Brief Communication

Emotional enhancement effect of memory: Removing the influence of cognitive factors

Tobias Sommer,[1,3,4] Jan Gläscher,[1,3] Steffen Moritz,[2] and Christian Büchel[1]

[1]NeuroImage Nord, Department of Systems Neuroscience, University of Hamburg Medical School, Hamburg 20246, Germany;
[2]Department of Psychiatry and Psychotherapy, University of Hamburg Medical School, Hamburg 20246, Germany

According to the modulation hypothesis, arousal is the crucial factor in the emotional enhancement of memory (EEM). However, the multifactor theory of the EEM recently proposed that cognitive characteristics of emotional stimuli, e.g., relatedness and distinctiveness, also play an important role. The current study aimed to investigate the individual contribution of arousal to the neural correlates of the EEM by controlling for these additional cognitive factors. We observed the characteristic neuronal correlates of the EEM, in particular enhanced activity in the amygdala and hippocampus, which provides evidence for an arousal-driven EEM in the amygdala as proposed by the modulation hypothesis.

Emotionally arousing events are usually better remembered than neutral ones (emotional enhancement of memory [EEM]). The modulation hypothesis of the EEM proposes that the basolateral amygdala enhances hippocampal consolidation of arousing stimuli via noradrenergic projections (Cahill and McGaugh 1998; McGaugh 2004). Consistent with the time scale of consolidation, the EEM is observed to be more pronounced and consistent after longer retention intervals (Kleinsmith and Kaplan 1963; Sharot and Yonelinas 2008). However, arousing items are often better remembered immediately after encoding as well, which cannot be explained by more efficient consolidation (Talmi et al. 2008).

Therefore, it was recently proposed that the EEM is additionally driven by memory enhancing cognitive characteristics of emotional stimuli, i.e., their distinctiveness, semantic relatedness, and deployment of selective attention. As predicted by this hypothesis, the immediate EEM is substantially reduced when the relative distinctiveness of emotional stimuli in a neutral context is removed by presenting pure lists of emotional and neutral items (Schmidt and Saari 2007; Talmi et al. 2007a). In addition, matching the semantic relatedness of the emotional and neutral stimuli by using categorized neutral items diminishes the immediate EEM (Manning and Julian 1975; Dewhurst and Parry 2000; Talmi and Moscovitch 2004; Buchanan et al. 2006; Talmi et al. 2007a). Importantly, controlling for both factors by using pure lists of categorized items eliminates the immediate behavioral EEM (Talmi et al. 2007a). On the other hand, a purely arousal-driven long term EEM could be observed after a 1 wk retention interval (Anderson et al. 2006). Finally, enhanced selective attention for emotionally arousing stimuli seems to play a more complex but less substantial role that may be valence specific (Kensinger and Corkin 2004; Sharot and Phelps 2004; Kern et al. 2005; Talmi et al. 2007b). The derived multifactorial theory of the EEM proposes that, on the one hand, emotional arousal directly modulates amygdala-driven consolidation but, on the other hand, enhances encoding mediated by the aforementioned cognitive factors (Talmi et al. 2007b).

The neural correlates of the EEM are commonly explored by contrasting brain activity during the successful encoding of arousing versus neutral stimuli (LaBar and Cabeza 2006). A consistent finding of positron emission tomography (PET) and func-

tional magnetic resonance imaging (fMRI) studies is enhanced amygdala activity as well as amygdala–hippocampal connectivity for the subsequently remembered arousing stimuli (Cahill et al. 1996; Canli et al. 2000; Kilpatrick and Cahill 2003; Dolcos et al. 2004b; Kensinger and Corkin 2004; Richardson et al. 2004; Kensinger and Schacter 2005, 2006; Dougal et al. 2007; Talmi et al. 2008). However, the previously employed neuroimaging paradigms could not disentangle the contributions of arousal and of the cognitive factors distinctiveness and semantic relatedness to the neuronal EEM. The aim of the current study was therefore to investigate the neural basis of an exclusively arousal-driven EEM by controlling the two crucial cognitive factors, semantic relatedness, and distinctiveness and to provide further evidence for the modulation hypothesis. Based on previous findings from pharmacological and animal studies, we hypothesized that also a purely arousal-driven EEM would be mediated by the amygdala and would have its effect during encoding on hippocampal activation (McGaugh 2004).

