

Memorability: A stimulus-driven perceptual neural signature distinctive from memory



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ABSTRACT

A long-standing question in neuroscience is how perceptual processes select stimuli for encoding and later retrieval by memory processes. Using a functional magnetic resonance imaging study with human participants, we report the discovery of a global, stimulus-driven processing stream that we call *memorability*. Memorability automatically tags the statistical distinctiveness of stimuli for later encoding, and shows separate neural signatures from both low-level perception (memorability shows no signal in early visual cortex) and classical subsequent memory based on individual memory. Memorability and individual subsequent memory show dissociable neural substrates: first, memorability effects consistently emerge in the medial temporal lobe (MTL), whereas individual subsequent memory effects emerge in the prefrontal cortex (PFC). Second, memorability effects remain consistent even in the absence of memory (i.e., for forgotten images). Third, the MTL shows higher correlations with memorability-based patterns, while the PFC shows higher correlations with individual memory voxels patterns. Taken together, these results support a reformulated framework of the interplay between perception and memory, with the MTL determining stimulus statistics and distinctiveness to support later memory encoding, and the PFC comparing stimuli to specific individual memories. As stimulus memorability is a confound present in many previous memory studies, these findings should stimulate a revisit of the neural streams dedicated to perception and memory.

Introduction

While visual perception and memory are classically supported by functionally distinct cortical circuits (visual perception: Kanwisher and Dilks, 2013; memory: Wixted and Squire, 2011), the transitional steps from perception to memory remain under debate. Memory is thought of as a function of an individual observer, yet there are many consistencies across people in memory performance based on the stimulus (Bainbridge et al., 2013; Isola et al., 2011b). Could the brain be sensitive to a high-level perceptual stimulus property that guides memory encoding?

This question touches upon the concept of *memorability* – an intrinsic, perceptual stimulus property correlated with the likelihood of an image being later remembered or forgotten. Behavioral and computational work finds that memorability is a highly consistent statistical property of visual information, regardless of the observer (Bainbridge et al., 2013; Isola et al., 2011b), and can be computationally predicted (Khosla et al., 2015, 2013). Memorability, like many

image properties (e.g., aesthetics, emotional content (Datta et al., 2008)), remains robust over different time lags (Isola et al., 2013) and viewing contexts (Bylinskii et al., 2015), and can be consistently measured in differing visual stimulus sets such as faces (Bainbridge, in press; Bainbridge et al., 2013), scenes (Isola et al., 2011b), and graphs and infographics (Borkin et al., 2013). A corpus of behavioral results has also shown that memorability can be isolated from other stimulus properties known to affect perception and memory. For instance, Isola et al. (2013, 2014) show that properties such as aesthetics, emotionality, subjective judgments of memorability, and low-level visual features are uncorrelated with scene memorability (Isola et al., 2013). Bainbridge et al. (2013) tested a comprehensive set of twenty face attributes to find that these attributes explained less than half of the variance in face memorability. Importantly, memorability is also found to be distinct from other cognitive processes known to influence memory behavior, and is dissociable from bottom-up attention, top-down attention, and priming effects (Bainbridge, in preparation). Memorability is thus particularly unique in that it serves as a

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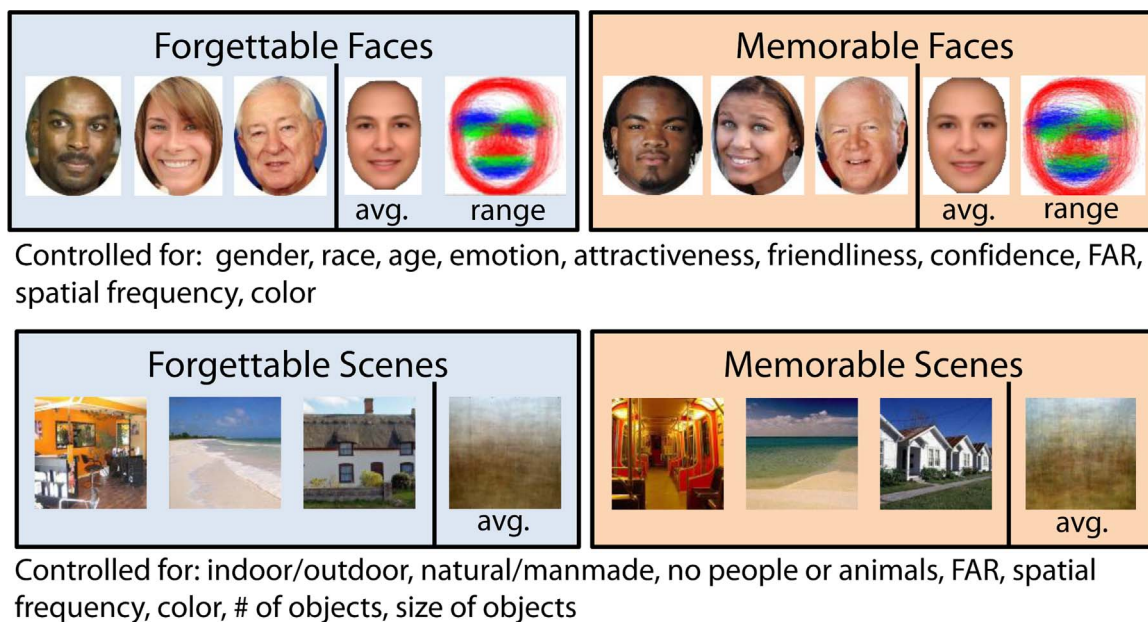


Fig. 1. Example stimuli used in the study, varying along two factors: 1) memorability (forgettable/memorable), and 2) stimulus type (face/scene). The stimuli were controlled for several low-level (e.g., color, spatial frequency) and high-level properties (e.g., emotion, attractiveness) that could be potentially confounded with memorability. Note that while it is not visually obvious which images would be memorable or forgettable, these images still result in very different memory behavior. The “avg.” images show the average face and scene image within each condition. Faces were averaged using Active Appearance Model averaging (Cootes et al., 2001) while scenes were average based on average color at each pixel. The “range” for the faces shows the outlines of the facial features (e.g., eyes, nose, lips) for each stimulus. As one can see, between memorable and forgettable images, the averages are extremely similar and in fact show no significant differences. The face images shown here were not used in the actual study but are visually similar example images at opposite ends of memorability, from the public domain and available for publication. The average and range are determined from the stimuli used in the study.

consistent, measurable, and predictable signature of the encoding of a visual stimulus.

Memorability may thus help pinpoint high-level perceptual processing that precedes memory encoding. One particularly interesting candidate region for memorability is the medial temporal lobe (MTL), here defined as the set of structures encompassing the hippocampus, perirhinal cortex, entorhinal cortex, amygdala, and parahippocampal cortex. It is still debated whether the MTL is a memory-based region sensitive to novelty and familiarity (Brown and Aggleton, 1991; Daselaar et al., 2006; Desimone, 1996; Eichenbaum et al., 2007; Kim, 2011; Kumaran and Maguire, 2009; Rissman et al., 2010), or a high-level perceptual region for object discrimination and identification (Buckley and Gaffan, 1998; Cate and Köhler, 2006; Devlin and Price, 2007; Olarte-Sánchez et al., 2015). Several individual subsequent memory studies identify two main regions – the MTL and the prefrontal cortex (PFC) – that show higher activation for stimuli that are later remembered than those that are forgotten by an individual participant (Brewer et al., 1998; Wagner et al., 1998). However, the PFC shows the strongest effects of subsequent individual memory (Kim, 2011) and has been proposed to be a locus of familiarity separate from the MTL (Kafkas and Montaldi, 2014).

Given that memorable images are more likely to be remembered by individuals, most behavioral and neuroimaging studies may have confounded some effects attributed to individual subsequent memory (based on neural comparisons with previous individual experiences) with stimulus-driven memorability (based on statistical properties of a stimulus). In fact, behavioral work has identified that these are two separate factors that influence later memory behavior; stimulus memorability determines ultimate memory behavior as much as all other factors combined, including individual experience and environmental factors (Bainbridge et al., 2013). Here, we demonstrate that stimulus-driven memorability effects can be neurally disentangled from individual subsequent memory effects: the MTL appears to be involved with a rapid processing stream sensitive to a normative perceptual marker of memory (memorability), while the PFC appears to be involved in processing individual memory.

