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Investigating the relationship between implicit and explicit memory: Evidence that masked repetition priming speeds the onset of recollection

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Memory theories assume that unconscious processes influence conscious remembering, but the exact nature of the relationship between implicit and explicit memory remains an open question. Within the context of episodic recognition tests research typical shows that priming impacts behavioral and neural indices of familiarity. By this account, implicit memory leads to enhanced fluency of processing, which is then attributed to 'oldness' in the context of recognition judgments. Recently, however, behavioral and neuroimaging evidence has emerged to suggest that priming can also influence recollection, suggesting that the rate of recollection increases following priming. Here, we examine the relationship between priming and recollection, using Event-Related Potentials (ERPs) to assess changes in the timecourse of processing. Participants studied a series of words, and episodic memory was assessed using a standard item recognition test, but masked repetition priming preceded half of the test cues. Results confirmed that implicit memory was engaged: priming produced robust facilitation of recognition Reaction Times (RTs), with larger effects for studied than unstudied words. Mapping onto the RT data, ERPs recorded during recognition testing over centro-parietal electrodes revealed N400-like priming effects (250–500 ms) that were larger in magnitude for studied than unstudied words. More importantly, priming also had a clear impact on explicit memory, as measured by recollection-related left-parietal old/new effects. While old/new effects for unprimed trials were present during the typical 500–800 ms latency interval, the old/new effects seen for primed trials were equivalent in magnitude and topography, but onset ~300 ms earlier. ERPs reveal that repetition priming speeds the onset of recollection, providing a novel demonstration that unconscious memory processes can have a measureable, functional, influence on conscious remembering.

Introduction

Within long-term memory a fundamental division is drawn between declarative (i.e., conscious or explicit) and non-declarative (i.e., unconscious or implicit) forms of memory (e.g., see Eichenbaum and Cohen, 2001; Tulving, 1985). Despite this division, a central assumption within memory theory is that unconscious memory processes influence and support conscious remembering. To date, however, the exact nature of the relationship between implicit and explicit memory remains unknown. Here we present the findings of an Event-Related Potential (ERP) study of episodic recognition memory in which we manipulated whether test cues received implicit priming. In doing so, we were able to demonstrate that priming can directly impact upon the timecourse of explicit recognition - producing changes in the speed of retrieval processing, as demonstrated by changes in the onset and duration of memory-related ERP effects. Before outlining our specific experimental design, we first provide a brief overview of the core memory processes supporting recognition and discuss prior evidence for interactions with priming.

Dual-process models of recognition are dominant in the episodic memory literature, proposing that separate familiarity and recollection processes support retrieval (see Yonelinas, 2002, for an extensive review). Familiarity is typically characterized as a relatively automatic process that assesses the degree of similarity between a current event and events experienced previously. By contrast, recollection is characterized as an effortful process that supports retrieval of contextual details associated with specific prior events. Importantly, some dual-process models suggest that common processes may underlie both familiarity in recognition memory and priming on implicit memory tests (see Jacoby and Dallas, 1981; Mandler, 1980). While growing evidence indicates that implicit priming does influence recognition during explicit memory tests (e.g., see Keane et al., 2006; Rajaram and Geraci, 2000; Wolk et al., 2005), the exact details of how and when priming influences explicit retrieval remain a matter of debate.

One approach that has proven useful for querying the relationship between priming and episodic memory involves combining a masked priming manipulation with standard recognition tests. Masked priming studies involve a very brief presentation of a prime item (prior to the

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onset of recognition targets), obscured by a pattern mask (e.g., letters or symbols) occupying the same visual space before and/or after the presentation of the prime. Using this approach it is possible to measure the contribution of priming in the absence of conscious awareness of the primes. In a seminal study focusing on illusory memory, Jacoby and Whitehouse (1989) investigated the impact of processing fluency on recognition using masked repetition priming of test cues, where target items were preceded by either a brief (50 ms) presentation of the target word (primed) or a different word (unprimed). Test words preceded by repetition were associated with an increase in the probability that they would be classified as studied, irrespective of whether or not they had been studied. This finding is important because it demonstrates that priming impacted recognition decisions, and was interpreted as evidence supporting a link between processing fluency and feelings of familiarity (Jacoby and Dallas, 1981). Critically, however, this early study did not employ process estimation methods, leaving the relationship between priming and specific episodic retrieval processes unclear.

Subsequent research employing similar paradigms, combined with the Remember/Know procedure (Rajaram, 1993; Rajaram and Geraci, 2000), have largely demonstrated changes in the proportion of Know responses, supporting the view that priming induced fluency selectively influences familiarity (e.g., see Lucas et al., 2012; Woollams et al., 2008). For example, Rajaram and Geraci (2000) demonstrated using the R/K procedure that presenting test items in an appropriately meaningful context (i.e., semantically primed) increases familiarity, but has no effect on recollection. While links between priming and familiarity are clear, equivalent evidence for links between priming and recollection have proved more elusive. Theoretically, a lack of priming effects on recollection could reflect a hard limit on the locus of interactions between implicit and explicit memory. Alternatively, however, the failure to find interactions between priming and recollection may reflect little more than methodological inadequacy and over-reliance on the use of binary R/K decisions (Higham and Vokey, 2004).

An alternative approach to dealing with concerns about the use of the binary R/K procedure has been to employ an alternative process estimation procedure, the independent scales methodology, where participants were asked to rate each item for both familiarity and recollection on a 4-point scale. Research using this approach has indicated that priming can also influence recollection (e.g., see Brown and Bodner, 2011; Higham and Vokey, 2004). For example, Kurilla and Westerman (2008) demonstrated that, using the independent scales methodology, the proportion of both R and K responses increased following repetition and conceptual primes. While the independent scales method has not been widely adopted in the literature, these findings nonetheless add weight to the claim that at least under certain circumstances priming can influence recollection.

