Benefits and Costs of Context Reinstatement in Episodic Memory: An ERP Study

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Abstract

■ This study investigated context-dependent episodic memory retrieval. An influential idea in the memory literature is that performance benefits when the retrieval context overlaps with the original encoding context. However, such memory facilitation may not be driven by the encoding–retrieval overlap per se but by the presence of diagnostic features in the reinstated context that discriminate the target episode from competing episodes. To test this prediction, the encoding–retrieval overlap and the diagnostic value of the context were manipulated in a novel associative recognition memory task. Participants were asked to memorize word pairs presented together with diagnostic (unique) and nondiagnostic (shared) background scenes. At test, participants recognized the word pairs in the presence and absence of the previously encoded contexts. Behavioral data show facilitated memory performance in the presence of the original context but, importantly, only when the context was diagnostic of the target episode. The electrophysiological data reveal an early anterior ERP encoding–retrieval overlap effect that tracks the cost associated with having nondiagnostic contexts present at retrieval, that is, shared by multiple previous episodes, and a later posterior encoding–retrieval overlap effect that reflects facilitated access to the target episode during retrieval in diagnostic contexts. Taken together, our results underscore the importance of the diagnostic value of the context and suggest that context-dependent episodic memory effects are multiple determined. ■

INTRODUCTION

Episodic memory enables mental time travel, allowing us to relive specific, personally experienced events tied in time and place (Tulving, 1983). This feat of human memory is considered to depend on the reinstatement of cortical processes that were active at the time of the previous event (e.g., Norman & O'Reilly, 2003; Marr, 1971). Accumulating evidence supports this notion by demonstrating that common neural systems are activated during perception and retrieval (see Rugg, Johnson, Park, & Uncapher, 2008, for a review). Given the ubiquitous nature of memory, a central goal within cognitive neuroscience is to unravel the factors that determine the accessibility of memories from our personal past. This study investigated the consequences of reinstating the encoding context at the time of retrieval and used electrophysiological recordings of brain activity to reveal the neural mechanisms associated with both benefits and costs of context reinstatement on episodic remembering.

Remembering occurs when retrieval cues interact with stored memory traces (Tulving, 1983), and the greater the overlap between the processing triggered by the cues during retrieval and the processing that took place during encoding, the greater the likelihood of successful retrieval (Tulving & Thomson, 1973; see also Morris, Bransford, & Franks, 1977). The importance of context encoding–retrieval (E–R) overlap has been underscored by a vast body of behavioral research that shows benefits in memory performance when the encoding and retrieval contexts overlap (see Smith & Vela, 2001; Roediger & Guynn, 1996, for reviews). The benefit of an E–R context overlap has been considered and explained in several theoretical models of episodic memory (e.g., Polyn & Kahana, 2008; Murnane, Phelps, & Malmberg, 1999) and represents a fundamental tenet in the memory literature.

Nevertheless, recent behavioral studies have shown that an E–R overlap can also be detrimental to memory performance (Goh & Lu, 2012; Poirier et al., 2012). These apparently counterintuitive findings may be explained by considering the diagnostic value of the retrieval cue (Nairne, 2002). Accordingly, memory retrieval may be considered a discrimination problem, and the effectiveness of a retrieval cue is relative to its ability to identify a single target memory as opposed to reactivate multiple memories. Closely related to this memory-as-discrimination idea, proposed by Nairne (2002), is the cue overload effect (Watkins & Watkins, 1975), also known as the fan effect (Anderson, 1974). The principle behind these effects is that the retrieval of a particular memory becomes less likely the more overloaded the cue is with other retrieval candidates (the greater the size of that cue's fan). Consequently, an E–R context overlap should only improve memory performance if there are diagnostic features in the context that help to discriminate the sought-after target memory from currently irrelevant memories. Previous

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behavioral studies, typically using word-list paradigms with task-relevant cues, have shown that the E–R overlap per se does not improve memory performance and may even carry detrimental effects when the retrieval cue is overloaded, that is, nondiagnostic (Goh & Lu, 2012; Poirier et al., 2012). However, it remains unclear the extent to which such findings with task-relevant retrieval cues correspond to the incidental environmental context effects observed in human episodic memory (e.g., Smith & Vela, 2001). In fact, studies using more task-irrelevant contextual cues have observed benefits of an E–R overlap even when the context is not diagnostic of the target episode (e.g., Smith & Manzano, 2010; Hockley, 2008).

In this study, we investigated the interaction between E–R overlap and the diagnostic value of the context using task-irrelevant contextual cues, promoting an incidental encoding of the context. ERPs measured during memory retrieval were used to disentangle the neural mechanisms underlying the benefits and costs of reinstating a diagnostic context versus a nondiagnostic context during memory retrieval. To the best of our knowledge, this is the first study to employ neuroimaging techniques to examine the consequences of an E–R overlap as a function of the contexts' diagnostic value.

The context-dependent nature of human episodic memory was first highlighted in the seminal study of Godden and Baddeley (1975), where it was shown that reinstating the encoding context at retrieval is beneficial for remembering. This idea has recently been corroborated by neuroimaging studies showing that brain oscillatory activity is strongly dependent of the encoding and retrieval context conditions (e.g., Staudigl, Vollmar, Noachtar, & Hanslmayr, 2015; Manning, Polyn, Baltuch, Litt, & Kahana, 2011; Summerfield & Mangels, 2005). During encoding, items and contexts are bound together, via medial temporal lobe regions (e.g., Horner et al., 2012; Staresina, Henson, Kriegeskorte, & Alink, 2012), and the reinstatement of the initial context improves memory retrieval (e.g., Jafarpour, Fuentemilla, Horner, Penny, & Duzel, 2014) by providing an effective route to remembering. However, successful memory retrieval is not only about accessing the target trace; it is also about rejecting incorrect ones. Thus, if the context is overloaded (i.e., not diagnostic of a particular episode), memory retrieval may be challenged by an interference from the reactivation of competing retrieval candidates. Recent memory research, using electrophysiological recordings of brain activity in episodic memory tasks where a cue is associated with multiple retrieval candidates, has reported EEG signatures of such retrieval competition and ensuing interference resolution (Hellerstedt & Johansson, 2014; Staudigl, Hanslmayr, & Bäuml, 2010).

Participants in our study were asked to memorize word pairs superimposed on a visual scene representative of a given context. Half of the word pairs were presented together with a unique context (diagnostic condition), and the remaining half was presented with a nonunique, shared context (nondiagnostic condition). An ensuing associative recognition memory test was employed to assess memory performance for the word pairs in the presence (E–R overlap) and absence (E–R nonoverlap) of the previously encoded contexts. Cueing participants with the encoded contexts increases the similarity between encoding and retrieval conditions. Therefore, according to the E–R overlap principle, participants are expected to be more efficient in remembering the word pair when the encoding context is present at retrieval. On the other hand, the memory-as-discrimination framework predicts that memory facilitation is limited to contextual retrieval cues that are diagnostic of the particular target event, that is, the unique contexts. Cueing participants with nondiagnostic contexts rather increases the likelihood that irrelevant memories, encoded in episodes that share the context, become activated. This reduces discriminability and leads to more interference and, consequently, to less efficient retrieval of the target word pair. Thus, memory for word pairs encoded together with nondiagnostic contexts is expected to suffer when the nondiagnostic context is presented at retrieval, despite a perfect overlap in context between encoding and retrieval.

