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Brief Communication

Age-related declines in the fidelity of newly acquired category representations

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We present a theory suggesting that the ability to build category representations that reflect the nuances of category structures in the environment depends upon clustering mechanisms instantiated in an MTL-PFC-based circuit. Because function in this circuit declines with age, we predict that the ability to build category representations will be impaired in older adults. Consistent with this prediction, we find that older adults are impaired relative to younger adults at learning nuanced category structures that contain exceptions to the rule. Model-based analysis reveals that this deficit arises from older adults' failure to engage clustering mechanisms to separate exception and rule-following items in memory.

[Supplemental material is available for this article.]

Is it a Tea Party or Occupy Wall Street Rally? Taquito or flauta? Throughout our lifespans, we are continuously bombarded with novel categories to learn. These categories perform a key role in day-to-day cognition by facilitating generalization and inference.

One critical aspect of category learning is the ability to flexibly build category representations that reflect the nuances of category structures as they exist in nature. Many category structures in the world are nuanced such that they cannot be easily described by simple rules or statistical averages. For example, most members of the categories, birds and mammals, can be accurately categorized based on the rule, "If it has wings, then it's a bird," but there are exceptions to this rule (e.g., bats) that must also be accommodated.

Cluster-based category learning models offer psychological accounts and formal methods of measuring the cognitive and neural mechanisms that allow people to build category representations that reflect the structure of categories in the environment (Anderson 1991; Love et al. 2004; Vanpaemel and Storms 2008). Cluster-based models represent categories by clusters that code a conjunction of an object's features and category membership. Clusters can take various forms to represent category structures, ranging from a single example to an abstraction, like a rule. For example, cluster-based models might represent the categories birds and mammals, with a cluster that contains winged animals for birds and another that contains nonwinged animals for mammals but require an additional cluster to form a separate representation for bats.

Neurobiologically, the ability to form new cluster representations is thought to depend on a circuit comprising the medial temporal lobes (MTL) and prefrontal cortex (PFC) (Love and Gureckis 2007; Davis et al. 2012a). Within this network, the MTL is thought to be the primary location where clusters are formed and stored. The PFC plays a critical role in directing the encoding of new clusters in response to surprise or prediction error and engages controlled retrieval processes. Recent fMRI studies (Davis et al. 2012a,b) have tested these neurobiological predictions using rule-plus-exception tasks. Rule-plus-exception tasks, like the birds and mammals example, require subjects to learn categories that can be primarily solved with a simple rule but also contain exceptions (like bats) that must be learned separately and, thus, place high demands on subjects' abilities to recruit new cluster representations. During rule-plus-exception learning, Davis et al. (2012a) found that MTL and PFC activation correlated with trial-by-trial cluster retrieval and error correction measures from SUSTAIN, a clustering model developed by Love et al. (2004). These results provide compelling evidence that the mechanisms that underlie formation and retrieval of new cluster-based representations depend upon an MTL-PFC circuit.

In the present study, we extend previous research on the neurobiological basis of clustering mechanisms by investigating how the ability to form new cluster-based representations is impacted by normal aging. By exploring how aging impacts cluster-based learning mechanisms, we can significantly add to previous results from fMRI studies. Anatomically, both the MTL and PFC exhibit decreases in volume over the course of normal aging (Hedden and Gabrieli 2004; Raz et al. 2005; Walhovd et al. 2011). In animal models, aging is associated with synaptic loss in the PFC (Peters et al. 2008) and deterioration of the paths through which information enters the hippocampus, a key structure in the MTL, from the cortex (Geinisman et al. 1992; Smith et al. 2000; for review, see Wilson et al. 2006). Thus, cognitive functions, like cluster formation, that depend upon the MTL-PFC circuit should be negatively impacted by the aging process.

Although the ability to form cluster-based category representations has not been directly investigated in older adults, declines in long-term memory (LTM), a cognitive function that depends upon similar MTL-PFC circuitry (Squire 1992; Eichenbaum et al. 2007; Preston and Wagner 2007), are well documented (e.g., Perlmutter 1979; Craik and McDowd 1987; McIntyre and Craik 1987). In terms of neural function, older adults activate the MTL less during tasks that tap LTM but show increased activation in the PFC, presumably as a compensatory mechanism for reduced MTL function (Daselaar et al. 2006; Park and Reuter-Lorenz 2009; Gutchess et al. 2011).