Using rapid event-related functional magnetic resonance imaging (fMRI) in a perceptual task with stimuli of predetermined memorability, we discover the human neural substrates of memorability, for both face and scene stimuli. First, we find clear sensitivity to memorability along the ventral visual stream (VVS) and the MTL for both face and scene categories, while no sensitivity exists in early visual cortex (EVC). This sensitivity to memorability is found to exist even in the absence of memory (i.e., for forgotten images). Lastly, we discover a double dissociation between stimulus memorability (in the MTL) and individual memory (in the PFC) in both univariate and multivariate measures. Taken together, these results point to a specialized neural stream that calculates stimulus-driven signatures of what people ultimately remember, at the speeds of perception.

Materials and methods

Participants

Eighteen adults (eight female, average age of 25.9 years) participated in the main event-related experiment. Seventeen separate adults (eight female, average age of 24.8 years) participated in a block-design study (see [Supplementary material, S4](#)), which serves as a replication of the results. Participants were healthy, right-handed, with normal or corrected vision, and US citizens, to reduce out-group effects (Chiroro and Valentine, 1995). They consented following guidelines approved by the MIT Institutional Review Board for fMRI studies and were compensated \$30/h. Two participants in the event-related experiment and one participant in the block-design experiment were excluded from analyses due to an inability to localize any ROIs at our chosen threshold of $p < 0.001$.

Stimuli

720 stimuli were put into four conditions of 180 each – 1) forgettable faces, 2) memorable faces, 3) forgettable scenes, and 4) memorable scenes. Stimuli were selected to be on opposite ends of

memorability, taken from the top and bottom 25% of the distribution of memorability. Example stimuli can be seen in Fig. 1.

The 360 face images were selected from the 10k US Adult Faces Database (Bainbridge et al., 2013), which contains a set of over 2000 faces labeled with memorability scores (hit rate HR and false alarm rate FAR) and various attributes from a large-scale online study with over 800 participants. The selected memorable faces had an average HR of 72.5% (SD=6.7%), while the forgettable faces had an average HR of 32.4% (SD=5.5%), with a significant difference between the two ($t(358) = -62.01$, $p = 1.48 \times 10^{-193}$). Memorability in these stimuli was also significantly consistent across participants (Spearman's rank correlation $\rho = 0.69$), indicating memorability can be used as an intrinsic attribute to these images. The memorable and forgettable groups of faces were equalized on age, race, gender, emotion, emotional magnitude, attractiveness, false alarm rate, and spatial frequency information (all $p > 0.10$).

For the 360 scene stimuli, memorability (HR) was also determined in a previous online memory experiment with 800+ participants (Isola et al., 2011b), and found to be highly consistent across groups of participants (Spearman's rank correlation $\rho = 0.75$). The selected memorable scenes had an average HR of 97.8% (SD=2.1%), while the forgettable scenes had an average HR of 69.0% (SD=7.9%), with a significant difference between the two conditions ($t(358) = -47.34$, $p = 4.73 \times 10^{-155}$). Memorable and forgettable groups of scenes were equalized for color, spatial frequency, number and size of objects, indoor/outdoor, and natural/manmade (all $p > 0.10$). Memorable and forgettable stimuli were selected to have equally small false alarm rates (FAR), to prevent effects of false memories.

fMRI in-scanner task

Participants viewed each novel face and scene stimulus *only once*, in a rapid event-related design, with conditions randomly interspersed with null fixation trials. For each stimulus, participants performed an orthogonal picture categorization task (male/female for faces, and indoor/outdoor for scenes). Response button mappings were counter-balanced across participants. Participants were unaware of any memory-related nature of the study and saw each image only a single time. Each image was presented for 1.2 s, with 1.8 s rest. Each run had 30 images per condition and 30 null trials, and each run ended in a 10 s rest period. The experiment had six runs, each lasting 7.1 min. A control fMRI experiment with the same stimulus set and task was also run using a block-design paradigm (see [Supplementary material, S4](#)).

Post-scan memory task

Participants completed an unexpected memory test after the fMRI task, outside the scanner. They saw randomly ordered face and scene images and indicated whether they had seen each image before or not. We used a binary-choice memory test (old/new) instead of a remember/know/new memory test, as the current study was not aiming to examine the role of familiarity (i.e., “know” judgements), and the false alarm rates between the stimulus conditions were equated to reduce differences in familiarity. Pilot data (N=14) testing memory using remember/know/new judgments on a subset of these images found that indeed, while memorable images received more “remember” judgments ($t(13) = 7.06$, $p = 8.57 \times 10^{-6}$) and fewer “new” judgments ($t(13) = 2.38$, $p = 0.03$) than forgettable images, there was no significant difference in “know” judgments between memorable and forgettable stimuli ($t(13) = 2.08$, $p = 0.06$). While image presentation was timed (1 s each), participant responses were self-paced. Participants were instructed to respond as accurately and as quickly as possible, and that their reaction times would be recorded. All 720 images from the in-scanner task were shown, in addition to 720 foil images taken from the center of the HR distribution. For faces, there were no differences between the target and foil images in gender, race distribution, FAR,

spatial frequency information, or higher-level attributes (attractiveness, emotion, etc). For scenes, there were no differences in indoor/outdoor, manmade/natural, spatial frequency information, or color statistics. The memory test took 40 min and participants were allowed breaks at every ¼ point through the test.

Functional localizers and regions of interest (ROIs)

Several visual, perceptual, and memory-related ROIs were localized in this study, using functional and anatomical ROIs, defined independently from the data in the main experiment. A 7.1 min functional localizer with an independent set of images was used to localize the fusiform face area (FFA; Kanwisher et al., 1997), occipital face area (OFA; Pitcher et al., 2011), parahippocampal place area (PPA; Epstein and Kanwisher, 1998), retrosplenial cortex (RSC), occipital place area (OPA; Dilks et al., 2013) and lateral occipital complex (LOC; Grill-Spector et al., 1999). A separate, 4.2 min meridian retinotopy mapping scan was used to locate early visual cortex (EVC) for each subject (Sereni et al., 1995). Anatomical ROIs were manually segmented based on currently accepted landmarks for segmentation (Insausti et al., 1998; Pruessner et al., 2002) in the MTL: the perirhinal cortex (PRC), entorhinal cortex (ERC), parahippocampal cortex (PHC), amygdala (Amg), and the hippocampus (Hipp) head, body, and tail. Additionally, a memory-based left prefrontal cortex region (LPFC) was defined for each participant based on overlap of the participant's individual grey matter map and a spherical anatomical ROI centered at Talairach coordinate (−48, 8, 30), taken from a review of subsequent memory literature and identified as one of the most consistent regions in subsequent memory findings (Kim, 2011). A spherical anatomical ROI was also defined at the intraparietal sulcus (IPS), identified as a region for memory and attention (Corbetta and Shulman, 2002), but ultimately no significant results were found for memorability nor individual subsequent memory, so it is not reported here.

MRI acquisition and preprocessing

Both experiments were conducted at the Athinoula A. Martinos Imaging Center at the MIT McGovern Institute, using a 3T Siemens Trio scanner with a 32-channel phased-array head coil. Anatomical scans used a high-resolution (1×1×1 mm voxels) T1 MPRAGE structural scan, and functional scans used a gradient echo-planar T2* sequence (33 axial slices parallel to the anterior commissure-posterior commissure line; 64×64 matrix; FoV=256×256 mm; TR=2000 ms; TE=30 ms; no gap; flip angle=90 degrees; 3.1×3.1×3.1 mm voxels). The scans were preprocessed using BrainVoyager QX 2.8 (<http://www.brainvoyager.com/>; Formisano et al., 2006), including slice time correction, linear trend removal, trilinear motion correction, 1/128 Hz temporal high pass filtering, and white-matter-based inhomogeneity correction on the anatomical scans. For the univariate analyses, the voxels were spatially smoothed using a 4mm full-width half-maximum kernel. Multivariate analyses used unsmoothed data. Functional data were aligned to the anatomical scans, and were normalized into the Talairach coordinate space.

