

Effects of Aging on Mnemonic Discrimination of Emotional Information

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Episodic memory loss is one of the hallmarks of age-related cognitive decline and a major symptom of Alzheimer's disease. The persistence and strength of memories is determined by modulatory factors such as emotional arousal. Whether emotional memories are preserved with age or if these memories are just as susceptible to loss and forgetting is not well understood. We have recently shown that emotion alters how similar memories are stored using nonoverlapping representations (i.e., pattern separation) in an emotional mnemonic discrimination task. Here, we extend this work to testing young and older adults at 2 time points (immediately after encoding and 24 hr later). Overall, older adults performed worse than young adults, a memory deficit that was not secondary to perceptual or attentional deficits. When tested immediately, older adults were impaired on neutral target recognition but intact on emotional target recognition. We also found that a pattern we previously reported in young adults (reduced emotional compared to neutral discrimination of similar items) was reversed in older adults. When tested after 24 hr, young adults exhibited less forgetting of emotional targets compared to neutral, while older adults exhibited more forgetting of emotional targets. Finally, discrimination of highly similar positive items was preserved in older adults. These results suggest that emotional modulation of memory interacts with age in a complex manner such that the emotion-induced memory trade-off reported in young adults is reversed in older adults. These findings shed light on how emotion and memory interact in the aging brain.

Keywords: emotion, memory, interference, hippocampus, age, pattern separation

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Changes in episodic memory performance are a hallmark feature of aging and a major symptom of mild cognitive impairment and Alzheimer's disease (AD). Episodic memory, or memory for personal events, is frequently reported to decline in the elderly (Craig & Simon, 1980; Glisky, 2007). The medial temporal lobes, which include the hippocampus, amygdala, and surrounding cortices, are crucial for the formation of episodic memories (Milner, Squire, & Kandel, 1998) and are one of the first sites of degeneration in aging and AD (Gómez-Isla et al., 1996). This network is implicated in age-related deficits in neurocognitive functioning. While general impairment of episodic memory has been well established, it is not clear whether there are existing mechanisms that may allow older adults to compensate for this memory loss by

altering modulatory influences. For example, altering the focus of attention, increasing repetition of events, or increasing the significance of events may alter the degree of memory impairment in older adults.

While episodic memory deficits are a hallmark characteristic of aging, emotion's modulatory influence on memory remains less well-characterized in aging. Decades of research in rodents have shown that emotional experiences are better remembered than nonemotional experiences (McGaugh, 2004; LeDoux, 2007). However, animal and human studies are inconsistent with respect to age-related changes in emotional modulation of memories. Several stimulus-specific factors may contribute to these discrepancies, such as valence, capacity to increase arousal, and degree of detail (Foster, DeFazio, & Bizon, 2012; McGaugh, 2006). Moreover, when deficits in the emotional modulation of memory manifest in aging, it is not clear whether these deficits are due to age-related hippocampal alterations, changes in the brain regions thought to play a modulatory role, such as the amygdala, or both.

Several human studies have shown that memory for emotional experiences is preserved with age (Denburg, Buchanan, Tranel, & Adolphs, 2003; Kensinger, Brierley, Medford, Growdon, & Corkin, 2002). However, not all aspects of an emotional event are remembered equally. Emotional arousal can enhance memory for the general theme or "gist-based" information but impair memory for detailed information (Adolphs, Denburg, & Tranel, 2001; Kensinger, 2009). This trade-off likely plays a critical role in the storage of long-lasting memories and may distinguish the aspects of those memories that are remembered with better accuracy. In aging, some studies have suggested that there is a "positivity

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effect,” where older adults may be more likely to attend to positive information in the environment (Wong et al., 2012; Mather & Carstensen, 2005). In contrast, some have suggested that memory for detailed information in older adults reveals no such positivity effect and may actually be biased toward remembering negative details (Kensinger, Garoff-Eaton, & Schacter, 2007). This suggests that the relationship between aging and emotional modulation of memory is complex and requires a more thorough investigation.

The hippocampus, which plays a key role in episodic memory (Milner, Squire, & Kandel, 1998), is thought to be involved in pattern separation—the process of reducing interference among similar inputs by using nonoverlapping representations (Marr, 1971; McClelland, McNaughton, & O’Reilly, 1995; O’Reilly & Norman, 2002; Treves & Rolls, 1994; Yassa & Stark, 2011). Older individuals show deficits in paradigms that tax the ability to discriminate highly similar information (i.e., a putative behavioral measure of hippocampal pattern separation; Toner, Pirogovsky, Kirwan, & Gilbert, 2009; Yassa, Lacy et al., 2010). We have also recently reported a specific perturbation in hippocampal activity thought to be reflective of impaired pattern separation in older adults, which is associated with poor discrimination performance (Yassa, Mattfeld, Stark, & Stark, 2011; Yassa, Lacy et al., 2010). This may be closely linked to degraded input from the perforant path (Kalus et al., 2006; Rogalski et al., 2009; Yassa, Muftuler, & Stark, 2010).

