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Marisa Knight University of San Francisco, mrknight@usfca.edu

M Mather

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Reconciling findings of emotion-induced memory enhancement and impairment of preceding items

Marisa Knight and University of San Francisco

Mara Mather University of Southern California

Abstract

A large body of work reveals that people remember emotionally arousing information better than neutral information. However, previous research reveals contradictory effects of emotional events on memory for neutral events that precede or follow them: in some studies emotionally arousing items impair memory for immediately preceding or following items and in others arousing items enhance memory for preceding items. By demonstrating both emotion-induced enhancement and impairment, Experiments 1 and 2 clarified the conditions under which these effects are likely to occur. The results suggest that emotion-induced enhancement is most likely to occur for neutral items that: (1) precede (and so are poised to predict the onset of) emotionally arousing items, (2) have high attentional weights at encoding, and (3) are tested after a delay period of a week rather than within the same experiment session. In contrast, emotion-induced impairment is most likely to occur for neutral items near the onset of emotional arousal that are overshadowed by highly activated competing items during encoding.

Effects of emotional arousal on memory: Reconciling findings of emotioninduced enhancement and impairment

When stimuli evoke emotional arousal, that emotion affects not only memory for the emotional stimuli but also memory for stimuli appearing just before or after the emotional item. Indeed, many studies reveal impaired memory for stimuli preceding or following an emotional item in a list of items (Bornstein, Liebel, & Scarberry, 1998; Detterman, & Ellis, 1972; Ellis, Detterman, Runcie, & Craig, 1971; Erdelyi & Blumenthal, 1973; Hadley & MacKay, 2006; Hurlemann et al., 2005; MacKay et al., 2004; Miu, Heilman, Opre, & Miclea, 2005; Runcie & O'Bannon, 1977; Schmidt, 2002; Strange, Hurlemann, & Dolan, 2003). However, a recent study provides an intriguing puzzle in its apparent contradiction with previous findings. Anderson, Wais and Gabrieli (2006) found that merely appearing before an emotionally arousing picture enhanced memory for a neutral picture a week later – rather than impairing memory for it, as would be expected given the prior studies. In the experiments outlined here, we attempted to demonstrate both the enhancement and impairment effects within the same experimental paradigm, with the hope that by revealing what leads arousing items to impair memory for nearby items in one case but enhance memory for nearby items in another case, we would gain insight into the fundamental mechanisms of how emotional arousal modulates memory.

Memorial Benefits of Emotional Arousal

A growing body of evidence supports the notion that emotional arousal influences memory by altering psychological and biological processes. For the most part, these processes make emotionally significant information more memorable than neutral information (see Dolan, 2002, Hamann, 2001, for reviews). Emotionally provocative events influence early stages of sensory processing and attention, speeding their detection (Adolphs, 2004; Mather & Knight, 2006; Öhman, Flykt & Lundqvist, 2000; Öhman, Lundqvist & Esteves, 2000, see Dolan, 2002 for a review). When lists of items are presented in rapid succession for very short durations (100-200 ms), emotionally arousing words are more likely to enter short-term memory, produce stronger repetition blindness, and are more likely to be recalled than neutral words (Hadley & MacKay, 2006; Silvert, Naveteur, Honore, Sequeira & Boucart, 2004). In addition, emotionally arousing words are less likely than neutral words to be missed by the perceiver due to the attentional blink period, i.e., the temporary blindness to a second stimulus after a first stimulus has been registered (Anderson, 2005; Anderson & Phelps, 2002).

Enhanced perception of and attention to emotional information is not limited to verbal stimuli. Compared with neutral scenes, participants' first eye fixations are more likely to be on emotionally arousing images and, once there, participants look longer (Isaacowitz, Wadlinger, Goren, & Wilson, 2006; Knight, et al., 2007; Lang, Greenwald, Bradley & Hamm, 1993; Rosler et al., 2005). Furthermore, when picture stimuli are paired with either neutral or aversive noise, attention is oriented preferentially to pictures that were paired with aversive noise, regardless of whether or not the pictures were recognized during acquisition and expression of the conditioned fear response (Beaver, Mogg & Bradley, 2005). Thus, the attention-demanding quality of emotionally arousing stimuli can be acquired by items that share a close temporal relationship with them (cf. Mather & Knight, 2008). The enhanced perception of and attention to emotionally arousing information involves early processing stages. However, once emotionally arousing information is registered, it also has a greater likelihood of engaging self-initiated processing relative to neutral information. Later stages of cognitive processing such as rumination, elaborative rehearsal and selective retrieval also contribute to emotional memory enhancement (e.g., Guy & Cahill, 1999; Lane, Mather, Villa, & Morita, 2001; Marsh, 2007; Mather & Knight, 2005).

While emotional memory enhancement is due, in part, to basic psychological processes such as attention and rehearsal, a growing body of work suggests that emotional memory enhancement also involves specialized neural mechanisms (Buchanan & Adolphs, 2004; Hamann, 2001; LaBar & Cabeza, 2006; Phelps, 2006). Enhanced explicit memory for information associated with emotional arousal has been linked to the amygdala (Adolphs, Cahill, Schull & Babinsky, 1997; Cahill, Babinsky, Markowitsch & McGaugh, 1995; Phelps et al., 1998) and activation of a β -adrenergic system that allows for modulation of hippocampal activity (Strange & Dolan, 2004). Amygdala activation is enhanced both during encoding of emotionally arousing information (Dolcos, LaBar & Cabeza, 2004; Hamann, Grafton, Ely, & Kilts, 1999; Mather et al., 2004) and during encoding of neutral information in an emotional context (Erk, Kiefer, Grothe, Wunderlich, Spitzer, & Walter, 2003). In several neuroimaging studies, amygdala activation during encoding has been found to correlate with later memory for emotional but not neutral stimuli (Canli, Zhao, Brewer, Gabrieli & Cahill, 2000; Hamann et al., 1999; Kilpatrick & Cahill, 2003; Mackiewicz, Sarinopoulos, Cleven, & Nitscke, 2006). Furthermore, emotional memory enhancement is absent in patients who no longer have a functioning amygdala or who have damage to this structure (Adolphs, Tranel & Buchanan, 2005; Adolphs et al., 1997), in particular the emotional memory enhancement due to arousal, rather than valence (Phelps et al., 1998).

The influence of emotion extends beyond rapid mechanisms that operate during episodic memory encoding. Even when encoding-related factors such as attention and rehearsal are equated, emotional stimuli are more likely to be remembered later (Harris & Pashler, 2005; Kensinger & Corkin, 2004; Sharot & Phelps, 2004). In a set of experiments by Sharot and Phelps (2004), participants fixated on a word presented for 250 ms in the center of a computer screen while neutral and arousing words flashed in the periphery. The results showed that memory for peripheral emotionally arousing words remained stable or slightly improved over a 24-hour delay, while memory for neutral peripheral items declined. These results suggest emotion-induced memory enhancement results, at least in part, from enhanced consolidation that is independent of attentional factors at the time of encoding (for a review see McGaugh, 2004).

Memorial Costs of Emotional Arousal for Nearby Information

The selective enhancement of emotional information in both perception and memory may come at a cost to information that is spatially or temporally contiguous with the emotion-inducing stimulus (Anderson & Shimamura, 2005; Burke, Heuer, & Reisberg, 1992; Christianson, 1984; Christianson & Loftus, 1991; Christianson, Loftus, Hoffman & Loftus, 1991; Hadley & MacKay, 2005; Hurlemann et al., 2005; Mather, Gorlick, & Nesmith, in press; Mather et al., 2006; Mitchell, Mather, Johnson, Raye, & Greene, 2006; Strange et al., 2003; Touryan, Marian, & Shimamura, 2007; see Mather, 2007 for a review). For instance, in mixed word lists that included both neutral and taboo words presented in rapid succession (170 ms per word), immediate recall of taboo words was enhanced at the expense of preceding and following neutral words (MacKay et al., 2004). Memory impairments for neutral stimuli preceding and following emotionally arousing material also occur in lists of verbal and visual stimuli at longer presentation rates, such as every 3 - 5 s (e.g., Hurlemann et al., 2005; Strange et al., 2003).

The present study follows the general outline of a procedure developed by Strange and colleagues (2003). They presented words in blocked lists consisting of several semantically related control nouns, one emotionally aversive noun (also semantically related to the list words), and one perceptually distinct semantically related noun (a "neutral oddball"). Immediately after the presentation of each list, participants were asked to verbally recall the list items. Strange et al. found that participants recalled more of the emotionally aversive nouns than the neutral control nouns. In addition, neutral items shown just before emotionally aversive nouns (hereafter referred to as E-1 stimuli) were significantly less likely to be recalled relative to control nouns.

Emotion-induced retrograde (E-1) and anterograde (E+1) amnesia were observed in a similar experiment that used lists of line drawings as control stimuli and substituted emotionally arousing pictures for emotionally aversive nouns (Hurlemann et al., 2005). In both the Strange et al. and the Hurlemann et al. experiments, beta-adrenergic blockade with propranolol reversed both the memory enhancement for emotional pictures and impairment of E+/-1 stimuli, indicating that beta-adrenergic activation plays a key role in both the retrograde and anterograde amnesia effects seen with emotional items (see Hurlemann, 2006, for a review).

The Exception: When Emotionally Arousing Items Enhance Memory for Associated Information

In contrast with studies revealing memory impairment for neutral items that are temporally adjacent to emotionally arousing material, Anderson et al. (2006) found memory enhancement for E-1 items. Participants were presented with pairs of stimuli consisting of a neutral item (a face or a house) followed by a scene that was either emotionally arousing or

neutral (see Figure 1). The interval between the neutral item and the subsequent scene varied between 4 and 9 seconds. At the shortest temporal lag (4 seconds), recognition accuracy for neutral items preceding emotionally arousing items was enhanced when recognition memory was tested one week later. No memory enhancement was found for faces/houses presented before emotionally provocative pictures at the longer stimulus onset asynchronies (SOAs). Because the emotion-induced retrograde enhancement was apparent only at the shortest SOA, there may be a critical window of time during which emotional arousal can enhance memory for temporally adjacent items.

How can the Anderson et al. findings be reconciled with those of other studies showing memory impairment for neutral items temporally adjacent to emotional material (e.g., Ellis et al., 1971; Hurlemann et al., 2005; Strange et al., 2003)? Based on the methodological differences between the studies, we came up with a list of hypotheses to test (please see Figure 1 A vs B for a comparison of the experimental designs).

First, Anderson et al. tested participants after a delay of one week, whereas previous studies showing emotion-induced retrograde impairment tested participants immediately. Consolidation processes may require an extended time course in order for E-1 enhancement to take hold. Therefore, in Experiment 1, we compared memory tested after a week with memory tested during the same session.

The next main methodological difference was the format of the retrieval test. Whereas Anderson et al. used a recognition test and found emotion-induced enhancement, most prior studies showing emotion-induced impairment used recall tests. In comparison with free recall tests, old/new recognition tests require less contextual information for successful performance. If emotional arousal allows for sufficient or enhanced encoding of E+/-1 item information, but selectively impairs the ability to contextualize the items, it may be possible to recognize items but difficult to retrieve them on free recall tests. In order to further clarify how emotional arousal influences the information remembered about E+/-1 items, we assessed recognition memory for both the general theme and specific visual details of items appearing in close proximity to neutral and emotional oddballs.

A third methodological factor we thought could be critical is the nature of the attention given to the neutral items preceding emotional or neutral modulator pictures. In the Anderson et al. paradigm, participants viewed only one neutral item before each modulator picture, and indicated whether or not they thought they would remember it later. This format should have fostered a high level of attention to each of the neutral items at the time of encoding. In contrast, studies using the oddball paradigm typically showed a series of neutral items with the modulator picture (an emotional or neutral "oddball") inserted randomly in one of several positions near the midpoint of each list. Requiring participants to hold numerous items simultaneously in working memory in anticipation of a memory test is likely to have spread attentional resources across multiple items, yielding less attentional weight on any one item from the list than to the face/house items in the Anderson et al. (2006) paradigm.

