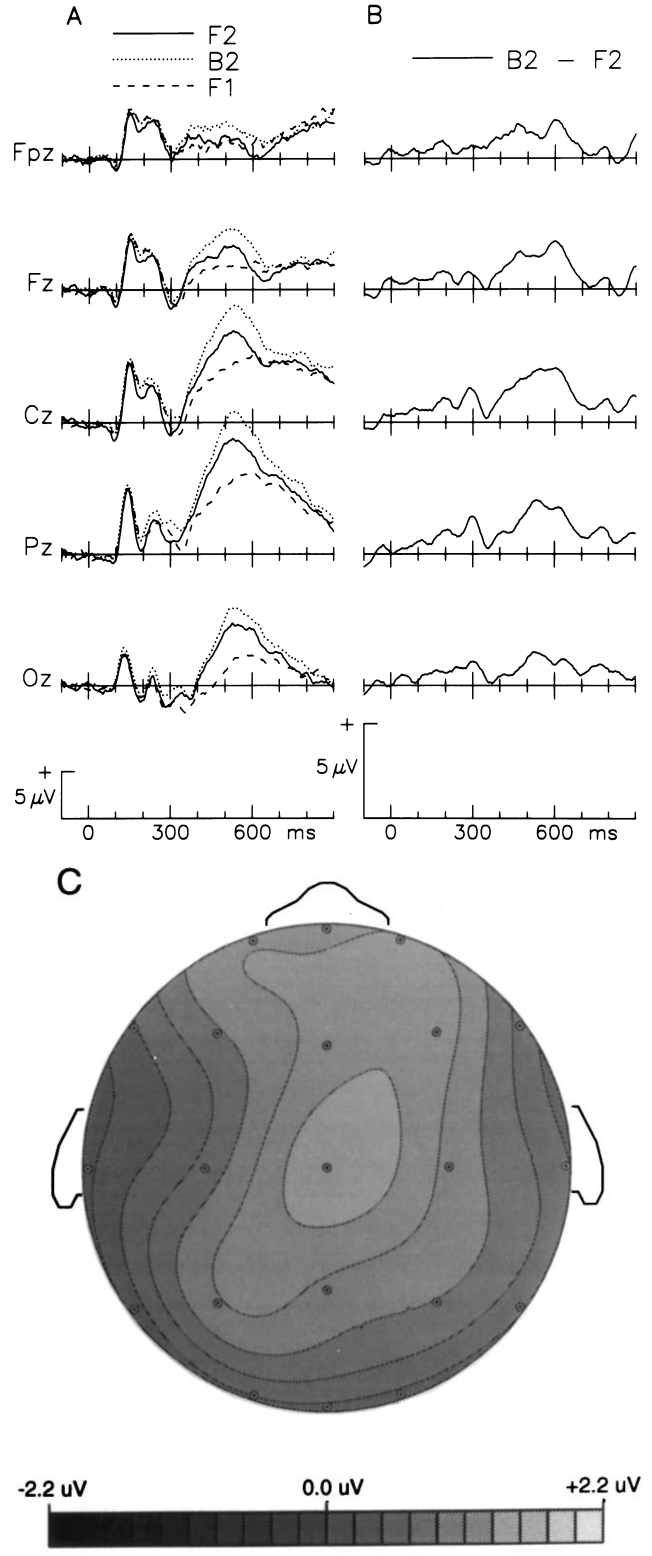

Fig. 4. (A) ERPs from Experiment 2 (electrode locations as in Fig. 2). (B) B2–F2 ERP difference waves, plotted at double the scale. (C) Topographic map of the mean amplitude of the B2–F2 ERP difference measured from 400–500 ms.

F1 condition. Furthermore, ERPs were generally more positive for the B2 condition than for the F2 condition. These observations were verified by a scalp regions analysis, showing for example that, for central, parietal, and occipital scalp regions, the response for B2 was greater than the response for F2 for the interval from 400–500 ms ($P = 0.0201$, 0.0033, and 0.1435, respectively) and the interval from 500–600 ms ($P = 0.0024$, 0.0001, and 0.0228, respectively). This pattern thus differed from the results of Experiment 1, wherein ERPs were less positive for the B2 condition than for the F2 condition.