The impact of emotional arousal on mnemonic computations, such as pattern separation, has not been examined in detail in older humans and has only been investigated recently in young adults (Leal et al., 2014). While pattern separation allows for the orthogonalization of information to distinguish highly similar events and experiences in our lives, the persistence and strength of memories is determined by modulatory factors such as emotional arousal. In the current study, we utilized an emotional mnemonic discrimination task similar to tasks used in the past (see Segal, Stark, Kattan, Stark, & Yassa, 2012; Stark, Yassa, Lacy, & Stark, 2013; Yassa et al., 2011) to examine the influences of emotional arousal on discrimination of emotional information. Our goal was to understand the emotional modulation of episodic memory in aging by first examining this putative modulation behaviorally in young and older adults. Furthermore, emotional arousal is thought to influence the consolidation of information over time; thus, we tested participants either immediately after encoding or 24 hr later.

Materials and Method

Participants

Participants were recruited from Johns Hopkins University as well as the local Baltimore, Maryland, community via local campus announcements, flyers, and ads in local newspapers. Participants were between the ages of 18 and 35 years for the young adult groups and 60 and 85 years for the older adult groups. Participants received either course credit or monetary remuneration for their participation. The young adult group tested immediately consisted of 24 participants (mean age = 21 years, $SD = 3$; 16 female). The young adult group tested 24 hr later consisted of 14 participants (mean age = 21 years, $SD = 1$; 6 female). The data from young participants in this paper have already been reported in Leal et al. (2014). The older adult group tested immediately consisted of 22

participants (mean age = 67 years, $SD = 4$; 14 female). The older adult group tested 24 hr later consisted of 16 participants (mean age = 71 years, $SD = 8$; 12 female). Informed consent was obtained from all participants, with all procedures approved by the Johns Hopkins University Institutional Review Board.

Inclusion/Exclusion Criteria

All participants were screened against major medical or psychiatric morbidities as well as substance abuse history. Older participants received a neuropsychological evaluation during their visit. The battery was designed to examine memory function, as well as other aspects of general cognition. The assessment included the following: (a) Mini-Mental State Exam to assess global cognitive status; (b) Rey Auditory Verbal Learning Test to assess verbal learning, immediate and delayed recall, and recognition; (c) Digit span backward and forward to assess working memory; (d) Trail Making Tests A and B to assess attention, visual search, and mental processing speed; (e) Beck Depression Inventory-II to assess depressive symptoms; and (f) Geriatric Depression Scale to assess depressive symptoms more specific to older adults (see Table 1). There were no significant differences between the older adult groups in age, education, and all other neuropsychological measures. All participants had normal or corrected to normal vision.

Emotional Mnemonic Discrimination Task

The stimulus set was comprised of novel scenes freely available online, sized to a width of 600 pixels. Images were categorized a priori for emotional valence (negative, neutral, positive), arousal (very calming to very exciting), and similarity (median split of similarity ratings into “high” and “low”; Leal et al., 2014). The experimental paradigm consisted of 149 images during the encoding phase and 291 images during the retrieval phase. Targets, lures (similar but not identical to images shown during encoding), and foils were roughly evenly distributed across emotional valence and

Table 1
Older Participant Demographics and Neuropsychological Test Results

Groups	Older immediate		Older 24-hr delay	
	Mean	SEM	Mean	SEM
Sample Size	22		16	
M : F	8 : 14		4 : 12	
Variables	Mean	SEM	Mean	SEM
Age	66.7	0.9	70.6	1.9
Education	16.0	0.5	15.4	0.7
Beck depression inventory-II	4.2	0.5	5.1	1.1
Geriatric depression scale	1.3	0.2	1.4	0.4
RAVLT* immediate recall	10.3	0.5	9.7	0.8
RAVLT delayed recall	10.0	0.6	9.4	0.8
Digit span forward	12.5	0.5	11.0	0.6
Digit span backward	8.3	0.5	7.1	0.5
Mini mental state exam	28.6	0.4	27.8	0.3
Trail making test A	28.6	2.1	34.7	3.7
Trail making test B	69.8	2.3	89.1	10.4

* = RAVLT: rey auditory verbal learning test.

similarity level (high-similarity and low-similarity lures). An Apple iMac equipped with MATLAB (Version R2010a, Natick, MA) software and PsychToolbox version 3.0 was used to present the stimuli and record keyboard responses. Each trial consisted of two displays: an image display (images were presented on the center of the screen with a black background for 2,500 ms) and a fixation display (a white fixation cross on the center of the screen with a black background for 500 ms). Timing was identical for encoding and retrieval phases.