Mather (2007) has proposed an object-based framework that can account for both emotion-induced impairments and enhancements in the memorial binding of emotional stimuli and contiguous neutral stimuli. Relative to neutral objects, emotionally arousing objects are more likely to elicit focused attention and receive enhanced processing at both early stages (perception, encoding) and later stages (consolidation) of episodic memory. According to this framework, the way in which emotional arousal influences episodic memory depends critically on how attention is directed when the emotional arousal occurs (Mather, 2007). Consistent with this notion that the effects of emotional arousal depend on how attention is

directed at the time the arousal is experienced comes from recent work showing that emotion-related tradeoffs in memory that disadvantage peripheral information can be eliminated when participants adopt encoding strategies that direct attention away from a visually arousing object and toward other aspects of a complex visual scene (Kensinger, Garoff-Eaton, & Schacter, 2006).

Previous research suggests that long-term memory depends, in part, on the nature of attention at the moment an event is experienced or reactivated later (see Johnson, 1992, Paller & Wagner, 2002, for reviews). When considering how arousal-attention interactions might relate to Anderson et al.'s finding of memory enhancement for neutral items temporally contiguous to arousing items, a key point is that the integration of the neutral item's features into a coherent memory record may depend on how attention is allocated to each item during encoding. Thus, according to the object-based framework, the specific way in which attention is allocated should play a crucial role in determining whether emotion-induced retrograde enhancement or impairment occurs. Specifically, arousing items may enhance memory for preceding items if those items currently have high attentional weights (as was the case in the Anderson et al. paradigm) but not if the attentional weights for those items are weak (as in the oddball paradigm).

Previous research suggests that emotional arousal can enhance memory for the specific visual or contextual details of emotional items relative to neutral items (see Mather, 2007, for a review). For example, participants are better able to distinguish identical items seen at encoding from visually similar items when the items are emotionally arousing than when they are neutral (Kensinger et al., 2006; Kensinger et al., 2007) and participants have better memory for the locations of arousing pictures than the locations of neutral pictures (Mather, Gorlick, & Nesmith, in press; Mather & Nesmith, 2008). There is also evidence to suggest that in complex scenes, emotional arousal can enhance memory for the general theme, or "gist," of an event (Denberg, Buchanan, Tranel, & Adolphs, 2003). Based on these findings, it is possible that emotion-induced memory enhancement may carry over to the visual details of E+/-1 items, the general theme of these items, or to both.

The Current Experiments

We designed Experiment 1 following the format of Hurlemann et al. (2005). Participants were shown short lists of neutral images of everyday objects (non-oddball stimuli) in a serial presentation format. In addition to a series of these objects shown on a white background, we also included one oddball photograph in each list. The oddball photographs depicted either neutral content or negative, emotionally arousing content, allowing us to examine how emotional arousal influenced participants' ability to remember everyday objects appearing before and after each oddball. As done by Hurlemann et al. (2005), we asked participants to recall the items after each list presentation. We predicted that emotionally arousing pictures would impair free recall for items that immediately preceded and followed them, as seen in previous studies (e.g., Hurlemann et al., 2005; Strange et al., 2003).

In addition, in one group of participants we tested recognition memory immediately after the encoding session and in another group we tested recognition memory after a delay of one week. We expected retrograde and anterograde impairment when testing recognition memory immediately after the encoding session, consistent with the impairments in immediate recall. However, it was less obvious what to expect for the delayed recognition test. If the impairments induced by the emotionally arousing item are caused by a disruption of encoding, retrograde and anterograde impairment should persist on a delayed recognition test. However, if the amnesia is due to temporary retrieval blockage or is countered by enhanced memory consolidation for items presented close to emotionally arousing items, a delayed recognition test should show a diminishment or reversal of the anterograde and

retrograde amnesia. Thus, we compared recognition memory at the end of the first session to recognition memory a week later to determine whether or not the typical retrograde amnesia effect would diminish over time or resemble the retrograde enhancement effect seen by Anderson et al. (2006).

Another goal of the present study was to clarify how emotional arousal influences the quality and quantity of information remembered about E+/-1 items. Therefore, we assessed memory for both the general theme and specific visual details of items appearing before and after emotional and neutral oddballs.

Emotional arousal is most likely to enhance aspects of episodic memory that are the focus of attention (see Mather, 2007 for a review). In most studies, it is the inherently emotionally arousing items within a scene that attract attention and receive a mnemonic boost. However, we propose that the mnemonic boost supplied by emotional arousal will occur not only for emotionally arousing items, but also for items having the highest attentional weights during the time emotional arousal is induced. In Experiment 1, we used whether an item was recalled immediately after each list presentation as a marker of the item's attentional weight at the time emotional arousal is induced. An item's attentional weight influences the efficacy of processes that maintain, manipulate and rehearse information, all of which have been shown to facilitate the creation and later accessibility of new memory traces (Blumenfeld & Ranganath, 2006). To compare memory performance for items with high versus low attentional weights, we measured participants' ability to correctly recognize recalled and non-recalled items after the end of the initial encoding session and after a one-week delay.

Experiment 2 provided a stronger test of the interaction between an item's attentional weight at the time of encoding and emotion-induced retrograde and anterograde effects. We directly manipulated the rehearsal of neutral items presented close in time to emotionally arousing stimuli to observe the relationship between an item's attentional weight at the time emotional arousal occurs and the likelihood of retrieving that item one week later.

Experiment 1

Methods

Participants—Undergraduate students (N = 52, $M_{\rm age}$ = 19.02, SD = .69, 12 males) received course credit for participating. All participants provided informed consent in writing prior to the experiment. The study involved two separate sessions. Of the 52 participants who were present for the first session, 45 returned for the second session one week later (22 in the immediate recognition test condition, 23 in the delayed recognition test condition). The participants who did not return were excluded from all analyses.

Stimuli—Similar to the presentation format used by Hurlemann et al. (2005), stimuli were selected to fit into one of two categories: oddball and non-oddball stimuli. Each stimulus was given a corresponding verbal label (semantically identical noun with 4 to 10 letters, presented in Times New Roman font). Non-oddball items consisted of neutral everyday objects (e.g. a lamp or a salad) selected from a database that consists of homogenous computer-generated images (Tarr, 2005). The computer-generated images were supplemented with a few additional computer-generated images from other online image databases. Each computer-generated object was matched with a corresponding real photograph of the object selected from the Internet. Although similar items (e.g. a computer generated image of a brush and real photograph of a brush) shared the same verbal label, they were allowed to differ in terms of orientation, color and shape. From this pool of objects, 24 lists of seven semantically different stimuli were constructed. Each list contained seven neutral everyday objects (non-oddball stimuli) from different semantic categories and

one oddball picture. Within each list, either 3 or 4 of the non-oddball items were real photographs of objects (natural stimuli) and the remaining items were computer-generated objects (artificial stimuli). Across all lists, half of the non-oddball items were real photographs and the remaining half consisted of computer-generated objects. Each list also included one emotionally arousing oddball or one neutral oddball inserted into list position 3, 4, 5 or 6. The serial position of oddballs was balanced to reduce primacy and recency effects. Neutral oddballs differed from non-oddball items in that they were all photographs depicting scenes in which one or more persons were engaging in a common activity (e.g., studying, cooking, cleaning, etc.). One third of the non-oddball items (56 items; 8 lists) were withheld as foils for a later recognition test (which third were foils was counterbalanced across participants). There were two versions of each foil (one computer-generated and one real photograph). The particular version of an object (natural or artificial) and the type of oddball it appeared with were counterbalanced across participants. No participant saw both the natural and artificial version of an object. Twenty-four oddball stimuli (12 perceptual and 12 emotional), equated in terms of human presence, were selected from the International Affective Picture System (IAPS; Lang, Bradley & Cuthbert, 1999) and from the Internet. An independent group of undergraduate students (N = 61, $M_{AGE} = 19.39$, SD = 1.36, 22 males) rated oddball stimuli in terms of valence and arousal on a 7-point scale (7 being most negative on the valence scale and most arousing on the arousal scale). The neutral (M = 1.35 \pm .10) and emotional oddballs ($M = 5.88 \pm .16$) differed significantly in terms of valence, $F(1, 60) = 2319.49, p < .0001, \eta_p^2 = .98$. In addition, neutral oddballs ($M = 1.52 \pm .11$) were rated as significantly less arousing than emotional oddballs ($M = 5.65 \pm .18$), F(1, 60) =1617.09, p < .0001, $\eta_p^2 = .96$.

Procedure—Stimuli were presented sequentially at a rate of one every three seconds (stimulus duration = 2 s + 1-s ISI) in the center of a 15-inch Macintosh computer screen. During the run, participants were presented with 24 lists, each signaled with the words "New List." To insure that participants attended to each item, they were asked to indicate with a key press whether the non-oddball item presented was "artificial" (a computer-generated image) or "natural" (a real photograph). Each list was followed immediately by a 25-s distracter task during which participants were presented with math problems and solutions and had to determine whether the solutions were correct or incorrect. Episodic memory was tested immediately after the 25-s math task and was signaled by the words "Please Recall." At this time, participants had 30 seconds to write down as many items from the list as they could remember. The computer displayed the time remaining and a beep occurred at the end of the elapsed time to alert the participant that a new list would appear (please see Figure 2A for a schematic of the trial structure).

Following the presentation of the 24 lists, half of the participants took an immediate recognition test for both the oddball and non-oddball items. The remaining half took the recognition test one week later. The early-test group also returned a week later, but did an unrelated study in the second session.

On each trial of the recognition test, participants were presented with a pair of items that shared the same verbal label (e.g., both were "spoons") but differed in other visual features (e.g., orientation, color, shape). In 2/3rds of the trials, one of the items in a pair was identical to a previously studied item. In the remaining 1/3rd of the trials a new item and a similar partner were shown on opposite sides of the computer screen. The word "old" appeared below each item either in red (item on the left) or blue (item on the right) font. The word "new" appeared in yellow and was centered below the two "old" labels. Participants were instructed to indicate which of the two items matched the non-oddball item seen previously, or if both of the items were new. To indicate a particular item was old, participants pressed a key on the keyboard that matched the color of the word "old" (red or blue) and the side of

the screen where the selected item appeared. To indicate that a pair of items was new, participants pressed the space bar, which had been marked with a yellow sticker. Following Kensinger et al. (2007), "old" responses to the items that were seen at encoding were used as a measure of memory for the specific details about the object's initial presentation and were categorized as "specific recognition." "Old" responses to either the identical version of the item or the similar version of the item were used as a measure of memory for the general characteristics or gist of an item and were categorized as "general recognition." The recognition test for non-oddball items was followed by a forced-choice recognition test for the oddball items. Foils were selected to match the oddballs in terms of human presence and thematic content.

Results

Memory performance (proportion of total items remembered in that position) was computed for the oddball and oddball +/-1 positions.

Immediate Recall—Free recall performance was determined for the emotional and perceptual conditions separately by calculating the proportion of items recalled for the following three list positions: oddball - 1, oddball, and oddball + 1. We compared items in each of these list position in the emotional condition to the items in the corresponding list positions in the perceptual condition.

A repeated measures ANOVA with oddball type (emotional, neutral) and list position (oddball - 1, oddball + 1) as within-subjects factors revealed a significant main effect of oddball type, F(1, 43) = 6.62, p < .05, $\eta_p^2 = .13$. Recall accuracy (oddball + 1 and oddball - 1 items collapsed) was lower for items near emotional oddballs ($M = .38 \pm .05$) than for items near neutral oddballs ($M = .43 \pm .04$). Replicating the results of Hurlemann et al. (2005), the results showed a significant emotion-induced retrograde amnesia for E-1 items ($M = .36 \pm .06$) relative to N-1 items ($M = .44 \pm .06$). In addition, recall of E+1 items ($M = .38 \pm .05$) was lower relative to N+1 items ($M = .42 \pm .04$) (see Figure 3). In contrast, the proportion of emotional oddballs recalled ($M = .96 \pm .02$) did not differ significantly from the proportion of neutral oddballs recalled ($M = .95 \pm .02$), F(1, 43) = 1.83, p > .10.

