Emotional Arousal Can Impair Feature Binding in Working Memory

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Abstract

■ To investigate whether emotional arousal affects memorial feature binding, we had participants complete a short-term source-monitoring task—remembering the locations of four different pictures over a brief delay. On each trial, the four pictures were all either high arousal, medium arousal, or low arousal. Memory for picture–location conjunctions decreased as arousal increased. In addition, source memory for the location of negative pictures was worse among participants with higher depression scores. Two subsequent functional magnetic resonance imaging experiments showed that relative to low-arousal trials, high- and medium-arousal trials resulted in greater activity in areas associated with visual processing (fusiform gyrus, middle temporal gyrus/middle occipital gyrus, lingual gyrus) and less activity in superior precentral gyrus and the precentral–superior temporal intersect. These findings suggest that arousal (and perhaps negative valence for depressed people) recruits attention to items thereby disrupting working memory processes that help bind features together. ■

INTRODUCTION

In this study, we investigated the impact of emotion on the encoding of episodic memories. People often seem to remember shocking events particularly vividly (Pillemer, Goldsmith, Panter, & White, 1988; Rubin & Kozin, 1984). People are also more likely to remember emotional than neutral stimuli (Charles, Mather, & Carstensen, 2003; Canli, Desmond, Zhao, & Gabrieli, 2002; Ochsner, 2000; Bradley, Greenwald, Petry, & Lang, 1992). Yet, emotional memories are often less accurate than we believe they are (e.g., Schmolck, Buffalo, & Squire, 2000).

In particular, although emotional events may result in excellent memory for their central aspects, the ''what'' of the event (Reisberg & Heuer, 2004), other elements of the event are often either forgotten or confused with elements of other events (Christianson & Loftus, 1991). For example, police officers recall fewer details from scenarios in which a shooting occurred than those without a shooting (Stanny & Johnson, 2000), and memory for contextual details is worse for emotionally arousing than nonemotional events (Kensinger, Piguet, Krendl, & Corkin, 2005; Schmidt, 2002). Memories for shocking events may import elements from other events, such as television footage seen later (Pezdek, 2003; Neisser & Harsch, 1992), and memory for peripheral details of such events is worst among people who find the event most emotionally powerful (Schmidt, 2004). Thus, the emotional nature of an event may enhance memory for its emotionally arousing components but impair binding of other aspects of the event to the emotional elements (Johnson, Nolde, & De Leonardis, 1996; but see MacKay & Ahmetzanov, 2005; Doerksen & Shimamura, 2001).

To study feature binding during encoding of neutral events (line drawings of objects in various locations), Mitchell, Johnson, Raye, and D'Esposito (2000) used a short-term source memory paradigm. In the present study, we used a similar working memory task (see Figure 1) to examine how the emotional content of a picture affects people's ability to remember where it appeared (a type of source memory, Johnson, Hashtroudi, & Lindsay, 1993). Our participants saw four pictures from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1999) presented sequentially in different locations on a computer screen. After each sequence of four pictures, there was a brief delay followed by one of those pictures in one of the locations occupied on that trial. Participants indicated whether the picture–location pairing was the same or different than at study. The critical manipulation was that all the pictures on a given trial were either high, medium, or low in arousal, based on normative ratings (Lang et al., 1999). For generality, the high- and medium-arousal pictures each included an equal number of negatively and positively valenced pictures; the low-arousal pictures were neutral in valence.

Experiment 1 was a behavioral study in which we also examined the relationship between individual differences in levels of depression and source memory.

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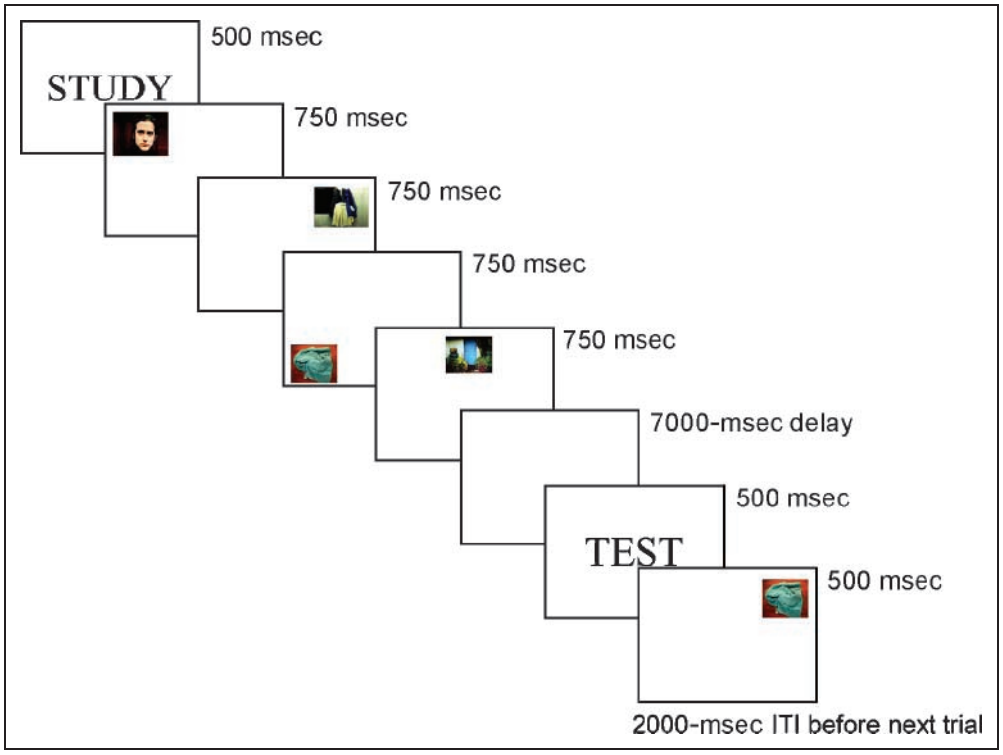

Figure 1. A schematic representation of one behavioral working memory trial with low-arousal, neutral pictures. Note that the picture to screen size proportion is not to scale.

