

Prior Emotional Context Modulates Early Event-Related Potentials to Neutral Retrieval Cues

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Abstract

■ Memory retrieval is thought to involve the reactivation of encoding processes. Previous fMRI work has indicated that reactivation processes are modulated by the residual effects of the prior emotional encoding context; different spatial patterns emerge during retrieval of memories previously associated with negative compared with positive or neutral context. Other research suggests that event-related potential (ERP) indicators of memory retrieval processes, like the left parietal old/new effect, can also be modulated by emotional context, but the spatial distribution and temporal dynamics of these effects are unclear. In the current study, we examined “when” emotion affects recognition memory and whether that timing reflects processes that come before and may guide successful

retrieval or postrecollection recovery of emotional episodic detail. While recording EEG, participants ($n = 25$) viewed neutral words paired with negative, positive, or neutral pictures during encoding, followed by a recognition test for the words. Analyses focused on ERPs during the recognition test. In line with prior ERP studies, we found an early positive-going parietally distributed effect starting around 200 msec after retrieval-cue onset. This effect emerged for words that had been encoded in an emotional compared with neutral context (no valence differences), before the general old/new effect. This emotion-dependent effect occurred in an early time window, suggesting that emotion-related reactivation is a precursor to successful recognition. ■

INTRODUCTION

Memory for highly emotional positive and negative events, such as a surprise party thrown in your honor or failing an important examination, is typically superior to memory for less emotional events, such as a conversation with your spouse about what to have for dinner (Bowen, Kark, & Kensinger, 2018; Kensinger & Schacter, 2008; Burke, Heuer, & Reisberg, 1992; Brown & Kulik, 1977). Empirical evidence also indicates that there are valence differences in memory. Young adults attend to and remember negative information better, and with more detail, than neutral or positive information (Kensinger, Garoff-Eaton, & Schacter, 2006; Kensinger & Schacter, 2006; Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Dewhurst & Parry, 2000; Ochsner, 2000). For instance, young adults are better at identifying exactly which object (e.g., a yellow snake coiled up) they have seen in the face of similar distractors (e.g., a yellow snake stretched out) when the items are negative versus when they are positive (Kensinger, Garoff-Eaton, & Schacter, 2007). Understanding why memories of positive and negative events differ in this way is important for understanding the basic operation of human memory because so many of the experiences we remember carry affective significance.

Much of the research on these valence differences has focused on encoding (Kensinger, 2009). For example, research using fMRI during encoding of negative and positive subsequently remembered items indicates that arousing negative information engages more sensory processing regions (Mickley Steinmetz & Kensinger, 2009; Mickley & Kensinger, 2008), leading these negative items to later be remembered with more vivid detail (Kensinger, Addis, & Atapattu, 2011). Encoding of positive information, in contrast, engages areas in prefrontal cortex that support conceptual processing and gist memory (Mickley & Kensinger, 2008).

In the current work, we focus on the effects of valence at retrieval. There is a long-standing hypothesis (James, 1890) that memory retrieval involves the reactivation or reinstatement of processes that were engaged when that information was encoded (Morris, Bransford, & Franks, 1977; Tulving & Thomson, 1973). Many modern theories of memory incorporate this idea, proposing that retrieval entails the recapitulation of distributed processes engaged during encoding (Bowen et al., 2018; Moscovitch et al., 2005; Mather, Shafir, & Johnson, 2000; Rolls, 2000; Alvarez & Squire, 1994), and empirical evidence has confirmed recapitulation of neural activity (Kark & Kensinger, 2015, 2019; Bowen & Kensinger, 2017b; Hofstetter, Achaibou, & Vuilleumier, 2012; Rugg, Johnson, Park, & Uncapher, 2008; Buckner & Wheeler, 2001; Wheeler, Petersen, & Buckner, 2000). For example, fMRI studies

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have demonstrated sensory-specific reactivation such that stimuli previously encoded visually or auditorily activate the visual and auditory cortex, respectively, at retrieval (Gottfried, Smith, Rugg, & Dolan, 2004; Slotnick, 2004; Wheeler & Buckner, 2004; Nyberg, Habib, McIntosh, & Tulving, 2000; Wheeler et al., 2000). Content-specific reactivation has also been demonstrated in the fusiform gyrus during the retrieval of information previously encoded with a face (Hofstetter et al., 2012; Skinner, Grady, & Fernandes, 2010).

This type of evidence supports the theory that neural processes at retrieval are similar to those engaged when the information was originally encoded, and these effects reflect reactivation of the associated information. To this end, our prior fMRI work has shown that neutral retrieval cues can reactivate some of the emotion-related properties associated with the prior encoding experience. Successful memory for neutral words (Bowen & Kensinger, 2017a, 2017b) and line drawings (Kark & Kensinger, 2015, 2019) is associated with greater recapitulation in regions including those within the ventral visual stream to a greater extent for items previously encoded in a negative compared with a neutral or positive context. This is true although the emotional content is no longer present at the time of retrieval (for a review, see Bowen et al., 2018).