Emotion-Induced Amnesia Effects in Recognition - Oddball +/-1 Positions

To assess the influence of emotional arousal on mean corrected recognition memory over an extended time course, a repeated measures ANOVA was conducted with memory type (general recognition, specific recognition), oddball type (emotional, neutral) and nonoddball position (oddball -1, oddball + 1) as within-subject factors and delay (immediate, one-week) as a between-subjects factor. The results revealed significant main effects of delay, F(1, 43) = 60.24, p < .001, $\eta_p^2 = .68$, and memory type, F(1, 43) = 98.16, p < .001, $\eta_p^2 = .70$. As expected, recognition performance was better on the immediate test (M = .69) \pm .08) than it was after a one-week delay ($M = .27 \pm .08$). In addition, general recognition scores were higher $(M = .53 \pm .05)$ than specific recognition scores $(M = .43 \pm .06)$. As expected, participants were more likely to retain at least the general theme of the nonoddball items than their specific details. There also was an interaction between memory type and delay, F(1, 43) = 17.50, p < .001, $\eta_p^2 = .29$, revealing that specific recognition declined more over the delay ($M_{IMMEDIATE} = .72 \pm .07$, $M_{DELAY} = .34 \pm .08$) than did general recognition (M_{IMMEDIATE} = .66 \pm .07, M_{DELAY} = .21 \pm .08). The results also showed a significant main effect of oddball type, F(1, 43) = 4.41, p < .05, $\eta_p^2 = .09^1$, as items occupying positions temporally adjacent to emotional oddballs ($M = .46 \pm .06$) were less likely to be correctly recognized than items in positions temporally adjacent to neutral oddballs ($M = .50 \pm .06$). This was qualified by an interaction between memory type and oddball type, F(1, 43) = 10.55, p < .01, $\eta_p^2 = .20$, as specific recognition was worse for

> items in emotional oddball lists ($M = .41 \pm .06$) than for items in neutral oddball lists ($M = .41 \pm .06$) than for items in $M = .41 \pm .06$ $46 \pm .06$). In contrast, memory for at least the general theme of items that appeared in emotional oddball lists (M = $.52 \pm .06$) and items that appeared in neutral oddball lists (M = . $54 \pm .06$) did not differ significantly. The main effect of oddball type did not interact with delay. Thus, the emotion-induced impairment in specific recognition observed for E +/- 1 items persisted across the delay period.

Recognition as a Function of Recall

We reasoned that non-oddball items that received enough of a benefit from reflective processes in working memory to be reported on the immediate free recall test had higher attentional weights in working memory than did non-recalled items when participants reacted to the oddball picture. We predicted that emotion-induced retrograde enhancement would occur for non-oddball items that had high attentional weights while participants were processing emotional oddballs. In contrast, we predicted that retrograde impairment would occur for non-oddball items with low attentional weights while participants were processing emotional oddballs.

We tested these hypotheses by assessing whether emotional arousal had a differential influence on later recognition of retrieved and non-retrieved items on the immediate free recall test. For each participant, the number of items recalled and correctly recognized was divided by the total number of items recalled for each list position (i.e., recalled items correctly recognized per list position / total items recalled per list position). Proportions of recalled items that were recognized were then compared to proportions of non-recalled items that were recognized (i.e., non-recalled items correctly recognized per list position / total items not recalled per list position). To avoid the loss of significant amounts of data where participants recalled zero items for a particular position, the number of correct recognition responses to previously seen items was collapsed across the four list positions preceding oddballs. The same procedure was followed to obtain an overall measure of recognition accuracy for items that followed oddballs².

Recognition for Recalled and Non-Recalled Items

Recognition accuracy (hits - false alarms) was submitted to a repeated-measures ANOVA with memory type (general, specific), recall status (recalled, not recalled), list position (items preceding oddballs, items following oddballs), and oddball type (emotional, neutral) as within-subjects factors, and delay (immediate vs. one-week recognition) as a betweensubjects factor. The results revealed a significant five-way interaction between all the factors, $(F(1, 40) = 10.27, p < .01, \eta_p^2 = .20)$. For the purpose of clarity, we present the ANOVA results for general and specific recognition separately.

General Recognition for Recalled and Non-Recalled Items

General recognition (hits [same + similar items] - false alarms) was submitted to a repeatedmeasures ANOVA with recall status (recalled, not recalled), list position (items preceding

¹The same result was obtained when recognition accuracy was assessed by computing the proportion of hits to old items (independent of false alarm rate). A repeated measures ANOVA with oddball type (perceptual, emotional) and list position (oddball +1, oddball - 1) as within-subjects factors and delay (immediate, one week) as a between-subjects factor was carried out on the proportion of hits in order to assess the influence of emotional arousal on recognition memory over an extended time course. The results revealed a significant main effect of oddball type, F(1, 42) = 12.49, p<.001, $\eta p^2 = .23$. Non-oddball items occupying positions immediately before and after emotional oddballs ($M = .63 \pm .04$) were less likely to be correctly recognized than were items immediately surrounding neutral oddballs ($M = .68 \pm .05$). In addition, there was a significant main effect of delay, F(1, 42) = 49.83, p < .001, pp^2 = .54. As expected, recognition performance was better on the immediate test $(M = .82 \pm .05)$ than it was after a one-week delay $(M = .82 \pm .05)$ $49 \pm .06$). No other main effects or interactions emerged. ²For this analysis, recall data was missing for three participants, leaving a total of 20 participants in the immediate condition and 22

participants in the delay condition.

oddballs, items following oddballs), and oddball type (emotional, neutral) as within-subjects factors, and delay (immediate vs. one-week recognition) as a between-subjects factor. The results revealed a significant main effect of recall, F(1, 40) = 639.39, p < .0001, $\eta_p^2 = .94$. Participants were more likely to correctly recognize items they retrieved on the immediate recall tests $(M = .61 \pm .06)$ than items they did not retrieve $(M = .28 \pm .06)$. As expected, there was a main effect of delay, F(1, 40) = 27.33, p < .0001, $\eta_p^2 = .41$. General recognition was higher on the immediate test $(M = .63 \pm .06)$ than after a one-week delay $(M = .26 \pm .06)$ 06). The results also showed a significant recall status by oddball type by position interaction, F(1, 40) = 9.79, p < .01, $\eta_p^2 = .20$. General recognition was higher for recalled items that appeared before emotional oddballs ($M = .64 \pm .06$) than for recalled items that appeared before neutral oddballs ($M = .60 \pm .06$). Thus, items with high attentional weights during oddball presentation were more likely to be recalled if the oddball was emotional than if it was neutral. General recognition performance for recalled items appearing after emotional oddballs ($M = .60 \pm .06$) and recalled items appearing after neutral oddballs ($M = .60 \pm .06$) $61 \pm .06$) did not differ significantly. A different pattern emerged for non-recalled items. General recognition was lower for non-recalled items that appeared before emotional oddballs ($M = .23 \pm .06$) than for non-recalled items that appeared before neutral oddballs $(M = .27 \pm .06)$. Thus, for items that had relatively low attentional weights during encoding, we observed emotion-induced retrograde impairment. In addition, general recognition was higher for non-recalled items that followed emotional oddballs ($M = .33 \pm .06$) than for nonrecalled items that followed neutral oddballs ($M = .29 \pm .06$). Emotional arousal had an enhancing effect on general recognition of non-recalled items appearing after emotional oddballs.

Critically, the results revealed a significant oddball type by delay interaction, F(1, 40) = 7.82, p < .01, $\eta_p^2 = .16$. To clarify how general recognition memory for neutral items that preceded and followed emotional oddballs changed as a function of delay, the data were split by delay condition and general recognition was examined on the immediate and delayed tests separately.

Immediate Test—The results showed a marginally significant main effect of oddball type, F(1, 19) = 4.23, p = .05, $\eta_p^2 = .18$. General recognition was higher for items in neutral oddball lists ($M = .64 \pm .08$) than for items in emotional oddball lists ($M = .62 \pm .08$). Results also showed a significant main effect of position, F(1, 19) = 12.20, p < .01, $\eta_p^2 = .39$. General recognition was lower for items preceding oddballs ($M = .60 \pm .08$) than for items following oddballs ($M = .66 \pm .08$). In addition, there was a significant recall status by position interaction, F(1, 19) = 17.83, p < .01, $\eta_p^2 = .49$. For items recalled, position made little difference in general recognition ($M_{\text{PRECEDING}} = .79 \pm .08$, $M_{\text{FOLLOWING}} = .80 \pm .08$). However, general recognition was lower for non-recalled items preceding oddballs ($M = .41 \pm .10$) than for non-recalled items following oddballs ($M = .51 \pm .08$). In other words, encoding was not disrupted as much for non-recalled items that followed the oddball as it was for non-recalled items that preceded the oddball (see Figure 4A).

Delayed Test—The results on the delayed test were quite different from those on the immediate test. There was a significant main effect of oddball type, F(1, 21) = 4.64, p < .05, $\eta_p{}^2 = .18$, but the pattern was reversed. That is, after a one-week delay, general recognition was higher for items in emotional oddball lists ($M = .28 \pm .06$) than for items in neutral oddball lists ($M = .24 \pm .06$). The emotion-induced amnesia apparent on the immediate test disappeared over the delay and emotion-induced enhancement emerged. The results also revealed a significant recall status by oddball type by position interaction, F(1, 21) = 8.95, p < .01, $\eta_p{}^2 = .30$ (see Figure 4B). General recognition was higher for recalled items that preceded emotional oddballs ($M = .49 \pm .10$) than for recalled items that preceded neutral oddballs ($M = .39 \pm .10$). In contrast, general recognition did not differ for recalled items

that followed emotional oddballs ($M = .41 \pm .09$) and recalled items that followed neutral oddballs ($M = .40 \pm .09$). This pattern suggests that items appearing before an emotional oddball that have high attentional weights at encoding are exceptional in their tendency to benefit from the memory enhancing effects of emotional arousal. Non-recalled items appearing before emotional oddballs ($M = .07 \pm .08$) were less likely to be correctly recognized than items appearing before neutral oddballs ($M = .10 \pm .08$). Thus, for items with lower attentional weights at encoding, retrograde enhancement was not observed in recognition memory after a one-week delay. In contrast, non-recalled items appearing after emotional oddballs ($M = .14 \pm .07$) were more likely to be correctly recognized than their counterparts in neutral oddball lists ($M = .07 \pm .07$).

Specific Recognition for Recalled and Non-Recalled Items

Specific recognition (hits [same items] – false alarms) was submitted to a repeated-measures ANOVA with recall status (recalled, not recalled), list position (items preceding oddballs, items following oddballs), and oddball type (emotional, neutral) as within-subjects factors, and delay (immediate vs. one-week recognition) as a between-subjects factor. The results revealed a significant main effect of recall, F(1, 40) = 377.64.07, p < .0001, $\eta_p^2 = .90$. Specific recognition was higher for recalled items ($M = .50 \pm .07$) than for non-recalled items ($M = .21 \pm .06$). As expected, there was a main effect of delay, F(1, 40) = 115.39, p < .0001, $\eta_p^2 = .74$. Specific recognition was higher on the immediate test $(M = .57 \pm .10)$ than after a one-week delay ($M = .14 \pm .10$). The results also showed a significant main effect of oddball type, F(1, 40) = 10.70, p < .01, $\eta_p^2 = .21$. Participants were more likely to remember visual details of items in neutral oddball lists ($M = .37 \pm .06$) than they were to remember visual details of items in emotional oddball lists ($M = .34 \pm .06$). The results also showed a main effect of item position (F(1, 40) = 9.47, p < .01, $\eta_p^2 = .19$), as specific recognition was lower for items appearing before oddballs ($M = .34 \pm .07$) than for items appearing after oddballs ($M = .38 \pm .06$). This was qualified by an oddball type by position interaction, F(1, 1)40) = 4.13, p < .05, $\eta_p^2 = .09$. The interaction showed that specific recognition was lower for items preceding emotional oddballs ($M = .31 \pm .06$) than for items preceding neutral oddballs ($M = .36 \pm .06$). Thus, the retrograde impairment effect was emotion-induced. Specific recognition of items that followed emotional oddballs ($M = .37 \pm .06$) and items that preceded $(M = .37 \pm .06)$ and followed neutral oddballs $(M = .38 \pm .06)$ did not differ significantly. Finally, the results revealed a significant interaction between oddball type and delay, F(1, 40) = 4.55, p < .05, $\eta_p^2 = .10$.

