

# Adaptive repulsion of long-term memory representations is triggered by event similarity

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## **AUTHOR CONTRIBUTIONS**

A.J.H.C. and B.A.K. designed the experiments. A.G.T.M. supervised and/or conducted all data collection. A.J.H.C. and B.A.K. performed data analyses. All authors contributed to writing and editing of the manuscript.

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1 **ABSTRACT**

2 We tested whether similarity between events triggers an adaptive repulsion of long-term  
3 memories. Subjects completed an associative learning task in which objects were paired with  
4 faces. Critically, the objects consisted of pairs that were identical except for their color values,  
5 which were parametrically varied in order to manipulate interference. Performance on  
6 associative memory tests confirmed that color similarity robustly influenced interference.  
7 Separate tests of color memory showed that high similarity triggered a repulsion of long-term  
8 memories, wherein remembered colors were biased away from colors of competing objects.  
9 This repulsion effect was replicated across three experiments. In a fourth experiment, the  
10 repulsion effect was fully eliminated when task demands promoted integration, instead of  
11 discrimination, of similar memories. Finally, we show that repulsion of color memory was highly  
12 adaptive: greater repulsion was associated with less memory interference. These findings  
13 reveal that similarity between events triggers adaptive distortions in how events are  
14 remembered.

## 15 INTRODUCTION

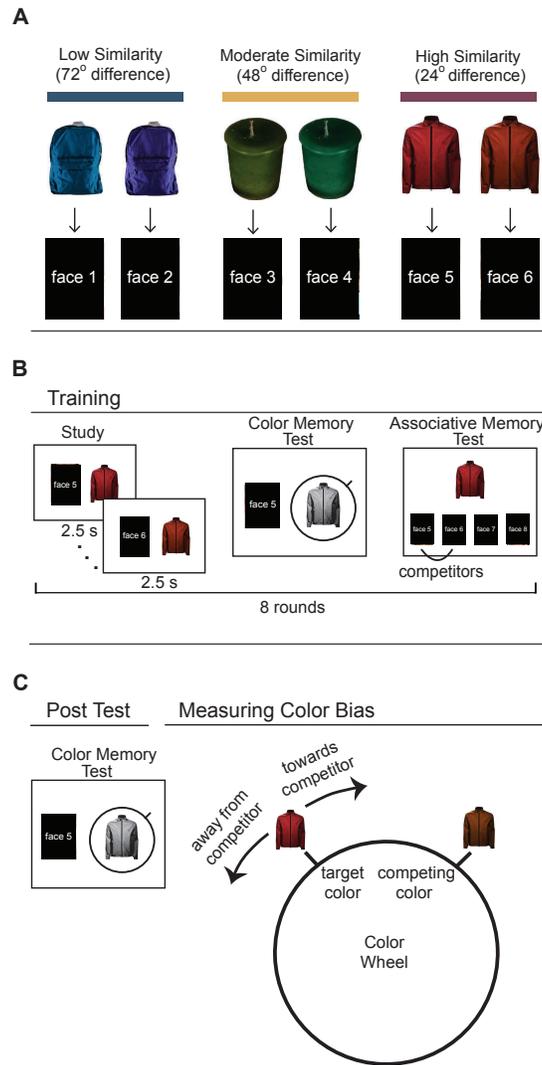
16 When episodic memories are similar, this creates interference and, ultimately, can lead to  
17 forgetting. Thus, an important challenge for the memory system is to resolve interference so that  
18 forgetting is minimized. The hippocampus is thought to play a critical role in resolving  
19 interference by pattern separating memory representations (Bakker, Kirwan, Miller, & Stark,  
20 2008; Colgin, Moser, & Moser, 2008; Yassa & Stark, 2011). Recently, several neuroimaging  
21 studies have found that hippocampal activity patterns associated with highly similar memories  
22 systematically ‘move apart’ from each other, suggesting that interference triggers a *repulsion* of  
23 memory representations (Ballard, Wagner, & McClure, 2019; Chanales, Oza, Favila, & Kuhl,  
24 2017; Dimsdale-Zucker, Ritchey, Ekstrom, Yonelinas, & Ranganath, 2018; Favila, Chanales, &  
25 Kuhl, 2016; Hulbert & Norman, 2015; Schlichting, Mumford, & Preston, 2015). However, these  
26 fMRI findings raise an important question: does a similar repulsion also occur with respect to  
27 how the specific *features* of competing events are remembered?

28 Here, we report a series of behavioral experiments—directly inspired by evidence of  
29 hippocampal repulsion—that test whether competition triggers repulsion of feature values  
30 associated with competing long-term memories. We had two central predictions. First, feature  
31 repulsion should be *competition dependent*—repulsion should be more likely to occur when  
32 memories are highly similar to each other (Chanales et al., 2017; Schapiro, Kustner, & Turk-  
33 Browne, 2012). Second, feature repulsion should be adaptive—repulsion should be associated  
34 with a reduction in memory interference (Favila et al., 2016; Hulbert & Norman, 2015).

35 To test these ideas, we conducted four experiments, each using a similar long-term, associative  
36 memory paradigm. In the paradigm, subjects repeatedly studied and were tested on object-face  
37 associations. Although each face was associated with a unique object, we created competition  
38 by including object pairs that were identical except for their color values (e.g., a blue backpack  
39 and a purple backpack; **Figure 1A**). Moreover, we parametrically manipulated the color distance  
40 between these object pairs to precisely control the degree of competition. In addition to  
41 measuring subjects’ associative memory (i.e., which face was paired with which object), we also  
42 probed subjects’ memory for the color of each object, providing a critical measure of whether  
43 subjects exaggerated the feature distance between competing objects. To the extent that  
44 competition triggers memory repulsion, we expected repulsion in color memory to specifically  
45 occur when color similarity was high. To the extent that repulsion is adaptive, we expected

46 greater repulsion to be associated with less associative memory interference.