Negative stimuli are especially likely to capture the attention of depressed people (Gotlib & Neubauer, 2000), and this selective attention might negatively affect memory-binding processes. That is, depressed people may be especially likely to process the content of negative stimuli at the expense of binding the content with location. To further clarify the cognitive processes associated with the arousal-induced deficits in source memory revealed in Experiment 1, in Experiments 2A and 2B we used functional magnetic resonance imaging (fMRI) to identify brain regions where activity differed depending on the arousal level of the pictures.

EXPERIMENT 1

Methods

Participants

Twenty undergraduates (15 women, mean age = 18 years) participated for course credit.

Materials

We compiled five categories of 16 pictures each from the IAPS (Lang et al., 1999):[1] (1) high arousal negative ($M_{arousal}$ = 6.38 on a scale of 1–9), (2) high arousal positive ($M_{arousal}$ = 6.38), (3) medium arousal negative ($M_{arousal}$ = 4.56), (4) medium arousal positive ($M_{arousal}$ = 4.53), and (5) low arousal/neutral ($M_{arousal}$ = 3.24). Each of the 80 pictures was randomly assigned to one set of four pictures from the same emotion category (e.g., high arousal negative).

Procedure

On each trial (see Figure 1), participants first saw the cue ''STUDY'' for 500 msec, followed by four pictures shown sequentially for 750 msec each. Each picture appeared in a different one of eight possible locations. After a 7000 msec delay a ''TEST'' cue appeared for 500 msec, followed by one of the four pictures from the trial for 500 msec in one of the locations used during that trial. Participants pressed one key to indicate the picture–location conjunction was the ''same'' as during study and another to indicate it was ''different.'' The intertrial interval (ITI) was 2000 msec, during which the screen was blank. Participants were given three practice trials with pictures not used during the experiment.

We were interested in people's memory for picture–location pairings (source memory). Half of the test pictures of each emotion type were presented in their correct location (''same'' trials) and half in a different location (these ''different'' test probes were a picture and a location from the current trial, but they were repaired). Each set of four pictures appeared in four different trials (picture location and ordinal position within trial was different across repetitions); each picture was tested once during the session (for a total of 80 trials). Whether a picture was tested in its correct location was counterbalanced across participants. Two

different versions of the sets varied which pictures appeared in the same set across participants. Thus, there were four versions of the session. The presentation order of picture sets was random.

Participants completed four 5-min blocks of the task. Between blocks, they completed various questionnaires for 5 min. In the last break, they completed a depression scale (Sheikh & Yesavage, 1986).

Results and Discussion

Short-term Source Memory Data

Participants' source accuracy when responding to the picture–location conjunctions is expressed as d' scores. Proportions of hits (H) and false alarms (FA) were adjusted as follows: $p(\mathrm{H}) = 1$ was recalculated as $1 - 1/(2N)$, $p(\mathrm{FA}) = 0$ was recalculated as $1/(2N)$, where N is the maximum number of hits or false alarms possible (Macmillan & Creelman, 1991). A linear contrast showed that the more arousing the pictures were, the less likely people were to remember where they had occurred, $F(1,19) = 10.16$, $MSE = .42$, $p < .01$, $\eta_p^2 = .35$ (see Figure 2). Omitting the low-arousal (neutral valence) items, a 2 (valence: negative, positive) × 2 (arousal: high, medium) repeated measures analysis of variance (ANOVA) showed only a main effect of arousal, $F(1,19) = 9.32$, $MSE = .28$, $p < .01$, $\eta_p^2 = .33$. There was no main effect of valence and no interaction of valence and arousal (both $F < 1$). Thus, unlike arousal, valence did not influence source accuracy.

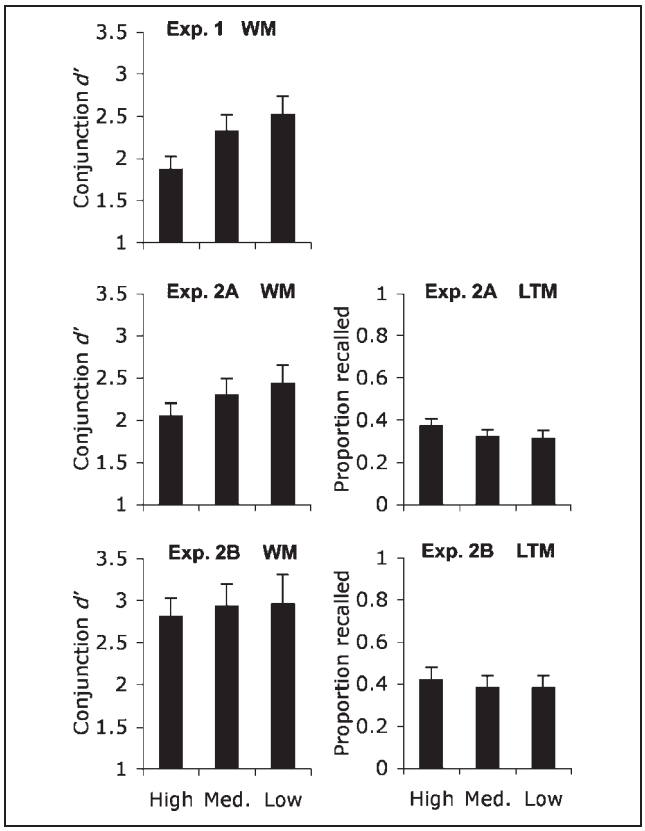

Figure 2. Source accuracy d' for high-, medium-, and low-arousal working memory (WM) trials in Experiments 1, 2A, and 2B (left); proportion of studied high-, medium-, and low-arousal pictures that were recalled (LTM) in Experiments 2A and 2B (right). Error bars are standard errors of the mean.

