

Emotional modulation of memorability in mnemonic discrimination

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ABSTRACT

Although elements such as emotion may serve to enhance or impair memory for images, some images are consistently remembered or forgotten by most people, an intrinsic characteristic of images known as memorability. Memorability explains some of the variability in memory performance, however, the underlying mechanisms of memorability remain unclear. It is known that emotional valence can increase the memorability of an experience, but how these two elements interact is still unknown. Hippocampal pattern separation, a computation that orthogonalizes overlapping experiences as distinct from one another, may be a candidate mechanism underlying memorability. However, these two literatures have remained largely separate. To explore the interaction between image memorability and emotion on pattern separation, we examined performance on an emotional mnemonic discrimination task, a putative behavioral correlate of hippocampal pattern separation, by splitting stimuli into memorable and forgettable categories as determined by a convolutional neural network as well as by emotion, lure similarity, and time of testing (immediately and 24-hour delay). We measured target recognition, which is typically used to determine memorability scores, as well as lure discrimination, which taxes hippocampal pattern separation and has not yet been examined within a memorability framework. Here, we show that more memorable images were better remembered across both target recognition and lure discrimination measures. However, for target recognition, this was only true upon immediate testing, not after a 24-hour delay. For lure discrimination, we found that memorability interacts with lure similarity, but depends on the time of testing, where memorability primarily impacts high similarity lure discrimination when tested immediately but impacts low similarity lure discrimination after a 24-hour delay. Furthermore, only lure discrimination showed an interaction between emotion and memorability, in which forgettable neutral images showed better lure discrimination compared to more memorable images. These results suggest that careful consideration is required of what makes an image memorable and may depend on what aspects of the image are more memorable (e.g., gist vs. detail, emotional vs. neutral).

1. Introduction

Memory plays a crucial role in our everyday lives as it allows information to be stored and retrieved for future use (Milner et al., 1998; Zlotnik & Vansintjan, 2019). Although elements such as emotion can impact the strength of a memory (McGaugh, 2013; Williams et al., 2022) some items are consistently better remembered or forgotten by most people (Bainbridge, 2019). A growing body of work aims to uncover what makes certain events more memorable. Most memory research has focused on participant performance rather than the properties of the encoded stimuli themselves. However, the properties of a stimulus play a major role in determining whether it will be remembered, even more so than other factors such as individual differences, environment, and noise (Bainbridge & Rissman, 2018). Memorability refers to the

systematic variation with which some events or stimuli are better remembered than others. It is described as an observer-independent intrinsic property of items (including faces, words, images, movements, etc.). In certain instances, it has been demonstrated to be consistent across time delays and in implicit encoding (Goetschalckx et al., 2017; Goetschalckx, Moors, et al., 2019). Memorability is also thought to be independent of attention and priming effects and of top-down and bottom-up influences (Bainbridge, 2020; Mancas & le Meur, 2013). Even though these effects have been shown to be shared and consistent across subjects (Bainbridge, 2019), most research on memorability has been conducted within the United States, hence our current knowledge might not be generalizable to other cultural contexts.

Although memorability has been explored across a variety of domains, most research has focused on the intrinsic memorability of

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images. Individual image memorability scores have been primarily measured from behavioral visual recognition memory tasks, where novel and repeated images are shown in a continuous stream and participants are instructed to indicate repeated images (Bylinskii et al., 2021). A behavioral memorability score is then computed as the proportion of subjects (0 to 1) that will correctly recognize the image upon it being repeated (Rust & Mehrpour, 2020). Recent advances now allow image memorability variation to be reliably quantified using Convolutional Neural Networks (CNNs), which have been trained to predict image memorability with high correlation success rates to ground truths (e.g., behavioral data). CNNs are deep learning algorithms that map images to a desired output – in this case memorability scores - when given a large input – in this case existing behavioral memorability datasets - by applying a sequence of linear and non-linear operations to the input (O'Shea & Nash, 2015). Deep features extracted by CNNs have been shown to be the most successful computational features approximating human memorability (Bylinskii et al., 2021). Hence, memorability can be a predictable, image-computable measure of information, eligible for automatic prediction.

While there are known factors that contribute to image memorability— including images with people, those that are colorful, clearer, and uncluttered, or pictures with atypical content; there is still ~25 % of variation in memory performance that cannot be explained purely by memorability (Rust & Mehrpour, 2020). Previous research has shown that images with emotional content tend to have higher memorability scores (Goetschalckx, Moors, et al., 2019; Khosla et al., 2015). Particularly images that evoke disgust, amusement, or fear tend to be more memorable (Bainbridge et al., 2013). While emotion is typically thought to enhance memory processing (McGaugh, 2013), human research has found evidence for a gist versus detail trade-off, where the gist, or central aspect, of an emotional experience is preserved at the expense of detailed, or peripheral, information (Kensinger, 2009; Loftus et al., 1987; Mather & Sutherland, 2011). This effect tends to be exaggerated after a time delay (Mather & Sutherland, 2011; Leal et al., 2014).

One approach toward investigating gist versus detail trade-offs during the emotional modulation of memory has been applying a pattern separation framework. Computational models propose that a key characteristic of episodic memory involves the ability to determine whether the information of an event overlaps with an already existing experience, or if it is a new event distinct from previous memories (Kumaran & Maguire, 2007; Treves & Rolls, 1994). These processes are respectively known as pattern completion and pattern separation. Pattern completion involves the use of existing representations to accurately generalize when given only partial cues, while pattern separation involves distinguishing overlapping representations as distinct and storing them separately (Yassa & Stark, 2011). It is the balance between the two computations that permit us to have rich episodic memories (Leal & Yassa, 2018). Mnemonic discrimination tasks can provide a behavioral correlate of hippocampal pattern separation (Stark et al., 2013). During encoding of a typical mnemonic discrimination task, participants view images and are asked to make an arbitrary judgment about them (e.g., indoor/outdoor, valence rating, etc.). After a delay, participants are shown repeated images (targets), similar, but not identical, images (lures), and completely new images (foils). Lure images are meant to increase interference in memory, taxing hippocampal pattern separation. While pattern completion and pattern separation have been hypothesized to help explain memorability variation and representation in the brain (Kramer et al., 2023), the impact of memorability on these processes and their interaction with emotion has not yet been investigated.

Image memorability has primarily been investigated using standard recognition memory paradigms but, to our knowledge, has yet to be applied within a pattern separation framework. Additionally, we aimed to explore how emotion interacts with image memorability and its influence on episodic memory measures. The current study utilized an existing dataset (Leal et al., 2014) using an emotional mnemonic

discrimination task and re-analyzed the data by splitting stimuli into memorable and forgettable categories as determined by a CNN, as well as by emotion (negative, neutral, positive), lure similarity (high, low), and time of testing (immediately and 24-hour delay). First, we hypothesized that we would find evidence of memorability for target recognition (e.g., memorable > forgettable), replicating previous findings and confirm that our task design is accurately characterizing memorability within our mnemonic discrimination task using CNNs on a novel set of stimuli. Second, we hypothesized that memorability effects would be observed for lure discrimination, with memorable images being better discriminated compared to forgettable images. Furthermore, these effects could depend on the lure similarity, emotion, as well as the time of testing. We hypothesized that that emotion would interact with memorability, such that there would be a larger emotional gist versus detail trade-off for memorable compared to forgettable images. For the interaction between memorability and similarity, we expected that low similarity and memorable items would facilitate discrimination, however, we had no *a priori* hypotheses as to which would be a better driver of discrimination. Finally, we expected our hypotheses to be reflected across both testing delays, with the 24-hour delay group showing decreased target recognition and lure discrimination, but memorability remaining resistant to these effects.

2. Materials and methods

2.1. Participants

This dataset was comprised of participants from a previously published study (Leal et al., 2014). Participants were recruited from Johns Hopkins University and were either paid or received course credit for their participation. All participants were screened for self-reported major medical, psychiatric, and substance use, and had normal or corrected to normal vision. Participants were randomly assigned to the immediate group, which had their memory tested immediately after encoding ($N = 24$, all mean age \pm SD, 21 ± 3 , 16 female), or the delay group, which had their memory tested 24 h later ($N = 14$, 20 ± 2 , 6 female). Importantly, the immediate and delay groups were independent of each other (between-subjects design) to explore the manipulation of time delay across the encoding and retrieval phases of the task. Moreover, we wanted to avoid retrieval-induced forgetting effects that can occur with a within-subjects design, in which recalling some information immediately may interfere with the ability to recall information from that same context at a later time point (Anderson et al., 2000; Bäuml, 2008). Informed consent was obtained from all participants, with all procedures approved by the Johns Hopkins University Institutional Review Board.

