

Table 1
Mean proportions of R, K, and G responses as a function of valence and age

		Young			Old		
		Negative	Neutral	Positive	Negative	Neutral	Positive
R	Hits	.74	.32	.47	.38	.25	.30
	FAs	.01	.01	.02	.05	.01	.03
K	Hits	.11	.35	.26	.19	.30	.26
	FAs	.03	.02	.05	.08	.05	.08
G	Hits	.04	.13	.10	.07	.11	.11
	FAs	.06	.04	.06	.07	.08	.08

Discussion

The results of the present study show that the effect of emotion on recollection is modulated by age differences. Consistent with a previous study (Ochsner, 2000), positive and negative pictures were richly recollected more often than neutral ones in younger adults. In contrast, older adults reported more R responses for negative but not for positive pictures. Furthermore, they reported less R responses than younger adults for emotional but not for neutral pictures. This is somewhat surprising given that age is generally associated with a decrease in R responses. However, Perfect, Williams, and Anderton-Brown (1995) found that the decrease in R responses in older adults disappeared when elaborative encoding was encouraged. The instructions we used in the present study encouraged such a detailed encoding by drawing attention to various aspects of the stimuli (their visual complexity, valence, and intensity) and this could explain the absence of age differences in the recollection of neutral stimuli. In contrast, older adults had a deficit in recollective experience for emotional stimuli. Despite the instructions which tried to draw attention to both emotional and perceptual details of the stimuli, it may be that, when confronted with emotional stimuli, older adults tend to focus on their feelings to a greater extent than younger adults. In consequence, less resources would be available to encode perceptual and contextual details of the stimuli and hence rich recollections would be less likely to occur. Future studies will be needed to examine this proposition.

References

- Gardiner, J. M., & Richardson-Klavehn, A. (2000). Remembering and knowing. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 229–244). Oxford: Oxford University Press.
- Hashtroudi, S., Johnson, M. K., Vnek, N., & Ferguson, S. A. (1994). Aging and the effects of affective and factual focus on source monitoring and recall. *Psychology and Aging*, *9*, 160–170.
- Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, visceral, and behavioral reactions. *Psychophysiology*, *30*, 261–273.
- Ochsner, K. N. (2000). Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. *Journal of Experimental Psychology: General*, *129*, 242–261.
- Perfect, T. J., Williams, R. B., & Anderton-Brown, C. (1995). Age differences in reported recollective experience are due to encoding effects, not response bias? *Memory*, *3*, 169–186.

34. Coactivation of the amygdala and hippocampus predicts better recall for emotional than for neutral pictures

F. Dolcos,^{a,b} R. Graham,^c K. Labar,^a and R. Cabeza^a

^a Center for Cognitive Neuroscience, Duke University, Durham, NC, USA

^b Centre for Neuroscience, University of Alberta, Edmonton, Alta., Canada

^c Department of Psychology, University of Alberta, Edmonton, Alta., Canada

Emotional events tend to be better remembered than nonemotional events. This memory-enhancing effect of emotion has been attributed to a modulatory influence of the amygdala on the hippocampus during encoding and consolidation (*modulation hypothesis*). We investigated this hypothesis using event-related fMRI. During scanning, subjects encoded pleasant, unpleasant, and neutral pictures under incidental learning conditions, and after scanning, they recalled details of the pictures. Confirming the memory-enhancing effect of emotion, emotional pictures were better recalled than neutral pictures. Compared to neutral pictures, encoding of emotional pictures was associated with activations in several regions, including amygdalar, anterior cingulate, parietal, and occipitotemporal regions. In the case of pictures that were subsequently remembered, emotional pictures were associated with greater activity in both the amygdala and the hippocampus than neutral pictures. These results are consistent with the modulation hypothesis, and shed light on the neural mechanisms of the memory-enhancing effect of emotion.

Report

Emotionally charged events tend to be better remembered than nonemotional events. This difference has been attributed to a modulatory effect of the amygdala on the hippocampus during memory encoding and consolidation (*modulation hypothesis*, e.g., McGaugh, 2000). This hypothesis is based mainly on animal evidence, but some functional neuroimaging evidence with humans is also available (Hamann, 2001). Here, we explore the neural mechanisms underlying the formation of emotional memory using event-related fMRI.

