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.]
Category representation and aging

A Category Structure

Hole A

Hole B

B Task

Does this one live in hole A or B?

Hole A

Hole B

Incorrect, This One Lives in Hole A

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

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

(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 rules. The role of the MTL in this process has been explored by a number of studies (e.g., Petrides and Pandya 1988; Glisky and Davachi 2005; Haxby and McDonald 2001; 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).

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In a hierarchical logistic regression, 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 ($t_{(51)} = 2.00$, $P < 0.05$, $d = 0.51$) (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 1. Abstract category structure

<table>
<thead>
<tr>
<th></th>
<th>Hole A beetles</th>
<th>Hole B beetles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exception</td>
<td>2 2 2 2</td>
<td>1 2 2 2</td>
</tr>
<tr>
<td>R1</td>
<td>1 2 2 1</td>
<td>2 2 2 1</td>
</tr>
<tr>
<td>R2</td>
<td>1 1 1 2</td>
<td>2 1 1 2</td>
</tr>
<tr>
<td>R3</td>
<td>1 1 1 1</td>
<td>2 1 1 1</td>
</tr>
</tbody>
</table>

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.

### Table 2. Neuropsychological tests scores for older adults

<table>
<thead>
<tr>
<th>Neuropsychological test</th>
<th>Raw scores Mean (SD) Range</th>
<th>Standard scores Mean (SD) Range</th>
<th>Task correlations</th>
<th>Rule-following</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAIS digit span</td>
<td>18 (4.2) 11–30</td>
<td>0.60 (0.83) −1.25</td>
<td>0.26</td>
<td>0.03</td>
</tr>
<tr>
<td>WAIS letter/number sequencing</td>
<td>10.9 (2.6) 7–17</td>
<td>0.68 (0.99) −1.4–2.5</td>
<td>0.12</td>
<td>0.04</td>
</tr>
<tr>
<td>WAIS arithmetic</td>
<td>15.4 (3.4) 6–21</td>
<td>0.82 (1.0) −1.7–2.5</td>
<td>0.32</td>
<td>0.22</td>
</tr>
<tr>
<td>WAIS working memory index</td>
<td>113.2 (12.6) 92–144</td>
<td>0.76 (0.84) −0.7–2.8</td>
<td>0.23</td>
<td>0.08</td>
</tr>
<tr>
<td>Trials A</td>
<td>32.2 (8.1) 19–52.4</td>
<td>−0.58 (0.56) −1.4–0.64</td>
<td>0.19</td>
<td>0.03</td>
</tr>
<tr>
<td>Trials B</td>
<td>77.7 (32.7) 19–177</td>
<td>−0.47 (0.59) −1.61–0.96</td>
<td>0.18</td>
<td>0.24</td>
</tr>
<tr>
<td>Stroop interference</td>
<td>3.9 (6.0) −7.1–17.6</td>
<td>0.29 (0.61) −0.8–1.6</td>
<td>0.13</td>
<td>0.25</td>
</tr>
<tr>
<td>Controlled oral word association</td>
<td>43.8 (10.2) 25–65</td>
<td>0.22 (0.79) −1.4–1.9</td>
<td>0.31</td>
<td>0.14</td>
</tr>
<tr>
<td>WCST # of categories</td>
<td>4.25 (2.3) 0–6</td>
<td>−0.18 (1.4) −2.72–2.03</td>
<td>0.14</td>
<td>0.10</td>
</tr>
<tr>
<td>WCST # of errors</td>
<td>29.0 (22.5) 0–83</td>
<td>0.09 (1.09) −2.3–2.5</td>
<td>0.37</td>
<td>0.05</td>
</tr>
<tr>
<td>WCST # of perseveres</td>
<td>13.56 (10.1) 0–37</td>
<td>0.26 (0.88) −1.6–2.5</td>
<td>0.28</td>
<td>0.19</td>
</tr>
<tr>
<td>WAIS information</td>
<td>22.84 (3.6) 11–28</td>
<td>1.35 (0.81) −1–2.5</td>
<td>0.14</td>
<td>0.16</td>
</tr>
<tr>
<td>WAIS vocabulary</td>
<td>54.63 (9.2) 17–65</td>
<td>1.27 (0.87) −1.7–2.5</td>
<td>0.24</td>
<td>0.05</td>
</tr>
<tr>
<td>WAIS similarities</td>
<td>26.6 (3.4) 19–32</td>
<td>1.27 (0.87) −1.7–2.5</td>
<td>0.14</td>
<td>0.19</td>
</tr>
<tr>
<td>CVLT short-delay free recall</td>
<td>10.9 (3.8) 1–16</td>
<td>0.73 (1.1) −2–2.5</td>
<td>0.19</td>
<td>0.07</td>
</tr>
<tr>
<td>CVLT long-delay free recall</td>
<td>11.75 (4.0) 0–16</td>
<td>0.78 (1.15) −2.5–3</td>
<td>0.15</td>
<td>0.06</td>
</tr>
<tr>
<td>WMS-III logical memory paragraphs immediate recall</td>
<td>44.25 (11.0) 23–63</td>
<td>1.04 (1.01) −1.3–2.5</td>
<td>0.29</td>
<td>0.07</td>
</tr>
<tr>
<td>WMS-III logical memory paragraphs delayed recall</td>
<td>13.56 (3.1) 7–19</td>
<td>1.19 (1.01) −1–2.5</td>
<td>0.41</td>
<td>0.24</td>
</tr>
<tr>
<td>Visual reproduction immediate recall</td>
<td>83.2 (15.5) 47–104</td>
<td>0.91 (1.16) −1.7–2.5</td>
<td>0.29</td>
<td>0.18</td>
</tr>
<tr>
<td>Visual reproduction delayed recall</td>
<td>12.9 (3.2) 9–99</td>
<td>0.99 (1.05) −1.7–2.5</td>
<td>0.35</td>
<td>0.20</td>
</tr>
<tr>
<td>Geriatric depression scale</td>
<td>5.06 (3.45) 0–13</td>
<td>−0.18 –0.04</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Uncorrected correlations of neuropsychological test scores with exception and rule-following item performance were included for exploratory purposes. (*) Significance at $P < 0.05$ level.
along with the rule-following items. The tendency to pattern separate aber-
rule-following items that they are pattern separated into their own specific
(codes depicted in bold font; last two trials) are inconsistent enough with
pattern separate items and store them in separate clusters, the exceptions
to the same category. For younger adults, who are more likely to
stored in shared clusters with other rule-following items that correspond
with previous clusters associated with a given category and so are
(cluster-based representations previously stored in memory, and a cou-
pling 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 aber-
rant 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 evi-
dence that the primary difference between groups was in the ext-
tent to which they could engage mechanisms to recruit and
store cluster-based representations for pattern-separating excep-
tions 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 these 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 mecha-
nisms can also account for declines in pattern-separation abilities
due to normal aging, the present results provide strong converg-
ing 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 the-
ory is intended to describe the function of the MTL-PFC circuit, it
may draw together aging-related findings in rule-based and proto-
type 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 de-
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 represen-
tations 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 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 (rep-
resented 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 present-
ed 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 cou-
ping 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

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


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