2.2. Emotional mnemonic discrimination task

Participants completed an emotional mnemonic discrimination task which included a total of 389 images sized to a width of 600 pixels. All images were rated by an independent sample of participants for emotional valence (on a scale 1–9, with 1 being the most negative, 9 being the most positive, and 5 being neutral), arousal on a scale 1–9 (1 being the least arousing, 9 being the most arousing), and relative similarity between lure pairs (on a scale 1–8, with 1 being unrelated, 3 low similarity, 5 high similarity, and 8 being identical), in *a priori* experiments as described in Leal et al., 2014. During the encoding phase of the task, 148 images were shown, evenly split between negative, neutral, and positive emotional valence. In the retrieval phase, 290 images were shown and were either targets (repeated images), lures (similar but not identical images to those shown during encoding), or foils (brand new images), and were evenly distributed across stimulus type. Lure images were evenly split into high and low similarity relative to their baseline images shown during encoding.

Images were presented using an Apple iMac equipped with MATLAB

7.10.0 (R2010a) (MATLAB, 2010) software using the Psychophysics Toolbox 3.0 extension (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). During both the encoding and retrieval phases, images were presented on the center of the screen with a black background for 2500 ms, followed by a fixation display consisting of a white fixation cross on the center of the screen with a black background for 500 ms.

During the incidental encoding phase, participants were shown non-emotional and emotional images in randomized order and were asked to rate the images for emotional valence (1 = most negative, 5 = neutral, 9 = most positive) spreading their responses across the scale. Then, immediately after encoding ($N = 24$), or after a 24-hour delay ($N = 14$), participants were shown another series of images during the retrieval phase. Some images were repeated from the encoding phase (targets), some were similar, but not identical to the ones shown in the encoding phase (lures), and some were completely new (foils) (Fig. 1). Some of the lures were very similar (high similarity) and others were less similar (low similarity) to the original baseline images as rated by a separate sample (Leal et al., 2014). Participants were asked to indicate whether the image shown during the retrieval phase was “new” or “old” by recording their responses on the keyboard.

2.3. Convolutional neural network

To assess image memorability, we obtained memorability scores for each image from *ResMem* (Needell & Bainbridge, 2022), a CNN that allows the extraction of stimulus information to create a memorability estimation process. *ResMem* takes 150 layers of residual neural networks and connects them across levels to produce a vector. The CNN can analyze any image and predict an intrinsic memorability score based on its edges, patterns, parts, and objects. It was trained on a combination of datasets, including *MemCat* (Goetschalckx & Wagemans, 2019) and *LaMem* (Khosla et al., 2015), two of the most prominent image memorability stimulus sets based on behavioral data. By using this open-

source deep learning tool on our existing stimulus set, we were able to obtain individual memorability scores for all images used in the emotional mnemonic discrimination task. *ResMem* has proven effective in several validation studies (Li et al., 2022; Wakeland-Hart et al., 2022; Zhao et al., 2022), however, it is important to note that it is still a relatively new tool that is not always successful in predicting behavioral memorability estimates (Geiger & Balas, 2021), and which had not been trained with emotionality in mind. Even though memorability has been shown to be independent of previous experience (Isola et al., 2011), individual differences in responses to emotional stimuli might account for some of the variability in memory performance. To analyze the relationship between emotional valence ratings obtained from the independent rater sample and the memorability scores predicted by *ResMem* for each image, we performed correlational analyses and found no significant relationship (either linear or quadratic) between emotional valence and memorability scores (Supplemental Fig. S3).

We successfully ran all 389 images used in the encoding and retrieval phases of the emotional mnemonic discrimination task through *ResMem*'s 150 layers, obtaining individual image memorability scores (0–1), with higher scores indicating more memorable items. Stimuli were then split into non-overlapping memorable and forgettable categories using a threshold of 0.80 based on previous work (Bylinskii et al., 2015; Rust & Jannuzzi, 2022; Rust & Mehrpour, 2020) and our dataset median (0.80). Given that no image ever scores 0, and few tend to score lower than 0.40, the threshold of 0.80 for distinguishing memorable and forgettable images resulted in an almost even split between the existing stimuli which also follows previous studies. We also performed k-means clustering to determine how the obtained memorability scores clustered together and results generally aligned with our 0.80 threshold (with a threshold of 0.78 from the model; see Supplemental Analyses 1 for details). We also considered removing stimuli in the middle tertile of images surrounding the 0.80 threshold; however, this approach would result in the removal of a substantial number of images, making it

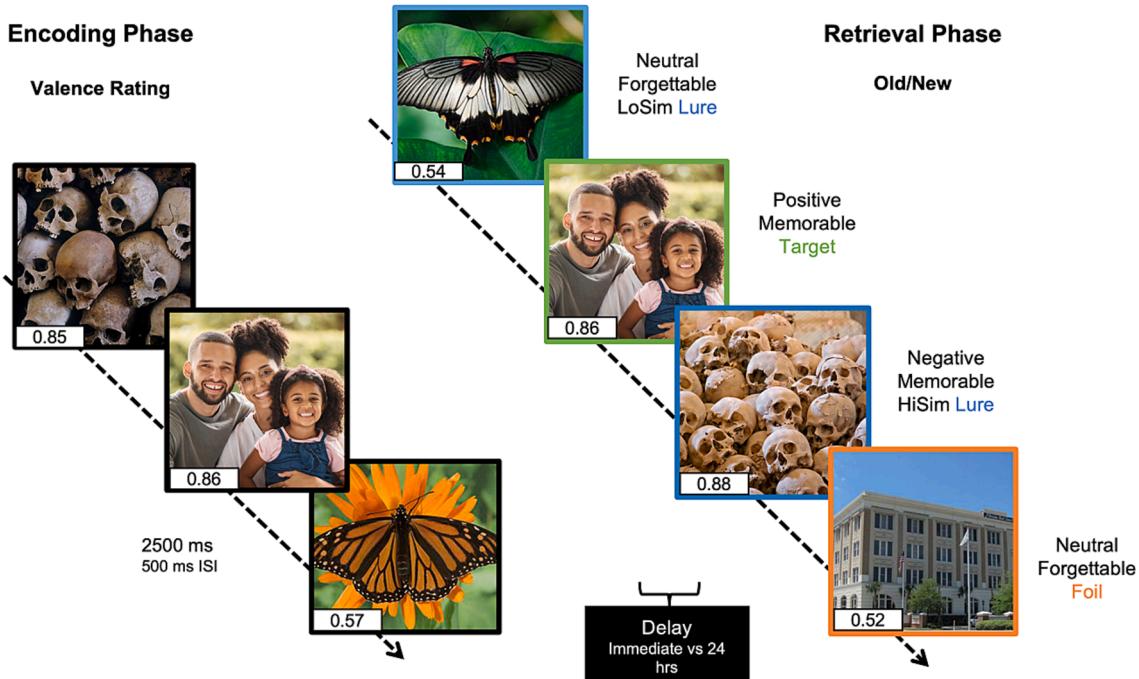


Fig. 1. Emotional mnemonic discrimination task design. During encoding, participants rated images according to their emotional valence from 1 (most negative) to 9 (most positive). Each image was presented for 2500 ms with a 500 ms inter-stimulus-interval (ISI). Either immediately after the encoding phase, or after a 24-hr delay, participants underwent a surprise retrieval phase which consisted of a surprise memory test where they viewed negative, neutral, and positive targets (green), foils (orange), and lures (blue) varying in similarity (high and low similarity) and were asked to indicate whether items were “old” or “new”. Numbers represent memorability scores (0–1, where higher scores indicate greater memorability). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

difficult to tease apart previously reported effects by memorability (Leal et al., 2014) and would result in too few images per condition.

2.4. Stimulus set

During encoding, out of the 148 images used, 75 were categorized as memorable (range of memorability scores between 0.80 and 0.95) and 73 as forgettable (scores between 0.51 and 0.79). Out of the 290 images used in the retrieval phase, 154 were categorized as memorable (scores between 0.80 and 0.96) and 136 as forgettable (scores between 0.47 and 0.79) (see Fig. S1 for individual score spread). The average memorability score distribution as well as statistical analyses comparing memorability scores across conditions for the encoding and retrieval phases can be found in Supplementary Table 1. Because the experimental paradigm and stimulus selection for this task was not created with memorability in mind, the number of stimuli in each category was not equally balanced across memorability like they were for emotional valence and lure similarity (see Table S1 and Fig. S2 for further detail).

2.5. Memory measures of interest

From participant responses, we obtained two measures of interest, target recognition and lure discrimination index (LDI). Target recognition provides a traditional recognition memory measure calculated by a discriminability index (d'), which is calculated as $d' = z[p(\text{'Old'}|\text{Target})] - z[p(\text{'Old'}|\text{Foil})]$. This corrects for response bias (calling a new item “old”). LDI provides a behavioral index that taxes hippocampal pattern separation calculated as $LDI = p(\text{'New'}|\text{Lure}) - p(\text{'New'}|\text{Target})$. This corrects for the tendency to reject (calling an old item “new”). We measured d' and LDI for overall performance in memorability (Section 3.1); the interaction between similarity and memorability (Section 3.2), how these interacted with emotion (Fig. S4); as well as the interactions between memorability and emotion (Section 3.3), the main analysis of interest. For analysis examining d' and LDI performance and the effects of emotional valence and lure similarity on these measurements, please refer to the original paper (Leal et al., 2014).