Another solution to concerns over reliance on behavioral measures is to provide convergent evidence from neuroimaging data. For example, Taylor and Henson (2012) employed a masked priming paradigm with a binary R/K decision to examine the effects of repetition and conceptual priming (e.g., brief prior exposure to meaningfully related words) on subjective reports of familiarity and recollection. Results demonstrated an increase in the proportion of R responses for studied words that were preceded by conceptual primes, but not for words preceded by repetition primes, which were associated with the standard increase in K responses for studied and unstudied words. Importantly, this behavioral finding was replicated in a follow-up fMRI study using the same design, which additionally demonstrated that conceptual priming led to an increase in activity within regions of the parietal cortex previously associated with recollection (Taylor et al., 2013). Here, however, the increase in R responses was found only when repetition and conceptual priming trials were intermixed (compared to presented in separate blocks), suggesting that the relationship between priming and recollection is paradigm dependent.

While convergent evidence has emerged in support of the view that priming can influence recollection, existing data points towards two quite different consequences - changes in either the amount or speed of processing. Claims for changes in the amount of recollection are supported by an fMRI study examining the impact of repetition priming at encoding on subsequent memory. Gagnepain et al. (2011) contrasted primed and unprimed auditory words presented along with distracting sounds, finding that priming at encoding increased the occurrence of recollection at test. In addition, the authors demonstrated that the repetition priming led to a reduction in the magnitude of neural activity at test, in regions of the Medial Temporal Lobes previously associated with recollection. The authors suggest that priming facilitates better encoding of contextual details, resulting in the observed increase in recollection, because it reduces the level of attentional resources tied up in processing item information. To our reading, the mismatch in the direction of behavioral and neural effects complicates interpretation of Gagnepain's findings, and the study focused primarily on the effects of priming at encoding rather than retrieval. Importantly, however, a recent ERP study has also demonstrated a relationship between repetition induced fluency and the amount of recollection, finding an increase in the magnitude of parietal old/new effects for repeated items receiving correct source judgments (Komes et al., 2014). Taken together, these results clearly point to a link between priming and changes in the amount of recollection.

Support for the view that priming impacts on the timing of recollection is provided by an alternative approach, based on the measurement of ERP correlates of retrieval. ERPs provide an ideal method for assessing the interaction between implicit and explicit memory, providing far higher temporal resolution than is available with fMRI data. Critically, ERPs are known to provide distinct neural correlates of priming and recognition, visible even within the confines of a single experiment (Rugg et al., 1998). In particular, recollection is associated with the left-parietal old/new effect (contrasting hits and correct rejections), which onsets around 500–800 ms post-stimulus. Importantly, as with fMRI signals of recollection, the ERP correlate has been shown to change in magnitude across a range of experimental manipulations designed to influence recollection (for reviews see Friedman and Johnson, 2000; Rugg and Curran, 2007; although see MacLeod and Donaldson, 2014). A separate literature has clearly identified an ERP correlate of priming: a broad negativity over posterior scalp sites (contrasting unprimed and primed), which peaks ~400 ms post-stimulus (see Kutas and Federmeier, 2011, for a review). Given the dissociable nature of the neural signals associated with priming and recollection, ERPs provide an excellent complimentary measure for assessing changes in recollection as a function of priming.

To date, only one ERP study, which aimed to capture neural signals associated with stimulus repetition, has reported an effect of priming on the neural correlate of recollection. Woollams et al. (2008) suggests that priming may influence the timing, rather than amount, of recollection. Memory was assessed using a standard word recognition test, combined with R/K decisions, and masked repetition. Priming was carried out at test, using a 50 ms pre-exposure of half the test cues (versus words unrelated to the test cues in an unprimed condition). Behavioral results revealed that priming led to an increase in K response rates, and although recollection was not the focus of the study, results also showed that R responses were faster following priming. As expected, R responses elicited left-parietal old/new effects, which onset 50 ms earlier when responses were primed. Critically, however, the change in latency of left-parietal effects observed in this study matched the duration of the prime, introducing a serious interpretative concern. Because no backwards masking procedure or measure of prime awareness was employed, it remains possible that explicit retrieval could simply have occurred in response to the prime rather than the target. From this perspective, changes in the timing of recollection simply reflect an artifact of the procedure, rather than showing a direct link between priming and recollection.

The studies outlined above point towards a link between priming and recollection, and suggest two independent hypotheses for how priming could influence the neural correlates of recollection. Firstly, based on existing fMRI findings, interactions between priming and recollection may be expected to modulate the magnitude of recollection-related effects, reflecting a change in the amount of cognitive resources engaged during retrieval of recently primed items. Secondly, based on the findings of Woollams and colleagues, repetition priming may produce observable changes in the timing of recollection-related effects, speeding their onset. The current investigation was designed to test these two predictions, using the ERP correlate of recollection, measured during a word recognition memory test, in combination with masked repetition priming. Our procedures are similar to those used by Woollams et al. (2008), but a backwards mask was introduced between prime and target words to reduce the accessibility of primes, and crucially, participants' awareness of primes was recorded. As we show below, by ensuring that participants were not aware of the primes, we were able to demonstrate that unconscious implicit memory really does produce a genuine increase in the speed of conscious explicit remembering.

Methods

Participants

34 right-handed English speakers with normal or corrected-to-normal vision were recruited from the undergraduate population at the University of Stirling. The local ethics committee approved the experiment prior to commencement and written informed consent was obtained from each participant in line with University of Stirling, Division of Psychology ethics procedures. Participants were compensated at a rate of £5 per hour, with the option of receiving payment for the first hour of participation in course credits. Data from two participants were discarded due to insufficient trials (<16) in critical response categories following artifact rejection (see below for criteria). The mean age of the remaining participants was 21 years (age range = 18–34, 15 males).

Materials & design

The stimulus set consisted of 524 medium frequency concrete nouns, between 4–9 letters in length, sampled from the MRC Psycholinguistic database (Coltheart, 1981). Words had a mean written frequency of 23 (±11) occurrences per million (Kučera and Francis, 1967), and a mean concreteness rating of 555 (±48). From the initial pool of words, 12 were randomly selected to be used in the practice block and another 32 were selected to act as fillers shown at the start of study and test phases. The remaining 480 critical words were divided into 4 blocks, matched on word length, concreteness and frequency. Each block consisted of 60 study and 120 test trials. At test, all 60 studied words were presented again, randomly intermixed with 60 unstudied new words. Half of the studied and unstudied test trials were primed (i.e., preceded by a repetition), and the remaining trials were unprimed (i.e., preceded by the word "blank"). The word "blank" was chosen as a neutral prime, as previous research has demonstrated that it is a suitable baseline for ERP investigations of priming (Dien et al., 2006), in particular because it avoids potential confounds introduced by orthnological/phonological/perceptual overlap when using different word primes. Assignment of stimuli to the factors of test status (old, new) and masked priming (unprimed, primed) was fully counterbalanced across participants.