Univariate analyses

Group whole-brain univariate analyses were carried out using a general linear model (GLM) with regressors for each of the four conditions, and the betas were z-transformed. These whole-brain analyses were conducted to look at generally where memorability sensitivity emerged in the brain. Specific GLMs were also applied separately within independently localized ROIs (see [Functional localizers and regions of interest \(ROIs\)](#)) to obtain beta estimates of the response of each region to the different conditions, to test specific ROI-based hypotheses. Analyses were also conducted with the stimuli regrouped into eight conditions (combinations of the three factors of

stimulus type, memorability, and memory test behavior) based on responses on the post-scan memory test, resulting in a GLM with eight regressors. Stimuli where participants responded incorrectly on the in-scanner perceptual task were removed from that participant's GLM to ensure that only perceived stimuli were used in the analyses. Whole-brain maps were corrected for multiple comparisons using cluster-size thresholding at a level of $\alpha=0.05$ (Forman et al., 1995; Goebel et al., 2006). For the ROI analyses, z-transformed beta estimates were determined for each ROI, and 3-way ANOVAs were applied on these to analyze stimulus selectivity within ROIs. Multiple comparison correction was implemented with an adjusted Benjamini-Hochberg (Benjamini and Hochberg, 1995) False Discovery Rate significance level of $\alpha=0.05$, $p=0.0286$. T-tests were additionally conducted to examine memorability or memory for a specific stimulus type. The ANOVAs and t-tests were dependent tests for comparisons of memorability and stimulus type due to balanced condition sizes, but independent samples tests for individual memory due to different numbers of remembered and forgotten stimuli.

To compare contrast overlap, the results of the GLMs for corresponding contrasts (e.g., memorable versus forgettable images) were plotted for each individual subject on a brain map with a significance threshold of $p < 0.05$. Volume of overlap was calculated based on overlap of shared clusters of over 10 contingent voxels between these contrasts (e.g., memorability contrast versus remembered contrast) for each participant. Percentage overlap was determined by averaging the percentage of the volume of overlap to the volume of the first contrast's set of clusters with the percentage of the volume of overlap to the volume of the second contrast's set of clusters. The conservative thresholds of $p < 0.05$ and 10 voxels were used to maximize any potential overlap.

Representational similarity analyses

Representational similarity analyses (RSAs) were conducted across the brain and compared to hypothesized model representational similarity matrices (RSMs), to see which regions of the brain showed significant representational geometries of memorability or subsequent memory, and if regions were more correlated with one process versus the other. RSAs allow one to examine the representational geometry of the neural patterns within a region (Kriegeskorte et al., 2008), and they easily accommodate for conditions with uneven numbers of stimuli, unlike classification-based multivariate analyses.

A depiction of the RSA used in this study can be seen in Fig. 2. A spherical searchlight of 7mm diameter was moved across each participant's brain, and from each searchlight the voxel patterns (beta values) for each stimulus were extracted. A *Data RSM* was constructed based on Pearson correlations of the beta values for each stimulus within that searchlight, between all stimulus pairs. This participant *Data RSM* was then correlated with a hypothesized memorability-based *Model RSM* using a Spearman's rank correlation. All combinations of memorability-based hypothesis models were tested, assigning high similarity (1), medium similarity (0.5), or low similarity (0) to different combinations of stimulus condition pairs¹, and the model most correlated with patterns in the brain was selected for the searchlight analysis. The ultimate hypothesized *Model RSM* was defined with high similarity between memorable-memorable image pairs (assigned a value of 1), moderate similarity between memorable-forgettable image pairs (assigned a value of 0.5), and low similarity between forgettable-forgettable image pairs (assigned a value of 0). Additionally, the *Data RSM* was also correlated with the same hypothesis *Model RSM* instead formed based on that individual participant's memory behavior rather than the memorability of the stimuli. These correlations resulted in a

¹ As these models were correlated using Spearman's rank correlations, the rankings of the values, rather than the actual values, are most relevant.

memorability-correlated whole-brain ρ -map and an individual subsequent memory-correlated whole-brain ρ -map for each participant (based around the same hypothesized representational geometry). A group ρ -map was then generated pitting memorability against individual subsequent memory, using signed-rank tests at each voxel of the ρ -maps of the sixteen participants for memorability versus their ρ -maps for individual memory. This map was then corrected for multiple comparisons using cluster-size thresholding at a level of $\alpha=0.05$ (Forman et al., 1995; Goebel et al., 2006).

Results

Behavioral results

Participants had high performance with the orthogonal in-scanner task (categorizing male/female for faces and indoor/outdoor for scenes), with an average performance of 93.1% and no significant difference between memorable and forgettable conditions in performance (faces: $t(15)=0.17$, $p=0.869$; scenes: $t(15)=0.77$, $p=0.452$) nor reaction time (faces: $t(15)=0.73$, $p=0.478$; scenes: $t(15)=0.574$, $p=0.575$), thus ensuring any brain differences we see are not due to behavioral differences with the task. For the subsequent post-scan memory test, as expected, participants significantly remembered memorable images more than forgettable images (faces: $t(15)=8.89$, $p=2.29 \times 10^{-7}$; scenes: $t(15)=6.19$, $p=1.72 \times 10^{-5}$), see [Supplementary material S1](#). For faces, the HR for forgettable images was not significantly different from the FAR for medium memorability foil images ($t(15)=1.45$, $p=0.167$), however it was for scenes ($t(15)=4.30$, $p=6.26 \times 10^{-4}$). On average, participants remembered 23.5% of forgettable faces, 44.8% of memorable faces, 27.1% of forgettable scenes, and 41.6% of memorable scenes. These levels of performance match those of other implicit image-based memory studies (Brewer et al., 1998), and are likely due to the implicit encoding task and the fact that the subsequent memory test may introduce a tendency to label items as “new” as the stimuli consist of 50% new images and 25% forgettable images. These levels of performance also allow us to separate memorability and subsequent memory – as both effects are correlated, but there are also trials where participants forget memorable images and remember forgettable ones, thus allowing us to search for a memorability effect in the absence of memory. Similar performance patterns were also seen in the replication block design study ([Supplementary material, S4-1](#)).

Memorability effect in ventral visual and medial temporal regions

The first important step is to see if sensitivity to memorability exists anywhere in the brain. Grouped whole-brain random-effects GLM contrasts of memorable versus forgettable images (Fig. 3) revealed a significant effect of memorability in the VVS, PRC, Amg, PHC, and Hipp. Region of interest-based (ROI) analyses, using a 2-way repeated-measures ANOVA (stimulus type: face, scene \times memorability: memorable, forgettable) on the z-transformed betas in independently localized ROIs confirm these results (Fig. 4). A significant main effect of memorability (with an FDR-corrected significance cutoff of $p < 0.028$) was found in several perceptual regions in the VVS: the FFA ($F(1,15)=34.39$, $p=3.11 \times 10^{-5}$), the OFA ($F(1,15)=35.01$, $p=2.83 \times 10^{-5}$), and the LOC ($F(1,15)=32.40$, $p=4.27 \times 10^{-5}$). As expected, we also found a significant main effect of stimulus type in several VVS regions (FFA: $F(1,15)=61.28$, $p=1.12 \times 10^{-6}$; OFA: $F(1,15)=51.24$, $p=3.29 \times 10^{-6}$; PPA: $F(1,15)=67.44$, $p=6.23 \times 10^{-7}$; RSC: $F(1,15)=53.97$, $p=3.64 \times 10^{-6}$; OPA: $F(1,15)=47.24$, $p=1.13 \times 10^{-5}$). However, no significant stimulus type by memorability interaction was found in any VVS regions (all $p > 0.10$), revealing that while category-selective regions still show category selectivity (e.g., the FFA for faces), their sensitivity to memorability is not modulated by category type. No significant main effect of memorability or stimulus type by memor-

