Ventromedial prefrontal cortex supports prototype representations in healthy older adults

Caitlin R. Bowman[1,2] and Dagmar Zeithamova[1]

[1] Department of Psychology, University of Oregon

[2] Department of Psychological and Brain Science, University of Wisconsin-Milwaukee

Abstract

The ability to learn broad concepts from individual instances is relevant throughout our lifespans as new concepts enter the world, and we seek to acquire new skills and hobbies that can enrich our lives. While older age has been associated with declines in the ability to remember individual instances, less is known about how these declines impact concept learning and generalization or the neural systems that older adults recruit to support abstraction. In the present study, young and older adults completed a category learning task while undergoing fMRI. We fit formal prototype and exemplar models to behavioral and brain data – models that differentially index concept learning based on abstraction versus memory for individual category members. We found that the fit of both models to behavior was poorer in older adults, but older adults were more likely than young adults to be best fit by the prototype model and less likely to be best fit by the exemplar model. We also found that young and older adults recruited anterior hippocampus and VMPFC to a comparable degree to support prototype-based generalization. In contrast, older adults showed weaker old/new discrimination of category members in a set of occipital and parietal regions. These results suggest that the age-related increase in prototype reliance in behavior may be driven by declines in memory for specific exemplars coupled with a relatively intact neural system for representing prototypes.

Keywords: memory, categorization, fMRI, prototype, exemplar, hippocampus, VMPFC

Highlights

- Young and older participants categorized cartoon animals while undergoing fMRI, and we fit prototype and exemplar models to their behavioral and brain responses.
- Prototype model fits to behavior were poorer in older adults than young adults, but the prototype model more consistently outperformed the exemplar model in older adults.
- A similar pattern of anterior hippocampus and VMPFC prototype correlates emerged across age groups, with numerically weaker effects in older adults.
- While age differences in neural exemplar correlates were minimal, young adults showed stronger discrimination of old versus new category members than older adults across several occipital and parietal regions.

1. Introduction

It is well established that decline in the ability to remember details of individual experiences is part of normal aging (Alghamdi & Rugg, 2020; Hashtroudi et al., 1989; Prull et al., 2006; Stark et al., 2010). Yet, remembering specific experiences is not the only way we use memory; we also use memory to extract commonalities across experiences to derive generalizable knowledge (Morton & Preston, 2021; Schapiro et al., 2017; Zeithamova & Bowman, 2020). Yet, how older age affects memory generalization is not well understood. On the one hand, some memory theories posit that the same memory representations underlie the ability to remember specific episodes and the ability to generalize (Hintzman, 1984; Kumaran & McClelland, 2012; Nosofsky, 1988), in which case we would expect declines in memory specificity to also have negative consequences for older adults' generalization abilities. On the other hand, there are a constellation of memory abilities that are relatively intact in older age that could, in theory, support generalization. Older adults tend to encode common features across experiences and extract their meaning, or 'gist' (Brainerd & Reyna, 2002, 2015) rather than the details that distinguish between similar experiences (Bowman et al., 2019; Bowman & Dennis, 2015; Gallo et al., 2006; Koutstaal & Schacter, 1997). Partial overlap with prior experience is more likely to trigger retrieval (i.e., pattern completion) in older compared to young adults (Vieweg et al., 2015; Wilson et al., 2006; Wynn et al., 2021). These findings point to ways that older adults' memory abilities may be well suited to forming memory representations that integrate across experiences, which can then support generalization.

Because categorization typically involves both learning of individual category members and generalization to new examples, it is well suited to addressing how older age impacts the ability to form specific vs. abstracted memory representations. Aging studies of categorization have generally shown age deficits in categorization

performance, with the degree of the deficit differing by category structure and task (for review see Bowman et al., 2023). Studies have shown small to no age deficit in learning typical category members, but larger age deficits for atypical or exception items (Bowman et al., 2022; T. Davis et al., 2012; Valdez et al., in press). Prior work has also shown that age differences in categorization arise primarily in learning, with little to no evidence of a generalization-specific deficit (Bowman et al., n.d.) and sometimes even age-matched generalization performance despite deficits in learning performance (Bowman et al., 2022). Thus, there is some evidence that older adults learn individual category members less well than young adults, but that this deficit does not always have a major impact on their ability to generalize.

Further, categorization is a useful domain for testing representations underlying memory judgments because there are longstanding models of categorization that differentially emphasize memory specificity versus integration and abstraction. The exemplar model posits that categories are represented by individual category members stored in memory and that generalization involves joint retrieval of these individual category members to determine the similarity between the to-be-categorized example and the stored examples (Medin & Schaffer, 1978; Nosofsky, 1991). The prototype model, in contrast, posits that categories are represented by prototypes – an idealized category representation that is abstracted from the individual examples (Minda & Smith, 2011; Posner & Keele, 1968). Prototype-based generalization involves determining the similarity between a to-be-categorized example and relevant category prototypes. Based on older adults' relatively intact gist-based memory and declines in memory specificity, one might expect older adults to be more likely than young adults to rely on prototype representations. Yet, the use of formal exemplar versus prototype modeling in aging studies has been limited, and the findings have been mixed. Formal model fits have sometimes pointed to older adults being less likely than young adults to rely on an

exemplar strategy and/or more likely to rely on prototypes (Bowman et al., 2022; Mata et al., 2012). Other findings showed similar strategies across age groups (Mata et al., 2012; Schenk et al., 2016; Valdez et al., in press). Thus, further evidence is needed to understand how older age affects prototype- and exemplar-based categorization.

Another advantage of the categorization domain is that latent variables from the prototype and exemplar models can be fit to fMRI data, allowing researchers to test whether the brain tracks the information needed to make prototype- or exemplar-based categorization judgments. In young adults, prototype correlates have been identified in the ventromedial prefrontal cortex (VMPFC) and the anterior hippocampus (Bowman et al., 2020; Bowman & Zeithamova, 2018; Z. Liu et al., 2025; but see Blank & Bayer, 2022). These findings are in line with the VMFPC and hippocampus playing a role in memory integration across multiple memory domains (Shohamy & Wagner, 2008; van Kesteren et al., 2010; Zeithamova et al., 2012). Notably, while some studies have shown only prototype (Bowman & Zeithamova, 2018) or only exemplar correlates (Mack et al., 2013) in the brain, other work has shown both prototype and exemplar correlates in the brain in the same task (Bowman et al., 2020) and even within the same individuals (Blank & Bayer, 2022). Thus, brain imaging can provide novel information about the kinds of representations available to make generalization judgments, even when one representational strategy is most prominent in behavior.

In the present study, we aimed to test for age-related increases in prototype reliance in categorization, the extent to which older adults recruit the VMPFC and anterior hippocampus to support prototype-based categorization, and the extent of any age differences in prototype correlates in the VMPFC and anterior hippocampus. To do so, young (aged 18-30) and older adults (aged 60+) learned and were tested on a prototype-based category structure (Figure 1A). Participants completed a category training task outside the scanner (Figure 1B), then underwent fMRI scanning during a

categorization test that included both training items and new generalization items (Figure 1C). We fit formal prototype and exemplar models to the behavioral categorization test responses and to brain activation levels measured with fMRI. We tested the extent of age differences in category learning and generalization performance, the extent to which behavioral responses were best explained by the prototype versus exemplar model, and the extent to which signals in the anterior hippocampus and VMPFC correlated with predictions from the prototype model.

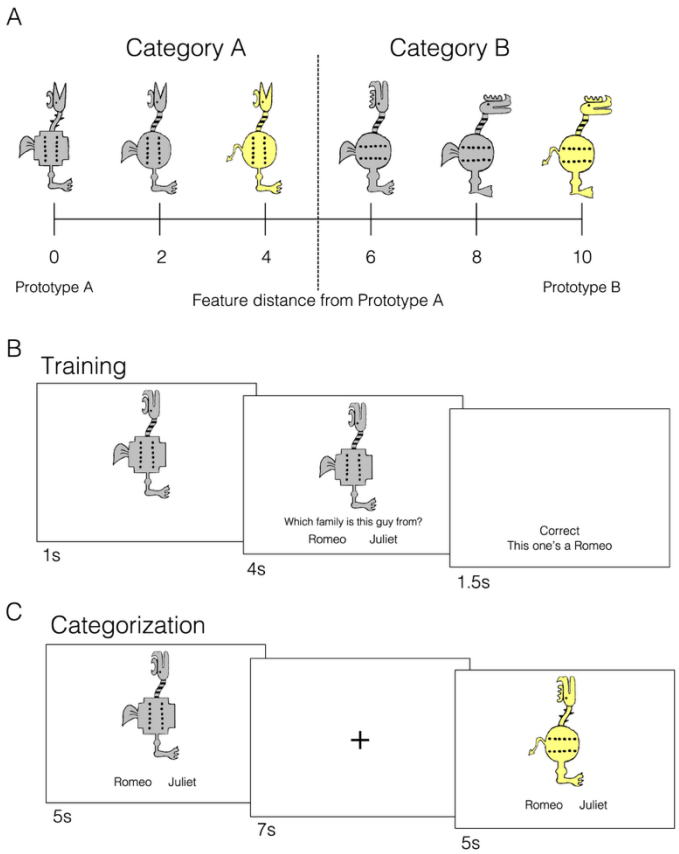

***Figure 1*. Category structure and task procedure**. A. The categories were designed around category prototypes. The prototypes had the typical version of each feature from the training items of their category. Items that shared more features with the category A prototype were members of category A ("Romeo"), and vice versa for category B ("Juliet"). B. Outside the scanner, participants completed feedback-based training with a set of eight distance 2 items and six distance 4 items. Immediately after training, participants also completed a brief old/new recognition test outside the scanner (not depicted). C. In the scanner, after structural scans and a rest scan, participants complete four runs of a categorization task. Participants categorized training items and new items without feedback. *Note*: s = seconds.

2. Method

2.1. Data and Code Availability

The de-identified behavioral and fMRI data and the analytic code are publicly available through OpenNeuro (LINK REDACTED PENDING REVIEW). The study was not pre-registered.

2.2. Participants

Forty-two young adults (recruitment range = 18-30 years) and forty older adults (recruitment range = 60+ years) were recruited from the University of Oregon and surrounding community and participated for financial compensation. All experimental procedures were approved by Research Compliance Services at the University of Oregon, and all participants provided written informed consent. Participants were screened to be right-handed, English-speaking, free of known neurological conditions, and not taking medications known to affect brain function. Older adults were also screened for signs of cognitive impairment using the Mini Mental State Exam (score > 24 for inclusion), with no exclusions based on this criterion (M = 28.7, SD = 1.3, range 26-30 for those included in analyses). One young adult and two older adults were excluded due to technical issues with the scan session that prevented data collection. One challenge with using prototype and exemplar-based regressors in fMRI analysis is that they are based on participants' responses rather than pre-defined conditions. In some cases, the two models' predictions end up highly correlated (Bowman et al., 2020). Five young adults and nine older adults were excluded for having fMRI model regressors that were highly correlated in three or more runs (r > .9). Following exclusions, 36 young adults (mean age = 20.5 years, range = 18-27, 24 females) and 28 older adults (mean age = 70.1 years, range = 62-86 years; 15 females) were included in all analyses. An additional four young adults and ten older adults had excessively correlated regressors

in one or two runs. We retained those participants but excluded those individual runs from analysis.