2.6. Statistical analyses and availability of data

All statistical analyses were conducted using JASP 0.16.2 (JASP Team, 2022) statistical software. We conducted t-tests and repeated-measures ANOVA, where appropriate. To determine the strength of the reported relationships Cohen's d and partial eta squared (η_p^2) are reported for effect sizes, where for Cohen's d 0.2 indicates a small effect, 0.5 a moderate effect, and 0.8 a large effect as established by (Cohen, 1988). For partial eta squared, 0.01 indicates a small effect, 0.06 indicates a medium effect and 0.14 indicates a large effect. Repeated-measures tests were corrected for error non-sphericity as measured by Mauchly's test using Greenhouse-Geisser correction. Post-hoc contrasts were conducted using Scheffé's method. Statistical values were considered significant at a final corrected alpha level of 0.05, which controlled for Type I error. All data was examined for outliers where any observation more than three standard deviations from the sample mean was considered an outlier, no data was identified as an outlier. We also conducted post-hoc effect size sensitivity analyses using G*Power 3.1 (Faul et al., 2007) to explore the effect sizes we could detect with 80 % power given our sample size ($N = 38$) and alpha of 0.05. For both our analyses of variance and difference between means explorations, we were powered to detect large effects across groups. In the separate groups, we were powered to detect large effects in the delay group ($N = 14$) and medium effects in the immediate group ($N = 24$). Given our limited sample size and lack of sensitivity to detect small effects, we also performed Bayesian statistics to explore whether any of our null results were more likely given the data without using a binary method such as null hypothesis significance testing. Overall, we found that when the frequentists approach showed no statistically significant differences,

these findings were supported by Bayesian prediction, where the null model provided the most evidence for explaining the observed data (see Supplementary Analyses 2). The data generated in the current study are available in a GitHub repository (https://github.com/lealmemory/emotion_memorability).

3. Results

3.1. Memorability impacts target recognition and lure discrimination performance

First, we examined overall performance (e.g., collapsed across emotion) on the emotional mnemonic discrimination task in the immediate versus 24-hour delay groups to determine if there was an effect of memorability on target recognition and lure discrimination. We hypothesized that we would find better d' and LDI for memorable relative to forgettable images across time delays. To measure this in target recognition, we conducted a repeated measures ANOVA with memorability (memorable, forgettable) as the within-subjects factor and group (immediate, 24-hour delay) as the between-subjects factor. We found a significant main effect of memorability [$F(1,36) = 5.25, p = .028, \eta_p^2 = 0.13$; Fig. 2A], with memorable images yielding better target recognition compared to forgettable images. Those tested immediately primarily drove this effect [$t(23) = 3.55, p = .002, d = 0.72$], as there was no significant difference between memorable and forgettable target recognition in the delay group ($p = .66$). An important caveat to keep in mind is that a null result in the delay group could be driven by the small sample size since we were underpowered to detect small-to-medium effects. There was also a significant main effect of time of testing [$F(1,36) = 18.88, p < .001, \eta_p^2 = 0.34$; Fig. 2A], where participants tested immediately showed better target recognition compared to those tested after a 24-hour delay. There was no significant interaction between memorability and time of testing [$F(1,36) = 2.03, p = .16$].

For lure discrimination, we conducted a repeated measures ANOVA with memorability (memorable, forgettable) as the within-subjects factor and time of testing (immediate, 24-hour delay) as the between-subjects factor. We found a significant main effect of memorability [$F(1,36) = 5.57, p = .024, \eta_p^2 = 0.13$; Fig. 2B], with memorable images yielding better lure discrimination compared to forgettable images. There was also a significant main effect of time of testing [$F(1,36) = 36.69, p < .001, \eta_p^2 = 0.50$; Fig. 2B], where participants tested immediately showed better lure discrimination compared to those tested after a 24-hour delay. There was no significant interaction between memorability and time of testing [$F(1,36) = 0.31, p = .58$]. The main effect of memorability was driven by the combined performance across immediate and delay participants, as there was no significant difference between memorable and forgettable lure discrimination in either the immediate ($p = .13$) or delay ($p = .12$) testing times independently.

3.2. Memorability differentially impacts high and low similarity lure discrimination

Next, we examined the effect of lure similarity interacting with memorability across testing times. We had hypothesized that both lower similarity and memorable images would facilitate discrimination at both time delays. We conducted a repeated measures ANOVA with memorability (memorable, forgettable) and lure similarity (low, high) as within-subjects factors and group (immediate, 24-hour delay) as the between-subjects factor. We found a main effect of memorability [$F(1,36) = 4.87, p = .034, \eta_p^2 = 0.11$], similarity [$F(1,36) = 119.25, p < .001, \eta_p^2 = 0.77$], and time of testing [$F(1,36) = 36.94, p < .001, \eta_p^2 = 0.50$], all in the expected directions (e.g., memorable > forgettable; low similarity > high similarity; and immediate > 24-hour delay; Fig. 3 A–B). There was a significant three-way interaction between memorability, similarity, and time of testing [$F(1,36) = 8.88, p = .005, \eta_p^2 = 0.19$], where memorable images were better remembered than

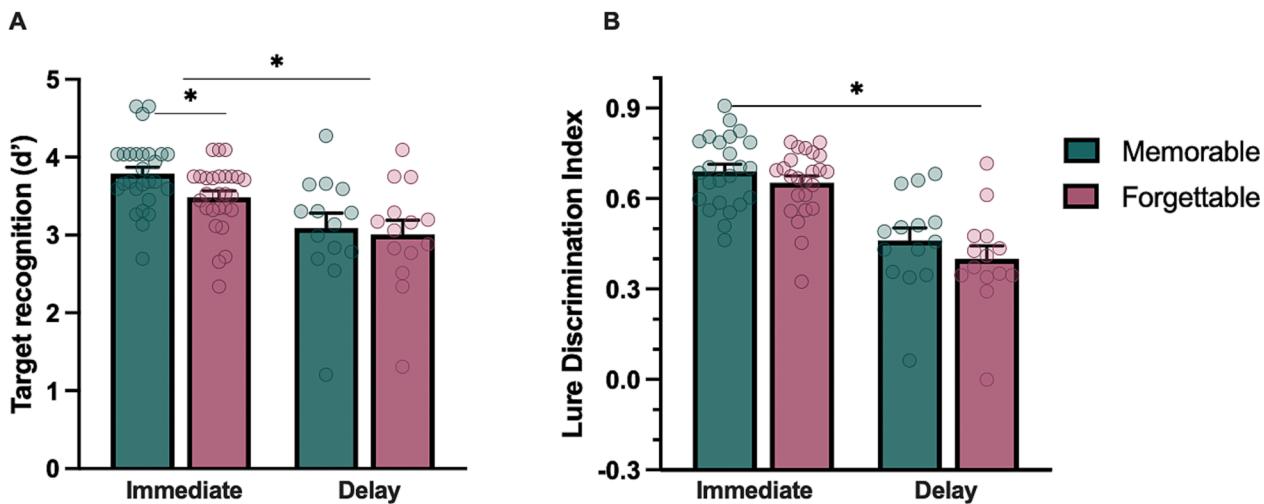


Fig. 2. The impact of image memorability on target recognition and lure discrimination when tested immediately or 24-hours later. Differences in average target recognition (A) and lure discrimination (LDI) (B) at immediate and delay testing times for memorable (teal) and forgettable (magenta) stimuli. Memorable images outperformed forgettable ones at immediate d' . When collapsed across groups, memorable images were significantly higher than forgettable at both immediate and delay d' and LDI. Error bars represent SEM. * = $p \leq .05$. Immediate N = 24, delay N = 14. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