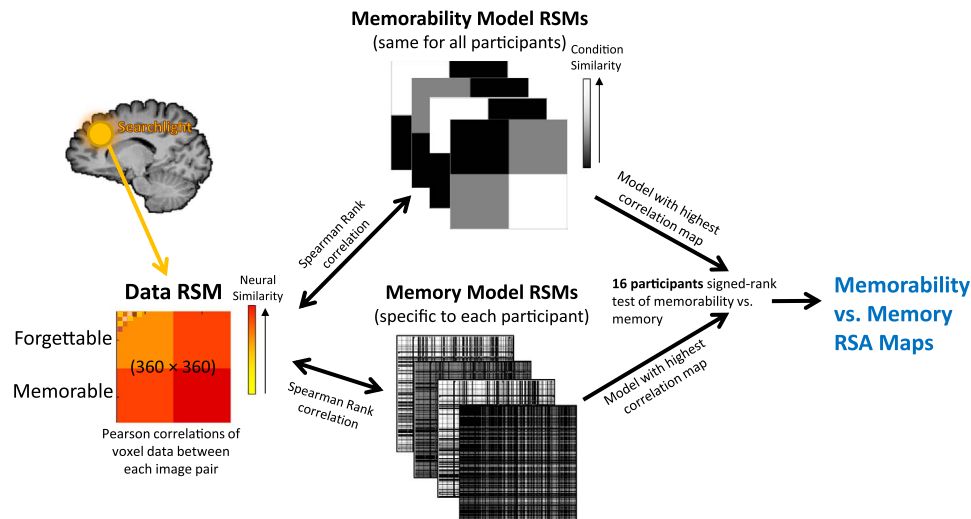


Fig. 2. The steps taken for the representational similarity analysis (RSA) searchlight in the current work. Essentially, beta values were extracted from a spherical searchlight and a representational similarity matrix (RSM) was constructed from pairwise correlations of the beta values for each pair of images. This RSM was then correlated separately with model RSMs constructed from hypothesized similarity structure based on memorability-based conditions (e.g., memorable images will be more similar than forgettable images) and models based on participant-specific memory conditions (e.g., images an individual remembered will be more similar than those they forgot). Correlations of the brain data with the two models were then compared using signed-rank tests, resulting in a map that shows regions more significantly correlated with memorability-based representations than individual memory-based representations and vice versa.

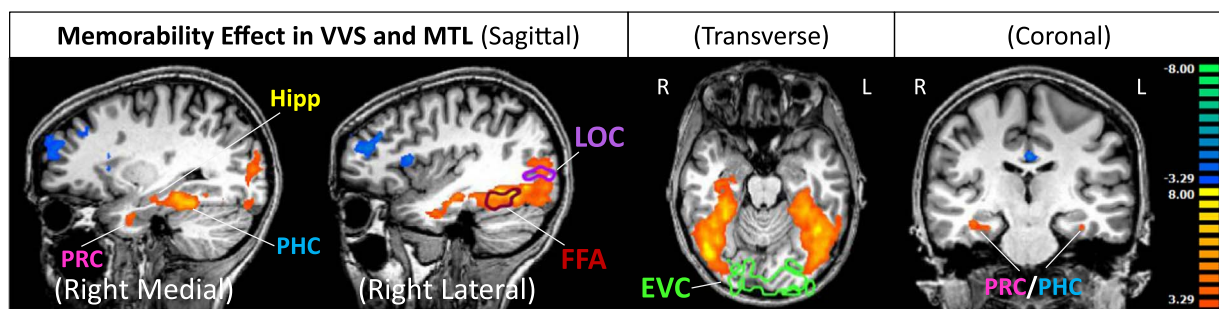


Fig. 3. Grouped ($N=16$) whole-brain results (t-statistic) of a random-effects univariate contrast of viewing memorable (red) versus forgettable (blue) images ($p < 0.005$, cluster-threshold corrected), displayed on a representative brain. Outlines of representative ROIs based on independent functional localizers (FFA, LOC, EVC) and anatomical segmentation (PRC, Hipp, PHC) are shown. A significant effect of memorability is found along the VVS to the MTL, with significant activation overlapping with regions including the FFA, LOC, Hipp, PRC, and PHC. However, no overlap is found with the EVC, suggesting these results are not due to low-level visual differences in the stimuli.

ability interaction was found in the scene-selective PPA, RSC, or OPA (all $p > 0.20$). The same significant regions for memorability emerge even when reaction time in the post-scan memory test (as a proxy for memory confidence) is regressed out in the GLM (Supplementary material, S2).

Additionally, a significant main effect of memorability was found in several regions in the MTL: the PRC ($F(1,15)=20.25$, $p=4.20 \times 10^{-4}$), the ERC ($F(1,15)=6.15$, $p=0.025$), the Amg ($F(1,15)=8.82$, $p=0.01$), the Hipp head ($F(1,15)=13.84$, $p=0.002$), and the PHC ($F(1,15)=12.13$, $p=0.003$). No significant main effect of memorability was found in the Hipp body ($F(1,15)=3.80$, $p=0.070$) or tail ($F(1,15)=1.05$, $p=0.321$). Finally, no significant stimulus type by memorability interactions were found in any MTL regions (all $p > 0.20$), indicating that these regions, like those in the VVS, exhibit content-general memorability. Notably, we found no significant main effect of memorability ($F(1,15)=1.38$, $p=0.258$) or stimulus type by memorability interaction ($F(1,15)=0.19$, $p=0.666$) in EVC, suggesting that the memorability differences found in VVS and MTL regions could not be explained by low-level visual differences. Finally, no significant effect of memorability emerged in the LPFC memory region ($F(1,15)=0.36$, $p=0.560$) defined based on the coordinates (see Functional localizers and regions of interest (ROIs)) for one of the most widely recognized regions for memory encoding effects (Kim, 2011).

To assess the replicability and generalizability of these effects, we ran a block-design fMRI experiment with identical stimuli and task, but

a separate pool of participants (Supplementary material, S4). VVS regions (OFA, FFA, LOC) and MTL regions (PRC, Amg, PHC) again showed a significant memorability effect, while EVC and LPFC did not.

Individual subsequent memory effects in the parahippocampal cortex and frontal regions

How do these candidate memorability ROIs respond to a more traditional individual-based subsequent memory contrast?

To address this question, we examined individual subsequent memory-related effects with a 2-way ANOVA ROI analysis (stimulus type: face, scene; memory: remembered, forgotten; see Fig. 4, results from a 3-way ANOVA ROI analysis of stimulus type \times memorability \times memory can be seen in Supplementary material S3). While memorability was determined *a priori* as a global measure of memory for a stimulus, individual subsequent memory was determined based on which images an individual remembered or forgot in the post-scan task. Significant individual memory effects were found in VVS regions similar to memorability: the FFA ($F(1,15)=6.60$, $p=0.021$) and the OFA ($F(1,15)=6.38$, $p=0.023$), but not the PPA, RSC, OPA, or LOC (all $p > 0.028$). No effect of individual subsequent memory was found in EVC ($F(1,15)=0.036$, $p=0.851$), indicating individual subsequent memory is not driven by low-level visual features. For individual memory effects within the MTL, the only significant main effect was found in the PHC ($F(1,15)=11.77$, $p=0.004$), with a significant interaction with stimulus