Principles that underlie LTM overlap with those that underlie cluster-based models (Love and Gureckis 2007; Davis et al. 2012a). LTM is thought to depend upon representations that are like the conjunctions encoded by clusters in that they flexibly bind

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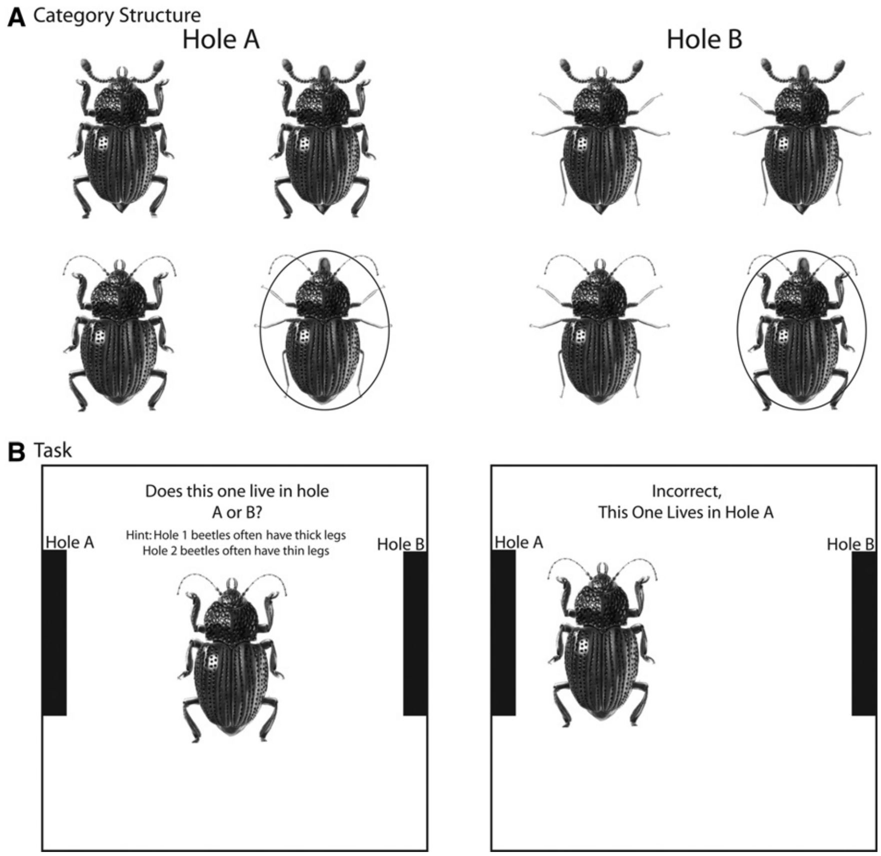

Figure 1. Category structure and task sequence. (*A*) An example category structure. The beetles vary on four of the following five perceptual dimensions where the fifth dimension is held fixed: eyes (green or red), tail (oval or triangular), legs (thin or thick), antennae (spindly or fuzzy), and fangs (pointy or round). The rule-relevant dimension in this example is legs. Most (75%) of Hole 1 beetles have thick legs, whereas most (75%) of Hole 2 beetles have thin legs. The two stimuli circled are the exceptions because they have legs consistent with the opposing category. The rest of the features are evenly distributed across the exemplars, with the exception of eyes, which is held constant in this example. (*B*) Trial structure. During stimulus presentation, a beetle was presented and subjects were asked to classify it as a Hole A or Hole B beetle. To focus on cluster formation processes, all subjects were given the rule that could be used to accurately categorize rule-following items prior to the beginning of the task and were reminded of it on each trial. Subjects then received feedback about whether they were correct or incorrect and the correct category assignment.

or associate multiple aspects of a memory trace into a single representation (Wallenstein et al. 1998; Eichenbaum and Cohen 2004; Preston et al. 2004; Staresina and Davachi 2009). Like cluster formation in cluster-based models, formation of new long-term memory representations is thought to depend upon pattern separation processes that differentiate new memories from older ones (O'Reilly and Rudy 2001; Norman and O'Reilly 2003). Interestingly, the aspects that overlap between cluster-based category learning and LTM are particularly disrupted during aging; older adults are increasingly impaired at forming new associative or conjunctive memories (Schacter et al. 1991; Henkel et al. 1998; Davidson and Glisky 2002; Li et al. 2005), and recent evidence suggests that this deficit may arise from failures to recruit MTL-based pattern separation mechanisms (Stark et al. 2010; Yassa et al. 2011a,b). Coupled with previous fMRI findings suggesting a role for the MTL-PFC circuit in cluster-based category learning (Davis et al. 2012a), these findings suggest that older adults should also be impaired at learning categorization problems that place higher demands on clustering mechanisms.

