Neural representations of reward-related memories shift across development

Alexandra O. Cohen[1]*, Susan L. Benear[2*+], Camille V. Phaneuf-Hadd[3], Lila Davachi[4], Catherine A. Hartley[2,5]

1. Department of Psychology, Emory University
2. Department of Psychology, New York University
3. Department of Psychology, Harvard University
4. Department of Psychology, Columbia University
5. Center for Neural Science, New York University

*Authors contributed equally

[+]Corresponding Author:

Susan Benear
Department of Psychology
New York University
6 Washington Pl.
New York, NY 10003
Email: susanbenear@nyu.edu

ABSTRACT

Rewards signal information in the environment that is valuable and thus useful to remember. Rewards benefit memory across development, but how reward-associated memories are represented in the brain has not been well characterized. Here we conducted pattern similarity analyses of fMRI data in participants aged 8-25 to elucidate how neural representations in key memory-related brain areas are influenced by reward, and how these relationships change across childhood and adolescence. We found that reward information was reflected in pattern similarity during encoding in ventral temporal cortex and in changes in similarity from encoding to retrieval in anterior hippocampus (aHC). Strikingly, aHC reward-sensitive representations also varied with age such that adults' memory benefitted from stability of hippocampal representations, while younger participants' memory improvements were associated with drift in representations over time. Moreover, reward-related univariate activation in the ventral tegmental area was associated with a tendency toward representational drift in aHC, the pattern seen in children. Taken together, our findings demonstrate that reward modulates neural memory representations, and that the representational patterns supporting reward-motivated memory shift with age.

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As we learn about the world across development, it is crucial to prioritize in memory the most important aspects of our experience. Rewards in the environment can promote the retention of information in memory, likely because they signal valuable experiences. Both reward and the motivation to obtain reward enhance subsequent memory in adults (Adcock et al., 2006; Patil et al., 2017; Wittmann et al., 2005; Wolosin et al., 2012). Reward motivation also enhances memory performance in children and adolescents (Davidow et al., 2016; Ngo et al., 2019), but how reward influences encoding and retrieval in the developing brain is less well characterized. Our recent work examining brain activation in cortical and subcortical regions associated with reward processing and memory demonstrated that although rewards similarly enhance memory performance in children, adolescents, and young adults, the underlying neural processes supporting these memory improvements differ across development (Cohen et al., 2022a). Beyond the engagement and functional connectivity of brain regions important for memory, research has demonstrated that variation in the distributed neural representations of the information being encoded also relates to successful memory retrieval. However, it is not well understood whether associations encoded in high- versus low-reward contexts are represented differently, how these representations relate to memory performance, and whether such brain-behavior relationships change across development.

Studies have begun to characterize how neural representations of visual stimuli are influenced by the encoding context as well as how similarity in neural patterns during memory formation relates to memory performance. These studies often examine multivariate patterns of activation across voxels within ventral temporal cortex (VTC), a set of brain regions that exhibit selectivity for representation of specific visual concepts and categories, such as faces or objects (Khan et al., 2011). VTC category selectivity increases through childhood and adolescence, and is

correlated with improved memory performance across this same developmental window (Golarai et al., 2007). Visual stimuli from a given conceptual category that are encountered in a similar encoding context (e.g., high- vs. low-reward or blue vs. yellow background) often exhibit more similar patterns of activation in VTC regions during encoding (Ward et al., 2013; Xiao et al., 2020; Xue et al., 2010). This increased neural similarity for stimuli encountered in shared contexts may be beneficial for memory, as it may lead to greater similarity in the mental states evoked during recall, facilitating associative retrieval. Several studies have also demonstrated that when the cortical neural activation pattern during retrieval of an episode from a partial cue more closely resembles the pattern when it was encoded, referred to as encoding-retrieval similarity (ERS), the complete episode is more likely to be successfully recalled (Kuhl et al., 2011, 2012). ERS in VTC is associated with better memory in adults (Kuhl et al., 2011), and has been found to increase with age across late childhood into adolescence (Schlichting et al., 2022), potentially reflecting increased precision in the categorical representations within these regions over development. However, it remains unclear whether and how reward associations impact the relationship between neural patterns in VTC and memory retrieval performance in children and adolescents.

In addition to VTC, neural patterns within the hippocampus have also been found to reflect features of to-be-remembered associations. Relational memory, or the binding of related items in memory, is a canonical function of the hippocampus, a subcortical region within the medial temporal lobe (Davachi et al., 2003). The hippocampus is proposed to encode relational memories using a sparse and distributed coding scheme, in which a small subset of neurons represent the relations between items in memory. Multivariate neural activation patterns in the hippocampus are dynamic, with memory-associated neural patterns at encoding, at retrieval, and between these two states showing either increased similarity or differentiation depending on factors such as stimulus or context overlap during encoding, and task goals at encoding or

retrieval (reviewed in Brunec et al., 2020). A large body of research suggests that the hippocampus represents different groups of items more similarly if they were encoded in the same spatial or temporal context, and this effect has also been shown for more abstract "contexts" such as attentional state or shared semantic content (Brunec et al., 2020). Reward can also serve as an abstract encoding context, with items from the same reward context (e.g., high- versus low-reward) exhibiting greater similarity in hippocampal response patterns both across encoding trials (Wolosin et al., 2013), as well as between encoding and retrieval (Zeithamova et al., 2018). The anterior hippocampus (aHC), in particular, plays an important role in associative memory and has been implicated in memory for motivational stimuli (Adcock et al., 2006; Murty et al., 2017) and in facilitating reward-motivated memory across development, especially during the childhood years (Cohen et al., 2022a). Burgeoning developmental work suggests that hippocampal pattern similarity at encoding can reflect shared contexts (Benear et al., 2022) and relate to later associative memory performance (Kazemi et al., 2022) even in young children. However, there is also age-related change in the degree to which aHC pattern similarity increases for pairs of stimuli encountered in the same context (Kazemi et al. 2022). These findings suggest that reinstatement of memories in the anterior hippocampus could be impacted by reward and that such hippocampal representations may also vary with age.