Event-Related Potential Evidence for Neural Recapitulation

The reactivation evidence presented above was from fMRI studies, but there is also a literature assessing content-dependent electrophysiological correlates and the time course of memory retrieval using event-related potentials (ERPs). Johnson, Minton, and Rugg (2008) examined recollection of words that differed according to their prior encoding history by either incorporating the word in a sentence or superimposing it on an image. They found that ERPs elicited by words previously encoded in a sentence compared with an image were more positive-going, and the effect was enhanced for recollective memory compared with familiarity responses. The discrepancy between the two waveforms began to emerge in anterior sites approximately 300 msec poststimulus continuing until about 1000 msec. These content-dependent ERPs had an onset as early as the general left parietal old/new effects demonstrating that content-dependent neural activity during retrieval can occur in a time frame, which suggests that it is guiding the retrieval process, and specifically recollection, of episodic information. A second effect beginning around 800 msec after stimulus onset distributed bilaterally over posterior sites and opposite in polarity to the early effect might reflect monitoring or maintenance of information retrieved.

In a more recent study, Johnson, Price, and Leiker (2015) employed multivariate pattern analysis to examine the timing of reactivation of encoding processes at retrieval. They found that reactivation was co-occurring

with ERP left parietal old/new effect (~500 msec after stimulus onset). The reactivation effects were also positively correlated with behavioral accuracy suggesting that reinstatement was capturing and is involved in successful retrieval. Effects that occurred later in the time course were consistent with the maintenance or monitoring and postretrieval processes. Finally, Waldhauser, Braun, and Hanslmayr (2016) found evidence that early sensory reactivation is actually necessary for episodic memory. Applying rhythmic TMS to lateral occipital cortex during retrieval cues disrupted desynchronization in the α/β band, thereby decreasing spatial source memory for those cues.

The novel findings from these studies are the temporal characterization of reactivation, such that reactivation is related to and potentially guides episodic retrieval success early in the time course, but that reactivation also contributes to postretrieval processing and stimulus evaluation.

Effects of Emotion at Encoding on ERPs at Retrieval

A few ERP studies have examined the effects of emotion on memory retrieval to neutral cues. These studies all use a similar design: Items (words or pictures) are initially encoded in emotional contexts. At retrieval, these items are presented without the previously presented context. The key question is whether the ERPs elicited at retrieval differ based on the emotional properties of the encoding context.

Maratos and Rugg (2001) presented sentences that contained neutral critical words in a broader context that was either negative or neutral. When the neutral critical word was re-presented at retrieval, there was a left parietal old/new effect beginning by 500 msec for all old items when compared with new items, but this effect was larger for words encoded in a negative context. There was also a later (after 800 msec) right frontal positivity that was larger to words that had been encoded in a negative context. Interestingly, these valence effects disappeared on both components in a second study when, at retrieval, participants were required to make a source judgment about the emotionality of the prior encoding context. The authors suggested that participants may have been more likely to spontaneously retrieve the source context for items encoded in negative contexts and that this effect therefore disappears when the task requires retrieval of source context for all items.

Smith, Dolan, and Rugg (2004) report a similar study using photos: Neutral objects were presented on neutral or emotional backgrounds. In contrast to the Maratos and Rugg study, the valence of the context primarily showed effects at frontal sites after 800 msec, with only weak evidence for earlier effects. These effects held whether source judgments were required or not. Jaeger, Johnson, Corona, and Rugg (2009) used a very similar picture-based paradigm to examine the effects

of study-test delay (see also Jaeger & Rugg, 2012). However, in the short-delay condition—a near replication of Smith et al.—more robust differences between items encoded in negative versus neutral contexts emerged early, around 200 msec at frontal sites, and continued at left central sites from around 300 msec through the end of the recorded epoch (1100 msec).

It is difficult to draw firm conclusions from this literature. On the one hand, it clearly suggests that traditional indicators of memory retrieval processes like the left parietal old/new effect can be modulated by emotion. On the other hand, the spatial distribution and reports of how early these emotion effects emerge in the retrieval process are variable, despite similar paradigms across studies.

One issue with evaluating the differences across studies is the statistical approach employed. These studies analyzed data using factorial ANOVAs with three spatial factors to explore effects across different regions of the scalp. Although this approach has long been common in ERP research, the field has recently become more aware that the inclusion of such spatial factors leads to significant multiple comparisons issues (see discussion in Fields & Kuperberg, 2019; Luck & Gaspelin, 2017). Although the later effects (after 800 msec) appear robust in these studies, early effects often emerged only in complex interactions with spatial factors and were not significant at levels that survive multiple comparisons correction.

In addition, most studies have only compared negative contexts with neutral contexts, which leaves open important questions about the effects of valence. Only Smith, Dolan, et al. (2004) included both positive and negative contexts during the encoding phase. That study showed effects of encoding in emotional versus neutral contexts but showed no differences between positive and negative contexts. This is in contrast to the fMRI literature reviewed above, which has shown greater neural recapitulation for stimuli encoded in negative contexts. It is unclear whether these differences are because of variation in the stimuli or paradigms employed or whether they reflect differences in the neural processes that fMRI and ERP are sensitive to.

This Study

In the current work, we employed a paradigm known to elicit greater recapitulation for negative versus positive contexts using fMRI (Bowen & Kensinger, 2017a, 2017b). Neutral words were paired with an unrelated neutral, positive, or negative picture during memory encoding. Each participant had a customized set of stimuli based on their individual valence and arousal ratings from a larger stimulus set, which ensured that participants were indeed seeing stimuli that they deemed negative, positive, and neutral. At retrieval, ERPs were recorded to presentation of the neutral words presented in

isolation. We analyzed the data using a mass univariate approach (similar to the way fMRI data are commonly analyzed); recent work has highlighted the value of this approach for controlling multiple comparisons issues while maintaining flexibility to find effects when the precise spatial and temporal distribution is not known in advance (Fields & Kuperberg, 2019; Groppe, Urbach, & Kutas, 2011). Given findings in the literature reviewed above, we employed analysis parameters that allowed us to identify effects at any scalp location and in both early and late time windows.