To investigate how normal aging impacts the ability to form new cluster-based category representations, we examined older ($n = 37$; mean age = 69.65; range = 59–82) and younger adults' ($n = 32$; mean age = 20; range = 18–26) abilities to master a rule-plus-exception task (Palmeri and Nosofsky 1995; Davis et al. 2012a; Supplemental Materials and Methods). In this task, subjects learn to categorize schematic beetles on the basis of trial and error (see Fig. 1A; Table 1 for the abstract category structure). On each trial, subjects are presented with a beetle in the center of the screen and are asked to classify it at their own pace (Fig. 1B). They then receive feedback for 2.5 sec indicating the correct answer. Each beetle belongs to one of two contrasting categories (Hole A or Hole B beetles) with membership determined by its features. Most of the beetles are rule-following items and can be categorized using a rule based on a single stimulus dimension (e.g., thick legs = Hole A) (Fig. 1A), but each category also contains an exception to this rule that must be represented separately from the rule-following items. In order to speed up learning and reduce demands upon hypothesis testing and rule-maintenance mechanisms that are also supported by the PFC (Ashby and Maddox 2005), subjects were given the rule prior to the experiment and reminded of it on each trial. The task consisted of 128 trials organized into blocks of eight in which each of the stimuli (Table 1; Fig. 1A) were presented once. All older adults were given a neuropsychological testing battery in a prior testing session (Table 2; Supplemental Materials and Methods).

Category learning models used to explain behavior in rule-plus-exception tasks posit that learning the task involves a balance between abstracting regularities, like rules, while pattern-separating items, like exceptions, that violate these regularities (Palmeri and Nosofsky 1995; Sakamoto and Love 2004, 2006). One cluster-based model that embodies these principles is the Rational Model of Categorization (RMC) (Anderson 1991). The RMC learns the task in the same way that subjects do. On each trial, the RMC compares a stimulus to stored clusters and makes a prediction for the category label based on how similar a stimulus is to these representations. The RMC then updates its representations on the basis of feedback. Critically, the RMC does not represent every item separately in memory but rather forms clusters that abstract over individual rule-following items, while pattern-separating exceptions that violate the rule by storing them in individual clusters (Fig. 2).

Here, one advantage of the RMC over other clustering models that have been used to explain rule-plus-exception tasks (Sakamoto and Love 2004) is that the RMC includes relatively few parameters, one of which, a coupling parameter, directly relates to cluster formation. When the value of the coupling parameter is high, the RMC tends to store items in shared clusters, whereas when the coupling parameter is low, the RMC tends to store all items separately. By providing an indicator of how readily the model is able to recruit new clusters, variations in the coupling

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Table 1. Abstract category structure

	Hole A beetles	Hole B beetles
Exception	2 2 2 2	1 2 2 2
R1	1 2 2 1	2 2 2 1
R2	1 1 1 2	2 1 1 2
R3	1 1 1 1	2 1 1 1

Each row represents a unique stimulus (i.e., beetle). The four values assigned to a stimulus denote the four stimulus dimensions (e.g., antenna, legs, etc.) assigned to a beetle. Each numeric value (1 or 2) represents a specific feature instantiation (e.g., red or green eyes). The first dimension represents the rule-relevant dimension. Most Hole A beetles have a 1 on the first dimension (e.g., thick legs), whereas most Hole B beetles have a 2 (e.g., thin legs). The first stimulus in each of the columns is, therefore, an exception.

parameter allow us to predict and model how decreases in MTL-PFC function relate to pattern separation mechanisms.

