Developmental change in prefrontal cortex recruitment supports the emergence of value-guided memory

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Abstract

Prioritizing memory for valuable information can promote adaptive behavior across the lifespan, but it is unclear how the neurocognitive mechanisms that enable the selective acquisition of useful knowledge develop. Here, using a novel task coupled with functional magnetic resonance imaging, we examined how children, adolescents, and adults (N = 90) learn from experience what information is likely to be rewarding, and modulate encoding and retrieval processes accordingly. We found that the ability to use learned value signals to selectively enhance memory for useful information strengthened throughout childhood and into adolescence. Encoding and retrieval of high- vs. low-value information was associated with increased activation in striatal and prefrontal regions implicated in value processing and cognitive control. Age-related increases in value-based lateral prefrontal cortex modulation mediated the relation between age and memory selectivity. Our findings demonstrate that developmental increases in the flexible recruitment of the prefrontal cortex support the emergence of adaptive memory.

Introduction

Memories of past experiences guide our behavior, promoting adaptive action selection throughout our lives (Biderman et al., 2020). But not all experiences are equally useful to remember — the information we encounter varies in its utility in helping us gain future reward. By adulthood, individuals demonstrate the ability to prioritize memory for information that is likely to be most rewarding in the future (Adcock et al., 2006; M. S. Cohen et al., 2014, 2019; Hennessee et al., 2019; Shigemune et al., 2014; Shohamy & Adcock, 2010; Wittmann et al., 2005). Children, however, demonstrate weaker memory selectivity, often remembering relatively inconsequential information at the expense of higher-value items or associations (Castel et al., 2011; Hanten et al., 2007; Nussenbaum et al., 2020). Behavioral studies have found that the use of value to guide encoding and retrieval processes emerges and strengthens gradually throughout childhood and adolescence, promoting more efficient acquisition of useful knowledge with increasing age (Castel et al., 2011; Hanten et al., 2007; Nussenbaum et al., 2020). It is unclear, however, how changes in brain activity support this observed emergence of motivated memory. Though a large literature has examined developmental change in the neural mechanisms that support memory from early childhood to young adulthood (Ghetti & Fandakova, 2020; Ofen, 2012; Shing et al., 2010), no prior studies have investigated how the developing brain prioritizes memories based on their relative utility.

Prioritizing valuable information in memory requires both determining the value of information and strategically modulating encoding accordingly. The vast majority of adult studies have focused only on the strategic *use* of value to guide memory — in most studies of motivated memory, *determining* the value of information is trivial for participants because experimenters label to-be-remembered information with explicit value cues (e.g., dollar signs, stars, point amounts) (Adcock et al., 2006; Castel et al., 2011; M. S. Cohen et al., 2014; Murty et al., 2017). However, in real-world contexts, individuals must derive the value of information from the statistics of their environments. In a recent behavioral study (Nussenbaum et al., 2020), we demonstrated that young adults could use naturalistic value signals to prioritize memory for useful information. Specifically, we manipulated information value via item *frequency.* Across many environments, the frequency of encountering something in the past predicts the frequency of encountering it in the future. In this way, frequency can signal information utility (Anderson & Milson, 1989; Anderson & Schooler, 1991; Liu et al., 2020; Pachur et al., 2014; Rich & Gureckis, 2018; Stevens et al., 2016) — if individuals are likely to encounter something often in the future, encoding information about it is likely to be valuable. For example, remembering the supermarket aisle of an ingredient with which one often cooks is likely to facilitate greater reward gain than remembering the aisle of an ingredient one almost never uses. In our prior study, we translated this feature of real-world environments to a laboratory task in which individuals could learn the potential reward value of associative information by first learning the relative frequency of items in their environments. We found that individuals exploited these naturalistic value signals and demonstrated better memory for information associated with high- relative to low-frequency items. Critically, this pattern of results varied with age; the strategic prioritization of high-value

information in memory increased from age 7 to age 25 (Nussenbaum et al., 2020). It is unclear, however, if developmental improvements in memory prioritization stemmed from change in learning the relative value of information based on environmental statistics or *using* learned value signals to strategically prioritize memory. Each of these processes likely engages separable neural systems.

Deriving value from the structure of the environment first requires the learning of statistical regularities. In the case of learning the frequency with which one might need to use information, individuals must differentiate novel occurrences (e.g., cooking with a rare ingredient) from oft-repeated experiences (e.g., cooking with a common food). Neurally, medial temporal lobe regions may support sensitivity to item repetitions. The parahippocampal cortex in particular demonstrates reduced responsivity to repeated relative to novel presentations of items (i.e., "repetition suppression") (Gonsalves et al., 2005; Kirchhoff et al., 2000; Köhler et al., 2005; O'Kane et al., 2005; Turk-Browne et al., 2006). Repetition suppression may index implicit learning of repeated items (Ward et al., 2013). Paralleling their robust implicit learning abilities (Amso & Davidow, 2012; Finn et al., 2016; Meulemans et al., 1998), children and adolescents also demonstrate neural repetition suppression effects (Nordt et al., 2016; Scherf et al., 2011; Turi et al., 2015), though repetition suppression — and the ability to learn the statistical structure of the environment — may increase throughout childhood (Scherf et al., 2011). When individuals need to remember information associated with previously encountered stimuli (e.g., the grocery store aisle where an ingredient is located), frequency knowledge may be instantiated as value signals, engaging regions along the mesolimbic dopamine pathway that have been implicated in reward anticipation, including the ventral tegmental area (VTA) and the striatum (Adcock et al., 2006; Shigemune et al., 2014).

Using these learned value signals to guide memory likely requires cognitive control (Castel et al., 2007; M. S. Cohen et al., 2014). Value responses in the striatum may signal the need for increased engagement of the lateral prefrontal cortex (lPFC) (Botvinick & Braver, 2015), which supports the implementation of strategic control. Enhanced recruitment of control processes promotes the use of deeper and more elaborative encoding strategies (M. S. Cohen et al., 2014, 2019; Miotto et al., 2006; Uncapher & Wagner, 2009) as well as the selection and maintenance of effective retrieval and post-retrieval monitoring strategies (Libby & Lipe, 1992; Scimeca & Badre, 2012), which may contribute to better memory for high-value information. The use of value to proactively upregulate cognitive control responses improves throughout development, though the specific trajectory of improvement may relate to the control demands of a given task (Davidow et al., 2018). Selectively enhancing the use of encoding and retrieval strategies requires not only tight coordination between subcortical regions involved in value processing and prefrontal areas implicated in control (Murty & Adcock, 2014), but also an available repertoire of memory strategies to implement. Even in the absence of value cues, children and adolescents demonstrate reduced use of strategic control (Bjorkland et al., 2009) and reduced lateral prefrontal engagement during encoding (Ghetti et al., 2010; Ghetti & Fandakova, 2020; Shing et al., 2016; Tang et al., 2018), suggesting that the availability of mnemonic control strategies may increase with age.