To eliminate the impact of cognitive factors to the EEM, we used valence pure lists of positive, negative, or neutral words that were moreover matched for their semantic relatedness within the list (Talmi et al. 2007a). The semantic relatedness of the study material was carefully matched between valence levels because the memory enhancing effect of "semantic cohesion" is well documented not only for recall, but also for recognition (Neely and Tse 2007a), and emotional stimuli are inherently semantically interrelated (Maratos et al. 2000; Dillon et al. 2006). We created six lists of 18 words for each of three valence levels (resulting in 108 words for each valence level): Words belonging to different theme words (e.g., love, funeral, air) were collected and rated with respect to their relatedness by 55 subjects. The experimental lists were then sorted based on these ratings. Twelve words from each list served as study items, the remaining six as distractors. We chose negative and positive words because the neural EEM in the amygdala is primarily driven by emotional arousal rather than valence (Kensinger and Schacter 2006). Sexual, threatening, and taboo words were not included, as it has been suggested that such stimuli might be preferentially processed (MacKay et al. 2004; Aquino and Arnell 2007).

The whole experiment consisted of three sessions, each with an encoding and a retrieval phase, which were scanned consecutively, but separated by a short break (due to space limitations the retrieval data will not be reported). To control for the relative distinctiveness of emotional items, the words from six lists (two

---

[3]These authors contributed equally to this work.
[4]Corresponding author.
E-mail tsommer@uke.uni-hamburg.de; fax 49-40-42803-9955.

from each valence level) were presented during an encoding phase in a pure list design, i.e., all 12 words of the particular list were presented one after another for 3 sec each. Subjects were asked to indicate by button press whether the word was a noun or not.

The behavioral EEM in recognition is very subtle, especially after short retention intervals, and demands sensitive measurement in order to be detected. For example, arousal-dependent differences in d′ and response bias (Danion et al. 1995; Windmann and Kutas 2001) as well as in the relative contribution of recollection and familiarity have been observed immediately after encoding (Dewhurst and Parry 2000; Ochsner 2000; Kensinger and Corkin 2003; Sharot et al. 2007; Sharot and Yonelinas 2008). Therefore, we employed a six-point confidence scale during the retrieval phases, in which old and new items from the three valence levels were presented in randomized order. Subjects were asked to indicate their memory confidence by moving a red rectangle located at a random position to one of the six response alternatives (6 = 100% confident old, 1 = 100% confident new). After the experiment, volunteers rated all words in randomized order with respect to arousal on a seven-point Likert-scale outside of the scanner.

Seventeen right-handed female volunteers (mean age 27.4 yr) participated in the study. Only female volunteers were included because previous work has shown a sex-related hemispheric lateralization of the EEM (Cahill et al. 2001; Canli et al. 2002; Cahill et al. 2004). Functional MRI was performed on a 3 T scanner (Siemens Trio) with a standard gradient-echo EPI T2*-sensitive sequence in 42 contiguous axial slices (2-mm thickness with 1-mm gap, repetition time [TR] = 2.41 sec, echo time [TE] = 25 msec, flip angle 70°, field of view 192 mm^2, 64 × 64 matrix resolution). The images were slice-time corrected, realigned, normalized into standard anatomical space (Montreal Neurological Institute [MNI] template), and smoothed with an isotropic Gaussian kernel of 10 mm full-width-half-maximum using SPM5.

For the fMRI and behavioral analyses, the words were individually categorized into three arousal levels based on the post-scanning arousal ratings: "non-arousing" (ratings 1–2), "slightly arousing" (ratings 3–4), and "arousing" (ratings 5–7). The naming of the categories as "slightly arousing" and "arousing" is based on informal post-experimental interviews where subjects commented that they did not experience reading the words as highly arousing. An event-related analysis was conducted for each subject on a voxel-by-voxel basis (first level analysis). To explore the EEM, a subject-specific design matrix was created containing the three encoding sessions. The data were high-pass filtered at a cutoff period of 120 sec. The events were divided into the three aforementioned arousal levels, each modeled as a separate regressor by convolving a delta function at the time of onset with the canonical hemodynamic response function. Each of these onset regressors was modulated by convolution with a parametric regressor containing the subsequent individual confidence ratings (six ranks) for each word during retrieval. These three parametric regressors (one for each arousal level) thereby modeled an arousal-dependent subsequent memory effect.