To clarify how specific recognition memory for neutral items that preceded and followed emotional oddballs changed as a function of delay, the data were split by delay condition and specific recognition was examined on the immediate and delayed tests separately.

Immediate Test—The results showed a main effect of oddball type, F(1, 19) = 15.66, p < 0.01, $\eta_p^2 = .45$. Specific recognition was higher for items in neutral oddball lists ($M = .60 \pm .10$) than for items in emotional oddball lists ($M = .54 \pm .10$). Results also showed a significant main effect of position, F(1, 19) = 18.39, p < .001, $\eta_p^2 = .49$. Specific recognition was lower for items preceding oddballs ($M = .53 \pm .10$) than for items following oddballs ($M = .61 \pm .10$).

Delayed Test—After a one-week delay, the main effect of oddball type was no longer significant, F < 1, ns.

In summary, there were oddball type by delay interactions for both general and specific memory measures; in both cases there was more emotion-induced retrograde impairment for

recalled items on immediate than delayed tests, however, the full reversal to emotion-induced retrograde enhancement over a week delay only occurred for general recognition.

Discussion

Replication and Extension of Previous Results – Recall and Recognition Scores for E +/- 1 Items

In Experiment 1, relative to their counterparts in neutral oddball lists, E - 1 and E + 1 items were significantly less likely to be recalled immediately after each list presentation. Our findings thus replicated emotion-induced retrograde and anterograde amnesia in tests of immediate recall (Hurlemann et al., 2005; Strange et al., 2003) with a novel stimulus set.

In addition to testing recall immediately after each list, we also tested recognition memory at the end of the session or a week later. To our knowledge, this is the first study to compare immediate and delayed emotion-induced retrograde and anterograde effects. Our findings replicate previous findings of anterograde amnesia in immediate recognition (e.g., Ellis et al., 1971; Detterman & Ellis, 1972; Schmidt, 2002). On both the immediate and delayed tests, emotion-induced amnesia was observed in recognition memory for E +/-1 items. Our findings further indicate that emotion-induced decrements in memory performance persist over time; a delay of one week did not mitigate the overall recognition advantage for N+/-1 items over E+/-1 items. In addition, by examining both specific and general recognition, we were able to show that the impairment in memory in emotional oddball lists is selective for the visual details of previously seen E+/-1 items. No significant difference emerged in memory for the general theme of items presented immediately before and after emotional oddballs. Thus, participants were able to at least remember that they had seen these items before. However, the appearance of the emotional oddball selectively compromised the ability to form item-context associations to support a detailed recollection of the particular E +/-1 item experienced. These findings suggest that the retrograde and anterograde amnesia in free recall observed in previous emotional oddball studies may reflect failures in selfdirected recollection that might not extend to gist recognition memory.

Recognition Memory as a Function of Recall Status - Recognition Scores for Before-Oddball and After-Oddball Items

In addition to replicating emotion-induced retrograde and anterograde effects, a second major goal of our study was to understand the mechanisms of contradictory findings of emotion-induced memory amnesia and enhancement for items appearing near an emotionally arousing item. We predicted that an item's attentional weight at the time of encoding would play a crucial role in whether emotion-induced amnesia or enhancement would be observed. In addition, based on Anderson et al.'s finding of emotion-induced retrograde enhancement after a one-week delay period, we examined whether or not an extended time course is necessary for emotion-induced retrograde enhancement to be expressed.

Recalling items that appeared before an oddball immediately after list presentation is an indication that the items were active in working memory (and therefore had higher attentional weights than non-recalled items) during the oddball presentation. This initial strength of before-oddball memory representations had an impact on how they were affected by emotional oddballs. We found enhanced general recognition of before-oddball items that were successfully recalled on the immediate free recall tests. However, the retrograde enhancement effect was not apparent on the recognition test administered during the same session as encoding; it emerged only after a delay period of one week. Thus we observed both emotion-induced impairment and enhancement within the same experimental

paradigm. However, the emotion-induced enhancement effect in general recognition required an extended time course to be expressed and was only seen for previously recalled items.

These findings suggest that highly activated items appearing near in time to the induction of emotion are endowed with emotion's memory enhancing effect. The neurobiological processes that accompany emotional arousal may act to stabilize representations that are most active within a specific temporal window. Consolidation of these representations may be enhanced over extended time periods (days to weeks).

Furthermore, the emotion-induced memory impairment observed in specific recognition was no longer present after a one-week delay. The fact that the emotion-induced amnesia for the visual details of non-oddball items was present after a short delay but did not occur after the long delay suggests that the impairment is relatively short-lasting. While emotion might impair immediate retrieval of an item's visual details, consolidation processes may remove this temporary retrieval blockage. In contrast, when we examined memory performance for E-1 items alone, memory impairment for visual details persisted across the delay [not clear how the data referred to by this sentence are different from those referred to by the beginning of the paragraph]. Taken together, these finding suggest that the representation of visual details of E-1 items are sensitive to encoding disruption by emotional oddballs when the interstimulus interval is short (1 second). The degree of disruption produced by an emotional oddball lessens with the temporal distance between the emotional oddball and the items that appear before it.

Our results further suggest that if items occurring near in time to emotional arousal are overshadowed when competing for limited attentional resources, their consolidation will not benefit from their original proximity to arousal. This was presumably the case for nonrecalled items that preceded emotional oddballs. Interestingly, emotion-induced enhancement was observed for non-recalled items that followed emotional oddballs. Nonrecalled items presented after oddballs had the advantage of occurring near in time to an emotionally arousing item. Because they appeared near the end of the list, the neural representation of these items did not have much time to be overshadowed or disrupted by previously rehearsed items and therefore may have been able to benefit from the memory enhancing effect of emotional arousal. Memory was not enhanced for recalled items appearing after emotional oddballs. The crucial difference between recalled items and nonrecalled items appearing after emotional oddballs seems to be the degree to which they actively compete for limited attentional resources. Overall, our findings show that the relative amount of rehearsal an object receives at encoding and the delay between encoding and test both play a crucial role in whether or not emotion-induced enhancement or impairment will be observed.

Experiment 2

The findings from Experiment 1 suggest that both an item's attentional weight at encoding and the delay period between encoding and test sessions are crucial factors in determining whether emotion-induced memory enhancement or impairment is observed. However, because the strength of an item's representation in working memory was not manipulated directly, we cannot be certain that this factor led to the retrograde enhancement and impairment observed in recognition memory. In Experiment 2, we compared the memory performance of participants who were instructed to recall the non-oddball items after viewing each list to those who did not have to recall the items. To increase the strength of this manipulation, and to create a closer analogue to the Anderson et al. (2006) presentation format, the number of non-oddball items in each list was reduced from seven to four. The

smaller memory load increased the chances that high levels of attention could be allocated to each list item in the recall condition, which should allow for the greatest chance of observing emotion-induced memory enhancement according to our hypothesis that emotion-induced memory enhancement for preceding list items depends on their attentional weight at the time of the emotional reaction.

As seen in Experiment 1, we predicted that emotion induced impairment would be evident on a test of immediate recall. In addition, for participants in the recall condition, we predicted that retrograde enhancement would be present when memory was tested after a one-week delay. For participants in the no-recall condition, we predicted no retrograde enhancement. However, in Experiment 1 non-recalled items that followed emotional oddballs were more likely to be recognized one week later than non-recalled items that followed neutral oddballs. Based on these results, we predicted a recognition advantage for items following emotional oddballs in the no-recall condition of Experiment 2.

Methods

Participants—Undergraduates (N = 63, 30 recall condition, 33 no recall condition, $M_{AGE} = 19.38$, SD = 1.38, 24 males) received course credit for participating and provided informed consent before beginning the experiment.

Stimuli—Twenty-four lists of four semantically different stimuli were constructed from the pool of non-oddball stimuli used in Experiment 1. Each list contained four everyday objects (non-oddball stimuli) from different semantic categories. Of the 144 total non-oddball stimuli, 96 were used to construct 24 encoding lists and 48 were reserved as foils for a later recognition test. Half of the list items were real photographs of objects (natural stimuli) and the remaining half were illustrations of objects (artificial stimuli). Each list also included one emotionally arousing picture or one neutral oddball inserted into list position 2, 3 or 4, making the list five items long. The emotional and neutral oddballs were the same as those used in Experiment 1. Non-oddball stimuli appearing as old items or as foils were counterbalanced across participants, as was the particular version of an object (natural or artificial) and the type of oddball it appeared with.

Procedure—Half of the participants were randomly assigned to a recall condition. For these participants, the encoding session was the same as in Experiment 1, with two minor changes to accommodate the shorter lists. The math task was reduced from 25 to 20 s and participants were allotted 25 s (instead of 30) to write down as many items from the list as they could remember. Prior to the presentation of the first list, all participants in the recall condition were instructed to remember the items because they would be tested after each list was presented. The remaining half of the participants in the no-recall condition saw each input list and completed the math distracter task, but did not engage in the 25-s recall session after each list. As in Experiment 1, participants in both conditions were asked to determine whether the stimulus presented was "artificial" (a computer-generated image) or "natural" (a real photograph) with a key. At the completion of the math task, the words "New List" appeared and a new input list was shown immediately thereafter.

Following the presentation of the 24 input sequences, all participants returned one week later to take the recognition tests for oddball and non-oddball stimuli. On each trial, participants were presented with pairs of items. The recognition test for non-oddball stimuli consisted of 144 total trials of two types: old items paired with similar foils, and new items paired with similar foils. In 96 of the trials, old items were presented along with a corresponding natural or artificial foil. In the remaining 48 trials, both the natural and artificial version of the new items was shown. Participants were asked to indicate on each

trial which version of the item was seen previously, or to indicate if both items were new. Participants responded by pressing a key corresponding to their selection. The recognition test for non-oddball stimuli was followed by a forced choice recognition test for the oddball items. Foils were selected to match the oddballs in terms of human presence and thematic content.

Results

Immediate Recall—Across the 24 input lists, participants recalled about two-thirds of the items presented (M = .65, SE = .02). There was no significant difference in the proportion of E-1 items recalled ($M = .58 \pm .07$) and the proportion of N-1 items recalled ($M = .57 \pm .08$). This suggests that at lower memory loads than those used in previous investigations (and in Experiment 1), arousing items do not lead to retrograde amnesia. There was marginally significant anterograde amnesia, t(31) = 2.02, p = .05. Participants recalled a smaller proportion of E+1 items ($M = .52 \pm .06$) than N+1 items ($M = .60 \pm .07$).

In the next analysis, we looked more broadly at all of the list items rather than just the items immediately before or after the oddballs. The proportion of items recalled for each list position that preceded and followed oddballs was calculated by dividing the total number of items recalled at each list position by the total number of items seen at that position. Recall proportion was submitted to a repeated-measures ANOVA with oddball type (emotional, neutral) and list position (preceding oddball, following oddball) as within-subjects factors. The results showed a significant main effect of oddball type, F(1, 31) = 4.64, p < .05, $\eta_p^2 = .13$. Participants recalled a larger proportion of items from lists with neutral oddballs ($M = .60 \pm .06$) than from lists with emotional oddballs ($M = .56 \pm .05$). This main effect was qualified by an emotion by position interaction, F(1, 31) = 5.72, p < .05, $\eta_p^2 = .16$ (see Figure 5). There was no significant difference in recall of items that appeared before emotional ($M = .60 \pm .07$) and before neutral oddballs ($M = .59 \pm .07$). However, recall of items that appeared after emotional oddballs ($M = .53 \pm .05$) was lower than items that appeared after neutral oddballs ($M = .61 \pm .07$).