2.3. Materials

In generating stimulus sets, pairs of young and older adults were yoked so that both the stimuli themselves and their presentation order were the same, minimizing the potential for item or order effects to drive age differences. Stimuli were novel cartoon animals with 10 binary dimensions (https://osf.io/8bph2/) (Bowman & Zeithamova, 2020; Bozoki et al., 2006). The two versions of each feature are visible across the example category A and category B prototypes in Figure 1A. For each participant, one stimulus was chosen to be the prototype of category A from a list of four possible prototypes, with prototypes counterbalanced across participants. All stimuli were coded in reference to the category A prototype. The stimulus that shared no features with the category A prototype was the category B prototype. Category A stimuli were those that shared more features with the category A prototype than the category B prototype. Category B stimuli were those that shared more features with the category B prototype than the category A prototype. Stimuli sharing an equal number of features with each prototype were not used in the study.

2.3.1. Training set

The training set included items that were near the category center (differing by two of ten features from their category prototype, ‘distance 2’ items) and items that were near the category boundary (differing by four of ten features from their category prototype, ‘distance 4’ items). This feature allowed us to test whether there were larger age differences in learning category typical (distance 2) versus category atypical (distance 4) items, as we have found previously (Bowman et al., 2022; Valdez et al., in press). We also chose a structure that had previously shown balanced prototype versus exemplar representations in young adults (Bowman & Zeithamova, 2020), allowing room

for age-related increases or decreases in prototype representations. Training sets included seven items per category (14 total items across categories). There were four distance 2 items and three distance 4 items per category (see Table 1 for the training set structure). The training set stimuli were constrained so that each feature was equally predictive of category membership. The overall structure of the training set was the same across subjects, but the exact stimuli depended on the prototypes selected.

Table 1
Category training set structure

	Dimension values									
Stimulus	1	2	3	4	5	6	7	8	9	10
Prototype A	1	1	1	1	1	1	1	1	1	1
A1	0	0	1	1	1	1	1	1	1	1
A2	1	1	0	0	1	1	1	1	1	1
A3	1	1	1	1	0	0	1	1	1	1
A4	1	1	1	1	1	1	0	0	1	1
A5	0	1	1	0	1	1	1	0	1	0
A6	1	0	1	1	0	1	0	1	0	1
A7	1	1	0	1	1	0	1	1	0	0
Prototype B	0	0	0	0	0	0	0	0	0	0
B1	1	1	0	0	0	0	0	0	0	0
B2	0	0	1	1	0	0	0	0	0	0
B3	0	0	0	0	1	1	0	0	0	0
B4	0	0	0	0	0	0	1	1	0	0
B5	1	0	0	1	0	0	0	1	0	1
B6	0	1	0	0	1	0	1	0	1	0
B7	0	0	1	0	0	1	0	0	1	1

Note: Prototypes were not included in the training set but are depicted here to illustrate the relationship between training items and the prototypes. A1-A7 represent category A training items. B1-B7 represent category B training items. Items 1-4 of each category were distance 2, and items 5-7 were distance 4.

2.3.2. Categorization set

Sixty-four unique items were included in the categorization test set. The test included the 14 (old) training items, each presented twice. It also included the two prototypes (considered new items as they were not encountered during study), each presented twice. Training items and prototypes were presented twice to increase the reliability of model fits, given their importance to predictions of each model and their

limited number (Bowman & Zeithamova, 2018; Kéri et al., 2001; J. D. Smith et al., 2008). An additional 48 new items were six new stimuli from each distance from the category A prototype (1-4, 6-9) each presented once. These new items were selected randomly for each yoked participant pair from the items not included in the training set.

2.4. Procedure

2.4.1. Overview

Participants completed the training phase and a brief old/new recognition test (not reported here) outside the scanner. They were then given information about the MRI environment, instructions for the categorization test, and were setup in the scanner. The scan began with a high resolution T1-weighted anatomical scan, followed by a resting state scan (not reported here). The categorization test followed the rest scan and was split across four runs. The scan ended with a T2-weighted anatomical image. After the scan, participants were given questionnaires about their strategies during the task, debriefed, and given their compensation.

2.4.2. Training

In each trial of the training task (Figure 1B), an individual training item was presented, and participants were instructed to decide which of two families (Romeo's family or Juliet's family) they thought the animal belonged to. The stimulus appeared on the screen alone for 1 second before the response options appeared, giving participants time to evaluate the stimulus without needing to respond. One second into the trial, the response options appeared alongside the stimulus. The stimulus remained on the screen for an additional 4 seconds (5 seconds total) regardless of when the participant responded so that all participants would have equal exposure to the stimulus. Once the participant responded, corrective feedback ("CORRECT" or "WRONG") appeared immediately alongside the exemplar's correct family membership ("It was Romeo's family" or "It was Juliet's family"). If the response was made while the stimulus was on

the screen, then the feedback replaced the response options and appeared alongside the stimulus. The feedback then stayed on the screen for an additional 1.5 seconds after the stimulus disappeared. If the participant did not respond while the stimulus was on the screen, they were prompted to respond immediately ("Please respond now") and given an additional 1 second to respond. If they responded within the 1 second, the corrective feedback was presented for 1.5 seconds. If they did not respond in time, the feedback "Respond faster" was presented with the item's family membership for 1.5 seconds. Each trial was followed by a 1-second fixation cross presented.

There were eight blocks of training separated by self-paced breaks. Each block contained four repetitions of each of the 14 training items, totaling 56 trials per block and 448 total training trials. Within each block, the order of stimuli was randomized with the constraint that all training items were presented before any were presented again and so that no more than three items from the same category were presented consecutively.

2.4.3. Categorization

The categorization test took place in the scanner following an anatomy scan and a rest scan. On each trial, an individual item was presented, and participants were asked to decide which family they thought it belonged to. The response options appeared immediately alongside the stimulus, and participants had 5 seconds to make their response while the stimulus was still on the screen. There was no feedback during the test phase. Each trial was followed by a 7-second fixation cross (i.e., slow-event related design (Dale, 1999; T. T. Liu, 2012; Zeithamova et al., 2017)). The 80 categorization trials were split evenly across four scan runs. Old items, prototypes, and new items at each distance were approximately evenly distributed across the four runs. The presentation order was randomized with the constraints that no more than two old items and no more than three items from the same category were presented consecutively.

2.5. MRI data acquisition

MRI data were acquired on a 3T Siemens MAGNETOM Skyra scanner at the University of Oregon Lewis Center for Neuroimaging. A 32-channel head coil was used. We minimized head motion with foam padding, monitored head motion using FIRMM online motion tracking software (Turing Medical, https://turingmedical.com/firmm/), and gave participants feedback about how well they held still in between runs.

The scanning session started with a localizer scan followed by a standard, high-resolution T1-weighted MPRAGE anatomical image (TR = 2500 ms; TE = 3.43 ms; TI = 1100 ms; flip angle = 7˚; matrix size = 256 x 256; 176 contiguous slices; FOV = 256 mm; slice thickness = 1 mm; voxel size = 1.0 x 1.0 x 1.0 mm; GRAPPA factor = 2). Five runs of functional data collection followed using a multiband gradient echo pulse sequence (TR = 2000 ms; TE = 25 ms; flip angle = 90˚; matrix size = 104 x 104; 72 contiguous slices oriented 15˚ off the anterior-posterior commissure line to reduce prefrontal signal dropout; FOV = 208 mm; voxel size = 2.0 x 2.0 x 2.0 mm; GRAPPA factor = 2; multiband acceleration factor = 3). The first functional run was a resting state scan (180 volumes lasting 6 minutes) followed by four categorization runs (122 volumes and lasting 4 minutes and 4 seconds each). The scan session ended with a T2-weighted coronal anatomical image (TR =13,520 ms; TE = 88 ms; flip angle = 150˚; matrix size = 512 x 512; 65 contiguous slices manually oriented perpendicularly to the hippocampal long axis; interleaved acquisition; FOV = 220 mm; voxel size = 0.4 x 0.4 x 2 mm; GRAPPA factor = 2).

2.6. MRI data pre-processing

2.6.1. Regions of interest

T1-weighted anatomical scans were processed using Freesurfer version 6.0.0 to generate cortical and subcortical regions of interest (ROIs) in each subject's native space. Because we did not have predictions about laterality effects, we used ROIs that averaged across the right and left hemispheres. We focused on the ventromedial

prefrontal cortex (medial orbitofrontal Freesurfer label) and anterior hippocampus based on our prior work in young adults showing prototype correlates in these regions (Bowman et al., 2020; Bowman & Zeithamova, 2018). We also included the posterior hippocampus to determine whether the strength of any prototype effects differed across the hippocampal long axis. The anterior versus posterior hippocampus was defined based on the middle slice, with the middle slice going to the posterior hippocampus when there was an odd number of slices. After anatomical definition in structural space, all ROI masks were registered to functional space using Advanced Normalization Tools (ANTs; https://stnava.github.io/ANTs/).

2.6.2. fMRI pre-processing

Raw dicom images were converted to Nifti format using the dcm2nii function from MRIcron (https://www.nitrc.org/projects/mricron). Skull tissue was removed from the functional images using FSL's brain extraction tool (BET) (www.fmrib.ox.ac.uk/fsl). Within-run motion correction was computed and applied using FSL's MCFLIRT, realigning all volumes to the middle volume. We then used ANTs to align volumes across runs with the first volume of the first functional run (rest) serving as the reference and the first volume of all other runs used to compute the transformation to the reference and then applied to all volumes in each run. We input the resulting motion corrected images into FSL's fMRI Expert Analysis Tool (FEAT) for high pass temporal filtering (100 s) and spatial smoothing (4 mm FWHM gaussian kernel).

In addition to ROI analyses conducted in native space, we also conducted exploratory whole-brain analyses. For whole-brain analyses, we registered each subject's brain to the MNI template (MNI152_T1_2mm_brain) using FSL's FMRIB's Linear Image Registration Tool (FLIRT). Functional images were first registered to the high-resolution structural image using a linear transformation, then registered to the MNI template using linear registration with 12 degrees of freedom.