Although the RMC was originally formulated as a computational-level description of category learning from a Bayesian perspective, it is also valid to view RMC as a mechanistic interpretation of the processes in which people engage when they learn novel categories (Jones and Love 2011). Predictions from the model such as parameter estimates and its internal states and representations can thus be used as psychological measures of how the brain instantiates specific processes (Davis et al. 2012b). Here, we use the RMC's coupling parameter, which determines the extent to which the RMC is able to form new clusters to measure differences between older and younger adults in their ability to engage pattern separation mechanisms in the MTL-PFC circuit. If older adults are impaired in their ability to pattern separate exception items from rule-following items during learning, fits of the RMC to their categorization performance at the end of training should yield higher values of the coupling parameter than fits to younger subjects' performance. In terms of behavior, older adults should be impaired at categorizing exception items at the end of training relative to younger adults, whereas both groups should perform equivalently with rule-following items, as rule-following items do not place as high a demand on pattern-separation mechanisms (see Fig. 2).

Following our predictions, we found that, while both older and younger adults achieved a high level of accuracy with rule-following items by the end of training (last five blocks), the older adults were impaired at categorizing exceptions (Fig. 3; Supplemental Figs. S2, S3; see Supplemental Table for response times). In a hierarchical logistic regression, we found a significant interaction whereby the difference between exceptions and rule-following item performance was greater for older adults compared to younger adults ($z = 2.41$, $P < 0.05$). This interaction is consistent with our prediction that older adults would be disproportionately impaired at categorizing the exception items due to a reduced ability to form separate clusters for exceptions.

The behavioral results provide compelling evidence that older and younger adults differed in their ability to pattern separate exception items, but in order to make stronger inferences regarding the mechanisms that lead to these behavioral differences, it is critical to use model-based analyses that directly relate the hypothesized clustering mechanisms to subjects' behavior. To this end, we fit the RMC to each subject's individual performance at the end of training by allowing the coupling parameter to vary between subjects (Supplemental Material). Consistent with our predictions, individual subject fits of RMC to younger subjects' data tended to have significantly lower coupling parameter values than fits to older subjects' data ($t_{(61)} = 2.00$, $P < 0.05$, $d = 0.51$) (Supplemental Fig. S3), indicating a reduced tendency to pattern separate items for older adults. To clarify how these group differences related to subjects' clustering of the rule-following and exception items, we also fit RMC to the group-averaged data for older adults and younger adults. Consistent with our predicted clustering (Fig. 2), we found that the RMC fit to younger subjects' behavior tended to form four clusters—one for each of the categories of rule-following items and another for each exception. In contrast, the RMC fit to older adults' behavior recruited only two clusters— one for each category—and did not form clusters to pattern-separate the exception items.

Table 2. Neuropsychological tests scores for older adults

	Raw scores		Standard scores		Task correlations	
Neuropsychological test	Mean (SD)	Range	Mean (SD)	Range	Exception	Rule-following
WAIS digit span	18 (4.2)	11–30	0.60 (0.83)	−1–2.5	0.26	0.03
WAIS letter/number sequencing	10.9 (2.6)	7–17	0.68 (0.99)	−1.4–2.5	0.12	0.04
WAIS arithmetic	15.4 (3.4)	6–21	0.82 (1.0)	−1.7–2.5	0.32*	0.22
WAIS working memory index	113.2 (12.6)	92–144	0.76 (0.84)	−0.7–2.8	0.23	0.08
Trials A	32.2 (8.1)	19–52.4	−0.58 (0.56)	−1.4–0.64	0.19	0.03
Trials B	77.7 (32.7)	19–177	−0.47 (0.59)	−1.61–0.96	0.18	0.24
Stroop interference	3.9 (6.0)	−7.1–17.6	0.29 (0.61)	−0.8–1.6	0.13	0.25
Controlled oral word association	43.8 (10.2)	25–65	0.22 (0.79)	−1.4–1.9	0.31	0.14
WCST # of categories	4.25 (2.3)	0–6	−0.18 (1.4)	−2.72–2.03	0.14	0.10
WCST # of errors	29.0 (22.5)	0–83	0.09 (1.09)	−2.3–2.5	0.37*	0.05
WCST # of perseverations	13.56 (10.1)	0–37	0.26 (0.88)	−1.6–2.5	0.28	0.19
WAIS information	22.84 (3.6)	11–28	1.35 (0.81)	−1–2.5	0.14	0.16
WAIS vocabulary	54.63 (9.2)	17–65	1.27 (0.87)	−1.7–2.5	0.24	0.05
WAIS similarities	26.6 (3.4)	19–32	1.27 (0.87)	−1.7–2.5	0.14	0.19
CVLT short-delay free recall	10.9 (3.8)	1–16	0.73 (1.1)	−2–2.5	0.19	0.07
CVLT long-delay free recall	11.75 (4.0)	0–16	0.78 (1.15)	−2.5–3	0.15	0.06
WMS-III logical memory paragraphs immediate recall	44.25 (11.0)	23–63	1.04 (1.01)	−1.3–2.5	0.29	0.07
WMS-III logical memory paragraphs delayed recall	13.56 (3.1)	7–19	1.19 (1.01)	−1–2.5	0.41*	0.24
Visual reproduction immediate recall	83.2 (15.5)	47–104	0.91 (1.16)	−1.7–2.5	0.29	0.18
Visual reproduction delayed recall	12.9 (3.2)	9–99	0.99 (1.05)	−1.7–2.5	0.35*	0.20
Geriatric depression scale	5.06 (3.45)	0–13			−0.18	−0.04