47



**Figure 1: Experimental Design.** (A) In each of four experiments, subjects learned object-face associations that contained pairs of competing objects (object images that were identical except for their color values). The similarity (color distance) between competing objects was parametrically manipulated within and across experiments. In Experiments 1, 2, and 4, there were three similarity conditions: high (24 degrees apart), moderate (48 degrees), and low (72 degrees). In Experiment 3, the conditions were: moderate (48 degrees), high (24 degrees), and ultra (6 degrees). Note: Actual faces are not shown here per biorxiv policy. (B) Each experiment began with 8 training rounds. Each training round contained a study, a color memory test, and associative memory test phase. During study (*left panel*), subjects viewed each object-face pair. During color memory tests (*middle panel*), subjects were presented with a face and a greyscale version of the associated object. Using a continuous color wheel, subjects selected (recalled) the color of the object. During associative memory tests (Experiments 1–3 only; *right panel*), an object image was presented and subjects selected the associated face from a set of four options. The four face options always included the correct face (target) and the face that had been paired with the competing object (competitor). Procedures for Experiment 4 are described in **Figure 5** and in Methods. (C) For all experiments, after the training rounds subjects completed a Post Test that only probed color memory. The procedure was identical to the color memory tests from the training rounds. The critical performance measure from the Post Test was the percentage of color memory responses that were biased away from

the color of the competing object.

## 48 **METHODS**

### 49 ***Participants***

50

51 For all Experiments, target sample sizes were identified in advance, but final sample sizes were  
52 determined by exclusion criteria. Because we did not have any way to estimate effect sizes in  
53 advance of the first Experiment, we chose a target sample of 40 subjects for Experiment 1.  
54 However, due to exclusion criteria, a total of 23 subjects (11 males, 18-32 years old) were  
55 included in analyses. Instead of adding additional subjects to increase the sample size for  
56 Experiment 1, we conducted a replication study (Experiment 2) with a larger sample: 36  
57 subjects included in analyses (13 male, 18-22 years old). For Experiments 3 and 4, the number  
58 of subjects included in analyses were: 38 subjects in Experiment 3 (6 males, 18-34 years old)  
59 and 26 subjects in Experiment 4 (1 male, 18-25 years old). The rationale for the smaller sample  
60 in Experiment 4 was that pilot data indicated that the critical manipulation in Experiment 4 was  
61 quite powerful and consistent across subjects. Exclusion criteria are described below, in  
62 Procedures. All subjects were right-handed and reported normal or corrected-to-normal vision.  
63 Informed consent was obtained in accordance with procedures approved by the University of  
64 Oregon Institutional Review Board.

### 65 ***Materials***

66

67 For all experiments, stimuli consisted of 18 object images and 36 face images (all images were  
68 250 x 250 pixels). The object images were selected from a set of images designed to be color-  
69 rotated (Brady et al., 2013). Objects were chosen that had no strong inherent associations with  
70 particular colors. To alter the color of each object, the hue of an image was rotated through a  
71 circular color space ranging from 0–360 degrees. Colors were altered by independently rotating  
72 every pixel through an equiluminant circle in  $L^*a^*b^*$  space. Face images were pictures of non-  
73 famous white males gathered from the internet. For each subject, 6 object images were  
74 randomly assigned to each of three color similarity conditions. For Experiments 1, 2, and 4,  
75 these conditions were: high similarity (24 degrees), moderate similarity (48 degrees), and low  
76 similarity (72 degrees) (**Figure 1A**). For Experiment 3, these conditions were: ultra similarity (6  
77 degrees), high similarity (24 degrees), and moderate similarity (48 degrees). Each object was  
78 then assigned a pair of colors separated by the hue angle degree difference of their respective

79 condition. For Experiments 1, 2, and 4, this was accomplished by randomly selecting 45 colors  
80 from the color space, each separated by 8 degrees ( $45 * 8 = 360$  degrees). This set of 45 colors  
81 represented the set of possible colors for each subject, but only 36 of these colors were actually  
82 used ( $18 \text{ objects} * 2 \text{ colors per object}$ ). For Experiment 3, the ultra similarity condition  
83 necessitated a slight modification to the color assignment procedure: 60 colors (instead of 45)  
84 were randomly selected from the color space, each separated by 6 degrees (instead of 8). This  
85 set of 60 colors represented the set of possible colors for each subject, but, again, only 36 of  
86 these colors were used. For all Experiments, the 36 colors were then assigned to objects,  
87 according to their similarity condition, without replacement (i.e., each color was only assigned to  
88 one object). One constraint on this assignment was that, for each condition, there was an even  
89 representation across each third of the color space (1-120, 121-240, 241-360 degrees).

## 90 **Procedures**

91  
92 The first part of each experiment was a series of training rounds (8 total) in which subjects  
93 learned and were tested on all of the object-face associations (**Figure 1B**). Specifically, each  
94 training round was comprised of a study phase, a color memory test phase, and an associative  
95 memory test phase. During the study phase, subjects were shown (encoded) each object-face  
96 association. During the color memory test phase, subjects were presented with a face image  
97 and a greyscale version of the object that was associated with that face. Using a continuous  
98 report scale (Brady, Konkle, Alvarez, & Oliva, 2013), subjects selected (recalled) the color of the  
99 object. During the associative test phase (with the exception of Experiment 4), subjects were  
100 presented with an object image along with four face images and they attempted to select  
101 (retrieve) the face that had been paired with that object. Importantly, the set of four faces  
102 included the face that was paired with the object ('target'), the face that was paired with the  
103 competing object ('competitor'), and two faces that had been paired with different objects ('non-  
104 competitors'). After the 8 training rounds, subjects completed a color memory Post Test which  
105 repeatedly tested subjects' memories for each object's color (**Figure 1C**). This Post Test was  
106 identical in format to the color memory tests during the training rounds, but served as a critical  
107 measure of the 'end point' of subjects' learning.

108  
109 **Experiment 1.** Experiment 1 consisted of 8 training rounds and two Post Tests. Each training  
110 round included study, color memory test, and associative memory test phases (in that order). In  
111 each study round, subjects viewed the same 36 face-object associations. For each trial, a face

112 and corresponding object image appeared on a white screen for 2.5 s, with the face image to  
113 left of the object. There was a 1 s inter-trial interval during which a blank white screen was  
114 presented. Each object-face association was studied once per study round.