All word stimuli were displayed in the centre of the screen in white on a black background using Courier New 18 point font. Masking symbols used to occlude prime words (>#########<) were also presented in white on a black background using Courier New font, but the size of the masking symbols was increased to 24 point font and placement on the screen was adjusted to ensure that prime words were fully concealed across trials. Study and target words were displayed in uppercase, while prime words were presented in lowercase. Prime and target words are typically presented in different cases during masked priming paradigms to ensure that resulting effects cannot merely be attributed to visual rather than lexical processing. Despite early research suggesting that repetition priming is highly sensitive to changes in case, more recent research on visual word recognition has clearly demonstrated case-independent priming under subliminal presentation conditions (Dehaene et al., 2001, 2004). Participants were seated in a testing cubicle approximately one meter away from a 17-inch LCD monitor. The experiment was implemented using the E-Prime software package (www.pstnet.com: version 1.2), running on a desktop computer in an adjacent room, and participants were monitored via a video link. The screen refresh rate was 16 ms and the accuracy and consistency of the prime duration across trials was verified using the Black Box Toolkit (www.blackboxtoolkit.com). Responses were recorded using a five button PST Serial Response Box (www.pstnet.com) resting on the desk in front of participants. Left and right index fingers were used to make all responses and the mapping of buttons for multiple response options was fully counterbalanced across participants. Words presented at study and test subtended a vertical visual angle of 0.5° and a maximum horizontal visual angle of 5.2°.

Procedure

After application of the electrode cap, participants were provided detailed instructions for the experiment and completed a short practice session. Fig. 1 illustrates the study and test procedures. Each study trial started with a warning signal (>#########<), shown in the centre of the screen for 500 ms, followed by a single word displayed for 300 ms; then a blank participant response screen was shown for 3700 ms. At encoding participants were either asked to read each word out loud, or to fit each word into a short sentence; initial exploration of the data revealed no differences in behavioral or ERP measures as a function of encoding task, and as a result all data are reported collapsed across task. The masking symbols used at test to occlude the prime were also employed for fixation at study to reduce the salience of the masking procedure, and were always described as a "warning signal" denoting that a word was about to appear. Upon completion of the study phase participants were instructed to count backwards from 50 in increments of 3; after 2 min the test phase instructions were presented.

Each test trial started with a screen instructing participants to press a button when they were ready to start the next trial, allowing participants control over the speed of the test presentation, and ensuring that attention was oriented appropriately. Following the participant's key press, and a 200 ms delay, a forward mask (>#########<) was presented for 250 ms, followed by a matching or non-matching prime word shown for 48 ms, and then a backward mask (>#########<) shown for 250 ms. Presentation of the prime sequence was followed by a blank screen for 100 ms, and then the target word was shown for 300 ms, before a blank response screen was presented for 3700 ms. During the blank response screen participants were required to indicate as quickly and as accurately as possible, by button press, whether the preceding target word was old or new.

When a word was classified as old, the screen then displayed details of response options for a subsequent R/K decision; once a response was made the screen went blank for 1000 ms, and then the next trial began. Participants were given detailed written and verbal instructions for the R/K decision (e.g., see Gardiner et al., 1996; Rajaram, 1993). Briefly, participants were instructed to make a 'Remember' response when retrieval was accompanied by specific contextual details from study exposure, and to make a 'Know' response when they felt that the word had appeared in the study list, but were unable to retrieve any specific contextual details. At the end of the experimental procedure participants were questioned to establish their awareness of the priming manipulation, before being fully debriefed.

There is no ideal method for measuring prime awareness. For example, post hoc testing (e.g., in a different set of participants) may reveal awareness that is only indirectly related to levels during actual testing. Equally, assessing awareness on each trial is more direct, but

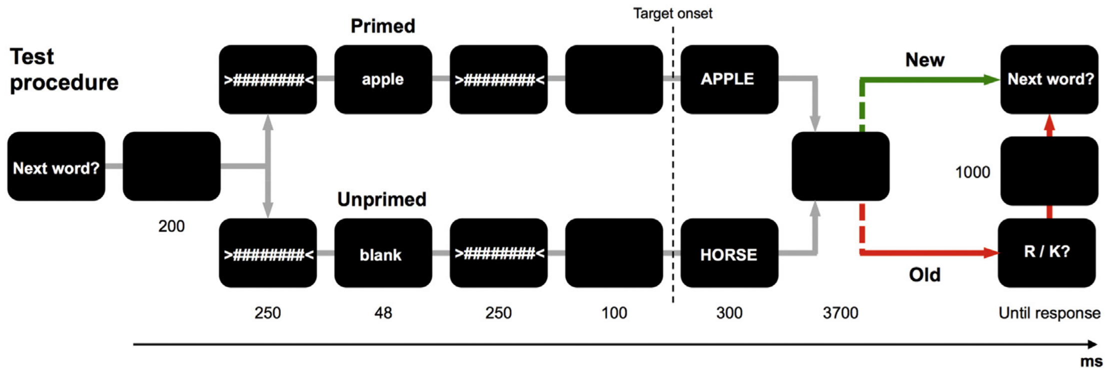

Fig. 1. Schematic illustration of the test procedure. At test, all 60 studied words were presented again randomly intermixed with 60 unstudied new words. Half of the studied and unstudied test trials were primed (i.e., preceded by a repetition), and the remaining trials were unprimed (i.e., preceded by the word "blank").

risks participants gradually becoming aware of the priming manipulation. Our approach of assessing awareness via subjective reports obtained at the end of the experiment links the measure to our specific test participants, and avoids the possibility of cuing participants to the presence of prime words. Responses to this questioning were classified into three broad levels of awareness (response categories that were identified based on responses collected during piloting). Participants were classified as 'not aware' when they were unable to report the presence of the prime during the initial questioning and also reported that they did not detect it after the manipulation was revealed. Participants were classified as 'aware of blank' when they were able to report its presence on some trials, but on further questioning, failed to report the presence of repetition primes. Finally, participants were classified 'aware of flickering' when they failed to report the manipulation, but reported that they had noticed a flicker on the screen once the manipulation had been revealed.