Our goal was to answer two key questions. First, we asked whether, consistent with the fMRI literature, negative and positive valence would show differing effects at retrieval or whether, like the Smith et al. studies describe above, emotional contexts would modulate retrieval when compared with neutral contexts without differences between positive and negative. Second, we examined the timing of these effects. Early modulation by previous emotional context would suggest that emotion at encoding affects processes that guide successful retrieval (cf. Johnson et al., 2008; Waldhauser et al., 2016). If such effects are only present in later time windows, this would suggest that emotion effects may emerge only after successful retrieval.

METHODS

Participants

All interested participants completed an extensive medical screening questionnaire to assess past and current medical conditions such as psychological disorders, head trauma or injuries, and medications. Reasons for ineligibility included currently taking antidepressants or anxiolytics, head trauma (e.g., concussion) in the last 2 years, seizures, diabetes, learning disorder (e.g., dyslexia, attention-deficit/hyperactivity disorder). We also required that participants be right-handed and native English speakers. All procedures were approved by the Boston College institutional review board, and all participants gave informed consent. Forty-one participants were tested, most of which were from the Boston College community with some additional participants recruited through a posting on Craigslist.org. Participants were either paid \$15/hr or given partial course credit. One participant withdrew before completion because of a headache, five participants were excluded because of technical errors or equipment failure, four were excluded because of poor behavioral performance (e.g., overall performance lower than chance or too few responses for reliable ERP analysis), and six data sets were unusable because of excessive artifact in the EEG (greater than 25% of trials lost to artifact—see artifact correction and rejection procedures in the Data Processing and Analysis section). This left 25 eligible participants (8 men) with an average age of 22 years (range = 18–32 years). All eligible participants completed the Beck

Depression Inventory (Beck, Epstein, Brown, & Steer, 1988) and scored below 11 ($M = 1.96$, $SD = 2.39$).

Stimuli

Three different types of stimuli were used in the study: faces, scenes, and words. The stimuli were gathered from a number of sources as detailed below. During encoding, stimuli stayed on screen for 3.5 sec and during retrieval until a response was made. Each stimulus was followed by a fixation that was jittered 500–4000 msec in both phases of the experiment.

Faces

Forty-two face stimuli were selected from the NimStim (www.macbrain.org/resources.htm) Set of Facial Expressions (Tottenham et al., 2009). These faces range in emotional expression, valence and arousal, gender, race, and ethnicity.

Scenes

Fifty-seven total images of scenes that contained no perceptible faces were used. To meet this requirement, some images were taken from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008) and some were taken from various sources on the Internet. The scenes depicted in the images ranged in content as well as emotional valence and arousal.

Words

Words were selected from a published data set (Warriner, Kuperman, & Brysbaert, 2013) consisting of 13,916 words with valence and arousal ratings. The large list was reduced to six-letter neutral words and then further restricted to 384 words using a random number generator ($M_{\text{valence}} = 5.71$, $SD_{\text{valence}} = 1.64$, range = 5.0–6.9; $M_{\text{arousal}} = 3.41$, $SD_{\text{arousal}} = 2.16$, range = 2.27–3.96). Words were then split into eight groups of 48 words. The eight lists did not differ on average valence or arousal ratings, $F(7, 383) = 0.85$, $p = .55$ and $F(7, 383) = 0.65$, $p = .72$, respectively.

Procedure

Before being scheduled to come to the laboratory on Boston College campus, all interested participants completed the medical screening questionnaire. Once eligibility was determined, participants were asked to complete an online questionnaire via SurveyMonkey.com. The online questionnaire had participants view 42 faces and 57 scenes to select the valence (negative, positive, or neutral) and rate the arousal (on a scale from 1 to 7) of all the stimuli. The purpose was to create an individualized subset of these images (four scenes and

four faces of each valence; 24 images in total) as experimental stimuli; the specific images selected for each participant were the eight negative and eight positive images that were given the highest arousal ratings during the initial ratings task, along with eight neutral images with the lowest arousal ratings. This ensured that participants were viewing images that indeed were emotional in their opinion. Valence and arousal from one participant are not included in analyses below because of experimenter error.

When participants came to the laboratory, they provided informed consent and demographic information and completed the Beck Depression Inventory. The EEG procedure was explained, they viewed the EEG equipment, and they were encouraged to ask questions before proceeding. After the EEG setup was completed, participants were given instructions about the task and completed a practice of six encoding and 12 retrieval trials.

Participants completed four alternating encoding–retrieval blocks with a short, filled retention interval separating the two phases. During the encoding phase (48 trials per block: 16 positive, 16 negative, 16 neutral), participants viewed a word and an image on the screen together. They were instructed to try and remember the word for the upcoming memory test and indicate via button press whether the image was of a face or a scene. The encoding block was followed by 10 multiple-choice math problems (e.g., $2 + 5$, 6×2). During the retrieval phase, participants viewed only the words and were asked to make a “remember,” “know,” “guessing,” or “new” judgment. There were 48 target items and 48 lures (96 items in total) during each retrieval block. Participants were given the “remember” and “know” instructions (Rajaram, 1993) and were encouraged to respond “guessing” if they had no inclination as to whether the word was old or new and to respond “new” if they had not seen the word during the encoding stage. ERPs were recorded during both the encoding and retrieval phases of the study. Participants were given a short break after the second block of trials. After the study was complete, participants were compensated, debriefed, and thanked for their participation.