115 On each color memory test trial, a studied face was presented to the left of its paired object and  
116 subjects used a color wheel (Brady et al., 2013) to select the remembered color of the object.  
117 The object image initially appeared in grayscale; once participants moved the mouse cursor, the  
118 object would appear in color. The hue was determined by the angle between the cursor location  
119 and the center of the object image. A line marker along a ring surrounding the object image  
120 indicated the current hue angle. Once subjects rotated to the desired color they clicked the  
121 mouse to finalize their choice. There was no time limit for these responses. The color wheel was  
122 randomly rotated across trials so there was no correspondence across trials between spatial  
123 position and color.

124 The associative memory tests probed memory for each object-face association. On each trial, a  
125 colored object was presented at the top of the screen and four faces images were presented  
126 beneath. Subjects were instructed to select the face that had been studied with the object  
127 image. The target face was always presented along with a face that was paired with the  
128 competing object. Thus, subjects had to discriminate between the objects' colors (in memory) in  
129 order to select the correct face. The other two face images were two randomly selected faces  
130 that had been paired with other, non-competing objects (non-competitor faces). Each face  
131 served as a non-competitor foil on exactly 2 trials. Subjects made a selection using a computer  
132 mouse with no time limit to respond. They then indicated confidence in their response by  
133 clicking either a 'sure' or 'unsure' button using the mouse (note: these confidence ratings are not  
134 considered here). A feedback screen was then presented for 1.25 s; the feedback screen  
135 indicated whether the selected face was correct or not and also displayed the correct object-  
136 face pair.

137 Following the 8 training rounds, subjects completed an immediate Post Test (Day 1 Post Test)  
138 and then returned the following day (~24 hours later) for a second Post Test (Day 2 Post Test).  
139 The Post Tests were identical to the color memory tests in the training rounds except that, in the  
140 Post Tests, each object was tested 5 times. The 180 post-test trials were divided into 5 blocks in  
141 which each object was tested exactly once. The order of the trials within a block was  
142 randomized with the constraint that an object and its competitor were not tested on successive

143 trials. To minimize fatigue, after trial numbers 60 (1/3 of trials completed) and 120 (2/3 of trials  
144 completed) a screen prompted subjects to “Take a quick break” and to press a key to continue.  
145 The Day 2 Post Test was identical to the Day 1 Post Test except that the order of trials was re-  
146 randomized.

147 **Experiment 2.** Experiment 2 was identical to Experiment 1 except for a few procedural  
148 changes. Because of the strict performance-based exclusion criteria in Experiment 1, and the  
149 time limit cutoff (1.5 hours), there was a high overall exclusion rate (45.2%) and relatively small  
150 final sample of subjects ( $n = 23$ ). Thus, the goal for Experiment 2 was to replicate the results  
151 from Experiment 1, but with a larger final sample (the target was a 50% increase) and lower  
152 overall exclusion rate. We retained the same exclusion criteria, but sought to shorten the  
153 experiment so as to reduce the number of subjects that failed to complete the experiment in the  
154 allotted time (1.5 hours). We opted to shorten the experiment rather than to extend the time limit  
155 due to concern for subject fatigue. Subject fatigue was of particular concern given that the most  
156 critical data from the entire experiment came from the Post Test (i.e., the last round of the  
157 experiment). To shorten the experiment, we reduced the number of color memory test rounds  
158 during training so that they only occurred during rounds 1, 3, 5, and 7, and we imposed a time  
159 limit of 10 s on the associative memory test trials and color memory test trials (both during the  
160 training rounds and the Post Test). The number of Post Test trials excluded because of the time  
161 limit in Experiment 2 was very small (mean across subjects = 0.78%; maximum = 3.3%).  
162 Additionally, since we observed qualitatively identical results across the Day 1 and Day 2 Post  
163 Tests in Experiment 1, we did not include the Day 2 Post Test in Experiment 2.

164 **Experiment 3.** Experiment 3 was identical in procedure to Experiment 2 except that color  
165 memory tests were included in each of the 8 training rounds (as in Experiment 1) and the time  
166 limit for the entire experiment was extended to 2 hours. The rationale for reverting to every-  
167 round color memory tests was that the magnitude of the repulsion effect in the high similarity  
168 condition was somewhat lower in Experiment 2 ( $M = 54.63\%$ ) than in Experiment 1 ( $M =$   
169  $60.80\%$ ) and we speculated that this difference might be partly attributable to the reduction in  
170 the number of color memory tests during training in Experiment 2. The rationale for extending  
171 the time limit was to reduce the number of subjects excluded for not completing the experiment  
172 in the allotted time.

173 **Experiment 4.** Experiment 4 differed in procedure from Experiments 1–3 most significantly in

174 that the associative memory test during the training rounds was replaced by an *inference test*  
175 that assessed generalization across object-face pairs. Specifically, on each trial in the inference  
176 test one of the 36 face images appeared at the top of the screen, with four face images  
177 presented beneath. Subjects were instructed to select which of the four face options were  
178 associated with the same object category (e.g., “backpack”) as the probe face at the top of the  
179 screen. Subjects made their selection using a computer mouse. The set of four face options  
180 always included the target face (correct response) and 3 other studied, non-target faces. Note:  
181 here, the ‘competitor’ face was the target face. Each face was tested once per round (i.e., 36  
182 trials per round) and each face served as a non-target face option on exactly 3 trials. Feedback  
183 was provided on each trial indicating whether the selected face was correct along with the  
184 correct face-face pairing displayed on screen for 1 second. Otherwise, all procedures were  
185 identical to Experiment 3 (for details of color similarity conditions, see Materials).