2.7. Statistical analyses

2.7.1. Behavioral statistical models

Our overall approach for accuracy analyses was to compute Age Group x Distance mixed factors ANOVAs on the data from the training and categorization phases. Where the sphericity assumption was violated, we used a Greenhouse-Geisser correction (denoted with 'GG').

To evaluate participants' categorization strategies, we fit the exemplar and prototype models to the behavioral categorization responses using the same approach as our prior work (Bowman et al., 2020, 2022; Bowman & Zeithamova, 2018, 2020, 2023), which is described in detail in Appendix A. Briefly, the exemplar model assumes that an item is categorized based on its similarity to members of relevant categories stored in memory. Thus, we compute the similarity of each categorization test item to the training items from each category, taking into account the fact that participants may not attend equally to all stimulus features and that there may be differences across subjects in the relationship between the number of differing features and subjective similarity. We then sum the similarity values across all members of each category to generate a single value per category that represents the subjective similarity of the to-be-categorized item to the exemplar-based category A and category B representations. Prototype-based similarity is the same except that the similarity is in reference to the prototype of each category rather than the individual training items. For both models, the probability of categorizing an item as a member of a given category is the similarity to that category divided by the summed similarity across both categories. We generated these probabilities for each model and for each trial of the categorization test, creating model predictions that we then compared to the observed responses using an error metric (negative log likelihood). The model with the lower error had a better fit. We then used a permutation testing approach (Zeithamova et al., 2025) to determine whether each

model fit better than one would expect by chance and whether one model fit significantly better than the other.

2.7.2. fMRI statistical models

Prototype and exemplar-based modeling of fMRI data was conducted as in prior work (Bowman et al., 2020; Bowman & Zeithamova, 2018). For each subject, for each of the four categorization runs, we conducted a first-level General Linear Model in FSL's FEAT that included three regressors: 1) item regressor: all trial onsets with a duration of 5 seconds (i.e., the length of the stimulus presentation) and constant weighting (i.e., weight = 1 for each trial), 2) exemplar regressor: the same as the item regressor but with the trial-by-trial summed similarity (category A similarity + category B similarity from the behavioral model fitting) as estimated by the exemplar model for the weight, and 3) prototype regressor: the same as the item regressor but with the trial-by-trial summed similarity as estimated by the prototype model for the weight. Using the prototype and exemplar summed similarity as the weight served to parametrically modulate the predicted BOLD response such that a larger amplitude BOLD response is predicted on trials with higher exemplar- or prototype-based similarity. These onsets were then convolved with a canonical hemodynamic response function (gamma function with a phase of 0 s, an SD of 3 s, and a mean lag time of 6 s) and used as predictors of the observed BOLD response.

For ROI analyses, we extracted the mean prototype and exemplar parameter estimates across each ROI from each run. For each model, we then computed the mean parameter estimate across runs, dividing by the standard deviation across runs. Normalizing the parameter estimates by their variability can de-weight values associated with higher uncertainty, similar to how lower-level estimates are used in group analyses in FSL (S. M. Smith et al., 2004). The resulting prototype and exemplar effects from each subject were then submitted to group-level analyses.

For whole-brain analyses, parameter estimates were averaged across runs within individual subjects using a fixed-effects analysis. Group-level contrasts were computed using mixed-effects FLAME 1 and 2 in FSL. We compared the prototype and exemplar regressors to the implicit baseline across the entire sample, within the young adult sample alone, and within the older adult sample alone. We also computed independent samples t-test contrasts comparing young and older adults for prototype and exemplar correlates separately. Whole-brain maps used a voxelwise threshold of $z > 3.1$ and were then cluster corrected at $p < .05$ with the false discovery rate method in FSL.

3. Results

3.1. Behavioral performance

3.1.1. Training

Mean accuracies for each training block separated by training item distance and age group are presented in Figure 2A. To test for age differences in category learning, we computed an age group (young vs. older) x item distance (2 vs. 4 features different from prototype) mixed factors ANOVA on accuracy in the final training block. There was a significant main effect of age group, $F(1,62) = 26.37$, $p < .001$, $\eta_p^2 = .30$, with young adults reaching higher overall performance than older adults (YA M = .86, SD = .12; OA M = .71, SD = .11). There was also a significant main effect of item distance, $F(1,62) = 113.07$, $p < .001$, $\eta_p^2 = .65$, with better learning of distance 2 items (M = .87, SD = .08) compared to distance 4 items (M = .70, SE = .16). Finally, there was also a significant age group x item distance interaction, $F(1,62) = 8.90$, $p = .004$, $\eta_p^2 = .13$. While young adults significantly outperformed older adults for both item types, that effect was smaller for distance 2 items, $t(62) = 3.99$, $p < .001$, $d = 1.01$, young-old M = .10, compared to distance 4 items, $t(62) = 4.97$, $p < .001$, $d = 1.25$, young-old M = .20. Thus, older adults

had more difficulty learning the categories, and that age deficit was particularly prominent for the items furthest from the prototypes.

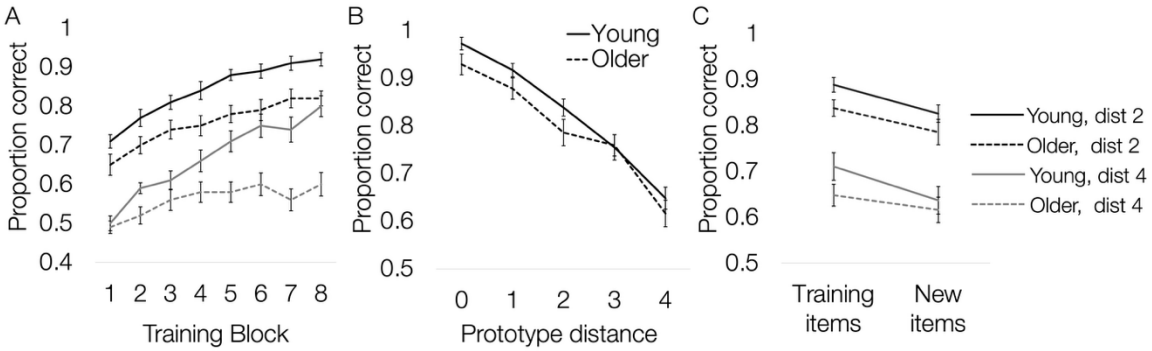

Figure 2. Behavioral accuracy results. A. The proportion of correct responses for each block of training separated by age group and training item distance (dark = distance 2, light = distance 4 as in legend at far right). B. The proportion correct for new items distance 0-4 on the categorization test. C. The proportion correct for training items (old) and new items at distance 2 and 4 on the categorization test. Only distances 2 and 4 are included because all training items came from those distances. For A-C, solid lines represent responses for the young adult group, and dashed lines represent responses for the older adult group. Error bars represent the standard error of the mean across subjects. dist = distance.

3.1.2. Categorization test

Mean accuracies for new items presented in the categorization test separated by age group and distance from category prototypes are presented in Figure 2B. To test for age differences in the ability to generalize category labels to a variety of novel items, we computed an age group (young, older) x item distance (0-4 features different from the prototype) mixed factors ANOVA on classification accuracy for new test items. Results revealed a significant main effect of item distance, $F(3.5,217.1) = 80.43$, $p < .001$, = .57, GG, with an accompanying significant linear effect of item distance, $F(1,62) = 258.29$, $p < .001$, = .06. Generalization performance was worse for items further from category prototypes. There was a non-significant trend toward better generalization in the young group (M = .83, SD = .08) compared to the older group (M = .79, SD = .07), $F(1,62) = 2.92$, $p = .09$, = .045. Age group and item distance did not significantly interact, $F(3.5,217.1) = .62$, $p = .64$, = .01, GG.

Finally, we compared accuracies of old and new items as one way to assess the role of exemplar memorization in category decision. We have often found a categorization advantage for old items relative to new items at the same distance from the prototype (Bowman et al., 2020, 2022; Bowman & Zeithamova, 2018), demonstrating some contribution of exemplar memorization even when the prototype model better fits behavior overall. Here we tested whether the old advantage is modulated by age group and item distance (typicality). Mean accuracies separated by age group, item distance (distance 2, distance 4), and item history (training item, new) are presented in Figure 2C. Only distance 2 and 4 items were considered since only those distances had both old and new items. Full results of a mixed factors ANOVA with age group (young, older), item distance (distance 2 or distance 4), and item history (training item, new) are presented in Table 2. As expected, there was a significant main effect of item history, with better classification of training items (M = .77, SD = .10) than new items (M = .72, SD = .10), demonstrating the advantage for old items. There was also a significant main effect of age group, with poorer categorization performance in the older group (M = .72, SD = .08) compared to the young group (M = .77, SD = .08). Finally, there was a main effect of item distance, with better classification of distance 2 items (M = .84, SD = .09) than distance 4 items (M = .65, SD = .13). However, none of the interaction effects reached significance. Thus, while there was categorization advantage for old items over new items indicative of exemplar memory contributing to categorization decisions, this effect was comparable across age groups.

Table 2

Age group x Item distance x Item history ANOVA results for categorization accuracy

Effect	*df*	*F* value	*p* value	η_p^2
Age group*	1,62	6.47	.01	.10
Item distance*	1,62	115.14	< .001	.65
Item history*	1,62	8.59	.005	.12
Age group x Item distance	1,62	0.02	.89	.00
Age group x Item history	1,62	0.78	.38	.01

Item distance x Item history	1,62	0.02	.90	.00
Age group x Item distance x Item history	1,62	.28	.60	.00

Note: * indicates a significant effect at alpha = .05.

Taken together, behavioral results show a clear age deficit in training accuracy but a less prominent deficit when generalizing. This was especially notable for the category boundary (distance 4) items, where young adults' training performance ended around 80% but dropped to around 65% during generalization. While older adults' mean distance 4 training accuracy did not quite reach 60%, generalization accuracy was slightly above 60%, meaning that there was no performance cost for generalization in older adults for items at that distance. We also show a slight performance advantage for classifying training items relative to new generalization items without strong age-related moderation.

3.2. Prototype and exemplar model fits

3.2.1. Fits to behavioral categorization responses

The group-level fit values for the prototype and exemplar models are presented in Figure 3A separately for young and older adults. An Age group x Model ANOVA on the fit values revealed a significant main effect of Age group, $F(1,62) = 11.10$, $p = .001$, $\eta_p^2 = .15$, with poorer overall fit in older adults (M = 23.74, SD = 7.7, higher values mean poorer fit) compared to young adults (M = 17.27, SD = 7.7). There was also a significant main effect of model, $F(1,62) = 9.13$, $p = .004$, $\eta_p^2 = .13$, with better fit of the prototype model (M = 19.40, SD = 7.7) compared to the exemplar model (M = 21.61, SD = 8.9). The Age group x Model interaction effect did not reach significance, $F(1,62) = 1.73$, $p = .19$, $\eta_p^2 = .03$. Thus, the prototype model fit both the young and older groups better than the exemplar model, and both models better explained the categorization responses of young adults than those of older adults.