ERP Acquisition and Processing

Data were collected using a BioSemi ActiveTwo EEG system and ActiView v6.05 EEG acquisition software (www.biosemi.com/). The EEG was recorded from 32 Ag/AgCl electrodes in an elastic cap placed according to the International 10–20 system.¹ In addition, electrodes below and to the left of the left eye and above and to the right of the right eye were recorded to monitor for blinks and eye movements, and electrodes on each mastoid were recorded to serve as the reference. The EEG signal was amplified, filtered online with a low-pass fifth-order sinc response filter with a half-amplitude cutoff at 104 Hz, and continuously sampled at 512 Hz.

Data Processing and Analysis

EEG and ERP data processing were conducted in EEGLAB v14.1.1 (scn.ucsd.edu/eeglab/index.php; Delorme & Makeig, 2004) and ERPLAB v6.1.4 (erpinfo.org/erplab; Lopez-Calderon & Luck, 2014).

The EEG was first referenced to the average of the two mastoid electrodes. For each segment of continuous EEG, we subtracted the average voltage of the entire segment and then applied a high-pass second-order Butterworth infinite impulse response filter with a half-amplitude cutoff of 0.1 Hz (Tanner, Morgan-Short, & Luck, 2015; Kappenman & Luck, 2010). We then extracted segments from 200 msec before to 1100 msec after all events of interest.

For the purposes of independent component analysis (ICA), the mean voltage was removed from each segment at each electrode (Groppe, Makeig, & Kutas, 2009). Segments containing a significant artifact that was not neural, ocular, or muscular in origin were identified via visual inspection and excluded from the data submitted to ICA. Independent components were calculated from the remaining segments using the extended infomax algorithm (Lee, Girolami, & Sejnowski, 1999) as implemented in EEGLAB. Independent components corresponding to ocular activity (blinks and eye movements) were identified by visual inspection and removed. This consisted of either two or three independent components for each participant.

After independent components were removed, all segments were rebaselined to the mean of the prestimulus period. Segments with remaining artifacts were identified via artifact detection algorithms implemented in ERPLAB. The parameters of these algorithms (e.g., voltage thresholds) were tailored to each participant via visual inspection of the data but were consistent across all trials and conditions within each participant. Trials containing a blink or large saccade within the first 200 msec of a trial were rejected even if the artifact was corrected via ICA, as these trials may have a delayed neural response because of the eyes being closed or averted during stimulus presentation. Rejection rates ranged from 2% to 24% across participants with an average of 11% and did not differ significantly across valence conditions.

After ICA-based correction and artifact rejection, the remaining trials were averaged within conditions of interest to form ERPs.

ERP Analysis

Statistical analysis of ERPs was conducted via the Mass Univariate Toolbox (Groppe et al., 2011) and Factorial Mass Univariate ERP Toolbox (github.com/ericcfields/FMUT/wiki). We used a cluster-corrected mass univariate approach (Groppe et al., 2011; Maris & Oostenveld, 2007). Briefly, this approach consists of conducting an ANOVA independently at each time point and electrode

of interest. Clusters are identified as adjacent time points/electrodes with effects surpassing a threshold, and all F values in the cluster are summed to form a cluster mass statistic. A permutation approach is used to estimate the null distribution for this statistic, which is then used to calculate a p value for each cluster. Recent simulation work has shown that this approach can provide power that compares well to traditional mean amplitude-based approaches while providing significantly greater flexibility (Fields & Kuperberg, 2019).

Because the relevant literature suggested effects may occur at frontal and posterior sites and in both early and late time windows, the cluster mass test was conducted at all time points from 200 to 1000 msec at all 32 scalp electrodes. The F value corresponding to $p = .05$ in an uncorrected parametric test was used as the threshold for cluster inclusion, and electrodes within approximately 7.5 cm of each other (assuming a head circumference of 56 cm) were considered neighbors. A total of 100,000 permutations were performed for each test. Statistical analysis was conducted on data that were first low-pass filtered at 10 Hz (half-amplitude cutoff, second-order Butterworth infinite impulse response filter) and downsampled to 128 Hz (Groppe et al., 2011; Luck, 2014). Cluster significance was evaluated at $\alpha = .05$.

RESULTS

Behavioral Data

Stimulus Arousal Ratings

Arousal ratings for the experimental stimuli were submitted to a one-way (Valence: negative, positive, neutral) repeated-measures ANOVA. There was a significant effect of Valence, $F(2, 46) = 113.08, p < .001, \omega_p^2 = .82$. This interaction was followed up with paired samples t tests, which indicated that negative stimuli ($M = 6.43, SD = 0.66$) were rated as more arousing than positive stimuli ($M = 5.46, SD = 0.86$), $t(23) = 6.06, p < .001, r = .78$, and positive stimuli were more arousing than neutral stimuli ($M = 3.94, SD = 0.27$), $t(23) = 8.24, p = .001, r = .86$.

Proportion of Responses

Table 1 displays the proportion of remember, know, guess, and new responses to target stimuli within each valence and to distractor items.