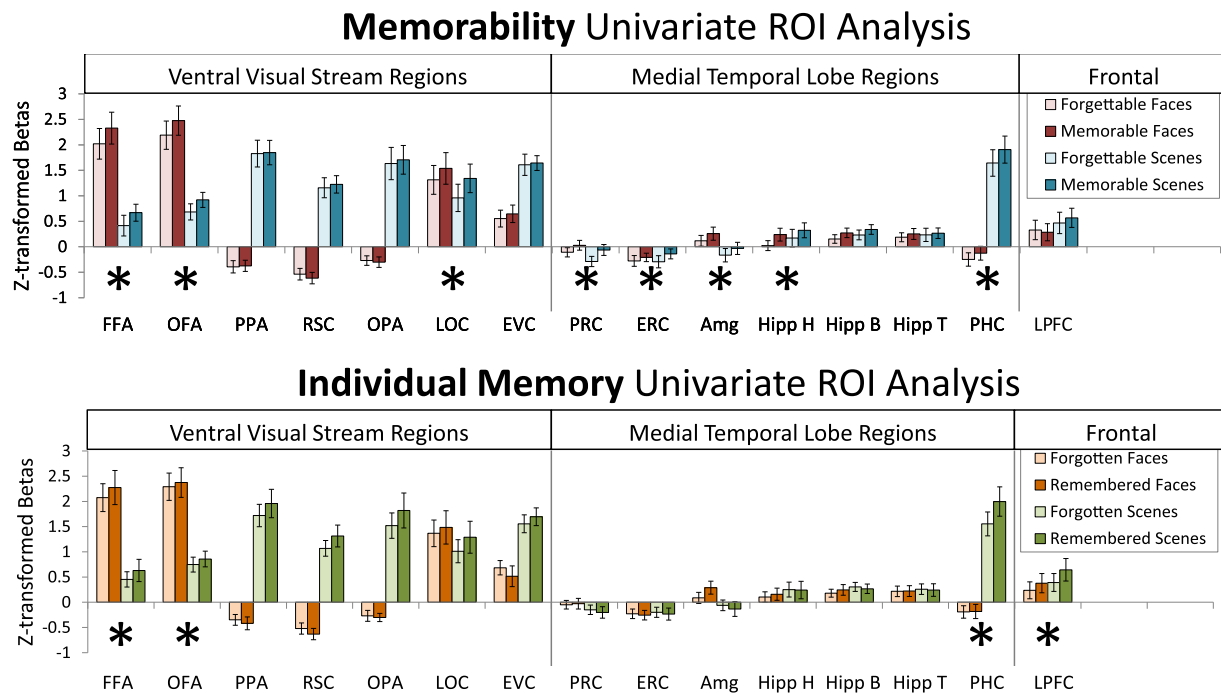


Fig. 4. (Above) Average z-transformed betas in ROIs for conditions grouped by memorability and stimulus type. Asterisks indicate a significant main effect of memorability in a 2-way ANOVA (memorability, stimulus type), at a corrected FDR level of $p < 0.0286$ ($\alpha=0.05$). Several regions within the VVS and MTL show a memorability effect: the FFA, OFA, LOC, PRC, ERC, Amg, Hipp H, and PHC. Notably, the EVC and LPFC memory region do not show memorability effects. (Below) Average z-transformed betas in ROIs for conditions grouped by individual memory and stimulus type. Asterisks indicate a significant main effect of individual memory in a 2-way ANOVA (individual memory, stimulus type), at a corrected FDR level of $p < 0.0286$ ($\alpha=0.05$). Like with memorability, individual memorability effects emerge in FFA, OFA, and PHC. However, no other MTL regions emerge, and there is an effect found in LPFC.

type ($F(1,15)=11.89$, $p=0.004$), showing content-specific memory for scenes only (post-hoc t-test: $t(15)=4.00$, $p=0.001$). No significant effect was found in the PRC, Amg, ERC, or Hipp. A significant individual subsequent memory effect was also found in the LPFC region ($F(1,15)=5.94$, $p=0.028$), with no significant interaction with stimulus type ($F(1,15)=0.64$, $p=0.435$), replicating the results of other individual subsequent memory studies (Kim, 2011).

Taken together, these results show that individual memory effects may be concentrated in the PHC and LPFC, rather than more anterior MTL regions, like memorability.

Significant memorability effect in the absence of memory (and vice versa)

Both memorability and individual memory show effects in subregions of the VVS and the PHC, however memorability also shows effects in the anterior MTL (e.g., PRC, Hipp H), while individual subsequent memory shows effects in frontal regions (e.g., LPFC). To what degree are these two processes separable, and do they have different regional loci?

To address this question, we conducted a 3-way (stimulus type: face, scene; memorability: memorable, forgettable; memory: remembered, forgotten; all modeled as fixed effects) repeated measures ANOVA whole-brain analysis, thresholded at $p < 0.001$ (Fig. 5). A main effect of memorability was found in the MTL, or specifically the PHC, PRC, Amg, and Hipp, while a main effect of individual subsequent memory was found in the PHC and frontal regions. Crucially, we found a significant memorability by subsequent memory interaction in the PRC, showing an effect of memorability but no effect of individual subsequent memory, and an interaction in the LPFC, showing an effect of individual subsequent memory but no memorability.

Indeed, a cluster overlap analysis (see [Univariate analyses](#)) reveals that there is only an average 2.41% overlap of voxels for memorability and individual subsequent memory contrasts. One can also specifically

probe this memorability/memory dissociation by examining the fringe cases: What happens to memorable images that are forgotten? While participants significantly remembered memorable images over forgettable ones, examining the cases where memorable images were forgotten can demonstrate whether individual differences account fully for differences in memorable versus remembered images. If memorability and memory encoding share a similar mechanism, then no significant clusters should appear with a contrast of memorable versus forgettable images for images that were later forgotten by the participant, as forgotten images would not have specialized processing based on memorability. In contrast, if memorability and memory encoding are indeed dissociable processes, then a similar set of regions to the memorability effect (Figs. 3 and 4) should emerge, even for forgotten images.

Fig. 6 shows a group whole-brain contrast of memorable versus forgettable for forgotten images only, as well as for remembered images only ($N=16$, fixed-effects, cluster threshold corrected at $\alpha=0.05$; note that the GLM accounts for differing numbers of item per condition). Fixed effects analyses were used here because these tests are examining participant-specific effects, and because of the decreased power by splitting the stimuli into smaller conditions. Both contrasts show significant activation for memorability along the VVS and the MTL (encompassing PRC and PHC). ROI analyses with paired t-tests confirm these results; the memorability effect for *forgotten images* was not diminished, as there was still significant activity in the FFA ($t(15)=5.79$, $p=3.60 \times 10^{-5}$), OFA ($t(15)=5.53$, $p=5.75 \times 10^{-5}$), LOC ($t(15)=4.83$, $p=2.20 \times 10^{-4}$), PRC ($t(15)=2.60$, $p=0.020$), Amg ($t(15)=2.27$, $p=0.038$), Hipp head ($t(15)=3.14$, $p=0.007$), Hipp body ($t(15)=2.75$, $p=0.015$), and PHC ($t(15)=3.15$, $p=0.007$). These regions also show a significant effect for memorability when examining *only remembered images*, in identical regions except for the Hipp body (FFA: $t(15)=3.78$, $p=0.002$; OFA: $t(15)=3.93$, $p=0.001$; LOC: $t(15)=4.21$, $p=7.55 \times 10^{-4}$; PRC: $t(15)=3.85$, $p=0.002$; ERC: $t(15)=2.38$, $p=0.031$; Amg: $t(15)=2.22$, $p=0.042$; Hipp head: $t(15)=2.50$,

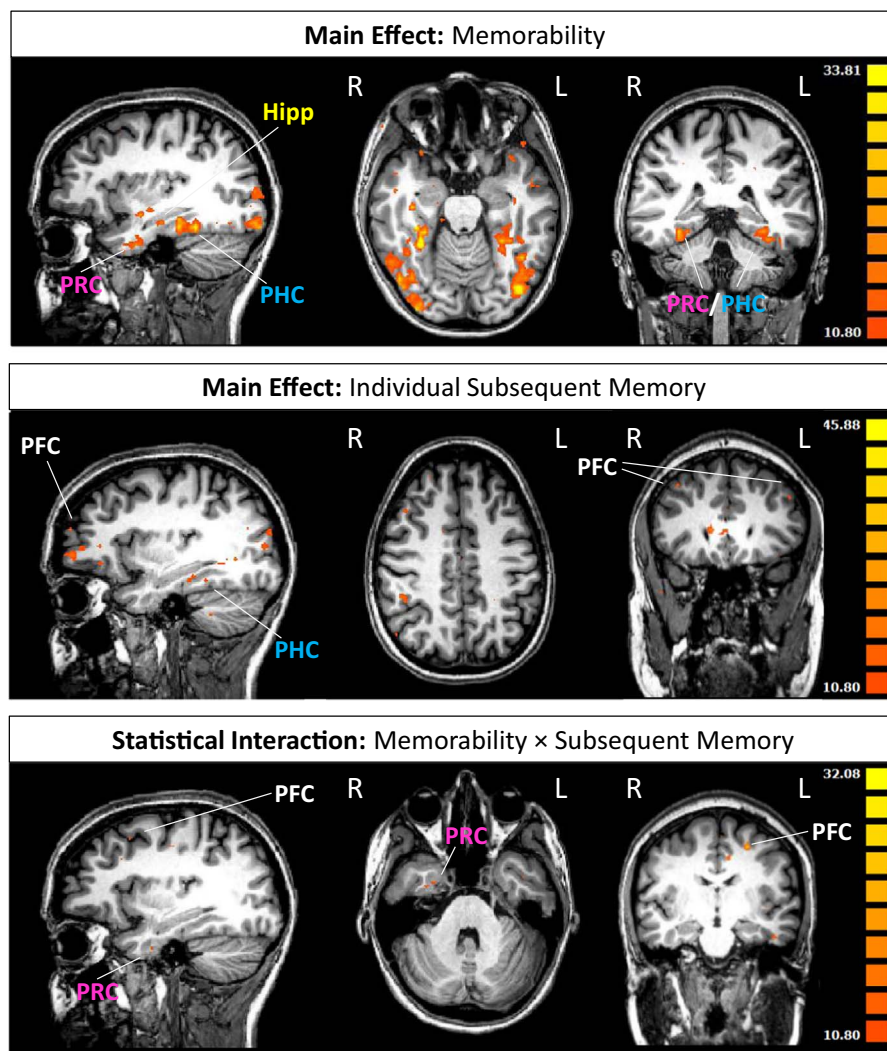


Fig. 5. Results from a group whole-brain 3-way repeated-measures ANOVA, $N=16$. At the top is the main effect of memorability, with activation in the VVS, PRC, PHC, and Hipp. In the middle is the main effect of individual subsequent memory, with activation only in the PHC and frontal regions. At the bottom is the statistical interaction of the two factors, with activation only in the PRC and PFC. All contrasts use a level of $p < 0.005$ uncorrected for illustration purposes, yet both main effects remain at a more stringent $p < 0.001$.

