Emotion enhances remembrance of neutral events past

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Emotional events are bestowed with special prominence in memory. This may reflect greater attention oriented to these events during encoding, and/or enhancement of memory consolidation after emotional events have passed. Here we show invoked emotional arousal results in a retrograde enhancement of long-term memory, determining what will later be remembered or forgotten. Subjects saw pictures of neutral faces and houses followed by emotionally arousing scenes at varying intervals. Self-reported emotional arousal responses predicted a retrograde enhancement of memory for preceding neutral events in a 1-week delayed recognition memory test. At longer picture–scene intervals, no enhancement was found, implicating a critical window in which emotional arousal must occur for retrograde memory enhancement. Postencoding manipulation of emotional arousal specifically enhanced conscious recollection rather than familiarity-based discrimination. An additional study revealed no retrograde enhancement for pictures preceding highly memorable, but nonarousing, distinctive scenes. These findings indicate an important role for emotional arousal in the postencoding enhancement of episodic memory consolidation.

amygdala | consolidation | hippocampus | memory | arousal

Recollection of the events surrounding the remote birth of a child or death of a loved one can persist in a manner unlike that of where we parked our car earlier in the day or the name of an acquaintance introduced moments prior. Psychological accounts of the powerful influence of emotion on human memory invoke the salience of emotional relative to neutral events and the commensurate increased attention and elaborative processes invoked during initial encoding, as well as potential continued ruminations on their past occurrence (1–4). By contrast, neurobiological accounts from research with nonhuman animals suggests that emotional arousal influences the processes by which memory traces are later consolidated (4–6), enhancing how these traces are inscribed in the cortex (7). This latter view suggests that enhanced memory for emotional events occurs because of critical neural processes that take place after the to-be-remembered event has passed (5, 6), not being under direct psychological control of the observer.

In studies of human memory for emotional events, the influence of emotional arousal on attention during encoding and on postencoding consolidation processes are often confounded. This is due to how, in nature as well as in empirical study, emotional arousal is evoked by the very same event that is later probed for memory. For instance, it is inherently problematic to dissociate the encoding (e.g., increased attention and/or elaboration) and postencoding (e.g., enhanced consolidation) processes that result in vivid memory for provocative events like a gory roadside accident. Emotionally provocative events result in emotional arousal that not only influences initial perceptual encoding (8, 9), but also persists after the provoking event has passed.

Seminal studies from nonhuman animals have used a postlearning treatment paradigm to demonstrate enhanced consolidation independent of encoding (10, 11). Postlearning influences of different systemic treatments from smoking to exercise have also been shown to alter human memory consolidation (12–19). However, the role of postencoding emotional arousal in enhancing long-term memory formation is largely unknown. It has been proposed that emotionally significant events result in imprinting remembrance of events immediately preceding, enhancing memory for ongoing activity in the recent past (20). The present study examined this thesis, specifically assessing how emotional arousal alters long term recollection for preceding neutral events and the precise time course of this influence.

The present study separated stimulus encoding and postencoding consolidation influences on memory formation by showing on each trial an emotionally neutral stimulus (referred to here as a test event) followed by an unrelated scene of varying emotional intensity (a modulator event). This design allowed for a dissociation between the effects of emotional arousal on attention during encoding from the influence of arousal on memory consolidation for preceding neutral events. Measurement of arousal was determined on a trial specific basis, as indicated by self reported intensity of emotional response to presented pictures, which has been shown to be highly correlated with peripheral and central measures of physiological arousal (21–23). It was later examined whether intensity of postencoding emotional response would enhance long term memory in an event-specific manner, increasing retention for the immediately preceding neutral events. Manipulating the interval between the neutral and subsequent emotional events further afforded an examination of the existence of a critical window in which emotional arousal can enhance memory for a prior neutral event.

Experiment 1: Postencoding Arousal

Results. ***Modulator ratings.*** Emotional intensity ratings and corrected recognition data were submitted to separate ANOVAs with modulator category (positive, negative, and neutral) as a repeated measure. Ratings significantly depended on modulator category, $F(2,74) = 465.09$, $P < 0.0001$, with both positive (mean, 4.38; SE, 0.09; $F(1,74) = 409.17$; $P < 0.0001$) and negative (mean, 5.59; SE, 0.08; $F(1,74) = 892.85$, $P < 0.0001$) modulator events rated as significantly more arousing than neutral (mean, 1.83, SE = 0.06).