Taken together, prior work suggests that adaptive memory requires the recruitment and coordination of multiple neural systems, including mechanisms for learning environmental structure, representing value, and engaging strategic control, all of which may undergo marked changes from childhood to adulthood. Here, we examined how the development of these neurocognitive processes supports the emergence and strengthening of value-guided memory from childhood to young adulthood. To pinpoint loci of developmental change in adaptive memory prioritization, we combined our novel motivated memory experiment (Nussenbaum et al., 2020) with functional neuroimaging. During the task, participants first learned the frequency of items in their environments, and then learned information associated with each item. Importantly, we structured our task such that the frequency with which participants first experienced each item indicated the frequency with which they would be asked to report the information associated with it, and therefore, the number of points they could earn by remembering the association. Immediately following encoding, we administered a memory test in which participants had to select each item's correct associate.

We examined neural activation during the learning of item frequency, and when participants were asked to encode and retrieve information associated with high- vs. low-frequency items. We hypothesized that while participants across our entire age range would demonstrate sensitivity to the frequency of items in their environments, with increasing age, participants would show improvements in transforming this experiential learning into value signals and modulating the engagement of strategic control processes during encoding. Neurally, we expected that at encoding and retrieval, the recognition of information value would be reflected in increased striatal activation in response to associations involving high- vs. low-frequency items, while the engagement of strategic control would be reflected in increased activation in lateral prefrontal cortex. Further, we hypothesized that increased recruitment of the striatum and prefrontal cortex during encoding and retrieval of high- vs. low-value information would underpin the strengthening of adaptive memory prioritization from childhood to early adulthood.

Methods

Participants

Ninety participants between the ages of 8.0 and 25.9 years took part in this experiment. Thirty participants (n = 16 females) were children between the ages of 8.0 and 12.7 years, 30 participants were adolescents between the ages of 13.0 and 17.7 years (n = 16 females), and 30 participants were adults between the ages of 18.32 and 25.9 years (n = 15 females). Ten additional participants were tested but excluded from all analyses due to excessive motion during the fMRI scan (n = 8; see exclusion criteria below) or technical errors during data acquisition (n = 2). We based our sample size on other functional neuroimaging studies of the development of goal-directed behavior and memory across childhood and adolescence (Insel et al., 2017; Tang et al., 2018) as well as on our prior behavioral study that showed age-related change in the use

of learned value to guide memory (Nussenbaum et al., 2020). According to self- or parental-report, participants were right-handed, had normal or corrected-to-normal vision, and no history of diagnosed psychiatric or learning disorders. Participants were recruited via flyers around New York University, and from science fairs and events throughout New York City. Based on self- or parent-report, 35.6% of participants were White, 26.7% were two or more races, 24.4% were Asian, 11.1% were Black and 2.2% were Native American. Additionally, 17.8% of the sample identified as Hispanic.

Research procedures were approved by New York University's Institutional Review Board. Adult participants provided written consent prior to participating in the study. Children and adolescents provided written assent, and their parents or guardians provided written consent on their behalf, prior to their participation. All participants were compensated $60 for the experimental session, which involved a 1-hour MRI scan. Participants were told that they would receive an additional bonus payment based on their performance in the experiment; in reality, all participants received an additional $5 bonus payment.

Prior to participating in the scanning session, child and adolescent participants who had never participated in a MRI study in our lab completed a mock scanning session to acclimate to the scanning environment. Mock scan sessions took place during a separate lab visit, at least one day in advance of scheduled scans. In the mock scanner, participants practiced staying as still as possible. We attached a Wii-mote to their heads, and set it to "rumble" whenever it sensed that the participant had moved. Participants completed a series of three challenges of increasing duration (10, 30, and 90 seconds) and decreasing angular tolerance (10, 5, and 2 degrees) in which they tried to prevent the Wii-mote from rumbling by lying very still (Casey et al., 2018).

Experimental tasks

Participants completed two blocks of three tasks (Figure 1), a variant of which we used in a previous behavioral study (Nussenbaum et al., 2020). Across tasks, participants made responses with two MRI-compatible button boxes, one for each hand. In between tasks, an experimenter reminded participants of the instructions for the next part, and participants viewed a diagram indicating which fingers and buttons they should use to make their responses. The tasks were presented using Psychtoolbox Version 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) for Matlab 2017a (Mathworks Inc, 2017) and displayed on a screen behind the scanner, visible to participants via a mirror attached to the MRI head coil. FMRI BOLD activity was measured over eight functional runs, which ranged in duration from approximately 4 to 7.5 minutes.

The structure of each block of tasks was identical, but their narratives and stimuli differed. In one set of tasks, participants were told that they had a collection of postcards they needed to mail. Each type of postcard in their collection required a different type of stamp.

In the *frequency-learning* task, participants were told they had to sort through their postcards to learn how many of each type they had. They were told that they had more of some types of

postcards relative to other types (e.g., they might have 5 postcards with the same, specific blue pattern but only 1 postcard with a specific red pattern (Figure 1)). Participants were instructed to try to keep track of how many of each kind of postcard they had, because it would be useful to them later on. Throughout the task, participants viewed 24 images of postcards. Twelve of these images were presented once and 12 of the images were presented five times, such that participants completed 72 trials total. On each trial, a postcard appeared in the center of the screen for 2 seconds. Across all tasks, stimulus presentation was followed by an inter-trial interval (ITI) of 2 - 6 seconds, which consisted of a black screen with a small, white fixation cross. Participants were instructed to press the button under their right index finger when they saw a new postcard they had not seen before and to press the button under their right middle finger when they saw a repeated postcard that they had already seen within the task. Participants were instructed to respond as quickly and as accurately as possible. The specific postcard assigned to each frequency condition (1 or 5) was counterbalanced across participants. The order of image presentation was randomized for each participant.

In the second task, the *associative encoding* task*,* participants were told that they would learn the correct stamp to put on each type of postcard. Participants were instructed that in the subsequent task, they would have to stamp all of their postcards, earning one point for each postcard stamped correctly. Critically, in the associative encoding task, regardless of the number of each type of postcard that they had (i.e., 1 or 5), participants saw each type of postcard with its corresponding stamp only *once*. Participants were instructed that they would earn more points if they focused on remembering the stamps that went on the types of postcards that they had the most of. Thus participants had equal exposure to the to-be-encoded associations across frequency conditions. On each trial, participants viewed one of the types of postcards from the frequency task next to an image of a unique stamp (5 s). The stamp-postcard pairs, order of the trials, and side of the screen on which the stamp and postcard appeared were randomized for each participant.

Next, participants completed *retrieval*. In the first part of the retrieval task, participants viewed all 24 unique postcards, one at time. When each postcard appeared, participants also saw four stamps: the correct stamp, a foil stamp that had been presented with a high-frequency postcard in the previous paired-associates task, a foil stamp that had been presented with a low-frequency postcard, and a novel stamp. Participants used the four fingers on their right hands to select one of these four stamps. Participants had six seconds to make their selection. Regardless of when they made their selection, the card and all four stamps remained on the screen for 6 seconds. After participants pressed a stamp, a faint, grey outline appeared around it. No feedback was given until the end of the set of tasks. The order of the postcard and the location of each stamp was randomized for each participant.