Dopamine plays a central role in reward processing, with the ventral tegmental area (VTA) being a primary source of dopaminergic signaling in the brain (Ranaldi, 2014). There is a robust literature demonstrating the role of VTA dopamine in human reward motivation (Daniel & Pollmann, 2014; Glimcher, 2011) and connectivity between the dopamine neurons in the VTA and the hippocampus (HC) is proposed to underpin the influence of reward on learning and long-term memory (Lisman & Grace, 2005; Luo et al., 2011). In animal models, coordination between reward-related dopaminergic signaling in VTA and hippocampal activity enhances goal-directed behavior (Ding et al., 2025) and artificial increases in VTA dopaminergic activity

can modulate pattern similarity in prefrontal cortical regions (Iwashita, 2014). In humans, associative memory performance is predicted by increased post-encoding connectivity between both VTA and HC (Tompary et al., 2015) as well as VTA and VTC (Murty et al., 2017), but there is limited work relating VTA activation to memory-related changes in neural pattern similarity. Moreover, although there are developmental changes in how VTA neurons respond to reward (Kim et al., 2016; McCutcheon et al., 2012), there is limited work characterizing VTA contributions to memory across human development. Whether VTA modulates neural patterns of learned reward associations and influences memory performance differentially across development remains underexplored.

The present study investigates the influence of reward motivation on neural memory representations, and whether reward impacts these representations differently in children, adolescents, and adults. To capture the representations of memories associated with reward, we used representational similarity analysis to quantify and compare the degree of neural pattern similarity between high- and low-reward encoding and retrieval trials in participants spanning the crucial developmental age window of 8-25 years, when children and teens might be particularly sensitive to reward. Specifically, we examined how reward modulated the similarity of neural representations within a reward context during encoding and retrieval and for a given memory across encoding and retrieval in VTC and aHC. We investigated the influence of neural sensitivity to reward encoding in VTA on neural representations, relationships with behavioral memory performance, and how these shift with age across childhood and adolescence into adulthood. We hypothesized that neural reinstatement of memory representations from encoding to retrieval would be associated with better memory. We further predicted that hippocampal memory representations would reflect the reward value of the encoding context, and that this effect might be linked to reward-related engagement of the VTA. Moreover, given our past findings demonstrating developmental changes in neural correlates of

reward-motivated memory (Cohen et al., 2022a), we expected that the contributions of these neural patterns to memory performance might exhibit age-related change.

METHODS

Participants

Analyses included 89 participants ages 8 to 25 years (M_{age} = 16.16, SD_{age} = 4.67; 45 F, 44 M). A target sample size of 90 participants distributed evenly across age and sex was determined based on previous research that used similar or smaller sample sizes to examine brain-behavior relations across comparable ages (Van Den Bos and Rodriguez, 2015; Insel et al., 2019; Callaghan et al., 2021). In addition to the final sample used in analyses, data from eight participants were excluded for excessive motion (participants without at least one complete set of encoding and retrieval runs due to runs with 15% or more timepoints censored with greater than 0.9 mm relative translational motion), data from seven participants were excluded for their choosing not to complete or prematurely terminating the fMRI scan, and incomplete data from five participants were excluded due to fMRI scanner malfunction. Participants were recruited from the local New York City community and self-identified as African American/Black (12.2%), Asian (24.4%), Caucasian/White (38.9%), more than one race (23.3%), and Hispanic (15.6%). Participants were right-handed and provided self or parental report of no: previous head injury, diagnosed psychiatric illness, developmental disability, serious neurological or medical illness, sensory impairment (e.g., vision or hearing loss), use of medications that impact central nervous system function or peripheral physiological responses (e.g., beta-blockers), or major contraindication for MRI. Informed written consent was obtained from participants ages 18 and over and assent was obtained from minor participants, consistent with approved research procedures by New York University's Institutional Review Board. Written consent on behalf of the child was obtained from parents or guardians of participants under age 18 prior to study

participation. Participants received $75 in compensation and up to $21 in bonus money for participating in two sessions. This sample of participants was used in two earlier reports focusing on different experimental questions (Cohen et al., 2022a; Cohen et al., 2022b).

Experimental design and statistical analyses

Participants completed a reward-motivated encoding and retrieval task in the fMRI scanner (Figure 1; Cohen et al., 2022a). All child and adolescent participants completed a mock scan to acclimate to the scanning environment prior to their fMRI scan. All participants completed a training that included instructions and sample trials for each scan. Tasks were programmed in Expyriment v0.9.1b2 (Krause & Lindemann, 2014) using Pygame v1.9.4 and Python v2.7.15. Images used in the reward-motivated encoding and retrieval task came from RADIATE (Conley et al., 2018), the Chicago Face Database (Ma et al., 2015), Harvard's Konkle Lab (Konkle et al., 2010), and MIT's Places Scene Recognition (Zhou et al., 2014) databases. After completing the training, participants underwent "pre-exposure" to the eight source images (four faces and four places) from the reward-motivated encoding and retrieval task to mitigate possible effects of source image category on memory performance (Mayes et al., 2007). Each source image was repeated five times each and for three-second presentations (total duration: three minutes).

Reward-motivated encoding and retrieval task. The reward-motivated encoding and retrieval fMRI task consisted of two runs of reward-motivated encoding and two runs of retrieval (Figure 1A). Each encoding phase comprised 64 trials (32 high- and 32 low-reward) that each contained two images. To promote deep encoding, participants were instructed to tell themselves a story involving both images. On each trial, participants first saw two gold or silver squares for one second. The squares indicated whether remembering that the upcoming pair of images went together would help them win a big bonus of $15 (gold high-reward) or a small bonus of $1 (silver low-reward). A trial-unique picture of a child-friendly object was overlaid on the left square

and one of eight repeated source images was overlaid on the right square for three seconds. Source images were four faces (two women, two men) and four places (two outdoor scenes, two indoor scenes). The high-reward category of images (faces or places) was evenly distributed across age and sex. Following the stimulus presentation, participants had two seconds to rate how well they imagined their story on a scale from one (very easy to imagine) to four (very hard to imagine). A randomized, jittered ITI of three-six seconds determined based on previous studies (J. A. Mumford et al., 2014), followed each six second trial. Each encoding run lasted 11.37 minutes.