Modulator item memory. Memory similarly depended on modulator category, $F(2,74) = 13.12$, $P < 0.0001$, being greater for both positive [mean, 65.6%, SE, 1.6, $F(1,74) = 15.24$, $P < 0.0002$] and negative scenes [mean, 63.5%; SE, 2.1; $F(1,74) = 23.24$; $P < 0.0001$] relative to neutral (mean, 54.4%; SE, 2.3), suggesting that degree of evoked arousal, rather than valence, predicted later memory (24). To increase power of the arousal independent variable, data were collapsed across valence and sorted by individually defined subjective arousal. This method allowed a

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Abbreviations: RME, retrograde memory enhancement; ISI, interstimulus interval.

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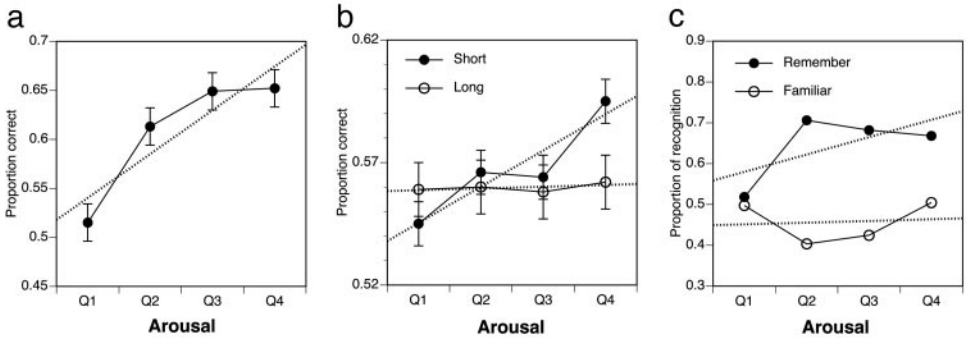

Fig. 1. Relation between modulator arousal and recognition memory for modulator and test events. (*a* and *b*) Overall recognition memory for modulator events (*a*) and preceding test events (*b*) sorted by trial specific arousal ratings (Q1 = low arousal quartile, Q4 = high arousal quartile). Test events are separated by test–modulator interstimulus interval (short = 4 s; long = 9 s). (*c*) Effect of modulator arousal on quality of test memory (remember vs. familiar responses proportional to overall recognition) at short test–modulator intervals. Dotted lines represent linear best fit.

tailoring of memory analyses to each individual participant's subjective emotional response on a given trial. This sorting resulted in graded manipulation of subjective emotional intensity with near equivalent steps from lowest to highest quartile. Consistent with the arousal modulation of memory, when sorted by individually defined arousal responses during viewing, there were pronounced linear ($F = 39.26$, $P < 0.0001$) and quadratic relations ($F = 8.78$, $P < 0.004$) between arousal rating quartile and later recognition memory (Fig. 1*a*). The quadratic component revealed that with increasing emotional intensity ratings there were diminishing returns for later memory. However, these findings cannot address whether arousal influences memory by increased attention and depth of processing during encoding (25), or via modulating the course of memory consolidation taking place after encoding.

Test item memory. We next examined recognition memory for preceding neutral events. At short test–modulator intervals, a linear contrast revealed memory for neutral test events was influenced by the degree of self-reported arousal for the following modulator event ($F = 4.15$, $P = 0.04$), with likelihood of recognition increasing from most to least arousing (Fig. 1*b*). This memory enhancement was approximately one-third of the size found for arousing events themselves. At longer intervals between encoding and evoked arousal, no linear or quadratic relationship was present ($F < 1$, P values > 0.75; Fig. 1*b*). This temporal dissociation was not associated with differences in the degree of evoked emotional intensity (short, 3.95; SE, 0.17 vs. long, 3.89; SE, 0.17; $F = 1.69$, $P > 0.20$) or recognition memory (short, 61.5%; SE, 1.5 vs. long, 60.0%; SE, 1.5; F = 1.79, $P > 0.18$) for modulators on short and long interval trials. Thus, emotional arousal evoked during a narrow window after stimulus offset, near the inception of memory consolidation for prior events, enhanced retrieval success 1 week later.