186

187 **Exclusion criteria.** Across Experiments 1–4, a total of 19, 18, 9, and 6 subjects, respectively,  
188 were excluded from analysis. Subjects were excluded from analyses if they failed to complete  
189 the experiment in the allotted time (1.5 hours for Experiments 1 & 2 and 2 hours for Experiments  
190 3 & 4). For Experiments 1–4, this resulted in exclusion of 12, 0, 1, and 3 subjects, respectively.  
191 Additionally, subjects were excluded if they did not satisfy each of two performance-based  
192 criteria. The first performance criterion was that, across the last two rounds of the associative  
193 memory test (see Procedures for details), *non-competitor* face images were selected on no  
194 more than 2% of trials. Importantly, this exclusion criterion was orthogonal to subjects’ ability to  
195 discriminate between similar colors in that it only required that subjects had ‘narrowed down’ the  
196 options to either the target or competitor face. This exclusion criterion therefore specifically  
197 ensured that subjects had learned that two different faces were paired with a common object  
198 category (e.g., “backpack”). Across Experiments 1–4, a total of 6, 15, 9, and 0 subjects,  
199 respectively, failed to meet this criterion. The second performance criterion was that the  
200 percentage of Post Test trials with reaction times less than 500 ms could not exceed 15%.  
201 Given that the Post Test trials required clicking and dragging a cursor along a color wheel,  
202 responses that were made in less than 500 ms were considered to be evidence of subjects  
203 rushing through the experiment—which was a particular concern given the repetitive and  
204 tedious nature of the experiment. Across Experiments 1–4, a total of 5, 3, 1, and 6 subjects,  
205 respectively, failed to meet this criterion. Note: some subjects failed to satisfy both of the  
206 performance-based criteria (Experiments 1–4: 4, 5, 3, and 0 subjects, respectively). It is  
207 important to emphasize that these performance-based exclusion criteria were established in

208 advance, they were orthogonal to our effects of interest (repulsion of color memory), and they  
209 were applied uniformly across all experiments.

210 **Measuring Color Memory.** For color memory tests (during training rounds and Post Test),  
211 responses were recorded as integer values (0–359 degrees) reflecting hue angle on the color  
212 wheel. Although the color memory tests were identical in procedure during the training rounds  
213 and Post Test, for narrative clarity we focus on different measures during each phase. During  
214 the training rounds, we focus on *color error* as a general measure of training-related  
215 improvement in color memory. Color error was computed as the absolute value of the hue angle  
216 difference between a subject's color response and the true color. During the Post Test,  
217 however, because we were critically interested in whether color memory responses exhibited  
218 bias, we focused on the *percentage of responses away from the competing object's color*. To  
219 illustrate how this measure was computed, the location of the target object's color value can be  
220 considered as being at 0 degrees on the color wheel and a competing object might, for  
221 example, be at 24 degrees. In this scenario, any responses between 181 and 359 degrees  
222 would be counted as 'away from' the competing color. Notably, the definition of 'away'  
223 responses would be identical if the competing object color was at 6, 48, or 72 degrees. For each  
224 subject and each condition, we computed the percentage of trials that fell in the 'away' bin. We  
225 used this measure as opposed to mean signed error because mean signed error is highly  
226 susceptible to influence from extreme responses whereas the percentage of away responses is  
227 not. While we focus on the color error measure during training rounds and the percentage of  
228 away responses during Post Test, we also report the percentage of away responses during  
229 training rounds in **Supplementary Figure 1** and mean color error during Post Test in  
230 **Supplementary Figure 3**.

