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## The Effect of Emotional Arousal and Retention Delay on Subsequent-Memory Effects

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## **Abstract**

Memory for emotional experiences often persists longer than memory for neutral experiences. The present study examined how encoding processes influence memory retention across 0.5 or 24-hour delays and whether these processes differ between emotionally arousing and neutral information. Participants encoded items during an fMRI scan. Immediately following the scan, and again 24-hours later, participants performed a recognition memory test. The results revealed that, for emotionally arousing information, most regions showed a correspondence to subsequent-memory performance that was at least as strong after the long delay as it was after the short delay. For neutral items, by contrast, many more regions, including portions of the hippocampus and lateral PFC, showed a stronger correspondence to subsequent-memory performance after the short delay than the long delay. These results suggest that the processes engaged at the moment of encoding have a longer-lasting relation to subsequent-memory for emotionally arousing information than for neutral information.

Some memories persist, while others fade soon after learning. Although many factors influence which memories will be most resilient, one key factor is the emotionality of an experience. Emotionally arousing events are more likely to be remembered over the long term, and the impact of emotion on memory can become exaggerated over time (e.g., Kleinsmith and Kaplan, 1963), even within the first 12 to 24 hours after encoding (Payne, Stickgold, Swanberg, & Kensinger 2008; Sharot & Phelps, 2004; Sharot & Yonelinas, 2008). Although these benefits can be relatively fast-acting, perhaps because synaptic consolidation processes act within this time frame (Dudai, 2002), most studies that have examined the neurobiological influence of emotion on memory have assessed memory either after relatively short delays of a few minutes (e.g., Kensinger & Corkin, 2004; Talmi, Anderson, Riggs, Caplan, & Moscovitch 2008) or after much longer delays of a week or more (Cahill et al., 1996; Canli & Brown, 1996; Hamann, Ely, Grafton, & Kilts, 1999; Mackiewicz, Sarinopoulos, Cleven, & Nitschke, 2006). Few studies have investigated how the neural correlates of memory change across a lengthening delay; therefore it is unclear to what extent the memory processes that change between minutes and weeks mirror those that transpire within the initial 24-hour delay period. The goals of the present study were to assess how encoding processes connect to memory retention over a short (0.5 hour) versus a longer (24-hour) delay and to elucidate whether the arousal elicited by a stimulus impacts those processes.

The ability to retrieve a memory requires the successful completion of a number of processes, beginning with the encoding of the information. A large number of studies have confirmed that the processes engaged at the moment of encoding can have a strong influence

over whether the information is later remembered or forgotten. When activation is elicited within the medial temporal-lobe (MTL) and lateral prefrontal cortex (PFC), the likelihood of subsequent-memory increases (reviewed by Paller & Wagner, 2002).

There is a large degree of overlap between the processes that support the successful encoding of neutral and emotionally arousing information, yet there are also some notable differences (see Murty, Ritchey, Adcock, & LaBar, 2010 for a meta-analysis). The most reliable difference is that the amygdala is engaged during the successful encoding of emotionally arousing information but not the successful encoding of neutral information (reviewed by LaBar & Cabeza, 2006). Regions within the orbital PFC also tend to have a stronger connection to the successful encoding of arousing information than neutral information, as do regions of the ventral visual processing stream, such as the fusiform gyrus (Murty et al., 2010).

The vast majority of studies that have examined subsequent-memory performance – either for neutral information or for emotionally arousing information – have assessed memory only for one delay (see Carr, Viskontas, Engel, & Knowlton, 2010; Ritchey, Dolcos, & Cabeza 2008; Uncapher & Rugg, 2005 for exceptions). To date, only one study has compared the encoding processes that support subsequent-memory within-subjects over delays similar to those employed here: Uncapher and Rugg (2005) tested memory, for neutral items, after a 0.5-hour delay and a 48-hour delay. Their results revealed that encoding activity within the MTL and dorsolateral PFC showed a delay-invariant correspondence to subsequent-memory. There was, however, a shift from reliance on posterior regions (fusiform gyrus) to frontal regions (ventrolateral PFC) as the delay interval increased; as noted by the authors, this shift is consistent with evidence that, over time, memories for neutral information contain fewer verbatim details and instead are comprised of gist-based information (reviewed by Koriat, Goldsmith, & Pansky, 2000).