Importantly, we used a sequential cue presentation paradigm (Figure 1) to temporally separate the neural correlates of memory reactivation triggered by the context from memory reactivated by the word and probe cues. This allowed us to directly test the prediction that cueing participants with a nondiagnostic context reactivates multiple currently irrelevant memory traces, previously encoded with that context, leading to retrieval competition. Competition-sensitive ERP correlates have recently been reported and are represented in reduced negativity over the frontal channels that starts 300 msec after stimulus onset (Hellerstedt & Johansson, 2014). This early frontal effect reflects the automatic reactivation of memories associated with and triggered by the presented retrieval cue. The memory-as-discrimination framework consequently predicts a larger E–R overlap effect over the frontal sites for the nondiagnostic condition compared with the diagnostic condition during the context presentation. Because the nondiagnostic contexts are more frequently presented during study, the participant's familiarity for these visual scenes is increased compared with that for the diagnostic ones. Familiarity is often associated with an early (200–500 msec) frontal old/new effect (for a review, see Wilding & Ranganath, 2011; Rugg & Curran, 2007) and is typically described as the feeling of having encountered an item before, without a reinstatement of episodic details specifying the previous encounter. An increased familiarity signal is a corollary feature of a nondiagnostic context. Thus, we expect an early frontal reduced negativity for the nondiagnostic ERPs also because of an increased familiarity with these visual scenes. Crucially, however, a mere increase in context familiarity should have no detrimental effect on memory accuracy for the associated information. Only retrieval competition

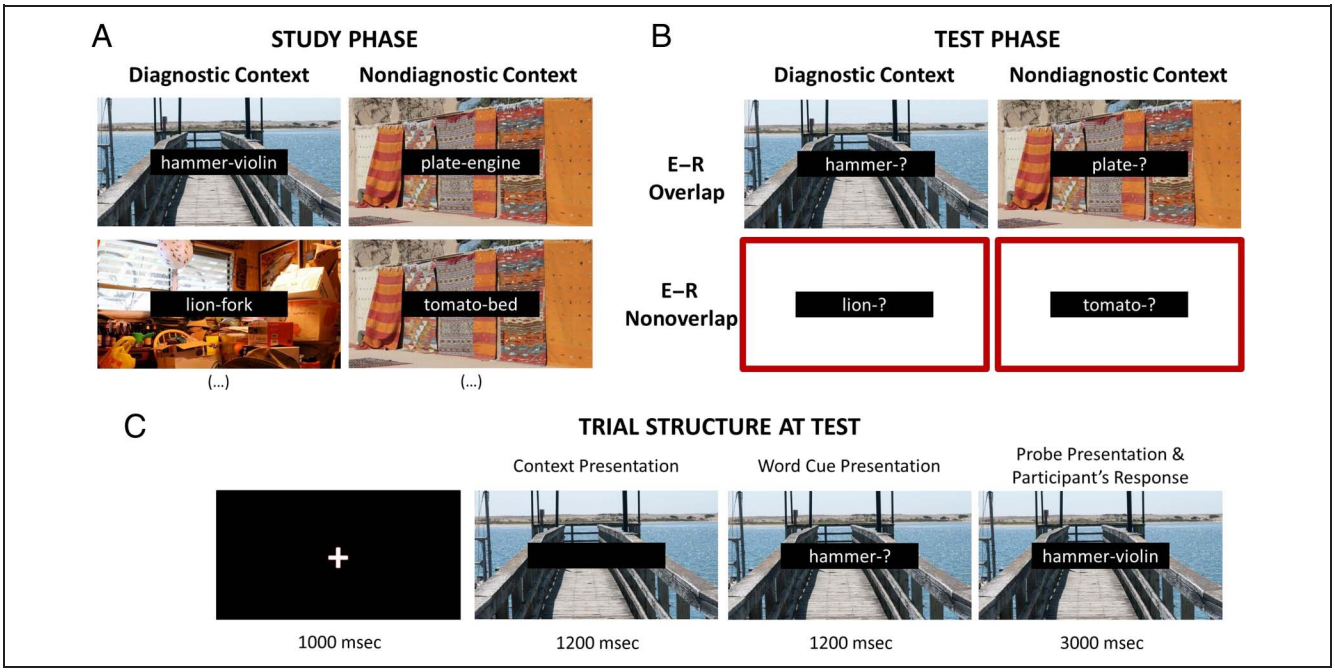

Figure 1. (A) In the study phase, word pairs were presented superimposed on a unique (diagnostic context) or shared (nondiagnostic context) visual scene. (B) In the test phase, the word pairs were presented in the presence (E–R overlap) or absence (E–R nonoverlap) of the encoded context, resulting in four different experimental conditions. (C) Schematic illustration of the trial structure at test. An associative recognition memory test was employed. The context (or a white frame) was presented followed by the word cue. Next, the complete word pair was presented, and participants were asked to respond if the word pair was intact or rearranged compared with the study phase.

should lead to a memory disadvantage of having a familiar nondiagnostic context presented at retrieval. We thus expected a reliable relationship between the early frontal ERP effect, sensitive to memory interference, and the mnemonic costs of retrieving in nondiagnostic contexts.

In addition, we examined induced theta power activity during the presentation of the context. Previous studies investigating brain oscillatory activity in retrieval competition paradigms have systematically found an increased theta power (4–7 Hz) in the high competition conditions, with an anterior distribution and early onset (~180 msec; Waldhauser, Johansson, & Hanslmayr, 2012; Hanslmayr, Staudigl, Aslan, & Bäuml, 2010; Staudigl et al., 2010). Accordingly, the memory-as-discrimination account predicts increased theta power activity for the nondiagnostic contexts compared with the diagnostic contexts where less interference is expected.

During the word cue and the probe time windows, we tracked the ERP correlates of target memory retrieval. The presentation of the word cue followed by the presentation of the probe will gradually specify the memory trace to be retrieved. Episodic memory accessibility has previously and consistently been associated with more positive-going ERP modulation for conditions where memory accessibility is increased (e.g., Wilding & Ranganath, 2011; Rugg & Curran, 2007; Rugg, Fletcher, et al., 1998; Rugg, Mark, et al., 1998; Allan & Rugg, 1997). More specifically, the ERP correlate of recollection, signaling associative memory retrieval of a particular word pair, is expected to be observed during these late time windows. Recollection involves the retrieval of the episodic details associated with the previously experienced event and is reflected, in the recognition memory literature, in a late (500–800 msec) left parietal old/new effect (for a review, see Wilding & Ranganath, 2011; Rugg & Curran, 2007). Therefore, we expected to observe late increased positive-going ERP amplitudes for E–R overlap compared with E–R nonoverlap, indicating facilitated access to the target memory when the context is re-presented at test. Crucially, following the memory-as-discrimination account, this E–R overlap effect should be more pronounced in the diagnostic contexts compared with the nondiagnostic contexts.

METHODS

Participants

Twenty-five students participated in exchange for a movie ticket (16 women; mean age = 23 years, range = 18–30 years). All participants were right-handed, native Swedish speakers with normal or corrected-to-normal vision and reported no history of neurological disease. The study was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki), and participants gave their written informed consent before taking part.