From these fit values, we determined which model fit best in each individual subject, testing whether a higher proportion of older adults were best fit by the prototype model compared to young adults. Our first step in model selection was to determine whether each model fit better than simply assuming that the participant responded randomly. In the present study, both the prototype and exemplar model fit better than a random model in all subjects. Next, we compared the prototype and exemplar models to one another. The proportions of young and older adults best fit by the prototype model, best fit by the exemplar model, and similarly fit by the two models ("similar") are depicted in Figure 3B. A chi-squared test revealed that the prototype model was the best fitting model in a significantly higher proportion of older adults (82%, n = 23 of 28) compared to young adults (58%, n = 21 of 36), χ^2 (1) = 4.16, p = .04. We also found that the exemplar model was the best fitting model in a significantly higher proportion of young adults (36%, n = 13 of 36) compared to older adults (11%, n = 3 of 28), χ^2 (1) = 5.42, p = .02. Taken together, we found that both the prototype and exemplar model fit more poorly in older adults compared to young adults, but that when the models were compared directly for each subject, older adults were biased toward a prototype strategy whereas young adults showed more mixed prototype and exemplar strategy use.

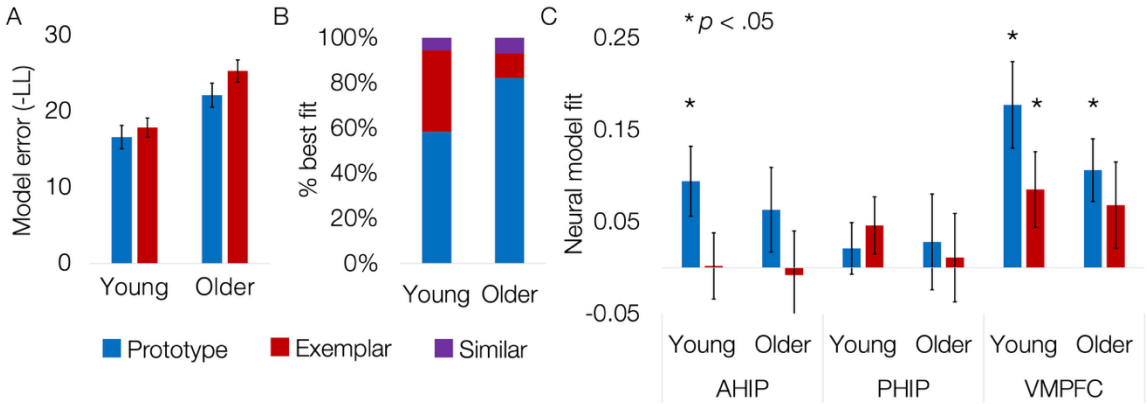

***Figure 3*. Prototype and exemplar model fits to behavior and neural regions of interest.** A. The degree of model error (in terms of negative log likelihood or '-LL') from the fitted prototype and exemplar models separated by age group. B. The percentage of young and older adults whose behavioral responses were best fit by the prototype

model, exemplar model, and those who had similar fits for the two models. C. The neural fit of the prototype and exemplar models in the anterior hippocampus (AHIP), posterior hippocampus (PHIP), and ventromedial prefrontal cortex (VMPFC) depicted separately for young and older adults. The neural model fit was the mean beta parameter for the model regressor in a given region divided by the standard deviation (i.e., an effect size). Stars represent significant one-sample t-tests at uncorrected alpha = .05.

3.2.2. Neural model fits: regions of interest

Mean prototype and exemplar responses from the anterior and posterior hippocampus and VMPFC are presented separately for young and older adults in Figure 3C. We replicated our prior findings by showing that the anterior hippocampus and VMFPC tracked prototype predictions in young adults (both t's > 2.5, p's < .01). As a first approach to understanding prototype-based generalization in older adults, we tested whether these regions also tracked prototype information in older adults. One-sample t-tests in the older adult group (one-tailed test, alpha corrected for two comparisons = .025) revealed significant prototype tracking in the VMPFC, $t(27) = 3.12$, $p = .002$, $d = .59$. There was a trend toward prototype tracking in the anterior hippocampus, but it did not reach significance, $t(27) = 1.37$, $p = .091$, $d = .26$.

We followed up on these prototype effects by testing whether prototype correlates were significantly stronger than exemplar correlates and whether any effects differed across age groups. First, we conducted an Age group (young, older) x Model (prototype, exemplar) mixed effects ANOVA in the VMPFC. The main effect of age was not significant, $F(1,62) = 1.42$, $p = .24$, $\eta_p^2 = .02$, nor was there a significant age x model interaction, $F(1,62) = .30$, $p = .59$, $\eta_p^2 = .01$. Thus, we found that effects in the VMPFC did not differ significantly across age groups.

Surprisingly, the main effect of prototype vs. exemplar model was also not significant, $F(1,62) = 1.75$, $p = .19$, $\eta_p^2 = .03$. Given prior findings in young adults showing that the VMPFC tracks prototype information significantly more than exemplars (Bowman et al., 2020; Bowman & Zeithamova, 2018), the lack of a main effect of model

was unexpected. We followed up on the lack of a prototype model advantage in the VMPFC by testing whether there was significant exemplar tracking in the VMPFC in either age group. One-sample t-tests revealed significant exemplar tracking in young adults, $t(35) = 2.08$, $p = .045$, $d = .35$, but the effect was not significant for older adults, $t(28) = 1.45$, $p = .16$, $d = .27$. Thus, with a training structure that included a mix of typical and atypical items and a young adult sample that showed a mix of prototype and exemplar strategy use, we found evidence of both prototype and exemplar correlates in the VMPFC in young adults. In older adults, the overall pattern of findings was similar to young adults, with effects that were non-significantly weaker for both prototype and exemplar tracking.

Next, we tested for effects of older age and prototype vs. exemplar model in the anterior hippocampus. Additionally, we tested whether any effects in the anterior hippocampus differed significantly from those in the posterior hippocampus. Once again, there was no significant main effect of age, $F(1,62) = .43$, $p = .52$, $\eta_p^2 = .01$, nor significant main effects of model, $F(1,62) = .82$, $p = .37$, $\eta_p^2 = .01$, or hippocampal subregion, $F(1,62) = .56$, $p = .46$, $\eta_p^2 = .01$. None of the age interaction effects were significant (all F's < .6, p's > .46). The model x hippocampal subregion interaction effect was marginally significant, $F(1,62) = 3.75$, $p = .057$, $\eta_p^2 = .06$. Although the interaction did not reach significance, the pattern was in the same direction as our prior work: prototype correlates (M = .08, SD = .23) were marginally stronger than the exemplar correlates (M = -.002, SD = .23) in the anterior hippocampus, $t(63) = 1.79$, $p = .077$, $d = .22$. In the posterior hippocampus, the exemplar correlates (M = .03, SD = .22) showed a minimal advantage over the prototype correlates (M = .02, SD = .22) that was not significant, $t(63) = .14$, $p = .45$, $d = .02$.

Taken together, our ROI results largely replicate what we have seen previously in young adults, with the exception of the VMPFC tracking exemplar information in addition to tracking prototype information. This may reflect the use of a training structure that contains less typical exemplars and promotes exemplar representations to a larger degree than our prior work. We newly show that older adults engage the VMPFC and hippocampus in ways similar to young adults, with numerically weaker effects. These findings indicate that young and older adults rely on a similar neural system to support prototype-based categorization and that this system is relatively intact in healthy aging.

3.2.3. Neural model fits: whole brain analyses

In addition to targeted tests of regions previously shown to track prototype information in young adults, we conducted exploratory whole-brain analyses to identify other regions that might support prototype-based and exemplar-based categorization. Figure 4 depicts regions tracking prototype and exemplar predictors across the entire sample with significant clusters identified in Table 3. Medial prefrontal cortex and the anterior cingulate along with temporal regions like middle temporal gyrus and temporal pole significantly tracked prototype predictors, which is consistent with prior work in young adults (Bowman & Zeithamova, 2018). However, there was also prototype tracking in several parietal regions like angular and supramarginal gyrus that we had not found previously. There was only one exemplar-tracking cluster that passed a whole-brain correction: in the VMPFC just posterior to the larger prototype-tracking cluster. Thus, it seems that there are mostly separate subregions of the VMPFC tracking prototype and exemplar information. When we examined prototype and exemplar tracking regions separately for each age group (Table 3), young adults generally showed activation across the regions that were significant across the entire sample for prototypes, but did not show suprathreshold activation for exemplars. For older adults, there were no clusters significantly tracking either the prototype or exemplar predictors.

Thus, despite showing a similar pattern of activation as young adults in the ROI analysis, we do not see older adults having the same kind of robust prototype response across the brain as young adults. These weaker effects in older adults likely reflect the smaller sample size for the older group, the poorer fit of both the prototype and exemplar models we found from behavior, or some combination of the these two factors.

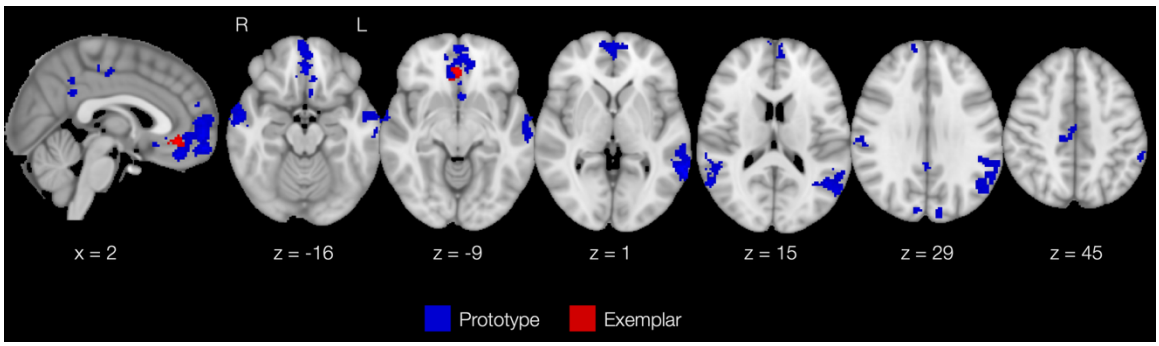

***Figure 4*. Whole-brain analysis depicting regions showing significant prototype > baseline (blue) and exemplar > baseline (red) across the entire sample**. x-, y- and z-values are in MNI space. R = right, L = left.