$p=0.024$; PHC: $t(15)=2.43$, $p=0.028$). Both memorability contrasts also continue to show no significant effect in the LPFC (forgotten images: $t(15)=1.47$, $p=0.162$; remembered images: $t(15)=1.18$, $p=0.256$). While there are different numbers of trials per condition (see Behavioral results), we find no significant difference between the number of voxels showing a significant effect for the memorability contrast for remembered images and the contrast for forgotten images ($t(15)=0.19$, $p=0.851$). In sum, these results provide strong evidence that memorability effects are stable, regardless of individual subsequent memory.

An opposite but similar question is whether individual subsequent memory could be handled by the same mechanism as memorability; as memorability is a group-based normative measure of memory, it is possible that individual memory is only a noisier version of memorability. Grouped whole-brain contrasts (Fig. 7; $N=16$, fixed-effects, cluster threshold corrected at $\alpha=0.05$) show significant effects of individual subsequent memory in the PFC (bilaterally), regardless of memorability, in addition to some VVS activation for memorable images only. In an ROI analysis, when contrasting remembered versus forgotten for *only forgettable images* (Fig. 7), significant effects emerge in the PHC ($t(15)=2.33$, $p=0.034$) and LPFC ($t(15)=3.10$, $p=0.007$; no significant effect in the right PFC), but in no other VVS or MTL regions. A contrast of remembered versus forgotten for *memorable images* shows significant activation in the FFA ($t(15)$

$=2.71$, $p=0.016$), OFA ($t(15)=2.91$, $p=0.011$), and PHC ($t(15)=3.28$, $p=0.005$), but no other MTL regions. Interestingly, while the LPFC shows the same trend for the memory contrast with only memorable images (Fig. 7, bottom), the effect is not significant ($t(15)=0.82$, $p=0.423$). It could be possible that if a forgettable image is to be remembered, additional LPFC activation would be needed to compensate for the lack of memorability-based activation; however, this hypothesis will need to be tested in future work.

Overall, these results support a dissociation of memorability and individual subsequent memory, where each effect exists regardless of the other, and the major locus of memorability is in the anterior MTL, while the major locus of individual subsequent memory is in the LPFC.

Dissociation of neural patterns of memorability and individual memory

These results show that several regions of the brain within the VVS and MTL have higher univariate activations for memorable images over forgettable images, and that these regions are separate from those of individual subsequent memory. However, is there a dissociation in the representations of information in these regions? Regions in the MTL and PFC have previously been shown to display neural pattern similarity based on individual subsequent memory (Gordon et al., 2013; LaRocque et al., 2013; Rissman and Wagner, 2012). Are there

Memorable vs. Forgettable, controlled for memory

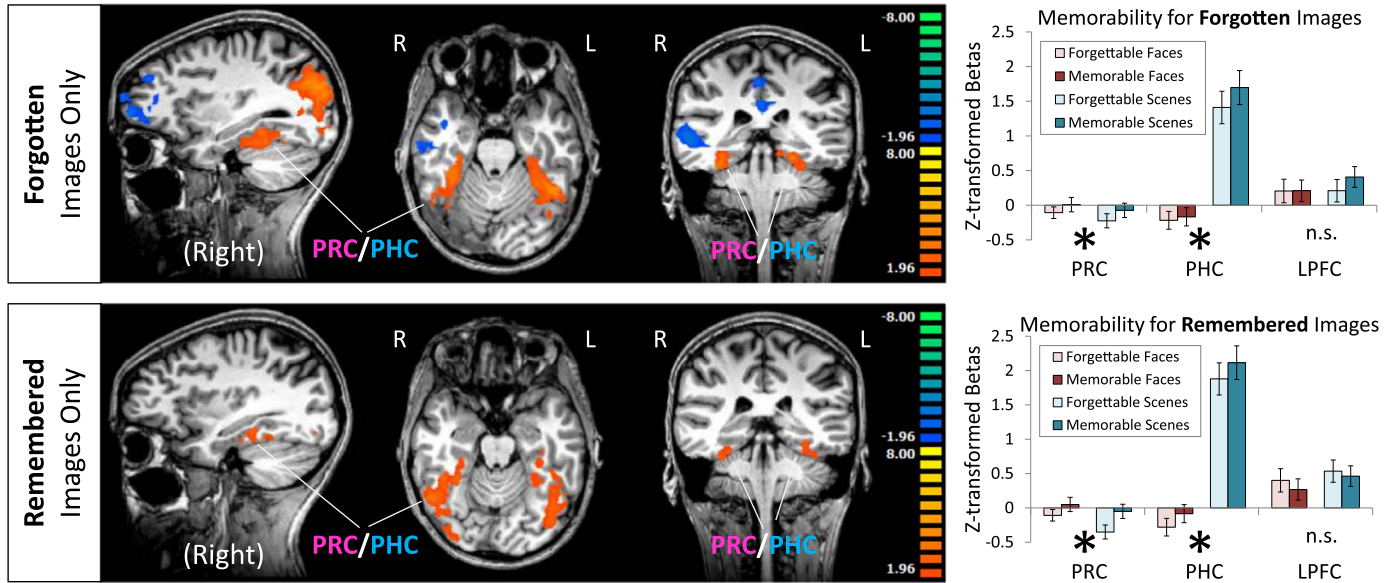


Fig. 6. The effect of memorability (t-map) when holding individual memory constant. At the top is three views of a group whole-brain analysis (N=16, fixed effects, cluster-threshold corrected at $\alpha=0.05$; activation for memorable images in red) and selected ROI analyses when looking at a memorability contrast for forgotten images. Asterisks indicate significance ($p < 0.05$) in a paired t-test for memorable versus forgettable images. At the bottom is a group whole-brain analysis and selected ROI analyses when looking at a memorability contrast for remembered images. Both share areas of activation and significance in the PRC and PHC (but not LPFC), providing evidence that effects of memorability exist independently of individual memory.

also regions in the brain significantly correlated with patterns of memorability, and do these differ from those for individual subsequent memory?

Representational similarity analysis (RSA) can unveil the representational geometry in these patterns throughout the brain, by finding which regions of voxels contain neural patterns correlated with hypothesized models organized based on a memorability-based similarity space or an individual subsequent memory-based similarity space

(Kriegeskorte et al., 2008; Rissman and Wagner, 2012). RSAs for memorability and individual subsequent memory were conducted in whole-brain searchlights and then statistically pitted against each other to find regions that were more correlated with one effect or the other (see [Representational similarity analyses](#)).