Stimulus Material

One-hundred sixty-nine color photographs, representative of different contexts (e.g., cities, landscapes, and street

views), were used in the experiment. A pool of 624 concrete nouns was selected from a comprehensive Swedish-language corpus (Borin, Forsberg, & Roxendal, 2012). The nouns were divided into four lists of 156 words each, ensuring that they were matched for frequency and length ($F < 0.3$, $p > .8$). Each word list was assigned to a different experimental condition and was subsequently divided into two smaller lists of 78 words each. Each of these two lists was assigned to either the first or second word of the word pair. To ensure that performance differences between conditions were not due to stimulus material, the assignment of the final eight word lists to experimental conditions was counterbalanced across participants.

Procedures

The experiment was composed of 13 blocks, each with a study phase, a distractor task, and a test phase. In the study phase, participants were presented with 24 word pairs and were asked to memorize them. Half of the word pairs were presented with a unique picture (diagnostic context), and the remaining half were presented with a shared picture (nondiagnostic context; Figure 1). In the study phase, each trial started with the presentation of a fixation cross for 1000 msec, followed by the presentation of the context picture for 2000 msec. Next, a word pair was displayed superimposed on the picture and remained on the screen for 3000 msec. After a counting-backward distractor task (performed during 1.5 min), an associative recognition memory test was administered. Memory retrieval for the word pairs was tested in the presence (E–R overlap) and absence (E–R nonoverlap) of the encoding contexts (Figure 1). Each test run was composed of 24 trials: 12 trials where intact word pairs (target) were presented and 12 where rearranged word pairs were presented (nontarget). The rearranged word pairs were created by switching the second word of the pair, ensuring that the switched words were from a word pair belonging to the same experimental condition. In the test phase, each trial started with a fixation cross presented for 1000 msec, followed by the presentation of the context picture or a white frame. After 1200 msec, the word cue (the first word of the pair) was presented superimposed on the picture (to keep the E–R overlap as close as possible). The second word of the pair (probe) was presented after 1200 msec. The whole word pair remained on the screen for 3000 msec. Participants were required to respond as quickly and accurately as possible if the word pair was intact or rearranged compared with the study phase (left and right index fingers; mapping counterbalanced across participants).

EEG Recording

The EEG was recorded continuously using a Neuroscan (Compumedics, El Paso, TX) NuAmps amplifier (1000-Hz sampling rate; left mastoid reference) from 30 Ag–AgCl scalp electrodes mounted in an elastic cap and positioned according to the extended 10–20 system. The montage included four midline electrode sites (Fz, Cz, Pz, and Iz) and 13 sites over each hemisphere (FP1/FP2, F7/F8, F3/F4, FC5/FC6, FC1/FC2, T7/T8, C3/C4, CP5/CP6, CP1/CP2, P7/P8, P3/P4, PO9/PO10, and O1/O2). Additional electrodes were used as ground (AFz) reference sites and for recording the EOG. EOG electrodes were placed above and below the left eye and at the left and right outer canthi.

EEG Data Analysis

The EEG data were analyzed using FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). Offline, the EEG data were high-pass filtered at 0.1 Hz and downsampled to 500 Hz. Bipolar EOG was computed using the electrodes placed horizontally and vertically around the eyes. The continuously recorded data were divided into epochs of 4.1 sec each, ranging from 500 msec before context presentation and 1200 msec after probe presentation. EEG epochs were visually inspected, and those containing muscle or other artifacts, not related to blinks and horizontal eye movements, were manually removed. Independent component analysis was computed, and components representing blink and other oculomotor artifacts that could be clearly distinguished from EEG were subtracted from the data. Before averaging, epochs associated with incorrect behavioral responses were also removed. According to the memory-as-discrimination account, diagnostic contexts should give rise to facilitated memory accessibility, which should be evident when both accepting targets and rejecting nontargets. A preliminary ERP analysis confirmed that this indeed was the case and showed no additional interactions involving the test probe, which was true also for the RT data. Thus, the reported ERP analysis was performed collapsed across test probe: target (intact word pairs) and nontarget (rearranged word pairs) epochs. An average of 68 trials (86%) for the diagnostic context (E–R overlap = 69 [range = 50–77] trials, E–R nonoverlap = 67 [range = 50–77] trials) and 67 trials (85%) for the nondiagnostic context (E–R overlap = 65 [range = 52–75] trials, E–R nonoverlap = 69 [range = 60–76] trials) remained for the final analysis.

For ERP analysis, two different epochs were created: (1) an epoch corresponding to the context and word cue presentation, with a length of 2600 msec, which started 200 msec before context presentation and ended 1200 msec after word cue presentation, and (2) an epoch corresponding to the probe presentation and participant's response, with a length of 1400 msec, which started 200 msec before probe presentation and ended 1200 msec after stimulus presentation. All epochs were filtered using a low-pass filter of 30 Hz and transformed to a linked-mastoid reference. The 200 msec before the stimulus onset served as the baseline for the amplitude measurement for each channel. Separate ERP averages were calculated for each epoch and experimental condition. The time–frequency

analysis was performed using a complex Morlet wavelet transform as implemented in FieldTrip. Conceptually, a Morlet wavelet transformation is related to a windowed short-term Fourier transformation. By applying the wavelet transform to successive intervals of EEG data, both temporal and spectral information can be extracted from the signal. Time–frequency was computed for frequencies ranging from 1 to 20 Hz, with a frequency step of 1 Hz, a time step of 0.01 sec, and a wavelet width of 5 cycles. This procedure was performed on the unfiltered data ranging from 1000 msec before context presentation until 1500 msec after context presentation. After Morlet wavelet decomposition was performed, oscillatory power, defined as the square of the modulus of the resulting complex number, was averaged separately for each experimental condition, and the power estimates for each time point were log transformed.

The statistical analyses of the E–R overlap effect (E–R overlap vs. E–R nonoverlap) for the diagnostic and nondiagnostic contexts were conducted using a nonparametric cluster-based permutation test implemented in FieldTrip (Maris & Oostenveld, 2007). In a first step, a dependent-sample t test was performed to compare the conditions (E–R overlap and E–R nonoverlap) at every data sample, and the data samples that reached statistical significance of .05 were identified. All adjacent data samples (either spatial or temporal neighbors) were then grouped into clusters, and the t values within each cluster were summed and used to generate a cluster-level t value. The Type 1 error rate for the complete spatiotemporal data matrix was controlled by evaluating the cluster-level test statistic under the randomization null distribution of the maximum cluster-level test statistic. This was obtained by randomizing the data between conditions within every participant. By creating a reference distribution from 4000 random draws, the p value was estimated according to the proportion of the randomization null distribution exceeding the observed maximum cluster-level test statistic (the so-called Monte Carlo p value). In this way, significant clusters extending over time and over electrodes can be identified, providing a measure of both the timing and distribution of the effect.