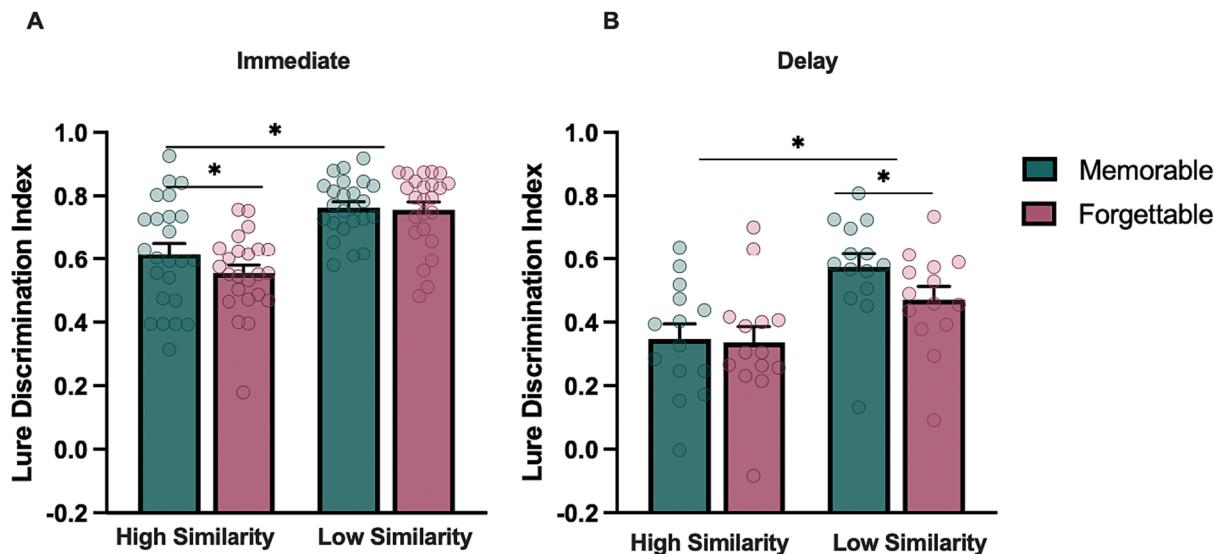


Fig. 3. The relationship between lure similarity and memorability immediately and 24 h later. Differences in average lure discrimination (LDI) at immediate (A) and delay (B) testing times for memorable (teal) and forgettable (magenta) images. At immediate testing, low similarity images performed better than high similarity ones. Only at higher similarity levels was there an effect for memorability. At delay, differences in memorability and similarity were present in the expected direction. The interaction between similarity and memorability was significant, with differences between memorability at low similarity items driving significance. Error bars represent SEM. * = $p \leq .05$. Immediate N = 24, Delay N = 14. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forgettable images, but only for high similarity lure images when tested immediately [$t(23) = 2.21, p = .04, d = 0.45$; Fig. 3A] and only for low similarity lure images when tested after a 24-hour delay [$t(13) = 2.63, p = .02, d = 0.70$ Fig. 3B].

Further, we included emotional valence as an additional within-subjects factor to the previously described ANOVA conducted within group to determine whether any of the above effects interacted with emotion. When tested immediately, we found a significant three-way interaction between emotion, similarity, and memorability [$F(2,46) = 5.11, p = .016, \eta^2_p = 0.18$; Fig. S4], where highly similar negative images showed stronger effects of memorability on lure discrimination (memorable > forgettable) compared to low similarity images [$F(1,23) = 5.11, p = .016, \eta^2_p = 0.18$]. Neutral images showed this effect to a

lesser degree, and positive images showed no such effects. This three-way interaction was not evident in the delay group (Fig. S4).

3.3. The interaction between memorability and emotion for target recognition and lure discrimination

Next, we wanted to determine how emotion may interact with memorability to impact target recognition and lure discrimination. We hypothesized that there would be an interaction between emotion and memorability, such that there would be a larger emotional gist versus detail trade-off for memorable images than forgettable ones. For target recognition, we conducted a repeated measures ANOVA with memorability (memorable, forgettable) and emotion (negative, neutral,

positive) as within-subjects factors. For those tested immediately, there was a significant effect of memorability [$F(1,23) = 13.92, p = .001, \eta_p^2 = 0.37$; Fig. 4A], where there was better target recognition for memorable images compared to forgettable images. There was a significant main effect of emotion [$F(2,46) = 4.99, p = .011, \eta_p^2 = 0.17$], where positive target recognition was worse than negative and neutral target recognition [$F(1,23) = 16.51, p < .001, \eta_p^2 = 0.42$]. We found no significant effects in those tested after a 24-hour delay (all p 's > 0.05 ; Fig. 4B), however, it is important to keep the delay group's small sample size in mind when interpreting these findings.

For lure discrimination, we conducted a repeated measures ANOVA with memorability (memorable, forgettable) and emotion (negative, neutral, positive) as within-subjects factors. For those tested immediately, we found a main effect of emotion [$F(2,46) = 36.76, p < .001, \eta_p^2 = 0.61$], where neutral images were better discriminated than emotional images [$F(1,23) = 57.95, p < .001, \eta_p^2 = 0.72$; Fig. 4C]. After a 24-hour delay, we found a main effect of emotion [$F(2,26) = 15.61, p < .001, \eta_p^2 = 0.55$], where neutral images were better discriminated than emotional images [$F(1,13) = 21.58, p < .001, \eta_p^2 = 0.62$; Fig. 4D]. We also found a significant interaction between emotion and memorability [$F(2,26) =$

$10.10, p = .004, \eta_p^2 = 0.44$], where lure discrimination was better for more memorable positive images followed by no difference in memorability for negative lure discrimination, but better neutral lure discrimination for forgettable images [$F(1,13) = 48.32, p < .001, \eta_p^2 = 0.79$]. When we conducted a three-way ANOVA including time of testing as a between-subjects factor, we additionally found a significant three-way interaction between memorability, emotion, and time of testing [$F(2,72) = 3.63, p = .031, \eta_p^2 = 0.09$], where lure discrimination for positive images was better for memorable than for forgettable images at a 24-hour delay. However, at immediate testing we observed that negative and neutral lure discrimination show similar relationships between memorable and forgettable images across time delays [$F(1,36) = 9.04, p = .005, \eta_p^2 = 0.20$].

4. Discussion

Many factors can influence what we remember and forget. Emotional experiences are more likely to be remembered than non-emotional ones (Williams et al., 2022), however, there are gist vs detail tradeoffs in emotional memory (Chipchase & Chapman, 2013; Waring & Kensinger,