Hit Rates, False Alarm Rate, and RT across "Remember" and "Know" Responses

Average hit rates² (i.e., proportion correct collapsed across trials given "remember" or "know" responses) were calculated for stimuli previously encoded with negative, positive, and neutral images and submitted to a

Table 1. Proportion of Remember, Know, Guess, and New Responses to Target and Distractor Stimuli within Each Valence Category

Response	Negative	Positive	Neutral	Distractor
	Target	Target	Target	
Remember	.45 (.03)	.45 (.04)	.41 (.04)	.07 (.02)
Know	.19 (.02)	.21 (.03)	.24 (.03)	.14 (.02)
Guess	.18 (.02)	.17 (.03)	.16 (.02)	.26 (.03)
New	.15 (.02)	.14 (.02)	.16 (.02)	.50 (.04)

Distractor (i.e., new) items did not vary by emotional context. Standard error values are in parentheses.

one-way repeated-measures ANOVA. The main effect of Emotion was not significant, $F(2, 48) = 0.18, p = .84, \omega_p^2 = -.012$, indicating that the hit rate for items previously encoded with negative images, $M = .63 (SE = .03)$, positive images, $M = .66 (SE = .04)$, and neutral images, $M = .64 (SE = .01)$ did not statistically differ. Because new stimuli presented at retrieval were never associated with a particular valence, only a single false alarm rate could be calculated. Overall, corrected recognition (hit rate minus false alarm rate) was $M = .14 (SE = .06)$. Median RTs for recognition of stimuli previously encoded with negative, positive, and neutral images were calculated and submitted to a one-way repeated-measures ANOVA. Again, the main effect of Emotion was not significant, $F(2, 48) = 0.18, p = .84, \omega_p^2 = -.033$, indicating that memory-related RTs to items encoded with negative, $Md = 1376$ msec ($SE = 88$), positive, $Md = 1372$ msec ($SE = 71$), and neutral, $Md = 1390$ msec ($SE = 69$), images did not statistically differ. The median RT for false alarms was 1554 msec ($SE = 102$).

Effects of valence on hit rates within experimental blocks. Next, we examined the possibility that emotion effects on memory were washed out over the four study-test blocks because each image was shown eight times over the experiment. Average hit rates (collapsed across “remember/know”) were calculated for each emotion within each of the four blocks and submitted to four separate one-way repeated-measures ANOVAs. These analyses revealed no significant effect of Emotion on hit rates within any of the four blocks, $F(2, 44) \leq 1.59, p \geq .22, \omega_p^2 \leq .024$.

Effects of experimental block on hit rates. To examine whether hit rate changed across the four study-test blocks (i.e., over time) as a function of Emotion, the average hit rates (collapsed across “remember/know”) were submitted to a 3 (Emotion: negative, positive, neutral) \times 4 (Experimental Block: 1, 2, 3, 4) repeated-measures ANOVA. Importantly, there was no main effect of Emotion or Block, nor a significant interaction between the two factors, $F(2, 44) \leq 0.54, p \geq .58, \omega_p^2 = -.010$.

Separate false alarm rates for each experimental block were also calculated, and a one-way ANOVA revealed no significant differences, $F(3, 66) = 1.67, p = .18, \omega_p^2 = .028$.

Hit Rates, False Alarm Rate, and RT for Remember Compared with Know Responses

The average hit rates (i.e., proportion correct) were calculated separately for “remember” and “know” responses (see Table 1 for means). To examine whether hit rates for “remember” compared with “know” responses varied by the prior emotional context, the proportions were submitted to a 3 (Emotion: negative, positive, neutral) \times 2 (Response: remember, know) repeated-measures ANOVA. As expected based on the prior analyses, there was no main effect of Emotion, $F(2, 48) = 0.70, p = .50, \omega_p^2 = -.012$, but there was a main effect of Response type, $F(1, 24) = 19.89, p < .001, \omega_p^2 = .421$, and an Emotion \times Response type interaction, $F(2, 48) = 6.48, p = .003, \omega_p^2 = .177$. The interaction was followed up with separate one-way ANOVAs for “remember” and “know.” For the proportion of “remember” responses, there was a significant main effect of Emotion, $F(2, 48) = 3.95, p = .03, \omega_p^2 = .104$. Follow-up paired t tests indicated that the proportion correct for “remember” responses was lower for stimuli previously encoded in a neutral context ($M = .410, SE = .04$) compared with negative contexts ($M = .45, SE = .03$), $t(24) = 2.56, p = .02, r = .46$, or to positive contexts ($M = .44, SE = .04$), $t(24) = 2.34, p = .03, r = .43$. The proportion correct for “remember” responses did not significantly differ between negative and positive contexts, $t(24) < .001, p = 1.0, r = .0$. The ANOVA for “know” responses revealed a main effect of Emotion, $F(2, 48) = 5.65, p = .01, \omega_p^2 = .15$, and follow-up paired t tests indicated that the proportion correct was higher for stimuli previously encoded in a neutral context ($M = .24, SE = .03$) compared with negative contexts ($M = .19, SE = .02$), $t(24) = 3.51, p = .002, r = .58$, and lower compared with positive contexts ($M = .21, SE = .03$), $t(24) = 2.03, p = .05, r = .38$. The proportion correct of “know” responses did not differ for negative and positive contexts, $t(24) = 1.30, p = .21, r = .26$. Finally, a paired t test indicated the false alarm rate for “remember” responses was significantly lower ($M = .07, SE = .02$) compared with the false alarm rate for “know” responses ($M = .14, SE = .02$), $t(24) = 3.06, p = .01, r = .53$.