Correlations with Depression Scale Scores

Scores on the depression scale ranged from 0 to 8 out of a possible 15 ($M = 2.9$, $SD = 3.36$). Scores of six or higher indicate probable depression (Ferraro & Chelminski, 1996). Participants' depression scores were negatively correlated with source accuracy for negative pictures ($r = -.52$, $p < .05$); participants with higher depression scores were less likely to remember the negative picture–location conjunctions correctly, but depression scores were not correlated with source accuracy for neutral ($r = .07$, $p = .80$) or positive ($r = .14$, $p = .50$) pictures.

EXPERIMENTS 2A AND 2B

In Experiment 1, the emotional arousal associated with pictures interfered with participants' ability to remember where the pictures were seen only a few seconds before. Source accuracy was poorest for highly arousing pictures, somewhat better for medium-arousal pictures, and best for the low-arousal pictures. One possible explanation is that emotionally arousing pictures recruit attention to picture content, which disrupts processes that help bind the pictures with location information. To explore this hypothesis, in Experiments 2A and 2B we assessed participants' brain activity during the short-term source memory task using fMRI. A long-term memory test was included to assess whether recall of high-arousal pictures was impaired, like conjunction accuracy, or enhanced, as might be expected if arousal recruits attention to the contents of the picture. Experiment 2A was conducted on a 1.5T scanner, Experiment 2B on a 3T scanner; otherwise, the procedures were identical.[2] Thus, for ease of exposition, they are discussed together. Minor changes to the timing used in Experiment 1 were made to accommodate fMRI constraints. See Figure 3 for the trial event sequence.

Methods

Participants

Participants were healthy, right-handed, college-aged students (Experiment 2A: $n = 16$, eight women, mean age = 22 years.; Experiment 2B: $n = 10$, four women, mean age = 20 years.). All participants reported being in good health, with normal (or corrected-to-normal) vision and no history of psychiatric diagnosis or primary

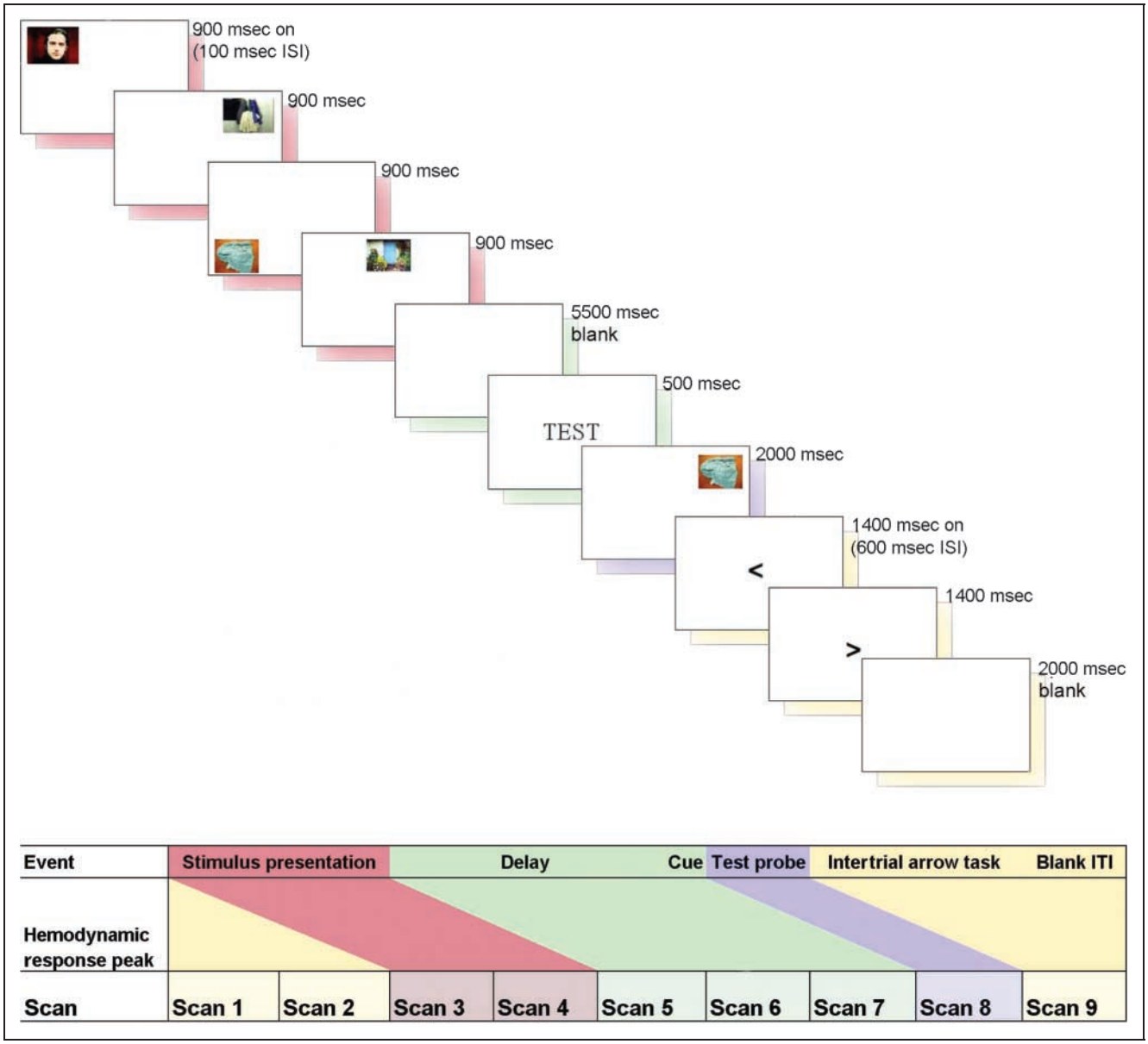

Figure 3. Trial timeline for the fMRI experiments, shown with low-arousal, neutral pictures. Note that the picture to screen size proportion is not to scale. Each trial included nine scans and the chart at the bottom approximates the lag in the hemodynamic response, with the first two scans in each trial reflecting activity from the ITI in the previous trial.

degenerative neurological disorder; none were taking psychotropic medications. All participants were paid.