After stamping all 24 unique postcards once, participants' memory for the postcards' original frequencies was then probed. Participants again saw all 24 unique postcards, one at a time this time with the numbers 1 – 7 underneath them, and they were asked to provide *frequency reports*. Participants used three fingers on their left hand and all four fingers on their right hand to select

the number that they believed matched the number of times they saw the card in the first task. As in the previous task, participants had six seconds to make their selection. Regardless of when they made their selection, the card and all seven numbers remained on the screen for 6 seconds. After participants selected a number, a faint, grey outline appeared around it. The order of the postcards was randomized for each participant.

Finally, participants stamped all remaining postcards, such that they completed 48 additional memory test trials (i.e. they stamped each of the postcards in the 5-frequency condition four more times.) These trials were not included in any analyses, but their inclusion ensured that correctly encoding the stamps that belonged on the high-frequency postcards would be more valuable for participants despite each retrieval trial being worth 1 point. Here, participants had 4 seconds to make each response. We did not record neural data for this run, so each trial was followed by a 500-ms black screen with a white fixation cross. At the end of the memory test, participants saw a screen that displayed how many postcards they stamped correctly.

After completing the three tasks, participants were told that they were going to play a second set of similar games. The second set of tasks was identical to the first, except that the stimuli were changed from postcards and stamps to landscape pictures and picture frames. The order of the stimulus sets was counterbalanced across participants.

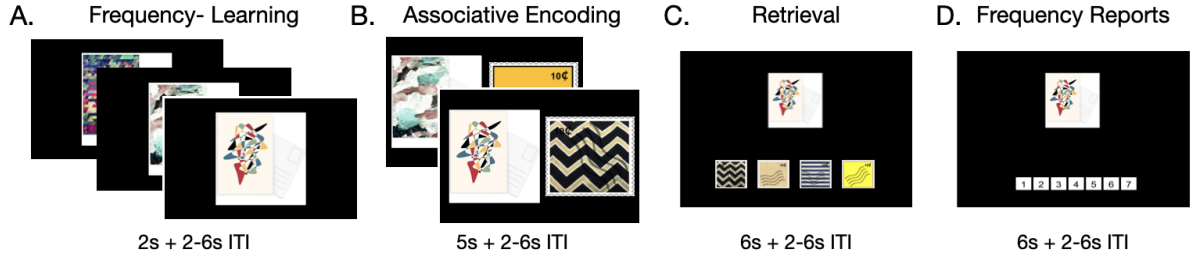

Figure 1. Task structure. Participants first learned the frequencies of each item (A) by viewing them in a continuous stream. They then were shown the information associated with each item (B). During retrieval, participants had to report the information associated with each item (C) as well as the item's original frequency (D).

Prior to entering the scanner, all participants completed a short task tutorial on a laptop to learn the overall task structure and the instructions for each part. The task tutorial comprised a full set of identical tasks but with only two stimuli within each frequency condition. Participants who first did the tasks with postcards completed a tutorial with four novel postcards and novel stamps; participants who first did the tasks with pictures completed a tutorial with four novel pictures and novel frames.

Child and adolescent participants were administered the Vocabulary and Matrix Reasoning subtests of the Wechsler Abbreviated Scale of Intelligence (WASI) (Wechsler, 2011) during the

mock scanning session. Adults were administered the same two subtests immediately following their scan. We followed the standard procedure to compute age-normed IQ scores for each participant based on their performance on these two sub-tests.

Analysis of behavioral data

All behavioral data processing and statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018). Data were combined across blocks. Trials in which participants failed to make a response were excluded from analyses. Mixed effects models were run using the 'afex' package version 0.21-2 (Singmann et al., 2020). Numeric variables were *z*-scored across the entire data set prior to their inclusion in each model. To determine the random effects structures of our mixed effects models, we began with the maximal model to minimize Type I errors (Barr et al., 2013). We set the number of model iterations to one million and use the "bobyqa" optimizer. When the maximal model gave convergence errors, we removed correlations between random slopes and random intercepts, and then random slopes for interaction effects. In all cases, these reduced models converged. For full details about the fixed- and random-effects structure of all models, see "Full Model Specification and Results" in the supplement. To test the significance of the fixed effects in our models, we used likelihood ratio tests for logistic models and F tests with Satterthwaite approximations for degrees of freedom for linear models. Mediation analyses were conducted with the "mediation" R package (Tingley et al., 2014) and significance of the mediation effects was assessed via 1,000 bootstrapped samples.

Across our behavioral analyses, to test for non-linear effects of age, we first compared the fit of models with a linear age term and with both a linear and quadratic age term (Braams et al., 2015; Somerville et al., 2013). We dropped the quadratic age term when it did not significantly improve model fit. Because we observed a significant relation between age and age-normed WASI scores in our sample (β = -.60, SE = .26, p = .0238), to control for age differences in reasoning ability, we included age-normed WASI scores as an interacting fixed effect in all analyses.

Image acquisition, preprocessing, and quality assessment

Participants were scanned at New York University's Center for Brain Imaging using a Siemens Prisma 3T MRI scanner with a 64-channel head coil. Anatomical data were acquired with high-resolution, T1- weighted anatomical scans 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 with the following parameters: 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).

All anatomical and functional MRI data were preprocessed using fMRIPrep v.1.5.1rc2 (Esteban et al., 2019), a robust preprocessing pipeline that adjusts to create the optimal workflow for the input dataset, and then visually inspected. Runs in which more than 15% of TRs were censored for motion (relative motion > .9 mm framewise displacement) were excluded from neuroimaging analyses (see Supplement for the number of participants included in each analysis). Participants who did not have at least one usable run of each task (frequency-learning, associative encoding, retrieval), were excluded from all behavioral and neuroimaging analyses (n = 8), leaving N = 90 participants in our analyzed sample.

Analysis of fMRI data

Statistical analyses were completed in FSL v. 6.0.2. (Jenkinson et al., 2012; Smith et al., 2004). Preprocessed BOLD data, registered to fMRIPrep's MNI152 template space and smoothed with a 5mm Gaussian kernel, were combined across runs via fixed-effects analyses and then submitted to mixed-effects GLM analyses, implemented in FEAT 6.0.0 (Mark W. Woolrich et al., 2004; M. W. Woolrich et al., 2001), to estimate relevant task effects. For all GLM analyses, nuisance regressors included six motion parameters and their derivatives, framewise displacement values, censored frames, the first six anatomical noise components (aCompCor) from fMRIPrep, and cosine regressors from fMRIprep to perform high-pass filtering of the data. All task-based temporal onset regressors were convolved with a double gamma hemodynamic response function and included temporal derivatives. Analyses were thresholded using a whole-brain correction of $z > 3.1$ and a cluster-defining threshold of $p < .05$ using FLAME 1.

Frequency-learning GLM. Our frequency-learning model included six task-based temporal onset regressors. Trials were divided based on appearance count and frequency condition to create the following regressors: 1) Low-frequency items the first (and only) time they appeared, 2) High-frequency items the first time they appeared, 3) High-frequency items the second time they appeared, 4) High-frequency items the third time they appeared, 5) High-frequency items the fourth time they appeared, 6) High-frequency items the fifth time they appeared.