After encoding and following a post-encoding active rest scan (see Cohen et al., 2022a for active rest details), participants completed a retrieval scan. Each retrieval phase included half of the trial-unique objects from the preceding encoding block. Thus, each retrieval run consisted of 32 trials (16 high- and 16 low-reward from encoding) and lasted 6.57 minutes. On each trial, images were overlaid on blue squares that were perceptually similar to the gold and silver squares presented during encoding. An object from the preceding encoding phase was overlaid on the left square and a frame overlaid on the right square for three seconds. Participants were instructed to imagine the source image that had been paired with the object in the empty frame. Participants then had two seconds to report whether a face or a place belonged in the frame. Finally, they were shown the four source images from the selected category and selected the specific source image within two and a half seconds. If a participant failed to respond, “Too slow!” was displayed on the screen for the remainder of the trial. As in encoding, each retrieval trial was followed by a random, jittered ITI of 3-6 seconds. Participants then completed a second set of encoding, active rest, and retrieval scans.

Participants also completed a behavioral memory retrieval test after 24 hours (reported in Cohen et al., 2022a). The retrieval test consisted of all 128 objects from the motivated encoding task the day prior and 128 new objects. Half of the previously viewed images had been

presented during both encoding and retrieval on day one and the other half were only viewed once during encoding. On each trial, participants first saw one object and first indicated if it was definitely old, maybe old, maybe new, or definitely new. If the object was endorsed as definitely or maybe old, they then indicated whether the object had been paired with a face or place (hereafter, associative memory), and then which specific face or place (hereafter, specific source memory). If the object was endorsed as new, there were no further queries. The day two retrieval test was self-paced.

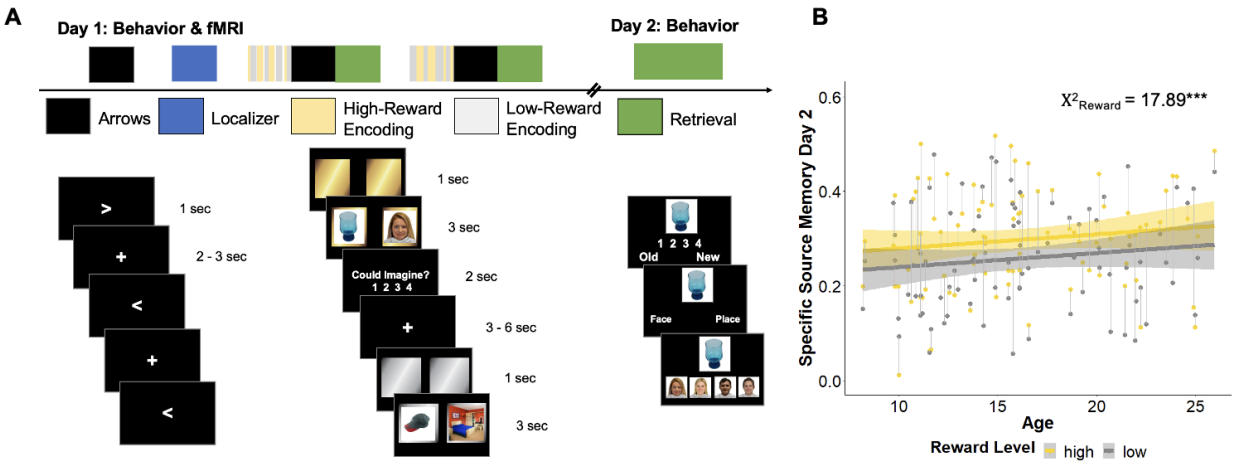

Figure 1. Experiment design. A) Participants completed a high- and low-reward motivated encoding and retrieval fMRI task. Participants also completed baseline and post-encoding active rest (arrows) tasks as well as a face/place functional localizer task. After 24 hours, they completed a behavioral retrieval task. B) Participants showed better memory for high- relative to low-reward memoranda across age after 24 hours. Shading depicts 95% confidence intervals around fitted lines. Thin gray lines connect individual subjects' data points. ***$p < 0.001$

MRI data acquisition and preprocessing. MRI data were acquired at the NYU Center for Brain Imaging using a 3 Tesla Siemens Prisma scanner and a 64-channel head coil. High-resolution, T1-weighted anatomical scans were acquired using a magnetization-prepared rapidly acquired gradient echo (MPRAGE) sequence (TR = 2.3s, TE = 2.3ms, TI = .9s; 8° flip angle; .9-mm isotropic voxels, field of view = 192 x 256 x 256 voxels; acceleration: GRAPPA 2 in the

phase-encoding direction, with 24 reference lines) and T2-weighted anatomical scans using a 3D turbo spin echo (TSE) sequence (T2: TR = 3.2s, TE = 564ms, Echo Train Length = 314; 120° flip angle, .9-mm isotropic voxels, field of view = 240 x 256 x 256 voxels; acceleration: GRAPPA 2x2 with 32 reference lines in both the phase- and slice-encoding directions). Functional data were acquired with a T2*-weighted, multi-echo EPI sequence (TR=2s, TEs=12.2, 29.48, 46.76, 64.04ms; MB factor = 2; acceleration: GRAPPA 2, with 24 reference lines; effective echo spacing: .245 ms; 44 axial slices; 75° flip angle, 3-mm isotropic voxels) from the University of Minnesota's Center for Magnetic Resonance Research (Feinberg et al., 2010; Moeller et al., 2010; Xu et al., 2013). Multi-band with multi-echo EPI sequences were used to aid with denoising of data and reducing signal dropout in subcortical brain regions. Total scan time was approximately 1 hour and 15 minutes, including short breaks between scans.