Task and Design

During scanning, stimuli were projected onto a screen, which participants viewed through a mirror mounted on the head coil (Experiment 2A used a front projection system, with the screen at the foot of the scanner; Experiment 2B used a back projection system with the screen at the back of the scanner). Sixteen low-arousal pictures were added to those from Experiment 1 for a total of 32 pictures at each arousal level (high, medium, low). Each trial took 18 sec (see Figure 3). Participants saw four pictures presented sequentially for 900 msec each, with a 100-msec ISI. Again, all pictures in a trial were similar in arousal level (high, medium, or low), each picture appeared in a different one of eight potential locations, and participants were told to study each item and its location for an upcoming test. After 5500 msec of unfilled time, a cue (TEST) appeared for 500 msec to alert participants that the next picture would be the test probe. As in Experiment 1, the probe was either a studied picture in its original location (same) or a studied picture in a location filled by a different picture on that trial (different). The probe was shown for 2000 msec and participants pressed a button on a response pad in their right (left) hand if the test

item was a picture–location conjunction that was the same (different) as at study. In both experiments, the test probe was followed by a 6000-msec ITI that included two arrows each presented for 1400 msec. Participants were told to press a button with their left hand if the arrow pointed left and with their right hand if it pointed right. The arrows provided a task common to all conditions to allow time for the hemodynamic response and to decrease variability among participants from uncontrolled mental activity between trials.

There were eight runs of 12 trials each, with high, medium, and low trials randomly intermixed in each run. Random assignment and counterbalancing procedures were similar to Experiment 1.

About 5 min after exiting the scanner, there was a surprise written recall test. Participants were told that there were 96 pictures shown during the scan session and that they should try to recall as many as possible, providing as much detail as possible so that the descriptions could be matched to the corresponding pictures.

Imaging Details

Anatomical images were acquired for each participant using a 1.5T Siemens (Malvern, PA) Sonata (Experiment 2A) or a 3T Siemens Trio (Experiment 2B) scanner at the Magnetic Resonance Research Center at Yale University. Functional scans were acquired with a single-shot echoplanar gradient-echo pulse sequence (TR = 2000 msec, TE = 35 msec [Experiment 2A] or 25 msec [Experiment 2B], flip angle = 80°, FOV = 24). The 26 axial slices (slice thickness 3.8 mm, resolution 3.75 × 3.75 mm in plane) were aligned with the AC–PC line. Each run began with 12 blank seconds to allow tissue to reach steady-state magnetization, and was followed by a 1-min rest interval. One volume was collected every 2 sec, or nine full brain scans for each trial (288 images per arousal level for each participant).

fMRI Analyses

Data were motion corrected using a 6-parameter automated algorithm (AIR, Woods, Cherry, & Mazziotta, 1992). A 12-parameter AIR algorithm was used to coregister participants' images to a common reference brain. Data were mean-normalized across time and participants, and spatially smoothed (3-D, 8 mm FWHM gaussian kernel).

fMRI data were analyzed using ANOVA with participant as a random factor (NIS software, University of Pittsburgh and Princeton University). Run (1–8), Arousal (high, medium, low), and Time within trial (scan 1–9) were fixed factors. Brain regions were identified that showed an Arousal by Time (scan) interaction. We report areas of activation identified using a cluster threshold of a minimum of six spatially contiguous voxels, each significant at $p < .001$ (Forman et al., 1995), except as noted in Table 1. We focus discussion on areas of activation that replicated across two independent experiments and therefore appear highly reliable. The resultant F maps were transformed to Talairach space using AFNI (Cox, 1996, version 2.50), and areas of activation were localized using Talairach Daemon software (Lancaster, Summerlin, Rainey, Freitas, & Fox, 1997), as well as manually checked using the Talairach and Tournoux (1988) and other brain atlases. For region-of-interest analyses of the amygdala and hippocampus, each anatomical area was drawn separately on the left and on the right side of the reference brain image and applied to each participant's data to extract timecourse information for each subject. Analyses were then conducted on the group-averaged time course information to determine which arousal levels differed.

The hemodynamic response that indexes brain activity in fMRI responds slowly, rising to a peak 4–6 sec after the critical event. Therefore, to determine which conditions significantly differed ($p < .05$, unless otherwise noted) in each region identified, subsequent analyses were conducted on the mean percent BOLD change (from time 1) at times 3 and 4 and at times 6 and 7, to assess activity that should include processing during picture presentation and during the retention interval, respectively.

Results and Discussion

Behavioral Data

As in Experiment 1, conjunction accuracy during the working memory task was measured using d'. A linear contrast indicated that, in Experiment 2A, the arousal-induced impairment in source memory was replicated, $F(1,15) = 10.16$, $MSE = .42$, $p < .05$, $\eta_p^2 = .27$ (see Figure 2). In Experiment 2B, the pattern of means was the same as in Experiments 1 and 2A, but failed to reach significance (see Figure 2).