EEG recording and analysis

EEG was recorded from 62 scalp sites using silver/silver chloride electrodes mounted in a Quick-Cap (Neuromedical Supplies: www.neuro.com) in accordance with an extended version of Jasper's (1958) International 10/20 system. A further six electrodes were used, two positioned on the mastoids (M1, M2) to serve as a reference, two positioned on the outer canthi to the left and right of the eyes (HEOG) to monitor horizontal eye movements, and two positioned above and below the left eye (VEOG) to monitor eye blinks. All electrodes were referenced online to an additional electrode (REF) positioned midway between the Cz and CPz. Before beginning the experiment impedances at each electrode were brought to below 2 kΩ. Signals were recorded with a band pass filter of 0.01–40 Hz, and digitized at a rate of 250 Hz.

Neuroscan software (www.neuroscan.org) was used to record the EEG data (Acquire, version 4.5) and to analyse the data offline (Edit, version 4.3). For each participant the raw EEG data was inspected and segments were removed if they contained artifacts, voltage drift, and excessive muscle movement. The effect of eye blinks was reduced using the Neuroscan ocular artifact reduction procedure, using 32 blinks for each participant to remove the contribution of the average blink from all channels. The continuous EEG data were then separated into 2000 ms epochs, starting 100 ms before prime onset. Data was re-referenced offline to linked mastoids and the individual epochs were baseline corrected and smoothed over a 5-point kernel. Epochs were rejected when they contained eye movements (HEOG) larger than 100 μV or when drift from baseline exceeded ±75 μV in any of the channels.

To examine priming and memory effects grand average ERPs were formed for hits and correct rejections relative to target onset, separately for the unprimed and primed conditions. ERPs were quantified by measuring the mean amplitude over specific time windows of interest (with respect to the mean pre-stimulus baseline). For priming contrasts a latency period from 250–500 ms was chosen to be consistent with previous identifications of N400 priming effects in the literature. For memory contrasts, ERPs were initially quantified over the 300–500 ms and 500–800 ms latency intervals, to be consistent with previous identifications of mid-frontal and left-parietal old/new effects (see Rugg and Curran, 2007, for a review). The mean number of trials contributing to the waveforms for hits was 78 (S.D. = 23) for the primed condition and 78 (S.D. = 25) for the unprimed condition. The mean number of trials contributing to waveforms for correct rejections was 94 (S.D. = 17) for the primed condition and 93 (S.D. = 18) for the unprimed condition. Statistical comparisons were performed using repeated measures ANOVA and paired samples *t*-tests as required (significance level $p = 0.05$). The Greenhouse-Geisser correction for non-sphericity was employed, and corrected degrees of freedom are reported where necessary.

Results

Behavioral results

85% of participants reported being unaware of the existence of the masked prime, 6% detected flickering on the screen but were unable to detect any of the words, and the remaining 9% reported that they were aware of seeing the word blank appear before the onset of the target on a few trials, but none of the participants reported being aware of the repetition of the target words. Memory performance, R/K proportions and response times for each condition are shown in Table 1. Mean accuracy data were analysed using ANOVA with the factors of masked priming (unprimed, primed) and test status (old, new), which revealed a significant main effect of test status [$F(1,31) = 28.60$, $p < 0.001$, $\eta p^2 = 0.48$], reflecting higher accuracy overall for new words. Discrimination rates did not differ (unprimed $Pr = 0.68$, primed $Pr = 0.68$), and measures of response bias were equally conservative (unprimed $Br = 0.25$, primed $Br = 0.27$), confirming that masked priming did not influence measures of recognition performance. Although the R/K data reveal a small increase in the proportion of K responses for old words that were primed, statistical analysis of the data failed to reveal significant differences in the proportion of K responses, or corrected estimates of familiarity, as a function of masked priming.

Response time data clearly evidenced faster responses for primed hits and correct rejections, and the magnitude of priming was also larger overall for hits than for correct rejections. Analysis confirmed a significant main effect of masked priming [$F(1,31) = 71.52$, $p < 0.001$, $\eta p^2 = 0.69$], and a significant interaction between masked priming and test status [$F(1,31) = 20.46$, $p < 0.001$, $\eta p^2 = 0.39$]. Subsidiary analysis performed on the difference in response times between the unprimed and primed conditions confirmed that the magnitude of priming was larger for hits

Table 1
Behavioral results. A: Memory performance and the proportion of Remember/Know responses at test (S.E.). B: Response times for hits and correct rejections, and the magnitude of priming effects (S.E.). RT data demonstrates the presence of robust priming effects, which were larger in magnitude for hits. Measures of recognition performance and estimates of familiarity and recollection did not differ across conditions.

(A)	Old		New	
	Unprimed	Primed	Unprimed	Primed
Accuracy (%)	75.11 (3.33)	75.69 (3.14)	93.05 (1.29)	92.44 (1.30)
Remember	56.64 (4.17)	56.06 (4.10)	1.62 (0.48)	1.68 (0.58)
Know	18.48 (2.70)	19.62 (2.84)	5.33 (1.15)	5.88 (1.15)

(B)	Hits		CRs	
	Unprimed	Primed	Unprimed	Primed
RT (ms)	959.65 (26.78)	844.05 (32.72)	947.25 (31.39)	877.24 (33.45)
Priming	115.60 (12.41)		70.01 (11.73)	

than for correct rejections ($t(31) = 4.52$, $p < 0.001$, $d = 0.68$). Examination of response time data for correct responses in the initial old/new decision, subsequently rated as Remembered, suggested faster response times for the primed (mean = 855.79 ms, S.E. = 33.23 ms) than for the unprimed (mean = 969.64 ms, S.E. = 28.86 ms) condition. In addition, analysis confirmed that response times for words subsequently reported to be Remembered were significantly faster for primed words than for unprimed words ($t(31) = 8.24$, $p < 0.001$, $d = 0.66$). In sum, response time data demonstrated the presence of robust priming effects, but measures of recognition performance and process estimates did not differ as a function of priming.