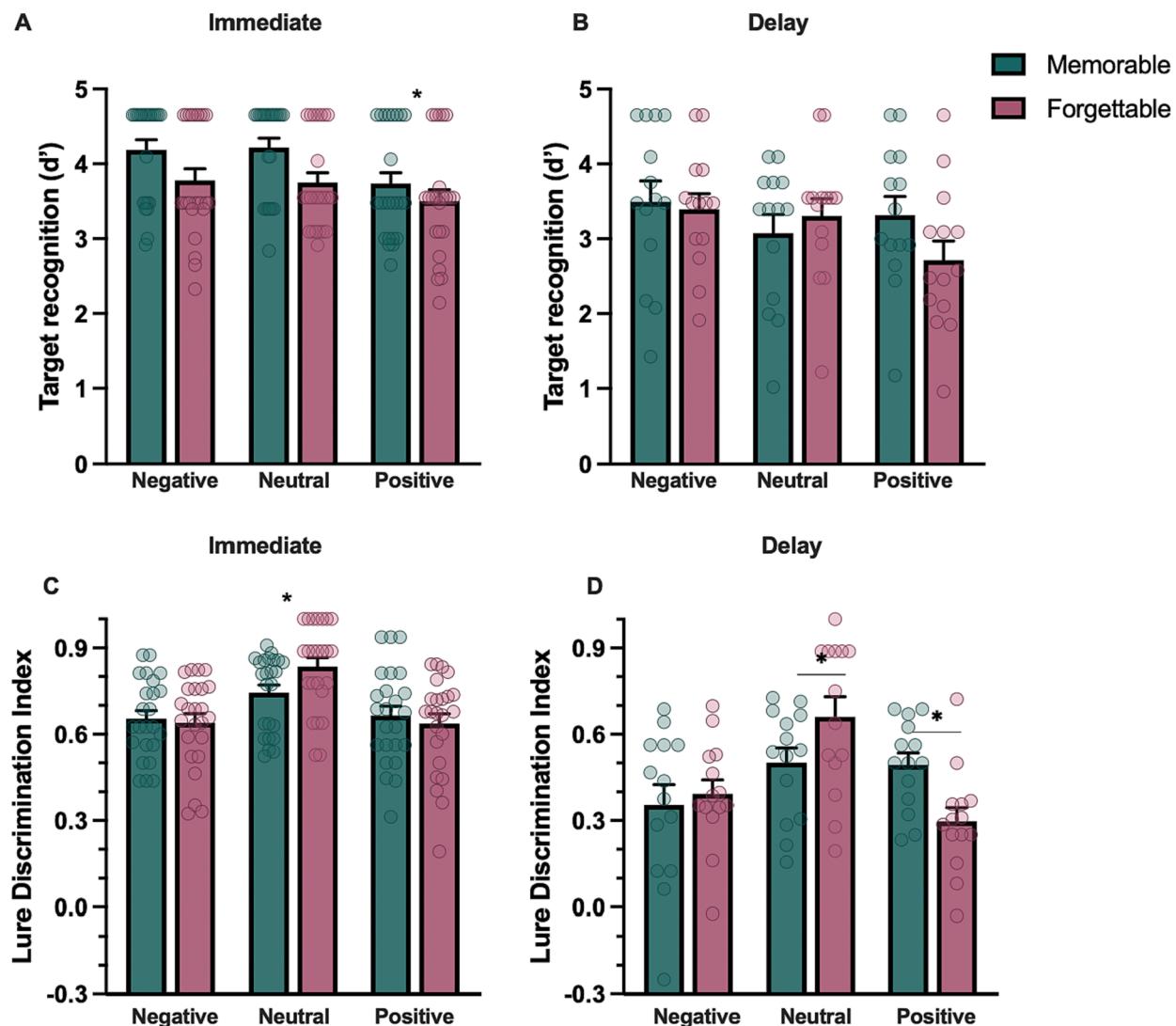


Fig. 4. The interaction between memorability and emotion for target recognition and lure discrimination. Differences in average target recognition (A and B) and lure discrimination (LDI) (C and D) at immediate (A and C) and delay (B and D) testing times for memorable (teal) and forgettable (magenta) images. Immediate d' was better for memorable images but no differences were found at delay testing. For LDI, we only see effects of memorability when interacting with emotion at delay, where we observe an opposing pattern in memorability across positive images vs negative and neutral. Error bars represent SEM. * = $p \leq .05$. Immediate N = 24, Delay N = 14. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2009). Thus, there is some emotional information we are more likely to remember (gist) and some that we are more likely to forget (details). There is growing interest in understanding what factors can enhance memory performance, as this has important implications for educational settings and postponement and treatment of cognitive decline. Additionally, intrinsic image properties such as memorability can also influence remembering and forgetting. Recent progress in training CNNs and the acquisition of large human behavioral datasets have allowed for better characterization and understanding of memorability. To our knowledge, memorability has not been previously examined using a pattern separation framework (e.g., with the inclusion of similar lures), nor how other factors may impact memorability within this context (i.e., emotional valence, time of testing). Through the investigation of the interaction of image memorability and an emotional mnemonic discrimination task, we were able to examine the potential effects these elements have on traditional recognition and mnemonic discrimination.

4.1. Both target recognition and lure discrimination for memorable images outperform forgettable ones

Prior ways of examining image memorability have done so through target recognition, but it is not clear whether memorability impacts lure discrimination. We hypothesized that memorability would facilitate target recognition and lure discrimination, with memorable items outperforming forgettable ones. Overall, we found that memorable images outperformed forgettable ones when collapsed across time delays, yielding higher target recognition and lure discrimination compared to forgettable images. We found this effect was largest for immediate target recognition, although this finding is not surprising given that immediate recognition tests are how memorability has been measured and characterized in the past. This finding provides support that our results are consistent with prior studies of memorability (Oliva & Isola, 2012) and that we were sensitive to previously reported findings of memorability when applying CNNs to a novel image dataset (Leal et al., 2014; Needell & Bainbridge, 2022). However, we did not find differences in memorability for either memory measure after 24 h. We showed that differences across memorability for target recognition were no longer significant after 24 h, suggesting that the effects of memorability were lost after a delay. It is important to bear in mind, however, that our sample sizes were unequal, and the delay group was quite small. Post-hoc power sensitivity analyses suggested that our sample size could detect large effect sizes; thus, we may not have been able to capture small effects across our groups. It will be important for future studies to test whether these effects are lost after a delay or may result in small effects at a delay.

For lure discrimination, there were no differences between memorable and forgettable items in LDI for either immediate or delay groups when examined separately. It is expected for memory performance to decline with increased retention intervals, which could also be expected of behavioral memorability scores, which have been stated to decline log-linearly (Khosla et al., 2015). Previous studies have investigated memorability across time delays; however, most have analyzed differences between approximately 5 to 40 min and not at extended time periods for retention intervals (Isola et al., 2014; Oliva & Isola, 2012). Very little research has been done looking at delays beyond a few minutes (Goetschalckx et al., 2017) and to our knowledge no studies have looked at 24-hour delays. It is important to note that our immediate and delay groups were independent of each other, so we could not examine forgetting within subjects immediately and after 24 h. Future studies would benefit from a within-subject design to test this more directly.

4.2. Differential effects of memorability and lure similarity immediately versus 24 hrs later

By including similar lure stimuli, we were able to measure a lure discrimination index, a behavioral measure that taxes hippocampal

pattern separation, and was a novel aspect of our task compared to traditional memorability recognition tests. Thus, examining the effect of lure similarity on memorability could provide novel insight into mechanisms underlying memorability. We found that lure discrimination was better for memorable versus forgettable lures, but only for high similarity lures when tested immediately. When we broke this down by emotion, we found that the effects were primarily driven by negative and neutral stimuli. After 24 hours, we observed that lure discrimination was better for memorable versus forgettable items, but only for low similarity lures. Hence, memorability effects were selective for low similarity lures after a 24-hour delay, but for high similarity lures when tested immediately. This suggests that lure similarity has less impact on emotional memory after 24 h, potentially because retrieval becomes more difficult after a delay; thus, lure similarity effects are lost in preference for emotional content. It would appear that, in the context of emotional pattern separation, memorability may offer a facilitating effect for harder-to-discriminate lures when memory is tested closer to baseline, whereas after a 24-hour delay we see this facilitating effect shift from harder to easier lures.

4.3. Emotion significantly interacts with memorability to impact lure discrimination

Although past research has explored the interactions of emotional valence on memory (Qasim et al., 2023; Ruetti et al., 2008); the precise underpinnings driving enhanced types of memory for emotional items are still unclear. The previously reported results from this study (Leal et al., 2014) examining the effects of emotion on mnemonic discrimination suggested that the gist versus detail trade-off observed for emotional memory was magnified after 24 hrs, where emotional target recognition was preserved relative to neutral target recognition, but emotional lure discrimination was impaired relative to neutral lure discrimination. This trade-off has been reported in the emotional memory literature (Kensinger, 2009), as well as studies suggesting that sleep enhances this effect (Payne et al., 2008). Here, we aimed to further parse these previously reported effects by examining the effects of image memorability on emotional memory in the same dataset, where we set out to explore if memorability modulated this known trade-off effect. We found that emotion did not significantly interact with memorability for target recognition at either immediate or delayed performance. Rather, a general effect of memorability was found when tested immediately, where memorable items outperformed forgettable ones across all emotional valences. Even though highly arousing emotional content (i.e., amusement, disgust) has been associated with greater memorability, some studies have shown that emotional valence and memorability can be driven by properties that are independent of each other (Goetschalckx, Leuven, et al., 2019).

For lure discrimination, we found no effects of memorability when tested immediately, however, after a 24-hour delay there was an interaction between emotion and memorability, where forgettable images showed the previously reported pattern (i.e., neutral > emotional lure discrimination) more strongly than memorable images. Forgettable neutral stimuli showed better lure discrimination than memorable neutral stimuli, and memorable positive stimuli showed better lure discrimination compared to forgettable positive stimuli. Negative stimuli showed similar patterns across memorable and forgettable stimuli. While this finding appears counterintuitive, one plausible explanation is that, given that “memorability” has been defined based on general target recognition, the definition of what makes something memorable might be based on the gist of the image, not its details. Previous research (Kensinger, 2009) speculates that affect can influence memory and lead to trade-offs, enhancing memory for some information while weakening memory for others. For the memorability of an image, it is possible that an image characterized as “forgettable” as based on a more general or gist-like memory measure (e.g., target recognition) may not account for how details of an image would be remembered, in which a lure

discrimination measure relies more heavily on memory for detail. As a result, a “forgettable” image could include memorable details, or peripheral aspects, of an image. Further, this may interact with emotional memory trade-offs, such that emotional images may exhibit larger gist vs detail trade-offs, where the central elements of emotional images (e.g., the gist) may be more memorable, while the peripheral, non-central elements (e.g., the details) of neutral, non-emotional images may be more memorable (or “forgettable” for the central/gist elements) (see Fig. 5).

In line with the Arousal Biased Competition model (Mather & Sutherland, 2011), gist versus detail trade-offs observed for emotional stimuli are consistent with what has the highest priority during encoding. This theory is harmonious with previous literature exploring drivers of memorability, where Khosla et al., (2015) developed memorability score heatmaps of intersecting image subregions, where each pixel in the heat map represented a memorability prediction across the subregions that contain it. Their maps tended to highlight more salient and central sections of the images (those containing people, animals, or text) as contributors to higher memorability scores. When these regions were emphasized, memory performance increased. In contrast, when said regions were removed from the images, their memorability scores decreased (see Fig. 7 in Khosla et al., 2015).

We propose that something similar is occurring when we behaviorally tax pattern separation. For memorable positive images, the gist, or central element, of the image is retained, but specific peripheral details are lost with the emotional trade-off after a delay. For positive lure images, which differ in subtle details from the baseline images shown, their discrimination tends to be worse due to the emotional trade-off, where details are lost in favor of central aspects. However, for non-emotional forgettable images, we see an opposing pattern, where the details may be more attended to, given the lack of emotional content, allowing participants to better discriminate lures due to their subtle peripheral differences. Hence, although termed “forgettable”, these images tended to be better remembered than their emotional counterparts characterized as “memorable” (see Fig. 5) within a pattern separation framework.