A key question to be addressed by the present study was whether similar regions to these would show delay-invariant and delay-dependent subsequent-memory effects for emotionally arousing information. There was reason to believe that the posterior-to-anterior shift would be less likely to occur for emotionally arousing items than for neutral items, because high-arousal items can be remembered with high fidelity not only over short delays but also over relatively long delays of days (e.g., Kensinger, Garoff-Eaton, & Schacter, 2006) or weeks (e.g., Sharot, Verfaellie, & Yonelinas, 2007). Indeed, in the only prior study to examine the effect of delay on subsequent-memory effects for high-arousal information (Ritchey et al., 2008), the authors found evidence that fusiform activity was connected to the persistence of memory over a 1 week delay, and not just to short-term retention of information. On the basis of these prior findings, we hypothesized that, in comparison to neutral items, high-arousal items would show fewer delay-dependent, and more delayinvariant, subsequent-memory effects. This pattern of results would be consistent with current theories regarding the modulation of memory by arousal (reviewed by McGaugh, 2004; LaBar & Cabeza, 2006), which state that the ability to retrieve emotional memories after long delays can be accounted for by arousal-induced processes that are initiated at the moment of encoding.

#### Method

## **Participants**

Participants included 24 young adults. Data from three participants were unusable due to scanner or image projection malfunction. The remaining 21 participants (9 female) were an average age of 23.6 years (range = 19–30 years) and had achieved an average of 15.8 years

of education (range = 12–20 years). Participants were right handed and had been screened to exclude anyone with a history of neurological or psychiatric disease.

#### **Materials**

Stimuli consisted of 300 high-arousal photos (half were positive: mean (SD) valence = 7.21 (.55), arousal = 5.79 (.57); half were negative<sup>1</sup>: valence = 2.96 (.83), arousal = 5.83 (.62) on 9-point scales), and 150 neutral photos (valence = 5.03 (.41), arousal = 3.12 (.86)). Images were from the International Affective Picture System database (Lang, Bradley & Cuthbert, 2008) with a few images supplemented from stimuli previously normed in our laboratory (Mickley Steinmetz & Kensinger, 2009). High-arousal and neutral pictures were matched on visual complexity, brightness [as indicated in Adobe Photoshop (Adobe Systems, San Jose, CA)], and picture content.

#### **Behavioral Procedure**

Participants underwent a functional magnetic resonance imaging (fMRI) scan as they viewed 300 pictures (100 from each emotion category). Each picture was presented for 2000 ms. During this time, participants rated the photographic quality of the picture; this particular task was chosen because it did not force participants to process the affective content of the pictures. Interstimulus intervals were jittered, ranging from 2 to 14 s (Dale, 1999).

Outside of the scanner, after participants changed into their street clothes, participants underwent a surprise recognition test. Participants viewed pictures on a computer and indicated which items they had seen in the scanner. If an item was deemed "old", the participant completed a modified Memory Characteristics Questionnaire (MCQ, Johnson, Foley, Suengas, & Raye, 1988); responses to these questions will not be discussed here. After approximately a 24-hour delay (range = 23.5–27 hours), participants returned to the laboratory and performed another recognition memory task; no pictures were repeated across the two memory tasks. At each delay, there were 225 pictures included on the recognition memory task: 2/3 of the images had been studied and 1/3 were included as nonstudied foils. This ratio of old:new items was selected to parallel the methods used by Ritchey et al. (2008).

### **Behavioral Data Analysis**

Corrected recognition scores were computed separately for items from each emotion category (high-arousal, neutral) and for items tested at each delay interval (short, long). Scores were calculated by subtracting the false alarm rate for each item type from its respective hit rate (e.g., % hit to neutral items at short delay minus % false alarms to neutral items at short delay).