To assess long-term memory for individual pictures, two coders matched each picture description from participants' picture recall to the studied pictures. Interrater reliability was 84% and discrepancies were resolved by a third judge. A linear contrast conducted on the proportion of recalled items that were from each arousal level showed that, in Experiment 2A, arousal increased the likelihood of recalling a picture, $F(1,15) = 5.96$, $MSE = .01$, $p < .05$, $\eta_p^2 = .28$ (see Figure 2). In Experiment 2B, high arousal items were recalled at a numerically higher rate, although not significantly so (see Figure 2).

fMRI Data

Table 1 summarizes areas of activation identified as showing Arousal × Time interactions in Experiments 2A

Table 1. Brain Areas Identified in Experiments 2A and 2B

Figure	*Experiment*	*L/R*	*BA*	*Anatomical Area*	*x*	*y*	*z*	*Max F*	*No. of Voxels*	*Contrasts*	
										t3,4	*t6,7*
Areas that replicated across Experiments 2A and 2B											
Areas where high and/or medium > low											
4	2A	R	37	GF	41	−51	−13	3.51	9	H > L† M > L	H > L
4	2B	R	37, (20) (36)	GF, (Gh)	36	−41	−11	4.35	16	H > L† M > L M > H†	H > L M > L
5	2A	R	39, 37/19, 18	GTm/GOm	45	−70	9	6.72	105	H > L M > L	H > L H > M
5	2B	R	39, 37, 19	GTm, GOm, (GTi)	42	−69	9	5.22	53	H > L M > L	
5	2A	L	17/18	GL, Sca, Cu, Gom	−9 −20	−85 −92	0 0	3.71, 3.67	78	M > L	H > L M > L H > M
5	2B	L	17, 18, (19)	Sca, GL, (GOm)	−21	−92	2	3.57	28	H > L†	H > L M > L
Areas where low > high and/or medium											
6	2A*	L	6	GPrC	−57	0	33	2.59	6		L > H
6	2B	L	6/4	GPrC	−53	−5	43	3.01	6	L > H L > M† M > H	L > H M > H
7	2A*	R	6, (44)	GPrC, (GFi)	57	5	10	2.94	15		L > H L > M
7	2B	R	44, (22, 6, 13)	GPrC (GTs, GFi, INS)	50	6	10	5.90	197		L > H M > H
7	2A	L	22/6	GTs/GPrC	−58	−1	9	3.39	10	L > M†	L > H L > M
7	2B	L	6, (22, 42, 44)	GPrC, (GTs, GFi)	−48	2	10	5.05	30		L > H M > H†
Other areas in Experiments 2A and 2B											
Areas where high and/or medium > low											
	2A	M	10/9	GFs, GFd	−11	57	29	4.34	72	H > M	H > L H > M
		R	47, (45/13)	GFi, (INS)	41	31	−4	4.01	13	H > L H > M	
		L	39/19	GTm, GOm	−38	−61	16	3.61	45	H > L M > L H > M	
		M	7	PCu	−12	−48	33	3.19	7	H > L M > L† H > M	H > L M > L
		L	40	LPi	−42	−51	42	3.11	37		H > L
	2B	R	19	GOm, GOi, (GL)	35	−76	−7	3.24	7		M > L†

Table 1. (*continued*)

Figure	Experiment	L/R	BA	Anatomical Area	x	y	z	Max F	No. of Voxels	Contrasts t3,4	Contrasts t6,7
Areas where low > high and/or medium											
	2A		NONE								
	2B	M	18	Cu, (Sca)	6	−80	20	3.24	6	L > H L > M† M > H	
		M	6, 24, 32	GFd, GC	1	−2	48	3.30	14	L > M	L > H L > M M > H
		R	7	LPs	17	−64	48	3.73	9		L > H
		L	6, (4)	GFs, (GFm)/ GPrC	−25	−12	51	4.12	7	L > H M > H	M > L† M > H
		L	40, 42, 22, (2)	LPi, GTs, (GPoC)	−65	−34	26	3.57	14		L > H†

All areas showed an Arousal × Time interaction with a minimum of six contiguous voxels, each significant at $p < .001$ (Forman et al., 1995), except for the two marked with an asterisk (*) in the Experiment column where $p < .01$. Subsequent contrasts between conditions, shown in the rightmost columns, were performed on percent signal change from Time 1 at Times 3, 4 (early) and Times 6, 7 (late), $p < .05$, except as indicated with a dagger (†), where $.05 < p < .10$. Abbreviations of brain areas follow Talairach and Tournoux (1988). L = left; M = medial; R = right; BA = Brodmann's area; Cu = cuneus; GC = cingulate gyrus; GF = fusiform gyrus; GFd = medial frontal gyrus; GFi = inferior frontal gyrus; GFm = middle frontal gyrus; GFs = superior frontal gyrus; Gh = parahippocampal gyrus; GL = lingual gyrus; GOi = inferior occipital gyrus; GOm = middle occipital gyrus; GPrC = precentral gyrus; GTi = inferior temporal gyrus; GTm = middle temporal gyrus; GTs = superior temporal gyrus; INS = insula; LPi = inferior parietal lobule; LPs = superior parietal lobule; PCu = precuneus; Sca = calcarine sulcus. BA and anatomical areas are listed left to right in descending order of approximate size, with approximately equal areas of activation indicated by a slash; parentheses indicate a small extent relative to other areas listed. Talairach coordinates are for the local maximum in each region of activation.

and 2B. Our discussion focuses on areas that replicated across experiments and that showed differences between arousing versus neutral pictures during the early (Times 3 and 4) or late (Times 6 and 7) portion of the trial (see event trial sequence in Figure 3 and subsequent analyses summarized in Table 1). These areas are shown in Figures 4–7.

As shown in Figures 4 and 5, emotional pictures resulted in greater activation than neutral pictures in regions associated with visual processing including the fusiform gyrus, middle occipital gyrus, and middle temporal gyrus. Because the number of face pictures did not differ in the high- and low-arousal picture sets, the different levels of fusiform activity between arousal conditions seen in Figure 4 cannot be attributed to differences in the number of face stimuli. The differences in activity in the visual processing regions shown in Figures 4 and 5 are consistent with greater attention to the high-arousal items, contributing to their higher likelihood of later being recalled (although we cannot rule out other factors that might be correlated with arousal level of the pictures, such as complexity).