The contrast images of these parametric regressors were then entered into a second level group analysis with subject as the random effect. We then looked for brain areas that encoded an arousal-dependent subsequent memory effect by applying a contrast that tested for an increase in retrieval success across the different arousal levels. The threshold for statistical significance was set to $P < 0.05$, corrected for multiple comparisons. Based on our a priori hypotheses, we applied a search volume in the entorhinal cortex, the hippocampus and the amygdala by employing anatomical masks derived from the statistical parametric mapping (SPM) anatomy toolbox (Amunts et al. 2005). In addi-

tion, a subset of studies on the neuronal correlates of the EEM reported areas beyond the medial temporal lobe for encoding (Dolcos et al. 2004a; Kensinger and Schacter 2005, 2006; Talmi et al. 2008). Therefore, areas observed in these studies were included in an exploratory analysis and the peak coordinates of activations as reported served as the center of reduced spherical search volumes (radius 10 mm).

Previous studies reported significant correlations between amygdala and hippocampus activity during the successful encoding of arousing but not of neutral items (Kilpatrick and Cahill 2003; Dolcos et al. 2004b; Kensinger and Corkin 2004). This correlation was interpreted as indication of the arousal-dependent functional interaction of these areas. Therefore, we conducted an additional first level analysis to calculate this correlation in voxels of interest that were identified by the foregoing analysis of the EEM. The items in each arousal-level were subdivided in subsequently remembered (confidence ratings 1 to 3) or forgotten words (confidence ratings 4 to 6), resulting in six event-types. These events-types were modeled as separate regressors. The mean parameter estimate across the three encoding sessions for each event-type was computed for each voxel. The mean parameter estimates for the subsequently remembered words in the hippocampus and amygdala peak voxels of the foregoing EEM analysis were extracted and correlated across subjects for each arousal level.

In the following behavioral analyses, a Greenhouse-Geisser adjustment for degrees of freedom was applied when appropriate to guard against violation of the sphericity assumption. An arousal × valence ANOVA revealed that positive and negative words were rated more frequently as arousing then neutral words ($F_{(1.90,30.41)} = 3.73$, mean square error [MSE] = 0.05, $P = 0.03$). The response time during encoding did not differ depending on the arousal level ($F_{(1.7,26.6)} = 0.27$, MSE = 0.002, $P > 0.7$).

To explore a behavioral EEM, we conducted repeated measures ANOVAs across the three arousal levels using a variety of memory performance parameters as dependent variables. First, we analyzed the hit rate and accuracy (hit rate corrected by false alarm rate) and found no significant effect of arousal level (hit rate: $F_{(1.83,29.20)} = 0.42$, MSE = 0.08, $P > 0.6$; accuracy: $F_{(1.88,30.10)} = 0.16$, MSE = 0.02, $P > 0.8$; Fig. 1, left panel). In addition, response bias and d′ did not differ depending on the arousal level (response bias: $F_{(1.98,31.76)} = 0.11$, MSE = 0.01, $P > 0.8$; d′: $F_{(1.48,23.75)} = 0.45$, MSE = 0.03, $P > 0.9$). Moreover, familiarity and recollection as calculated from the individual distribution of confidence ratings did not differentially contribute to recognition depending on the arousal level ($F_{(1.89,30.36)} = 0.07$, MSE = 0.01, $P > 0.9$; $F_{(1.12,17.84)} = 0.01$, MSE = 0.84, $P > 0.9$; Fig. 1, middle panel). The ROC-curves and parameters for both processes were estimated from the confidence ratings based on a widely accepted dual process model of recognition memory (Yonelinas et al. 1998). In conclusion, even if it is not statistically possible to accept the null hypothesis, there seems to be no behavioral indication for systematic memory differences dependent on the arousal level.