In addition, the proportion of emotional oddballs recalled (M = .94 \pm .04) was significantly larger than the proportion of neutral oddballs recalled (M = .85 \pm .04), F(1, 31) = 17.56, p < .05, η_p^2 = .36.

Delayed Recognition—Recognition accuracy (hits - false alarms) was submitted to a repeated-measures ANOVA with memory type (general, specific), oddball type (neutral, emotional) and list position (preceding oddball, following oddball) as within-subjects factors and encoding condition (recall, no recall) as a between-subjects factor 3 . There was a significant main effect of memory type, F(1, 61) = 137.51, p < .001, $\eta_p^2 = .69$, as participants were more likely to recognize the general theme of previously seen non-oddball items ($M = .40 \pm .04$) than they were to recognize the visual details of those items ($M = .31 \pm .04$). There also was a significant oddball type by encoding condition by position

³Running the same recognition ANOVA with just the oddball +/- 1 items yielded a significant four-way interaction between all factors, F(1, 61) = 4.12, p < .05, $\eta p^2 = .06$. For the purpose of clarity, we present the results for the recall and no recall conditions separately. In the no recall condition, there was a significant memory type by oddball type by position interaction, F(1, 32) = 6.77, p < .05, $\eta p^2 = .18$. In the no recall condition, general recognition was lower for E-1 items ($M = .37 \pm .06$) than for N-1 items ($M = .44 \pm .06$). For items with low attentional weights at encoding, emotion-induced retrograde impairment was observed after a one-week delay. General recognition did not differ for E+1 items ($M = .32 \pm .06$) and N+1 items ($M = .32 \pm .06$). In contrast, specific recognition did not differ significantly for E-1 items ($M = .28 \pm .06$) and N-1 items ($M = .32 \pm .06$). Similarly, specific recognition did not differ for E+1 items ($M = .23 \pm .06$) and N+1 items ($M = .24 \pm .06$). In the recall condition, there was no main effect of oddball type. In addition, add in other condition, the position of the other factors. Thus, in summary, these oddball +/- 1 analyses reveal a pattern of emotion-induced retrograde impairment in the no-recall condition, this emotion-induced retrograde impairment was eliminated, but there was not a reversal to emotion-induced enhancement, as shown when we examined all the before oddball items, as reported in the results section.

> interaction, F(1, 61) = 5.27, p < .05, $\eta_p^2 = .08$ (see Figure 6). When participants were not required to recall the five items from each list immediately after seeing them, recognition a week later did not differ for items that appeared before emotional oddballs ($M = .34 \pm .04$) and items that appeared before neutral oddballs ($M = .33 \pm .04$). These findings are consistent with the findings from Experiment 1, in which non-recalled items that appeared before emotional oddballs showed no emotion-induced retrograde enhancement. Recognition for items that appeared after emotional oddballs ($M = .34 \pm .06$) was numerically higher than for items that appeared after neutral oddballs ($M = .30 \pm .06$). As in Experiment 1, for items with low attentional weights, participants were more likely to recognize items that appeared after emotional oddballs than they were to recognize items appearing after neutral oddballs. However, a post hoc test showed that the difference for post-oddball items in Experiment 2 was only marginally significant, t(33) = 1.81, p = .07.

In addition, as predicted, the recall condition produced a different pattern than the no-recall condition. Recognition memory was better for items that preceded emotional oddballs (M = ... $41 \pm .06$) than for items that preceded neutral oddballs ($M = .34 \pm .06$) ⁴. This finding suggests that increased rehearsal gave the memory enhancing effects of emotional arousal a better chance to strengthen representations of items that appeared before emotional oddballs in the recall condition and mark them for consolidation into long-term memory. Recognition memory for items in the recall condition that followed emotional oddballs ($M = .42 \pm .06$) did not differ significantly from items that followed neutral oddballs ($M = .44 \pm .06$). Thus, as in Experiment 1, emotion-induced enhancement depended on the nature of attention at the time of encoding.

The results also revealed a significant memory type by oddball type by position interaction, $F(1, 61) = 4.94, p < .05, \eta_p^2 = .08$ (see Figure 7). General recognition a week later for items that appeared before emotional oddballs ($M = .42 \pm .04$) and items that appeared before neutral oddballs ($M = .39 \pm .04$) did not differ significantly. Similarly, general recognition for items that appeared after emotional oddballs ($M = .40 \pm .04$) and items appearing after neutral oddballs ($M = .39 \pm .04$) did not differ. In contrast, specific recognition for items that appeared before emotional oddballs was higher ($M = .33 \pm .05$) than for items that appeared before neutral oddballs ($M = .28 \pm .05$)⁵. Specific recognition for items that appeared after emotional ($M = .31 \pm .05$) and neutral oddballs did not differ ($M = .31 \pm .05$). Figure 8 displays this effect separately for the two conditions.

Discussion

The replication of retrograde memory enhancement after direct manipulation of the intention to maintain, manipulate and rehearse each list item permits stronger conclusions about the role of an item's level of activation at the time that emotion is experienced. In Experiment 1, we used whether an item was recalled immediately after each list presentation as a marker of its attentional weight in working memory during the list presentation. In Experiment 2, the attentional weight given to items was manipulated by having participants in one condition recall each list of items after it was presented during the encoding session; the remaining participants were not asked to recall each list of items. We expected that participants in the recall condition would be more likely than participants in the no-recall condition to try to maintain and rehearse list items while seeing the lists. Thus, items in the no-recall condition presumably had lower attentional weights relative to their counterparts in the recall

 $^{^4}$ A paired samples t-test confirmed the difference in recognition memory for items preceding emotional oddballs (M = .41, SE = .03) and items preceding neutral oddballs (M = .34, SE = .03) was significant in the recall condition, t(29) = 2.57, p < .05.

A paired samples t-test confirmed that specific recognition for items preceding emotional oddballs (M = .33, SE = .02) was

significantly higher than for items preceding neutral oddballs (M = .28, SE = .02), t(62) = 2.93, p < .01.

condition and were also less likely to compete for limited attentional resources at encoding. Consistent with the result from Experiment 1, retrograde enhancement was observed in the recall condition for items that appeared before emotional oddballs and were presumably in a state of high activation when emotional arousal occurred. In contrast, in both experiments, emotion-induced retrograde enhancement was not apparent for items that had relatively low attentional weights. In addition, in both Experiments 1 and 2, emotion-induced impairment was observed on tests of immediate recall.

Finally, in both experiments, emotion-induced enhancement emerged after a one-week delay. The findings are consistent with the idea that memory enhancement is less likely to occur after a period of consolidation if items occurring near in time to emotional arousal are overshadowed when competing for limited attentional resources. Being asked to recall the items after each list presentation places pressure on participants to rehearse the items in working memory so that they are available when the test occurs. Thus, items are likely to compete for limited attentional resources prior to the retrieval attempt. One possibility is that recalled pre-oddball items were the ones that had the highest activation levels at the time that emotional arousal evoked by the emotional oddball was experienced. Therefore, these non-oddball items could benefit the most from emotion-induced memory enhancement. The fact that in both experiments, emotional memory enhancement occurred for items with high attentional weights only if they appeared before emotional oddballs suggests that items that are potential predictors of the onset of an emotionally arousing item may be marked for enhanced consolidation. Both an item's attentional weight at encoding and its potential value as a predictor of an important future outcome may be important in determining whether emotion induced enhancement will occur.

There were also some interesting differences between the results of Experiment 2 and those in Experiment 1. The recall data in Experiment 1 replicated the results of previous studies by showing poorer memory for items that preceded and followed emotional oddballs relative to control items on immediate tests of free recall. In Experiment 2, only emotion-induced anterograde amnesia was observed on the free recall test, suggesting that retrograde amnesia effects may depend on list length. In Experiment 1, emotion-induced retrograde impairment reversed over a delay of one week and retrograde enhancement emerged in general recognition. In Experiment 2, emotion-induced memory enhancement was observed after one week in specific recognition. The combination of high attentional weights at encoding and lighter working memory load in Experiment 2 may have allowed participants to hold more detailed information about items that preceded emotional oddballs in working memory. This suggestion is further supported by the fact that immediate recall of items preceding emotional oddballs was not compromised relative to items preceding neutral oddballs in Experiment 2. In summary, emotion-induced enhancement emerged in specific recognition for items appearing before emotional oddballs with performance in the recall and no-recall conditions collapsed. The same trend was apparent in general recognition, but the emotion-induced enhancement effect was not strong enough to be significant. However, as Figure 8 shows, with specific and general recognition performance separated by condition, it was in general recognition that performance was most different according to attentional weight. In accord with the findings in Experiment 1, whereas no retrograde enhancement in general recognition was observed for items in the no-recall condition, retrograde enhancement did emerge for items in the recall condition.

General Discussion

Experiment 1 replicated previous findings of emotion-induced retrograde and anterograde impairment for E +/-1 stimuli in immediate free recall (Hurlemann et al., 2005; Strange et al., 2003). An emotional oddball inserted into a list of neutral items disrupted encoding of

temporally contiguous items. Experiment 1 also showed that memory impairments for E \pm 1 items occur not only on tests of immediate free recall but also on tests of immediate and delayed recognition. Mean corrected recognition scores for items appearing immediately before and after emotional oddballs were significantly lower than mean corrected recognition scores for items appearing immediately before and after neutral oddballs. Thus, emotion-induced amnesia for E \pm 1 items in a list operates over short time scales (seconds) and can persist across a longer time scale (a week). Furthermore, the results from Experiment 1 show that the presentation of an emotional oddball selectively compromises memory for the visual details of E \pm 1 items, as no significant difference was observed in memory for the general theme of items temporally adjacent to emotional oddballs relative to their counterparts in neutral oddball lists.

Thus, the dominant result from Experiment 1 was that arousing items led to forgetting of preceding and subsequent items, both on tests given in the same session and a week later. These results conflict with Anderson et al.'s finding that appearing before an arousing picture led to enhanced memory for a neutral picture a week later. However, by categorizing non-oddball items as having been recalled or not immediately after each list presentation, we were able to observe emotion-induced memory enhancement and impairment within the same experimental paradigm. Items recalled on the immediate tests presumably received high enough activation during strategic rehearsal in working memory to establish memory traces linking them to aspects of the initial learning episode. Consistent with our predictions, for items with high attentional weights at encoding, emotion-induced retrograde enhancement was observed on a recognition test one week after encoding. In contrast, when we examined subsequent recognition memory for items that were not recalled immediately after seeing the list, we observed emotion-induced retrograde impairment, suggesting that items that received relatively fewer encoding resources were even more likely to be forgotten a week later when they had originally appeared near emotional oddball items than near neutral oddball items.

In addition, this analysis revealed that the passage of time made a difference in whether retrograde enhancement or impairment was expressed. On the session-1 test, recognition memory was worse for both the visual details and the general theme of items in emotional oddball lists than for items in neutral oddball lists. This main effect of oddball type did not interact with whether an item was retrieved or not during free recall. In contrast, one week after encoding, emotion-induced enhancement emerged in general recognition. Participants were more likely to remember the general theme of non-oddball items that appeared before emotional oddballs than they were to remember the general theme of their counterparts in neutral oddball lists. For emotion-induced retrograde enhancement to operate on a trial-to-trial basis, a rapid mechanism would have to be involved to tag items for later consolidation. The findings from Experiment 1 confirm Anderson and colleagues' speculation that in order for the retrograde enhancement to be expressed fully, enough time has to pass to let consolidation strengthen recently formed memory representations.