Each participant was given oral and written instructions. Participants underwent an incidental encoding phase where they were shown emotional and non-emotional images, presented in randomized order, and were asked to rate the images for emotional valence. Young adults rated images on a 9-point scale from 1 (*most negative*) to 9 (*most positive*), with 5 being *neutral*, and older adults used a similar scale, but without the large range of responses (limited to three button responses of 1 = *negative*, 5 = *neutral*, and 9 = *positive*). In pilot studies, we observed that allowing older adults the full 9-point scale to respond led to frustration and increased latency beyond the response window. Thus, we chose to limit the response options in order to make the decision process easier and remove this potential difficulty. Participants were given a subsequent surprise memory test either immediately after encoding or after a 24-hr delay, in which participants saw another series of stimuli, some of which were seen once before in the incidental task (targets), some were similar to ones seen in the incidental task but not identical (lures), and some were new (foils). Participants were asked to indicate whether items were “old” or “new” by button responses on the keyboard. Participants were explicitly told that in order for an image to be called “old,” it had to be the exact same image they saw before (see Figure 1). Participants who

returned 24 hr later were told that they would be coming in for another hour of testing and were not explicitly told what tasks they would be performing.

Our two key outcome measures of interest were target recognition (D') and Lure Discrimination Index (LDI). Target recognition was measured by a discriminability index (D'), which was calculated as $z(\text{Hits}) - z(\text{False Alarms})$, which is thought to assess gist knowledge or general familiarity (Norman, 2010; Yonelinas, Aly, Wang, & Koen, 2010). This was calculated for each emotion (negative, neutral, and positive). From a computational perspective, this process requires pattern completion but not pattern separation (Kim & Yassa, 2013; Yassa & Stark, 2011). In order to measure how well participants discriminated similar items (lures), we examined performance using a response bias-corrected LDI operationalized as $p(\text{New}|\text{Lure}) - p(\text{New}|\text{Target})$. One potential problem with using correct rejections (i.e., $\text{New}|\text{Lure}$) as a behavioral correlate for pattern separation is that it is likely contaminated by rejections that are the result of insufficient or inattentive encoding (i.e., misses, $\text{New}|\text{Target}$). In order to account for this possibility, we subtract the probability of rejecting an old item (which quantifies such misses) from the probability of rejecting a lure to generate the LDI metric we use in the task. This corrected for the general tendency to reject (i.e., call an item “New”) and is similar to other metrics we used in prior work (Leal et al., 2014; Yassa & Stark, 2011; Yassa, Lacy et al., 2010; Yassa, Muftuler, & Stark, 2010). This was also calculated for each emotion (negative, neutral, and positive). From a computational perspective, this process requires both pattern completion as well as pattern separation (Kim & Yassa, 2013; Yassa & Stark, 2011). Raw response proportions and reaction time data for all experimental groups are in Supplemental Information (Table S1 and Figure S1).

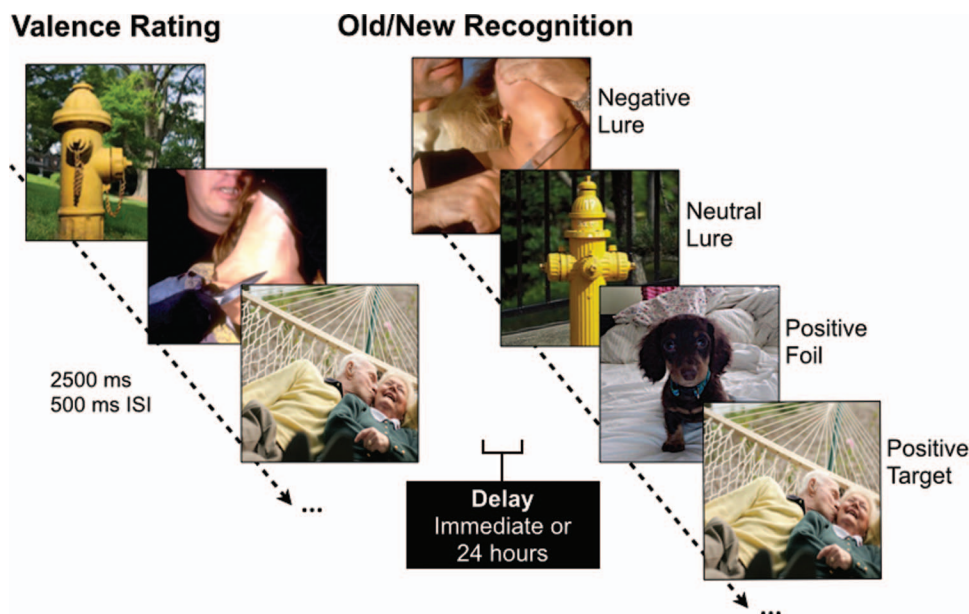


Figure 1. Emotional mnemonic discrimination task. During encoding, participants rated images according to their emotional valence. Each image was presented for 2,500 ms with a 500-ms interstimulus interval. Immediately after study or 24 hr later, participants underwent a surprise recognition test where they viewed negative, neutral, and positive targets, foils, and lures varying in similarity and were asked to indicate whether items were “old” or “new.” See the online article for the color version of this figure.