The following analyses are restricted to the group of words that were rated as arousing (arousal level 3). The aim of these analyses was to identify the characteristics of the arousing events that correlate with subsequent retrieval success. This knowledge can inform the interpretation of the neuronal EEM that is based on contrasting arousing events dependent on subsequent memory performance. Therefore, we conducted a series of repeated measures ANOVAs across the six confidence levels using dependent variables that varied across the arousing words. To begin with, there was no influence of valence or reaction time during encoding on memory confidence (valence: $F_{(3.6,53.3)} = 0.81$, MSE = 0.001, $P > 0.5$; reaction time:
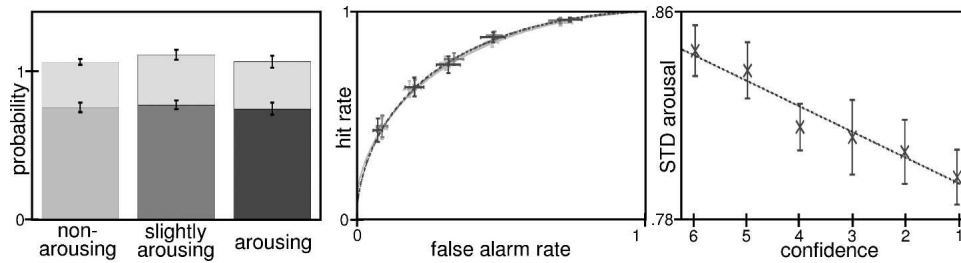
Figure 1. (*Left* panel) hit rate (mean ± SEM; light gray, medium gray, and dark gray bars) and false alarm rate (very light gray bars) in the three arousal levels. (*Middle* panel) ROC-curves in probabilistic space fitted according to the dual process model (Yonelinas et al. 1998) to the data (mean ± SEM; light gray, non-arousing words; medium gray, slightly arousing words; dark gray, arousing words). (*Right* panel) Inter-rater consensus for the arousing words (expressed in standard deviations, STD, of post-experimental arousal ratings; higher STD corresponds to higher subjective arousal) for the six confidence levels (6 = high confidence old, 1 = high confidence new; mean ± SEM, dashed line represents linear trend line).

$F_{(2.9,23.4)} = 1.03$, MSE = 12,347, $P > 0.4$). Another characteristic that varied between the arousing words was their micro-context within the list, as some were preceded by an equally arousing word, whereas others were preceded by a word rated as non- or only slightly arousing. The arousing words thereby differed with respect to the slope of arousal between the preceding and the current trial, and this can be coded as 0, 1, or 2. The analysis of the relationship between the steepness of the arousal slope and memory performance revealed no significant result (ANOVA: $F_{(3.90,58.53)} = 0.16$, MSE = 0.16, $P > 0.3$). Finally, the rating of a word as "highly arousing" can be based either on a subjective experience of arousal or on a more rationally based normative attribution of arousal, i.e., cultural norms suggesting which words should be considered as highly arousing. High "normative arousal" of a word is expressed as a high interindividual consensus. However, high "normative arousal" is not necessarily accompanied by the subjective experience of arousal, which is reflected in amygdala activity. The "normative arousal" of each word was computed as the standard deviation of the individual arousal ratings for this word across subjects (higher standard deviation corresponds to lower "normative arousal"). The lower the "normative arousal" of a word rated by an individual subject as highly arousing, the more likely this rating was based on the subjective experience of arousal. The "normative arousal" × confidence

ANOVA revealed that words rated more subjectively as highly arousing (higher standard deviation of ratings) were better remembered ($F_{(3.4,54.8)} = 4.75$, $P = 0.004$; Fig. 1).