The passage of time also influenced emotion-induced memory impairment in specific recognition. The retrograde impairment in memory for the visual details of non-oddball items was no longer present after a one-week delay. This finding suggests that while emotion impairs immediate retrieval of the specific details of preceding non-oddball items, consolidation processes counteract this retrieval blockage. Overall, our findings help resolve the contradiction of how emotionally arousing items can enhance memory for preceding items in one study (Anderson et al., 2006) but impair memory for preceding items in many other studies (Bornstein et al., 1998; Detterman, & Ellis, 1972; Ellis et al., 1971; Erdelyi & Blumenthal, 1973; Hadley & MacKay, 2006; Hurlemann et al., 2005; MacKay et al., 2004; Miu et al., 2005; Runcie & O'Bannon, 1977; Schmidt, 2002; Strange et al., 2003).

Retrieving recently acquired information can place that information in a labile state that requires reconsolidation to restabilize the memory trace (see Dudai, 2006; Tronson & Taylor, 2007 for reviews). Reconsolidation is thought to play an important role in allowing for memories to be updated, modified and strengthened. In the present studies, the repeated rehearsal of the encoded items in anticipation of immediate free recall tests may have played a role in sensitizing these traces to the memory-enhancing influence of emotional arousal. However, competition in working memory among items may have also sensitized these traces to disruption by stronger competitors.

In Experiments 1 and 2, retrograde enhancement was observed a week later for items that preceded emotional oddballs and were presumably in a state of high activation when emotional arousal occurred. One possible explanation for this pattern of results is that the predictive relationship shared by items that precede an emotionally provocative event increases the likelihood of memory enhancement. Another possibility is that the key factor was the activation level of an item at the time that the arousal was experienced. Those neutral items that had high activation when an arousing item was seen would be marked for subsequent enhanced consolidation, whereas post-oddball items would not receive the same benefit. A related possibility is that the quality of rehearsal in working memory may determine which items are endowed with enhanced recollective experience. Items in early list positions should have received the most rehearsal and so could have dominated or interfered with representations that were formed when working memory capacity limits were challenged.

In Experiment 2, we manipulated the attentional weight given to non-oddball items. Participants in one encoding condition were under pressure to recall each list of items after it was presented during the encoding session. The remaining half of our participants did not engage in free recall of each list. As with recalled items in Experiment 1, in the recall condition we found emotion-induced retrograde enhancement in recognition memory one week later. Consistent with our prediction, our findings suggest that what made these items sensitive to the mnemonic boost provided by emotion was their high level of activation during the initial learning session. The findings in the recall condition of Experiment 2 and for recalled items in Experiment 1 are consistent with the idea that memory enhancement is more likely to occur after a period of consolidation for items occurring near in time to emotional arousal that dominate the competition for limited attentional resources.

Furthermore, among non-oddball items with high attentional weights, in both experiments, emotion-induced memory enhancement was observed for items poised to predict the onset of an emotionally arousing event. For items that were highly activated at encoding but appeared after emotional oddballs, memory enhancement was not observed. Such a finding indicates that items that have high attentional weights and that have the potential to predict the onset of an important future event might be exceptional in their sensitivity to memory enhancement by emotional arousal. Consistent with this idea, previous research has shown that key areas of the brain involved in emotional memory enhancement are also activated in anticipation of an emotional event (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Nitchke, Sarinopoulos, Mackiewicz, Schaefer, & Davidson, 2006). Participants might have been in a state of anticipation prior to experiencing an oddball in each list. However, the anticipation of a distinctive and memorable event alone cannot readily explain the retrograde enhancement we observed. If this were the case, retrograde enhancement should have been observed for neutral items that preceded both emotional and neutral oddballs because both were memorable and distinctive. In addition to modulation by activation level at encoding, our findings suggest an emotion-induced enhancement of consolidation that is independent of attention and rehearsal. Overall, our findings suggest that both activation strength and position relative to the emotional item may be important in determining whether emotion

induced enhancement will occur. However, the current experiments do not allow us to examine the influences of these factors separately.

In Experiment 1, emotional arousal enhanced general recognition for non-recalled items that followed emotional oddballs. This finding is consistent with the contention that neutral items occurring near in time to emotionally arousing items can benefit from emotional arousal's memory enhancing influence after a period of consolidation. Non-recalled items that followed emotional oddballs in Experiment 1 were presented when working memory capacity was heavily loaded and had little or no opportunity to enter and compete with items already in the rehearsal loop. The reduced interference experienced by these representations may have made them less vulnerable to disruption and allowed emotion to enhance their consolidation.

The findings in Experiments 1 reveal that some of the effects of emotionally arousing items only emerge after the passage of time, and thus presumably reflect consolidation processes. On the immediate recognition test in Experiment 1, participants were less likely to correctly recognize the general theme and the visual details of items in emotional oddball relative to items in neutral oddball lists. This emotion-induced amnesia reversed over the delay and retrograde enhancement emerged in general recognition. This finding is intriguing because it suggests that although emotional arousal may mark highly activated preceding items for enhanced consolidation, these items may also become temporarily inaccessible to retrieval attempts in the short term. Although emotion-induced retrograde enhancement was not observed in specific recognition, the impairment in memory for the visual details of items that appeared before emotional oddballs was no longer present when recognition was tested one week later. Over time, consolidation may make memory for the general theme and visual details of these items more resistant to disruption.

There are also some interesting differences between the results in Experiment 2 and those in Experiment 1. The recall data in Experiment 1 replicated results of previous studies by showing poorer memory for items that preceded and followed emotional oddballs relative to control items on immediate tests of free recall. In Experiment 2, only emotion-induced anterograde amnesia was observed on the free recall test, suggesting that retrograde amnesia effects may depend on list length. In Experiment 2, the working memory load was reduced to four neutral items in each list, compared with seven in Experiment 1. Nevertheless, the emotion-induced enhancement observed for recalled items in Experiment 1 was again observed for items in the recall condition of Experiment 2 in spite of the rehearsal differential across experiments.

Another interesting difference to emerge was that in Experiment 1, emotion enhanced memory for the general theme more than for specific details of items that appeared before emotional oddballs after a one-week delay. In Experiment 2, the memory enhancing effect of emotion was also observed in specific recognition for items that preceded emotional oddballs. The combination of high attentional weights at encoding and lighter working memory load in Experiment 2 may have allowed participants to form more detailed representations of items that preceded emotional oddballs in working memory.

Our findings have clarified the circumstances under which emotion-induced enhancement and impairment is most likely to occur. Emotion-induced impairment is most likely when interference in working memory is high and emotionally arousing items consume attentional resources that might otherwise be devoted to rehearsing temporally contiguous neutral items (e.g., Mather et al., 2006). In contrast, emotion-induced enhancement is most likely to occur for items that receive the benefit of rehearsal in working memory and that precede the onset of emotional arousal. In addition, emotion-induced impairment is most likely when memory

is tested shortly after encoding⁶ whereas emotion-induced enhancement is most likely to occur when memory is tested after a delay period. Thus, our findings reveal that emotion-induced enhancement requires an extended time course to be expressed.

An interesting question for future research concerns the flexibility of representations that have undergone enhanced consolidation by virtue of their appearance near an emotional item and the high level of activation they receive at encoding. Recent research suggests that emotional items can produce stronger proactive interference than neutral items, which may make it more difficult to update these representations with new information (Mather, in press; Novak & Mather, in press). In addition, a recent study has shown impairment in the ability to learn new associations to neutral items that were previously associated with emotionally arousing items (Mather & Knight, 2008). Based on this recent evidence, it is possible that neutral items endowed with emotion's memory enhancing influence also produce high levels of proactive interference and may be more resistant to change. Overall, our findings highlight some important features of human memory that may serve an adaptive function, but also can backfire under extreme or extraordinary circumstances. Endowing emotionally arousing stimuli with memory-enhancing potential makes good evolutionary sense, as these events are likely to be instructive.

The fact that the memory-enhancing effect of emotional arousal can radiate outward to encompass neutral information occurring before, and, in some circumstances, after the onset of emotional arousal is intriguing. However, a memory system that randomly marks and records information occurring near in time to an emotionally consequential event without recourse to some protocol for selection would not be very efficient. Consistent with the central tenet of the object-based framework, our findings demonstrate that attention is the ephemeral glue that determines how emotional memory enhancement will later manifest (Mather, 2007). Because several aspects of attention can be consciously controlled, the information most likely to become a long-lasting part of memory has passed a litmus test either because it is inherently salient and therefore attention-grabbing or because of one's deliberate efforts to hold onto it.

Acknowledgments

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References

Adolphs R. Emotional vision. Nature Neuroscience 2004;7:1167–1168.

Adolphs R, Cahill L, Schul R, Babinsky R. Impaired declarative memory for emotional material following bilateral amygdala damage in humans. Learning & Memory 1997;4:291–300. [PubMed: 10456070]

Adolphs R, Denburg NL, Tranel D. The amygdala's role in long-term declarative memory for gist and detail. Behavioral Neuroscience 2001;115:983–992. [PubMed: 11584931]

Adolphs R, Tranel D, Buchanan TW. Amygdala damage impairs emotional memory for gist but not details of complex stimuli. Nature Neuroscience 2005;8:512–518.

Anderson A. Affective influences on the attentional dynamics supporting awareness. Journal of Experimental Psychology: General 2005;134:258–281. [PubMed: 15869349]

⁶Although our research design did not allow for a measurement of the separate influences of the valence and arousal levels of our emotional oddballs, the results of previous studies suggest that valence and arousal may differentially influence memory for items in emotional oddball lists (Hurlemann et al., 2005). Hurlemann and colleagues included both positive and negative arousing oddballs in their design. In lists with negative arousing oddballs, retrograde impairment occurred in immediate free recall. In contrast, retrograde impairment was not obtained when the lists contained positive arousing oddballs. Thus, it is possible that our replication of emotion-induced retrograde impairment may be due to the valence of the emotional oddball, the arousal level, or both.

Anderson A, Phelps EA. Is the human amygdala critical for the subjective experience of emotion? Evidence of intact dispositional affect in patients with amygdala lesions. Journal of Cognitive Neuroscience 2002;14:709–720. [PubMed: 12167256]

- Anderson A, Wais P, Gabrieli JDE. Emotion enhances remembrance of neutral events past. Proceedings of the National Academy of Sciences 2006;103:1599–1604.
- Anderson L, Shimamura AP. Influences of emotion on context memory while viewing film clips. American Journal of Psychology 2005;118(3):323–337. [PubMed: 16255123]
- Atkinson, RC.; Shiffrin, RM. Human memory: A proposed system and its control processes. In: Spence, KW.; Spence, JT., editors. The psychology of learning and motivation. Vol. 2. New York: Academic Press; 1968.
- Beaver JD, Mogg K, Bradley BP. Emotional conditioning to masked stimuli and modulation of visuospatial attention. Emotion 2005;5:67–79. [PubMed: 15755220]
- Blumenfeld RS, Ranganath C. Dorsolateral prefrontal cortex promotes long term memory formation through its role in working memory organization. Journal of Neuroscience 2006;26:916–925. [PubMed: 16421311]
- Bornstein BH, Liebel LM, Scarberry NC. Repeated testing in eyewitness memory: A means to improve recall of a negative emotional event. Applied Cognitive Psychology 1998;12:119–131.
- Buchanan, TW.; Adolphs, R. The neuroanatomy of emotional memory in humans. In: Reisberg, D.; Hertel, P., editors. Memory and emotion. Oxford: University Press; 2004. p. 42-75.
- Burke A, Heuer F, Reisberg D. Remembering emotional events. Memory and Cognition 1992;20:277–290.
- Cahill L, Babinsky R, Markowitsch HJ, McGaugh JL. The amygdala and emotional memory. Nature 1995;377:295–296. [PubMed: 7566084]
- Cahill L, McGaugh JL. Mechanisms of emotional arousal and lasting declarative memory. Trends in Neuroscience 1998;21:294–299.
- Cahill L, Prins B, Weber M, McGaugh JL. Beta-adrenergic activation and memory for emotional events. Nature 1994;371:702–704. [PubMed: 7935815]
- Canli T, Zhao Z, Brewer J, Gabrieli JDE, Cahill L. Activation in the human amygdala associates event-related arousal with later memory for individual emotional experience. The Journal of Neuroscience 2000;20:1–5. [PubMed: 10627575]
- Christianson SÅ. The relationship between induced emotional arousal and amnesia. Scandinavian Journal of Psychology 1984;25:147–160. [PubMed: 6463613]
- Christianson SÅ, Loftus EF. Remembering emotional events: The fate of detailed information. Emotion & Cognition 1991;5:81–108.
- Christianson SÅ, Loftus EF, Hoffman H, Loftus GR. Eye fixations and memory for emotional events. Journal of Experimental Psychology 1991;17:693–701. [PubMed: 1832433]
- Cohen JD, MacWhinney B, Flatt RR, Provost J. PsyScope: an interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. Behavioral Research Methods, Instruments, and Computers 1993;25:257–271.
- Debiec J, Doyere V, Nader K, LeDoux JE. Directly reactivated, but not indirectly reactivated, memories undergo reconsolidation in the amygdala. Proceedings of the National Academy of Sciences 2006;103:3428–3433.
- Delplanque S, Lavoie ME, Hot P, Silvert L, Sequeira H. Modulation of cognitive processing by emotional valence studied through event-related potentials in humans. Neuroscience Letters 2004;356:619–633.
- Denberg NL, Buchanan TW, Tranel D, Adolphs R. Evidence for preserved emotional memory in normal older persons. Emotion 2003;3:239–253. [PubMed: 14498794]
- Detterman DK, Ellis NR. Determinants of induced amnesia in short-term memory. Journal of Experimental Psychology 1972;95:308–316. [PubMed: 5071912]
- Dolan RJ. Emotion, cognition, and behavior. Science 2002;298:1191-1194. [PubMed: 12424363]
- Dolcos F, LaBar KS, Cabeza R. Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. Proceedings of the National Academy of Sciences 2004;102:2626–2631.