To assess the relationship between the ERP effects and the behavioral performance, we correlated the magnitude of each participant's ERP effect with the behavioral benefit/cost of having a context re-presented at test in terms of discrimination memory accuracy (PR = hits − false alarms) and RTs of the correct responses. For each participant, we subtracted the PR obtained in the E–R nonoverlap from the one obtained in the E–R overlap, for both the diagnostic and nondiagnostic contexts. The opposite was done for the RTs of the correct responses: The average RT obtained in the E–R overlap was subtracted from the one obtained in the E–R nonoverlap. In this way, we obtained an index of the behavioral impact of having the context presented at test, where positive values always indicate a benefit and negative values indicate a cost of the context. These measures where then correlated with the E–R overlap ERP effect observed for the diagnostic and nondiagnostic contexts. The participant's E–R overlap ERP effect was calculated as the average differences in amplitude, between the E–R overlap and the E–R nonoverlap conditions, across electrodes that reached significance in the cluster-based permutation test. For the context time window, the participant's E–R overlap ERP effect was calculated for the interaction, as this represents the effect of interest, that is, as the average differences in the amplitude of the E–R overlap effect between diagnostic and nondiagnostic contexts. Nonparametric Spearman correlations were calculated.

RESULTS

Behavioral Results

Average memory performance is presented in Tables 1 and 2. A measure of discrimination memory accuracy (PR = hits − false alarms) and response bias [BR = false alarms / (1 − PR)] was calculated for each experimental condition and participant (Snodgrass & Corwin, 1988). RTs were quantified as the time between the presentation of the second word of the pair (probe) and the onset of the participant's response. Correct RTs were individually normalized within a mean of 0 and an *SD* of 1, providing z scores. A median z-normalized RT was extracted for each condition and participant. To explore if memory performance varied according to the diagnostic value of the context and the E–R overlap, a repeated-measures ANOVA, including the factors E–R overlap (overlap vs. nonoverlap)

Table 1. Average (*SD*) Memory Performance Rates for Hits, False Alarms, PR, and BR for Each Experimental Condition

	Diagnostic Context		*Nondiagnostic Context*	
	E–R Overlap	*E–R Nonoverlap*	*E–R Overlap*	*E–R Nonoverlap*
Hits	0.88 (0.11)	0.86 (0.11)	0.85 (0.10)	0.87 (0.09)
False alarms	0.06 (0.08)	0.09 (0.08)	0.09 (0.07)	0.08 (0.06)
PR	0.82 (0.17)	0.78 (0.17)	0.76 (0.16)	0.79 (0.12)
BR	0.33 (0.29)	0.33 (0.27)	0.35 (0.22)	0.39 (0.21)

Table 2. Average (*SD*) Median RT for Each Experimental Condition

	Diagnostic Context		*Nondiagnostic Context*	
	E–R Overlap	*E–R Nonoverlap*	*E–R Overlap*	*E–R Nonoverlap*
Target	930 (225)	949 (198)	918 (203)	948 (231)
Nontarget	999 (249)	1039 (220)	1098 (252)	1033 (240)

and Context diagnosticity (diagnostic vs. nondiagnostic contexts), was performed for PR and BR. For the RT analysis, Test probe (target vs. nontarget word pairs) was also included as a factor in the repeated-measures ANOVA.

In terms of PR, no significant main effects of E–R overlap and Context diagnosticity were observed ($F < 1.3$, $p > .3$). Critically, however, the two-way interaction was significant ($F(1, 24) = 7.9$, $p = .01$, $\eta_p^2 = 0.25$; see Figure 2). Planned pairwise comparisons showed that memory discrimination increased in the E–R overlap compared with the nonoverlap condition ($F(1, 24) = 4.6$, $p = .04$, $\eta_p^2 = 0.16$) for word pairs encoded in diagnostic contexts. On the other hand, for word pairs encoded in nondiagnostic contexts, memory discrimination tended to decrease as a function of the E–R overlap ($F(1, 24) = 3.4$, $p = .08$, $\eta_p^2 = 0.13$). In addition, memory discrimination was greater for word pairs encoded in diagnostic compared with nondiagnostic contexts, but only when the E–R overlapped ($F(1, 24) = 5.2$, $p = .03$, $\eta_p^2 = 0.18$). When the E–R did not overlap, memory discrimination for word pairs encoded in diagnostic and nondiagnostic contexts was comparable ($F(1, 24) = 0.9$, $p = .3$). For the BR, there were no significant effects observed ($Fs < 1.8$, $ps > .2$).

The RT analysis revealed a significant main effect of Context diagnosticity ($F(1, 24) = 8.4$, $p = .007$, $\eta_p^2 = 0.26$)—participants were faster responding to word pairs encoded in diagnostic compared with nondiagnostic contexts. The main effect of E–R overlap was not significant ($F(1, 24) = 0.7$, $p = .4$). In addition, the main effect of Test probe was significant ($F(1, 24) = 22.3$, $p < .001$, $\eta_p^2 = 0.48$)—participants were faster responding to targets compared with nontargets. Again, the two-way interaction between E–R overlap and Context diagnosticity was significant ($F(1, 24) = 9.0$, $p = .006$, $\eta_p^2 = 0.27$; see Figure 2). Planned pairwise comparisons showed faster recognition times in the E–R overlap compared with the nonoverlap condition for word pairs encoded in diagnostic contexts ($F(1, 24) = 4.4$, $p = .05$, $\eta_p^2 = 0.16$) but not for word pairs encoded in nondiagnostic contexts ($F(1, 24) = 1.3$, $p = .3$). In addition, when the E–R overlapped, participants were faster responding to word pairs presented with diagnostic contexts compared with word pairs presented with nondiagnostic contexts ($F(1, 24) = 18.2$, $p < .001$, $\eta_p^2 = 0.43$). On the other hand, if the E–R did not overlap, participants responded equally fast to word pairs encoded with diagnostic and nondiagnostic contexts ($F(1, 24) < 0.1$, $p = .9$). All the other interactions were not significant ($Fs < 0.3$, $ps > .5$).

In summary, both accuracy and RTs reveal facilitated access to episodic memory after a contextual overlap between encoding and retrieval, but importantly, such benefits are only observed for contexts that are diagnostic of the target episode. We next turn to the electrophysiological data to elucidate the potential neural processes mediating these influences of context on episodic remembering.

Electrophysiological Results

Figure 3 shows the ERP waveforms at representative electrodes for the context and word cue epoch (Figure 3A) and for the probe and response epoch (Figure 3B). During the context time window, there is an increased negativity over the frontal and central channels for the E–R overlap compared with the nonoverlap condition, which starts

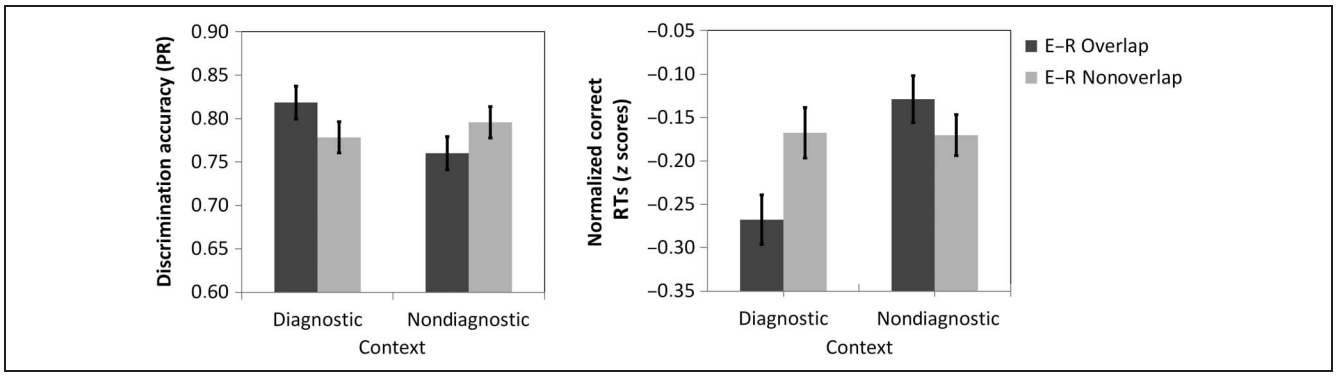

Figure 2. Two-way interaction between Context diagnosticity and E–R overlap for PR and correct RTs. Error bars represent *SEM*.