## MRI Image Acquisition and Preprocessing Procedure

Data were acquired on a 1.5 Tesla Siemens whole body Avanto MRI scanner (Erlangen, Germany) using a 32-channel, high-resolution head coil. Anatomic data were acquired with an MP-RAGE sequence (TR = 2,730 ms, TE = 3.39 ms, Field of view =  $256 \times 256$  mm, acquisition matrix  $256 \times 256 \times 128$ , slice thickness = 1.33 mm). Functional images were

<sup>&</sup>lt;sup>1</sup>All effects reported here were consistent for positive and negative stimuli. Valence did, however influence Dm effects (Stronger Dm effects for negative items in posterior regions and for positive items in anterior regions, consistent with Mickley Steinmetz & Kensinger, 2009). At a reduced threshold, Dm effects for emotionally arousing items also were influenced by the interaction of valence and delay. The posterior-to-anterior effects were more pronounced at the short delay than the long delay, and laterality differences (right = negative Dm, left = positive Dm) were more pronounced at the long delay. Because these effects were not hypothesized a priori and did not meet the typical significance we do not discuss them further.

acquired via a T2\* weighted echo planar imaging sequence sensitive to the blood oxygenation level dependent (BOLD) signal (TR = 2000 ms, TE = 40 ms, flip angle 90°). Twenty-six interleaved axial-oblique slices were collected in a 3.125 mm  $\times$  3.125 mm  $\times$  3.84 mm matrix, with the z dimension including a 20% gap. If full brain coverage was not achieved for any participant, slices were aligned such that orbitofrontal and ventral occipital-temporal cortex were always included within the field of view. Standard preprocessing (slice time correction, motion correction, normalization, and smoothing with a 5 mm kernel) and data analysis were completed using SPM5 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, London, UK).

#### **Event-Related fMRI Data Analysis**

Encoding events were divided based upon the emotion category of the pictures (high-arousal, neutral), the subsequent-memory performance of the item (remembered, forgotten), and the delay after which memory for that item had been assessed (short delay, long delay). For each emotion category, participants had an average of 35 hits (and 15 misses) at the short delay, and 25 hits (and 25 misses) at the long delay. No participant had fewer than 7 items in any hit or miss category.

A first-level, event-related subsequent-memory analysis (Dm) was completed: for each participant, on a voxel by voxel basis, event types were modeled through convolution with a canonical hemodynamic response function, comparing hits for a particular emotion category to misses for that emotion category. These Dm contrast images were then used for a second-level, random-effects group analysis, in which ANOVAs were computed with emotion category and delay as factors. We additionally computed first-level, event-related analyses for just the remembered items (vs. baseline) and for just the forgotten items (vs. baseline). These contrast images were used for additional second-level, random-effects ANOVAs with emotion category and delay as factors.

For all whole-brain analyses, differences in activation were considered to be significant within regions consisting of at least 5 voxels, active at p < .001, unless otherwise specified. Monte Carlo simulations (Slotnick, Moo, Segal, & Hart, 2003) confirmed that this p value and voxel extent combination corrected results for multiple comparisons at p < .05. Voxel coordinates are reported in Talairach coordinates at the most significant voxel in each cluster (Talairach & Tournoux, 1988), and data are displayed on canonical images provided within SPM5.

## **Results**

#### **Behavioral Results**

An ANOVA conducted on the corrected recognition rates (see Table 1 for hit and false alarm values) revealed a main effect of emotion category,  $\underline{F}(1,20) = 20.8$ , p < .001,  $^2 = .51$ , with better memory for high-arousal items than for neutral items. The ANOVA also revealed a main effect of delay,  $\underline{F}(1,20) = 146.9$ , p < .001,  $^2 = .88$ , with better memory after the short delay than the long delay. There was no interaction between emotion category and delay,  $F(1,20) \leq 1$ ,  $p \geq .15$ .

#### **Dm Effects**

Collapsing across emotion and delay, we replicated the standard Dm effects (reviewed by Paller & Wagner, 2002) within the lateral PFC, MTL (TAL coordinates: 22, -5, -15), lateral parietal cortex, precuneus, and ventral visual processing stream (see Figure 1A, regions in red and the top portion of Table 2 for a list of all regions). Analyses also replicated prior findings (see Murty et al., 2010) with regard to Dm effects modulated by emotion. When

collapsing across delay, regions within the medial and orbital PFC, amygdala (TAL coordinates: -34, -1, -18), and posterior hippocampus (TAL coordinates coordinates 34, -20, -7) showed a stronger Dm effect for emotionally arousing items than neutral items (see Figure 1B, regions in yellow and the lower panel of Table 2 for a list of all regions).