This RSA searchlight revealed two different sets of regions for memorability and individual memory (Fig. 8). Regions in the VVS and MTL (including the PRC and PHC) show significantly higher correla-

Remembered vs. Forgettable, controlled for memorability

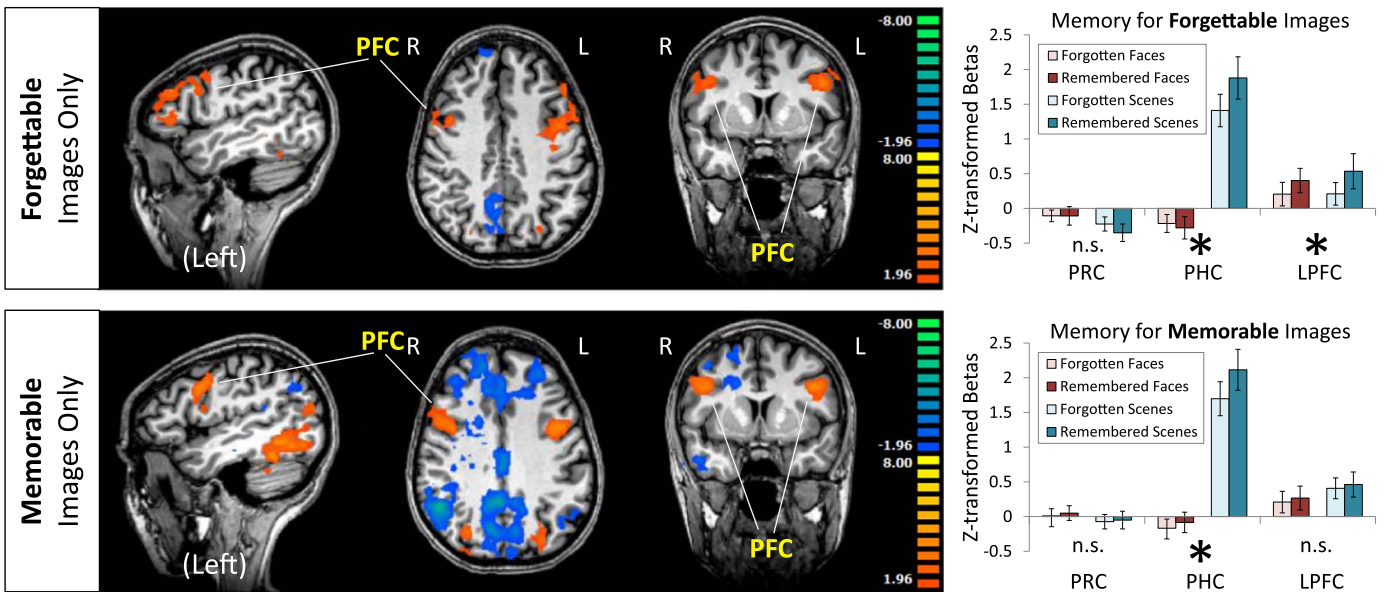


Fig. 7. The effect of individual memory (t-map) when holding memorability constant. At the top is three views of a group whole-brain analysis (N=16, fixed effects, cluster-threshold corrected at $\alpha=0.05$; activation for remembered images in red) and selected ROI analyses when looking at a memory contrast for forgettable images. Asterisks indicate significance ($p < 0.05$) in a paired t-test for remembered versus forgotten images. At the bottom is a group whole-brain analysis and selected ROI analyses when looking at a memory contrast for memorable images. Both share areas of activation and significance in the PHC and LPFC, but not the PRC, providing evidence that effects of individual memory exist independent of memorability.

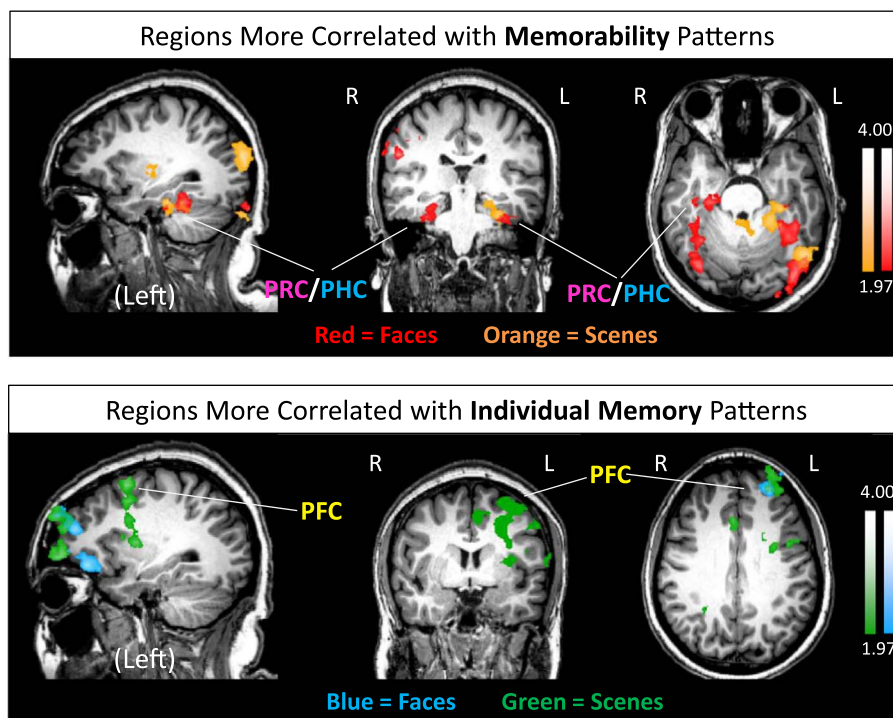


Fig. 8. Multiple views of grouped whole-brain maps of a RSA searchlight showing where neural patterns are significantly more correlated with models of memorability (above; faces in red, scenes in orange) or models of individual memory (below; faces in blue, scenes in green). The scale indicates the test statistic of the signed rank test. The VVS and MTL show correlations with memorability patterns, while the LPFC and other prefrontal regions show correlations with individual memory patterns. $N=16$, cluster-threshold corrected at $\alpha=0.05$.

tions with memorability pattern models than with individual memory pattern models. These regions are replicated across stimulus types – showing largely similar and overlapping correlation maps for both faces and scenes. In contrast, regions in the LPFC show significantly higher correlations with individual memory pattern models than with memorability pattern models. Again, these effects replicate for both faces and scenes. These results show multivariate evidence that memorability and individual memory are represented in dissociable systems, and one effect cannot be fully explained by the other.

Discussion

Memorability sensitivity in the brain

Memorability provides a new way to investigate the conjunction of perception and memory, pinpointing a high-level perceptual property that influences future memory behavior. Memorability is highly consistent across participants despite their diversity of individual experiences (Bainbridge et al., 2013; Isola et al., 2011a) and can be consistently predicted by deep learning neural networks (Khosla et al., 2015). These results find that the human brain is highly sensitive to memorability, showing stereotyped patterns of memorability in the VVS and MTL in terms of both activation levels as well as representational geometry. These memorability effects also differ from those of low-level vision and individual memory, providing evidence that memorability may pinpoint a stimulus-driven perceptual process that influences the ultimate memory encoding fate of that stimulus.

What might be a reason for memorability sensitivity to exist in the brain? Extensive evidence shows that memorability is unique and separate from other known stimulus properties including low-level features, attractiveness, emotionality, and subjective judgments of what is memorable or familiar (Bainbridge et al., 2013; Isola et al., 2013). Unlike most other properties, memorability has also been found to be intrinsic to an entity (e.g., a face identity) and invariant to transformations of that entity (Bainbridge, *in press*), indicating that memorability is a highly stable property to entities in our environment.

A current working hypothesis is that memorability is a high-level perceptual property reflecting the statistical distinctiveness of a stimulus along a multidimensional set of axes, beyond a simple single measure like physical distinctiveness of points in a face. Rapidly and automatically identifying the memorability of a person or place may be crucial to quickly identifying items essential for later memory (e.g., threats, or essential information about the environment) and prioritizing them for processing and storage.

Memorability is not low-level vision, nor attention

The current study uses a unique set of stimuli that are closely matched for low-level visual features yet highly different in terms of memorability. As expected, we found no effect of memorability in the EVC. Memorability effects in the brain thus cannot be explained by low-level visual differences (e.g., color, brightness, spatial frequency; Isola et al., 2011b), and indeed, other work finds that memorability also cannot be fully predicted by higher-level attributes, such as aesthetics, emotion, or subjective judgments of memorability (Bainbridge et al., 2013; Bylinskii et al., 2015; Isola et al., 2011b). The current study also finds memorability-based activation for both faces and scenes, showing that memorability may be agnostic to perceptual categories. These results validate that sensitivity to memorability occurs beyond low-level perception in the brain.

These memorability effects also cannot be explained by attention-based accounts or priming. Using the same stimulus set, memorability has been found to be separate from bottom-up attentional capture (i.e., memory does not cause spatial cueing, nor does it influence visual search times; Bainbridge, *in preparation*). Thus, while the memorability effects we find here occur at the stages of perception, they are not driven by attention-grabbing visual features in the stimuli. They are also known to not be driven by priming effects (Bainbridge, *in preparation*), a similarly automatic cognitive phenomenon known to influence later memory. At the same time, the effects of memorability are also stronger than those of top-down attention (i.e., you cannot make yourself forget a memorable image or remember a forgettable

image; Bainbridge, in preparation), explaining partially why memorability effects do not appear in frontal or parietal (Functional localizers and regions of interest (ROIs)) regions. In sum, the results in the current study are due to a specific, isolated sensitivity to memorability itself – not low level features, attention, or priming effects.