Repetition suppression analyses. For each stimulus in the high-frequency condition, we computed an index of repetition suppression by measuring the reduction in neural activation from the *first* to the *last* appearance of the item during frequency-learning within a parahippocampal ROI. We defined our ROI by taking the peak voxel ($x = 30$, $y = -39$, $z = -15$) from the group-level first > last item appearance contrast for high-frequency items during frequency-learning and drawing a 5 mm sphere around it. This voxel was located in the right parahippocampal cortex, though we observed widespread and largely symmetric activation in bilateral parahippocampal cortex. To encompass both left and right parahippocampal cortex within our ROI, we mirrored the peak voxel sphere. For each participant, we modeled the neural response to the first and last appearance of each item using the Least Squares-Separate approach (Mumford et al., 2014).

Each first-level model included a regressor for the trial of interest, as well as separate regressors for the onsets of all other items, grouped by repetition number (e.g., a regressor for item onsets on their first appearance, a regressor for item onsets on their second appearance, etc.). We then created a "repetition suppression index" for each high-frequency item by computing the difference in mean beta values within our ROI on its first and last appearance. Repetition suppression indices that fell outside three standard deviations from the mean index across all subjects were excluded from subsequent analyses (16 out of 2040 values).

Associative encoding and retrieval GLMs. Our associative encoding and retrieval models included six task-based temporal onset regressors. Trials were divided based on frequency condition (high- vs. low-) and subsequent memory (remembered, forgotten, missed). Missed trials were included as nuisance regressors and not included in any contrasts.

Associative encoding regions of interest (ROIs). Given our *a priori* hypotheses about the role of the prefrontal cortex and striatum in value-guided encoding, we examined neural activation within a prefrontal cortex and striatal ROI. The specific ROIs were determined by taking the peak prefrontal voxel ($x = -51$, $y = 42$, $z = 9$) and the peak striatal voxel ($x = -18$, $y = 12$, $z = 6$) from the group-level high > low value associative encoding contrast and drawing 5mm spheres around them.

Results

Experiential learning of environmental statistics improved with age

During frequency learning, participants across our age range responded to new and repeated items with a high degree of accuracy (new Items: *mean* = .90, *SD* = .30; repeated items: *mean* = .92, *SD* = .27). Participants' accuracy in correctly identifying both new and repeated items improved with increasing age (*new items:* $\chi2(1) = 25.54$, $p < .001$, *repeated items:* $\chi2(1) = 33.81$, $p < .001$). Participants were also more accurate in identifying items as 'repeated' as the number of times they saw each item increased, $\chi2 = 138.20$, $p < .001$, indicating learning throughout the task. This effect varied as a function of age — younger participants demonstrated a larger effect of the number of item repetitions on response accuracy, as indicated by a significant interaction, $\chi2(1) = 17.52$, $p < .001$.

Response times to both new and old items decreased nonlinearly with age (*new items:* age: $F(1, 84.37) = 8.60$, $p = .004$, quadratic age: $F(1, 83.07) = 4.61$, $p = .035$; *old items:* age: $F(1, 83.85) = 11.61$, $p = .001$, quadratic age: $F(1, 83.39) = 7.69$, $p = .007$), such that reaction times decreased steeply throughout childhood before leveling off into late adolescence and early adulthood. Finally, response times for old items also decreased as the number of item repetitions increased, $F(1, 73.49) = 286.87$, $p < .001$.

Participants' ability to distinguish old from new items was associated with a wide network of neural regions, some of which demonstrated greater activation in response to the last vs. first appearance of each item, and others of which demonstrated suppressed activation across repetitions. Specifically, whole-brain contrasts revealed greater recruitment of regions of the lateral occipital cortex, the frontal pole, precuneus, angular gyrus, and caudate (among other regions, see Figure 2A and Supplementary Table S12), on the last vs. first appearance of each item. We observed widespread repetition suppression effects, reflected in *decreases* in neural responsivity in the lateral occipital cortex and temporal occipital cortex on the last vs. first appearance of each item. In line with our hypothesis, we also observed a robust decrease in activation in the parahippocampal cortex (Figure 2B, Supplementary Table S13).

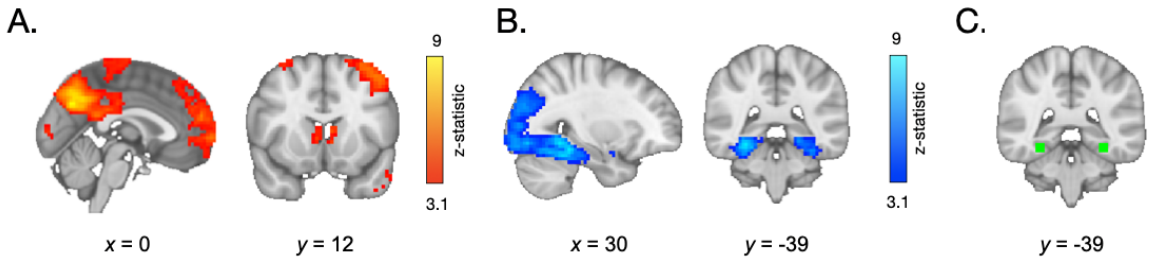

Figure 2: (A) During frequency-learning**,** participants demonstrated increased recruitment of regions in the frontal cortex, angular gyrus, and striatum on the last vs. first appearance of high-frequency items. (B) They demonstrated *decreased* activation in the lateral occipital cortex, temporal occipital cortex, and parahippocampal cortex. (C) Within a parahippocampal ROI (shown in green), the decrease in responses to each stimulus on its last vs. first appearance was greater in older participants.

We next examined whether repetition suppression in a parahippocampal region of interest changed with age (Figure 2C). Here, we observed a positive main effect of linear age, $F(1, 79.73) = 4.04$, $p = .048$ and a negative effect of quadratic age, $F(1, 79.94) = 5.15$, $p = .026$. This pattern of age-related change suggests that repetition suppression increased into adulthood, with the steepest increases occurring in late adolescence and early adulthood (Supplementary Figure S2). Taken together, our behavioral and neural results suggest that sensitivity to the frequency of items in the environment was prevalent from childhood to adulthood, but increased with age.

Age-related change in explicit knowledge of environmental structure

Could participants transform their sensitivity to environmental statistics into explicit reports of item frequency? To address this question, we computed participants' frequency report error magnitudes by taking the absolute value of the difference between the item's true frequency (i.e., 1 or 5) and participant's explicit report of its frequency (i.e., 1 - 7). We then examined how these report error magnitudes varied as a function of age and frequency condition. We observed main effects of both age ($F(1, 82.79) = 12.55$, $p < .001$) and quadratic age ($F(1, 82.73) = 8.68$, $p = .004$); error magnitudes decreased sharply throughout childhood before leveling off in late adolescence and into adulthood (Children: *Mean* = 1.48, *SD* = 1.34; Adolescents: *Mean* = 1.10, *SD* = 1.12; Adults: *Mean* = 1.13, *SD* = 1.05). Error magnitudes were not related to frequency

condition (p = .894), indicating that participants were not systematically better at representing the 'true' frequencies of items that appeared once or items that appeared five times.