Match-to-Sample Task

It is possible that behavioral performance on the discrimination task is affected by perceptual/attentional deficits that manifest with aging. To control for these potential confounds, we employ a match-to-sample task using the same stimuli, except yoking similar image pairs together (separated by a static noise mask to eliminate sensory memory). Two separate samples of young and older adults were tested on a match-to-sample task using the same exposure time as in the primary experiment (2,500 ms; young: $N = 18$, 22 ± 3 , 12 female; old: $N = 13$, 65 ± 6 , 7 female). The young adult group is from Leal et al. (2014). The match-to-sample task consisted of trials that were composed of four sequential displays: first image (presented for 2,500 ms), followed by a pixelated noise mask display for 1,000 ms, a second image for 2,500 ms, and finally an intertrial fixation display (500 ms). Images were identical to those used in the discrimination experiments. Participants were told to determine whether the two images were exactly the same or different via button press on the keyboard. Subjects were told to respond while the second image was still on the screen. Image pairs were either identical (repetitions) or similar (lures). We have used a similar design in our past work to control for perceptual or attentional influences, which can vary with age (Yassa, Lacy et al., 2010; Ly, Murray, & Yassa, 2013).

Statistical Analysis

All statistical analyses were conducted in SPSS v. 20.0 (IBM Corp., Armonk, NY). For immediate testing, two-way repeated-measures ANOVAs (age and emotion) were performed for target recognition and lure discrimination index (high- and low-similarity ANOVAs conducted separately). For 24-hr delay testing, three-way repeated-measures ANOVAs (age, emotion, time of testing) were performed for target recognition and lure discrimination index (again, high- and low-similarity ANOVAs conducted separately). Forgetting rates were calculated post hoc for visualization purposes only (i.e., no statistics were run on the forgetting rates). This was a between-subjects design, thus, forgetting rates were calculated on the group means (e.g., mean D' [immediate] – mean D' [delay] and not on individual subject scores). Repeated measures tests were corrected for error nonsphericity using Greenhouse-Geisser correction where appropriate. Post hoc statistical tests were corrected for multiple comparisons using Scheffé's correction, with critical F values indicated in the text corresponding to the degrees of freedom (df) of the F test (mentioned only once for each pair of dfs). Statistical values were considered significant at a final corrected alpha level of .05, which appropriately controlled for Type I error.

Results

Impaired Neutral but Preserved Emotional Target Recognition in Older Adults

We investigated the effect of emotion (negative, neutral, and positive) on target recognition when tested immediately across age groups (young and old) using a two-way ANOVA, which revealed a significant effect of emotion, $F(2, 88) = 5.3$, $p = .01$, where negative targets were better remembered compared

to neutral and positive targets, $F(1, 88) = 9.7$, critical Scheffé = 6.2. There was a significant effect of age where young adults performed better than older adults, $F(1, 44) = 7.7$, $p = .01$. In addition, there was a significant interaction between emotion and age, $F(2, 88) = 3.7$, $p = .04$. We parsed this interaction using a post hoc contrast examining the effect of emotional valence (positive and negative vs. neutral) across groups (young vs. old). We found that older adults were impaired relative to young adults on neutral target recognition but were preserved on emotional (positive and negative) target recognition, on par with young adults, $F(1, 88) = 6.7$, critical Scheffé = 6.2 (Figure 2A). We will refer to "emotional target recognition or lure discrimination" as comprised of both negative and positive stimuli unless otherwise noted.

Reversed Emotional Modulation of Lure Discrimination in Older Adults

Next, we assessed the effect of emotion on discrimination of low-similarity LDI across age groups using a two-way ANOVA, which revealed a significant effect of age, in which young adults performed better than old adults, $F(1, 44) = 47.6$, $p < .001$. We also found a significant interaction between emotion and age, $F(2, 88) = 4.5$, $p = .02$. We parsed this interaction using a post hoc contrast examining the effect of emotional valence (positive and negative vs. neutral) across groups (young vs. old). We found that older adults show increased emotional versus neutral lure discrimination, while young adults show reduced emotional versus neutral lure discrimination, $F(1, 88) = 8.2$, critical Scheffé = 6.2 (Figure 2B). While discrimination of emotional stimuli was better compared to neutral stimuli in older adults, it is important to note that even with a boost in memory performance for emotional items, older adults do not overcome the overall memory deficit.

We evaluated the effect of emotion on high-similarity LDI across age groups using a two-way ANOVA, which revealed a significant effect of age, $F(1, 44) = 47.6$, $p < .001$, where young adults performed better than older adults. There were no significant differences between age groups for emotion or an interaction between age and emotion. While young adults show a similar pattern of reduced emotional versus neutral lure discrimination, older adults show no differences in discrimination across highly similar emotional and nonemotional items (Figure 2C).