## Effect of Delay and Emotion on Dm Effects

When examining the effect of delay on Dm effects for neutral items, many regions showed a stronger Dm effect after the short delay than after the long delay (blue regions in top left panel of Figure 2), including regions within the ventromedial PFC (TAL coordinates: 8, 21, -1), the parahippocampal gyrus (TAL coordinates: -20, -43, 2) and throughout the ventral visual processing stream (Brodmann areas 19 and 37). By contrast, only a single region of the superior temporal gyrus (TAL coordinates: -48, -6, -10) showed a stronger Dm effect for neutral items after a long than a short delay.

The pattern was not the same for emotionally arousing items, however (see upper right panel of Figure 2). Confirming this difference, a number of regions showed a Dm effect that was influenced by the interaction between emotion and delay (see Table 3). In nearly all regions that showed this interaction, including regions of the ventromedial PFC (TAL coordinates: 8, 23, -1), fusiform (TAL coordinates: -30, -47, -16), and hippocampus (TAL coordinates: 36, -29, -5), there was a stronger Dm effect after a short than a long delay only for the neutral items; for emotionally arousing items, there was either an equally strong correspondence to subsequent-memory regardless of the delay after which memory was tested, or the correspondence to subsequent-memory was stronger when memory was tested after the long delay.

Among the regions that showed a Dm effect that was influenced by the interaction between emotion and delay, we examined whether this interaction arose for remembered items or for forgotten items. For items later forgotten, differential activation at the short versus the long delay was present for neutral but not for emotional items. By contrast, for items later remembered, activation generally was equally strong regardless of emotion category or delay. In other words, the effect of emotion and delay on the Dm effect may be driven by the pattern of activation to forgotten items (see the right columns of Table 3).

Although most regions showed the interaction because of the activation to forgotten items, there were two exceptions to this pattern. The first was within medial regions, which showed an interaction for both remembered and forgotten items (ventromedial PFC, cingulate gyrus) or for only remembered items (precuneus). The second exception was within regions connected to sensory processing; these regions seemed particularly tied to the relative activation differences between remembered and forgotten items, showing an interaction either for both remembered and forgotten items (lingual and parahippocampal gyrus) or for neither item type when considered in isolation (middle occipital gyrus, fusiform gyrus).

#### **Delay-Invariant Dm Effects**

To reveal regions showing a delay-invariant Dm effect, we used exclusive masking to isolate regions that showed an overall Dm effect (at p < .001) and also no significant effect of delay on that Dm effect (p > .05). For neutral stimuli (red regions in lower panel of Figure 2), a number of regions showed this delay-invariant correspondence to subsequent-memory, including a region of the parahippocampal cortex (TAL coordinates: 34, -28, -15) in close proximity to a region identified previously by Uncapher & Rugg (2005; TAL coordinates: 30, -24, -19). A number of regions showed this correspondence for emotionally arousing items as well (yellow regions of Figure 2), and there was extensive overlap in delay-invariant Dm effects for the two item types.

#### **General Discussion**

Our results confirm that there are both delay-dependent and delay-invariant Dm effects. For neutral items, the delay-dependent effects generally revealed a more tenuous link between encoding processes and subsequent-memory at the longer (24-hour) delay than the shorter (0.5-hour) one. For arousing items, more of the processes engaged at the moment of encoding had a long-lasting impact on subsequent-memory performance, consistent with modern theories which state that when arousal is elicited during encoding, it initiates a cascade of processes that lead to the creation of durable memory traces (reviewed by McGaugh, 2004; LaBar & Cabeza, 2006).

## Effect of Delay on Subsequent-Memory Effects for Neutral Information

For neutral items, the majority of delay-dependent effects reflected activity that showed a strong correspondence to subsequent-memory after a short delay but that failed to show a relation to subsequent-memory after the long delay. In many of the regions, encoding activity was equivalently high whenever the items were remembered, regardless of the emotion category or the delay after which memory was assessed, but activation was particularly low when neutral items were forgotten after a short delay. These results suggest that forgetting over the 0.5-hour delay may reflect a fault in the encoding process, whereas forgetting over longer delays may occur even when encoding processes were engaged.