Dudai Y. Reconsolidation: The advantage of being refocused. Current Opinion in Neurobiology 2006;16:174–178. [PubMed: 16563730]

- Ellis NR, Detterman DK, Runcie RB, Craig EM. Amnesic effects in short-term memory. Journal of Experimental Psychology 1971;89:357–361. [PubMed: 5567140]
- Erdelyi MH, Blumenthal DG. Cognitive masking in rapid sequential processing: The effect of an emotional picture on preceding and succeeding pictures. Memory & Cognition 1973;1:201–204.
- Erk S, Kiefer M, Grothe J, Wunderlich AP, Spitzer M, Walter H. Emotional context modulates subsequent memory effect. NeuroImage 2003;18:439–447. [PubMed: 12595197]
- Guy SC, Cahill L. The role of overt rehearsal in enhanced conscious memory for emotional events. Consciousness and Cognition 1999;8:114–122. [PubMed: 10072696]
- Hadley CB, MacKay DG. Does emotion help or hinder immediate memory? Arousal versus priority-binding mechanisms. Journal of Experimental Psychology: Learning, Memory, and Cognition 2006;32:79–88.
- Hamann SB. Cognitive and neural mechanisms of emotional memory. Trends in Cognitive Sciences 2001;5:394–400. [PubMed: 11520704]
- Hamann SB, Cahill L, McGaugh JL, Squire LR. Intact enhancement of declarative memory for emotional material in amnesia. Learning & Memory 1997;4:301–309. [PubMed: 10456071]
- Hamann SB, Ely TD, Grafton ST, Kilts CD. Amygdala activity related to enhanced memory for pleasant and aversive stimuli. Nature Neuroscience 1999;2:289–293.
- Harris CR, Pashler H. Enhanced memory for negatively emotionally charged pictures without selective rumination. Emotion 2005;5:191–199. [PubMed: 15982084]
- Hurlemann R, Hawellek B, Matusch A, Kolsch H, Wollersen H, Madea B, Vogeley K, Maier W, Dolan RJ. Noradrenergic modulation of emotion-induced forgetting and remembering. The Journal of Neuroscience 2005;25:6343–6349. [PubMed: 16000624]
- Isaacowitz DM, Wadlinger HA, Goren D, Wilson HR. Selective preference in visual fixation away from negative images in old age? An eye-tracking study. Psychology and Aging 2006;21:40–48. [PubMed: 16594790]
- Johnson MK. MEM: Mechanisms of recollection. Journal of Cognitive Neuroscience 1992;4:268-280.
- Kensinger EA, Corkin S. Two routes to emotional memory: Distinct neural processes for valence and arousal. Proceedings of the National Academy of Sciences 2004;101:3310–3315.
- Kensinger EA, Garoff-Eaton RJ, Schacter DL. Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. Journal of Memory and Language 2007;56:575–591.
- Kilpatrick L, Cahill L. Amygdala modulation of parahippocampal and frontal regions during emotionally influenced memory storage. NeuroImage 2003;20:2091–2099. [PubMed: 14683713]
- Kirkpatrick EA. An experimental study of memory. Psychological Review 1894;1:602-609.
- Knight M, Seymour TL, Gaunt JT, Baker CA, Nesmith K, Mather M. Aging and goal-directed emotional attention: Distraction reverses emotional biases. Emotion 2007;7:705–714. [PubMed: 18039037]
- LaBar KS, Cabeza R. Cognitive neuroscience of emotional memory. Nature Reviews Neuroscience 2006;7:54–64.
- Lane S, Mather M, Villa D, Morita S. How events are reviewed matters: Effects of varied focus on eyewitness suggestibility. Memory & Cognition 2001;29:940–947.
- Lang, PJ.; Bradley, MM.; Cuthbert, BN. International Affective Picture System (IAPS): Technical manual and affective ratings. Gainesville: University of Florida, Center for Research in Psychophysiology; 1999.
- Lang PJ, Greenwald MK, Bradley MM, Hamm AO. Looking at pictures: Affective, facial, visceral, and behavioral reactions. Psychophysiology 1993;30:261–273. [PubMed: 8497555]
- LeDoux J. Fear and the brain: Where have we been, and where are we going? Biological Psychiatry 1998;44:1229–1238. [PubMed: 9861466]
- Mackiewicz KL, Sarinopoulos I, Cleven KL, Nitscke JB. The effect of anticipation and the specificity of sex differences for amygdala and hippocampus function in emotional memory. Proceedings of the National Academy of Sciences 2006;103:14200–14205.

MacKay DG, Shafto M, Taylor JK, Marian DE, Abrams L, Dyer JR. Relations between emotion, memory, and attention: Evidence from taboo stroop, lexical decision, and immediate memory tasks. Memory & Cognition 2004;32:474–488.

- Marsh EJ. Retelling is not the same as recalling: Implications for memory. Current Directions in Psychological Science 2007;16:16–20.
- Mather M. When emotion intensifies memory interference. Psychology of Learning and Motivation 51 in press.
- Mather M. Emotional arousal and memory binding: An object-based framework. Perspectives on Psychological Science 2007;2:33–52.
- Mather M, Canli T, English T, Whitfield SL, Wais P, Ochsner KN, et al. Amygdala responses to emotionally valenced stimuli in older and younger adults. Psychological Science 2004;15:259–263. [PubMed: 15043644]
- Mather M, Gorlick M, Nesmith K. The limits of arousal's memory impairing effects on nearby information. American Journal of Psychology. in press.
- Mather M, Knight M. Goal-directed memory: The role of cognitive control in older adults' emotional memory. Psychology and Aging 2005;20:554–570. [PubMed: 16420131]
- Mather M, Knight M. Angry faces get noticed quickly: Threat detection is not impaired among older adults. Journal of Gerontology: Psychological Sciences 2006;61:P54–P57.
- Mather M, Knight M. The emotional harbinger effect: Poor context memory for cues that previously predicted something arousing. Emotion 2008;8:850–860. [PubMed: 19102596]
- Mather M, Mitchell KJ, Raye CL, Novak DL, Greene EJ, Johnson MK. Emotional arousal can impair feature binding in working memory. Journal of Cognitive Neuroscience 2006;18:614–625. [PubMed: 16768364]
- Mather M, Nesmith K. Arousal-enhanced location memory for pictures. Journal of Memory and Language 2008;558:449–464. [PubMed: 19190722]
- McGaugh JL. The amygdala modulates the consolidation of memories of emotionally arousing experiences. Annual Review of Neuroscience 2004;27:1–28.
- Mitchell KJ, Johnson MK, Raye CL, Greene EJ. Prefrontal cortex activity associated with source monitoring in a working memory task. Journal of Cognitive Neuroscience 2004;16:921–934. [PubMed: 15298780]
- Mitchell KJ, Mather M, Johnson MK, Raye CL, Greene EJ. A functional magnetic resonance imaging investigation of short-term source and item memory for negative pictures. NeuroReport 2006;17:1543–1547. [PubMed: 16957605]
- Miu AC, Heilman RM, Opre A, Miclea M. Emotion-induced retrograde amnesia and trait anxiety. Journal of Experimental Psychology: Learning Memory and Cognition 2005;31:1250–1257.
- Mogg K, Bradley BP. Time course of attentional bias for fear-relevant stimuli in spider-fearful individuals. Behaviour Research and Therapy 2006;44:1241–1250. [PubMed: 16870133]
- Murdoch BB. A theory for the storage and retrieval of item and associative information. Psychological Review 1982;89:609–626.
- Murdoch BB Jr. The serial position effect of free recall. Journal of Experimental Psychology 1974;64:482–488.
- Öhman, A.; Flykt, A.; Lundqvist, D. Unconscious emotion: Evolutionary perspectives, psychophysiological data and neuropsychological mechanisms. In: Lane, RD.; Nadel, L., editors. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000. p. 296-327.
- Öhman A, Lundqvist D, Esteves F. The face in the crowd revisited: A threat advantage with schematic stimuli. Journal of Personality and Social Psychology 2001;80:381–396. [PubMed: 11300573]
- Paller KA, Wagner AD. Observing the transformation of experience into memory. Trends in Cognitive Sciences 2002;6:93–102. [PubMed: 15866193]
- Phelps EA. Emotion and cognition: Insights from studies of the human amygdala. Annual Review of Psychology 2006;57:27–53.
- Phelps EA, LaBar KS, Anderson AK, O'Connor KJ, Fulbright RK, Spencer DD. Specifying the contributions of the human amygdala to emotional memory: A case study. Neurocase 1998;4:527–540.

Reisberg, D.; Heuer, F. Memory for emotional events. In: Reisberg, D.; Hertel, P., editors. Memory and emotion. New York: Oxford University Press; 2004. p. 3-41.

- Rosler A, Ulrich C, Billino J, Sterzer P, Weidauer S, Bernhardt T, Steinmetz H, Frohich L, Kleinschmidt A. Effects of arousing emotional scenes on the distribution of visuospatial attention: Changes with aging and early subcortical vascular dementia. Journal of the Neurological Sciences 2005:229–230. 109–116.
- Runcie D, O'Bannon RM. An independence of induced amnesia and emotional response. American Journal of Psychology 1977;90:55–61. [PubMed: 871179]
- Schmidt SR. Outstanding memories: The positive and negative effects of nudes on memory. Journal of Experimental Psychology: Learning, Memory, and Cognition 2002;28:353–361.
- Sharot T, Phelps EA. How arousal modulates memory: Disentangling the effects of attention and retention. Cognitive, Affective & Behavioral Neuroscience 2004;4:294–306.
- Silvert L, Naveteur J, Honore J, Sequeira H, Boucart M. Emotional stimuli in rapid serial visual presentation. Visual Cognition 2004;11:433–460.
- Strange BA, Dolan RJ. β-Adrenergic modulation of emotional memory-evoked human amygdala and hippocampal responses. Proceedings of the National Academy of Sciences 2004;101:11454–11458
- Strange BA, Hurlemann R, Dolan RJ. An emotion induced retrograde amnesia in humans is amygdalaand β-Adrenergic dependent. Proceedings of the National Academy of Sciences 2003;100:13626– 13631.
- Tarr, MJ. The object databank. 2005. http://www.tarrlab.org/
- Touryan SR, Marian DE, Shimamura AP. Effect of negative emotional pictures on associative memory for peripheral information. Memory 2007;15(2):154–166. [PubMed: 17534109]
- Tronson NC, Taylor JR. Molecular mechanisms of memory reconsolidation. Nature Reviews Neuroscience 2007;8:262–275.