We measured two effects: the *emotion effect* and the *subsequent memory effect*. The *emotion effect* refers to brain activity that is greater for emotional than for neutral stimuli. Previous functional neuroimaging studies have identified emotion effects in several regions including the amygdala, prefrontal cortex, anterior cingulate, posterior parietal, and insula (Davidson & Irwin, 1999). The *subsequent memory effect* refers to encoding activity that is greater for items that are subsequently remembered than for items that are subsequently forgotten. Previous event-related fMRI studies have identified subsequent memory effects in hippocampal and prefrontal regions (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998). On the basis of emotion and subsequent memory effects we investigated two issues.

1. *Co-activation of the amygdala and hippocampus during emotional encoding*. Previous neuroimaging studies have reported that amygdalar activity was correlated with the number of subsequently remembered emotional items (for a review, see Hamann, 2001). However, the modulation hypothesis assumes not only an amygdalar activation, but also an effect of the amygdala on the hippocampus, and therefore it predicts that both the amygdala and the hippocampus are involved in emotional encoding. To investigate this issue,

we compared activity in these regions for subsequently remembered emotional and subsequently remembered neutral pictures, using event-related fMRI.

2. *The role of the amygdala in the processing of pleasant stimuli.* Neuroimaging studies of emotion have strongly associated the amygdala with the processing of unpleasant stimuli, but it is less clear how this region is involved in the processing of pleasant stimuli (Davidson & Irwin, 1999). To investigate this issue, we measured amygdalar activity during the processing of pleasant and unpleasant pictures.

Methods

Participants

Fourteen young (mean age = 24.3 years) healthy right-handed female Duke University students/staff participated in this study. All subjects gave informed consent to a protocol approved by the Duke University Institutional Review Board. Female participants were chosen because previous studies using similar stimuli have found that women are more physiologically reactive to emotional stimuli, and because women are more likely to report intense emotional experiences.

Materials

Stimuli consisted of a pool of 180 pictures selected mainly from the International Affective Picture System (IAPS) and complemented with additional neutral pictures equated for complexity and human presence. IAPS pictures are rated on a nine-point scale both in terms of emotional arousal (1, calm and 9, excited) and emotional valence (1, unpleasant; 5, neutral; 9, pleasant). Based on these scores, we selected 60 high-arousing and pleasant, 60 high-arousing and unpleasant, and 60 low-arousing and neutral pictures. The pleasant and unpleasant pictures differed from each other in terms of emotional valence, but not in terms of emotional arousal, whereas both pleasant and unpleasant pictures differed from neutral pictures in terms of both arousal and valence.

Behavioral methods

Similar to the procedure we employed in a previous event-related potential (ERP) study (Dolcos & Cabeza, submitted), subjects completed six consecutive study blocks of 30 pictures each (10 pleasant, 10 unpleasant, and 10 neutral), randomly presented using an LCD projector. Pictures were presented for 3 s, and followed by a 12-s fixation. Participants were instructed to rate the pictures for pleasantness, using a three-point scale (1, unpleasant; 2, neutral; 3, pleasant). No subsequent memory test was mentioned during encoding, so that learning was incidental. Following the scanning session, subjects performed a 45 min cued-recall test, in which they were provided with a written cue for each of the pictures, and had to describe in writing as many details as they could remember. Subjects were asked to provide enough details so that an outsider could identify each picture and discriminate it from similar studied pictures. Only pictures whose description was detailed enough to allow both identification and discrimination were classified as remembered.

fMRI methods

Anatomical scanning. Thirty-four axial high-resolution T1-weighted structural images were acquired with a 450-ms TR (repetition time), a 9-ms TE (echo time), a 24-cm FOV (field of view), a 256² matrix, and a slice thickness of 3.75 mm. Forty-six coronal T1-weighted images were then acquired using the same imaging parameters.