It is also interesting to note that, like Uncapher & Rugg (2005), activation in the fusiform gyrus was more predictive of subsequent-memory over the short delay than the longer one, consistent with the proposal that the link between sensory engagement and memory degrades as time progresses (Koriat et al., 2000). We did not find evidence of increased lateral PFC activity for longer-lasting subsequent-memory effects, although we did find increased superior PFC and anterior temporal-lobe reliance, which could be consistent with a shift toward dependence on extracted semantic information rather than sensory detail (Koriat et al., 2000). Thus, both studies reveal that there can be a shift in the encoding processes that correspond with subsequent-memory even over delays that are within a relatively narrow time frame (0.5-hour to 24-hours in this study, and 0.5-hour to 48-hours in Uncapher & Rugg, 2005).

### Effect of Delay on Subsequent-Memory Effects for Emotionally Arousing Information

Consistent with our hypothesis, there was no evidence of a posterior-to-anterior shift in the Dm effects for emotionally arousing items as the delay interval increased. Also, in contrast to neutral items, Dm effects for emotionally arousing information were rarely stronger at the short delay than the long delay; Dm effects were either delay-invariant or intensified with the longer delay. This finding is consistent with Ritchey et al. (2008), who found no differences in the activation levels corresponding with memory performance for emotional items at 20-min and 1-week delays (although they did find some connectivity differences). What is particularly novel about the present study, however, is that it emphasizes that emotionally arousing items have a greater tendency than neutral items to have delay-invariant Dm effects, or to have Dm effects that strengthen, rather than weaken, over a delay. Thus, the processes engaged at the moment of encoding have a longer-lasting connection to whether information will be remembered or forgotten if that information elicits arousal than if it does not.

#### **Concluding Remarks**

The current study reveals that, even when memory is assessed over a relatively narrow time frame (i.e., 0.5-hours to 24-hours), there are diminishing returns on the efficacy of encoding processes for predicting subsequent-memory for neutral items. Yet there is a longer-lasting

relation between encoding processes and subsequent-memory performance when information elicits arousal. These findings are consistent with the proposal that arousal-induced processes at the moment of encoding trigger a cascade of processes that continue to preserve a memory, even over longer delays.

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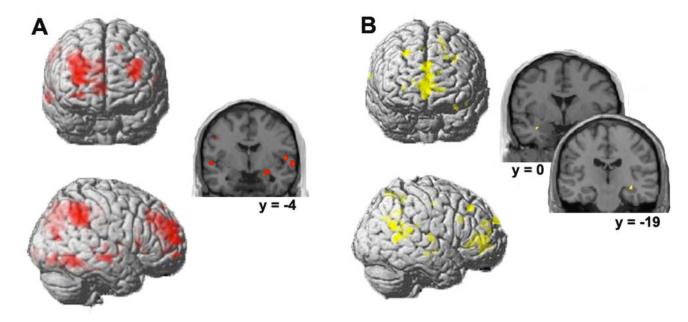


Figure 1. When collapsing across delay, the results replicated prior findings with regard to the regions that showed a Dm effect, collapsing across all items (panel A, regions in red) or those that showed a stronger Dm effect for emotionally arousing items than for neutral items (panel B, regions in yellow). The y value of the Talairach coordinates are indicated for each coronal slice.

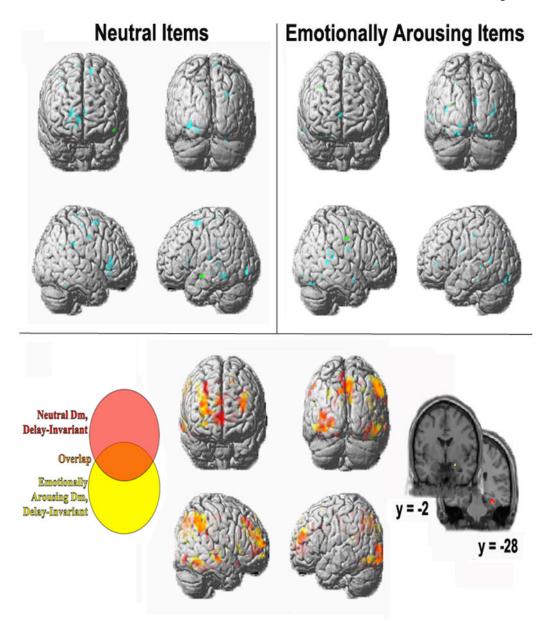


Figure 2. Regions showing a Dm effect that interacted with delay (top panels) or that was delay invariant (bottom panel). All activations are shown at p < .001 (see text for details). In the top panels, blue regions showed a stronger Dm effect at the short than the long delay; green regions showed the opposite pattern. In the bottom panel, all regions showed a significant Dm effect (p < .001) and no influence of delay on the magnitude of that Dm effect (p > .05). Red regions showed the delay-invariant Dm effect for neutral items, and yellow regions showed the delay-invariant effect for emotionally arousing items. Orange reveals the area of overlap of those two whole-brain maps. The y Talairach coordinates are indicated for each coronal slice.