ERP Data

Visual inspection of the EEG and ERPs at encoding suggested that participants were variable from trial to trial in terms of when they were looking at the word versus the picture (which were presented simultaneously). Because neural processes must be aligned in time across trials to form meaningful ERPs, and because the key research

Table 2. Average Number of Trials per Participant That Contributed to the ERP Analyses Broken Down by Response Type

Response	Negative Target	Positive Target	Neutral Target	Distractor
Remember	26 (10–41)	26 (11–48)	24 (6–43)	16 (0–100)
Know	11 (1–28)	12 (1–40)	14 (1–29)	24 (0–61)
Guess	10 (0–22)	10 (0–32)	10 (2–21)	47 (3–87)
New	9 (2–24)	8 (0–20)	10 (0–24)	85 (21–163)
Remember/know	37 (21–55)	39 (17–55)	38 (22–59)	40 (0–119)
Guess/new	19 (6–39)	18 (3–37)	19 (3–38)	132 (57–174)

Values in parentheses indicate the range in number of trials across participants. ERP analyses were collapsed remember/know and guess/new, and the bottom two rows reflect the average number of trials included in those analyses. Distractor stimuli (i.e., new items) did not vary by emotional context.

questions in this study were about neural processes at retrieval, the data recorded at encoding are not considered further.

For all analyses reported below, ERPs were collapsed across “remember/know” (considered together as an “old” response) and “guess/new” (considered together as a “new” response) to ensure enough trials (> 15 per condition for each participant) went into each average to provide stable ERPs and reasonable power. Visual inspection revealed that effects of valence were similar for “remember” and “know” trials, but the “know” trials were noisier because of smaller bin sizes (see Table 2). Separate results for each of the four judgments can be seen in the supplementary materials (available on the Open Science Framework osf.io/jyd5c/).

We first examined the ERP signature of recognition by contrasting new words correctly categorized as new to words that had been presented with a neutral picture and correctly categorized as old. This provided a test that was independent of any effects of emotion and therefore most comparable with previous ERP investigations of recognition memory. As can be seen in Figure 1, this contrast revealed the standard old/new ERP effects that have been reported in many ERP studies (Wilding & Ranganath, 2012; Rugg & Curran, 2007): A frontally distributed negativity was reduced to old words from around 400–700 msec, followed by a larger left parietally distributed positivity to old words from around 500–700 msec, and a right frontally distributed positivity larger to old words from around 900 msec. As shown in

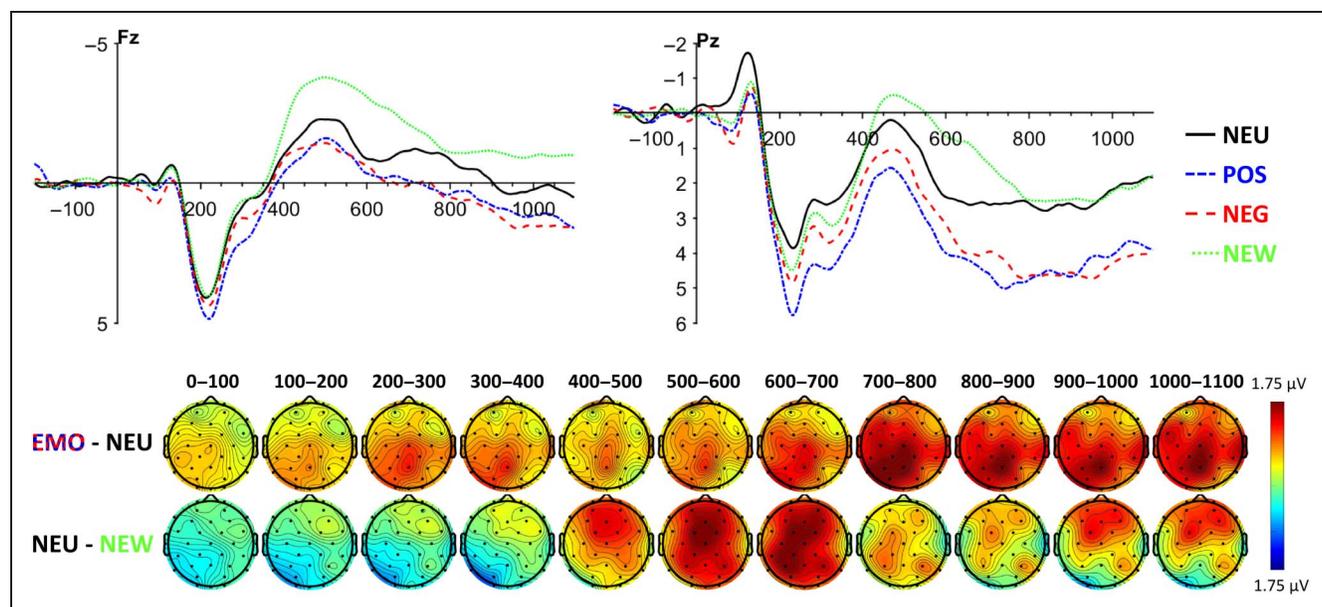


Figure 1. ERP waveforms show the response at retrieval to words previously encoded with neutral, positive, and negative photos and given a “remember” or “know” judgment as well as new words given a “guess” or “new” judgment. Scalp maps show the emotion (collapsed across positive and negative) minus neutral effect and the old/new (neutral – new) effect. ERPs are filtered at with a 10-Hz half-amplitude low-pass filter, matching the data used for statistical analysis (see Methods). EMO = emotion; NEU = neutral; NEG = negative; POS = positive.

difference between positive and neutral was significant ($p = .007$).