The way emotion shapes memory for central and peripheral aspects of a scene has been found to change across time delays and across emotional valences. One caveat to our findings is that the interaction between the emotional trade-off and memorability is only present in positive images after a 24-hr delay. However, the emotional mnemonic discrimination task from which the current data was obtained (Leal et al., 2014) showed an emotional gist vs detail trade-off in both positive and negative stimuli.

Previous studies have found an enhanced emotional trade-off specific to negative images when compared to positive ones (Kensinger et al., 2007a, 2007b; Waring & Kensinger, 2009), where there was better memory for central aspects of negative objects and impaired memory for the neutral backgrounds (peripheral aspects) the stimuli were presented. The most common example of these findings is the weapon focus effect (Loftus et al., 1987). Additionally, another study found these same effects to be amplified after an increased delay (12 h) when compared directly after encoding (30 min) (Payne et al., 2008).

It is possible that negative and positive emotions influence memory through different mechanisms. Previous studies have suggested that positive emotion can lead to attention broadening (Fredrickson, 2001; Rowe et al., 2006) with negative emotion conversely leading to attention narrowing (Christianson et al., 1991). However, researchers have also found no evidence of attentional effects with memory enhancement for details in both positive and negative emotions (Chipchase & Chapman, 2013), calling for factors beyond attentional enhancement. Other researchers have posited that positive information is processed faster (Unkelbach et al., 2008) and thus better encoded than negative information; while others have argued that positive emotion bias leads to increased levels of familiarity (Verde et al., 2010).

Within the current study, our findings point towards an alternative factor that can further elucidate the explanation of the enhancement of emotional memory specificity. When interacting with memorability, we showed an enhanced gist versus detail trade-off selective to positive images; therefore, the influence of memorability on emotional trade-offs of memory may be more sensitive to changes in positive versus negative stimuli. However, further investigation into the interactions between

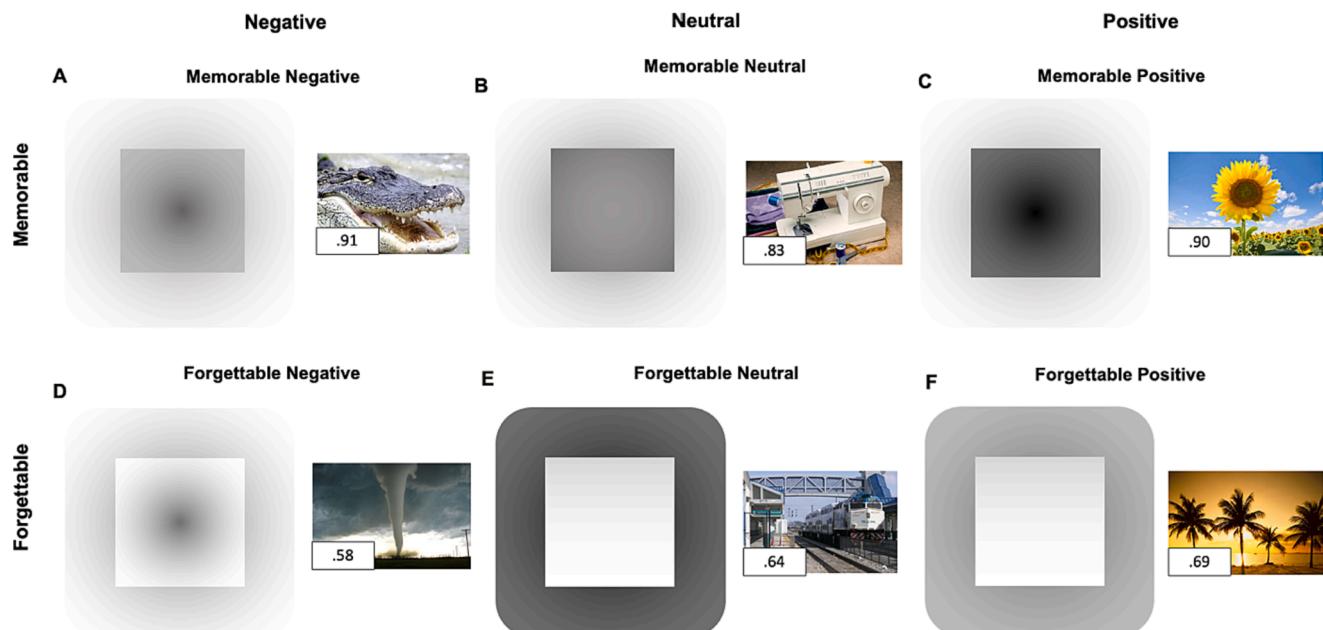


Fig. 5. Proposed mechanisms shown in the interaction between emotion and memorability in lure discrimination after a delay. Memorable items (top panel) are not impacted by details (outer ring) given that what is defined as “memorable” is based on target recognition, which is characterized by general, gist-like features, or central aspects, of an image (central ring), and not lure discrimination. This interaction can be expected as emotional gist vs detail trade-offs between neutral and emotional images have been previously reported. Forgettable images (bottom panel), defined as “forgettable” based on their central elements, may lead to better memory for details (outer ring), where there are greater emotional gist vs detail trade-offs in peripheral aspects of the image.

memorability, emotion, and mnemonic discrimination are required to disentangle the drivers of the observed results. A study design controlled and balanced for memorability levels across emotional valences could better tap into these effects.

4.4. Neural correlates of mnemonic discrimination and memorability

The hippocampus, amygdala, and cortical regions such as the pre-frontal cortex work jointly to process emotional memories (Cahill & McGaugh, 1995; Dolcos et al., 2005). In particular, the connections between basolateral amygdala and the hippocampus are thought to modulate the strength of emotional memories (McGaugh, 2004). However, amygdala-hippocampal connectivity may be increased or decreased depending on the memory conditions being studied (Fasenrath et al., 2014).

Studies examining memorability have discussed the importance of understanding its neural mechanisms given that memorability could provide insights into the interactions between perception and memory by explaining the extent to which MTL structures are selective to particular stimuli, as well as identifying brain regions or networks sensitive to abstract representations of memorability beyond perceptual features (Bainbridge et al., 2013). It has been previously proposed that hippocampal pattern separation, the computation that orthogonalizes overlapping experiences as distinct from one another, could be a candidate mechanism underlying memorability (Kramer et al., 2023). Previous research has shown that the brain is sensitive to image memorability, regardless of memory performance (Bainbridge & Rissman, 2018), where there is a representational organization in the brain based on memorability; with memorable items showing a tendency to be highly similar, while forgettable images are highly dissimilar from one another (Bainbridge et al., 2017). This is akin to work showing higher representational similarity in pattern completion and higher distinctiveness in pattern separation (Larocque et al., 2013).

While we cannot directly infer information about the neural processes underlying our findings, we hypothesize that the interactions between emotion and memorability are supported by underlying amygdala-hippocampal connectivity. Future studies using high-resolution functional MRI are necessary to understand the interactions between memorability and encoding/retrieval memory processes, specifically in hippocampal subfields important for pattern separation. Prior work in animals has suggested that the amygdala is sensitive to interference based on reward value (Kesner et al., 2002). Thereby, we hypothesize that the amygdala may modulate the interaction between emotional valence and memorability in mnemonic discrimination. We hypothesize higher representational organization in DG/CA3 during the encoding of memorable when compared to more forgettable items. We expect the amygdala to impact DG/CA3 subfield activity, which is more sensitive to lure discrimination (varying similarity of images) compared to other hippocampal subfields (e.g., CA1) and target recognition measures (repeated images), which would likely show stronger connectivity during processing of memorable compared to forgettable images. Nonetheless, these effects may be independent of memorability representation in the brain; ventral visual areas and memory related areas have been shown to be associated with stimulus memorability but independent of memory performance (Bainbridge et al., 2017, Bainbridge & Rissman, 2018), pointing towards a role in supporting visual recognition memory behavior during memory encoding. Studying hippocampal subfields and MTL connectivity within the context of perceptual influences using high resolution imaging techniques will allow us to explore whether there is differential activation between memorable and forgettable items, and how emotion may influence this network.

5. Conclusions, limitations, and future directions

To explore the influence of image memorability on emotional mnemonic discrimination, we examined memory performance by splitting

stimuli into memorable and forgettable categories as determined by a CNN. We measured target recognition, which is a general memory measure that can be used to determine memorability scores; as well as lure discrimination, which taxes hippocampal pattern separation and, which to our knowledge, had not yet been examined within a memorability framework.

We showed that more memorable images were better remembered across both target recognition and lure discrimination measures. However, for target recognition, this was only true upon immediate testing, not after a 24-hour delay. These effects will need to be replicated with a larger sample to increase sensitivity to smaller effects. For lure discrimination, we had two major findings. First, that memorability interacts with lure similarity, but this interaction depends on the time of testing; where memorability primarily impacts high similarity lure discrimination when tested immediately but impacts low similarity lure discrimination after a 24-hour delay. Second, only lure discrimination showed an interaction between emotion and memorability, in which forgettable neutral images showed better lure discrimination compared to more memorable images. While a particular image may generally be memorable, this does not necessarily tell us what information is retained. Lure discrimination measures can help get at some of these trade-offs by behaviorally taxing pattern separation. Finally, emotion is another element that can increase image memorability. In the current study, we showed that emotion more significantly interacts with memorability for lure discrimination measures than target recognition, potentially due to gist vs detail trade-offs that exist with emotional memory.