Table 1

Mean (SD) recognition performance as a function of emotion category and delay.

	Short Delay	Long Delay
High Arousal		
Hits	.74 (.03)	.53 (.20)
False Alarms	.02 (.03)	.03 (.04)
Neutral		
Hits	.67 (.17)	.43 (.20)
False Alarms	.05 (.04)	.05 (.04)

Table 2

Regions showing an overall Dm effect (top portion) and a Dm effect that is greater for emotional than neutral items (bottom portion). Regions significant at p < .001. Hemi = hemisphere, BA = Brodmann Area, TAL = Talairach, MNI = Montreal Neurological Institute, K = cluster size (voxel extent).

Overall Dm Effect	Effect						
Location	Region	Hemi	BA	TAL Coordinates (x,y,z)	MNI Coordinates (x,y,z)	K	Z
Frontal	inferior frontal gyrus	Left	45	-55, 28, 12	-56, 28, 14	13	3.54
		Right	45	46, 19, 21	46, 18, 24	10	3.53
		Left	44	-38, 9, 18	-38, 8, 20	9	3.51
	middle frontal gyrus	Right	10	30, 60, –5	30, 62, -2	62	5.67
		Right	6	8, 40, 20	8, 40, 24	379	5.46
		Right	10	28, 57, 5	28, 58, 8	1483	5.38
		Left	46	-36, 46, 22	-36, 46, 26	592	4.97
	cingulate gyrus/dorsomedial prefrontal coretx	Right	5	8, -25, 44	8, –28, 46	612	5.28
	superior frontal gyrus	Left	8	-14, 49, 42	-14, 48, 48	38	4.79
Limbic	anterior cingulategyrus	Right		12, 25, -3	12, 26, –2	67	4.4
	amygdala/anterior hippocampus	Right		22, -5, -15	22, -4, -18	8	3.8
	posterior cingulate gyrus	Left		-10, -45, 23	-10, -48, 22	18	3.66
Occipital	cuneus	Left	19	-26, -86, 37	-26, -90, 36	39	4.48
	fusiform gyrus	Left	19	-32, -80, -6	-32, -82, -12	1122	5.26
	middle occipital gyrus	Left	18	-38, -89, 10	-38, -92, 6	100	5.03
		Left	19	-36, -77, 20	-36, -80, 18	13	3.81
		Right	18	22, –93, 6	22, –96, 2	7	3.37
Parietal	precuneus	Right		10, –74, 28	10, -78, 26	1400	5.72
	inferior parietal lobule	Right	40	53, -52, 41	54, -56, 42	837	6.17
		Left	40	-50, -60, 44	-50, -64, 44	125	4.57
	superior parietal lobule	Right	7	30, -64, 40	30, -68, 40	92	4.09
		Left	5	-10, -36, 50	-10, -40, 52	11	3.59
Temporal	fusiform gyrus	Right	36	28, -28, -17	28, -28, -22	99	4.23
	inferior temporal gyrus	Right	37	48, -51, -8	48, -52, -12	539	5.6
	middle temporal gyrus	Right	21	63, -16, -8	64, -16, -10	214	5.28