The full results of all mass univariate analyses are available in the supplementary materials at osf.io/jyd5c/.

DISCUSSION

In the current study, we sought to investigate the electrophysiological correlates and time course of memory retrieval for neutral words previously encoded in a neutral, positive, or negative context. Using ERPs, we found evidence that, compared with a neutral encoding context, words encoded in a positive or negative context began to show a more positive-going amplitude in parietal electrodes beginning around 200 msec after stimulus onset. This occurred before the general old–new recognition effect, which began around 400 msec.

Early Effects of Emotional Encoding Context at Retrieval

Theories of memory suggest that processes engaged at encoding are reactivated at retrieval and that this recapitulation plays an important role in determining retrieval success (Morris et al., 1977; Tulving & Thomson, 1973). In line with such views, a large empirical literature using fMRI shows substantial overlap in neural activation during encoding and retrieval (for reviews, see Bowen et al., 2018; Buckner & Wheeler, 2001). However, the temporal resolution of fMRI means that it is unclear whether these reactivations occur before, during, or after successful retrieval. Although the EEG literature on this question is still small, a few studies have suggested that neural recapitulation can be observed quite early during retrieval (Waldhauser et al., 2016; Johnson et al., 2008, 2015).

In previous fMRI work, including a study using the same paradigm employed in this study, our laboratory has shown that neural recapitulation is greater for negatively valenced stimuli than neutral or positive stimuli (Bowen & Kensinger, 2017a, 2017b). Only a few studies have examined how emotional content from encoding affects the ERP response at retrieval (Jaeger et al., 2009; Smith, Henson, Dolan, & Rugg, 2004; Maratos & Rugg, 2001). Although these studies have suggested that emotion effects may emerge early during retrieval, these effects have been inconsistent and most of these studies have not examined both negative and positive valence.

The present results showed that encoding a neutral word in an emotional context—either positive or negative—can affect the neural response from the very earliest stages of memory retrieval. Indeed, the effect of emotion in our data began around 200 msec after the onset of the neutral retrieval cue. Not only is this coincident with the earliest old/new differences generally observed in ERP (Wilding & Ranganath, 2012), it is earlier than we were able to distinguish words encoded in neutral contexts from new words in the present data. This suggests that

the emotion of the encoding context modulates the earliest stages of memory retrieval and may play a role in guiding the retrieval process.

It is not entirely clear what neural process is represented by the emotion effect we observed. One interpretation is that it reflects modulation of the left parietal old/new effect that has been associated with memory recollection in a large ERP literature (Wilding & Ranganath, 2012). Some work has suggested that emotion of the encoding context can modulate this component (Maratos & Rugg, 2001), and the effect of emotion in this study showed a scalp distribution that is consistent with this effect (see Figure 1). Under this interpretation, participants showed greater episodic recollection for items that had been encoded with an emotional image, perhaps because the emotional properties of the image led it to be encoded and then recalled in greater detail. Alternatively, the effect we observed could be interpreted as the late positive potential (LPP) that is generally observed to emotional stimuli and that appears as a very similar parietal positivity (Hajcak, Weinberg, MacNamara, & Foti, 2012). This interpretation would be in line with a more direct recapitulation account: It would suggest that the same neural processes that are observed when emotional stimuli are being viewed can be elicited by the incidental retrieval of emotional stimuli, even when the retrieval cue is neutral.

Under either of these interpretations, the timing of the effect is somewhat surprising. The left parietal old/new effect generally begins around 400–500 msec and lasts a few hundred milliseconds. If the present effect is identified with this component, it would suggest that emotional contexts can lead retrieval processes to begin earlier than they are usually observed. The LPP generally begins between 300 and 500 msec in response to emotional pictures and usually lasts at least a few hundred milliseconds but can last longer depending on the task (Gable, Adams, & Proudfit, 2015). If the present effect is identified with this component, it suggests that cued retrieval of emotional information can be faster than initial recognition of the emotional properties of stimuli.

Of note, when responses were collapsed across “remember” and “know,” we report emotion-related differences in the electrophysiological signature, but we did not find any behavioral differences in memory performance as a function of encoding context. This is not entirely surprising given the short delay between encoding and retrieval blocks. Most findings of an emotion effect on memory have retention intervals upwards of 24 hr to allow for consolidation processes to unfold (Sharot & Yonelinas, 2008). Furthermore, the to-be-remembered stimuli were not emotional themselves, but were neutral words, and participants were never explicitly asked to associate the word and emotional context, nor make a judgment about the emotionality of the encoding stimuli at any point during the experiment. These procedural details likely contributed to no differences in behavior but

also made for a strong test of emotion effects on memory. When behavioral performance was examined separately for “remember” and “know” responses, we did find that memory was better for stimuli encoded in an emotional context (both negative and positive) compared with a neutral context for “remember,” whereas the opposite pattern was true of “know.” Because of the limited number of “know” responses, we could not reliably compare the ERPs for “remember” versus “know” to more closely compare with the fMRI findings reported in Bowen and Kensinger (2017a, 2017b).