For comparisons of scalp distributions, B2–F2 ERP difference waves (Fig. 4B) were measured over the latency range from 400–500 ms. The corresponding topography displayed maximal amplitudes over central scalp regions (Fig. 4C). The distribution of this B2–F2 ERP difference was more anterior and asymmetric compared to that of the F2–B2 ERP difference in Experiment 1 (Fig. 2C). Topographic comparisons using the Geisser–Greenhouse correction revealed significant differences using either the five midline electrode locations [$F(4,56) = 5.16$, $P = 0.016$] or all electrode locations [$F(20,280) = 3.74$, $P = 0.029$].

Discussion

In Experiment 1, word processing was influenced by the nature of prior word presentations: forward presentations, relative to backward presentations, led to faster behavioral responses to subsequent forward presentations of the same word. Brain potentials recorded from parietal and occipital scalp locations 400–500 ms after word onset were reliably associated with this differential priming effect. We use the term “ERP format effect” to refer to this ERP difference and hypothesize that it represents differential processing of visual word-form in the brain. This interpretation is consistent with prior observations from both neuropsychology and neuroimaging indicating that certain posterior regions of the cerebral cortex are specifically involved in the processing of visual word-form.

An alternative interpretation of these ERP effects is that they reflect explicit remembering rather than visual word-form processing, but evidence from Experiment 2 argues against this interpretation. The recognition requirements in Experiment 2 led to a different sort of ERP repetition effect, with a larger late positive amplitude and longer peak latency (as can be seen by comparing Fig. 2 and Fig. 4). In addition, the ERP repetition effect in Experiment 2 displayed a broad scalp distribution without the distinct posterior focus of the presumptive visual word-form correlate. Most importantly, ERP differences between B2 and F2 conditions went in opposite directions in the two experiments; late positive ERPs were larger for B2 in Experiment 2, but for F2 in Experiment 1. This pattern of results can be interpreted by supposing that the recollective experience for words earlier presented in the backward format tended to include retrieval of contextual details such as aspects of the earlier presentation format, and that this enhanced

Table 4. Statistical results from scalp regions analysis of ERP priming effect (F2–F1) and ERP format effect (F2–B2) in Experiment 2, showing *P*-values for the main effect of condition in each ANOVA

Latency (ms)	Effect	Region						
		fronto-polar	frontal	central	parietal	occipital	left-lateral	right-lateral
0–100	F2–F1							
	F2–B2							
100–200	F2–F1			0.0045				
	F2–B2			0.03	0.008			
200–300	F2–F1							
	F2–B2			0.02	0.002	0.02	0.02	
300–400	F2–F1						0.0413	
	F2–B2				0.01			
400–500	F2–F1			0.0269	0.0123	0.0064		
	F2–B2	0.05		0.02	0.03		0.004	0.04
500–600	F2–F1		0.0068	0.0001	0.0003	0.0014	0.0021	
	F2–B2	0.04	0.02	0.002	0.0001	0.02	0.004	0.002
600–700	F2–F1							
	F2–B2			0.03	0.0031			0.01
700–800	F2–F1				0.02			
	F2–B2							
800–900	F2–F1							
	F2–B2							

Nonsignificant *P* values are omitted.

recollection led to a larger ERP repetition effect for B2, but only in Experiment 2 in which recollection was encouraged. Results from other sorts of experiments have likewise suggested that ERPs can be sensitive to aspects of contextual retrieval or source memory [24, 25]. Furthermore, enhanced recollection for B2 may have encompassed better memory for the words per se, not just the contextual details. Although behavioral results from Experiment 2 suggested that an equivalent level of recognition accuracy was achieved for F and B words, recognition results from Experiment 2 may have been influenced by ceiling effects, and recognition results from the delayed test in Experiment 1 hinted at a recognition advantage for B words over F words, suggesting that B words may have indeed engaged more recollection in Experiment 2. In any event, the most likely explanation for ERP repetition effects in Experiment 2 is that they reflect some aspect of episodic recollection.

The finding that the polarity of ERP differences between F2 and B2 conditions switched between Experiments 1 and 2 provides support for the notion that explicit remembering is responsible for the ERP differences in Experiment 2 but not those in Experiment 1. Recollection in Experiment 1 was presumably less robust than in Experiment 2 due to the differing performance requirements. The later portion of the ERP repetition effect in Experiment 1 from 500–700 ms, which was quite similar for F2 and B2 conditions, may have reflected a small amount of recollective processing, although further evidence to support this speculation is lacking.