Test item memory predictions. Participant predictions of remembering during encoding were not related to arousal quartile for either short ($F < 1$) or long ($F = 1.17$, $P > 0.28$) interval trials. Thus, there was no evidence that the neutral test events preceding highly arousing modulator events were inherently memorable. Rather, memory for test events was modulated by postencoding manipulations that could not be predicted during stimulus encoding.

Emotional Arousal and Recollective Experience. Emotion acts not only to increase the likelihood of memory retrieval, but also may change the subjective quality of memory (26–29), enhancing the retrieval of information that evokes a robust subjective experience of recollection or mere familiarity (2). We next examined these qualitative aspects of memory retrieval to determine whether enhanced recollective experience is restricted to distinctive emotional events, or can be induced for neutral nondistinct events by evoking an emotional response after encoding. During recognition, subjects were asked to indicate whether they remembered seeing the stimulus (remember responses), or found it familiar, not able to retrieve specific information about its prior occurrence (familiar responses).

Modulator event memory. Remember responses were strongly associated with arousal. Significant linear ($F = 48.85$, $P < 0.0001$) and quadratic components ($F = 8.55$, $P < 0.005$) demonstrated that likelihood of recollection increased from the least to most arousing quartile, but again with diminishing returns. By contrast, familiar responses were only weakly linearly associated with arousal ($F = 3.41$, $P < 0.07$), with familiarity slightly decreasing from most to least arousing.

Test event memory. Enhanced recollection was not restricted to the emotional modulator events, but extended to the neutral test events that preceded them (Fig. 1*c*). Recollection of the neutral test events was significantly related to arousal. Significant linear ($F = 3.95$, $P < 0.05$) and quadratic ($F = 4.46$, $P < 0.04$) components revealed the most prominent enhancement occurred relative to the lowest arousal quartile ($F = 9.17$, $P = 0.005$). By contrast, no relationship was found between arousal and familiarity ($F < 1$), with no evidence of enhancement relative to lowest arousal trials ($F < 1$). When directly contrasting memory quality, likelihood of recollection of neutral test events was equivalent with familiarity at the lowest postencoding arousal levels, ($F < 1$). This equivalence in remember and familiar responses was likely due to overall poor corrected memory for the indistinctive test events after a 1-week delay. However, as post encoding arousal increased, the likelihood of recollection relative to familiarity was significantly enhanced (proportional advantage for quartile 2 = 75%, $F = 15.64$, $P < 0.0001$; quartile 3 = 61%; $F = 11.12$, $P < 0.002$; quartile 4 = 32%, $F = 4.57$, $P < 0.04$). Thus, arousal enhancement of recollection is not restricted to highly distinctive and emotionally salient events, which may be subject to enhanced attention during encoding. Nondistinct stimuli may be endowed with enhanced recollective experience when arousal is manipulated after their encoding has passed.

Gender Differences in Emotional Modulation of Memory. Men and women are thought to differ in their behavioral and neural expression of enhanced memory for emotional events (30–32), with women typically demonstrating greater emotional enhancement of episodic memory. Such gender differences may reflect how men and women differently construe or attend to emotional events, or in subsequent neural processes supporting consolida-

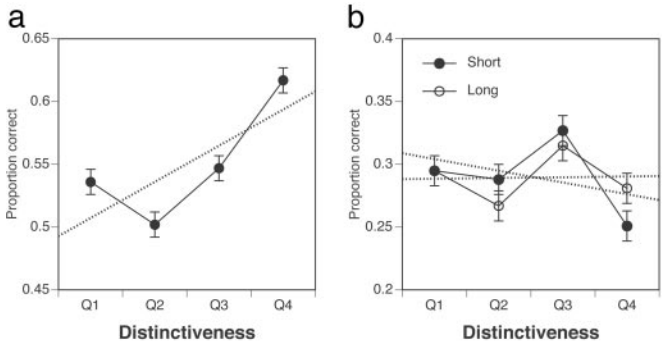

Fig. 2. Relation between modulator distinctiveness and recognition memory for modulator and test events. Overall recognition memory for modulator events (*a*) and preceding test events (*b*) sorted by trial specific distinctiveness ratings (Q1 = low distinctive quartile, Q4 = high distinctive quartile) (short = 4 s; long = 9 s, interstimulus interval). Dotted lines represent linear best fit.

tion. In the present study, both genders reported statistically equivalent subjective arousal reactions to the emotionally arousing events ($F = 1.35$, $P > 0.26$). Mirroring this equivalence in subjective arousal responses, enhanced recollection for emotionally arousing modulator items did not significantly differ between genders ($F < 1$). This lack of a significant effect of gender on modulator events extended to recognition of preceding test stimuli, with gender not interacting with the effect of arousal quartile on test stimuli recognition, nor when remember or familiar responses were considered separately, all F values $<$ 1.05. This null finding with respect to gender differences in the effect of postencoding arousal may reflect the lack of power to demonstrate gender differences during encoding.