MRI data were preprocessed using fMRIPrep 20.0.6 (Esteban et al., 2019). The default options were used with slice timing disabled and MNI and T1w output spaces specified. The T1w space functional runs were used as input files in the reported analyses. Anatomical processing steps implemented via fMRIPrep included intensity nonuniformity correction, skull-stripping, spatial normalization, brain tissue segmentation, and surface reconstruction. FMRIPrep uses the tedana T2* workflow (DuPre et al., 2021; Kundu et al., 2017) to generate an optimally combined timeseries across echoes. This combined timeseries was then used in all subsequent preprocessing steps (e.g. registration estimation of head motion and confounds, susceptibility distortion estimation). All raw and preprocessed data were visually inspected. All subsequent processing and statistical analyses were completed in FSL version 5.0.10 (Jenkinson et al., 2012). Registration matrices were estimated by concatenating the transformations between the T1w functional to structural and structural to MNI space fMRIPrep outputs. Updated registration using these matrices derived from the fMRIPrep outputs were visually inspected.

Encoding and retrieval fMRI analyses. Trial-specific activation patterns were modeled using the least squares single (LSS) method (J. Mumford, 2013). Each generalized linear model (GLM) included a regressor for the trial of interest, a regressor with all other trials belonging to the same reward level as the trial of interest, a regressor with all trials belonging to the other reward level, and a regressor for onsets of no interest (during encoding, the onsets of the squares indicating reward level and during retrieval, the onsets of the four possible source images). Each task regressor was convolved with a double gamma hemodynamic response function. In addition to timepoints censored for excessive motion, the following nuisance regressors derived from fMRIPrep for each run were also included in these models: average signal within anatomically-derived eroded CSF mask, average signal within anatomically-derived eroded white matter mask, six motion (translational and rotational) parameters and their derivatives, a framewise displacement regressor, the first six anatomical noise components (aCompCor), and the cosine components to perform high-pass filtering of the data. Data were spatially smoothed with a 3-mm FWHM Gaussian kernel. T-statistic maps for each stimulus were then used in subsequent analyses.

Univariate encoding analyses used run-level GLMs for each participant. Each GLM had two task regressors: high-reward trials and low-reward trials. Each task regressor was convolved with a double gamma hemodynamic response function and included temporal derivatives. The following nuisance regressors derived from fMRIPrep for each encoding run were also included: six motion (translational and rotational) parameters and their derivatives, a framewise displacement regressor, the first six anatomical noise components (aCompCor), and the cosine components to perform high-pass filtering of the data. Encoding runs were combined using fixed-effects analyses. FSL's FLAME 1 was used to perform a group-level mixed-effects analysis. The group average was calculated for the high reward > low reward contrast-of-interest and included demeaned age and demeaned age-squared as covariates.

ROI definition. We investigated pattern similarity and encoding activation using several a-priori ROIs that have been previously implicated in reward-motivated memory processes: ventral temporal cortex (VTC), anterior hippocampus (aHC), and ventral tegmental area (VTA). A VTC ROI was created using the Harvard-Oxford cortical probabilistic structural atlas available in FSL. Parahippocampal cortex, temporal fusiform cortex, and temporal occipital fusiform cortex were merged to create the VTC ROI. This ROI was then warped into subject T1w space and thresholded at 50%. Bilateral aHC was defined in standard space using a probabilistic atlas at conventional MRI resolution (Ritchey et al., 2015). The bilateral aHC ROI was warped into subject T1w space and thresholded at 75%. The VTA ROI was defined in standard space using a probabilistic atlas that reliably defines this area at conventional MRI resolution (Murty et al., 2014). The ROI was warped into subject T1w space and thresholded at 75%. All ROIs were visually inspected.

Behavioral data analyses. Data processing and statistical analyses were conducted using R version 4.2.1 (de Micheaux et al., 2014). Mixed-effects models were run using the “lme4” package (Bates, 2011). Age was treated as a continuous variable in all analyses and was z-scored across all participants. We examined day two specific source memory because we previously observed reward-motivated memory enhancements in this measure after the 24 hour delay (Cohen et al., 2022a). Correct specific source memory was defined as trials where the specific source image (i.e., the specific woman, man, indoor place, or outdoor place) was accurately identified. Because day two associative memory (i.e., face or place) was only queried on items identified as old, the denominator for the day two measure was computed as the total number of items correctly identified as old for each participant. Trials were subdivided into paired associates that had been retrieved on both days or only on day two to account for effects of testing on memory performance.

As reported previously (Cohen et al., 2022a), we fit models to the memory data using a mean-centered, scaled linear age predictor and a squared mean-centered, scaled age predictor to test for nonlinear effects of age. A likelihood ratio chi-square test showed that the data were not better fit by quadratic age models ($\chi^2(4) = 1.98$, $p = 0.74$), indicating that a linear age model provided a better fit to the data. We fit a maximal model, including a single random intercept per participant and random slopes for within-subject fixed effects (reward level [high or low] and, for the day two data, retrieval condition [retrieved day 1 or not tested]) and their interaction, and simplified the models that failed to converge by removing random slopes until we identified the most complex random effects structure supported by the data (Bates et al., 2015). The model included a random intercept for participant and random slopes for retrieval condition. The high reward category of source image (face or place) for each subject was included as a covariate of no interest in all analyses. Statistical significance of the fixed effects is reported from the analysis of variance (Type III using Satterthwaite's method).

Neural pattern similarity analyses. The input data for similarity analyses were extracted t-statistics for each voxel of every trial within our ROIs of interest (VTC and aHC) that had been warped into subject T1w space. We computed three different pattern similarity measures within each ROI: encoding similarity, retrieval similarity, and encoding-retrieval similarity. Encoding similarity and retrieval similarity were computed as Pearson correlations between every trial with every other trial within the same reward level (high or low) and the same memory phase (encoding or retrieval). This analysis was intended to capture the representation of a "brain state" associated with both the reward level and the memory phase. Importantly, these correlations were computed across runs to avoid overinflating correlation values. Thus, these analyses – and all subsequent analyses using these measures – included 73 subjects (16 subjects only had partial data; i.e., one of two encoding and/or retrieval runs). Encoding-retrieval similarity was computed as Pearson correlations between corresponding encoding and retrieval

activation patterns for each trial. Correlation scores were Fisher *r*-to-*z* transformed so that they could be submitted to further analyses and then averaged, resulting in measures of high-reward and low-reward pattern encoding similarity, retrieval similarity, and encoding-retrieval similarity.