Neutral trials, on the other hand, showed more activity than emotional trials in the left superior precentral gyrus (see Figure 6) and in an area at the intersect of inferior precentral gyrus and superior temporal gyrus (see Figure 7). It is interesting that differences between conditions in the areas shown in Figures 6 and 7 tended to emerge later in the trial than the differences in the areas shown in Figures 4 and 5. This pattern is consistent with a positive impact of arousal on attention given to visual features of individual pictures and a negative impact of arousal on rehearsal processes important for binding individual pictures to their locations, although our experimental design does not allow definitive separation of activity during the early and late portions of the trial (e.g., Zarahn, 2000).

In addition to the whole-brain analyses summarized in Table 1, we also conducted region-of-interest analyses of the hippocampus and amygdala because previous findings indicate that the hippocampus is important for memory binding (Olson, Chatterjee, Page, & Verfaellie, 2005; Mitchell et al., 2000) and the amygdala modulates hippocampal activity to enhance memory for emotional stimuli (McGaugh, 2002). There were no significant differences between arousal conditions in these areas in Experiment 2A. In Experiment 2B, there was greater activation for emotional than neutral trials in both the right ($p < .004$) and left ($p < .06$) hippocampus[3] and in right amygdala ($p < .09$). Because the pattern did not replicate across experiments, we do not discuss these

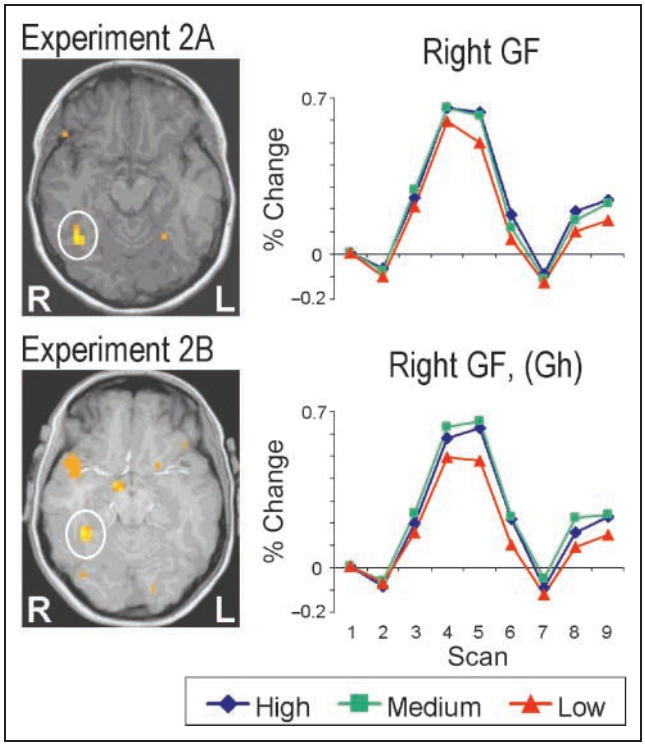

Figure 4. Areas of the fusiform gyrus (GF) in Experiments 2A and 2B showing significant Arousal × Time interactions, shown with the associated average within-trial time courses. In all figures, for the time courses, the *x*-axis represents scan within a trial (TR = 2000 msec, each trial 18 sec), and the *y*-axis represents mean percent signal change from the first within-trial time point. Abbreviations of brain areas follow Talairach and Tournoux (1988) (see footnote, Table 1), and for each region of activation, areas are listed in descending order of approximate size, with approximately equal areas of activation indicated by a slash and minor areas in parentheses. Slices in all figures were chosen to show representative activations; Talairach coordinates are given in Table 1.

findings further, although they do suggest an avenue for further investigation.

GENERAL DISCUSSION

In the three experiments presented here, participants showed poorer short-term source memory for the location of highly arousing pictures than for pictures lower in arousal. Such a pattern suggests that emotional arousal disrupts encoding processes necessary for memorial feature binding, at least in the short term. The fMRI results of Experiments 2A and 2B are consistent with the idea that emotionally arousing pictures recruit more attention, reflected in activation in visual processing areas, at the expense of activity in other areas (the intersect of precentral and superior temporal gyrus, superior precentral gyrus) that likely contribute to feature maintenance and binding during working memory. This greater attention to item than relational information (in this case, item plus location) produces a short-term disadvantage in source memory, but a long-term advantage in item memory.

Previous studies indicate that attending to emotional stimuli can disrupt attention to other information (MacKay et al., 2004; McKenna & Sharma, 2004). For example, the presence of an emotional word together with two neutral words in a briefly presented display makes it more difficult to immediately think back to (i.e., ''refresh'') either of the neutral words in the display (Johnson et al., 2005). Johnson et al. called this lingering reflective attention to a salient item that is no longer perceptually present ''mental rubbernecking.'' This rubbernecking has some benefits, such as improved memory for the item lingered upon, as shown in this and other studies demonstrating better memory for emotional than neutral items (e.g., Ochsner, 2000). However, the present results reveal a cost; namely, poorer source memory—in this case, for the location in which the item appeared. In all three experiments, short-term source memory was lowest for high-arousal trials and best for low-arousal trials. Thus, it seems that emotional content disrupted reflective processes by which the conjunction of item and location are bound in working memory (Mitchell et al., 2000). In addition, Experiment 1 suggests that mildly depressed participants engage in mental rubbernecking for negative stimuli, in particular.

Experiments 2A and 2B provide information about the neural correlates of the arousal-induced source memory deficit. First, the suggestion that arousing pictures evoked greater attention than neutral pictures is supported by the finding that in both Experiments 2A and 2B there was more activity in higher-order visual areas during processing of emotional than neutral picture sets (Figures 4 and 5; see also Phan, Wager, Taylor, & Liberzon, 2002), and that the emotional pictures were remembered better later. Visual attention tasks produce activity in the fusiform gyrus (Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Heinze et al., 1994) and BA 17, 18, and 19 (for a review see Cabeza & Nyberg, 2000). Second, participants in Experiments 2A and 2B showed activation in a superior area of the precentral gyrus that was greater for low- than for medium- or high-arousal pictures. That this area contributes to memory binding is supported by the fact that Mitchell et al. (2000) found the same area ($x = -54$, $y = -5$, $z = 35$) showing greater activity during working memory for ''combination'' trials on which participants had to remember where (neutral) items were located than on trials where they had to remember only individual features (items or locations, see also Henke, Weber, Kneifel, Wieser, & Buck, 1999).