ERPs

Priming effects

ERPs from the test phase were first analysed separately for hits and correct rejections to characterize priming effects, before comparing the magnitude and distribution of these priming effects. Fig. 2 shows grand average ERPs from a selection of representative sites, evidencing the presence of positivity for primed words during the 250–500 ms latency interval over centro-parietal sites, consistent with the timing and distribution of N400 effects. Critically, mapping onto the response time data, these N400-like effects appeared larger in magnitude for hits than for correct rejections.

ERP comparisons of N400 effects during the 250–500 ms latency interval were performed on two rings of eight electrodes surrounding CPz to adequately capture the distribution of effects (Greve et al., 2007). ANOVAs were initially performed separately for hits and correct rejections, including the factors of masked priming (unprimed, primed), ring (outer, inner) and site (FCz, FC4, CP4, PO6, POz, PO5, CP3, FC3, Cz, C2, CP2, P2, Pz, P1, CP1, C1). Analysis for hits revealed a significant effect of masked priming [$F(1,31) = 42.32$, $p < 0.001$, $\eta p^2 = 0.57$], a two-way interaction between masked priming and ring [$F(1,31) = 49.71$, $p < 0.001$, $\eta p^2 = 0.61$] and a three-way interaction between masked priming, ring and site [$F(2.79,86.75) = 10.20$, $p < 0.001$, $\eta p^2 = 0.24$]. Analysis for correct rejections also revealed a main effect of masked priming [$F(1,31) = 59.96$, $p < 0.001$, $\eta p^2 = 0.65$], a two-way interaction between masked priming and ring [$F(1,31) = 46.35$, $p < 0.001$, $\eta p^2 = 0.59$] and a three-way interaction between masked priming, ring and site [$F(4.40,136.37) = 11.31$, $p < 0.001$, $\eta p^2 = 0.26$]. As can be seen in Fig. 2, for both hits and correct rejections, the initial analyses confirm the presence of centrally distributed N400 priming effects with a focus over superior centro-parietal sites, maximal at electrode CPz.

The next level of analysis was performed on amplitude differences between primed and unprimed words to compare the pattern of N400 priming effects for hits and correct rejections. To investigate whether the hit and correct rejection effects exhibit differences in distribution, analysis employed data rescaled with the min/max procedure (McCarthy and Wood, 1985). Analysis were performed using ANOVA

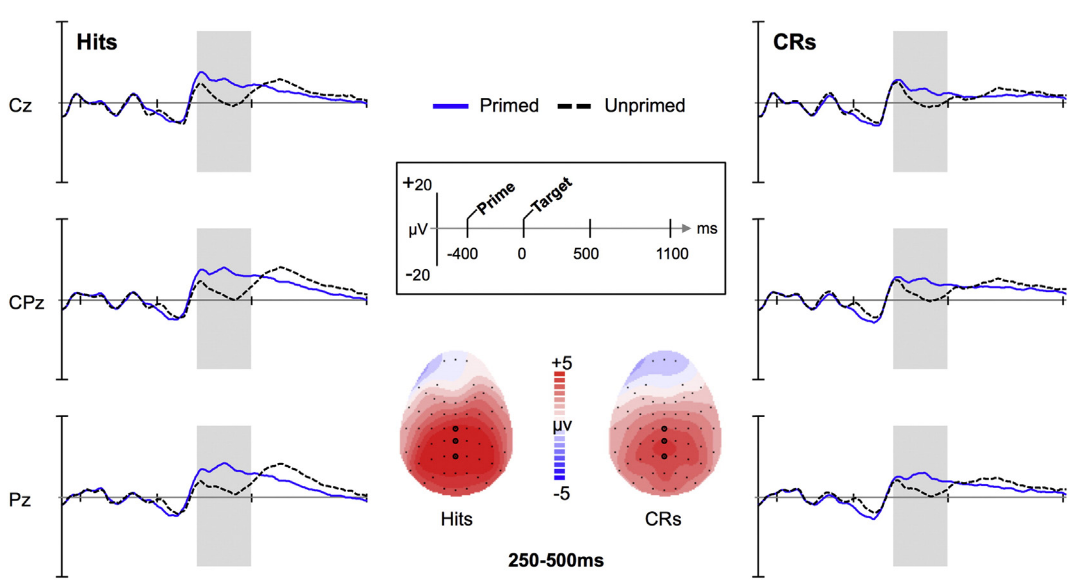

Fig. 2. Grand average ERPs for hits and correct rejections from representative electrode sites. Boxes highlight the latency interval of interest for N400 priming effects (250–500 ms). Topographic maps depict ERP differences between primed and unprimed trials for hits and correct rejections during the 250–500 ms latency interval.

with the factors of test status (old, new), ring (outer, inner) and site (FCz, FC4, CP4, PO6, POz, PO5, CP3, FC3, Cz, C2, CP2, P2, Pz, P1, CP1, C1), and revealed no main effect or interactions including the factor of test status, indicating that N400 effects for hits and correct rejections did not differ in distribution. Follow up analyses were then carried out to compare the magnitude of priming effects across conditions, using data from CPz. The priming effect was larger in size for hits (5.15 μV) than correct rejections (3.56 μV), a difference that was statistically reliable ($t(31) = 2.49$, $p < 0.05$, $d = 0.46$).

Memory effects

A second set of analyses was carried out to examine memory related ERP effects, investigated effects for the 300–500 ms and 500–800 ms latency intervals consistent with prior literature. Fig. 3 shows grand average ERPs elicited for correct responses during the test phase at electrode site P3, where left parietal old/new effects are maximal. As can be seen from the topographic distribution of effects shown in Fig. 3, early (300–500 ms) mid-frontal old/new differences (normally associated with familiarity, cf. Rugg and Yonelinas, 2003) were not present. More critically, waveforms for unprimed words were more positive going for hits than for correct rejections between 500–800 ms, with the greatest differences at left-parietal locations. By contrast, for primed words old/new differences with a left-parietal distribution were evident during 300–500 ms latency interval. As is clear from Fig. 3 the onset time of left-parietal old/new effects for unprimed and primed words differs, with waveforms for primed words diverging ~300 ms earlier. Given the pattern of effects, analysis focused solely on characterizing and comparing left-parietal old/new effects. Initial analysis was designed to identify variations in the pattern of old/new effects across conditions and time windows. ANOVA with the factors of masked priming (unprimed, primed), test status (old, new), hemisphere (left, right), site (inferior: P5, P6; medial: P3, P4; superior: P1, P2) and time window (300–500 ms, 500–800 ms), revealed a significant main effect of masked priming [$F(1,31) = 22.15$, $p < 0.001$, $\eta p^2 = 0.42$], and a five-way interaction between masked priming, test status, hemisphere, site and time window [$F(1.2,37.6) = 4.59$, $p = 0.032$, $\eta p^2 = 0.13$], evidencing changes in the pattern of parietal old/new effects over time as a function of priming.