Mixed-effects models examining whether pattern similarity in a-priori ROIs varied as a function of reward level and age were fit in the same manner as described for behavioral analyses above. All models converged with a random intercept per participant and were best fit by linear age models, except for the encoding retrieval similarity model for VTC, in which quadratic age provided a better fit to the data ($\chi^2(2) = 7.43$, $p = 0.024$). Statistical significance of fixed effects is reported from the analysis of deviance (Type III Wald chi-square tests) performed on the *lmer* models.

Brain-behavior relation analyses. We examined the trial-wise relation between VTC encoding-retrieval similarity and memory, controlling for reward, age, and the high-reward category of source image. Statistical significance of fixed effects was reported from an analysis of deviance (Type III Wald chi-square tests) performed on the *glmer* model. Additionally, several multiple regressions were run. We examined the relations between reward-sensitive neural similarity measures and the high-reward memory benefit (high - low reward specific source memory after 24 hours) in a single multiple regression with each of the two neural similarity measures as predictors, controlling for each other, and controlling for age and the high-reward category of source image. In a separate multiple regression, we then examined the relation between VTA encoding activation and high versus low reward aHC encoding-retrieval similarity, modelling age as a covariate of interest and controlling for the high-reward category of source image.

RESULTS

Reward-motivated memory enhancements are evident across age. We previously reported that this sample of participants showed better memory for specific high-reward relative to low-reward associations across all ages after 24 hours (see Cohen et al., 2022a for a more thorough description of the memory results). Specifically, we ran a linear mixed effects model examining specific source memory as a function of reward level (high or low), age, and retrieval condition (whether the association was retrieved on both days or just day two), controlling for the high-reward source image category. There was a significant effect of reward level ($\chi^2(1, N = 89) = 17.89$, $p < 0.001$), with high-reward associations better remembered than low-reward associations. As expected, there was also a significant effect of retrieval condition, indicating better memory for associations that were retrieved twice rather than just once ($\chi^2(1, N = 89) = 49.56$, $p < 0.001$). However, there was no reward level-by-retrieval condition interaction, so we collapsed across conditions for visualization and subsequent analyses (Figure 1B). There were no other significant main effects or interactions (χ^2s < 2.00, ps > 0.15). These findings show that reward similarly enhances specific associative memory across age.

Ventral temporal cortex encoding similarity increases with age and greater reward value. We first examined neural pattern similarity in ventral temporal cortex (VTC). Using a series of linear mixed-effects models, we examined VTC encoding similarity, retrieval similarity, and encoding-retrieval similarity as a function of reward level and age, controlling for the high-reward source image category (faces vs. places). We observed significant main effects of reward level ($\chi^2(1, N = 73) = 13.85$, $p = 0.002$) and age ($\chi^2(1, N = 73) = 4.38$, $p = 0.036$) on encoding similarity, such that encoding similarity was greater for high- relative to low-reward memoranda and increased with age (Figure 2A). There was not a significant interaction between reward level and age or an effect of high-reward source image category (χ^2s < 1.2, ps > 0.23). We did not observe any significant differences in VTC retrieval similarity as a function of reward level,

age, or source image category (χ^2s < 1.5, *p*s > 0.21). Finally, we only observed a significant main effect of quadratic age ($\chi^2(1, N = 89) = 7.02$, $p = 0.008$) on VTC ERS such that similarity increased nonlinearly with age. There were no main effects of reward level, linear age, high-reward source image category, or interactions between reward level and age (χ^2s < 1.6, *p*s > 0.20). These findings suggest that paired associates were encoded more similarly with greater reward value and increasing age and that individual memory representations increase in similarity with age, regardless of reward level.

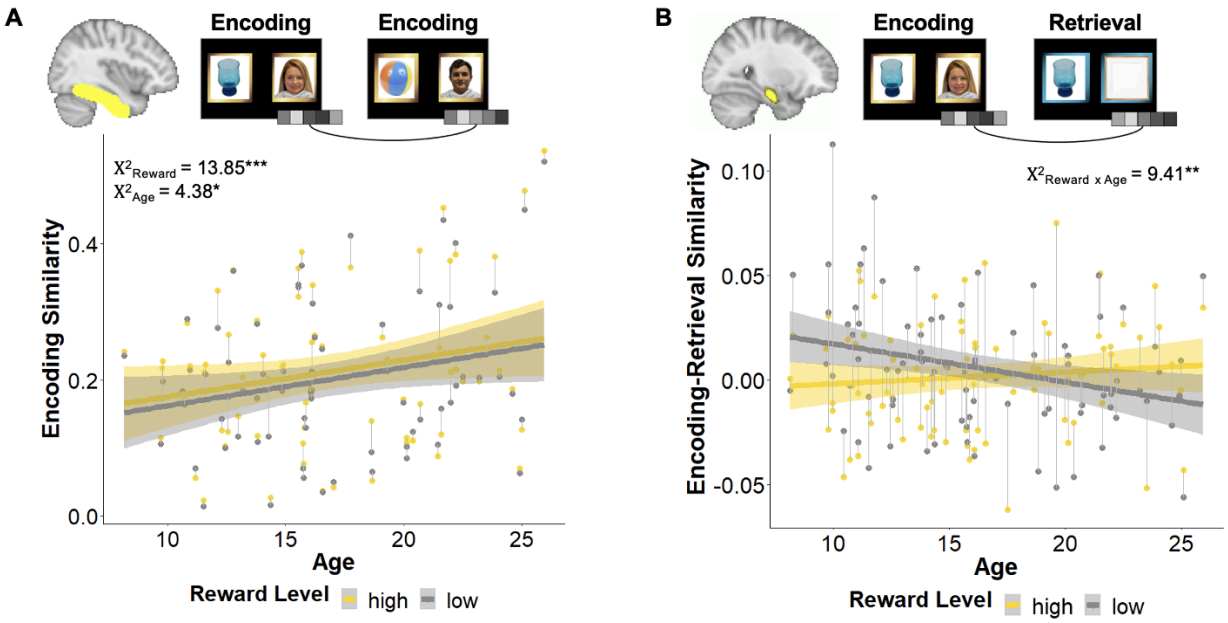

Figure 2. Reward-sensitive neural pattern similarity in ventral temporal cortex (VTC) and anterior hippocampus (aHC). A) VTC encoding similarity increased with age and was increased for high- relative to low-reward memoranda across age. B) aHC encoding-retrieval similarity varied by both reward level and age, such that pattern similarity for high-relative to low-reward memoranda was differentiated for younger and older participants (reward level by age interaction). Shading depicts 95% confidence intervals around fitted lines. Thin gray lines connect individual subjects' data points. *p < 0.05, **p < 0.01, ***p < 0.001