231

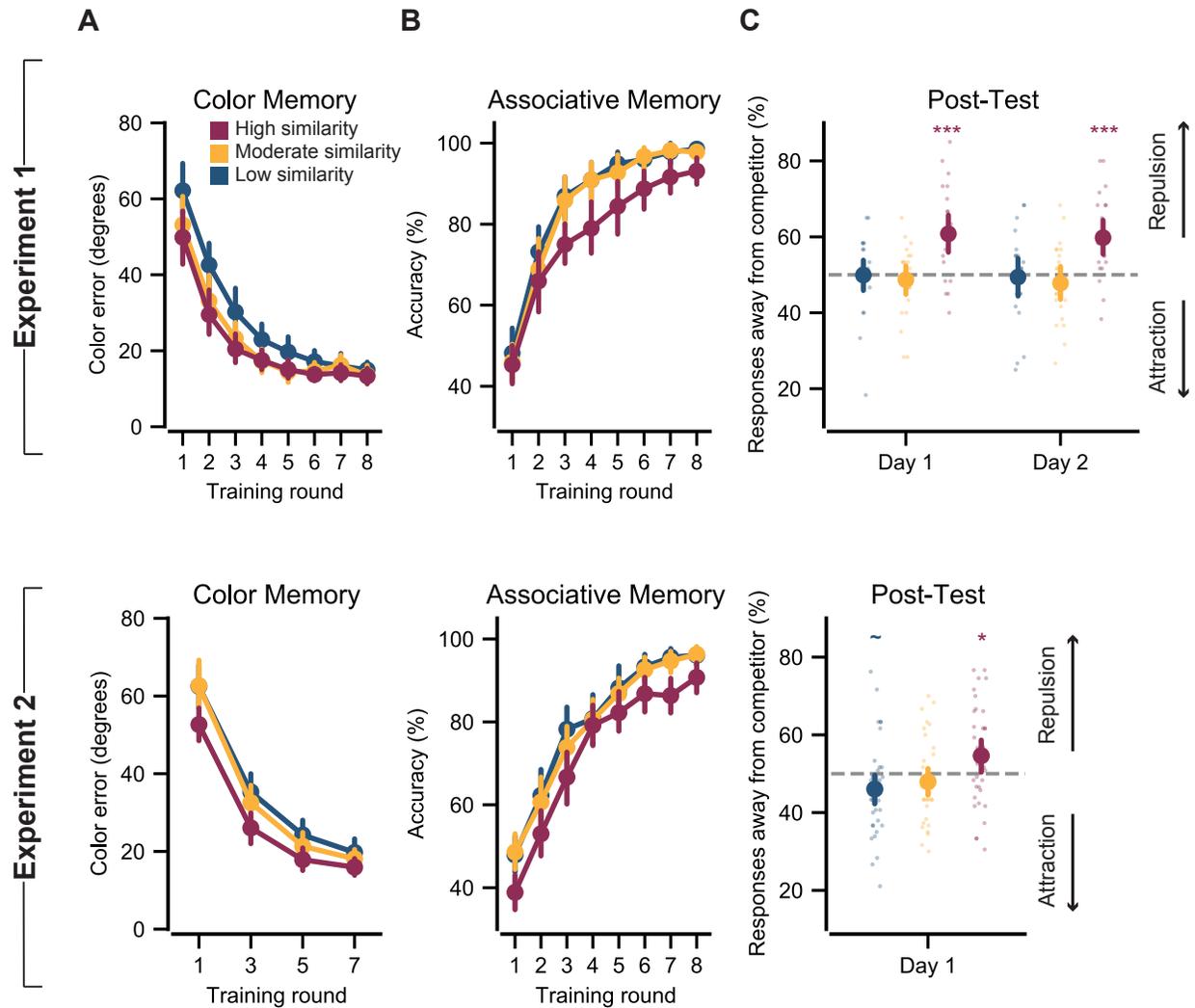
## 232 RESULTS

233

234 **Experiment 1.** Across the training rounds in Experiment 1, there were marked reductions in  
235 error on the color memory tests (**Figure 2A**) and increases in accuracy on the associative  
236 memory tests (**Figure 2B**) (see **Supplementary Figures 1** and **2** for additional data from the  
237 training rounds). Critically, accuracy on the associative memory tests was strongly influenced by  
238 color similarity (**Figure 2B**). In particular, subjects were much more likely to select the face  
239 associated with the competing object (hereinafter, *interference errors*) when color similarity was  
240 high (**Supplementary Figure 2**), confirming that our interference manipulation was successful.

241 In order to test for repulsion effects in color memory, we focused on the Post Tests. We  
242 predicted that repulsion would specifically occur when competition was high (i.e., the high  
243 similarity condition). The critical dependent measure was the percentage of trials in each  
244 similarity condition for which subjects reported a color that was ‘*away from*’ the color of the  
245 competing object (measures of unsigned color error are reported in **Supplementary Figure 3**).  
246 For example, if the target object’s color was located at 0 degrees on the color wheel and the  
247 competing object’s color was at 24 degrees, a color response at 350 degrees would be  
248 considered ‘*away from*’ the competing object’s color (**Figure 1C** and see Methods). We defined  
249 a repulsion effect as occurring for a condition if the mean percentage of away responses was  
250 greater than 50% (i.e., that most color reports were biased *away from the color of the competing*  
251 *object*).

252 For the Day 1 Post Test, an ANOVA with similarity condition as a factor revealed a robust main  
253 effect of similarity on the percentage of responses away from the competitor ( $F_{2,44} = 10.11$ ,  $P =$   
254  $0.0002$ ,  $\eta^2 = 0.22$ ; **Figure 2C**). Critically, there was a strong repulsion effect in the high similarity  
255 condition ( $M = 60.80\%$  ;  $SD = 12.00\%$ ;  $t_{22} = 4.31$ ,  $P = 0.0003$ , 95% CI: 5.61 – 15.99, Cohen’s  $d$   
256 = 1.27), but not in the moderate similarity ( $M = 48.70\%$  ;  $SD = 9.37\%$ ;  $t_{22} = -0.67$ ,  $P = 0.51$ , 95%  
257 CI: -5.36 – 2.75, Cohen’s  $d = -0.20$ ) or low similarity conditions ( $M = 49.93\%$  ;  $SD = 10.16\%$  ;  $t_{22}$   
258 = -0.03,  $P = 0.97$ , 95% CI: -4.46 – 4.32, Cohen’s  $d = -0.01$ ). Thus, when similarity between  
259 competing objects was high, color memory for a target object was systematically biased away  
260 from the color of the competing object. Follow-up comparisons confirmed that the percentage of  
261 away responses was significantly greater in the high similarity condition compared to both the  
262 moderate similarity ( $t_{22} = 4.47$ ,  $P = 0.0002$ , 95% CI = 6.49 – 17.71, Cohen’s  $d = 1.12$ ) and low  
263 similarity conditions ( $t_{22} = 3.80$ ,  $P = 0.001$ , 95% CI: 4.93 – 16.81, Cohen’s  $d = 0.98$ ). The  
264 selectivity of the repulsion effect to the high similarity condition is striking when considering that  
265 interference errors during the associative memory tests in the training rounds were much more  
266 common in the high similarity condition than in the moderate or low similarity conditions  
267 (**Supplementary Figure 2**).



**Figure 2. Color similarity induces interference and triggers memory repulsion.** Results from Experiment 1 (top row) and Experiment 2 (bottom row). **(A)** Mean color memory error (absolute distance between reported and target color values from the color memory tests) decreased across training rounds (main effect of round, Experiment 1:  $F_{1,22} = 166.2$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.77$ ; Experiment 2:  $F_{1,22} = 166.2$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.83$ ) **(B)** Accuracy on the associative memory tests (percentage of trials for which the target face was selected; chance = 25%) increased across training rounds (main effect of test round, Experiment 1:  $F_{1,22} = 435.4$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.83$ ; Experiment 2:  $F_{1,35} = 690.4$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.85$ ). Accuracy differed across color similarity conditions (main effect of similarity, Experiment 1:  $F_{2,44} = 13.04$ ,  $P = 0.00003$ ,  $\eta^2 = 0.23$ ; Experiment 2:  $F_{2,70} = 18.77$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.19$ ), driven by relatively lower accuracy (higher interference) in the high similarity condition (also see **Supplementary Figure 1**). **(C)** On the color memory Post Tests, the mean percentage of responses away from the competitor varied across similarity conditions (main effect of similarity,  $P$ s  $< 0.005$  for all Days/Experiments). Repulsion effects ( $> 50\%$  of responses away from competitor) were selectively observed in the high similarity condition ( $P$ s  $< 0.05$  for all Days/Experiments). Small dots reflect data from individual subjects. Notes: Error bars reflect  $\pm$  S.E.M.; \*\*\*  $P < 0.001$ , \*  $P < 0.05$ , ~  $P < 0.10$ .