Experiment 2: Postencoding Distinctiveness

In addition to being associated with greater subjective and physiological arousal (21), emotional events are inherently distinctive, deviating from normal everyday experience. Novel experiences, of relatively neutral emotional tone, also result in enhanced recollection (33). It is possible that the distinctiveness of arousing events is responsible for enhanced memory for prior test events. We examined this in an additional study by varying the distinctiveness rather than the emotional significance of subsequent modulator events.

Results. ***Modulator ratings.*** As expected, sorting each individual's distinctiveness ratings resulted in a linear manipulation of modulator event distinctiveness ($F = 842.90$, $P < 0.0001$).

Modulator event memory. These ratings of increasing distinctiveness were associated with later enhanced recognition memory, with both linear, $F = 7.63$, $P < 0.008$, and quadratic components ($F = 4.91$, $P < 0.04$), as indicated by the inverted U-shaped profile, with a small dip in accuracy from the first to second quartile (Fig. 2*a*). As such, recognition accuracy was maximally different from the second to the most distinct quartile ($F = 12.10$, $P < 0.001$). With respect to memory quality, like the influence of emotional arousal, increasing distinctiveness was associated with greater recollection, as indicated by its relation with remember ($F = 11.11$, $P < 0.002$), but not familiarity based responses ($F < 1$).

Test event memory. By contrast with the effects of emotional modulators in experiment 1, distinctive modulator events were not associated with enhanced recollection of preceding neutral test items at either short or long intervals (F values < 1; Fig. 2*b*), or for remember or familiar responses (F values < 1). These overall null results might reflect a difference in power between the arousal and distinctiveness manipulations on memory. To examine this, a median split analysis was performed. Subjects with the most pronounced memory for distinctive modulators [$F(1,27) = 26.29$, $P < 0.0001$], resulting in larger effect size for the distinctiveness than arousal manipulation ($r = 0.69$ vs. 0.51), demonstrated no significant enhancement of memory for preceding neutral test items ($F <$ 1). Enhanced memory for modulator events was thus not sufficient to augment memory for preceding neutral items, suggesting that a critical threshold of emotional arousal must be reached (22).

Discussion

The present studies demonstrated that on an event-by-event basis increased intensity of an emotional experience enhanced memory for prior neutral events, a phenomenon that may be termed "retrograde memory enhancement" (RME). RME was specifically tied to the magnitude of emotional arousal, and did not occur after highly distinctive events of low arousal value. RME occurred in a restricted temporal window, effective after a 4-s interval but no longer effective after 9 s. Finally, RME for neutral events was expressed specifically in terms of enhanced recollective experience, similar to what is typically ascribed to memory for emotionally arousing events themselves (2).

Emotional arousal can influence event encoding (8, 9) as well as attention to events that follow (34). Investigations of memory for the emotional event itself or those closely following in time (35) are then confounded with increased attentional or elaborative processes. The present findings suggest that RME is an automatic consequence of a subsequent, independent experience, such that processing of the second experience enhances memory for a prior event that is no longer under consideration by the observer. As such, rather than an orienting of attention or invocation of elaborative psychological processes during initial encoding (36), poststimulus RME implicates the importance of arousal in modulating how memory traces are consolidated into long-term memory. Emotional enhancement of memory may result from the work of effortful psychological processes, bestowing these events with special salience, but also as the present results suggest, via a direct augmentation of the neurobiological mechanisms by which memory traces are laid down. As William James proposed long ago (7), emotional activation may invoke a special mechanism whereby these events are inscribed more readily and deeply into the cortex.