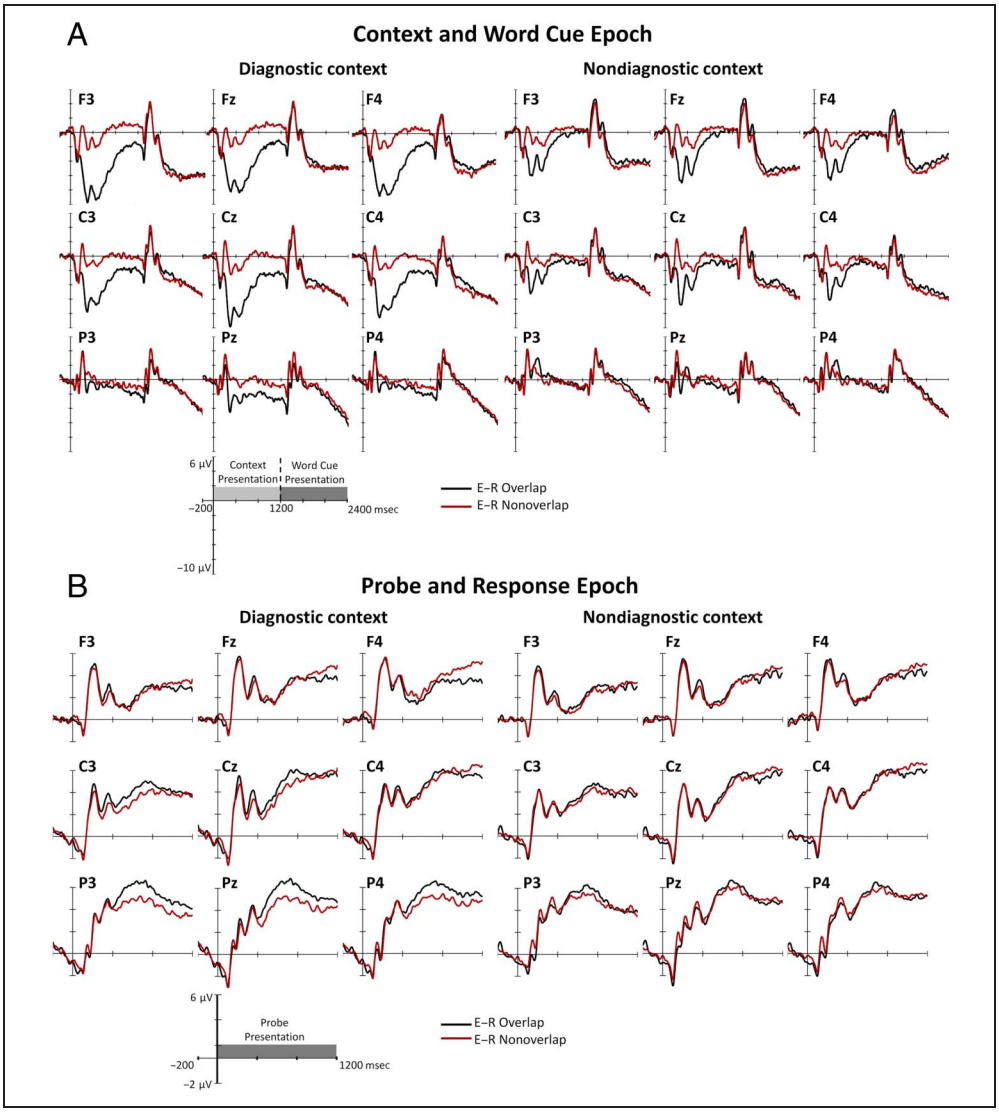

Figure 3. Average ERP waveforms from representative electrodes for the diagnostic and nondiagnostic contexts for the (A) context and word cue epoch and (B) probe and response epoch. The trial structure is highlighted in grayscale.

at an early onset after context presentation (~200 msec). As predicted, this difference is more pronounced for the diagnostic than for the nondiagnostic contexts. At the time of word cue presentation, E–R overlap, compared with the nonoverlap, is associated with reduced negative amplitudes over the frontal and central sites. This difference is evident for both the diagnostic and nondiagnostic contexts and starts around 300 msec after word cue presentation (Figure 3A). Finally, during the probe and response time window, we observe increased positive-going amplitudes over the central and posterior channels for the E–R overlap compared with the nonoverlap condition, starting around 300 msec after probe onset and larger for the diagnostic contexts (Figure 3B).

In summary, both the early anterior and late posterior E–R overlap effects are observed and appear to be modulated by our experimental manipulations according to our predictions. We next turn to the statistical qualification of these findings. To investigate if the E–R overlap differences are modulated by the diagnostic value of the context, a cluster-based permutation procedure was used to test the E–R overlap effect (overlap vs. nonoverlap) in the diagnostic and nondiagnostic contexts in three different time windows: (1) context time window (200–1000 msec), (2) word cue time window (300–1000 msec), and (3) probe and response time window (300–1000 msec).

Context Time Window

In the context time window, the cluster-based permutation test revealed a significant negative E–R overlap effect, comprising frontal and central channels, from 250 to 1000 msec after context presentation, for both the diagnostic ($p < .001$) and nondiagnostic ($p = .001$) contexts. To compare the effects, a statistical comparison between the E–R overlap effects for the diagnostic and nondiagnostic contexts was performed. Importantly, the cluster-based permutation test revealed a significant negative-going effect, comprising frontal and central channels, from 250 to 1000 msec after context presentation ($p < .001$; Figure 4A).