Location	Region	Hemi	BA	TAL Coordinates (x,y,z)	MNI Coordinates (x,y,z)	K	Z
		Right	19	44, –73, 18	44, –76, 16	191	4.5
		Right	21	65, -4, -1	66, -4, -2	6	3.52
		Left	39	-42, -62, 3	-42, -64, 0	14	3.4
	superior temporal gyrus	Right	22	46, –33, 3	46, –34, 2	22	3.93
		Right	22	63, -19, 6	64, -20, 6	22	3.8
		Left	22	-53, -2, 0	-54, -2, 0	12	3.62
		Right	22	53, -4, 8	54, -4, 8	8	3.59
		Left	22	-50, -40, 20	-50, -42, 20	22	3.46
Cerebellum		Right		14, -61, -12	14, -62, -18	8	3.58
		Right		40, -61, -15	40, -62, -22	5	3.32
Dm Effects I	Dm Effects Emotion > Neutral						
Location	Region	Hemi	BA	TAL Coordinates	MNI Coordinates	K	Z
				$(\mathbf{z}'\mathbf{\hat{A}}'\mathbf{x})$	(x,y,z)		
Frontal	superior frontal gyrus	Bilateral	10	0, 61, 25	0, 62, 30	39	3.68
		Г	6/94	-22, 31, 33	-22, 30, 38	9	2.91
		R	6/8	24, 33, 39	24, 32, 44	28	3.34
		Г	6	-12, 40, 18	-12, 40, 22	9	2.81
		R	32	2, 46, 20	2, 46, 24	32	3.38
		Г	10	-2, 51, 12	-2, 52, 16	34	3.12
		Г	9	-16, -11, 54	-16, -14, 58	35	3.37
	cingulate/superior frontal gyrus	R	24	6, -9, 45	6, -12, 48	10	2.94
Limbic	cingulate gyrus	R	23	8, -51, 27	8, –54, 26	10	2.95
		R	24	4, 21, 25	4, 20, 28	44	3.23
		R	32	18, 43, 7	18, 44, 10	5	2.76
	hippocampus	R	41	34, -20, -7	34, -20, -10	11	3.32
	amygdala	Г	34	-34, -1, -18	-34, 0, -22	10	2.75
	insular gyrus	R	41	44, -13, 8	44, -14, 8	21	3.24
		R	41	36, -10, -6	36, -10, -8	5	3.13

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Overall Dm Effect	Effect						
Location	Region	Hemi	BA	TAL Coordinates (x,y,z)	MNI Coordinates (x,y,z)	K	Z
Parietal	angular gyrus	Г	19	-38, -78, 37	-38, -82, 36	9	2.69
	precuneus	Г	7	-2, -61, 58	-2, -66, 60	23	3.24
		Г	31	-2, -61, 33	-2, -64, 32	17	2.99
	superior parietal lobule	Г	7	-8, -38, 52	-8, -42, 54	2	2.86
		R	2//2	16, -44, 54	16, –48, 56	14	2.87
Temporal	middle temporal gyrus	R	21/22	59, –54, 8	60, –56, 6	72	2.88
	superior temporal gyrus	R	39	42, -64, 31	42, -68, 30	2	2.76
		R	39/22	46, –55, 23	46, –58, 22	92	3.87
		R	22	55, -45, 24	56, -48, 24	2	2.86
		R	22	40, -42, 11	40, -44, 10	17	2.92
		R	22	67, -38, 18	68, -40, 18	11	2.95
Other	caudate nucleus	Г	24	-12, -1, 24	-12, -2, 26	12	3.21
	hypothalamus	R	near 34	2, -10, -5	2, -10, -6	10	2.99
	thalamus	Г	27	-20, -27, 5	-20, -28, 4	5	3.46

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# Table 3

trials, or only remembered trials, were entered into an ANOVA. Regions are significant at p <.001 except where highlighted in gray (p < .005). Hemi = Regions showing a Dm effect that is influenced by the interaction of emotion category and delay. The top portion of the table lists regions that show a regions that show the opposite pattern. Right columns indicate if this interaction between delay and emotion was also significant when only forgotten larger Dm effect at the short delay than the long delay for neutral items but not for emotionally arousing items. The bottom portion of the table lists hemisphere, BA = Brodmann Area, TAL = Talairach, MNI = Montreal Neurological Institute, K = cluster size (voxel extent).