To examine relations between online frequency learning and explicit knowledge, we tested whether repetition suppression indices for each item related to frequency reports. We hypothesized that participants would report the items that elicited the greatest repetition suppression as the most frequent. However, in line with other studies suggesting dissociations between repetition suppression and explicit memory (Ward et al., 2013), we did not observe any relation between repetition suppression and frequency reports, $F(1, 1068.02) = 0.00$, $p = .962$. Thus while we observed parallel developmental improvements in online frequency learning and subsequent explicit reports, they may be driven by separable processes.

Age-related change in value-guided memory

Participants' frequency-learning performance and their explicit frequency reports indicate that older participants were better both at tracking repetitions of items within their environments and at explicitly representing item frequencies. Were participants able to use these representations of the structure of their environment to prioritize memory for high-value information? To address this question, we examined how frequency condition and age influenced memory accuracy. Memory accuracy varied as a function of both linear ($\chi2(1) = 8.71$, $p = .003$) and quadratic age ($\chi2(1) = 4.28$, $p = .039$), such that older participants demonstrated higher memory accuracy, with the steepest improvements in memory accuracy occurring from childhood into early adolescence (Figure 3). In line with our hypothesis, we observed a main effect of frequency condition on memory, $\chi2(1) = 21.51$, $p <.001$, indicating that individuals used naturalistic value signals to prioritize memory for high-value information. Critically, this effect interacted with both linear age ($\chi2(1) = 11.03$, $p < .001$) and quadratic age ($\chi2(1) = 9.51$, $p = .002$), such that the influence of frequency condition on memory increased to the greatest extent throughout childhood and early adolescence.

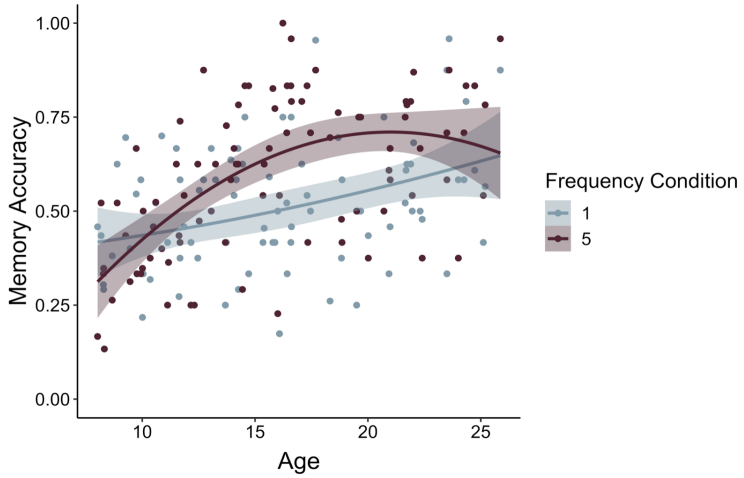

Figure 3. Participants demonstrated prioritization of memory for high-value information, as indicated by higher memory accuracy for associations involving items in the five- relative to the one-frequency condition. The effects of item frequency on associative memory increased throughout childhood and into adolescence.

Neural mechanisms of value-guided encoding

We next examined how neural activation during encoding supported the use of learned value to guide memory. Specifically, we examined whether participants demonstrated different patterns of neural activation during encoding of information associated with high- vs. low-frequency items. In line with our hypothesis, a whole-brain contrast revealed increased engagement of the left lateral PFC and bilateral caudate (1765 voxels at $x = -51$, $y = 42$, $z = 9$; 232 voxels at $x = 18$, $y = 12$, $z = 6$; and 54 voxels at $x = 18$, $y = 18$, and $z = 12$; Figure 4A) during encoding of the pairs involving high-frequency items. To examine how this pattern of activation related to behavior, we computed a 'memory difference score' for each participant by subtracting their memory accuracy for associations involving low-frequency items from their accuracy for associations involving high-frequency items. We then included these memory difference scores as a covariate in our group-level GLM examining neural activation during encoding of pairs involving high- vs. low-frequency items. Participants who demonstrated the greatest difference in memory accuracy for pairs involving high-frequency vs. low-frequency items also demonstrated greater value-based modulation of left lateral PFC activation (232 voxels at $x = -48$, $y = 21$, $z = 27$; Figure 4B).

Because participants demonstrated effects of value on memory, neural signatures of encoding high vs. low-value information may reflect successful vs. unsuccessful encoding. To de-confound the effects of value vs. subsequent memory accuracy on neural activation at encoding, we re-ran our high vs. low-value contrast but restricted our analysis to associations that were subsequently retrieved correctly. We observed similar neural effects — increased recruitment of the left lateral prefrontal cortex and left caudate during encoding of high- vs. low- value pairs (1042 voxels at $x = -42$, $y = 15$, $z = 30$; 124 voxels at $x = -12$, $y = -3$, $z = 9$). Further, neural signatures of successful vs. unsuccessful encoding differed from those of high- vs. low-value encoding. Though we observed similar activation in left lateral PFC (1273 voxels at $x = -48$, $y = 9$, $z = 27$), here, we did not observe differential recruitment of the caudate. In addition, consistent with previous observations of subsequent memory effects (Davachi, 2006), successful encoding was associated with increased activation in the right hippocampus (21 voxels at $x = 24$, $y = -6$, $z = -21$).

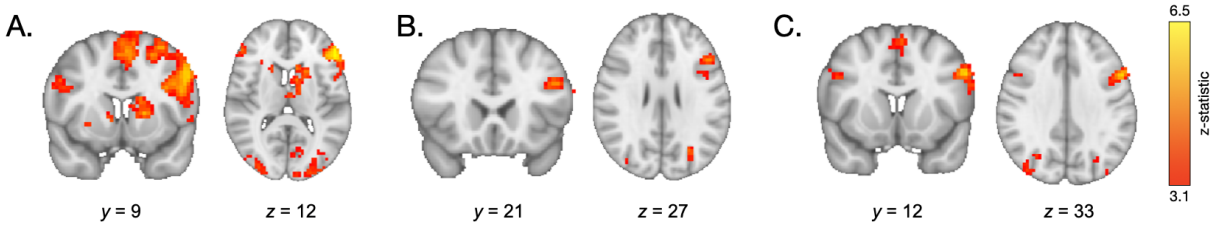

Figure 4: (A) During encoding of associations involving high- vs. low-frequency items, participants demonstrated greater engagement of the lateral PFC and caudate. (B) Participants who demonstrated the greatest value-based modulation of memory also demonstrated the greatest modulation of left prefrontal cortical activation during encoding of high- vs. low-value associations. (C) During encoding of both high- and low-value pairs**,** older participants demonstrated greater recruitment of the PFC relative to younger participants.

Age-related change in neural activation during encoding

Next, we examined how neural activation during encoding changed with age. Across trial types, during encoding, we observed widespread age-related increases in neural activation (Supplementary Table S14), in regions including the left lateral PFC (120 voxels at x = -54, y = 12, z = 33) and the right lateral PFC (24 voxels at x = 48, y = 12, z = 30; Figure 4C).