Emotional Modulation Not Secondary to Attention or Perceptual Effects

A potential interpretation of the emotional modulation effects we report is that age-related changes in attentional focus or working memory capacity could influence behavioral performance. For example, participants may not have perceptually encoded all of the details of the emotional images during the encoding phase, and this lack of attention to detail may have affected subsequent memory performance. Consistent with this idea, Mather and Sutherland (2011) proposed that arousal during an event can either enhance or impair memory for events, depending on attentional factors that bias competition in favor of high-priority stimuli (Mather & Sutherland, 2011).

To examine the possibility of extramnemonic influences on task performance, we tested 31 new participants (13 older adults) on a

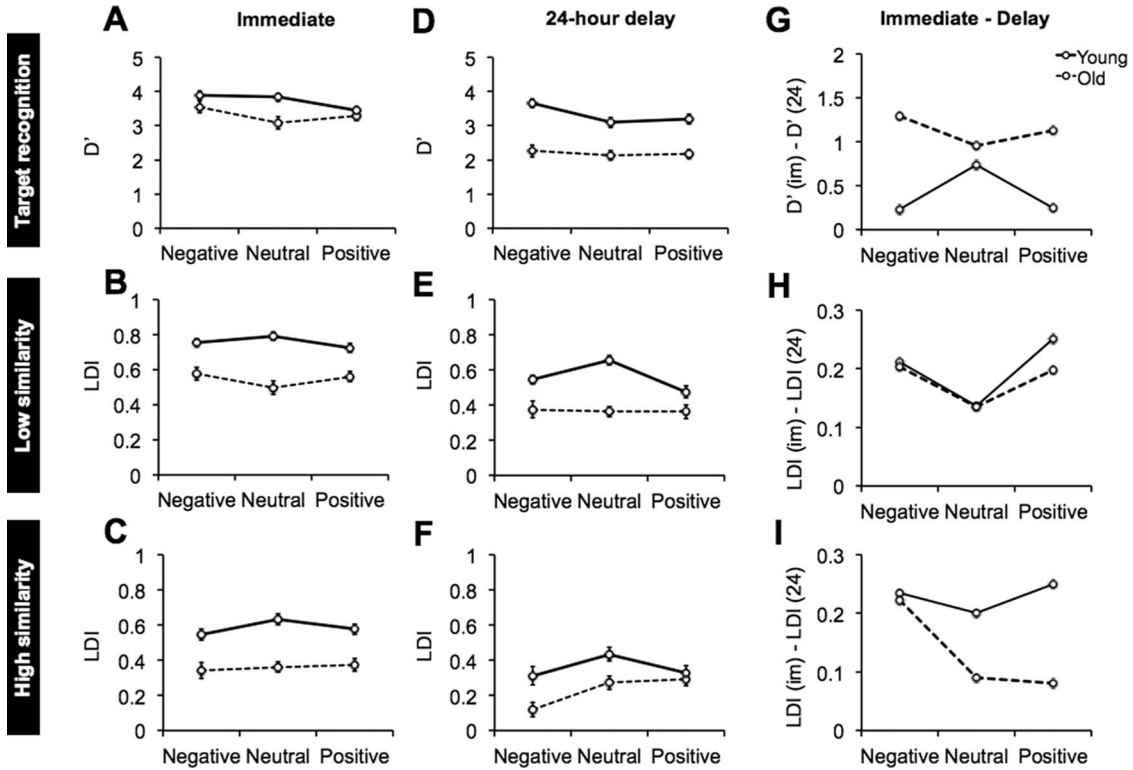


Figure 2. Performance in young and older adults. (A) Target recognition (D') in the immediate condition. (B) Low-interference Lure Discrimination Index (LDI) in the immediate testing condition. (C) High-interference LDI in the immediate testing condition. (D) Target recognition (D') in the 24-hr delay condition. (E) Low-interference LDI in the 24-hr delay condition. (F) High-interference LDI in the 24-hr delay condition. (G) Target recognition forgetting rate plotted as the difference between immediate target recognition [$D'(\text{im})$] and 24-hr delay target recognition [$D'(24)$]. (H) Low-interference lure discrimination forgetting rate plotted as the difference between immediate lure discrimination [$\text{LDI}(\text{im})$] and 24-hr delay lure discrimination [$\text{LDI}(24)$]. (I) High-interference lure discrimination forgetting rate plotted as the difference between $\text{LDI}(\text{im})$ and $\text{LDI}(24)$. See main text for data interpretation and statistical comparisons.

match-to-sample task using the same stimuli that were used in the emotional mnemonic discrimination task. Participants were shown yoked pairs of similar or repeated images with a static noise mask in between and asked to determine if the images were the same or different. We measured target hit rate and lure rejection rate and found a main effect of age for target hit rate, $F(1, 29) = 6.88, p = .014$ (Figure S2a), where older adults performed slightly better than young adults. There were no significant differences across age groups for lure rejection rate (all p 's $> .05$; Figure S2b). This suggests that while attention may play a role in emotional processing, it did not significantly contribute to the effects observed here. A related possibility is that encoding and consolidation mechanisms interact so that emotionally arousing items are differentially processed during encoding, in such a manner that their long-term consolidation is also altered (Hamann, 2001).