268 Interestingly, the repulsion effect strongly persisted the following day: the main effect of  
269 similarity condition was again significant at the Day 2 Post Test ( $F_{2,42} = 9.82$ ,  $P = 0.0003$ ,  $\eta^2 =$   
270  $0.19$ ; **Figure 2C**) and there was a selective repulsion effect in the high similarity condition (high  
271 similarity:  $M = 59.77\%$ ;  $SD = 11.17\%$ ;  $t_{21} = 4.11$ ,  $P = 0.0005$ , 95% CI:  $4.82 - 14.72$ , Cohen's  $d =$   
272  $1.24$ ; moderate similarity:  $M = 47.80\%$ ;  $SD = 10.55\%$ ,  $t_{21} = -0.98$ ,  $P = 0.34$ , 95% CI:  $-6.87 -$   
273  $2.48$ , Cohen's  $d = -0.29$ ; low similarity  $M = 49.39\%$ ;  $SD = 12.05\%$ ,  $t_{21} = -0.24$ ,  $P = 0.82$ , 95% CI:  
274  $-5.95 - 4.73$ , Cohen's  $d = -0.07$ ).

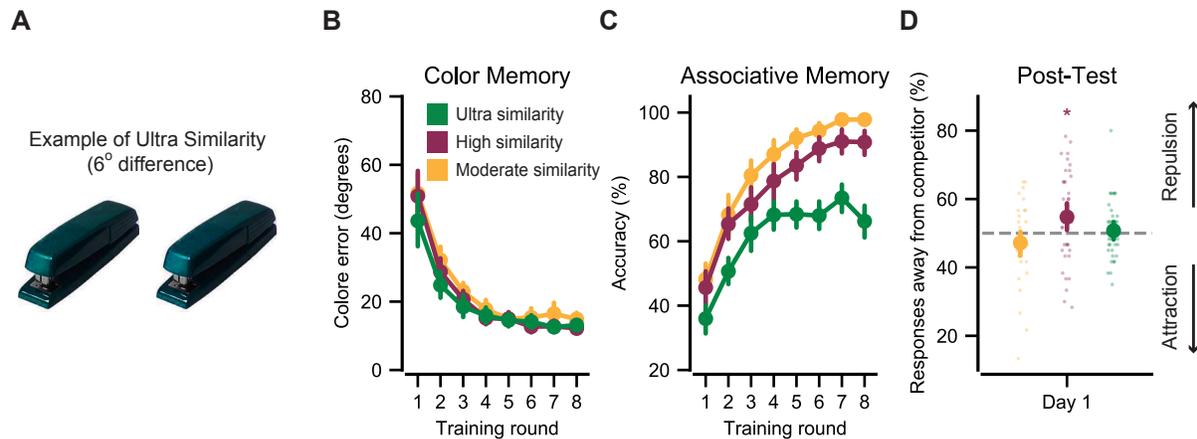
275 **Experiment 2.** In a replication study (Experiment 2) we used the same procedure as  
276 Experiment 1 except for a few minor changes (see Methods for details and rationale). In  
277 particular, we reduced the number of color memory tests during the training rounds (by 50%)  
278 and eliminated the Day 2 Post Test. Performance across the training rounds is reported in  
279 **Figure 2A,B** and **Supplementary Figures 1** and **2**. As in Experiment 1, the percentage of  
280 responses away from the competitor during the color memory Post Test robustly varied across  
281 color similarity conditions ( $F_{2,70} = 6.79$ ,  $P = 0.002$ ,  $\eta^2 = 0.09$ ; **Figure 2C**). Critically, we again  
282 observed a significant repulsion effect in the high similarity condition ( $M = 54.63\%$ ;  $SD =$   
283  $12.74\%$ ;  $t_{35} = 2.16$ ,  $P = 0.036$ , 95% CI:  $0.32 - 8.95$ , Cohen's  $d = 0.51$ ). The percentage of away  
284 responses did not significantly differ from 50% in the moderate similarity condition ( $M = 47.95\%$ ;  
285  $SD = 10.42\%$ ;  $t_{35} = -1.18$ ,  $P = 0.25$ , 95% CI:  $-5.57 - 1.48$ , Cohen's  $d = -0.28$ ) and there was a  
286 marginally-significant effect in the opposite direction (below 50%) in the low similarity condition  
287 ( $M = 46.05\%$ ;  $SD = 12.07\%$ ;  $t_{35} = 1.96$ ,  $P = 0.057$ , 95% CI:  $-8.04 - 0.13$ , Cohen's  $d = -0.46$ ).  
288 Follow-up tests confirmed that the percentage of away responses was again significantly higher  
289 in the high similarity condition compared to both the moderate similarity condition ( $t_{35} = 3.10$ ,  $P =$   
290  $0.004$ , 95% CI:  $2.30 - 11.06$ , Cohen's  $d = 0.57$ ) and the low similarity condition ( $t_{35} = 3.36$ ,  $P =$   
291  $0.002$ , 95% CI:  $3.40 - 13.77$ , Cohen's  $d = 0.69$ ). Thus, as in Experiment 1, we observed a  
292 selective repulsion effect in color memory specifically when there was high similarity between  
293 competing objects.

294 **Experiment 3.** Experiments 1 and 2 strongly establish that the repulsion effect is competition  
295 dependent in that it was selective to the high similarity condition. Interestingly, however, while  
296 hippocampal repulsion effects are also competition dependent, the relationship between  
297 competition and repulsion is thought to be non-monotonic: that is, with sufficiently strong  
298 competition, representations will fail to diverge (Ritvo, Turk-Browne, & Norman, 2019). In  
299 Experiment 3, we tested whether there was a non-monotonic relationship between color  
300 similarity and repulsion by shifting the range of color similarity to include a moderate similarity

301 condition (again, 48 degrees), a high similarity condition (again, 24 degrees) and a new 'ultra  
302 similarity' condition (6 degrees; **Figure 3A**).

303 Performance across the training rounds is reported in **Figure 3B,C** and **Supplementary**  
304 **Figures 1** and **2**. Of particular relevance, associative memory test accuracy (during the training  
305 rounds) was significantly lower in the ultra similarity condition than the high similarity condition  
306 ( $t_{37} = -11.39$ ,  $P < 0.00000001$ , 95% CI: -17.95 – -12.53, Cohen's  $d = -1.85$ ) or moderate  
307 similarity condition ( $t_{37} = -16.26$ ,  $P < 0.00000001$ , 95% CI: -24.26 – -18.86, Cohen's  $d = -2.96$ )  
308 (**Figure 3C** and **Supplementary Figure 2**). Nonetheless, in the last associative memory test  
309 round, subjects selected the target faces at above-chance rates in all similarity conditions  
310 (chance = 25%, all means > 66%,  $P$ s < 0.0000001). Thus, the ultra similarity condition clearly  
311 increased interference relative to the high similarity condition, but subjects were still generally  
312 successful at memory-based discrimination between these extremely similar colors.