The analysis of the fMRI data revealed an effect of arousal on encoding activity. We found a greater subsequent memory effect for arousing words in the bilateral amygdala ($xyz = -33$, -3, -21, $Z = 3.47$; $xyz = 30$, -6, -12, $Z = 4.04$), in the bilateral hippocampus and left hippocampal tail ($xyz = -30$, -18, -27, $Z = 5.07$; $xyz = -24$, -39, 3, $Z = 4.34$; $xyz = 30$, -15, -27, $Z = 4.06$) as well as in the bilateral entorhinal cortex ($xyz = -24$, -12, -33, $Z = 4.54$; $xyz = 27$, -12, -33, $Z = 4.01$; Fig. 2). The peak voxels of the bilateral amygdala activity are located within a cytoarchitectonic-defined MRI-mask for its basolateral nuclei (Amunts et al. 2005). However, a definitive assignment of the activity to the basolateral amygdala is not possible due to scanning and imaging parameters. The parameter estimates in all areas revealed that activity was equally low for non- and slightly arousing words, but significantly greater for the arousing words (Fig. 2). The exploratory analysis based on the reported peak voxels of previous studies revealed significant arousal-dependent subsequent memory effects in dorsolateral prefrontal cortex ($xyz = -15$, 36, 39; $Z = 3.87$; Dolcos et al. 2004a), in right superior frontal gyrus ($xyz = 15$, -12, 36; $Z = 3.21$), and in right anterior cingulate ($xyz = 12$, 18, 19; $Z = 3.99$), in right superior parietal lobe ($xyz = 12$, -48, 63; $Z = 3.83$), in left inferior/middle temporal gyrus ($xyz = -45$, -39, -6; $Z = 4.13$; Kensinger and Schacter 2006), and in left superior temporal gyrus ($xyz = -33$, -3, -15; $Z = 3.76$; Talmi et al. 2008). In addition, activity differences in the right postcentral gyrus reached significance ($xyz = 30$, -33, 63; $Z = 4.99$, corrected for entire brain volume).

The correlation between amygdala and hippocampus activity during encoding of subsequently remembered words was significant only for the arousing words (left hemisphere $r = 0.87$, $P < 0.0001$; right hemisphere $r = 0.93$, $P < 0.0001$; Fig. 3). However, one outlier (the same subject in both hemispheres) may have disproportionally increased the correlation. After removal of this subject, the left hemispheric correlation showed a strong trend toward significance ($r = 0.51$, $P = 0.056$); the right hemispheric correlation was still highly significant ($r = 0.82$, $P < 0.0005$).
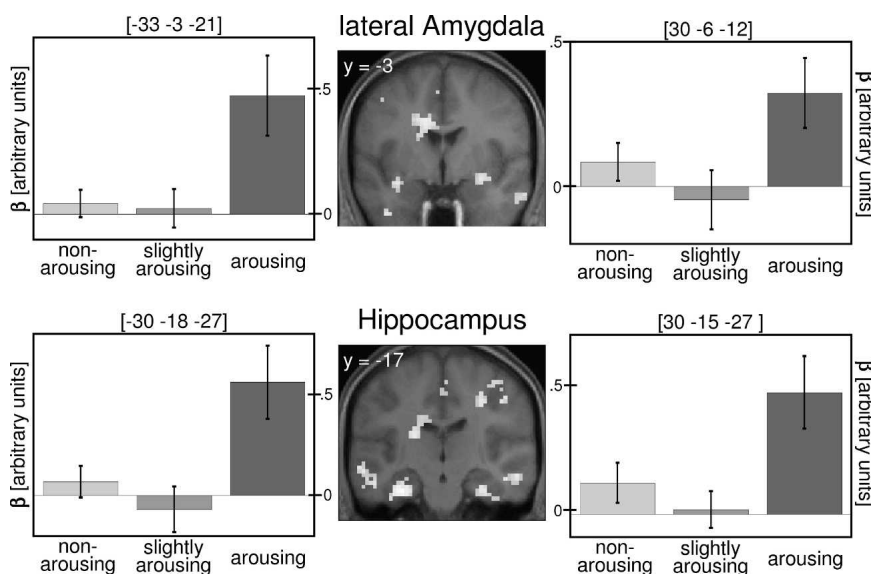
Figure 2. Emotional subsequent memory effect in the lateral amygdala, hippocampus, and entorhinal cortex. The parameter estimates (mean ± SEM) in the peak voxels of the parametric confidence regressors of the three arousal levels are shown (see main text for a detailed description of the model).
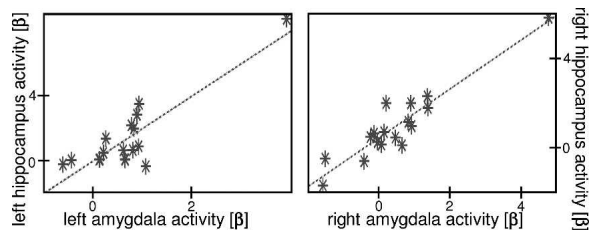
Figure 3. Activity in the hippocampus and amygdala (β, arbitrary units) during encoding of arousing words that were later remembered (confidence rating 1 to 3) correlated significantly only for arousing words (*left*: $r = 0.87$, $P < 0.01$; *right*: $r = 0.93$, $P < 0.01$; without the outlier, *left*: $r = 0.51$, $P = 0.056$; *right*: $r = 0.82$, $P < 0.01$; dashed line represents linear trend lines).