Table 3
Cluster information for whole-brain prototype and exemplar correlates

Region label(s)	n voxels	Maximum z-value MNI coordinate x	y	z
Contrast: Prototype > baseline across both age groups				
Middle temporal gyrus, supramarginal gyrus, angular gyrus, and operculum	1704	-64	-54	4
Ventromedial and medial PFC	1526	0	38	-20
Middle temporal gyrus	499	-56	-2	-20
Middle temporal gyrus	331	60	-8	-16
Angular gyrus	296	58	-58	16
Supramarginal gyrus and operculum	212	60	-18	20
Temporal pole	139	50	18	-30
Precuneus and posterior cingulate	123	-4	-42	38
Occipital cortex (cuneus)	113	20	-90	22
Posterior cingulate	101	12	-26	46
Occipital cortex (cuneus)	100	-12	-92	26
Subcollosal cortex	81	-4	18	-14
Superior parietal cortex and postcentral gyrus	72	20	-48	70
Contrast: Prototype > baseline in young adults				

Ventromedial and medial PFC and anterior cingulate	1951	0	60	-8
Supramarginal gyrus, angular gyrus, operculum, and lateral occipital cortex	1849	-48	-60	14
Supramarginal gyrus, angular gyrus, and operculum	1138	58	-36	18
Middle temporal gyrus and temporal pole	851	-56	-2	-22
Middle temporal gyrus	235	60	-2	-26
Temporal pole	211	44	24	-30
Posterior cingulate	164	8	-16	44
Precuneus and posterior cingulate	94	-12	-44	34
Lateral orbitofrontal cortex	93	-46	28	-10
Subcollosal cortex	88	-4	18	-12
Superior temporal gyrus and insula	83	50	0	-14
Postcentral gyrus	81	-22	-38	74
Lateral orbitofrontal cortex	77	40	32	-18
Pre- and post-central gyrus	75	-58	-6	20
Contrast: Prototype > baseline in older adults				
no suprathreshold clusters				
Contrast: Exemplar > baseline across both age groups				
Ventromedial PFC	77	2	38	8
Contrast: Exemplar > baseline in young adults				
no suprathreshold clusters				
Contrast: Exemplar > baseline in older adults				
no suprathreshold clusters				

Next, we tested for significant age differences in prototype and exemplar activation across the whole brain (Table 4). There were no clusters that showed significant age differences in exemplar model correlates. Figure 5A depicts the single cluster in the right inferior frontal gyrus (IFG) showing stronger prototype-based activation in young adults compared to older adults. To test whether right inferior frontal gyrus significantly tracked prototype information in each age group and whether any prototype effects differed from exemplar tracking, we extracted the prototype and exemplar neural effects from each subject. Note that we did not compute age comparisons at this stage since it was an age comparison that generated the cluster.

The neural model fits are depicted in Figure 4B. A one-sample t-test showed significant prototype tracking in young adults, $t(35) = 2.62$, $p = .013$, $d = .44$, but the difference between prototype and exemplar correlates was not significant, $t(35) = .437$, $p = .665$, $d = .07$. There was also significant prototype tracking in older adults, but in the negative direction, $t(27) = -3.74$, $p < .001$, $d = -.71$. That means that trials with higher levels of prototype similarity led to lower activation in this region. However, as with young adults, the difference between the prototype and exemplar correlates was not significant, $t(27) = .588$, $p = .561$, $d = .11$. Thus, there was an age difference in how the right IFG responded to the typicality of category members: stronger response to typical category members in young adults versus stronger response to atypical category members in older adults. Further, this effect was comparable regardless of the definition of category typicality: based on exemplar similarity or prototype similarity.

Table 4
Cluster information for age differences in whole-brain prototype an exemplar correlates

		Maximum z-value MNI coordinate		
Region label(s)	n voxels	x	y	z
Contrast: Young > Older adults for Prototype > baseline				
Inferior frontal gyrus	77	48	34	-8
Contrast: Older > Young adults for Prototype > baseline				
Lateral occipital cortex and superior parietal cortex	89	18	-72	54
Contrast: Young > Older adults for Exemplar > baseline				
no suprathreshold clusters				
Contrast: Older > Young adults for Exemplar > baseline				
no suprathreshold clusters				

Figure 4D depicts the single cluster in the right lateral occipital/superior parietal cortex showing older adult > young adult activation for prototypes. Yet, we see that the differences are in levels of negative prototype effects, meaning that activation was higher in this region for items further from the prototype (near category boundary). Both young and older adults showed significant negative prototype tracking in this region,

young $t(35) = -6.537$, $p < .001$, $d = -1.09$, older $t(27) = -3.213$, $p = .003$, $d = -.61$. Young adults also showed significantly more negative tracking of prototype relative to exemplar similarity, $t(35) = -2.795$, $p = .008$, $d = -.47$, whereas older adults did not differentiate between prototype and exemplar tracking in this region, $t(27) = .114$, $p = .910$, $d = .02$. Thus, despite showing older > young adult activity, this occipitoparietal region was one that was again showing stronger prototype tracking in young adults, just in a negative direction.

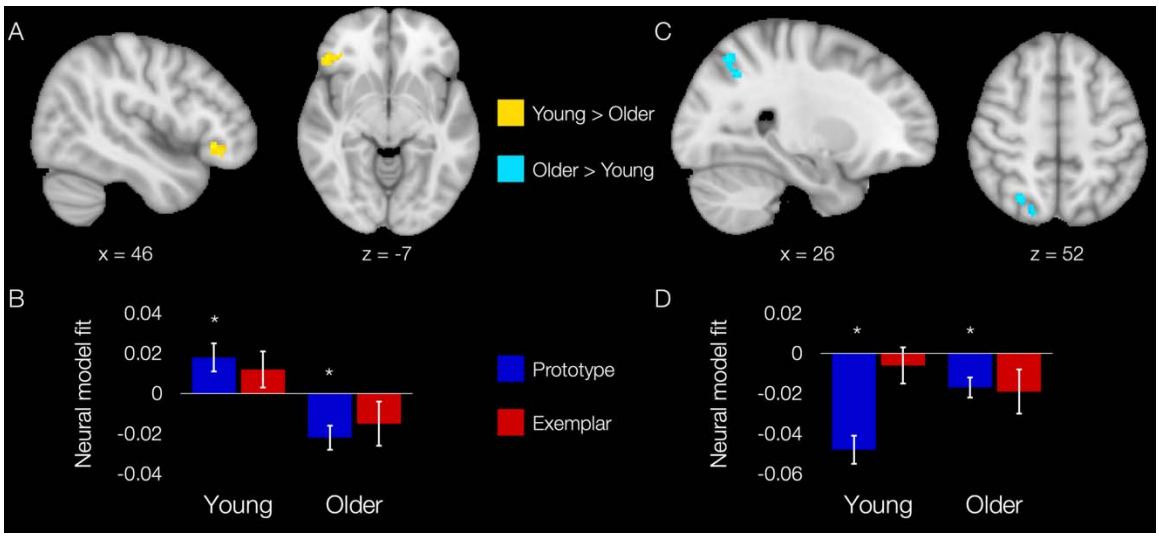

***Figure 5*. Whole-brain age differences in prototype correlates**. A. A cluster (shown in two views) in the right inferior frontal gyrus showing young > older adult activity. B. Mean neural model fit (mean beta/variance) for the prototype and exemplar models in the right inferior frontal gyrus cluster. C. A cluster (shown in two views) in the right lateral occipital/superior parietal cortex showing older > young adult activity. B. Mean neural model fit (mean beta/variance) for the prototype and exemplar models in the right lateral occipital/superior parietal cortex cluster. * represents a significant difference from zero (one-sample t-test) at alpha = .05.

3.3. Exploratory analysis of neural old vs. new differences

Some previous studies have identified exemplar correlates in the brain (Blank & Bayer, 2022; Bowman et al., 2020; Mack et al., 2013), but here we found a mix of prototype and exemplar strategies in behavior in young adults without corresponding exemplar representations in the brain. One key prediction of the exemplar model is that the individual training items should be stored in memory and should have a strong

response during generalization since they are the basis of the exemplar representation. In line with this exemplar model prediction, we found a categorization advantage of old items over new items in behavior. We thus conducted an exploratory fMRI analysis testing old/new differentiation of items during the categorization test, which would suggest some degree of memory for the specific training items as predicted by the exemplar model. We further explored whether any old/new effects were stronger in young adults than in older adults, as would be expected from the mixture of prototype and exemplar strategies in this age group. To do so, we computed an exploratory univariate GLM where old and new stimuli and stimuli of different distances each had their own regressor (i.e., old distance 2 items, old distance 4 items, new distance 0 items (prototypes), new distance 1 items, etc.), leading to 7 separate regressors. All regressors had a duration of 5 seconds (as with the model-based analyses) and all onsets had a weight of 1 (no parametric modulation). We then contrasted old vs. new items at distance 2 and old vs. new at distance 4 to test for neural old/new discrimination while equating for distance from the prototype. We computed those contrasts within each age group and computed age difference (young vs. older) contrasts.

Table 5 presents the results of these old > new contrasts for young adults, older adults, and for age group comparisons. Group comparisons are also visualized in Figure 6. No old/new differences were found in older adults at either distance; we also did not find any reliable older > young effects. In contrast, young adults show a differentiation of old and new items for both distance 2 and 4, with several clusters showing reliable age differences in the old/new effects. At distance 2, the old > new contrast for distance 2 items yielded two suprathreshold clusters in young adults, and two cluster also reliably greater activation in young adults compared to older adults. Figure 6A depicts the two clusters showing suprathreshold young > older adult activation: one in left frontal pole and one that spanned the cuneus and precuneus. At distance 4, young adults showed

significantly more activation in the old > new contrast in a set of occipital and parietal regions (Table 5). Further, activation across several overlapping occipital and parietal clusters showed greater old > new activity in young adults than in older adults (Table 5, Figure 6B). In summary, young adults but not older adults showed neural discrimination of old from new items, consistent with young adults being more likely than older adults to be best fit by the exemplar model.