Functional scanning

Thirty-four contiguous gradient-echo echoplanar axial images (EPIs) sensitive to blood-oxygen level dependent contrast were acquired using the same slice prescription described above for the near-axial structural images. The EPIs were acquired as follows: TR = 3 s, TE = 40 ms, one radio frequency excitation, FOV = 24 cm, image matrix = 64², and flip angle (FA) = 90°. Slice thickness was 3.75 mm, resulting in cubic 3.75-mm³ isotropic voxels.

Image preprocessing

All image preprocessing and statistical analyses were performed using SPM99. Functional images were corrected for acquisition order, and realigned to correct for motion artifacts. Anatomical images were coregistered with the first functional images for each subject, and both anatomical and functional images were spatially normalized to a standard stereotactic space. Functional images were spatially smoothed using an 8-mm isotropic Gaussian kernel.

Statistical analyses. For each subject, task-related activity was identified by a convolving vector of the onset times of the stimuli with a synthetic hemodynamic response and its temporal derivative. The general linear model, as implemented in SPM, was used to model the effects of interest. Group analyses were conducted using random-effects models, as follows. To identify brain areas involved in emotional processing, we compared brain activity for pleasant, unpleasant, and neutral pictures (emotion effect). To reveal brain regions involved in successful encoding operations, we compared brain activity for subsequently remembered and subsequently forgotten pictures (subsequent memory effect). The significance threshold was set at $p < .001$, uncorrected ($t > 3.85$). Additionally, ANOVAs were performed on percent signal change measures extracted from regions of interest (ROIs) drawn on amygdala and hippocampus using custom software from the Brain Imaging and Analysis Center of Duke University.

Results

Behavioral results

As expected, recall was better for emotional pictures (pleasant: 54%, unpleasant: 54%) than for neutral pictures (40%). An ANOVA yielded a significant picture type effect ($F(2, 13) = 73.07, p < .0001$), and post-hoc contrasts indicated that recall of pleasant and unpleasant pictures was similar ($p > .05$) and higher than recall of neutral pictures (both $p < .001$).

fMRI results

Emotion effect

Compared to neutral pictures, emotional pictures (pleasant and unpleasant) were associated with activations in several regions including amygdalar, anterior cingulate, lateral parietal, precuneus, and occipitotemporal regions (see Fig. 1A). The amygdala was activated by both unpleasant and pleasant pictures, and in the right amygdala activity was greater for unpleasant than for pleasant pictures (see Fig. 1B).

Subsequent memory effect

Compared to forgotten pictures, remembered pictures were associated with activations in hippocampal, prefrontal, temporal, and occipital regions. Compared to remembered neutral pictures, remembered emotional pictures elicited greater activity in both the amygdala and the hippocampus (see Figs. 1C and D).