To address our main question of interest — how age-related change in differential neural activation during the encoding of high- vs. low-value information may support the development of adaptive memory — we conducted two ROI analyses focused on the caudate and PFC (see 'methods'). Specifically, for the high- vs. low-value encoding contrast, we examined how the mean parameter estimate across voxels within each ROI related to both linear and quadratic age. Caudate activation did not vary significantly as a function of either linear (β = -.90, SE = .75, p = .237) or quadratic (β = 1.08, SE = .74, p = .15) age, indicating that participants across our age range demonstrated similarly increased recruitment of the caudate while encoding high- vs. low-value associations. PFC activation, however, demonstrated a different pattern, varying as a function of both linear (β = 1.97, SE = .74, p = .01) and quadratic age (β = -1.73, SE = .73, p = .021), such that the difference in PFC engagement during encoding of high- vs. low-value associations increased to the greatest extent throughout childhood and early adolescence (Supplementary Figure S3).

The pattern of age-related change that we observed in the PFC recruitment mirrored the age-related differences we observed in value-based memory. Given these parallel age effects across brain and behavior, we next asked whether age differences in PFC recruitment could account for our observed age differences in adaptive memory prioritization. First, we confirmed that in line with our whole-brain analysis, PFC modulation predicted memory difference scores, even when controlling for age (β = .34, SE = .10, p = .001). Next, we confirmed that these difference scores did in fact vary with age (β = .22, SE = .10, p = .041), with older participants demonstrating a larger difference in memory accuracy for high- vs. low- value associations. Critically, however, when controlling for PFC activation, age no longer related to memory difference scores (β = .15, SE = .10, p = .14). A formal mediation analysis revealed that PFC activation fully mediated the relation between linear age and memory difference scores (standardized indirect effect: .07, 95% confidence interval: [.011, .15], p = .02; standardized direct effect; .15, 95% confidence interval: [-.03, .33], p = .108; Figure 5). This relation was directionally specific; age did *not* mediate the relation between PFC activation and memory difference scores (standardized indirect effect: .03, 95% confidence interval: [-.006, .08], p = .13; standardized direct effect; .34, 95% confidence interval: [.14, .53], $p < .001$). Further, when we included quadratic age and IQ as control variables in the mediation analysis, PFC activation continued to mediate the relation between linear age and memory difference scores (standardized indirect effect: .58, 95% confidence interval: [.11, 1.29], p = .008; standardized direct effect; 1.91, 95% confidence interval: [.72, .3.48], p = .012).

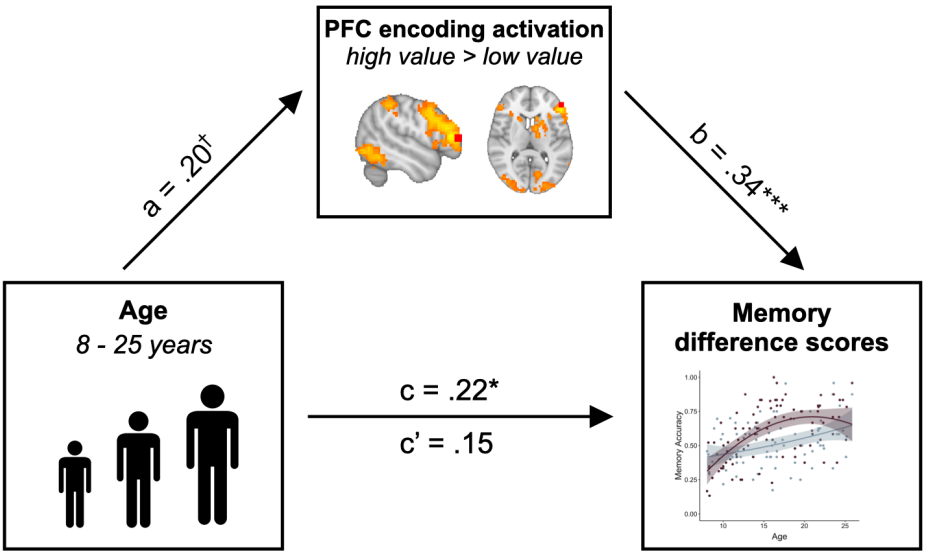

Figure 5. The increased engagement of left lateral PFC (ROI depicted in red) during encoding of high- vs. low-value information mediated the relation between age and memory difference scores. Path a shows the regression coefficient of the relation between age and PFC modulation. Path b shows the regression coefficient of the relation between PFC activation and memory difference scores, while controlling for age. Paths c and c' show the regression coefficient of the relation between age and memory difference scores without and while controlling for PFC activation, respectively. † denotes $p < .06$, * denotes $p < .05$, ** denotes $p < .01$.

Age- and value-based modulation of neural activation during retrieval

We next examined how the neural mechanisms of memory retrieval were influenced by both age and learned value signals. As during encoding, we observed age-related differences in bilateral PFC recruitment (Figure 6A; 42 voxels at $x = 51$, $y = 3$, $z = 21$; 36 voxels at $x = -60$, $y = 6$, $z = 21$) as well as regions of occipital cortex (see Supplementary Table S18) across trials during retrieval. We further tested whether participants demonstrated value-based modulation of neural activation at retrieval. During retrieval of associations involving high- vs. low-frequency items, we continued to observe increased engagement of the left lateral PFC (Figure 6B; 116 voxels at $x = -48$, $y = 21$, $z = 24$) and the bilateral caudate (128 voxels at $x = -12$, $y = -6$, $z = 15$ and 77 voxels at $x = 15$, $y = -3$, $z = 21$). This activation was not modulated by age or memory difference scores.

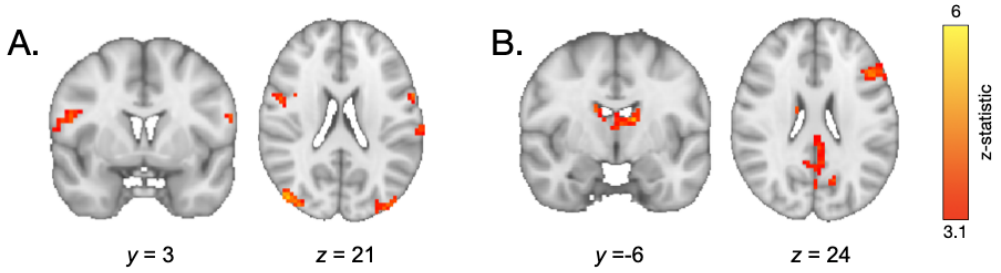

Figure 6: (A) During retrieval**,** older participants demonstrated greater recruitment of the inferior frontal cortex relative to younger participants. (B) During retrieval of associations involving high- vs. low-frequency items, participants demonstrated greater engagement of the left lateral PFC and bilateral caudate.

Two distinct value representations influence memory

The overlap between the engagement of the neural systems we observed during encoding of high- vs. low-value information and those observed in prior studies of motivated memory that have used explicit value cues (M. S. Cohen et al., 2014, 2019) suggests that participants did indeed use learned regularities as value signals to guide memory. To what extent was memory supported by explicit representations of item frequency versus sensitivity to statistical regularities during frequency-learning? To examine the influence of these two types of value representations across age, we ran additional mixed-effects models. First, we examined how participants' explicit representations of item frequency related to memory. Participants demonstrated better associative memory for pairs involving items they reported were more frequent, $\chi2(1) = 31.93$, $p < .001$ (Figure 7A). This effect was modulated by age ($\chi2(1) = 10.69$, $p = .001$) and quadratic age ($\chi2(1) = 9.89$, $p = .002$), indicating that participants' beliefs about item frequency influenced memory to the greatest degree in adolescence and early adulthood. Further, replicating our previous behavioral findings (Nussenbaum et al., 2020), we found that the linear model including explicit frequency reports (BIC = 5417.7) fit the data *better* than the linear model including the true frequency condition (BIC = 5433.6, $\chi2 = 15.39$, $p < .001$), indicating that participants' *representations* of item frequency influenced memory to a greater extent than the true item frequencies.