Table 5
Cluster information for whole-brain old > new analysis for distance 4 items

		Maximum z-value MNI coordinate		
Region label(s)	n voxels	x	y	z
Contrast: Old > New – distance 2 items in young adults				
Pre/post-central gyrus	85	-58	-14	42
Frontal pole	67	-44	44	-12
Contrast: Old > New – distance 2 items in older adults				
no suprathreshold clusters				
Contrast: Young > Older adults for Old > New – distance 2 items				
Frontal pole	84	-18	44	48
Cuneus and precuneus	68	-6	-80	36
Contrast: Older > Young adults for Old > New – distance 2 items				
no suprathreshold clusters				
Contrast: Old > New – distance 4 items in young adults				
Lateral occipital cortex	155	30	-68	8
Superior parietal cortex	153	34	-54	62
Superior parietal cortex	98	-26	-54	66
Precuneus	91	2	-52	66
Precentral gyrus	89	30	-20	70
Lateral occipital cortex	75	-40	-72	10
Precuneus	60	2	-46	50
Lateral occipital cortex	56	52	-74	10
Contrast: Old > New – distance 4 items in older adults				
no suprathreshold clusters				
Contrast: Young > Older adults for Old > New – distance 4 items				
Lateral occipital cortex	331	-40	-78	12
Superior parietal cortex	320	-22	-54	56
Precentral gyrus	208	16	-18	74
Precuneus	161	-2	-52	64
Lateral occipital cortex	148	36	-82	28
Lateral occipital cortex	82	38	-86	4
Superior parietal cortex	76	36	-54	62
Precuneus	56	-4	-74	56
Contrast: Older > Young adults for Old > New – distance 4 items				
no suprathreshold clusters				

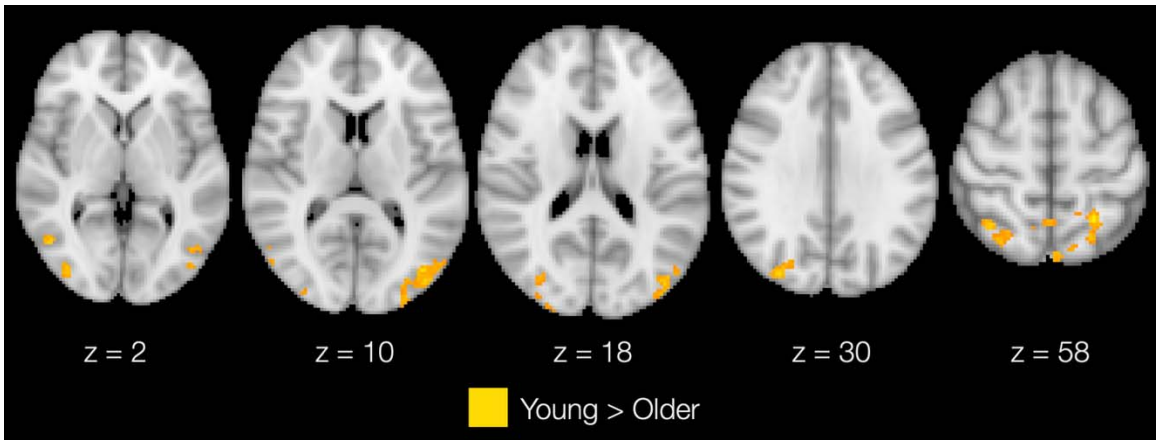

***Figure 6*. Whole-brain age differences in old vs. new discrimination**. A. Distance 2 items (category-typical items close to the category prototypes): two clusters showed greater old vs. new discrimination in young compared to older adults. B. Distance 4 items: (less typical items near category boundary): nine clusters across occipital and parietal cortex showed greater old vs. new discrimination in young compared to older adults. No suprathreshold clusters showed the opposite age difference (older > young) for either distance 2 or distance 4 items.

4. Discussion

In the present study, we tested whether the VMPFC and anterior hippocampus support prototype representations in older adults as they do in young adults. As expected, older adults were more likely than young adults to be best fit by the prototype model, although the overall fit of both models was poorer in older compared to young adults. In the brain, we found a similar pattern of prototype-based activation in the VMPFC and anterior hippocampus across age groups. This relatively intact prototype processing was coupled with minimal age deficits in behavioral generalization performance, demonstrating that prototype representations can support successful generalization in older adults. We also saw that older adults had weaker neural discrimination of old versus new category members than young adults primarily in occipital and parietal regions. Thus, increased reliance on prototype representations may be due at least in part to declines in representations of individual category members paired with a relatively intact VMPFC-anterior hippocampus neural prototype system.

As in our prior behavioral study that used the same category structure and a similar task procedure (Bowman et al., 2022), we found that older adults' categorization responses tended to be best fit by the prototype model, and that older adults were more likely to be best fit by the prototype model than young adults were. We also replicated two other behavioral patterns: 1) there was a smaller age deficit in learning typical training items that were close to category prototypes (10% accuracy difference) compared to more atypical items near the category boundary (20% accuracy difference), and 2) age deficits in category generalization were minimal despite robust age deficits in category training. Together, these findings suggest that older adults' memory is sufficiently equipped to extract the commonalities among members of the same category, which is adequate for learning typical category members and for generalization. In contrast, memorization of specific training items—a strategy that young adults seem to use to boost training performance for atypical items—may be hindered in aging. These findings are also consistent with memory and aging findings outside of category learning, which have shown that the ability to remember the general meaning or 'gist' of an experience is intact in older age (Brainerd & Reyna, 2002, 2015) while memory for specific, unique details of individual experiences declines (Bowman et al., 2019; Bowman & Dennis, 2015; Gallo et al., 2006; Koutstaal & Schacter, 1997). Thus, across multiple memory domains, the older brain seems to prioritize building abstract, generalizable knowledge over remembering individual experiences.

We also show for the first time that older adults engage a similar medial PFC and hippocampal neural system as young adults to support prototype-based categorization. Although the prototype effect in the anterior hippocampus was significant only in young adults, there was a trend toward prototype representations in older adults and there was no significant age difference in hippocampal prototype correlates. The hippocampus has long been known to support rapid learning and retrieval of unique

experiences (Chadwick et al., 2010; Fortin et al., 2004; Leutgeb et al., 2007; Scoville & Milner, 1957), but more recent work has also identified a role for the hippocampus in integration of related experiences and in generalization (Bowman et al., 2020; Bowman & Zeithamova, 2018; Schlichting et al., 2015; Shohamy & Wagner, 2008; Zeithamova et al., 2012). It is thought that the hippocampus can form relationships between separate but related experiences very rapidly before they have had time to be consolidated into neocortical networks (Schapiro et al., 2017). Here, we find evidence that, although the hippocampus is known to undergo structural and functional decline in older age (Driscoll et al., 2003; Leal & Yassa, 2015; Lister & Barnes, 2009), this rapid abstraction function may be relatively intact, potentially allowing older adults to maintain performance on generalization tasks that are well suited to abstraction.

Further, both young and older adults showed significant prototype tracking in the VMPFC, which is consistent with prior work in young adults alone (Bowman et al., 2020; Bowman & Zeithamova, 2018; Z. Liu et al., 2025; but see Blank & Bayer, 2022). In addition to tracking prototype information, the VMPFC is known to integrate across related experiences (Audrain & McAndrews, 2022; Schlichting et al., 2015; Tompary & Davachi, 2017; Zeithamova et al., 2012) and support schema-based memory (Ghosh et al., 2014; Reagh & Ranganath, 2023; van Kesteren et al., 2010). The VMPFC may therefore broadly support formation of abstract representations that summarize across experiences and apply those abstract representations to new situations. Here, we show that this function of the medial prefrontal cortex is relatively intact in older age, which stands in contrast to lateral prefrontal cortex that tends to show age-related differences in memory function (S. W. Davis et al., 2008; Rajah & D'Esposito, 2005). Thus, older adults' ability to maintain memory performance in terms of category generalization, schema-based memory, and gist-based memory may be due in part to relatively intact medial PFC function.

We also found novel evidence of *exemplar* correlates in the VMPFC in addition to the prototype correlates we have seen previously. VMPFC exemplar tracking was significant in young adults when we considered the VMPFC as a whole, and there was also a cluster in the VMPFC that was significant in the whole-brain analysis across age groups. The exemplar-tracking cluster was smaller than the prototype-tracking cluster we also identified at the whole-brain level, and the exemplar and prototype clusters overlapped only minimally. While the exemplar effect was not significant in older adults alone in the ROI analysis, there was also no age difference in the VMPFC exemplar effect. Thus, it seems that the VMPFC is capable of maintaining both abstract and item-specific representations during categorization and does so in a similar manner across age groups. This finding is also consistent with findings showing that the VMPFC can represent categories at multiple levels of complexity (Mack et al., 2020), that it can contain a mix of integrated and separated representations in an associative inference task (Schlichting et al., 2015) and with its role as a hub region that integrates many sources of information (Buckner et al., 2009). Further, work on schema memory shows that the VMPFC is involved in tracking the congruity of individual items with a broader context, suggesting role of the VMPFC both in representing the larger, abstract context and in integration of individual items into that context (van Kesteren et al., 2012). Yet, we have also seen prototype correlates most strongly and most consistently in this region (Bowman et al., 2020; Bowman & Zeithamova, 2018; Z. Liu et al., 2025), suggesting that its primary role is in representing the abstract, generalized information, at least in the context of categorization tasks.

We did not find significant age differences in prototype correlates in the hippocampus or VMPFC, but we found two regions showing age differences in our whole-brain analysis. One region in the prefrontal cortex seemed to track item typicality generally, irrespective of whether category typicality was based on prototype- or exemplar-

similarity. Interestingly, the age difference in this region was driven by a flip of the direction of the effect: positive tracking in young adults and negative tracking in older adults. In other words, young adults were activating this region more strongly for items near category center while older adults were activating this region more strongly for atypical items near category boundary. Thus, there seems to be an age differences in whether prefrontal cortex prioritizes more typical versus atypical feature combinations when making categorization judgments.

A region in right occipitoparietal cortex showed stronger negative prototype tracking in young adults than in older adults: this region showed higher activation for less prototypical category members (items near category boundary) and that effect was stronger in young than older adults. This occipitoparietal region also differentiated prototype from exemplar correlates in young but not older adults. Thus, there seem to be age differences in visual processing of category members, with young adults showing stronger response to less prototypical category members, potentially reflecting visual attention to additional visual features when the most highly attended features are not sufficient to determine category membership (Nosofsky, 1986). Another possibility is that this activation functions as a novelty signal for less typical items because their combination of features is less familiar (Kafkas & Montaldi, 2018). That older adults showed reduced tracking of prototype information in this visual region suggests there may be age differences in the level of visual detail in the prototypes, which can be explored in future studies.

Lastly, although we found that older adults were more likely than young adults to be best fit by the prototype model, the fit of the prototype model was poorer in older adults, and we did not see age-related increases in prototype correlates in the brain. This pattern indicates that the age-related increase in prototype reliance could be driven by a lack of exemplar processing rather than an increase in prototype processing. A

deficit in exemplar processing could leave prototypes as the only viable option for representing categories, whereas young adults may have the flexibility to use a mix of representations. We saw some evidence for this proposal: young adults were more likely than older adults to be best fit by the exemplar model and showed stronger neural differentiation between old and new items across several occipital and parietal regions. We also found that age reduction in old/new differentiation was particularly prominent for the category boundary items, suggesting that young adults may have relied more on memory for individual, atypical category members. These results align with our prior behavioral study (Bowman et al., 2022), indicating that young adults but not older adults supplement prototype learning with exemplar memorization especially for atypical exemplars. Nevertheless, the interpretation of old/new activation differences across age groups should be taken with some caution, as the analysis was exploratory and we did not see any corresponding age moderation of the behavioral advantage for the old items over new items. Thus, it is also possible that young adults' increased old/new neural differentiation in visual and parietal regions was not a strong contributor to their explicit decision-making. Future research will be necessary to test the extent to which such old/new effects in the brain contribute to exemplar-based categorization.