Anterior hippocampus encoding-retrieval similarity varies by reward level and age. We next examined neural pattern similarity in our primary region of interest, the anterior hippocampus

(aHC). We used a series of linear mixed-effects models to assess whether aHC encoding similarity, retrieval similarity, and encoding-retrieval similarity varied as a function of reward level and age, controlling for the high-reward category source image. There were no significant differences in either encoding or retrieval similarity in aHC as a function of reward level, age, or source image category (all χ^2s < 1.2, ps > 0.28). There were also no significant main effects of reward level, age, or high-reward source image category on aHC encoding-retrieval similarity (χ^2s < 1.6, ps > 0.22). However, there was a significant reward level by age interaction ($\chi^2(1, N = 89) = 9.41$, $p = 0.002$), such that high-reward paired associates showed relatively greater encoding-retrieval similarity than low-reward pairs in older participants, but less encoding-retrieval similarity relative to low-reward pairs in younger participants (Figure 2B). These results suggest that individual memory representations in aHC were differentiated by reward level in both older and younger individuals, but with opposite patterns of neural similarity for stimuli from high- and low-reward categories as a function of age.

Ventral temporal cortex encoding-retrieval similarity predicts trial-wise memory accuracy. We found that VTC encoding-retrieval similarity did not vary by reward level but increased with age. We assessed whether VTC reinstatement was associated with trial-wise memory accuracy after 24 hours. Specifically, we fit a generalized linear mixed-effects model to examine the trial-wise relation between VTC encoding-retrieval similarity and memory accuracy, controlling for reward level, age, and high-reward source image category. As expected, we found a robust positive relationship between VTC encoding-retrieval similarity and memory performance ($\chi^2(1, N = 89) = 17.04$, $p < 0.001$; Figure 3), suggesting that the reinstatement of neural patterns from encoding in visual regions during retrieval may have supported successful memory for specific source images. As anticipated based on analyses of the behavioral data, we also found that memory performance increased with age ($\chi^2(1, N = 89) = 4.22$, $p = 0.04$), and that high-reward associations were better remembered than low-reward associations ($\chi^2(1, N = 89) = 7.26$, $p =$

0.007). There was no significant effect of source image category ($\chi^2(1, N = 89) = 0.01$, $p = 0.93$). Thus, we find that VTC reinstatement supports memory performance regardless of age or the reward level of stimuli.

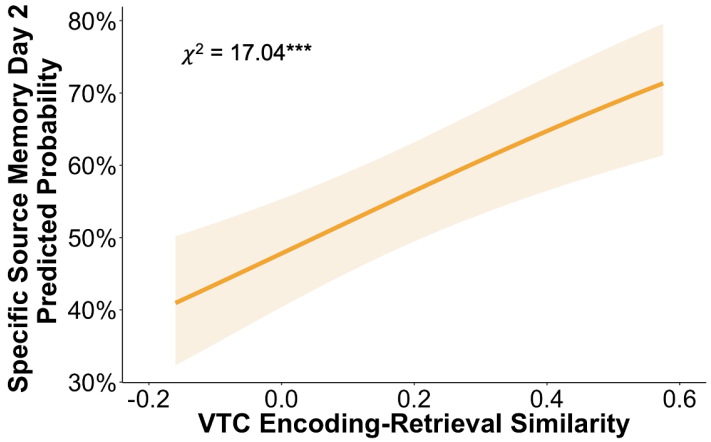

Figure 3. Trial-wise ventral temporal cortex (VTC) pattern similarity relates to memory performance across age. Trial-wise VTC encoding-retrieval similarity was related to memory after 24 hours, such that greater encoding-retrieval similarity predicted better memory performance. Shading depicts 95% confidence intervals around the predicted probability line. ***$p < 0.001$

Neural similarity measures relate to reward-motivated memory enhancements. We found that VTC encoding similarity and aHC encoding-retrieval similarity patterns both reflected an influence of reward value on memory. To assess how each of these neural measures related to reward-motivated memory enhancements, we ran a multiple regression including the neural similarity measures from each of these two regions as covariates predicting memory performance after 24 hours. Specifically, because we observed greater encoding similarity for high- versus low-reward items in VTC, which did not vary by age, we included the difference score between high- and low-reward encoding similarity in VTC as the covariate for this region. However, we observed reward value-related differentiation of encoding-retrieval pattern similarity that differed in older compared to younger participants in aHC, such that adults

showed greater pattern similarity for high-reward pairs, while children showed lower similarity for these pairs. We reasoned that the magnitude of differentiation, regardless of the sign of the difference, might relate to the strength of the reward-modulated memory effect. Thus, for the aHC covariate, we computed the absolute value of the difference score between high- versus low-reward encoding-retrieval similarity. The dependent variable in the model was a high-reward memory benefit measure, which was simply the difference between high- versus low-reward memory performance after 24 hours. Both the VTC and aHC difference scores were included as predictors, controlling for each other, along with age and the high-reward source image category.