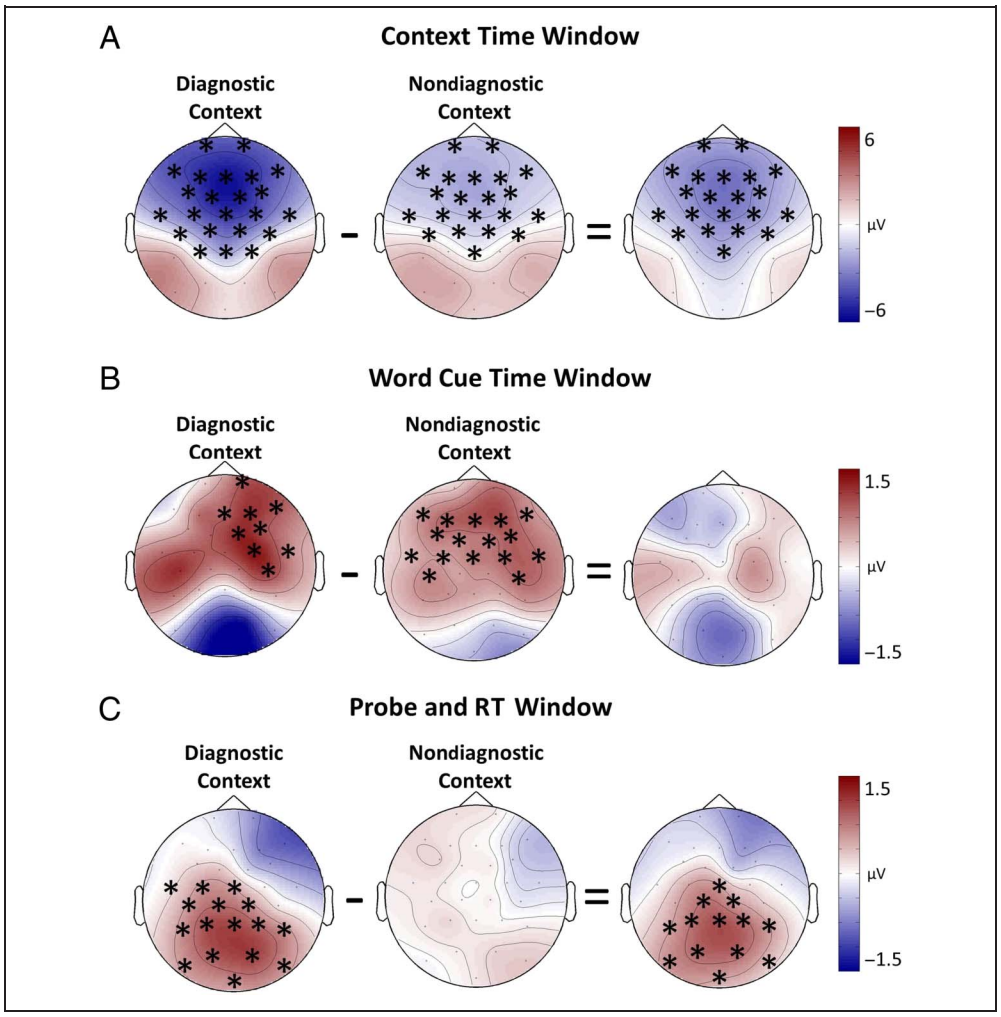

Figure 4. Topographic distribution of the ERP E–R overlap effects (E–R overlap vs. E–R nonoverlap) for the diagnostic and nondiagnostic contexts and for the difference between them. Electrodes that reached significance in the cluster-based permutation test are highlighted (*). Topographies are shown for the time windows in which the cluster-based permutation test identified statistical effects. (A) Context time window (250–1000 msec after context onset). (B) Word cue time window (300–600 msec after word cue onset). (C) Probe and response time window (440–1000 msec after probe onset).

This interaction effect indicates that, when the E–R overlapped, the ERPs associated with the nondiagnostic contexts exhibit an attenuated fronto-central negativity compared with the ERPs associated with the diagnostic contexts. Crucially, this ERP effect was associated with the mnemonic costs of having a nondiagnostic context presented at test in terms of PR ($r = -.45, p = .02$; Figure 5A). This result is consistent with the idea that the early anterior E–R overlap effect cannot merely reflect familiarity but also retrieval competition resulting from the reactivation of multiple associates encoded within the shared nondiagnostic context.

To further substantiate the claim that nondiagnostic contexts reactivate the memory traces previously associated with them, we conducted a time–frequency analysis in the context time window. Previous studies have reported

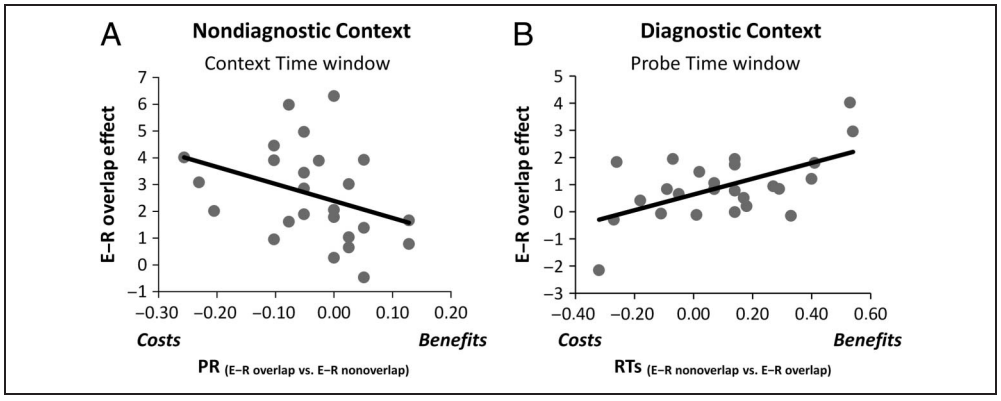

Figure 5. Relationships between the size of the E–R overlap effects (vertical axis) and the behavioral impact of having a context presented at test, where positive values indicate a benefit and negative values indicate a cost of the context (horizontal axis). (A) Relationship shown for the nondiagnostic contexts in terms of discrimination accuracy (PR). (B) Relationship shown for the diagnostic contexts in terms of RTs of the correct responses.

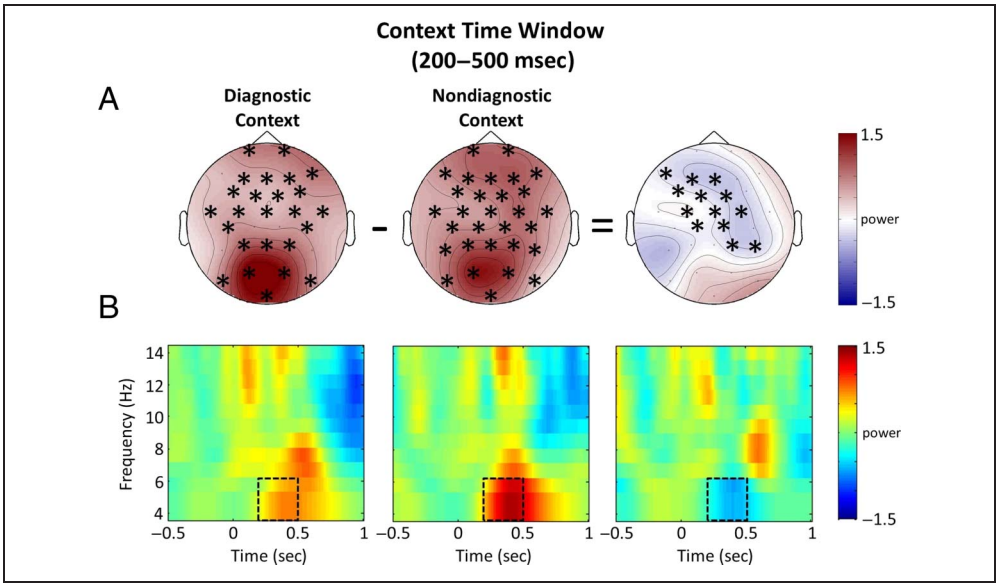

Figure 6. (A) Topography and significant clusters of the increased theta power (4–6 Hz) effect found between 200 and 500 msec after context presentation for the diagnostic and nondiagnostic contexts and for the difference between them. Electrodes that reached significance in the cluster-based permutation test are highlighted (*). (B) Time–frequency spectrograms for a representative channel (Fz) for the diagnostic and nondiagnostic contexts and for the difference between them.

an increased theta power with an anterior distribution in an early time window related with memory interference (Waldhauser et al., 2012; Hanslmayr et al., 2010; Staudigl et al., 2010).