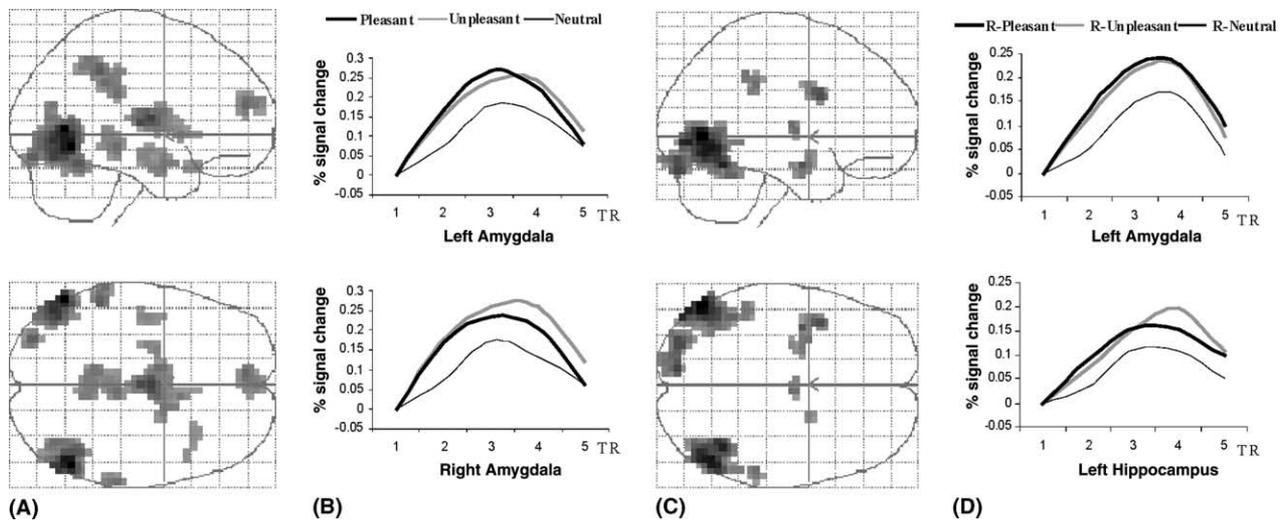


Fig. 1. (A) Regions more active for emotional than for neutral pictures. (B) Percent signal change in the amygdala. (C) Regions more active for remembered emotional than for remembered neutral pictures. (D) Percent signal change in the amygdala and hippocampus. Activations are displayed at $p < .005$, uncorrected. R, remembered; TR, repetition time.

Discussion

The main result of the study was the finding that both the amygdala and the hippocampus were more activated for remembered emotional than for remembered neutral pictures. This finding provides strong support for the modulation hypothesis. Neural activity of these two structures paralleled the difference in memory performance, which was greater for emotional than for neutral pictures. These results suggest that emotional stimuli exert their beneficial effect on memory performance by enhancing activity in the medial-temporal lobe system.

A second finding of the present study is that, when the emotional stimuli are equated for arousal, the amygdala is involved in the processing of both positive and negative emotions. At the same time, the finding that the right amygdala was more activated for unpleasant than for pleasant pictures is consistent with evidence suggesting that the amygdala is particularly sensitive to negative emotions (Davidson & Irwin, 1999). Thus, the present results suggest that the amygdala is involved in the processing of both positive and negative emotions, and that the right amygdala may have some preference for negative emotions.

Acknowledgments

We thank Harlan Fichtenholtz, Barry Giesbrecht, Daniel Weissman, and Kevin Wilson for assistance with data collection and analyses. The study was supported by Duke University, AHFMR (Alberta, Canada), NSERC (Canada), and Chia PhD Scholarship (University of Alberta, Canada).

References

- Brewer, J. B., Zhao, Z., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1998). Making memories: Brain activity that predicts how well visual experience will be remembered. *Science*, *281*, 1185–1187.
- Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, *3*, 11–20.
- Dolcos, F., & Cabeza, R. (submitted). Subsequent memory effect at centroparietal electrodes predicted better recall for high-arousing than for low-arousing pictures.

Hamann, S. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*, *5*, 394–400.

McGaugh, J. L. (2000). Memory—A century of consolidation. *Science*, *287*, 248–251.

35. Effect of divided attention on the memory benefit for negative as compared to neutral words

E.A. Kensinger and S. Corkin

Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA, USA

Individuals are better able to remember in rich detail (“recollect”) negative as compared to neutral stimuli. No studies have addressed whether divided attention alters this benefit. We examined the effect of divided attention on memory for negative versus neutral words. Divided attention at encoding reduced the ability to recollect negative words (Experiments 1 and 2) and to remember source information (Experiment 3); divided attention at retrieval had no effect. Even with divided attention at encoding, however, memory for negative words was better than for neutral words. Automatic and attention-demanding processes at encoding may contribute to the memory benefit for negative items.

Report

Background and motivation

Declarative memory is typically better for negative than neutral stimuli. This benefit may result from an increased ability to remember, in rich detail, negative as compared to neutral stimuli. Thus, Ochsner (2000) found that negative stimuli are better recollected (i.e., participants feel they are re-experiencing the item when they encounter it on a recognition test) than neutral stimuli. Similarly, Doerksen and Shimamura (2001) found that individuals remember more “source” information (i.e., contextual details of an item’s presentation) for negative than neutral words.