Increased Forgetting of Emotional Compared to Neutral Targets After 24 Hours in Older Adults

Next, we had separate groups of young and older adults perform the same task, but perform the surprise memory test 24 hr later. We investigated the effect of emotion, age, and time of testing (im-

mediate vs. 24-hr delay) on target recognition using a three-way ANOVA, which revealed a significant effect of emotion, $F(2, 144) = 8.8, p < .001$, where negative targets were better remembered compared to neutral and positive targets, $F(1, 144) = 14.3$, critical Scheffé = 6.12. There was a significant effect of age where young adults performed better than older adults, $F(1, 72) = 49.8, p < .001$. There was a significant effect of time of testing where immediate performance was better than after 24 hr, $F(1, 72) = 49.1, p < .001$. In addition, there was a significant interaction between age and time of testing, $F(1, 72) = 10.8, p = .002$. We parsed this interaction using a post hoc contrast examining the effect of time of testing (immediate vs. delay) across groups (young vs. old). We found that old and young adults performed similarly on target recognition when tested immediately, while older adults had worse target recognition (i.e., more forgetting) after a 24-hr delay. Interestingly, we found a three-way interaction between time of testing, emotion, and group, $F(2, 144) = 3.5, p = .037$. We performed a post hoc contrast examining the effect of time of testing (immediate vs. delay) and emotional valence (negative and positive vs. neutral) across groups (young vs. old). We found that young adults exhibited less forgetting of emotional

targets compared to neutral, while older adults exhibited more forgetting of emotional targets compared to neutral, $F(1, 144) = 6.8, p = .011$ (Figure 2D, G).

Increased False Recognition of Emotional Compared to Neutral Lures After 24 Hours Across Both Young and Older Adults

We also assessed the effect of emotion, age, and time of testing for low-similarity lure discrimination index using a three-way ANOVA, which revealed a significant effect of emotion, $F(2, 144) = 3.2, p = .048$, where positive and negative lures were more poorly discriminated compared to neutral lures, $F(1, 144) = 3.5, p < .05$. There was a significant effect of age, where young adults performed better than older adults, $F(1, 72) = 69.9, p < .001$. There was a significant effect of time of testing, where performance was better when tested immediately versus at a 24-hr delay, $F(1, 72) = 61.1, p < .001$. We also found a significant interaction between emotion and time of testing. We performed a post hoc contrast examining the interaction between emotional valence (negative and positive vs. neutral) and time of testing (immediate vs. delay), where emotional lures were more falsely recognized over time compared to neutral lures across age groups, $F(1, 144) = 6.0, p = .017$ (Figure 2E, H). We also found a significant interaction between emotion and age, $F(2, 144) = 9.3, p < .001$, where a post hoc contrast of emotional valence across age groups showed that older adults have increased emotional versus neutral lure discrimination, while young adults have decreased emotional versus neutral lure discrimination, $F(1, 144) = 18.0, p < .001$, suggesting that the aforementioned reversal of the emotional modulation of lure discrimination in older adults continues at a delay of 24 hr.

Preserved Discrimination of Highly Similar Positive Lures in Older Adults

We assessed the effect of emotion, age, and time of testing on high-similarity LDI using a three-way ANOVA, which revealed a significant effect of emotion, $F(2, 144) = 10.5, p < .001$, where discrimination of highly similar emotional lures was worse than neutral lure discrimination, $F(1, 144) = 12.2, p = .001$. There was a significant effect of age, $F(1, 72) = 34.6, p < .001$, where young adults performed better than older adults. There was a significant effect of time of testing, $F(1, 72) = 35.5, p < .001$, where performance was better when tested immediately versus after a 24-hr delay. Additionally, we found an emotion by age interaction, $F(2, 144) = 3.1, p = .048$. A post hoc contrast of emotional valence across age groups revealed that young adults had worse discrimination on both positive and negative items relative to neutral. Older adults, on the other hand had worse discrimination only on negative items relative to neutral, but were preserved on positive items, $F(1, 144) = 3.5, p < .05$ (Figure F, I).

In order to determine if older adults show greater impairment when discriminating high-similarity lures compared to low-similarity lures, we conducted an additional ANOVA in older adults with emotion and similarity as within-subject factors and time as a between-subjects factor and found a significant effect of similarity, where older adults were more impaired when discriminating high-similarity lures compared to low-similarity lures, $F(1, 36) = 109.11, p < .001$.