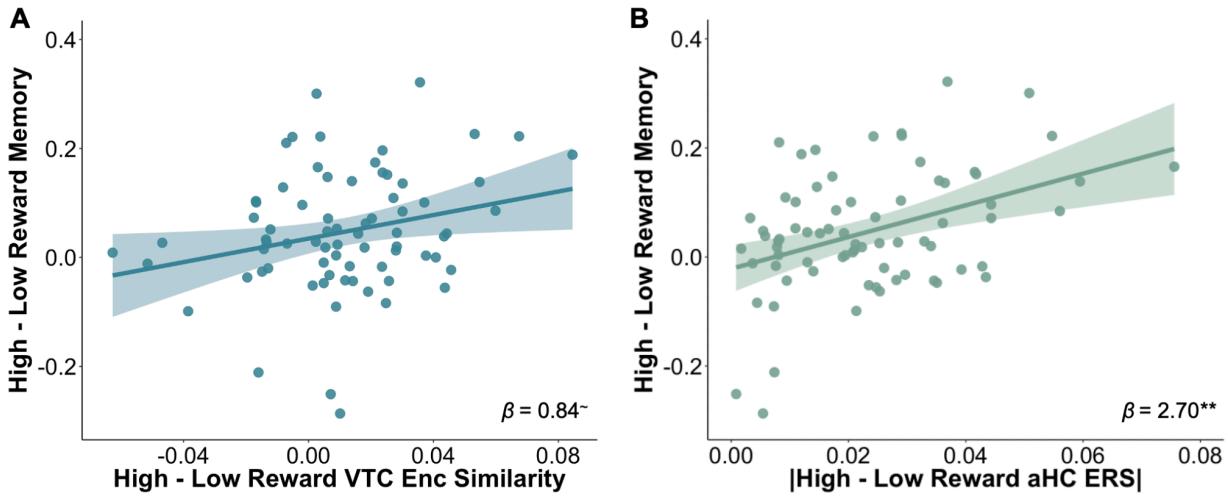

Figure 4. Reward-sensitive neural similarity measures relate to high-reward memory benefits. A) Greater high- versus low-reward ventral temporal cortex (VTC) encoding similarity relates to better high- versus low-reward memory after 24 hours. B) Greater magnitude of the difference between high- and low-reward anterior hippocampus (aHC) encoding-retrieval similarity relates to better high- versus low-reward memory after 24 hours. Results come from a single multiple regression model. Shading depicts 95% confidence intervals around fitted lines. ~$p < 0.1$, **$p < 0.01$

There was a marginal positive relationship between high- versus low-reward VTC encoding similarity and the high-reward memory benefit ($\beta = 0.84$, $t_{(68)} = 1.82$, $p = 0.074$; Figure 4A), suggesting that the enhanced encoding similarity for high-reward items in VTC may support

better memory for these items. We also observed a significant positive relationship between the magnitude of high- versus low-reward aHC encoding-retrieval similarity and the high-reward memory benefit ($\beta = 2.70$, $t_{(68)} = 3.42$, $p = 0.001$; Figure 4B), suggesting that the magnitude of the difference between high and low-reward ERS, regardless of sign, may facilitate memory for high-reward items. There were no significant effects of age or the high-reward stimulus category (ps > 0.80). These findings suggest that reward-sensitive adaptations of neural representations in both VTC and aHC support reward-motivated memory enhancements.

Ventral tegmental area encoding activation relates to reward and age varying hippocampal encoding-retrieval similarity. While the magnitude of the difference between high- and low-reward aHC ERS robustly related to reward-motivated memory benefits across age, high-reward paired associates were represented more similarly in older participants while low-reward paired associates were represented more similarly in younger participants (Figure 2B). Our prior published work in this dataset revealed that reward-motivated memory enhancements in younger individuals related to increased post-encoding functional connectivity between the ventral tegmental area (VTA) and aHC (Cohen et al., 2022a). Given the VTA's relevance to associative memory (Tompary et al., 2015) and this increased putative communication between VTA and aHC following reward-motivated encoding, we reasoned that VTA encoding activation may relate to the aHC representational pattern observed in younger participants more so than the pattern observed in older participants. We examined whether univariate encoding activation of VTA for high- versus low-reward memoranda related to aHC ERS. Specifically, we used an a priori anatomically and functionally defined VTA ROI to examine activation in the high-reward > low-reward encoding contrast and related it to the difference in high- versus low-reward aHC ERS. Here, we did not take the absolute value of the hippocampal encoding-retrieval similarity metric specifically to attempt to capture potential relations between

differential VTA activation and the more “child-like” or more “adult-like” pattern of differentiation of memory representations for pairs of stimuli from each reward level within the hippocampus.

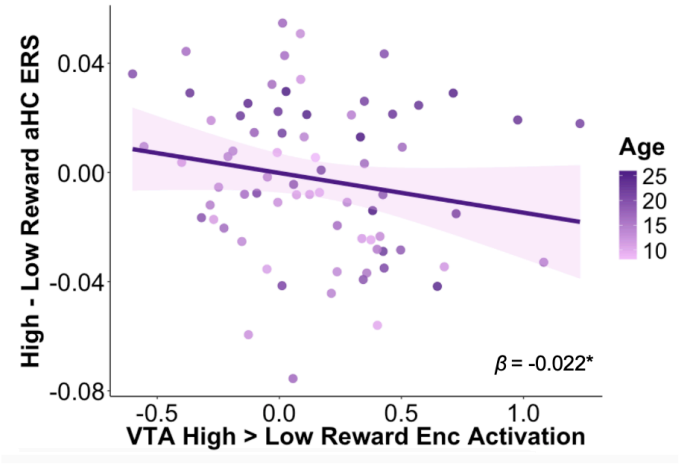

Figure 5. Ventral tegmental area (VTA) encoding activation for high-reward memoranda relates to anterior hippocampal (aHC) high versus low reward pattern similarity. Greater VTA encoding activation for high- relative to low-reward memoranda is associated with lower encoding-retrieval similarity for high- relative to low-reward memoranda in anterior hippocampus, the aHC pattern more frequently observed in younger participants. *$p < 0.05$

We found a significant relationship between VTA encoding activation and high- versus low-reward aHC encoding-retrieval similarity, such that greater VTA activation for high- versus low-reward stimuli was associated with increased low- relative to high-reward aHC encoding-retrieval similarity ($\beta = -0.022$, $t_{(68)} = -2.27$, $p = 0.026$; Figure 5), which was the similarity pattern observed in younger participants (Figure 2B). There was a marginal main effect of age ($\beta = 0.007$, $t_{(68)} = 1.81$, $p = 0.075$), such that high- versus low-reward aHC ERS increased with age. There was no significant main effect of the high-reward source image category or an interaction between age and VTA encoding activation (ps > 0.54). These findings suggest that greater VTA encoding activation for high-reward memoranda may facilitate the differentiation of hippocampal reward-related neural patterns from encoding to retrieval, facilitating memory performance specifically in children. This finding is consistent with our prior

work showing a preferential role for VTA and aHC in reward-related memory processing in younger participants.