Emotion X	Delay Interaction: (Neut	ral Short > ]	Long) > (	Emotion X Delay Interaction: (Neutral Short > Long) > (Emotionally Arousing Short > Long)	t > Long)								
Cocation Cocation	Region	Hemi	BA	TAL Coordinates	MNI Coordinates	K	z	Significant	z	TAL For	Significant	z	TAL For
gn Neurosc				(z,y,x)	(x,y,z)			interaction for Forgotten Trials?*		Forgotten ANOVA	interaction for Remembered Trials?		Kemembered ANOVA
Frontal	spanning cingulate gyrus and ventromedial PFC	R	24	8, 23, -1	8, 24, 0	23	4.59	yes	3.77	8, 23, –3	yes	3.32	10, 25, 1
пап	middle frontal gyrus	R	4	34, -10, 37	34, -12, 40	6	3.74	yes	3.9	same	ou		
uscrij	orbital gyrus	R	32	22, 25, –8	22, 26, –8	12	3.85	yes	3.3	22, 27, –6	no		
ot; av	precentral gyrus	R	4	26, –25, 51	26, -28, 54	10	3.45	yes	3.62	same	no		
ailal		R	1	34, -20, 34	34, –22, 36	8	3.89	yes	3.51	34, -18, 34	ou		
ole in	superior frontal gyrus	Т	9	-12, 7, 57	-12, 4, 62	9	3.62	yes	2.81	-12, 5, 57	ou		
M Limbic	cingulate gyrus	R	24	18, 28, 8	18, 28, 10	20	3.82	yes	2.81		yes	3.12	18, 29, 6
C 20	hippocampus	R	20	36, -29, -5	36, -30, -8	<i>L</i>	3.37	yes	3.96	20, 26, 12	ou		
Occipital	middle occipital gyrus	L	19	-34, -79, 17	-34, -82, 14	10	3.31	ou		same	no		
over	insular gyrus	R	45	30, 18, 6	30, 18, 8	9	3.6	yes	3.58	-38, -1, 11	ou		
nber	insular gyrus	Т	4	-40, -3, 11	-40, -4, 12	9	3.64	yes	3.56	32, -28, 27	ou		
9 Parietal	inferior parietal lobe	R	40	30, –30, 29	30, -32, 30	11	3.46	yes	3.49		ou		
	sneuncend	Т	31/39	-24, -63, 23	-24, -66, 22	9	3.43	no		4, 16, 3	yes	2.91	-22, -65, 24
Temporal	fusiform gyrus	Г	37	-30, -47, -16	-30, -48, -22	7	3.38	no			no		
	spanning lingual gyrus and parahippocampal gyrus	L	35	-20, -43, -6	-20, -44, -10	21	4.15	yes	3.27	38, -27, -4	yes	3.29	-18, -43, -8
Other	striatum	Bilateral	33	0, 16, 8	0, 16, 10	28	3.58	yes	3.46	-22, -43, -8	yes	3.18	0, 18, 10
Emotion X	Emotion X Delay Interaction: (Emotionally Arousing Short $>$ Lon	tionally Aro	using Sh	ort > Long) > (Neutral Short > Long)	t > Long)								

Emotion X Delay Interaction: (Neutral Short > Long) > (Emotionally Arousing Short > Long)

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TAL For	ANOVA	TAL For Remembered ANOVA							
Z		Z							
Significant	meraction for Remembered Trials?	Significant interaction for Remembered Trials?	ou	ou	no	no	no	no	no
TAL For	r orgonen ANOVA	TAL For Forgotten ANOVA							-59, -37, 4
Z		z							3.27
Significant	interaction for Forgotten Trials?*	Significant interaction for Forgotten Trials?	ou	ou	no	no	no	no	yes
Z		z	2.99	3.03	2.91	3.03	3.29	2.85	3.53
K		К	9	9	13	8	II	01	9
MNI Coordinates	(x,y,z)	MNI Coordinates (x,y,z)	-18, -24, 44	8, 52, 24	10, –42, 22	-28, 12, 20	46, –34, 34	36, 12, –28	-58, -38, 0
TAL Coordinates	(z',k'x)	TAL Coordinates (x,y,z)	-18, -21, 42	8, 51, 20	10, –40, 22	-28, 13, 18	45, –31, 33	36, 10, –24	-58, -37, 2
BA		BA	4	6	23	44	40	38/21	21/22
Hemi		Hemi	T	R	R	T	R	R	L
Region		Region	precentral gyrus	superior frontal gyrus	cingulate gyrus	insular gyrus	supramarginal gyrus	inferior temporal gyrus	middle temporal gyrus
Location Region		Location	Frontal	euro	E. Limbic	xutho	Parietal	Temporal	т <del>ірt;</del> а

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