We also found an area at the intersect of the inferior precentral gyrus and superior temporal gyrus that was greater for low-arousal sets of pictures than for medium- or high-arousal sets. Activity in these areas has been associated generally with working memory (Chein & Fiez,

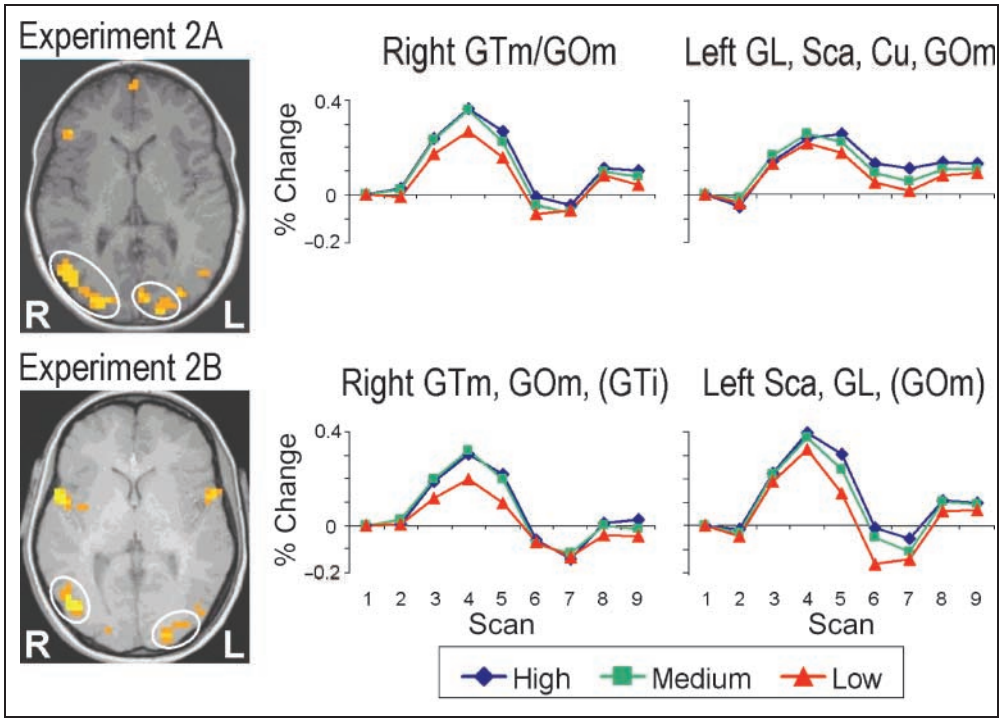

Figure 5. Visual processing areas, including most notably the middle temporal gyrus (GTm), middle occipital gyrus (GOm), lingual gyrus (GL), and calcarine sulcus (Sca), in Experiments 2A and 2B showing significant Arousal × Time interactions, shown with the associated average within-trial time courses.

2001; Cornette, Dupont, Salmon, & Orban, 2001), and extracellular recording in awake patients showed that activity in this area of the superior temporal gyrus at encoding predicted correct working memory trials (Ojemann, Schoenfield-McNeill, & Corina, 2004). The pattern seen in the present experiments suggests that this area contributed to more effective short-term source memory for low-arousal pictures. This area is also near one reported by Wright, Pelphry, Allison, McKeown, and McCarthy (2003) in which activity was greater for the combination of auditory and visual stimuli than for either alone, consistent with the idea that the superior temporal gyrus plays a role in feature integration (e.g., Calvert, Hansen, Iverson, & Brammer, 2001). The superior temporal gyrus may help integrate disparate features for a brief period in order to maintain a coherent overall representation (see also Jung-Beeman et al., 2004). Our data suggest that when emotional features dominate encoding and/or rehearsal at the expense of other features, integration is less likely, as evidenced by poorer source memory (e.g., Johnson et al., 1996).

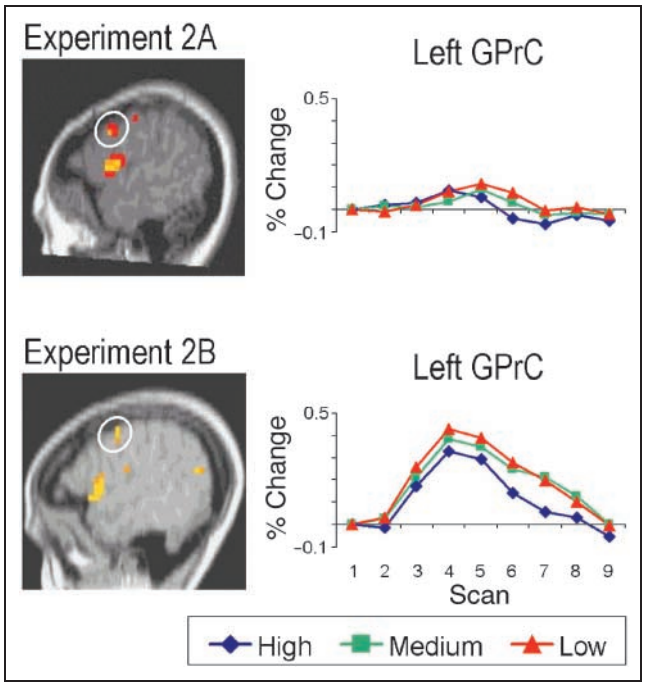

Figure 6. Area of the precentral gyrus (GPrC) in Experiments 2A and 2B, and associated average within-trial time courses, with significant Arousal × Time interactions.