Thus, in the current study, we observed the characteristic effect of arousal on memory encoding at the neural level. In particular, the subsequent memory effect was greater in the amygdala, hippocampus, and entorhinal cortex for emotionally arousing than for only slightly and non-arousing words. Moreover, a correlation in the activity between the amygdala and the hippocampus during successful encoding was only found for arousing words, suggesting an arousal-dependent interaction of both areas. This pattern of the emotional subsequent memory effect is highly consistent with previous PET and fMRI studies (Cahill et al. 1996; Canli et al. 2000; Kilpatrick and Cahill 2003; Dolcos et al. 2004a,b; Kensinger and Corkin 2004; Richardson et al. 2004; Kensinger and Schacter 2005, 2006; Dougal et al. 2007; Talmi et al. 2008). The activity in the amygdala was greater in the left than in the right hemisphere, which is in agreement with previous reports of a sex-related hemispheric lateralization (Cahill et al. 2004). However, the various performance parameters—i.e., hit rate, accuracy, d′, response bias, and relative contribution of recollection—did not reveal any immediate behavioral EEM, indicating the intended absence of differences in relatedness and distinctiveness. In addition, the response time during encoding was equal across the arousal levels, suggesting that arousing stimuli did not attract more selective attention (Schmidt and Saari 2007; Talmi et al. 2008). Altogether, these data imply that the cognitive factors contributing to the EEM in the standard experimental paradigm were, at least for the most part, eliminated. This indicates that the observed neuronal EEM reflects almost exclusively arousal-dependent differences in encoding. The present data thereby provide important evidence for the modulation hypothesis, which proposes that the correlation between amygdala activity and memory encoding is driven by the arousal of stimuli that activates the amygdala. Consistent with this hypothesis, we found the strongest subsequent memory effect bilaterally in the amygdala, putatively in its basolateral nuclei, and in its hippocampal projection targets (McGaugh 2004).

The neuronal EEM indicated that the amygdala activity during encoding correlated strongest with the memory confidence for arousing words. Our behavioral analysis of the arousing events revealed that neither the slope of arousal, nor their valence, nor the reaction time during encoding predicted memory performance. This suggests that indeed neither relative distinctiveness of some arousing words nor the differential attraction of selective attention contributed to the differences in encoding efficiency (Kensinger and Corkin 2004; Schmidt and Saari 2007; Talmi et al. 2008). Only when we separated the arousal ratings into subjective and normative we found that experienced rather than normative arousal led to better subsequent memory performance (Fig. 1). In other words, the more an item was momentarily perceived as arousing, the more its processing was accompanied by increased amygdala activity and the more efficiently it was encoded. This behavioral analysis thereby provides further

evidence, that the neuronal EEM in the current study is indeed a reflection of differences in experienced arousal, but not of cognitive factors. In conclusion, this study, by controlling for the confounding cognitive factors, is the first fMRI evidence for a purely arousal-driven EEM in the amygdala as proposed by the modulation hypothesis. This does not, of course, imply that cognitive factors do not play a role in the etiology of the EEM under standard experimental conditions.

Acknowledgments

References

Amunts, K., Kedo, O., Kindler, M., Pieperhoff, P., Mohlberg, H., Shah, N.J., Habel, U., Schneider, F., and Zilles, K. 2005. Cytoarchitectonic mapping of the human amygdala, hippocampal region and entorhinal cortex: Intersubject variability and probability maps. *Anat. Embryol.* **210:** 343–352.

Anderson, A.K., Wais, P.E., and Gabrieli, J.D. 2006. Emotion enhances remembrance of neutral events past. *Proc. Natl. Acad. Sci.* **103:** 1599–1604.