313 Results from the Post Test again revealed that color similarity influenced the percentage of  
314 responses away from the competitor ( $F_{2,74} = 5.45$ ,  $P = 0.006$ ,  $\eta^2 = 0.06$ ; **Figure 3D**). However,  
315 the relationship between similarity and repulsion followed the predicted non-monotonic pattern.  
316 As in Experiments 1 and 2, there was a significant repulsion effect in the high similarity condition  
317 ( $M = 54.74\%$ ;  $SD = 13.42\%$ ;  $t_{37} = 2.17$ ,  $P = 0.036$ , 95% CI: 0.32 – 9.15, Cohen's  $d = 0.50$ ), no  
318 repulsion effect in the moderate similarity condition ( $M = 47.19\%$ ;  $SD = 10.93\%$ ;  $t_{37} = -1.58$ ,  $P =$   
319  $0.12$ , 95% CI: -6.40 – 0.79, Cohen's  $d = -0.36$ ) and a significant difference between the high and  
320 moderate similarity conditions ( $t_{37} = 3.04$ ,  $P = 0.004$ , 95% CI: 2.51 – 12.58, Cohen's  $d = 0.61$ ). In  
321 the ultra similarity condition, however, the percentage of away responses did not differ from  
322 50% ( $M = 50.75\%$ ;  $SD = 8.52\%$ ;  $t_{37} = 0.54$ ,  $P = 0.59$ , 95% CI: -2.06 – 3.55, Cohen's  $d = 0.12$ )  
323 confirming that, with sufficiently high similarity, the repulsion effect was eliminated. While the  
324 percentage of away responses was numerically lower in the ultra similarity condition than the  
325 high similarity condition, this difference did not reach significance ( $t_{37} = -1.63$ ,  $P = 0.11$ , 95% CI:  
326 -0.10 – 8.94, Cohen's  $d = 0.35$ ). Interestingly, despite the much higher rate of interference  
327 errors in the ultra similarity condition compared to the moderate similarity condition  
328 (**Supplementary Figure 2**), the percentage of color responses away from the competing  
329 object's color was marginally higher in the ultra similarity condition than in the moderate  
330 similarity condition ( $t_{37} = 1.89$ ,  $P = 0.067$ , CI: -0.026 – 7.37, Cohen's  $d = 0.36$ ). Taken together,  
331 performance across the three similarity conditions suggests a 'local maximum' in the repulsion  
332 effect that occurred when similarity was high (24 degrees) but not too high (6 degrees).



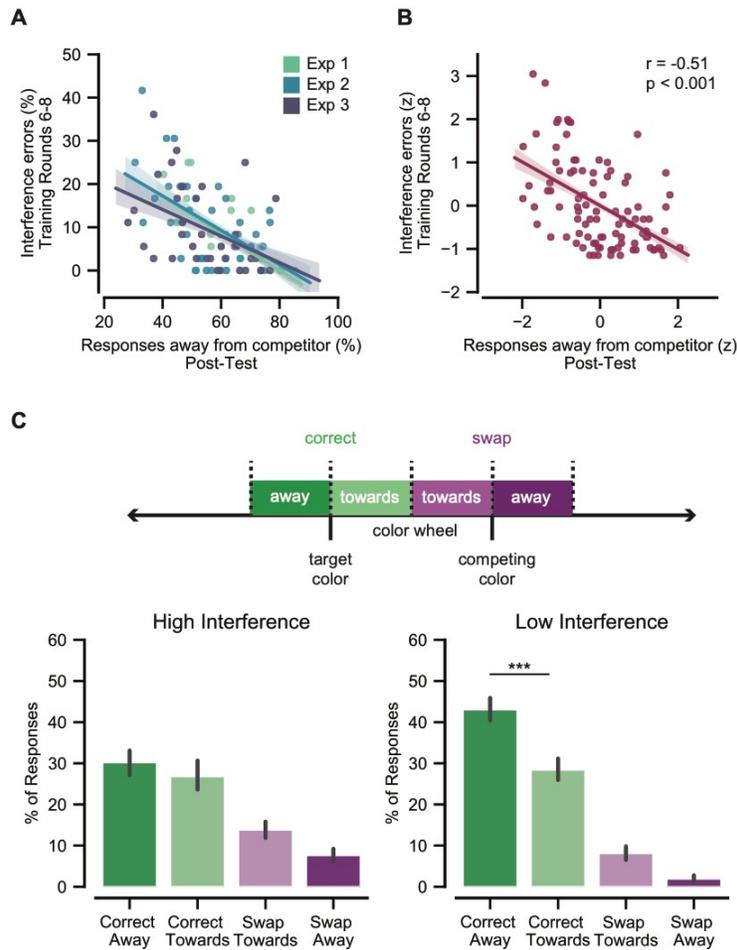
**Figure 3: Non-monotonic relationship between color similarity and repulsion.** (A) Experiment 3 used three color similarity conditions: moderate (48 degrees apart), high (24 degrees), and ultra (6 degrees). An example of competing images from the ultra similarity condition is shown. (B) Mean color memory error decreased across training rounds (main effect of round:  $F_{1,37} = 186.5$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.70$ ). (C) Accuracy on the associative memory tests increased across training rounds (main effect of test round:  $F_{1,37} = 326.9$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.75$ ). Accuracy differed across color similarity conditions (main effect of similarity:  $F_{2,74} = 129.9$ ,  $P < 0.00000001$ ,  $\eta^2 = 0.60$ ), driven by relatively lower accuracy (higher interference) in the ultra similarity condition (also see **Supplementary Figure 2**). (D) On the color memory Post Test, the mean percentage of responses away from the competitor varied across similarity conditions (main effect of similarity:  $P = 0.006$ ). A repulsion effect was selectively observed in the high similarity condition ( $P = 0.036$ ). Small dots reflect data from individual subjects. Notes: Error bars reflect  $\pm$  S.E.M.; \*  $P < 0.05$ .