5. Conclusion

We tested for age differences in the neural basis of prototype-based category generalization and found that young and older adults recruited anterior hippocampus and VMPFC to a comparable degree to support prototype representations. Age differences were most prominent for neural old/new discrimination of category boundary items, suggesting that the age-related increase in prototype reliance in behavior may be

driven by declines in memory for specific training items coupled with a relatively intact neural system for representing prototypes.

References

Alghamdi, S. A., & Rugg, M. D. (2020). The effect of age on recollection is not moderated by differential estimation methods. *Memory*, *28*(8), 1067–1077. https://doi.org/10.1080/09658211.2020.1813781

Audrain, S., & McAndrews, M. P. (2022). Schemas provide a scaffold for neocortical integration of new memories over time. *Nature Communications*, *13*(1), 5795. https://doi.org/10.1038/s41467-022-33517-0

Blank, H., & Bayer, J. (2022). Functional imaging analyses reveal prototype and exemplar representations in a perceptual single-category task. *Communications Biology*, *5*(1), 896. https://doi.org/10.1038/s42003-022-03858-z

Bowman, C. R., Ashby, S. R., & Zeithamova, D. (n.d.). Age effects on category learning and their relationship to deficits in memory specificity. *PsyArXiv*.

Bowman, C. R., Chamberlain, J. D., & Dennis, N. A. (2019). Sensory representations supporting memory specificity: Age effects on behavioral and neural discriminability. *Journal of Neuroscience*, *39*(12), 2265–2275. https://doi.org/10.1523/JNEUROSCI.2022-18.2019

Bowman, C. R., & Dennis, N. A. (2015). Age differences in the neural correlates of novelty processing: The effects of item-relatedness. *Brain Research*, *1612*, 2–15.

Bowman, C. R., Iwashita, T., & Zeithamova, D. (2020). Tracking prototype and exemplar representations in the brain across learning. *eLife*, *e59360*, e59360. https://doi.org/10.7554/elife.59360

Bowman, C. R., Iwashita, T., & Zeithamova, D. (2022). The effects of age on prototype- and exemplar-based categorization. *Psychology and Aging*, *37*(7), 800–815. http://dx.doi.org/10.1037/pag0000714

Bowman, C. R., Valdez, M. R., & Obarski, S. A. (2023). Learning New Categories in Older Age: A Review of Theoretical Perspectives and Empirical Findings. *Psychology and Aging*. https://doi.org/10.1037/PAG0000715

Bowman, C. R., & Zeithamova, D. (2018). Abstract memory representations in the ventromedial prefrontal cortex and hippocampus support concept generalization. *The Journal of Neuroscience*, *38*(10), 2605–2614. https://doi.org/10.1523/JNEUROSCI.2811-17.2018

Bowman, C. R., & Zeithamova, D. (2020). Training set coherence and set size effects on concept generalization and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *46*(8), 142–1464.

Bowman, C. R., & Zeithamova, D. (2023). Coherent category training enhances generalization in prototype-based categories. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *49*(12), 1923–1942. https://dx.doi.org/10.1037/xlm0001243

Bowman, C. R., & Zeithamova, D. (in press). High coherence among training exemplars promotes broad generalization of face families. *Journal Of Experimental Psychology-Learning Memory And Cognition*.

Bozoki, A., Grossman, M., & Smith, E. E. (2006). Can patients with Alzheimer's disease learn a category implicitly? *Neuropsychologia*, *44*(5), 816–827. https://doi.org/10.1016/j.neuropsychologia.2005.08.001

Brainerd, C. J., & Reyna, V. F. (2002). Fuzzy-Trace Theory and False Memory. *Https://Doi.Org/10.1111/1467-8721.00192*, *11*(5), 164–169. https://doi.org/10.1111/1467-8721.00192

Brainerd, C. J., & Reyna, V. F. (2015). Fuzzy-trace theory and lifespan cognitive development. *Developmental Review*, *38*, 89–121. https://doi.org/10.1016/J.DR.2015.07.006

Buckner, R. L., Sepulcre, J., Talukdar, T., Krienen, F. M., Liu, H., Hedden, T., Andrews-Hanna, J. R., Sperling, R. A., & Johnson, K. A. (2009). Cortical Hubs Revealed by Intrinsic Functional Connectivity: Mapping, Assessment of Stability, and Relation to Alzheimer's Disease. *The Journal of Neuroscience*, *29*(6), 1860–1873. https://doi.org/10.1523/JNEUROSCI.5062-08.2009

Chadwick, M. J., Hassabis, D., Weiskopf, N., & Maguire, E. A. (2010). Decoding Individual Episodic Memory Traces in the Human Hippocampus. *Current Biology*, *20*(6), 544–547. https://doi.org/10.1016/j.cub.2010.01.053

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping*, *8*(2–3), 109–114. https://doi.org/10.1002/(SICI)1097-0193(1999)8:2/3<109::AID-HBM7>3.0.CO;2-W

Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Qué PASA? the posterior-anterior shift in aging. *Cerebral Cortex*, *18*(5), 1201–1209. https://doi.org/10.1093/cercor/bhm155

Davis, T., Love, B. C., & Maddox, W. T. (2012). Age-related declines in the fidelity of newly acquired category representations. *Learning and Memory*, *19*(8), 325–329. https://doi.org/10.1101/lm.024919.111

Driscoll, I., Hamilton, D. A., Petropoulos, H., Yeo, R. A., Brooks, W. M., Baumgartner, R. N., & Sutherland, R. J. (2003). The Aging Hippocampus: Cognitive, Biochemical and Structural Findings. *Cerebral Cortex*, *13*(12), 1344–1351. https://doi.org/10.1093/CERCOR/BHG081

Fortin, N. J., Wright, S. P., & Eichenbaum, H. (2004). Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature*, *431*(7005), 188–191. https://doi.org/10.1038/nature02853

Gallo, D., Bell, D., Beier, J., & Schacter, D. (2006). Two types of recollection-based monitoring in younger and older adults: Recall-to-reject and the distinctiveness heuristic. *Memory*, *14*(6), 730–741. https://doi.org/10.1080/09658210600648506

Ghosh, V. E., Moscovitch, M., Melo Colella, B., & Gilboa, A. (2014). Schema representation in patients with ventromedial PFC lesions. *The Journal of Neuroscience*, *34*(36), 12057–12070. https://doi.org/10.1523/JNEUROSCI.0740-14.2014

Hashtroudi, S., Johnson, M. K., & Chrosniak, L. D. (1989). Aging and source monitoring. *Psychology and Aging*, *4*(1), 106–112. https://doi.org/10.1037/0882-7974.4.1.106

Hintzman, D. L. (1984). MINERVA 2: A simulation model of human memory. *Behavior Research Methods, Instruments, & Computers*, *16*(2), 96–101. https://doi.org/10.3758/BF03202365

Kafkas, A., & Montaldi, D. (2018). How do memory systems detect and respond to novelty? *Neuroscience Letters*, *680*, 60–68. https://doi.org/10.1016/j.neulet.2018.01.053

Kéri, S., Kelemen, O., Benedek, G., & Janka, Z. (2001). Intact prototype learning in schizophrenia. *Schizophrenia Research*, *52*(3), 261–264. https://doi.org/10.1016/S0920-9964(00)00092-X

Koutstaal, W., & Schacter, D. L. (1997). Gist-Based False Recognition of Pictures in Older and Younger Adults. *Journal of Memory and Language*, *37*(4), 555–583. https://doi.org/10.1006/jmla.1997.2529

Kumaran, D., & McClelland, J. L. (2012). Generalization through the recurrent interaction of episodic memories: A model of the hippocampal system. *Psychological Review*, *119*(3), 573–616. https://doi.org/10.1037/a0028681

Leal, S. L., & Yassa, M. A. (2015). Neurocognitive Aging and the Hippocampus across Species. *Trends in Neurosciences*, *38*(12), 800–812. https://doi.org/10.1016/J.TINS.2015.10.003

Leutgeb, J. K., Leutgeb, S., Moser, M.-B., & Moser, E. I. (2007). Pattern separation in the dentate gyrus and CA3 of the hippocampus. *Science (New York, N.Y.)*, *315*(5814), 961–966. https://doi.org/10.1126/science.1135801

Lister, J. P., & Barnes, C. A. (2009). Neurobiological Changes in the Hippocampus During Normative Aging. *Archives of Neurology*, *66*(7), 829–833. https://doi.org/10.1001/ARCHNEUROL.2009.125

Liu, T. T. (2012). The development of event-related fMRI designs. *NeuroImage*, *62*(2), 1157–1162. https://doi.org/10.1016/j.neuroimage.2011.10.008

Liu, Z., Zhang, Y., Wen, C., Yuan, J., Zhang, J., & Seger, C. A. (2025). Emergence of Categorical Representations in Parietal and Ventromedial Prefrontal Cortex across Extended Training. *Journal of Neuroscience*, *45*(9). https://doi.org/10.1523/JNEUROSCI.1315-24.2024

Mack, M. L., Preston, A. R., & Love, B. C. (2013). Decoding the brain's algorithm for categorization from its neural implementation. *Current Biology*, *23*(20), 2023–2027. https://doi.org/10.1016/j.cub.2013.08.035

Mack, M. L., Preston, A. R., & Love, B. C. (2020). Ventromedial prefrontal cortex compression during concept learning. *Nature Communications*, *11*(1), 46. https://doi.org/10.1038/s41467-019-13930-8

Mata, R., von Helversen, B., Karlsson, L., & Cüpper, L. (2012). Adult age differences in categorization and multiple-cue judgment. *Developmental Psychology*, *48*(4), 1188–1201. https://doi.org/10.1037/a0026084

Medin, D. L., & Schaffer, M. M. (1978). Context theory of classification learning. *Psychological Review*, *85*(3), 207–238. https://doi.org/10.1037/0033-295X.85.3.207

Minda, J. P., & Smith, J. D. (2011). Prototype models of categorization: Basic formulation, predictions, and limitations. In E. M. Pothos & A. J. Wills (Eds.), *Formal approaches in categorization* (pp. 40–64). Cambridge University Press.