Aquino, J.M. and Arnell, K.M. 2007. Attention and the processing of emotional words: Dissociating effects of arousal. *Psychon. Bull. Rev.* **14:** 430–435.

Buchanan, T.W., Etzel, J.A., Adolphs, R., and Tranel, D. 2006. The influence of autonomic arousal and semantic relatedness on memory for emotional words. *Int. J. Psychophysiol.* **61:** 26–33.

Cahill, L. and McGaugh, J.L. 1998. Mechanisms of emotional arousal and lasting declarative memory. *Trends Neurosci.* **21:** 294–299.

Cahill, L., Haier, R.J., Fallon, J., Alkire, M.T., Tang, C., Keator, D., Wu, J., and McGaugh, J.L. 1996. Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proc. Natl. Acad. Sci.* **93:** 8016–8021.

Cahill, L., Haier, R.J., White, N.S., Fallon, J., Kilpatrick, L., Lawrence, C., Potkin, S.G., and Alkire, M.T. 2001. Sex-related difference in amygdala activity during emotionally influenced memory storage. *Neurobiol. Learn. Mem.* **75:** 1–9.

Cahill, L., Uncapher, M., Kilpatrick, L., Alkire, M.T., and Turner, J. 2004. Sex-related hemispheric lateralization of amygdala function in emotionally influenced memory: An fMRI investigation. *Learn. Mem.* **11:** 261–266.

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J.D., and Cahill, L. 2000. Event-related activation in the human amygdala associates with later memory for individual emotional experience. *J. Neurosci.* **20:** RC99. http://www.jneurosci.org/cgi/content/full/20004570v1.

Canli, T., Desmond, J.E., Zhao, Z., and Gabrieli, J.D. 2002. Sex differences in the neural basis of emotional memories. *Proc. Natl. Acad. Sci.* **99:** 10789–10794.

Danion, J.M., Kauffmann-Muller, F., Grange, D., Zimmermann, M.A., and Greth, P. 1995. Affective valence of words, explicit and implicit memory in clinical depression. *J. Affect. Disord.* **34:** 227–234.

Dewhurst, S.A. and Parry, L.A. 2000. Emotionality, distinctiveness, and recollective experience. *Eur. J. Cogn. Psychol.* **12:** 541–551.

Dillon, D.G., Cooper, J.J., Grent-'t-Jong, T., Woldorff, M.G., and LaBar, K.S. 2006. Dissociation of event-related potentials indexing arousal and semantic cohesion during emotional word encoding. *Brain Cogn.* **62:** 43–57.

Dolcos, F., LaBar, K.S., and Cabeza, R. 2004a. Dissociable effects of arousal and valence on prefrontal activity during emotional evaluation and subsequent memory: An event-related fMRI study. *Neuroimage* **23:** 64–74.

Dolcos, F., LaBar, K.S., and Cabeza, R. 2004b. Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron* **42:** 855–863.

Dougal, S., Phelps, E.A., and Davachi, L. 2007. The role of medial temporal lobe in item recognition and source recollection of emotional stimuli. *Cogn. Affect. Behav. Neurosci.* **7:** 233–242.

Kensinger, E.A. and Corkin, S. 2003. Memory enhancement for emotional words: Are emotional words more vividly remembered than neutral words? *Mem. Cognit.* **31:** 1169–1180.

Kensinger, E.A. and Corkin, S. 2004. Two routes to emotional memory: Distinct neural processes for valence and arousal. *Proc. Natl. Acad. Sci.* **101:** 3310–3315.

Kensinger, E.A. and Schacter, D.L. 2005. Emotional content and reality-monitoring ability: fMRI evidence for the influences of encoding processes. *Neuropsychologia* **43:** 1429–1443.

Kensinger, E.A. and Schacter, D.L. 2006. Amygdala activity is associated

with the successful encoding of item, but not source, information for positive and negative stimuli. *J. Neurosci.* **26:** 2564–2570.

Kern, R.P., Libkuman, T.M., Otani, H., and Holmes, K. 2005. Emotional stimuli, divided attention, and memory. *Emotion* **5:** 408–417.

Kilpatrick, L. and Cahill, L. 2003. Amygdala modulation of parahippocampal and frontal regions during emotionally influenced memory storage. *Neuroimage* **20:** 2091–2099.