These results suggest that careful consideration is required of what makes an image “memorable” or “forgettable” and may depend on what aspects of the image are more memorable or forgettable (e.g., gist vs. detail, emotional vs. neutral). In addition, by using our emotional mnemonic discrimination task, a putative behavioral correlate of hippocampal pattern separation, we were able to capture differential effects of memorability only shown in a pattern separation framework. Our results not only illustrate that memorability and emotional valence interact when we behaviorally tax pattern separation through lure discrimination, but they also demonstrate that novel paradigms are important in the understanding and conceptualization of memorability research and its neural underpinnings.

There are some limitations in our current study. First, task development and dataset compilation were not created with individual image memorability scores in mind. We analyzed an existing task and dataset (Leal et al., 2014), making the image set unbalanced for an equal number of memorable and forgettable stimuli across both the encoding and retrieval phases. However, they were generally matched throughout the task design. Future studies may benefit from developing a novel stimulus set with memorability in mind such that images with the highest and lower memorability scores could be selected to increase the sensitivity of memorability rather than implementing a threshold on a continuous scale. Second, the number of subjects in the immediate and delayed testing groups was not equal and were relatively small samples. Our samples were powered to detect large and medium, but not small effects, thus, larger samples will be important to include in future studies to detect potential small effects as well. Null results should be interpreted with this caveat in mind. Thus, future studies with a larger dataset designed with memorability in mind will be important to replicate the current findings. In addition, the immediate and delay groups were independent of each other so we could not measure within-subject forgetting over time. This will be an important future direction to better understand the dynamics of memory changes over time. An additional limitation to our study is the representativity of emotional content within memorability datasets, where the emotional distribution of the datasets *ResMem* was trained on is not specified. Even though it has been shown to accurately approximate ground truth predictions of memorability scores, the CNN uses features of an image to assign it a memorability score, without considering higher-level content, such as

emotional valence. Previous research has shown that the performance of memorability CNN predictions is tied to the emotional scores of images (Baveye et al., 2017). Hence, the emotion elicited by the input image can negatively modify the success rate of existing trained prediction models. It is possible the memorability scores obtained on our emotionally-valenced set using a CNN are not accurately representing the memorability scores that would have been obtained in a behavioral memory task. Nonetheless, we were able to capture effects of memorability bin differences across target recognition, where we replicated traditional memorability findings. Moreover, individual differences and previous experiences which might evoke greater emotional responses might also interact with memorability performance. An individual differences approach will be an essential future direction for memorability studies to explore how these variations might drive memory performance and interact with the ability to accurately discriminate emotional experiences.

This discussion highlights the importance of having memorability datasets that are well-distributed across emotional valence and arousal to allow for the fine-tuning of deep learning models to predict both visual features as well as scene semantics, since both concepts can influence memorability scores. Despite these limitations, we report significant effects of memorability interacting with lure similarity, emotion, and time of testing in an emotional mnemonic discrimination task. Memorability has primarily been measured at immediate recognition tests; however real-life memory is occurring beyond this short time window. This suggests that the definition and conceptualization of memorability could be incomplete when analyzing how we remember in naturalistic settings. While what memorability is capturing is complex, especially after longer time delays or when there is interference, our results suggest that image memorability can have a significant impact on emotional memory. It is possible memorability is tapping into specific mechanisms involved in immediate target recognition; however, more novel elements like lure discrimination or extended time delays between encoding and retrieval have not been examined with image memorability interactions being accounted for. Different mechanisms may be involved in the distinction between memorability for repeated items versus similar ones. Future studies using neuroimaging will be important for elucidating the underlying mechanisms of memorability in the context of temporal delays and interference in memory. Our current findings highlight the need to explore memorability beyond traditional recognition tests.

CRediT authorship contribution statement

Fernanda Morales-Calva: Conceptualization, Formal analysis,

Visualization, Writing – original draft, Writing – review & editing.

Stephanie L. Leal: Conceptualization, Data curation, Methodology,

Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.nlm.2024.107904>.

References

- Anderson, M. C., Bjorkand, E. L., & Bjork, R. (2000). Retrieval-induced forgetting: Evidence for a recall-specific mechanism. *Psychonomic Bulletin & Review*, 7(3).
- Bainbridge, W. A. (2019). Memorability: How what we see influences what we remember. In *Psychology of learning and motivation - Advances in research and theory* (Vol. 70, pp. 1–27). Academic Press Inc.. <https://doi.org/10.1016/bs.plim.2019.02.001>
- Bainbridge, W. A. (2020). The resiliency of image memorability: A predictor of memory separate from attention and priming. *Neuropsychologia*, 141. <https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2020.107408>
- Bainbridge, W. A., Dilks, D. D., & Oliva, A. (2017). *Memorability: A stimulus-driven perceptual neural signature distinctive from memory*. doi: 10.1016/j.neuroimage.2017.01.063.
- Bainbridge, W. A., Isola, P., & Aude, O. (2013). The intrinsic memorability of face photographs. *Journal of Experimental Psychology: General*. <https://doi.org/10.1037/a0033872.supp>
- Bainbridge, W. A., & Rissman, J. (2018). Dissociating neural markers of stimulus memorability and subjective recognition during episodic retrieval. *Scientific Reports*, 8(1), 1–11. <https://doi.org/10.1038/s41598-018-26467-5>
- Bäuml, K.-H. (2008). *2.13 inhibitory processes*. *Learning and memory: A comprehensive reference*. Elsevier.
- Baveye, Y., Cohendet, R., Perreira da Silva, M., & le Callet, P. (2017). Deep learning for image memorability prediction: The emotional bias. In *ACM multimedia 2016, Oct 2016, Amsterdam, Netherlands* (pp. 491–495).
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436. <https://doi.org/10.1163/156856897X00357>
- Bylinskii, Z., Research, A., & Goetschalckx, L. (2021). *Memorability: An image-computable measure of information utility*.
- Bylinskii, Z., Isola, P., Bainbridge, C., Torralba, A., & Oliva, A. (2015). Intrinsic and extrinsic effects on image memorability. *Vision Research*, 116, 165–178. <https://doi.org/10.1016/j.visres.2015.03.005>
- Cahill, L., & McGaugh, J. L. (1995). A novel demonstration of enhanced memory associated with emotional arousal. *Consciousness and Cognition*, 4(4), 410–421. <https://doi.org/10.1006/coco.1995.1048>
- Chipchase, S. Y., & Chapman, P. (2013). Trade-offs in visual attention and the enhancement of memory specificity for positive and negative emotional stimuli. *Quarterly Journal of Experimental Psychology*, 66(2), 277–298. <https://doi.org/10.1080/17470218.2012.707664>
- Christianson, S.-A., Loftus, E. F., Hoffman, H., & Loftus, G. R. (1991). Eye fixations and memory for emotional events. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 17(4).
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences second edition*.
- Dolcos, F., LaBar, K. S., & Cabeza, R. (2005). Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proceedings of the National Academy of Sciences of the United States of America*, 102. <https://doi.org/10.1073/pnas.0409848102>
- Fastenrath, M., Coynel, D., Spalek, K., Milnik, A., Gschwind, L., Roozenendaal, B., Papassotiropoulos, A., & de Quervain, D. J. F. (2014). Dynamic modulation of amygdala-hippocampal connectivity by emotional arousal. *Journal of Neuroscience*, 34(42), 13935–13947. <https://doi.org/10.1523/JNEUROSCI.0786-14.2014>
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2), 175–191.
- Frederickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions perspectives on emotions and affect NIH public access. *American Psychologist*, 56(3).
- Geiger, A. R., & Balas, B. (2021). Robot face memorability is affected by uncanny appearance. *Computers in Human Behavior Reports*, 4. <https://doi.org/10.1016/j.chbr.2021.100153>
- Goetschalckx, L., Leuven, K., Andonian, A., Oliva, A., & Isola, P. (2019). *GANalyze: Toward visual definitions of cognitive image properties*. <http://ganalyze.csail.mit.edu/>.
- Goetschalckx, L., Moors, P., & Wageman, J. (2017). Image memorability across longer time intervals. *Memory*, 26(5), 581–588. <https://doi.org/10.1080/09658211.2017.1383435>
- Goetschalckx, L., Moors, P., & Wageman, J. (2019). Incidental image memorability. *Memory*, 27(9), 1273–1282. <https://doi.org/10.1080/09658211.2019.1652328>
- Goetschalckx, L., & Wageman, J. (2019). MeMCAT: A new category-based image set quantified on memorability. *PeerJ*, 2019(12). <https://doi.org/10.7717/peerj.8169>