As discussed in the Introduction, previous research suggests that the disruption caused by mental rubbernecking has deleterious effects on long-term source memory for complex emotional events (Schmidt, 2002; Johnson et al., 1996; Burke, Heuer, & Reisberg, 1992; Christianson & Loftus, 1991). However, there may be contexts in which mental rubbernecking is less of an issue. For example, when only one item is the focus of attention at a time the enhanced attention devoted to a single emotional item may improve long-term memory for its context. Consistent with this possibility, several studies that presented one word at a time, and did not include a working memory task where several items had to be maintained simultaneously, found better memory for the color of emotional than neutral

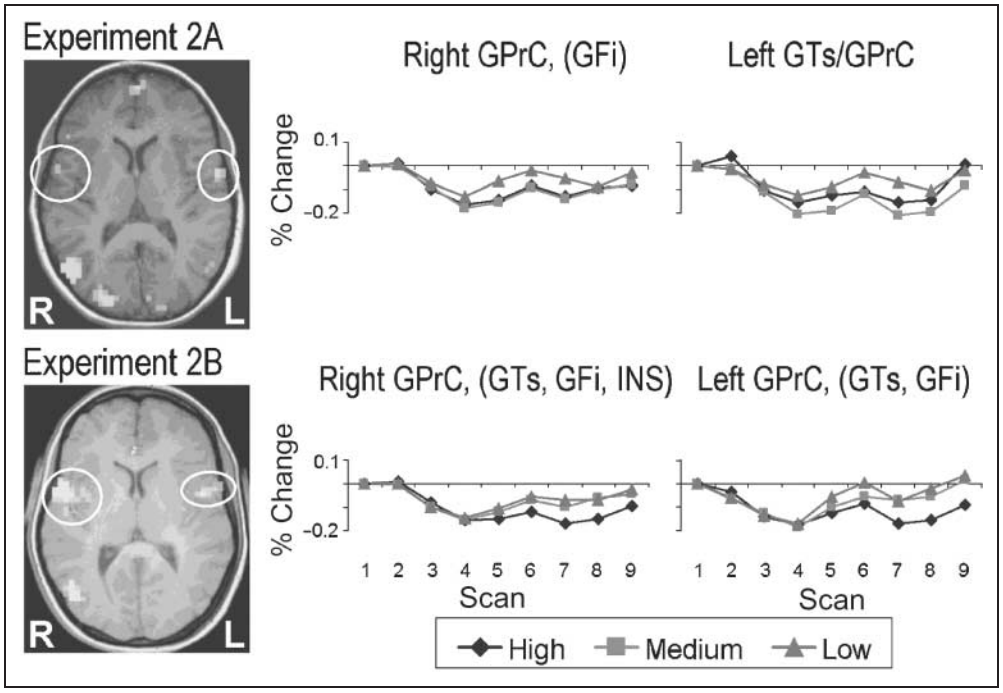

Figure 7. Bilateral areas at the intersect of the inferior precentral gyrus (GPrC) and superior temporal gyrus (GTs), in Experiments 2A and 2B, and associated average within-trial time courses, with significant Arousal × Time interactions.

words (D'Argembeau & Van der Linden, 2004; MacKay et al., 2004; Kensinger & Corkin, 2003; Doerksen & Shimamura, 2001).

Finally, we note that our findings may also bear on the cognitive deficits associated with schizophrenia. Patients with schizophrenia show deficits in memory for the conjunction of neutral features even when they are equated with controls for memory of the features themselves (Burglen et al., 2004; Waters, Maybery, Badcock, & Michie, 2004; Rizzo et al., 1996). The dominant hypothesis is that these deficits are due to decreased hippocampal volume in schizophrenia (Shenton, Dickey, Frumin, & McCarley, 2001). However, our findings provide converging evidence for another (not necessarily mutually exclusive) hypothesis. A review of MRI findings in studies of schizophrenia showed that all 12 studies examining gray matter volume of the superior temporal gyrus found reductions in patients with schizophrenia (Shenton et al., 2001). Furthermore, the smaller the patients' left superior temporal gyrus, the more severe their hallucinations (Onitsuka et al., 2004), and a small superior temporal gyrus seems to be a predisposing factor for the disease rather than a result of it (Rajarethinam, Sahni, Rosenberg, & Keshavan, 2004). The correlation between size of the superior temporal gyrus and degree of hallucination makes sense if this area aids in the formation of associations among aspects of an event that are critical for later remembering its source (e.g., Johnson et al., 1993). Consistent with this hypothesis, controls show greater superior temporal activation than patients with schizophrenia when imagining sentences being spoken in someone else's voice or listening to external speech, suggesting that this area helps create associations between the source of speech and what is said (Woodruff et al., 1997; McGuire et al., 1995). Our findings that feature binding is associated with activation in an area that includes the superior temporal gyrus is consistent with the idea that schizophrenic patients' reduced volume or dysfunction (or both) of this area may contribute to their source-monitoring deficits.

In summary, emotion is important for directing attention, and emotional stimuli are likely to be remembered later. Our study demonstrates that this attention to emotional stimuli, reflected in activity in visual processing areas, sometimes has a cost. During a working memory task, it can disrupt binding of features such as location associated with the emotionally arousing information, as reflected in less activity in the precentral and superior temporal areas.

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The data reported in this experiment have been deposited with the fMRI Data Center (www.fmridc.org). The accession number is 2-2005-1209B.

Notes

1. Two of the pictures in the neutral set were not from the IAPS set.
2. Due to time limitations and the lower *n* for the fMRI studies, we did not administer depression scales in Experiments 2A and B.
3. Given evidence that hippocampal activity is most likely to be seen when stimuli are novel (e.g., Ranganath & Rainer, 2003), we examined only the first half of the trials (i.e., runs 1–4, where items had been repeated only once).

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