Subsequent ANOVAs performed for primed and unprimed words within each time window included the factors of test status (old, new), hemisphere (left, right) and site (inferior: P5, P6; medial: P3, P4; superior: P1, P2). Analysis for unprimed words during the 300–500 ms interval revealed a main effect of test status [$F(1,31) = 4.52$, $p = 0.042$, $\eta p^2 = 0.12$], and a three-way interaction between test status, hemisphere and site [$F(1.16,36.19) = 6.95$, $p = 0.009$, $\eta p^2 = 0.18$], reflecting a slight positivity for hits extending from superior sites in the right hemisphere across sites in the left hemisphere. Analysis for primed words between 300–500 ms revealed a main effect of test status [$F(1,31) = 24.89$, $p < 0.001$, $\eta p^2 = 0.44$], and a two-way interaction between test status and hemisphere [$F(1,31) = 8.03$, $p = 0.008$, $\eta p^2 = 0.20$], confirming the presence of an old/new difference over the left hemisphere at parietal locations. The distribution of the old/new effects from 300–500 ms is shown in Fig. 3 (column A maps); while the effects seen for unprimed words are small and broadly distributed, a clear left parietal old/new effect is evidenced for the primed condition. To compare the magnitude of effects at left-parietal locations for primed and unprimed words, the next level of analysis was performed on subtraction data using activity averaged over three electrode sites (LP: P5, P3, P1). Results confirmed the presence of significantly larger effects over left-parietal sites for primed words during the 300–500 ms latency interval ($t(31) = 2.76$, $p = 0.01$, $d = 0.71$).

Analysis for unprimed words during the 500–800 ms interval revealed a main effect of test status [$F(1,31) = 39.91$, $p < 0.001$, $\eta p^2 = 0.56$] and a three-way interaction between test status, hemisphere and site [$F(1.4,42.8) = 7.03$, $p = 0.006$, $\eta p^2 = 0.19$], reflecting the presence of an old/new difference in the left hemisphere, with a maxima over mid electrode sites. Analysis for primed words during the 500–800 ms time window produced a significant main effect of test status [$F(1,31) = 9.86$, $p = 0.004$, $\eta p^2 = 0.24$] and a significant interaction between test status and electrode [$F(1.3,40.4) = 7.63$, $p = 0.005$, $\eta p^2 = 0.19$], reflecting more positive going activity for hits than for correct rejections at parietal locations, focused over mid and inferior electrodes. As can be seen in Fig. 3 (column B maps) a clear left parietal old/new effect is visible for the unprimed condition, which was not present in the earlier time window. By contrast, for the primed condition, the pattern of effects is consistent with the continuation of the left-parietal effect seen in the earlier time window. Comparing the magnitude of old/new effects at left-parietal sites revealed significantly larger effects for unprimed words during the 500–800 ms latency interval ($t(31) = 3.66$, $p = 0.001$, $d = 0.53$).

The next level of analysis was performed on amplitude differences between hits and correct rejections to compare the pattern of left-parietal old/new effects evident in 300–500 ms time window for primed words and the 500–800 ms time window for unprimed words. To look for differences in the distribution of effects, analysis was performed on rescaled data using ANOVA with the factors of time window (300–500 ms, 500–800 ms), location (frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital), hemisphere (left, right) and site

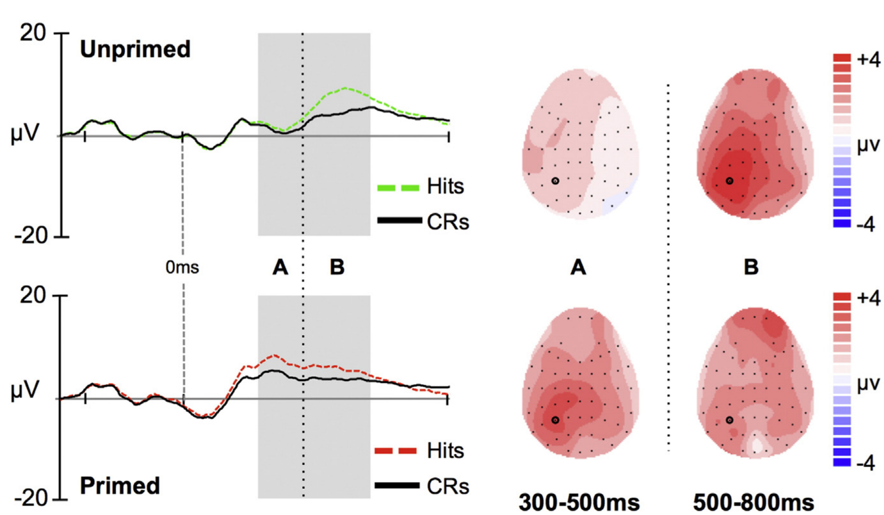

Fig. 3. Grand average ERPs for hits and correct rejections at electrode P3. Boxes highlight the latency intervals of interest for left-parietal old/new effects (A: 300–500 ms, B: 500–800 ms). Topographic maps depict ERP differences between hits and correct rejections for primed and unprimed trials between 300–500 ms and 500–800 ms.

(inferior, mid, superior). Results revealed no main effects or interactions including the factor of time window, indicating that early onsetting (300–500 ms) parietal old/new effect found for primed words did not differ in distribution from the later effect (500–800 ms) found for unprimed words. Overall, the foregoing pattern of results support a difference in the onset latency of left-parietal effects for unprimed and primed words, with effects for primed words apparent earlier.