To see if the reinstatement of a nondiagnostic context was associated with increased theta power, a cluster-based analysis that compared the spectral power (4–6 Hz) between the E–R overlap and nonoverlap conditions was performed, for both the diagnostic and nondiagnostic contexts, in an early time window (100–500 msec). The E–R overlap effect was reflected in an increased theta power in both the diagnostic ($p < .001$) and nondiagnostic ($p < .001$) conditions (see Figure 6). Next, a cluster-based permutation test was conducted to investigate the interaction effect and revealed, as predicted, a relatively greater theta power increase in the nondiagnostic context over fronto-central channels ($p = .02$; Figure 6). However, no correlations between the theta power effect and the mnemonic benefits/costs of the context were observed.

Word Cue Time Window

In the word cue time window, a significant positive E–R overlap effect was found for both the diagnostic (between 450 and 550 msec; $p = .04$) and nondiagnostic (between 300 and 370 msec; $p = .05$) contexts (Figure 4B), with E–R overlap being associated with a more pronounced positivity over anterior sites. The interaction between E–R overlap and Diagnosticity was investigated by running a cluster-based permutation test in the channels and in the time window (300–550 msec) where the main effect of the E–R overlap was observed. However, this analysis yielded no significant effects. In addition, no significant correlations were found between the ERP effects and the behavioral performance.

It should be noted that the E–R overlap difference appears somewhat bigger for the diagnostic compared with nondiagnostic contexts immediately before the word cue onset. Consequently, the observed word cue effects may also reflect carry-over E–R overlap effects related with the preceding context presentation and not only word cue processing.

Probe and Response Time Window

During the probe and response time window, we observed a significant E–R overlap effect for the diagnostic contexts ($p = .003$; see Figure 4C). As expected, the ERPs in the E–R overlap condition exhibited a more pronounced positivity over the central and left posterior sites, starting 440 msec after the stimulus presentation and lasting until the end of the epoch. The interaction between E–R overlap and Diagnosticity was investigated by running a cluster-based permutation test in the channels and in the time window where the main effect of the E–R overlap was observed. This analysis revealed a significant effect ($p = .04$; Figure 4C) showing that the E–R overlap effect was, as predicted, only reliable for the diagnostic contexts. Interestingly, the late posterior E–R overlap effect was positively related to the mnemonic benefits of having a diagnostic context re-presented at retrieval in terms of shorter RTs (overall: $r = .42$, $p = .04$; Figure 5B).

DISCUSSION

We used electrophysiological recordings of brain activity to investigate the context-dependent nature of episodic memory retrieval. The idea that an overlap between encoding and retrieval contexts improves memory performance has been highly influential and represents a widely

accepted principle in the memory literature (Tulving & Thomson, 1973). Although the E–R overlap principle has received extensive support, a complementary—memory-as-discrimination—account argues that an E–R overlap per se predicts nothing about subsequent memory performance (Nairne, 2002). Rather, memory performance is improved by the presence of features in the retrieval cue that help to discriminate relevant target memories from irrelevant competitors—that is, the diagnostic value of the retrieval cue. In the current study, we introduced a novel paradigm to investigate the consequences of context on memory performance and the underlying neural processes when the E–R overlap and the diagnostic value of the context were independently manipulated. Participants were asked to memorize word pairs presented together with task-irrelevant unique (diagnostic) and shared (nondiagnostic) contexts. In a later associative recognition memory test, participants were asked to retrieve the encoded information in the presence (E–R overlap) and absence (E–R nonoverlap) of the previous encoding contexts. Interestingly, our data reveal both benefits and costs associated with reinstating the encoding context at retrieval and further that these mnemonic consequences may be explained by variations in at least two functionally distinct processes.

Our behavioral data showed increased memory discrimination and also faster RTs in the E–R overlap compared with the E–R nonoverlap, but only if the context was diagnostic. It is important to note that our manipulation of context diagnosticity, with the increased familiarity signal carried by the nondiagnostic contexts, did not induce a more liberal response bias (i.e., the tendency to respond "old" was unaffected; cf. Anderson, Jacoby, Thomas, & Balota, 2011). When the context is diagnostic, it offers discriminatory power to separate the target episode from other retrieval candidates, improving memory performance. Conversely, when the context overlaps with other currently irrelevant episodes as well, which is the case for the nondiagnostic contexts, memory performance shows no facilitation regardless of a perfect overlap between encoding and retrieval. In fact, for the nondiagnostic contexts, there was even a tendency for memory discrimination to decrease when the E–R overlapped compared with when it did not. Previous studies have reported facilitatory E–R context overlap effects even for nondiagnostic, shared contexts (e.g., Diana, Yonelinas, & Ranganath, 2013; Smith & Manzano, 2010; Hockley, 2008). These apparently contradictory results may be due to the use of paradigms that arguably overestimate the E–R context overlap effect, for example, simultaneous presentation of the context scenes and target memories (Hockley, 2008), instructing the participants to create associations between context and target memory (Smith & Manzano, 2010) or using a mismatch context condition as a baseline (Diana et al., 2013). Here, instead, we employed a paradigm that promoted an incidental encoding of task-unrelated context. Our data provide support for the memory-as-discrimination framework (Nairne, 2002) and extend previous behavioral findings (Goh & Lu, 2012; Poirier et al., 2012) to a novel paradigm. In addition, our study reveals the neural processes associated with mnemonic benefits and the costs of reinstating diagnostic and nondiagnostic contexts.

The sequential cue presentation paradigm, where the presentation of the context and the word cue was temporally separated, made it possible to measure the neural correlates of memory interference, as predicted by the memory-as-discrimination framework, when nondiagnostic contexts were presented during retrieval. Indeed, our electrophysiological data provided evidence that the nondiagnostic contexts resulted in increased memory interference from currently irrelevant memories, which explains the decreased memory performance observed in this condition. Early after context presentation, we observed a reduced anterior negativity in the ERPs elicited by the nondiagnostic contexts that continued until the word cue was presented. The spatiotemporal characteristics of the effect match the competition-sensitive ERP modulation described by Hellerstedt and Johansson (2014). In their article, the electrophysiological correlates associated with memory competitor reactivation were measured in a retrieval-induced forgetting paradigm. By comparing the ERPs associated with high and low competition conditions, the authors observed that the high competition condition was associated with an attenuated anterior negativity between 300 and 600 msec after stimulus onset. The effect mimicked the FN400 effect observed in previous ERP studies of associative recognition (Opitz & Cornell, 2006) and conceptual priming (Paller, Voss, & Boehm, 2007), and it was interpreted as reflecting the automatic retrieval of the cue's associates. Likewise, the attenuated anterior negativity here observed, for the nondiagnostic contexts, is also most likely reflecting the automatic reactivation of the previous memory traces encoded together with the contextual cues. Because the contexts are nondiagnostic, such reactivation reduces the discriminability between the target memory trace and other retrieval candidates, imposing increased memory interference and, in turn, lowered memory performance. Corroborating this functional interpretation, the early anterior effect co-varied reliably with the costs of having a nondiagnostic context represented at retrieval.