DISCUSSION

In the present study, we investigated how reward influences neural memory representations across development. Specifically, we examined neural pattern similarity in the ventral temporal cortex (VTC) and the anterior hippocampus (aHC). We found that VTC encoding similarity and aHC encoding-retrieval similarity reflected reward value in different ways. VTC encoding similarity was greater for high- relative to low-reward memoranda and increased with age, regardless of reward level. aHC encoding-retrieval similarity varied by reward level as well as by age—mean neural pattern similarity between encoding and retrieval was higher for low-reward stimulus pairs and lower for high-reward pairs with age, such that older participants exhibited greater similarity for high-reward memoranda whereas younger participants exhibited lower similarity. The increase in VTC encoding similarity for high- relative to low-reward memoranda and the magnitude of the high- versus low-reward ERS difference in aHC were both associated with high-reward memory benefits after 24 hours. Furthermore, greater high-reward encoding activation in VTA was associated with decreased similarity between neural patterns for high-reward memoranda from encoding to retrieval in aHC, the pattern more commonly observed in younger participants. These results highlight differences in how VTC, aHC, and VTA incorporate reward-related information within long-term memory and in how hippocampal representations support reward-motivated memory across development.

Although VTC encoding similarity predicted memory performance and related to reward value regardless of age, the degree of similarity for both high- and low- reward memoranda increased with age. One explanation for our findings comes from work demonstrating that VTC regions become more robust in their category-specific responses with increasing age, leading to the

potential for greater similarity in response patterns for objects from the same reward category with development (Golarai et al., 2007; Grill-Spector et al., 2008). However, it has also been suggested that over development, multivariate neural representational similarity between items of the same category is present prior to the emergence of univariate neural category selectivity (M. A. Cohen et al., 2019), highlighting the provisional nature of this literature. Specificity in neural responses to objects, faces, and scenes in VTC has been demonstrated in infants, but category selectivity in these regions continues to develop into early adulthood (Grill-Spector et al., 2008). In particular, although object-selective neural activation and behavioral recognition are at adult-like levels by middle childhood, activation in face- and place-selective regions and memory for exemplars from these two categories continue to develop into adulthood (Golarai et al., 2007), which is proposed to be due to experience-related plasticity (Golarai et al., 2015; Nordt et al., 2021). Although category-selective functional activation grows stronger across childhood and adolescence, activation in VTC correlates with category-specific memory performance even among children as young as 7 years old (Golarai et al. 2007). Given that faces and scenes were the categories paired with each of the reward levels (low and high) in our study, increases in the degree of pattern similarity in VTC across development in our sample may reflect this protracted developmental trajectory of cortical representations.

Strikingly, reward facilitated memory in adults by promoting stability of neural patterns for high-reward stimuli, whereas children's memory was instead facilitated by lower similarity or "drift" in hippocampal activation patterns. Representational drift refers to shifts in neural patterns or "engrams" representing a particular stimulus over time (Rule et al., 2019), reflecting a distributed neural code that dynamically shifts with ongoing experience (Hainmueller & Bartos, 2018; Rule et al., 2019). A prior study reporting that reward expectation reduces drift of spatial representations in the CA1 subregion of HC in adult mice (Krishnan & Sheffield, 2023) is consistent with the greater hippocampal neural pattern similarity (i.e., reduced drift) for

high-reward pairs we observed in adults. However computational accounts proposing that drift in the CA3 subregion of the HC may actually facilitate memory performance (Antony et al., 2024) suggest that stability does not always benefit memory, consistent with our finding that younger participants exhibited better memory but lower neural pattern similarity for high-reward pairs. The CA1 and CA3 subregions of the hippocampus exhibit distinct maturational trajectories (Keresztes et al., 2018; Lavenex & Banta Lavenex, 2013), and animal models indicate there may also be differences in the rates of representational drift across these regions (Hainmueller & Bartos, 2018). One possibility is that children's and adults' comparable reward-motivated memory enhancements reflect differential contributions of dynamic representations within these HC subfields, a hypothesis that could be explored in future developmental studies using approaches that afford better spatial resolution of neural representations. Further work in this area may also clarify the nature of hippocampal representations in adolescence. We did not observe a prevailing reward-differentiating representational scheme employed by the hippocampus during adolescence. Adolescents' value-related hippocampal memory representations may exhibit greater variation as teens transition from "child-like" to the "adult-like" patterns.

The magnitude of reward-related VTA activity during encoding related to the differential degree of stability versus drift in hippocampal patterns from encoding to retrieval for high- versus low-reward memoranda. Our prior work showed that pre- to post-encoding increases in VTA-aHC functional connectivity were associated with reward-motivated memory to the greatest extent in younger participants (Cohen et al., 2022a), suggesting that increased communication between VTA and aHC following reward-motivated encoding was particularly beneficial for children's memory. Consistent with this evidence of a central role for VTA-aHC interactions in reward-motivated encoding earlier in development, here we found that greater VTA encoding activation for high-reward memoranda was associated with lower aHC pattern similarity for

these stimuli from encoding to retrieval, the pattern that was observed to a greater extent in younger participants. While few studies to date have examined how reward modulates hippocampal memory representations, these findings suggest that the contributions of the dopaminergic system to the stability or flexibility of these representations may vary with age.

Reward associations impact the formation and retention of memory across the lifespan. Here, we provide evidence for developmental differences in how reward influences the neural representations that support associative memory. Taken together, our findings align with a nascent body of research suggesting that distinct representational schemes benefit memory over development (Schlichting et al., 2022; Varga et al., 2023). Our work points to important avenues for future research into the mechanisms that underpin variation in the neural representations of motivated memories over development.

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