Uncorrected correlations of neuropsychological test scores with exception and rule-following item performance were included for exploratory purposes. (*) Significance at $P < 0.05$ level.

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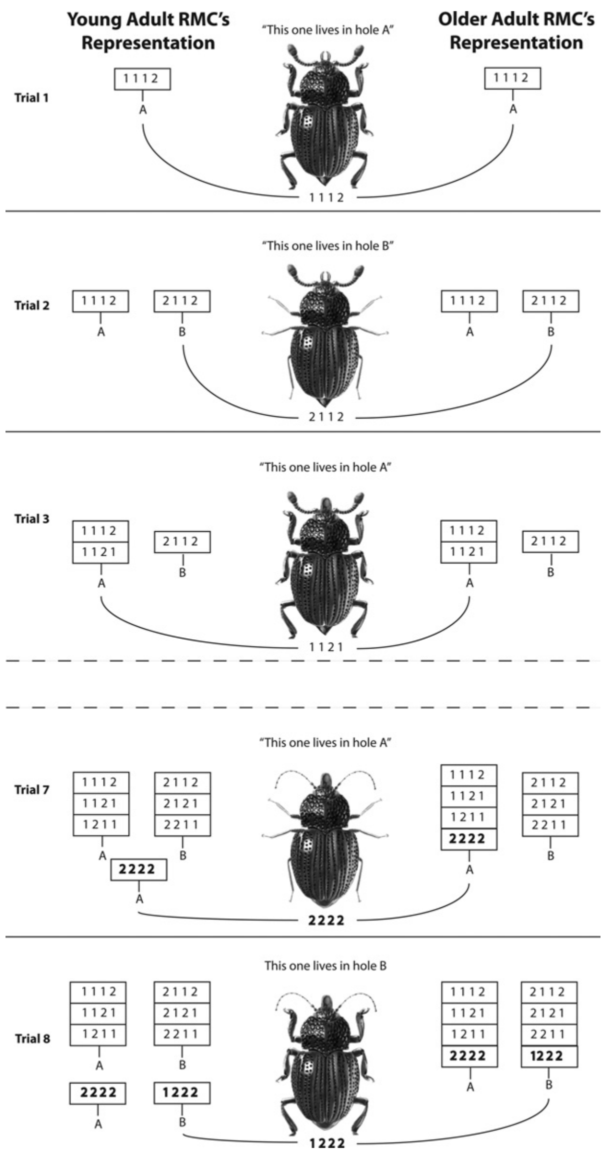