The final level of analysis sought to more precisely quantify the onset time of left parietal-effects old/new effects for primed and unprimed words. Data were split into eight consecutive time bins starting from target onset (0–100 ms, 100–200 ms, 200–300 ms, 300–400 ms, 400–500 ms, 500–600 ms, 600–700 ms, 700–800 ms). Bonferonni corrected paired *t*-tests were performed on data from each bin, contrasting activity for hits and correct rejections, at electrode P3, for primed and unprimed words. The distribution of effects, and statistical outcomes, are shown in Fig. 4, highlighting the earlier onset of the left parietal old/new effect following priming. Results demonstrated a significant old/new difference for primed words onsetting between 100–200 ms of target onset ($t(31) = 3.02$, $p = 0.035$, $d = 0.31$), with differences for unprimed words only becoming evident 400 ms after target onset ($t(31) = 4.38$, $p < 0.001$, $d = 0.27$); in both cases, clear left parietal maxima are visible.

Discussion

The aim of the current experiment was to examine the relationship between priming and recollection. Two independent predictions were made concerning how priming could impact neural correlates of recollection. Firstly, following Gagnepain et al. (2011) priming might reduce the magnitude of old/new effects, indexing a reduction in the amount of cognitive resources engaged during retrieval. Secondly, following Woollams et al. (2008) repetition priming might produce observable changes in the timing of left-parietal old/new effects, speeding their onset. Here, to address these predictions, we used ERPs to measure the neural correlates of retrieval during a recognition memory task - including masked priming of half of the cues presented at test. Critically, the behavioral data demonstrated facilitation of response times for primed words, which was greater for hits than for correct rejections. Despite this strong evidence of the operation of priming at test, measures of accuracy, discrimination, bias, and process estimates of familiarity and recollection were unaffected by the priming manipulation. Mapping onto the RT data, however, N400-like priming-related ERP effects were evident over centro-parietal locations during the 250–500 ms latency interval and were larger in magnitude for studied than unstudied test items. Most importantly, memory contrasts demonstrated that priming influenced the left-parietal old/new effects associated with recollection, speeding their onset. In short, the findings confirmed the prediction derived from Woollams et al. (2008), providing evidence of a genuine change in the onset latency of recollection following priming.

In light of prior work demonstrating an increase in the proportion of recollection following priming (i.e., Taylor and Henson , 2012; Taylor et al., 2013), the absence of differences in behavioral measures of memory in the current study appears somewhat surprising, although not inconsistent with prior work using a similar methodology to the one reported here (i.e., Woollams et al., 2008). One key difference in design that could account for failure to find performance differences is the nature of the prime itself. For example, Taylor and Henson (2012) report an increase in the R responses for conceptual primes but no changes in recollection following repetition primes. By contrast, Higham and Vokey (2004) report an increase in illusory R responses for targets preceded by repetition primes. Taken together, findings from studies examining the relationship between priming and recollection suggest that the influence of priming on behavioral measures of recollection is highly material/context specific. As such the findings of the current study serve to highlight the importance of obtaining concurrent neural measures to elucidate interactions between priming and recollection.

Before discussing the theoretical implications of the current findings, we outline prior evidence that the timing of recollection is not inherently fixed - despite it typically being described as a slow form of retrieval. For example, De Chastelaine et al. (2009) found that parietal old/new effects decreased in latency over multiple study-test repetitions, moving into the time window for the FN400 (decreasing from 400 ms to 300 ms), and were associated with a matched increase in discrimination and reduction in reaction times across test repetitions. In another ERP study, Vilberg et al. (2006) reported an early onsetting left-parietal effect similar to the one found here, during a source memory task employing a modified R/K procedure, where participants were required to indicate whether visual objects were fully or partially recollected. Crucially, the authors found that full recollection of contextual information was associated with earlier onsetting left-parietal effects between 200–500 ms after stimulus onset. In a more recent study, Murray et al. (2015) linked early onsetting left parietal effects (300–500 ms) with high precision, using a novel source memory task that allowed the quantity and quality of retrieval to be examined independently. In short, all of the preceding studies associate superior recollection with changes in the onset of parietal old/new effects. In this context, the current data adds weight to the view that the timing of retrieval processing can vary: manipulating unconscious repetition priming selectively influences the onset and duration of recollection.

Priming can potentially facilitate processing at a number of stages, each of which could contribute to observed change in the timing of recollection related ERP old/new effects reported here. For example, faster visual (perceptual) or semantic (conceptual) processing could produce

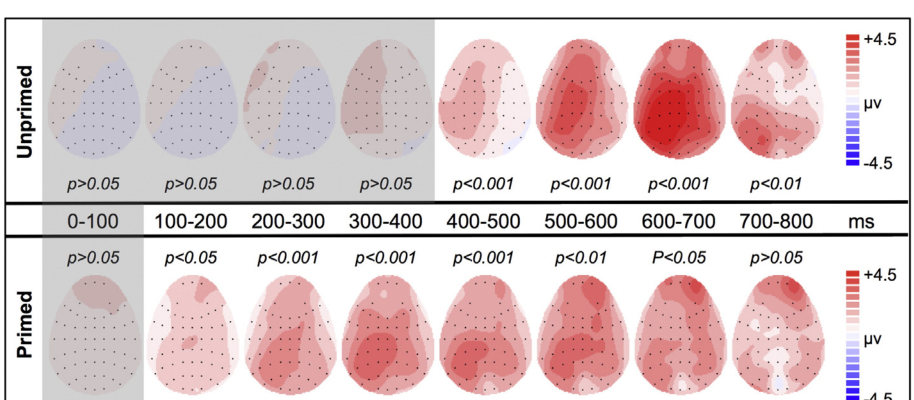

Fig. 4. Topographic maps depict the difference between the hits and correct rejections for both conditions from target onset (0 ms), split into the 100 ms time bins that were used to establish the onset time of left-parietal old/new effects across conditions. Statistical outcomes confirm the earlier onset of the left-parietal old/new effect following priming.

a reduction in the amount of time taken to access item information, leading to a reduction in the onset time of recollection. Similarly, Gagnepain et al. (2011) proposed that priming facilitates better encoding and results in an increase in recollection because it reduces the level of attentional resources tied up in processing item information. While this explanation was posited to explain changes in the magnitude of neural activation and behavioral indices of recollection following priming, faster processing of item information could also account for the current findings, leading to changes in the timing of neural signals. In the current data, N400-like effects for primed and unprimed words differed in magnitude but not in onset time, suggesting that the early onsetting recollection effect was not merely a result of knock-on facilitation from processing occurring earlier (i.e., downstream). Overall, therefore, the present data suggest that recollection onsets earlier following priming, but that this effect cannot be attributed simply to changes in the speed of initial processing or reading of test items that would allow for more rapid visual identification of the word itself.