The early anterior effect observed for the nondiagnostic contexts can also be attributed to an increased familiarity with the repeated visual scenes. It is well documented that familiarity is reflected in an early (200–500 msec) frontal old/new effect (for a review, see Rugg & Curran, 2007). In fact, the nondiagnostic contexts were presented 12 times during the study, whereas the diagnostic contexts were presented a single time. However, the effect cannot merely be reflecting context familiarity as the analyses revealed significant relationships between this early anterior E–R overlap effect and memory performance. Such functional relationships are not readily interpreted solely in

terms of familiarity. Moreover, recent studies investigating the effects of visual scene repetition in memory found that the old/new frontal effect (400–600 msec) is not modulated by the number of repetition (one vs. several) and the kind of repetition (massed vs. distributed). Such repetition effects have a different topographical distribution maximum over the centro-parietal sensors (Ferrari, Bradley, Codispoti, & Lang, 2015; Ferrari, Bradley, Codispoti, Karlsson, & Lang, 2013). Thus, the early anterior ERP effect observed here is better described in terms of interference resulting from the automatic reactivation of multiple memories encoded with the shared nondiagnostic context.

In support of this interpretation, we also found a frontal increased theta power activity, with an early onset, for the nondiagnostic condition compared with the diagnostic condition. This time–frequency effect paralleled the ERP results and is in line with previous studies showing that theta oscillatory activity co-varies with memory reactivation (for recent reviews, see Hanslmayr & Staudigl, 2014; Hsieh & Ranganath, 2014) and that the relationship between increased theta power and memory performance decreases when the reactivation of the memory associates increases memory interference (Waldhauser et al., 2012; Hanslmayr et al., 2010; Staudigl et al., 2010). The increased theta power presumably reflects interference because of the reactivation of memory traces previously encoded with the contextual scenes. The nondiagnostic contexts reduce the discrimination between the target and other irrelevant candidates, which leads to the reactivation of irrelevant memory traces. However, because no correlations were found between the theta effect and the mnemonic benefits/costs of context, we are reluctant to draw strong conclusions. An alternative interpretation is that the effect reflects increased recognition for the nondiagnostic context scenes, which are shown more frequently.

During the word cue time window, we found an E–R overlap effect for both diagnostic and nondiagnostic contexts. The onset and topography of this effect mimic in several ways the early midfrontal (200–500 msec) old/new effect described in the ERP studies of recognition memory (e.g., Addante, Ranganath, & Yonelinas, 2012; Wilding & Ranganath, 2011; Rugg & Curran, 2007; Mecklinger, 2000). Accordingly, the effect observed here might reflect increased familiarity for a specific context–word association irrespective of the diagnostic value of the retrieval context. Alternatively, the effect might reflect the automatic reactivation of the memory associates previously encoded with the contexts. If so, the reduced negativity in the nondiagnostic contexts should be associated with a mnemonic cost in terms of behavioral performance. However, because this was not observed, we hesitate to make any strong interpretation.

During the probe time window, we found an E–R overlap effect for the diagnostic contexts, characterized by a larger posterior positivity with a left distribution in a late (400–1000 msec) time window. These spatiotemporal characteristics mimic the left parietal old/new effect associated with recollection (for a review, see Rugg & Curran, 2007). Recollection refers to the conscious retrieval of contextual details of the original study episode in which an item occurred and is known to be hippocampally dependent (O'Reilly & Rudy, 2001; Donaldson & Rugg, 1998). The late posterior E–R overlap effect, observed for the diagnostic contexts, suggests that the specific memory representation of a word pair is more accessible at retrieval in the presence of the original study context but, importantly, only if the reinstated context is discriminatory of the target episode. In line with this interpretation, we found an association between this effect and the behavioral benefit of having a diagnostic context represented at test in terms of shorter RTs. However, it should be acknowledged that our paradigm differs from the classical recognition memory paradigm and that this may complicate a direct translation of our effects into ERP recognition memory effects. For example, in the diagnostic condition, it was possible to retrieve the target episode already during the context time window when the E–R overlapped, which may have resulted in the faster recognition observed for the diagnostic context compared with the nondiagnostic context in terms of RTs. Nevertheless, the present results are consistent with the interpretation that a diagnostic context cue provides facilitated access to a target episodic memory trace.

So far, we have been discussing the effects of diagnostic and nondiagnostic contexts during retrieval. However, diagnostic contextual information might also impose a benefit during encoding. One of the features that clearly distinguish a diagnostic context from a nondiagnostic context is the novelty status. Novelty has long been considered an important factor in learning (e.g., Wagner, Maril, & Schacter, 1998; Tulving & Kroll, 1995), and research suggests that, when novelty is detected, information is transferred to the hippocampus for effective episodic encoding (e.g., Fernández & Tendolkar, 2006). A growing body of literature suggests that the hippocampus is inhibited when familiar information is detected (Schlichting & Preston, 2015; Preston & Eichenbaum, 2013; van Kesteren, Ruiter, Fernández, & Henson, 2012). Accordingly, the presence of novel diagnostic contexts might have engaged hippocampal encoding and promoted ensuing recollection-based retrieval, which would explain both the behavioral benefit and the greater left posterior E–R overlap effect observed in the diagnostic contexts.

The repeated presentation of the nondiagnostic contexts may thus promote hippocampal inhibition. The word pairs presented in nondiagnostic contexts, associated with a strong familiarity signal, might instead have been encoded by adjacent medial temporal regions, such as the perirhinal cortex (e.g., Norman & O'Reilly, 2003). The perirhinal cortex is considered to play a key role in unitizing paired associates into a single representation and in mediating familiarity-based recognition (e.g., Mayes, Montaldi, & Migo, 2007). Furthermore, the reoccurrence of a nondiagnostic context might promote the integration of word pairs

across episodes with the shared context (Schlichting & Preston, 2015). This would cause interference and explain the behavioral cost observed in later memory tests as well as the reduced early anterior E–R overlap effect.

Importantly, however, we observed similar memory performance in the diagnostic and nondiagnostic contexts when the E–R did not overlap, indicating that processes during encoding are not sufficient to fully explain the observed pattern of results (see Skinner & Fernandes, 2010, for a similar result). Thus, our results are more comprehensively explained in terms of an interaction between processes occurring during encoding and retrieval. Specifically, the consequences of different encoding operations are contingent on the nature of the context reinstated during memory retrieval.

Conclusion

This study investigated the consequences of reinstating the original encoding context in a novel memory paradigm, where the E–R overlap and the diagnostic value of the context were independently manipulated. Although context was incidental to the task, our results demonstrate both beneficial and detrimental effects of context reinstatement. Furthermore, two different neural mechanisms accounted for the discriminatory power of a diagnostic context: an early anterior ERP E–R overlap effect associated with memory interference and a later posterior E–R overlap effect, reflecting target memory accessibility. The reinstatement of a diagnostic context offers a high discriminatory signal of the target episode, facilitating episodic remembering. On the other hand, reinstating a nondiagnostic context promotes the reactivation of multiple episodes sharing the contexts, reducing the ability to discriminate between target and irrelevant memory traces. Taken together, our results suggest that context-dependent episodic memory effects are multiple determined.

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