We further examined whether our neural measure of online frequency learning related to associative memory. Specifically, we asked whether greater sensitivity to item repetitions — as indexed by greater repetition suppression within the parahippocampal cortex — promoted better encoding of associative information. Because we only had repetition suppression indices for items that appeared five times, our analysis was restricted to associations involving high-frequency items. We found that repetition suppression during frequency-learning did indeed predict subsequent associative memory, $\chi2(1) = 9.95$, $p = .002$ (Figure 7B). This effect did not interact with age, $\chi2(1) = .46$, $p = .499$. Further, when we included both repetition suppression indices and explicit frequency reports in our model, *both* predictors continued to explain significant variance in memory accuracy (Frequency reports: $\chi2(1) = 24.82$, $p < .001$, Repetition suppression: $\chi2(1) = 8.45$, $p = .004$), suggesting that learned value signals that guide memory may be derived from multiple, distinct representations of prior experience.

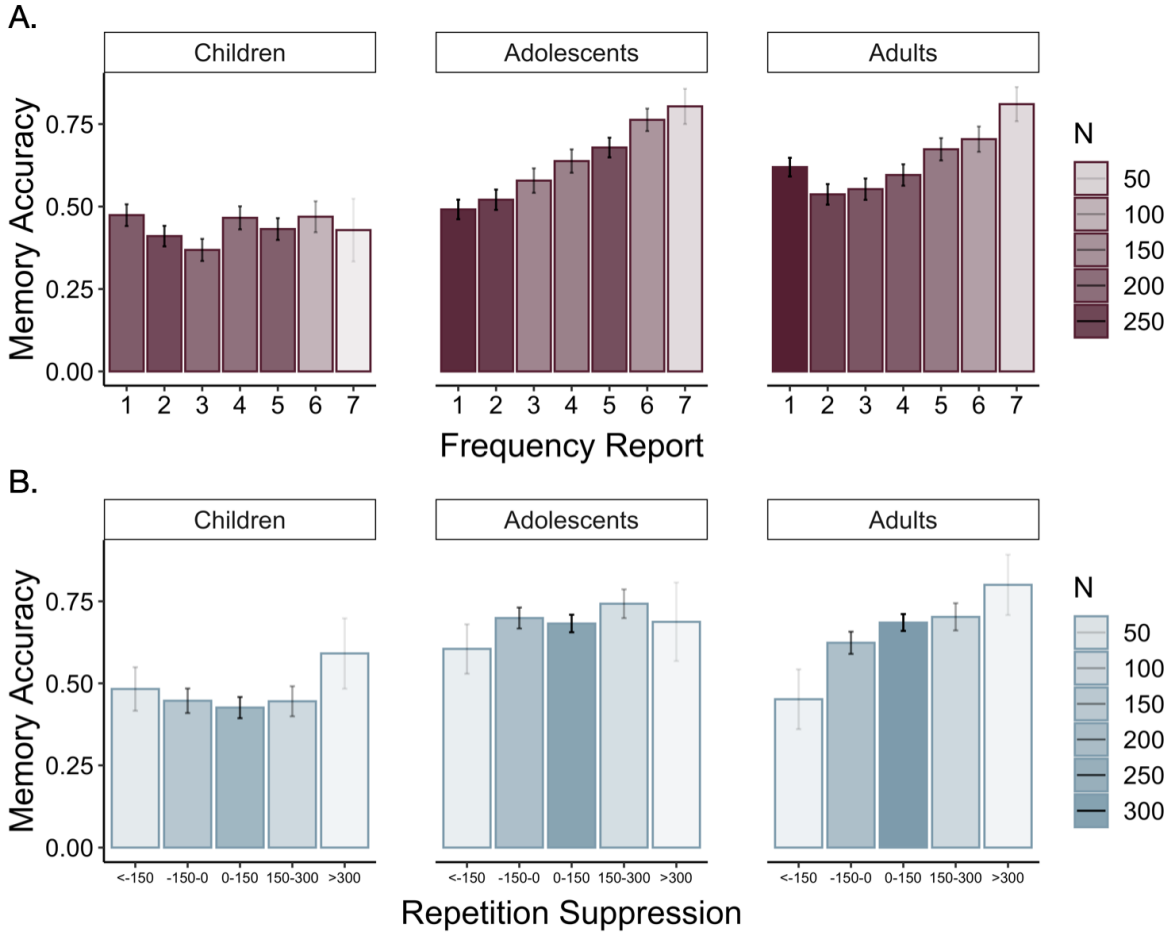

Figure 7. (A) Participants demonstrated increased associative memory accuracy for items that they reported as being more frequent. This effect strengthened with increasing age. (B) Participants also demonstrated better memory for associations involving high-frequency items to which they demonstrated the greatest repetition suppression during frequency-learning. In both panels, the shading of the bars represents the number of trials in which participants provided that frequency report.

Discussion

Prioritizing memory for useful information is essential throughout individuals' lifetimes, but no prior work has investigated the development of the neural mechanisms that support value-guided memory prioritization from childhood to adulthood. The goal of the present study was to characterize how developmental change in the neurocognitive processes that support both the *learning* and *use* of information value support improvements in adaptive memory from childhood to adulthood. In line with studies of motivated memory in adults (M. S. Cohen et al., 2014), we found that during encoding and retrieval, high- relative to low-value stimuli elicited increased activation in regions sensitive to value and motivational salience, including the caudate (Delgado et al., 2004), and those associated with strategic control processes, including the lateral PFC

(Badre & Wagner, 2007; Cole & Schneider, 2007; Power & Petersen, 2013). Further, replicating previous work, we found that value-guided memory selectivity improved across childhood and adolescence (Castel et al., 2011; Hanten et al., 2007; Nussenbaum et al., 2020). Critically, here we demonstrate that increased engagement of the lateral PFC during encoding mediated the relation between age and memory selectivity. This relation was specific to the lateral PFC — though the caudate similarly demonstrated increased activation during encoding of high- vs. low-value information, value-based modulation of caudate activation did not vary as a function of age and did not relate to memory selectivity.