- Isola, P., Xiao, J., Torralba, A., & Oliva, A. (2011). What makes an image memorable? In *Proceedings of the IEEE computer society conference on computer vision and pattern recognition* (pp. 145–152). doi: 10.1109/CVPR.2011.5995721.
- Isola, P., Xiao, J., Parikh, D., Torralba, A., & Oliva, A. (2014). What makes a photograph memorable? *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 36(7), 1469–1482. <https://doi.org/10.1109/TPAMI.2013.200>
- JASP Team (2022). JASP (0.16.2). <https://jasp-stats.org/>.
- Kensinger, E. A. (2009). Remembering the details: Effects of emotion. *Emotion Review*, 1 (2), 99. <https://doi.org/10.1177/1754073908100432>
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007a). Effects of emotion on memory specificity in young and older adults. *The Journal of Gerontology: Series B*, 62(4), P208–P215. <https://doi.org/10.1093/GERONB/62.4.P208>
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007b). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, 56(4), 575–591. <https://doi.org/10.1016/J.JML.2006.05.004>
- Kesner, R. P., Gilbert, P. E., & Barua, L. A. (2002). The role of the hippocampus in memory for the temporal order of a sequence of odors. *Behavioral Neuroscience*, 116 (2), 286–290. <https://doi.org/10.1037/0735-7044.116.2.286>
- Khosla, A., Raju, A. S., Torralba, A., & Oliva, A. (2015). *Understanding and predicting image memorability at a large scale*. <http://memorability.csail.mit.edu>.
- Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3?. 36, 1–235. <https://doi.org/10.1177/03010066070360S101>
- Kramer, M. A., Hebart, M. N., Baker, C. I., & Bainbridge, W. A. (2023). The features underlying the memorability of objects. *Science Advances*, 9(17). <https://doi.org/10.1126/SCIADV.ADD2981>
- Kumaran, D., & Maguire, E. A. (2007). Which computational mechanisms operate in the hippocampus during novelty detection? *Hippocampus*, 17(9), 735–748. <https://doi.org/10.1002/HIPO.20326>
- Larocque, K. F., Smith, M. E., Carr, V. A., Witthoft, N., Grill-Spector, K., & Wagner, A. D. (2013). Global similarity and pattern separation in the human medial temporal lobe predict subsequent memory. *The Journal of Neuroscience*. <https://doi.org/10.1523/JNEUROSCI.4293-12.2013>
- Leal, S. L., Tighe, S., & Yassa, M. A. (2014). Asymmetric effects of emotion on mnemonic interference. *Neurobiology of Learning and Memory*, 111, 41–48. <https://doi.org/10.1016/j.nlm.2014.02.013>
- Leal, S. L., & Yassa, M. A. (2018). Integrating new findings and examining clinical applications of pattern separation. *Nature Neuroscience*, 21(2), 163. <https://doi.org/10.1038/S41593-017-0065-1>
- Li, X., Bainbridge, W. A., & Bakkour, A. (2022). Item memorability has no influence on value-based decisions. *Scientific Reports*, 12(1). <https://doi.org/10.1038/s41598-022-26333-5>
- Loftus, E. F., Loftus, G. R., & Messo, J. (1987). Some facts about "weapon focus". *Law and Human Behavior*. https://psycnet.apa.org/fulltext/1987-18758-001.pdf?auth_toke=n=82d313058cf294d5734d900cea329cac0338216f.
- Mancas, M., & le Meur, O. (2013). Memorability of natural scenes: The role of attention. In *IEEE International conference on image processing*. <https://doi.org/10.1109/ICIP.2013.673804>
- Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Undefined*, 6(2), 114–133. <https://doi.org/10.1177/1745691611400234>
- MATLAB. (2010). version 7.10.0 (R2010a) (7.10.0). The MathWorks Inc.
- McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, 27, 1–28. <https://doi.org/10.1146/annurev.neuro.27.070203.144157>
- McGaugh, J. L. (2013). Making lasting memories: Remembering the significant. *Proceedings of the National Academy of Sciences of the United States of America*, 110 (SUPPL2), 10402–10407. <https://doi.org/10.1073/pnas.1301209110>
- Milner, B., Squire, L. R., & Kandel, E. R. (1998). Cognitive neuroscience and the study of memory. *Neuron*, 20(3), 445–468. [https://doi.org/10.1016/S0896-6273\(00\)80987-3](https://doi.org/10.1016/S0896-6273(00)80987-3)
- Needell, C. D., & Bainbridge, W. A. (2022). Embracing new techniques in deep learning for estimating image memorability. *Computational Brain & Behavior*, 5(2), 168–184. <https://doi.org/10.1007/s42113-022-00126-5>
- O'Shea, K., & Nash, R. (2015). *An introduction to convolutional neural networks*.
- Oliva, A., & Isola, P. (2012). Image memorability differences are stable over time delay. *Journal of Vision*, 12(9), Article 1097. <https://doi.org/10.1167/12.9.1097>
- Payne, J. D., Stickgold, R., Swanberg, K., & Kensinger, E. A. (2008). Sleep preferentially enhances memory for emotional components of scenes. *Psychological Science*, 19(8), 781. <https://doi.org/10.1111/J.1467-9280.2008.02157.X>
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442. <https://doi.org/10.1163/156856897X00366>
- Qasim, S. E., Mohan, U. R., Stein, J. M., & Jacobs, J. (2023). Neuronal activity in the human amygdala and hippocampus enhances emotional memory encoding. *Nature Human Behaviour*, 2023, 1–11. <https://doi.org/10.1038/s41562-022-01502-8>
- Rowe, G., Hirsh, J. B., & Anderson, A. K. (2006). *Positive affect increases the breadth of attentional selection*. doi: 10.1073pnas.0605198104.
- Ruett, E., Mustaca, A., & Bentosela, M. (2008). Memoria emocional: Efectos de la corticosterona sobre los recuerdos. *Revista Latinoamericana de Psicología*, 40, 461–474.
- Rust, N. C., & Jannuzzi, B. G. L. (2022). Identifying objects and remembering images: Insights from deep neural networks. *Current Directions in Psychological Science*, 31(4), 316–323. [https://doi.org/10.1177_09637214221083663-FIG2.JPG](https://doi.org/10.1177/09637214221083663/ASSET/IMAGES/LARGE/10.1177_09637214221083663-FIG2.JPG)
- Rust, N. C., & Mehrpour, V. (2020). Understanding image memorability. In *Trends in cognitive sciences* (pp. 557–568). Elsevier Ltd.. <https://doi.org/10.1016/j.tics.2020.04.001>
- Stark, S. M., Yassa, M. A., Lacy, J. W., & Stark, C. E. L. (2013). *A task to assess behavioral pattern separation (BPS) in humans: Data from healthy aging and mild cognitive impairment*. doi: 10.1016/j.neuropsychologia.2012.12.014.
- Treves, A., & Rolls, E. T. (1994). Computational analysis of the role of the hippocampus in memory. *Hippocampus*, 4(3), 374–391. <https://doi.org/10.1002/HIPO.450040319>
- Unkelbach, C., Fiedler, K., Bayer, M., Stegmüller, M., & Danner, D. (2008). Why positive information is processed faster: The density hypothesis. *Journal of Personality and Social Psychology*, 95(1), 36–49. <https://doi.org/10.1037/0022-3514.95.1.36>
- Verde, M. F., Stone, L. K., Hatch, H. S., & Schnall, S. (2010). Distinguishing between attributional and mnemonic sources of familiarity: The case of positive emotion bias. *Memory and Cognition*, 38(2), 142–153. <https://doi.org/10.3758/MC.38.2.142>
- Wakeland-Hart, C. D., Cao, S. A., deBettencourt, M. T., Bainbridge, W. A., & Rosenberg, M. D. (2022). Predicting visual memory across images and within individuals. *Cognition*, 227, Article 105201. <https://doi.org/10.1016/j.COGNITION.2022.105201>
- Waring, J. D., & Kensinger, E. A. (2009). Effects of emotional valence and arousal upon memory trade-offs with aging. *Psychology and Aging*, 24(2), 412–422. <https://doi.org/10.1037/a0015526>
- Williams, S. E., Ford, J. H., & Kensinger, E. A. (2022). The power of negative and positive episodic memories. *Cognitive, Affective, & Behavioral Neuroscience*, 2022(1), 1–35. <https://doi.org/10.3758/S13415-022-01013-Z>
- Yassa, M. A., & Stark, C. E. L. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, 34(10), 515–525. <https://doi.org/10.1016/j.tins.2011.06.006>
- Zhao, C., Fukuda, K., Park, S., & Woodman, G. F. (2022). Even affective changes induced by the global health crisis are insufficient to perturb the hyper-stability of visual long-term memory significance statement. *Cognitive Research: Principles and Implications*, 7–62. <https://doi.org/10.1186/s41235-022-00417-2>
- Zlotnik, G., & Vansintjan, A. (2019). Memory: An extended definition. *Frontiers in Psychology*, 10. <https://doi.org/10.3389/fpsyg.2019.02523>