Kleinsmith, L.J. and Kaplan, S. 1963. Paired-associate learning as a function of arousal and interpolated interval. *J. Exp. Psychol.* **65:** 190–193.

LaBar, K.S. and Cabeza, R. 2006. Cognitive neuroscience of emotional memory. *Nat. Rev. Neurosci.* **7:** 54–64.

MacKay, D.G., Shafto, M., Taylor, J.K., Marian, D.E., Abrams, L., and Dyer, J.R. 2004. Relations between emotion, memory, and attention: Evidence from taboo stroop, lexical decision, and immediate memory tasks. *Mem. Cognit.* **32:** 474–488.

Manning, S.K. and Julian, L. 1975. Recall of emotional words. *J. Gen. Psychol.* **92:** 237–244.

Maratos, E.J., Allan, K., and Rugg, M.D. 2000. Recognition memory for emotionally negative and neutral words: An ERP study. *Neuropsychologia* **38:** 1452–1465.

McGaugh, J.L. 2004. The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annu. Rev. Neurosci.* **27:** 1–28.

Neely, J.-H. and Tse, C.-S. 2007. Semantic relatedness effects on true and false memories in episodic recognition: A methodological and empirical review. In *The foundations of remembering: Essays in honor of Henry L. Roediger, III* (ed. J.S. Nairne), pp. 313–351. Psychology Press, New York.

Ochsner, K.N. 2000. Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. *J. Exp. Psychol. Gen.* **129:** 242–261.

Richardson, M.P., Strange, B.A., and Dolan, R.J. 2004. Encoding of emotional memories depends on amygdala and hippocampus and their interactions. *Nat. Neurosci.* **7:** 278–285.

Schmidt, S.R. and Saari, B. 2007. The emotional memory effect: Differential processing or item distinctiveness? *Mem. Cognit.* **35:** 1905–1916.

Sharot, T. and Phelps, E.A. 2004. How arousal modulates memory: Disentangling the effects of attention and retention. *Cogn. Affect. Behav. Neurosci.* **4:** 294–306.

Sharot, T. and Yonelinas, A.P. 2008. Differential time-dependent effects of emotion on recollective experience and memory for contextual information. *Cognition* **106:** 538–547.

Sharot, T., Verfaellie, M., and Yonelinas, A.P. 2007. How emotion strengthens the recollective experience: A time-dependent hippocampal process. *PLoS ONE* **2:** e1068. doi: 10.1371/journal.pone.0001068.

Talmi, D. and Moscovitch, M. 2004. Can semantic relatedness explain the enhancement of memory for emotional words? *Mem. Cognit.* **32:** 742–751.

Talmi, D., Luk, B.T.C., McGarry, L.M., and Moscovitch, M. 2007a. The contribution of relatedness and distinctiveness to emotionally-enhanced memory. *J. Mem. Lang.* **56:** 555–574.

Talmi, D., Schimmack, U., Paterson, T., and Moscovitch, M. 2007b. The role of attention and relatedness in emotionally enhanced memory. *Emotion* **7:** 89–102.

Talmi, D., Anderson, A.K., Riggs, L., Caplan, J.B., and Moscovitch, M. 2008. Immediate memory consequences of the effect of emotion on attention to pictures. *Learn. Mem.* **15:** 172–182.

Windmann, S. and Kutas, M. 2001. Electrophysiological correlates of emotion-induced recognition bias. *J. Cogn. Neurosci.* **13:** 577–592.

Yonelinas, A.P., Kroll, N.E., Dobbins, I., Lazzara, M., and Knight, R.T. 1998. Recollection and familiarity deficits in amnesia: Convergence of remember-know, process dissociation, and receiver operating characteristic data. *Neuropsychology* **12:** 323–339.

Emotional enhancement effect of memory: Removing the influence of cognitive factors

Tobias Sommer, Jan Gläscher, Steffen Moritz, et al.

References	This article cites 40 articles, 8 of which can be accessed free at: **http://learnmem.cshlp.org/content/15/8/569.full.html#ref-list-1**
License	
Email Alerting Service	Receive free email alerts when new articles cite this article - sign up in the box at the top right corner of the article or **click here.**