Two different signatures of value-learning predicted subsequent associative memory: Individuals demonstrated better memory for associations involving items that elicited stronger repetition suppression as well as for items that they reported as being more frequent. Moreover, the relation of these learning signals to memory performance varied with age. While all participants demonstrated a similar relation between repetition suppression and subsequent associative memory, the association between explicit frequency reports and memory was greater in older participants. These divergent developmental trajectories suggest that the influence of learned value on memory arises through distinct cognitive processes. One possibility is that while explicit beliefs about information value triggered the engagement of strategic control, stimulus familiarity (as indexed by repetition suppression (Gonsalves et al., 2005)) may have facilitated encoding of novel associations, even in the absence of controlled strategy use. Indeed, prior work suggests that stronger memory traces for constituent components enhances associative memory (Popov & Reder, 2020; Reder et al., 2016). However, in our previous behavioral work (Nussenbaum et al., 2020), we found that removing the relation between item frequency and reward value eliminated the memory benefit for associations involving high-frequency items, suggesting that stimulus familiarity itself did not account for the influence of item frequency on memory in our task. Still, when frequency does predict value, stimulus familiarity may serve as a proxy for information utility. This familiarity signal may exert age-invariant effects on subsequent memory, whereas explicit beliefs about item frequency may more strongly facilitate subsequent memory with increasing age.

Beyond these developmental differences in the processes involved in learning the value of information, our neural results further suggest that developmental differences in memory were driven strongly by the *use* of prior learning to guide encoding. Specifically, we observed age-related increases in both overall PFC engagement as well as its value-based modulation, which may reflect developmental changes in the engagement of strategic control. The PFC may support enhanced attention (Uncapher et al., 2011; Uncapher & Wagner, 2009) and semantic elaboration (Kirchhoff & Buckner, 2006) during encoding, and more focused (Wais et al., 2012) and organized search and selection (Badre & Wagner, 2007; Yu et al., 2018) during retrieval. From childhood to young adulthood, individuals demonstrate improvements in the implementation of strategic memory processes (Bjorkland et al., 2009; Yu et al., 2018), which are paralleled by increases in PFC recruitment during both encoding and retrieval (Ghetti et al., 2010; Ghetti & Fandakova, 2020; Ofen et al., 2007; Shing et al., 2016; Tang et al., 2018). In line with this prior work, we

similarly observed age-related improvements in overall memory performance and in prefrontal recruitment during encoding and retrieval of novel associations. However, the development of adaptive memory requires not just the implementation of encoding and retrieval strategies, but the flexibility to up- or down-regulate the engagement of control in response to momentary fluctuations in information value (Castel, 2007; Castel et al., 2013; Hennessee et al., 2017). Importantly, here, we found that value-based modulation of lateral PFC engagement during encoding mediated the relation between age and memory selectivity, suggesting that developmental change in value-guided control may underpin the emergence of adaptive memory prioritization. Prior work examining other neurocognitive processes, including response inhibition (Insel et al., 2017) and selective attention (Störmer et al., 2014), has similarly found that increases in the flexible upregulation of control in response to value cues enhance goal-directed behavior across development (Davidow et al., 2018), and may depend on the engagement of both striatal and prefrontal circuitry (Hallquist et al., 2018; Insel et al., 2017). Here, we extend these past findings to the domain of memory, demonstrating that learned value signals increasingly elicit prefrontal cortex engagement and strengthen goal-directed encoding across development.

We did not observe differences in hippocampal engagement during encoding or retrieval of high- vs. low-value associates. This is somewhat surprising, as prior work has suggested that value cues bolster memory through their influence on medial temporal lobe activity (Adcock et al., 2006). However, because our task required the use of *learned* value signals, memory retrieval processes may have been required on every encoding trial to recall the frequency of each item. Thus, all items presented at encoding may have triggered the engagement of hippocampal-dependent retrieval processes (Squire, 1992) that underpin many forms of memory-guided behavior including attention (Stokes et al., 2012; Summerfield et al., 2006) and decision-making (Murty et al., 2016; Shadlen & Shohamy, 2016; Wang et al., 2020). Further, in line with prior work (Davachi, 2006), we did observe increased activation in the hippocampus during encoding of associations that were subsequently remembered vs. those that were subsequently forgotten. Medial temporal activation, including hippocampal activation, may thus more strongly reflect successful memory formation — whether or not it was facilitated by value — whereas the caudate and lateral prefrontal cortex may be more sensitive to fluctuations in the engagement of value-guided cognitive control.

There are multiple routes through which value signals influence memory (M. S. Cohen et al., 2019), and in many contexts, reward-motivated memory may not require strategic control. Value anticipation and reward delivery lead to dopaminergic release in the VTA, which projects not only to corticostriatal circuits that implement goal-directed strategy selection (Liljeholm & O'Doherty, 2012), but also directly to the hippocampus and medial temporal lobes (Adcock et al., 2006; Lisman & Grace, 2005; Murty et al., 2017; Shohamy & Adcock, 2010; Stanek et al., 2019). Given the earlier development of subcortically restricted circuitry relative to the more protracted development of cortical-subcortical pathways (Somerville & Casey, 2010), it may be the case that the *direct* influence of reward on memory develops earlier than the controlled pathway we studied here. Rather than eliciting strategic control through incentivizing successful memory, this pathway

can be engaged through direct delivery of rewards or reinforcement signals at the time of encoding (Ergo et al., 2020; Jang et al., 2019; Rosenbaum et al., 2020; Rouhani et al., 2018). In one such study, adolescents demonstrated greater reward-based modulation of hippocampal-striatal connectivity than adults, and the strength of this connectivity predicted reward-related memory (Davidow et al., 2016). However, other studies have not found evidence for developmental change in the influence of valenced outcomes on memory (A. O. Cohen et al., 2019; Katzman & Hartley, 2020). The influence of different motivational and reward signals on memory across development may not be straightforward — individual and developmental differences in neurocognitive processes including sensitivity to valenced feedback (Ngo et al., 2019; Rosenbaum et al., 2020), curiosity (Fandakova & Gruber, 2021), and emotional processing (Adelman & Estes, 2013; Eich & Castel, 2016) may interact, leading to complex relations between age, motivation, and memory performance. Further work is needed to characterize both the influence of different types of reward signals on memory across development, as well as the development of the neural pathways that underlie age-related change in behavior.

The present study contributes to our understanding of the neurocognitive mechanisms that support memory across development. Specifically, we addressed the question of how motivated memory may operate in the absence of explicit value cues by examining the development of the neurocognitive mechanisms that support the *learning* and *use* of information value to guide encoding and retrieval. The present findings suggest that while development is marked by improvements in the ability to learn about the statistical structure of the environment, the emergence of adaptive memory also depends centrally on age-related changes in prefrontal control. Our findings demonstrate that prefrontal cortex development has implications not just for general memory processes but for the selective prioritization of useful information — a key component of adaptive memory throughout the lifespan.

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Author contributions

K.N. and C.A.H. designed the experiment. K.N. collected and analyzed the data under the supervision of C.A.H. K.N. drafted the manuscript and C.AH. provided critical feedback and revisions. All authors approved the final manuscript prior to submission.

Competing interests

The authors have no competing interests to declare.

Data and code availability

Task code, behavioral data, and analysis code are available on the Open Science Framework:
https://osf.io/2fkbj/?view_only=87caf5ce7c924e14a41bb09e83a64866

Unthresholded *z*-statistic maps from the neuroimaging analyses are available on Neurovault:
https://neurovault.org/collections/BUMNZQXA/

Upon publication, BIDS-formatted neuroimaging data will be made public on Open Neuro:
https://openneuro.org/datasets/ds003499