Effects of Negative vs. Positive Valence

Notably, when the present paradigm was employed in fMRI, there was greater recapitulation in sensory processing regions during recollection of words encoded in a negative context compared with a positive or neutral context (Bowen & Kensinger, 2017b). In the ERP results, negative and positive valence showed an equally increased positivity compared with neutral, consistent with the ERP findings of Smith, Dolan, et al. (2004). Although ERP and fMRI are complementary techniques, they are sensitive to different aspects of the neural response for a number of reasons (Murta, Leite, Carmichael, Figueiredo, & Lemieux, 2015; Lau, Gramfort, Hämäläinen, & Kuperberg, 2013; Ekstrom, 2010; Logothetis, 2008). In the present paradigm, it is likely that the timing of the visual activity at retrieval is variable across trials. Because the time course of the BOLD signal in MRI is slow and because the processing of MRI data generally presents activation that is a weighted average across several seconds of data, this variability would make little difference to the MRI results. However, in ERP, the visual response consists of a series of fast deflections of opposite electrical polarity (Pratt, 2012). If these are not aligned precisely in time across trials, they are likely to cancel out when averaging. Thus, the ERP response may have captured broader effects of emotion present in both positive and negative conditions, while missing sensory-specific valence differences. Future work using time–frequency analysis methods that ignore phase and/or methods that make sensory recapitulation more clearly identifiable may be able to use the temporal resolution of EEG to examine the time course of valence-modulated sensory recapitulation (see, e.g., Waldhauser et al., 2016, who were able to show rapid recapitulation of visual activity by combining time–frequency analysis with lateralized presentation at encoding).

Limitations and Future Directions

One interesting question is whether the emotion effects on memory retrieval and reactivation are stronger for recollected compared with familiar stimuli. Prior ERP work has shown that reactivation effects were enhanced for “remember” compared with “know” responses (Johnson

et al., 2008), and using fMRI, we also found evidence that there was greater recapitulation for “remember” compared with “know” responses, suggesting that the reactivation may be more strongly associated with recollection processes (Bowen & Kensinger, 2017b). When the behavioral data were analyzed separately for “remember” and “know” responses, trials given a “remember” response were associated with better memory for items previously encoded in an emotional context (both positive and negative) compared with a neutral context, but the opposite pattern was true of “know” responses. We broadened our ERP analyses to trials given either a “remember” or “know” response, rather than comparing effects for these response types, because we did not have enough “know” trials to adequately assess this. The ability to examine “remember” and “know” trials separately may also help to determine the relationship of the emotion effect we observed to the left parietal old/new effect, because this effect is generally associated specifically with recollection (i.e., remember trials). On the other hand, if the effect we observed is a recapitulation of the emotional LPP effect, this effect could appear in the absence of recollection if the neutral cues have been imbued with some of the emotional properties of the pictures they were paired with (cf. Jaeger & Rugg, 2012).

A limitation of our encoding procedure was the placement of target words above the picture. As a result of this stimulus placement, the EEG and ERPs at encoding indicated that participants were switching their gaze from the word to the picture in a way that was not consistent across trials and participants. This resulted in difficulty time-locking the ERP to a particular stimulus or process at encoding, so the encoding data were not analyzed. We couch our findings within the recapitulation literature, and our results suggest that emotional encoding context can affect neural responses early in retrieval and are consistent with increased recollection and/or recapitulation of the emotional LPP. However, it is important to note that we could not examine directly the similarity between the ERPs elicited at encoding and retrieval, as we have done in our fMRI work (Bowen & Kensinger, 2017b; Kark & Kensinger, 2015). As a result, we cannot conclude with confidence that the effects we observed at retrieval reflect reactivation or reengagement of neural processes elicited during encoding. Future work with encoding procedures that allow for a reliable recording of the emotional response at encoding—perhaps with one stimulus superimposed on the other (cf. Jaeger & Rugg, 2012) or the stimuli after each other temporally—would allow for a more detailed analysis of recapitulation by allowing for a direct comparison of similarity in the EEG at encoding and retrieval.

Another possible limitation was participants’ exposure to the same emotional stimuli repeatedly during encoding. Participants completed online arousal ratings of many stimuli before coming to the laboratory for the EEG session, and an individualized subset of these

images was chosen as experimental stimuli based on their arousal ratings. From this subset, participants viewed the same eight negative, eight positive, and eight neutral stimuli twice in each experimental block over four blocks, but paired with different neutral words at each exposure. It is possible that participants habituated to the emotional content of these images over the course of the experiment, but our behavioral results do not support this. We reported that hit rates did not significantly decrease over the experiment, and there were no Block \times Valence interactions on hit rate, nor did hit rates differ as a function of valence within each experimental block. Nonetheless, future studies could include unique emotional stimuli on each trial.

Conclusions

The study of emotion on memory has primarily focused on encoding processes, with little emphasis on how emotion might influence downstream processes, including retrieval. Prior fMRI work has revealed that emotion modulates the patterns of reactivation during successful memory retrieval but does not reveal the time course of these effects. The current ERP findings show that effects of emotion at retrieval are not simply a result of successful retrieval. Instead, our findings show that effects of the emotionality of the encoding context are present very early during the retrieval process and thus may play a role in guiding successful retrieval.

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Notes

1. The electrodes were Fp1, AF3, F7, F3, FC1, FC5, T7, C3, CP1, CP5, P7, P3, Pz, PO3, O1, Oz, O2, PO4, P4, P8, CP6, CP2, C4, T8, FC6, FC2, F4, F8, AF4, Fp2, Fz, and Cz.
2. The guess response was instructed to be used when participants were unsure whether the stimulus was old or new. Given this ambiguity, these responses could not be categorized as correct or incorrect, but these trials were included to calculate proportion.

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