Observations in many previous ERP studies were not sufficient for identifying an ERP correlate of perceptual priming. Despite the resemblance between an ERP measure and a behavioral measure obtained in an implicit memory test (i.e., the fact that neither is obtained in response to an explicit memory query), it does not follow that the ERP measure necessarily bears a close relationship to the implicit memory measure. Such a relationship must be demonstrated empirically.

In a set of studies in normal subjects, Bentin *et al.* [33, 34] attempted to relate ERP repetition effects to priming effects. ERP repetition effects elicited during implicit memory tests were found to vary in amplitude with the number of times a word had previously been presented during the session and with the amount of elapsed time, and these effects appeared to be independent of whether words were accurately recognized. However, one difficulty with interpreting these effects is that variables such as number of repetitions and elapsed time commonly influence performance on both implicit and explicit memory tests. Recordings during recognition tests showed that ERPs elicited by words categorized as "new" differed according to whether they had actually been presented earlier [33, 34]. These findings could arise if ERPs were sensitive to processing responsible for perceptual priming, in that some words could conceivably be primed but not be recognized. Alternatively, a variety of other factors could produce trials in which explicit retrieval occurred but erroneous recognition responses were made. In short, although the authors suggested that "ERPs are sensitive to both implicit and explicit aspects of memory performance" ([34], p. 1280), their results did not allow such effects to be dissociated such that ERPs associated with perceptual priming could be identified.

Evidence from other experiments are subject to similar limitations. For example, studies comparing within- versus across-modality priming effects may in some circumstances allow for dissociations between recognition and priming [35–38]. Although scores on explicit memory tests may be similar for within- versus across-modality conditions, the retrieved information is quite different in the cross-modal case. Thus, the modality manipulation represents a much more extreme manipulation than the within-modality manipulation in the present experiment, which focuses specifically on priming of visual word-form. Another approach has been to investigate ERPs in neurological populations. In three patients with damage in right parahippocampal and lingual gyri and adjacent regions, a reduction was found both in priming of lexical decision RTs and in ERPs associated with word and nonword repetition [39]. This result lends support to an association between occipito–temporal regions and visual word-form priming, although a contribution related to recollective processing cannot be ruled out. Findings that patients with Alzheimer's disease showed normal ERP repetition effects under some conditions, particularly when words were repeated after relatively short delays [40, 41], might be interpreted as evidence that ERPs reflect priming phenomena. In general, Alzheimer's patients show intact perceptual priming but are impaired in recognizing repeated words (e.g., [42]). However, recognition memory was not assessed in the ERP studies, and the experimental designs did not allow specific associations to be made between ERP repetition effects and priming versus recognition. Therefore, connections between priming and ERPs observed in these studies are unwarranted.

A research strategy well-suited to overcome these problems involves the use of experimental manipulations with differential effects on performance measures in implicit and explicit memory tests. Memory dissociations can thus be used to isolate ERP correlates of priming. In particular, Paller *et al.* [32] sought to determine whether ERPs are sensitive to processing underlying priming of visual word-form. Words were presented under two different presentation conditions: whole word presentations (the usual manner) and letter-by-letter presentations (isolated letters presented in rapid succession to form a word). Results from a subsequent lexical decision test showed (1) that ERPs recorded from all scalp locations were more positive for repeated words than for new words and (2) that ERPs recorded from occipital scalp locations were more positive for words previously presented as whole words than for words previously presented letter-by-letter. Furthermore, lexical decision times were speeded for studied words more so when the prior presentation format was whole word rather than letter-by-letter. The differential ERP response as a function of prior presentation format was thus construed as an ERP correlate of visual word-form processing subject to priming.

The ERP format effect in Experiment 1 is similar to that reported by Paller *et al.* [32] in many respects, although the experimental paradigm differed as follows: (a) the two critical conditions were repetitions after prior presentation in forward versus backward format; (b) repetitions occurred after a shorter delay in a continuous rather than a study-test design; (c) the task was name detection rather than lexical decision. In both cases, ERP correlates of priming were isolated by virtue of manipulations that selectively influenced priming measures. Moreover, similarities between results in these experiments support the conclusion that ERPs are specifically sensitive to processing underlying perceptual priming, as opposed to other processing unique to the B2 condition in Experiment 1 and responsible for RT slowing in that condition.