Discussion

While general impairment of episodic memory in age-related cognitive decline has been well established, it is not clear whether there are existing mechanisms that may allow older adults to compensate for this memory loss by altering modulatory systems in the brain. The current study examined whether there were age-related changes in the emotional modulation of memory, specifically in the context of interference and pattern separation changes associated with aging. Because emotion's influence on memory can occur during encoding and furthermore during consolidation, we tested separate groups of participants immediately after encoding and 24 hr later.

Emotional Modulation of Memory Encoding in Aging

When testing participants immediately after encoding, we found an overall enhancement in young adult performance compared to older adults in general recognition and discrimination. Older adults showed a preservation of emotional target recognition compared to young adults, but showed an impairment of neutral target recognition compared to young adults. This finding is consistent with previous findings that emotional memory may be preserved across the lifespan (Denburg et al., 2003; Kensinger, Krendl, & Corkin, 2005; Waring & Kensinger, 2009). While older adults show a general decline in episodic memory, memories tied to an emotional context are remembered with more fidelity. Although forgetting increases with age, these results and others suggest that there is a selective remembering of emotional experiences, serving to create lasting memories of our more important experiences.

Whereas older adults were impaired in discriminating similar items relative to young adults overall, the effect of emotion was reversed with age. Young adults were more likely to falsely recognize similar emotional lures than older adults. This effect was evident at least for the low-similarity lure items. The shift in emotional modulation could be due to at least two possible explanations: (a) a compensatory effect such that emotional arousal can boost discrimination performance on similar items and help increase memory for more important emotional events or (b) an aberration of emotional-mnemonic processing in older adults such that the boost in emotional discrimination is actually maladaptive, as it would be better to remember the gist for emotional events rather than the details. Young adults' discrimination (ability to suppress false recognition) was enhanced on neutral items compared to emotional items presumably due to a trade-off between gist and detail. Thus, it may be more adaptive to forget minute details of emotional experiences in favor of retaining the bigger picture (Adolphs et al., 2001; Kensinger, 2009; Loftus, Loftus, & Messo, 1987). Older adults, on the other hand, appear to suppress false alarms better for emotional items, suggesting that they may be engaging in a more costly mnemonic operation without clear adaptive value.

Emotional Modulation of Memory Consolidation in Aging

We then conducted the study with a 24-hr delay between the study and test phase and compared immediate and delayed perfor-

mance across groups. Young adults exhibited less forgetting of emotional targets compared to neutral after 24 hr, while older adults exhibited more forgetting of emotional targets after 24 hr. Thus, with the passage of time, emotional gist memory seems to be preserved in young adults and reduced in older adults. Initially, memories tied to an emotional context seem to be better remembered in older adults, but these memories may not undergo consolidation to the same extent as in young adults. Over time, emotional arousal does not seem to provide an additional boost for remembering the same image seen before.

For stimuli that were somewhat similar but not identical to previously viewed stimuli (i.e., low-similarity lures), false recognition was higher for emotional compared to neutral items across both age groups. This suggests that both young and older adults discriminate emotional and neutral information similarly after consolidation has occurred (i.e., both age groups falsely recognize more emotional vs. neutral information over time). For stimuli that were very similar but not identical to previously viewed stimuli (i.e., high-similarity lures), false recognition of negative items (but not neutral or positive items) was higher in older adults. The ability of older adults to recall the details of positive stimuli to correctly discriminate them from highly similar lures seems to be unaffected by age. This is consistent with the positivity bias reported in past literature (Mather & Carstensen, 2005). In addition, the effects we find on memory consolidation may be associated with changes in the sleep-wake cycle, where typical findings have shown that older adults have irregular sleep patterns (Buckley & Schatzberg, 2005), which may affect their ability to consolidate emotional memories (Payne & Kensinger, 2010).

Potential Mechanisms for Shifts in Emotional Modulation of Memory With Age

Paradigms that vary mnemonic interference offer a robust empirical framework by which hippocampal function can be assessed (Hunsaker & Kesner, 2013). Indeed, much work has already been done using this framework including the assessment of changes in neurocognitive aging (Stark, Yassa, & Stark, 2010; Toner et al., 2009; Yassa & Stark, 2011; Yassa, Lacy et al., 2010), mild cognitive impairment (Yassa, Stark et al., 2010), perforant path degradation (Yassa et al., 2011; Yassa, Muftuler, & Stark, 2010), and neurogenesis loss of function (Clelland et al., 2009), as well as gain of function (Sahay et al., 2011). In human high-resolution blood-oxygen-level dependent (BOLD) fMRI studies, behavior on discrimination tasks has been specifically associated with pattern separation signals in the hippocampal DG and CA3 (Yassa et al., 2011) as well as the integrity of the perforant path input to the hippocampus from the entorhinal cortex (Yassa, Muftuler, & Stark, 2010). Here, we extended the pattern separation framework to investigate the impact of emotional modulation on hippocampal memory in aging. Although pattern separation was not directly assessed here, our manipulation of the similarity of lure stimuli allows us to examine a potential behavioral correlate of hippocampal pattern separation (Yassa & Stark, 2011).