The restricted temporal window of this retrograde influence appears distinct from other findings related to the effects of postencoding arousal. Research in nonhuman animals has shown that injections of adrenaline and or a β-adrenergic antagonists subsequent to newly acquired learning can enhance or impair retention for prior learning, respectively, in the minutes or hours after memory encoding (6, 37). Similar effects have been observed in humans administered epinephrine (14) or partaking in physical exertion (17) after encoding. Several studies in human and nonhuman animals (13, 14, 17, 38) also suggests that postlearning arousal is most effective at modulating memory for intrinsically arousing events. Results of the above studies have been attributed to the release of stress hormones into the bloodstream (5, 12). Because of the slower peripheral release of steroid hormones, they are unlikely to support the restricted time course of retrograde enhancement shown here. The steep temporal gradient of arousal modulation of neutral events presented at 4 but not 9 s prior implicates a short-term consolidation process initiated during the very first seconds of stimulus consolidation (10). Thus, a fast-acting mechanism of central origin is needed to account for such temporally restricted selection effects in memory, whereby events closely associated in time with emotional activation are subject to greater retention.

The neural mechanisms of this rapid and event specific selection for later memory are unclear. Consistent with the importance of the amygdala in hippocampal long-term potentiation (LTP) (39), there are robust amygdala efferents to parahippocampal and hippocampal targets, including the ento-

rhinal and perirhinal cortices, as well as the subiculum and CA1/CA3 subfields of the hippocampus (40). These connections may support direct and rapid augmentation of memory traces in the hippocampus and surrounding cortices, whereby amygdala activation acts as a tetanic stimulus, selectively enhancing consolidation of recently experienced events through increased induction of LTP. The limited temporal extent of this mechanism may reflect an adaptation whereby the events leading to and coinciding with an emotional response are most pronounced in memory (20, 35), allowing memory strength to be modulated by memory importance (5).

In contrast to our supposition of the influence of post encoding arousal on consolidation, RME may reflect additional cognitive factors, e.g., the greater association between memorable emotionally arousing events and preceding neutral events. Unlike studies that explicitly ask subjects to form associations between simultaneously presented neutral items and surrounding contexts (41), in the present study, test and modulator events were separated by at least 4 s, and no instruction was given to employ a strategy of associating modulator events with test events (e.g., associating seeing a picture of a white elephant with a prior house). More directly, if memorability of following modulators was critical for the observed postencoding enhancement, then increased distinctiveness should similarly result in enhanced neutral test event memory. Unlike highly arousing events, distinctive events did not result in enhanced memory for prior neutral stimuli. Emotional arousal appears to influence memory for prior events in a way that is not readily explained by increased memory or association with distinctive and memorable contexts. Rather, we suggest that emotionally arousing events result in a direct neurobiological enhancement of memory consolidation, independently of attention to and elaboration with the to-be-remembered event.

Distinctive and unexpected events are sometimes associated with impaired memory for surrounding items (42, 43). Such learning paradigms differ with the present study, where the presentations of distinctive and emotionally arousing events were not infrequent or unexpected. This intralist distinctiveness is critical for finding impaired retention of surrounding items, referred to as the von Restorff or isolation effect (42, 43). Emotionally incongruent and unexpected events have been shown to result in von Restorff effects in immediate recall (44), suggesting that in addition to the influence of emotional arousal on long term memory consolidation shown here, emotional significance can have a detrimental influence on immediate retrieval (45, 46). This observation suggests the possibility that postencoding arousal may impair immediate access but result in later memory enhancement or reminiscence, as has been shown for arousing events themselves (47).

Pharmacological, lesion, and neuroimaging studies have implicated the human amygdala in the emotional enhancement of episodic memory (22, 24, 48–55) via influences on the hippocampal formation (56, 57). Consistent with the present findings, many studies now suggest that amygdala activation near the inception of memory consolidation is correlated with enhanced long term memory. Activation in the amygdala during viewing of emotionally arousing events predicts later memory (22, 24, 49, 51, 58), with amygdala activation and degree of arousal conjointly predicting memory on an event-by-event basis. However, the amygdala has also been shown in both human and nonhuman animals to play an important role in the allocation of attention to emotionally significant events (9, 59–61). Thus, evidence for the amygdala's role in human memory enhancement for emotional events is inconclusive regarding whether greater amygdala activation during encoding reflects modulation of attention to these events or influences on memory consolidation after event encoding has passed. The present behavioral results suggest that enhanced memory for emotional events is at least in part a reflection of amygdalar influences on the effectiveness of memory consolidation. Future studies demonstrating correlations between postencoding amygdala activation and memory for prior neutral events will be needed to demonstrate this directly.