Morton, N. W., & Preston, A. R. (2021). Concept formation as a computational cognitive process. *Current Opinion in Behavioral Sciences*, *38*, 83–89. https://doi.org/10.1016/j.cobeha.2020.12.005

Nosofsky, R. M. (1986). Attention, similarity, and the identification–categorization relationship. *Journal of Experimental Psychology: General*, *115*(1), 39–57. https://doi.org/10.1037/0096-3445.115.1.39

Nosofsky, R. M. (1988). Exemplar-based accounts of relations between classification, recognition, and typicality. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *14*(4), 700–708. https://doi.org/10.1037/0278-7393.14.4.700

Nosofsky, R. M. (1991). Tests of an exemplar model for relating perceptual classification and recognition memory. *Journal of Experimental Psychology: Human Perception and Performance*, *17*(1), 3–27. https://doi.org/10.1037/0096-1523.17.1.3

Posner, M. I., & Keele, S. W. (1968). On the Genesis of Abstract Ideas. *Journal of Experimental Psychology*, *77*(3, Pt.1), 353–363. https://doi.org/10.1037/h0025953

Prull, M. W., Dawes, L. L. C., Martin III, A. M., Rosenberg, H. F., & Light, L. L. (2006). Recollection and familiarity in recognition memory: Adult age differences and

neuropsychological test correlates. *Psychology and Aging*, *21*(1), 107–118. https://doi.org/10.1037/0882-7974.21.1.107

Rajah, M. N., & D'Esposito, M. (2005). Region-specific changes in prefrontal function with age: A review of PET and fMRI studies on working and episodic memory. *Brain*, *128*(9), 1964–1983.

Reagh, Z. M., & Ranganath, C. (2023). Flexible reuse of cortico-hippocampal representations during encoding and recall of naturalistic events. *Nature Communications 2023 14:1*, *14*(1), 1–15. https://doi.org/10.1038/s41467-023-36805-5

Schapiro, A. C., Turk-Browne, N. B., Botvinick, M. M., & Norman, K. A. (2017). Complementary learning systems within the hippocampus: A neural network modelling approach to reconciling episodic memory with statistical learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*. https://doi.org/10.1098/rstb.2016.0049

Schenk, S., Minda, J. P., Lech, R. K., & Suchan, B. (2016). Out of sight, out of mind: Categorization learning and normal aging. *Neuropsychologia*, *91*, 222–233. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2016.08.013

Schlichting, M. L., Mumford, J. A., & Preston, A. R. (2015). Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex. *Nature Communications*, *6*, 8151. https://doi.org/10.1038/ncomms9151

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *The Journal of Neuropsychiatry and Clinical Neurosciences*, *20*(11), 11–21. https://doi.org/10.1136/jnnp.20.1.11

Shepard, R. N. (1957). Stimulus and response generalization: A stochastic model relating generalization to distance in psychological space. *Psychometrika*, *22*(4), 325–345. https://doi.org/10.1007/BF02288967

Shohamy, D., & Wagner, A. D. (2008). Integrating Memories in the Human Brain: Hippocampal-Midbrain Encoding of Overlapping Events. *Neuron*, *60*(2), 378–389. https://doi.org/10.1016/j.neuron.2008.09.023

Smith, J. D., Redford, J. S., & Haas, S. M. (2008). Prototype abstraction by monkeys (Macaca mulatta). *Journal of Experimental Psychology. General*, *137*(2), 390–401. https://doi.org/10.1037/0096-3445.137.2.390

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., Bannister, P. R., De Luca, M., Drobnjak, I., Flitney, D. E., Niazy, R. K., Saunders, J., Vickers, J., Zhang, Y., De Stefano, N., Brady, J. M., & Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, *23*(SUPPL. 1). https://doi.org/10.1016/j.neuroimage.2004.07.051

Stark, S. M., Yassa, M. A., & Stark, C. E. L. (2010). Individual differences in spatial pattern separation performance associated with healthy aging in humans. *Learning & Memory*, *17*(6), 284–288. https://doi.org/10.1101/LM.1768110

Tompary, A., & Davachi, L. (2017). Consolidation promotes the emergence of representational overlap in the hippocampus and medial prefrontal cortex. *Neuron*, *96*(1), 228-241.e5. https://doi.org/10.1016/j.neuron.2017.09.005

Valdez, M., Kimura, K., & Bowman, C. R. (in press). Age-related differences in the stability of categorization performance and prototype versus exemplar strategy use. *Journal Of Experimental Psychology-Learning Memory And Cognition*.

van Kesteren, M. T. R., Rijpkema, M., Ruiter, D. J., Fernandez, G., & Fernández, G. (2010). Retrieval of associative information congruent with prior knowledge is

related to increased medial prefrontal activity and connectivity. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(47), 15888–15894. https://doi.org/10.1523/JNEUROSCI.2674-10.2010

van Kesteren, M. T. R., Ruiter, D. J., Fernández, G., & Henson, R. N. (2012). How schema and novelty augment memory formation. *Trends in Neurosciences*, *35*(4), 211–219. https://doi.org/10.1016/j.tins.2012.02.001

Vieweg, P., Stangl, M., Howard, L. R., & Wolbers, T. (2015). Changes in pattern completion—A key mechanism to explain age-related recognition memory deficits? *Cortex*. https://doi.org/10.1016/j.cortex.2014.12.007

Wilson, I. A., Gallagher, M., Eichenbaum, H., & Tanila, H. (2006). Neurocognitive aging: Prior memories hinder new hippocampal encoding. *Trends in Neurosciences*, *29*(12), 662–670. https://doi.org/10.1016/J.TINS.2006.10.002

Wynn, J. S., Buchsbaum, B. R., & Ryan, J. D. (2021). Encoding and retrieval eye movements mediate age differences in pattern completion. *Cognition*, *214*, 104746. https://doi.org/10.1016/J.COGNITION.2021.104746

Zeithamova, D., & Bowman, C. R. (2020). Generalization and the hippocampus: More than one story? *Neurobiology of Learning and Memory*, *175*, 107317.

Zeithamova, D., de Araujo Sanchez, M.-A., & Adke, A. (2017). Trial timing and pattern-information analyses of fMRI data. *NeuroImage*, *153*, 221–231.

Zeithamova, D., Dominick, A. L. L., & Preston, A. R. R. (2012). Hippocampal and ventral medial prefrontal activation during retrieval-mediated learning supports novel inference. *Neuron*, *75*(1), 168–179. https://doi.org/10.1016/j.neuron.2012.05.010

Zeithamova, D., Houser, T., & Bowman, C. (2025). *Monte Carlo approaches to model selection: Application to the prototype and exemplar models of categorization*. OSF. https://osf.io/vhm7r_v2

Appendix A

Prototype and exemplar model fitting to behavioral responses

The prototype and exemplar models were fit to trial-by-trial categorization data in individual subjects. The prototype model assumes that items are categorized based on their similarity to category prototypes. Prototype similarity is computed as an exponential decay function of the distance in psychological space between the to-be-categorized item and the prototype of a given category (Shepard, 1957). Estimated model parameters include the amount of attention paid to individual features (attention weights) and the steepness of the function relating distance to subjective similarity (sensitivity). Formally, the similarity of item x to the category A representation is computed as:

(1) $$S_A(x) = \exp\left[-c\sum_{i=1}^{m}(w_i|x_i - proto_{Ai}|^r)^{\frac{1}{r}}\right]$$

where $S_A(x)$ is the similarity of item x to the category A representation, x_i is the value of the i-th dimension of item x, m is the number of feature dimensions (m = 10 in the present study), $proto_A$ is the prototype of category A, r is the distance metric (fixed at 1 for the city-block metric in the present study), w is a vector with attention weights for each of the 10 stimulus features (constrained to sum to 1), and c is the sensitivity (constrained to be between 0-100).

The exemplar model is the same except that the underlying similarity computation is the summed similarity across training exemplars from a given category, but it includes the same estimated attention weights and sensitivity parameters. Similarity of item x to the category A representation is computed as:

(2) $$S_A(x) = \sum_{y\in A}\exp\left[-c\sum_{i=1}^{m}(w_i|x_i - y_i|^r)^{1/r}\right]$$

where y represents the individual training stimuli from category A, and the remaining notations are as in Equation 1.

For both models, the probability of assigning a given stimulus to category A is equal to the similarity to category A divided by the summed similarity across categories A and B:

(3) $$P(A|x) = \frac{s_A(x)}{s_A(x) + s_B(x)}$$

For each trial and each model, we estimated the probability of the participant having made their observed response. We then generated an error metric, computing the negative of log-transformed response probabilities (negative log likelihood) across all trials in the categorization phase and summing them. We used standard maximum likelihood methods implemented with fminsearch in MATLAB (MathWorks) to minimize this error metric separately for each model in each participant, adjusting the attention weights and sensitivity values to minimize model error. After minimization, the resulting negative log likelihoods were carried forward for model selection and the denominator from Equation 3 (summed similarity) for each model was used as a parametric modulator in fMRI analyses.

Model selection

Our model selection approach had two steps: we first determined whether each model (prototype, exemplar) fit better than a model assuming random responding, and we then determined whether either the prototype or exemplar model fit better than the other. For both steps, we used a permutation approach that we have used previously (Bowman et al., 2020, 2022; Bowman & Zeithamova, 2018, 2020, 2023, in press) and described in detail (Zeithamova et al., 2025).

To determine whether each model fit better than one would expect by chance, we randomly shuffled each participant's responses, maintaining any overall response bias but removing any relationship between the stimuli and the responses. We then fit

each model to the permuted data and stored the resulting negative log likelihood value. We repeated this process 10,000 times, generating a distribution of negative log likelihood values that one would expect from chance responding. We then compared the fit of each model to the observed responses. Each model was considered to fit better than chance if the observed negative log likelihood value was smaller than 95% or more of the fits in the null distribution (i.e., alpha = .05, one-tailed). In the present study, both the prototype and exemplar model fit better than one would expect by chance for all included subjects.

To determine whether the prototype model fit better than the exemplar model or vice versa, we computed a null distribution of differences in model fits using the fits to permuted responses from above. We subtracted the null prototype model fits from the null exemplar model fits and divided by their sum (i.e., exemplar fit – prototype fit / exemplar fit + prototype fit). Dividing by the sum of model fits accounts for how well the models fit overall in determining whether the difference in fits is significant. We computed the same difference for the fit of the prototype and exemplar models to the observed data. We then tested whether the difference in prototype and exemplar model fits was greater than would be expected by chance based on the null distribution of model fits (alpha = .05, two-tailed). Participants for whom the prototype model fit significantly better than the exemplar model were given the ‘prototype’ strategy label. Participants for whom the exemplar model fit significantly better than the prototype model were given the ‘exemplar’ strategy label. Participants for whom neither model significantly outperformed the other were given the ‘similar’ fits strategy label, indicating that we did not have enough evidence to say that one model fit better than the other.