We observed a shift in the balance of processing similar emotional information with age, which may be due to a shift in amygdala-hippocampal interactions. St. Jacques, Dolcos, and Cabeza (2009) suggested that an age-related reduction in the contribution of amygdala-hippocampal mechanisms may be com-

pensated by enhanced contribution of amygdala-prefrontal mechanisms to the formation of emotional memories (Murty et al., 2009; St. Jacques et al., 2009). In normal aging, the DG/CA3 regions seem to be affected such that there is hyperactivity in the CA3 region (likely driven by the region's excitatory recurrent collaterals that are disinhibited with age) concurrent with a decrease in input from the entorhinal cortex (Gallagher & Koh, 2011; Jagust, 2013; Yassa, Lacy et al., 2010; Yassa, Muftuler, & Stark, 2010). The amygdala is relatively well preserved, but still shows age-related change, especially in the basolateral amygdala (BLA; Dere, Pause, & Pietrowsky, 2010; Herzog & Kemper, 1980; Verweken, Vogels, & Nieuwenhuys, 1994).

It is hypothesized that emotional arousal, via norepinephrine release in the BLA, strengthens hippocampal memory representations (Gallagher, Kapp, Musty, & Driscoll, 1977; McGaugh, 2004). Decreases in peripheral epinephrine levels (Sternberg, Martinez, Gold, & McGaugh, 1985) and noradrenergic involvement in age-related memory dysfunction (Kubanis & Zornetzer, 1981) have been reported in animal models of aging. Alterations in synaptic plasticity in the amygdala-hippocampal network with age have also been reported. Young rodents display early long term potentiation (LTP) when stimulating the perforant path, which is prolonged into late-LTP when the BLA is stimulated 15 min later. However, aged rodents show no enhancement of perforant path—dentate gyrus LTP after BLA stimulation (Almaguer, Estupiñán, Uwe Frey, & Bergado, 2002). A combination of deficient synaptic plasticity and alterations in the noradrenergic system may therefore impair amygdala-hippocampal interactions with aging. Additionally, studies have shown that there is no upregulation of phosphorylated CREB in the BLA and hippocampus in low- and moderate-intensity shock, although aged rodents do show behavioral enhancements in the moderate shock condition (Morris & Gold, 2012). Findings such as this suggest that increasing the level of arousal may allow for compensation in aged rodents. It is not clear whether these deficits are due to hippocampal alterations or an age-related decrease in activity in modulatory regions such as the amygdala. Future studies utilizing high-resolution neuroimaging methods in combination with the current task may allow us to gain insight into subtle behavioral and neurobiological changes occurring in the medial temporal lobe in aging.

There are some limitations of the current study. It is difficult to rule out the possibility that our older adult group includes individuals with preclinical AD, which may present with different behavioral effects on emotional memory. While we attempted to minimize this possibility by excluding any individuals who presented with deficits in neuropsychological test performance, we cannot be certain that some of the behavioral effects observed are not driven at least in part by incipient AD pathology.

Furthermore, while we screened all of our young adults against major cognitive disorders, we did not perform detailed neuropsychological testing, thus investigating correlations between task performance and neuropsychological test performance was not feasible. Additionally, sample sizes were too small to thoroughly investigate gender differences, which have been demonstrated in some prior studies of emotional memory (Cahill, 2006). Finally, we used naturalistic stimuli and not computer-generated, controlled morphs, thus specific features (e.g., orientation, color, etc.) were quite variable. It is possible that future studies with more controlled stimuli can be used to examine mnemonic asymmetry

for emotional items in more detail by directly manipulating individual aspects of the images. In addition, as mentioned in the Materials and Method section, young and older adults used different scales for rating the valence of the images seen during the study phase. Young adults rated images on a 1–9 point scale while older adults used a similar scale, but without the large range of responses (limited to three button responses vs. 9). We chose to limit the response options for older adults to make the decision process easier and remove this difficulty; however, this could potentially underlie differences seen in task performance between young and older adults. This possibility can be examined in future studies by changing the young adults' rating scale to the same three-button response as older adults to match across groups.

In conclusion, our data suggest that there may be age-related changes to how emotional memories are processed, such that emotional details of the experience may be remembered with higher fidelity in older adults. These results highlight an interesting behavioral phenomenon with age and a novel neuropsychological paradigm that can be used in conjunction with high-resolution neuroimaging to test the neural mechanisms of pattern separation of emotional information and how they change with age and disease.

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