RME implies a mechanism by which memory is enhanced reflexively. Similarly, the amygdala may operate relatively automatically (62–65), without the intentions of the observer. Such automaticity is in contrast to the greater attention dependency of higher-order prefrontal cortical contributions that are thought to contribute to enduring memory retention (25, 66, 67). Mirroring the relative attentional independence of amygdala responsiveness (62, 63), enhanced memory for emotionally arousing events is relatively unaffected by divided attention (68). Studies examining emotional–cognitive interactions often demonstrate that lateral prefrontal regions supporting higher-order cognitive processes are often disrupted by ongoing emotional activation (69). Enhancement of memory for emotionally arousing events may then critically depend on direct amygdala-hippocampal interactions (24, 51, 52, 70), which are less limited by attention (68). Decreased reliance on higher order cognitive resources during emotionally stressful events may help to ensure later enhanced memory for the events surrounding life's significant experiences.

Methods

Experiment 1. ***Participants.*** Paid volunteers (arousal condition: $n = 38$; 19 males and 19 females; mean age, 22.9 years) were recruited under the cover of evaluating a series of pictures on two occasions 1 week apart. Five participants were disqualified due to shielding their eyes during presentation of aversive events or the failure to enter ratings for events on numerous trials. All subjects gave informed consent before participating.

Stimuli. The experiment comprised two event types. Test events were neutral nondistinct events used to probe the effect of postencoding arousal evoked by modulator events. Test events were human faces and houses obtained from various sources. Face and house stimuli were chosen as homogenous stimulus classes, to limit interitem variability in memorability and for future use in mapping extrastriate representations during fMRI scanning. Of the test events, 108 were neutral face images (54 male and 54 female full-face photographs of Caucasian faces) and 108 were uniformly formatted images of private homes. Modulator events were scenes designed to evoke an emotional arousal response compiled from the International Affective Picture Survey (IAPS) library. The 216 modulator events were selected on the basis of IAPS normative ratings to sample equally from negative ($n = 72$), positive ($n = 72$), and neutral events ($n = 72$). The negative and positive events were selected to be equidistant from neutral events in terms of valence and arousal. Of these selections, 24 from each valence were reserved for foils during a later recognition test. For each of the face and house stimuli, 36 were reserved for foils.

Procedure. Experiments were administered with PSYSCOPE 1.2.5 on a Macintosh desktop computer. In the first session, participants received a brief orientation to the experiment and the computer keyboard commands before performing a three-trial practice session. A schematic representation of the trial structure is presented in Fig. 3, which is published as supporting information on the PNAS web site. During the encoding session, a 1-s fixation point preceded each trial. One second before the test event (3 s), participants were prompted with "Will you remember [Y of N?]". Participants were given instruction to judge whether a particular item was memorable or not to examine whether test events were intrinsically distinctive. To ensure equal looking time at the test stimulus, responses were entered during a 1-s poststimulus interval while the question remained on the screen. During presentation of the modulator event (3 s), participants were prompted with "How intense do you feel [1 (low) to 7

(high)]?". The questions appeared underneath each photograph. Interposed between test and modulator events was a central fixation point for either 1 or 6 s, during a test–modulator interstimulus interval (ISI) of 4 or 9 s, for short and long trials, respectively. To limit the carry over of emotional response between trials, after a 2.5-s fixation interval, participants performed a rapid response flanker task for 8 s. The flanker task required participants to determine the direction of the middle of three arrows and press the corresponding key for each of eight consecutive 1-s trials. Each trial lasted between 23 and 28 s, allowing the arousal for each modulator event to subside before the next trial. In the arousal condition, there were 12 trials per factorial combination of modulator valence (positive, negative, neutral), test–modulator ISI (short, long), and test event type (faces, houses), yielding a total of 144 trials. Assignment of test and modulator exemplars was randomized for each participant.

At the end of the first session, participants were scheduled for a second session to take place ≈7 days later. They were not advised that the next session would be a memory test. When participants arrived for their second session they were instructed that three separate series of photographs would be presented: faces, houses, and scenes, in this order; their task was to indicate whether they recognized any images from the first session. To assess potential qualitative differences in memory, the recognition task asked whether the images were "remembered," "familiar," or "new".