The orthogonal nature of the analysis employed for priming and memory contrasts in the current study adds weight to the suggestion that semantic processing is not a necessary pre-cursor for recollection. For primed words the left-parietal old/new effect onset around 100 ms post-target in the memory contrast, while N400-like effects in the priming contrast were not evident until around 250 ms post-target. Theoretically, these findings suggest the need to reconceptualize how priming is characterized, including the nature of its influence on cognitive processing. Our view is that priming is not a process per se (i.e., that can be linked to a specific neural correlate), but is instead something that happens to processes (i.e., reflects a change in the operation of processes). By this view, priming can exert influence over a wide range of cognitive processes (e.g., at perceptual and conceptual stages), leading to different measurable changes in associated neural correlates, depending on what is being primed. This view sits at odds with traditional systems models of memory, where priming is seen as a form of procedural memory, analogous to recollection as a form of declarative memory (e.g., see Squire, 2004), adding weight to calls for alternative frameworks (e.g., see Henke, 2010).

While, our findings clearly demonstrate that priming directly influences recollection, the question remains of exactly how priming speeds the onset of retrieval, particularly as this appears not to be attributable to faster processing of item/semantic information, due to the later onset of N400 effects. One possibility is that priming results in test items crossing the threshold for retrieval more quickly (e.g., due to priming providing items with an elevated baseline). Currently, the precise nature of recollection itself remains a matter of debate (e.g., see Harlow and Donaldson, 2013; Slotnick et al., 2014; Wixted et al., 2010; Yonelinas et al., 2010), with all-or-none thresholded, continuous and combined descriptions of recollection all being proposed in the literature. Combined models of recollection would accommodate an activation account of the influence of priming on recollection, but the onset time of N400 effects and the lack of a difference in the magnitude of left-parietal effects in the current study appears to negate this explanation of the data. While most models consider recollection to be a univariate retrieval process responsible for retrieval of contextual details of prior episodes, it has recently been suggested that recollection is bivariate (Brainerd et al., 2014). In essence, these authors distinguish between target and context forms of recollection, providing a potential explanation for the timing changes reported here: while occurring concurrently under standard recognition testing, subcomponents of recollection could be differentially engaged following priming, resulting in the observed change in onset time across conditions.

Our view is that recollection is unlikely to reflect a unitary process, and the rise of models that fractionate recollection into subcomponents is inevitable. We are not entirely convinced, however, that item versus context distinctions reflect real divisions within memory. Assuming that the retrieval of item and contextual occurs separately, and contextual recollection takes longer than item recollection, this would suggest that LP effects in the current study for unprimed words index context recollection, while effects for primed words index pure item recollection. On this basis, repetition pushes items over the threshold for item recollection, which in the absence of contextual reconstruction, occurs earlier, potentially accounting for the difference in onset time found here. While theoretically possible, to our minds, it is not compelling to argue that a single neural correlate arbitrarily reflects different processes in this way. We are also unclear how a flexible memory system could distinguish between item and context information a priori - given that definitions reflect experiment specific control over stimuli (such that a single piece of information could be considered item or context, depending on how memory is tested).

More broadly, we highlight the fact that the idea of two forms of recollection is not entirely new. For example, Moscovitch (2008) proposed a two-stage model of recollection. By this account, the first stage is a rapid automatic retrieval process that occurs when a retrieval cue interacts with stored information, but its products are not accessible to consciousness. The second stage is more closely aligned with dual-process accounts of recollection, being slower and accessible to consciousness. Within this characterization of recollection, repetition primes in the current study acted as a proximal retrieval cue, engaging the first stage of recollection in the primed condition, while the unprimed condition relied on conscious recollection to bridge the temporal gap between study and test, resulting in the observed difference in onset time. While Moscovitch's model could be characterized as closer to the dual-process distinction between recollection and familiarity, than the dual-routes to recollection account of Brainerd et al., the ability of this kind of account to accommodate the current findings adds weight to the need for more sophisticated models of recollection.

What is clear from the preceding discussion is that the precise nature of recollection remains to be fully established. Proposals that recollection is multifaceted have had limited impact on the field to date, presumably due to difficulties inherent in isolating the operation of sub-types of recollection during recognition testing. Crucially, the two formulations of dual recollection outlined above differ on whether the products of retrieval are implicit or explicit. On the basis of the current study, whether implicit priming merely speeds the onset of recollection as traditionally conceived, or facilitates a specific sub-type of recollection that occurs more rapidly remains an open question. Equally, it remains unclear whether recollection is best fractionated in terms of distinctions between item versus context information (cf. Brainerd et al., 2014), proximal versus distal cueing (cf. Moscovitch, 2008), or quantity versus quality of retrieval (cf. Murray et al., 2015). Regardless, the current data clearly demonstrates that priming can directly influence recollection. Moreover, the findings highlight that gaining a better understanding of the influence of priming could play a critical role in elucidating the nature of recollection.

Conclusion

Here we aimed to investigate interactions between priming and recollection by employing ERPs to monitor neural markers of memory processing during recognition with masked priming of test cues. Overall, our findings clearly demonstrate that priming can influence the time at which neural signals of recollection will be observed, leading to faster retrieval processing. While early onsetting recollection effects have been reported previously, the exact nature of the early onsetting recollection effect reported here following priming remains an open question. Future work is required to establish whether these changes in recollection merely reflect a change in timing or also reflect changes in the quality, quantity or type of retrieval. The addition of an incidental source task or the introduction of context priming in the current design would help to differentiate between these options. Nonetheless, the current data contributes additional insights to a slowly growing literature demonstrating that priming does influence recollection, and underlines the importance of obtaining neural measures for further progress in understanding the complexities of recognition, and more importantly, the true nature of priming and recollection.

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