However, several VVS regions downstream of the EVC (e.g., FFA, LOC) show sensitivity to image memorability. These regions could be picking up on high-level perceptual features of memorability, similarly to how later layers within a deep learning network can distinguish image memorability (Khosla et al., 2015). Indeed, regions in the VVS contain representations of stimulus similarity linked to idiosyncratic memory (Charest et al., 2014). It is possible that this VVS activation is a result of feedback from the MTL, as it is widespread and content generic across the VVS. However, importantly, this effect is again unlikely to be driven by top-down attention, as no significant memorability effect was found in frontal regions, and there was no global increase in brain activity for memorable stimuli. These results thus present evidence for memorability as an automatically processed high-level perceptual property, late in the perceptual processing stream, that is important to influencing memory encoding behavior.

Memorability is not individual subsequent memory

By definition, memorability is a strong predictor of later memory – and indeed, participants significantly remembered memorable images over forgettable ones. However, this correspondence is not one-to-one; not all memorable images are remembered by all participants. Our results indicate a dissociation between memorability processing and memory encoding. Memorability effects are focused in the VVS and MTL, even when controlling for individual subsequent memory, while individual subsequent memory effects are focused in the LPFC, even when controlling for memorability. Importantly, when directly pitting the representational geometries of these two effects against each other across the whole brain, the VVS and MTL again emerge as specific to memorability, while the LPFC emerges as specific to individual memory. These results show that memorability is not just a proxy for subsequent memory, nor is subsequent memory just a noisy measure of memorability.

These results strongly suggest that memorability and subsequent memory paradigms are capturing two separate memory phenomena. Memorability is a normative measure of memory largely based on the stimulus and how it relates to the visual statistics of the world (Bylinskii et al., 2015; Isola et al., 2011b). In contrast, subsequent memory is an idiosyncratic measure of memory, based on comparisons between a stimulus and a specific individual's experience. Previous work has combined the two of these measures into a single measure of “memory,” where normative stimulus-driven memorability and individual subsequent memory are completely intercorrelated, as memorable images are also more likely to be remembered. However, these two measures (stimulus-driven effects and observer-driven effects) are found to make up two separate halves of ultimate memory behavior (Bainbridge et al., 2013). This study is the first to disentangle the two phenomena, and demonstrate that they contribute to different aspects of the stream leading up from perception to memory encoding. One hypothesis from these data is that memorability drives rapid identification of stimuli in one's environment essential for memory, while individual subsequent memory compares stimuli with one's own experiences to pinpoint the true novelty of that stimulus.

Memorability as a bridge between perception and memory

Memorability represents an important transition between perceptual and memory processes. With memorability-sensitive neural patterns in the VVS and MTL, it appears that memorability plays a role in automatically tagging a perceived stimulus as memorable, or distinctive or significant (Inhoff and Ranganath, 2015), to be later encoded into

memory. There is debate as to whether regions in the MTL, such as the PRC and PHC, are mainly perceptual or memory-based regions (Aminoff et al., 2013; Cate and Köhler, 2006; Devlin and Price, 2008). Memorability is a stimulus property that bridges both domains – signaling the distinctiveness of a stimulus in comparison to past experience, with the rapid automaticity of perception. While previous work has proposed the PRC as a novelty detector (Brown and Aggleton, 2001; Daselaar et al., 2006; Desimone, 1996; Eichenbaum et al., 2007; Kumaran and Maguire, 2009), as playing a role in object discrimination and oddball tasks (Eacott et al., 2001; Meunier et al., 1993; LaRocque et al., 2013; Murray et al., 2007; Schapiro et al., 2012), or as relating to difficulty of information processing (Dew and Cabeza, 2013), the current results demonstrate that the PRC may instead be sensitive to stimulus distinctiveness (LaRocque et al., 2013; Xue et al., 2010). In this sense, the PRC would be sensitive to more novel (i.e., memorable) stimuli, be successful at object discrimination and oddball tasks (i.e., assessing distinctiveness), and also exhibit greater activity for more deeply encoded images (i.e., memorable images (Bartlett et al., 1984; Light et al., 1979)). In fact, the current study uses completely novel stimuli controlled for depth of encoding and attentional effects (Bainbridge, in preparation; Tulving et al., 1996), isolating memorability as the sole factor driving these neural effects. The PRC could serve as a bridge between incoming perceptual connections with IT to outgoing memory-encoding connections with the PHC (Brown and Aggleton, 2001; Eichenbaum et al., 2007) and hippocampus, converting perceptual information into a signal for whether a stimulus should be encoded into memory or not.

In contrast, “subsequent memory”, which has often found effects in both the MTL and PFC, may in fact be made up of two main components: memorability processing within the MTL and individual subsequent memory within the PFC. In fact, LPFC activations are the most consistent and reliable across subsequent memory studies (Kim, 2011). The current study finds these same LPFC activations, specific to individual subsequent memory and separate from memorability. Previous work has found this region to be sensitive to the organization and selection of memories (Moscovitch and Winocur, 2002), individual memory differences (Kuhl et al., 2012), and familiarity (Kafkas and Montaldi, 2014). There are strong bidirectional anatomical connections between the PFC and MTL, and direct connections from the PFC to the hippocampus (Brown and Aggleton, 2001; Fernández and Tendolcar, 2001). Memory work recording event-related potentials in the human brain also find that the MTL and PFC show generally simultaneous processing, while hippocampal activation occurs later (Fernández et al., 1999; Fernández and Tendolcar, 2001). We propose that the MTL and PFC work in conjunction to determine the eventual encoding fate of a perceived stimulus – where the PRC rapidly determines the memorability of a stimulus, while the PFC determines the individual-based memory of a stimulus. The PHC works as an intermediary between the PFC and MTL, as it has been shown to handle familiarity (Daselaar et al., 2006), serves as the main bidirectional connection between the PRC and PFC (Brown and Aggleton, 2001), and shows sensitivity to both memorability and individual memory in the current study. The hippocampus then encodes the stimulus into memory based on these two factors.

Memorability also offers a new way to conceptualize memory experiments, and revisit previous memory findings. Previously, memory work reported on effects confounding individual memory with stimulus memorability, however reanalyzing activation patterns based on stimulus memorability could show whether these dissociations emerge across different paradigms and stimulus sets. For example, amnesic patients such as H.M. have been found to show residual learning for images after the onset of amnesia (Corkin, 2002), and analyzing the memorability of these successfully remembered images and their neural signatures from older fMRI scans could give deeper insight into the nature of his lesions, which has recently been found to include a left-lateralized frontal lesion in addition to partial MTL

lesions (Annese et al., 2014). Further work could explore the temporal signatures of memorability, individual subsequent memory, and memory encoding, to see the temporal ordering of these three processes (Khaligh-Razavi et al., submitted for publication). The current study explores memorability and individual subsequent memory as binary values and finds dissociable effects even when incorporating reaction time as a continuous measure of memory strength (Supplementary material S2). However, rather than being binary measures, these two phenomena are likely to be more continuous metrics, varying along a scale of memorability or subsequent memory confidence, and further studies should explore how these continuous metrics may be represented in the brain. Additionally, as in other explicit memory studies, memorability shows decodable neural patterns, yet emerges in this implicit task in implicit memory-sensitive regions such as the PRC (Ward et al., 2013). Positioning memorability within the framework of explicit versus implicit memory, recognition versus recollection, as well as encoding versus retrieval will be important next steps for understanding how this stimulus-driven property plays into current perspectives of perceptual and memory processes. Using this predictor of later memory also opens up a wide range of novel paradigms – creating a functional memorability “localizer,” comparing cortical patterns for patient populations (e.g., Alzheimer’s disease) upon viewing stimuli of a determined memorability, or for even identifying and manipulating forgettable stimuli (Khosla et al., 2013, 2015).

Overall, our results support a reformulated framework of the interplay between perception and memory – with the MTL picking up on stimulus-driven memorability to determine stimulus distinctiveness to support later memory encoding, and the PFC comparing stimuli to specific individual experience. Ultimately, these calculations of memorability serve as an essential, automatic step of processing bridging from what we see to what we remember.

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Conflicts of interest

The authors declare no competing financial interests.

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Appendix A. Supporting material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neuroimage.2017.01.063](https://doi.org/10.1016/j.neuroimage.2017.01.063).

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