Analysis. The manipulation of arousal was indexed by sorting participants' individual emotional intensity ratings for modulators into quartiles, from least to most emotionally intense. This allowed an examination of individually tailored emotional response to each of the modulator events, which has been shown to be important for paired associate learning (47). Furthermore, use of graded emotionally intensity levels afforded examination of the shape of the relation between evoked subjective emotional response and later memory. Separate quartile sorts were undertaken for both the short and long ISI conditions. Mean corrected recognition scores for modulator and test events were calculated separately by assessing the proportion of hits (collapsing across remember and familiar responses to old events) for each the faces and houses and subtracting the proportion of false alarms. All analyses collapsed across face and house test stimuli. Mean corrected remember and familiar scores were similarly calculated, with the proportion of hits (remember or familiar considered separately) subtracted from the proportion of false alarms for the indicated memory type (remember or familiar).

Arousal level (four arousal quartiles, from low to high) was submitted to repeated measures ANOVA for each ISI (short and long). To limit number of pairwise comparisons and to more precisely examine the association between arousal and later memory, the arousal modulation hypothesis was tested by using *a priori* linear and quadratic polynomial contrasts (df = 1,111).

Experiment 2. ***Participants.*** Paid volunteers (n = 21, 10 males and 11 females, age = 22.4) were recruited under the cover of evaluating a series of pictures on two occasions 1 week apart. All subjects gave informed consent before participating.

Stimuli. Modulator events were compiled from various sources. The 144 modulator events were preselected to represent high (n = 72) and low (n = 72) distinctive but emotionally neutral events. Distinctive images were defined as those with unusual content (e.g., a white elephant, a person spray painted in silver; example of a distinctive image is provided in Fig. 4*a*, which is published as supporting information on the PNAS web site). Twenty-four images from each the high and low distinctiveness categories were reserved as foils during a later recognition test. Test events were the same as those used in experiment 1. Of the test events, 72 were neutral face images (1/2 male) and 72 were uniformly formatted images of private homes. For each the face and house stimuli, an additional 24 were reserved for recognition test foils.

A stimulus characterization study (n = 11) was undertaken where participants were asked to rate the distinctiveness (1 low to 7 high) and arousal (1 low to 7 high) value of modulator events in the present study as well as the arousing modulator events from experiment 1. Distinctive modulators in the present experiment were judged much more distinctive than arousing [$F(1, 10) = 126.33$, $P < 0.0001$]. By contrast, arousing modulators from experiment 1 were more arousing than distinctive [$F(1, 10) = 7.80$, $P < 0.02$]. To more closely examine the relationship between arousal and distinctiveness of modulators in experiment 1, distinctiveness and arousal ratings were submitted to a two-way ANOVA with rating type (distinctiveness vs. arousal) and arousal quartile (sorted from least to most arousing) as separate variables. Arousing modulator events were judged overall as equally distinctive and arousing ($F < 1$) yet at the most arousing quartile were judged as significantly more arousing than distinctive [$F(1,30) = 27.72$, $P < 0.0001$; Fig. 4*b*]. This parallel increase in distinctiveness for arousal of modulators from experiment 1 underscores the need to separate the contributions of arousal and distinctiveness to retrograde memory enhancement. A similar analysis was performed on distinctive modulators from the present experiment, with ratings sorted by distinctiveness quartile. By contrast with arousing modulators from experiment 1, distinctive modulators overall were judged to be significantly more distinctive than arousing [$F(1,10) = 41.19$, $P < 0.0001$] and at the most distinctive quartile being much more distinctive than arousing [$F(1,30) = 368.69$, $P < 0.0001$; Fig. 4*c*]. This pattern allowed an examination of the effect of manipulations of distinctiveness under conditions of decreased arousal in the present study.

Procedure. The procedure was highly similar to that of experiment 1, with the exception that participants were asked to rate each modulator stimulus according to question "How distinctive?" on a scale from 1 (not at all) to 7 (very much). There were 12 trials per factorial combination of modulator distinctiveness (low and high), test–modulator ISI (short, long), and test stimulus type (faces, houses), yielding a total of 96 trials.

Analysis. As in the arousal condition, the manipulation of distinctiveness was indexed by sorting participants' individual distinctiveness ratings for modulators into quartiles. Distinctiveness level (four quartiles, from low to high) was submitted to repeated measures ANOVA for each ISI (short and long). The distinctiveness hypothesis was tested by using focused linear and quadratic contrasts (df = 1,60).

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