Figure 2. Illustration of the RMC's clustering mechanisms for the first eight trials of the experiment and how the representations differ between RMC fit to younger adults (*left*) and RMC fit to older adults (*right*). On each trial of the task, the RMC is presented with a beetle (represented by a four-digit code) (see Table 1), just like human subjects, and it makes a guess about the correct category by matching the stimulus to stored cluster representations. After it makes a guess, the RMC is presented with the correct category label (shown *above* each beetle) and updates its representations based on this feedback. After the feedback is delivered on each trial, the RMC can either assign an item to a current cluster or recruit a new cluster to represent the item. Whether an item is stored in a new or old cluster depends upon two factors: the match between an item's unique conjunction of features and category label and those of cluster-based representations previously stored in memory, and a coupling parameter that determines how likely the model is to store items in shared or separate clusters. For both groups, the rule-following items (codes presented in standard font; first six trials) tend to be consistent with previous clusters associated with a given category and so are stored in shared clusters with other rule-following items that correspond to the same category. For younger adults, who are more likely to pattern separate items and store them in separate clusters, the exceptions (codes depicted in bold font; last two trials) are inconsistent enough with rule-following items that they are pattern separated into their own specific clusters. However, for older adults, the tendency to pattern separate aberrant items is lower, and so the exceptions are stored in shared clusters along with the rule-following items.

Taken with the behavioral and neuropsychological analysis presented above, our model-based analysis provides strong evidence that the primary difference between groups was in the extent to which they could engage mechanisms to recruit and store cluster-based representations for pattern-separating exceptions and rule-following items in memory. Importantly, however, the model-based results go beyond what is possible using behavior alone in that they directly relate a concrete mechanistic process (i.e., cluster recruitment) to subjects' performance in the task.

The present results illustrating how older and younger adults differ in their abilities to form new clusters extend previous results examining predictions from cluster-based models in fMRI studies of rule-plus-exception tasks. In theses studies, Davis et al. (2012a,b) used trial-by-trial predictions from clustering models to track how signals in the MTL-PFC circuit related to recognition, error correction, and uncertainty unfold as healthy younger adults learn. By showing that the same basic clustering mechanisms can also account for declines in pattern-separation abilities due to normal aging, the present results provide strong converging evidence for our cluster-based account of category learning.

Although we focus on rule-plus-exception learning, there are many different category learning tasks that have been studied; some tasks, like rule-based and prototype learning tasks, engage MTL-PFC circuitry (e.g., Nomura et al. 2007; Ziethamova et al. 2008), but others depend upon implicit neurobiological systems that do not include the MTL (Ashby and Maddox 2005; Poldrack and Foerde 2008; Smith and Grossman 2008; Seger and Miller 2010; but see Gureckis et al. 2010; Nosofsky et al. 2012). As our theory is intended to describe the function of the MTL-PFC circuit, it may draw together aging-related findings in rule-based and prototype learning (Hess 1982; Hess and Slaughter 1986; Filoteo and Maddox 2004; Maddox et al. 2010; Glass et al. 2012). For example, findings suggesting that older adults are increasingly impaired at rule-based tasks as rule complexity increases (Racine et al. 2006; Maddox et al. 2010) lend well to our theory, as complex rules tend to require more clusters than simple rules (Anderson 1991; Love et al. 2004). In this way, our theory suggests that the MTL-PFC circuit is not only critical for learning categories that contain exceptions but should be engaged in many types of category learning tasks. The extent of MTL-PFC engagement should depend on the demands placed upon clustering mechanisms.

In conclusion, we present a cluster-based category-learning theory, which suggests that the ability to build category representations to meet the demands of a learning context depends upon an MTL-PFC circuit. Based on this theory, we predicted that, throughout the course of normal aging, the ability to recruit

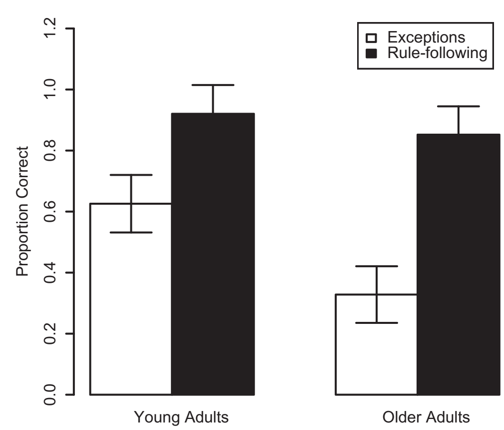

Figure 3. Learning performance for last five blocks of learning. Error bars depict 95% confidence intervals.

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new cluster-based category representations would diminish, altering older adults' abilities to represent the nuances of category structures. Consistent with this theory, using model-based analysis, we found that older adults were impaired at recruiting clusters to pattern separate exceptions from rule-following items. Our findings draw together a number of related findings in category learning and memory and help to solidify the relationships between a variety of category learning and LTM tasks.

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