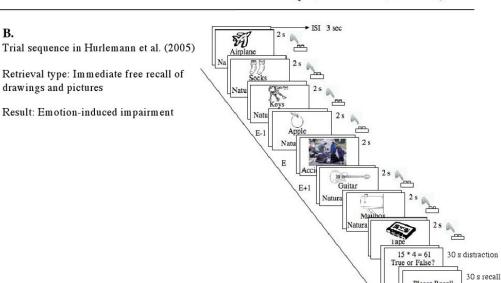


Figure 1.

Figure 1A. The experimental timeline used in Anderson et al. (2006) for each encoding trial. Modulator items were rated on arousal during each trial. Retrograde enhancement of memory was observed for faces and houses that preceded emotionally arousing scenes in a one-week delayed recognition test.

Figure 1B. The experimental timeline used in Hurlemann et al. (2005) for each encoding trial (list). Retrograde amnesia was observed for items that preceded emotionally arousing oddballs in tests of immediate free recall after each trial.

A. Trial sequence in Experiment 1 Session I retrieval: Immediate free recall of each list; end-of-session recognition of all list items Session II retrieval: One-week delayed recognition of all list items Apple Apple OLD OLD 15 * 4 = 61 25 s distraction True or False 30 s recall Please Recall

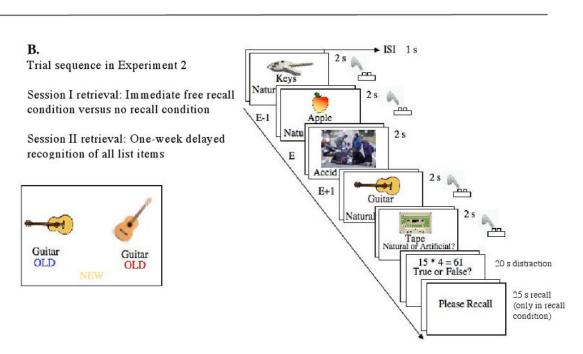


Figure 2A. The experimental timeline used in Experiment 1 for each encoding trial (list) and the format of the recognition memory test. Within each encoding list, either three or four of the non-oddball items were real photographs of objects (natural stimuli) and the remaining items were computer-generated objects (artificial stimuli). Across all lists, half of the items were real photographs and the remaining half consisted of computer-generated objects. Participants were asked to indicate with a key press whether the non-oddball item presented

was "natural" (a real photograph) or "artificial" (a computer-generated image). Each list also included one emotionally arousing oddball or one neutral oddball inserted into list position 3, 4, 5 or 6. During the run, participants were presented with 24 lists. Each list was followed

Figure 2.

immediately by a 25-second distracter task during which participants were presented with math problems and solutions and had to determine whether the solutions were correct or incorrect. Episodic memory was tested immediately after the 25-second math task and was signaled by the words "Please Recall." At this time, participants had 30 seconds to write down as many items from the list as they could remember. The computer displayed the time remaining and a beep occurred at the end of the elapsed time to alert the participant that a new list would appear. Following the presentation of the 24 lists, half of the participants took an immediate recognition test for both the oddball and non-oddball items. The remaining half took the recognition test one week later. On each trial of the recognition test, participants were presented with a pair of items that shared the same verbal label (e.g., both were "apples") but differed in other visual features (e.g., orientation, color, shape). The word "old" appeared below each item either in red (item on the left) or blue (item on the right) font. The word "new" appeared in yellow and was centered below the two "old" labels. Participants were instructed to indicate which of the two items matched the non-oddball item seen previously, or if both of the items were new.

Figure 2B. The experimental timeline used in Experiment 2 for each encoding trial (list) and the format of the recognition memory test. Within each encoding list, two of the items were real photographs of objects (natural stimuli) and the two remaining items were computergenerated objects (artificial stimuli). Each list also included one emotionally arousing picture or one neutral oddball inserted into list position 2, 3 or 4. Because of the shorter lists than in Experiment 1, the math task was reduced from 25 to 20 seconds and participants were allotted 25 seconds (instead of 30) to write down as many items from the list as they could remember. Participants in the no-recall condition started with a new encoding list instead of recalling the list items after the distraction task. Following the presentation of the 24 input sequences, all participants returned one week later to take the recognition tests for oddball and non-oddball stimuli.

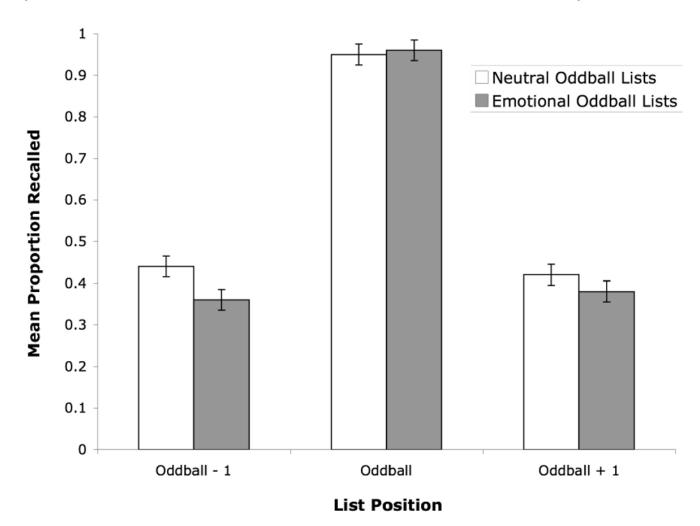
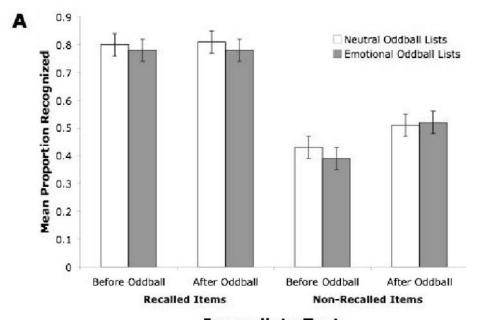


Figure 3. Probability of recall (hits - false alarms) for emotional and neutral oddballs and non-oddball items in list positions immediately preceding and following oddballs in Experiment 1. No significant difference emerged in memory for the neutral and emotional oddball pictures themselves. Recall for items in E+/-1 positions was depressed relative to memory for items in N+/-1 positions.



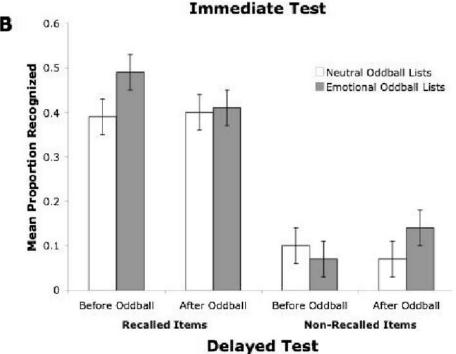


Figure 4.

General recognition [hits (same + similar items collapsed) - false alarms] for non-oddball items preceding and following oddballs as a function of recall status at the immediate test (A) and the delayed test (B) in Experiment 1. Recognition performance was collapsed across the 4 positions that preceded oddballs to obtain an overall "before-oddball" measure. The same procedure was followed to yield an overall "after oddball" measure.

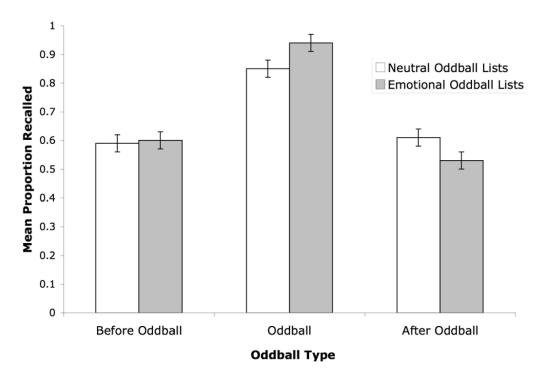


Figure 5. Probability of recall as a function of list position in Experiment 2.

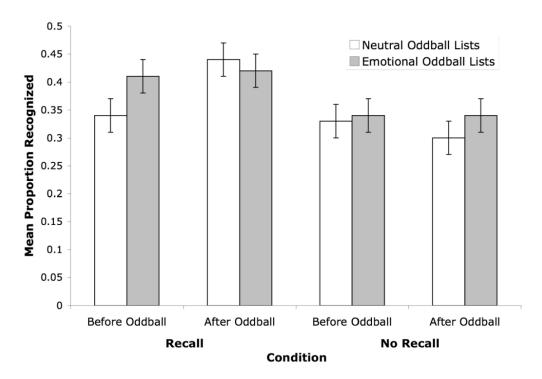


Figure 6.

Recognition accuracy [hits - false alarms] for non-oddball items that preceded and followed oddballs in the recall and no recall conditions in Experiment 2. Recognition performance was collapsed across the three positions that preceded and followed oddballs to obtain an overall "before-oddball" and "after-oddball" measure.

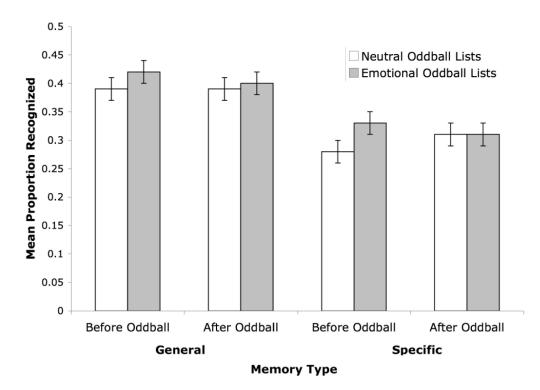


Figure 7.

Recognition accuracy [hits - false alarms] for non-oddball items that preceded and followed oddballs as a function of memory type in Experiment 2. Recognition performance was collapsed across the three positions that preceded and followed oddballs to obtain an overall "before-oddball" and "after-oddball" measure.

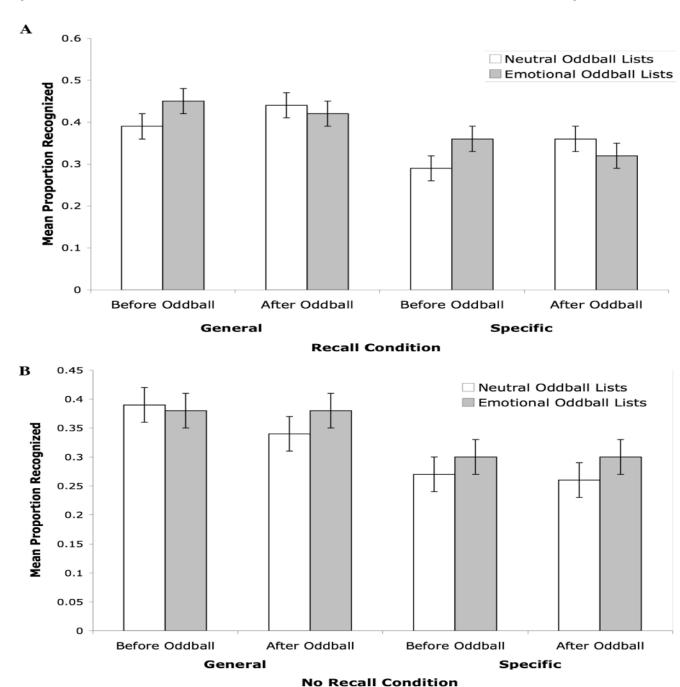


Figure 8.

Recognition accuracy [hits - false alarms] for non-oddball items that preceded and followed oddballs as a function of memory type in the recall condition (A) and the no recall condition (B) in Experiment 2. Recognition performance was collapsed across the three positions that preceded and followed oddballs to obtain an overall "before-oddball" and "after-oddball" measure.