Neuropsychological evidence as well as evidence from normal subjects has been used to support the prevailing assumption that essential analyses of visual word-form take place in the left hemisphere, although some authors have suggested that both hemispheres are capable of processing visual word-form (e.g., [43]). Moreover, various results from normal subjects have demonstrated intriguing contrasts between visual word-form processing in left and right cortical regions [44–46]. Our results revealed no hemispheric differences and thus cannot speak to the question of whether the two hemispheres are responsible for distinctive types of processing of visual word-form. However, the present demonstration of an ERP correlate of priming opens the door for further studies that can probe possible hemispheric differences and also examine the location of intracranial generators more precisely.

Although scalp topographic data were not sufficient for determining the intracranial source of the ERP format effect, some speculation can be made with assistance from neuroimaging results. In particular, Buckner *et al.* [13] reported that bilateral occipito-temporal regions showed cerebral blood flow reductions in a priming condition compared to a baseline condition. In both conditions, lists of three-letter word-stems were displayed visually and subjects attempted to complete each stem with the first word to come to mind. In the priming condition, but not in the baseline condition, some of the stems could be completed to form words viewed in a prior study phase, as in prior experiments with amnesic patients [47]. The blood flow reduction was interpreted as a neural correlate of priming, as less neural activity was apparently required to complete stems to previously viewed words [13]. This occipito–temporal region in the left hemisphere corresponds with the location of prior PET activations presumably related to visual word-form processing ([12], but see [48, 49]).

Accordingly, we can speculate that the ERP format effect was also derived from cortical activity in occipito–temporal regions that was less pronounced after a prior forward presentation than after a prior backward presentation. This electrophysiological effect reached a maximum amplitude at about 450 ms after word onset. The latency and scalp distribution of the effect did not match deflections apparent in the unsubtracted ERPs and it is unlikely that previously characterized ERP components are responsible for this effect. Whether our scalp recordings of the ERP format effect were produced predominantly by generators in a visual word-form area in the left hemisphere or whether there were significant contributions from both hemispheres remains to be determined. In addition, if a close connection between the ERP format effect and occipital activations based on neuroimaging studies (PET or functional magnetic resonance imaging) could be substantiated, the ERP data could be used to indicate the time-course of those activations.

It can be useful to contrast these ERP correlates of priming of visual word-form with prior results in which memory dissociations were used to isolate ERP correlates of recollection. For example, Paller *et al.* [22, 23] used study conditions that led to differential recognition but similar levels of priming. The anterior scalp distribution of the associated ERP correlates of recollection, as well as their generally later onset compared to the approximately 300 ms onset of the ERP format effect in Experiment 1, are consistent with conceptions of memory functions that emphasize distinctions between the brain mechanisms of priming and recollection (e.g., [50]).

Finally, these ERP results carry new prospects for connections between studies of visual word-form processing in normal subjects and neuropsychological studies of pure alexia. A variety of conceptions of the functional deficit underlying pure alexia are currently under active debate (for review, see [51]). Whereas Warrington and Shallice [10] postulated that a dysfunctional visual word-form system is responsible, Patterson and Kay [52] emphasized deficient access to the visual word-form system with respect to the parallel transmission of letter information. Counterarguments to both of these views have been developed through studies of *implicit reading* (i.e., reading demonstrated indirectly via lexical decision, semantic categorization, and context effects in word and letter identification), suggesting that parallel access to the visual word-form system is still possible in pure alexia (e.g., [53–57]). Furthermore, results showing preserved word-identification priming in a patient with pure alexia led Schacter *et al.* [58] to conclude that the patient's preserved priming was mediated by an intact visual word-form system. Given that pure alexia generally arises after left hemisphere damage [59], the patterns of deficit can also be related to lateralization of function across the two hemispheres. Accordingly, Coslett and Saffran [43] have attributed letter-by-letter reading to intact right-hemisphere processing, a speculation supported by evidence that additional reading disruption in a recovered alexic patient could be produced by right-hemisphere transcranial magnetic stimulation [60]. In line with this idea, it is interesting to note that in normal subjects both hemispheres can mediate word identification via serial letter processing, whereas left-hemisphere regions appear to be specialized for processing words directly without mediation through letter representations [45]. Explanations for pure alexia thus face the challenge of accounting for the reading deficit, concomitant abnormalities in letter identification, possibly normal word-form access in examples of priming and implicit reading, as well as hemispheric laterality with regard to these functions. Considerable controversy still surrounds the findings of residual reading capabilities in patients with alexia and relationships to the normal functioning of visual word-form areas. The ability to specifically monitor the processing of visual word-form in real time, using this ERP approach, may be helpful for clarifying some of these issues, as well as issues pertaining to perceptual priming and its relationship to other types of memory.

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