333 **Relationship between repulsion and memory interference.** Thus far, we have shown that  
334 the repulsion effect is *triggered* by similarity between memories. This raises the complementary  
335 question: what is the *consequence* of repulsion? From an adaptive perspective, repulsion may  
336 carry an important benefit in that, by exaggerating the differences between similar memories, it  
337 serves to *reduce* memory interference. To test for a relationship between repulsion and  
338 interference, we considered data from Experiments 1–3 and focused specifically on the high  
339 similarity condition since a significant repulsion effect was observed in this condition across all  
340 three experiments. For each subject in each experiment, we computed (1) the mean percentage  
341 of responses away from the competitor based on data from the immediate Post Test and (2) the  
342 mean number of interference errors across the last three rounds of the associative memory test  
343 (during the training rounds). As a first step, we tested for across-subject correlations between  
344 mean percentage of away responses on the color memory Post Test and mean interference  
345 errors on the associative memory test. Strikingly, a highly significant, negative correlation was  
346 observed for each experiment (Experiment 1:  $r = -0.61$ ,  $P = 0.002$ ; Experiment 2:  $r = -0.51$ ,  $P =$   
347  $0.001$ ; Experiment 3:  $r = -0.44$ ,  $P = 0.006$ ; **Figure 4A,B**). Thus, stronger color memory repulsion

348 was associated with fewer interference-related errors during the associative memory test.  
349 One potential caveat with the correlations described above is that they may partly reflect that  
350 subjects who suffered more interference errors during associative memory tests had a higher  
351 probability of remembering the wrong color (i.e., the competing object's color) during the color  
352 memory Post Test. From this perspective, it is possible that all subjects showed comparable  
353 levels of repulsion *when they recalled the correct color*, but subjects with more interference  
354 errors also recalled the 'wrong color' with greater frequency, thereby pulling down their  
355 percentage of responses away from the competitor. To address this concern, we performed a  
356 second, more targeted analysis that focused on the distribution of *correct* color memory  
357 responses. We first median split all subjects (within each experiment) into 'high interference'  
358 and 'low interference' groups based on the mean number of interference errors during the last  
359 three associative memory tests in the training rounds (high interference group:  $M = 18.45\%$ ,  $SD$   
360  $= 7.58\%$ ; low interference group:  $M = 2.12\%$ ,  $SD = 2.59\%$ ). We then computed the frequency of  
361 Post Test responses that fell in each of four color space bins. Two of these bins were centered  
362 around the target color value ( $\pm 11$  degrees from the target color) and two of these bins were  
363 centered around the competitor color value ( $\pm 11$  degrees from the competitor color) (**Figure**  
364 **4C**). This allowed us to separate out color memory responses that were 'correct' ( $\pm 11$   
365 degrees from the target) vs. 'swap errors' ( $\pm 11$  degrees from the competitor). Note:  
366 responses that were precisely equal to the target or competitor color were excluded from this  
367 analysis.

368 Not surprisingly, high interference subjects tended to commit more swap errors in the color  
369 memory test ( $M = 21.47\%$  of responses,  $SD = 9.51\%$ ) than did low interference subjects ( $M =$   
370  $10.07\%$ ,  $SD = 7.28\%$ ); ( $t_{82} = 6.17$ ,  $P = < 0.001$ , 95% CI: 7.73 -15.10, Cohen's  $d = 1.35$ ). Of  
371 critical interest, however, was the distribution of correct responses—i.e., whether there was a  
372 difference in the frequency of 'correct towards' vs. 'correct away' responses. For high  
373 interference subjects, correct color memory responses were evenly distributed around the  
374 actual target value (no difference in frequency of 'correct towards' vs. 'correct away':  $F_{1,39} =$   
375  $2.07$ ,  $P = 0.16$ ,  $\eta^2 = 0.03$ ; left panel **Figure 4C**). For low interference subjects, however, there  
376 was a strong asymmetry, with significantly more responses in the 'correct away' bin as  
377 compared to the 'correct towards' bin ( $F_{1,39} = 58.00$ ,  $P < 0.0001$ ,  $\eta^2 = 0.39$ ; right panel **Figure**  
378 **4C**). The interaction between high vs. low interference subjects and 'correct away' vs. 'correct  
379 towards' bins was also highly significant ( $F_{1,78} = 33.33$ ,  $P = 0.0006$ ,  $\eta^2 = 0.08$ ). None of these  
380 effects interacted with experiment number ( $P$ s  $> 0.4$ ). Thus, even when restricting focus to color

381 memory responses that were correct (i.e., removing swap errors), there was clear evidence for  
 382 an adaptive distortion of color memory: subjects that made the fewest interference errors during  
 383 the associative memory test exhibited a robust repulsion effect wherein color memory was  
 384 systematically biased away from the color of the competing object.



**Figure 4. Memory repulsion is adaptive.** (A) Across-subject correlations between mean percentage of Post Test (Day 1) color memory responses that were away from the competitor and mean percentage of interference errors during the last three associative memory test rounds (high similarity condition only). Interference errors were defined as selecting the face associated with the competitor object (see **Figure 1B** and **Supplementary Figure 2**). Significant, negative correlations were observed for Experiments 1, 2, and 3 ( $r_s > .43$ ,  $P_s < 0.007$ ), indicating that stronger color memory repulsion was associated with fewer interference errors during the associative memory test. (B) Same as (A), except that each measure was z-scored within experiment, allowing for a single correlation to be calculated for the pooled data ( $r = -0.51$ ,  $P < 0.001$ ). (C) High interference subjects evenly distributed ‘correct’ color memory responses around the target value (correct toward vs. correct away:  $P = 0.16$ ). In contrast, low interference subjects exhibited a strong bias in their distribution of correct color responses, with significantly more correct responses ‘away’ from the competing color than ‘towards’ the competing color ( $P < 0.0001$ ). The distribution of correct responses (correct towards vs. correct away) significantly interacted with subject group (high vs. low interference;  $P = 0.0006$ ). Notes: Error bars reflect  $\pm$  S.E.M.; \*\*\*  $P < 0.001$ .

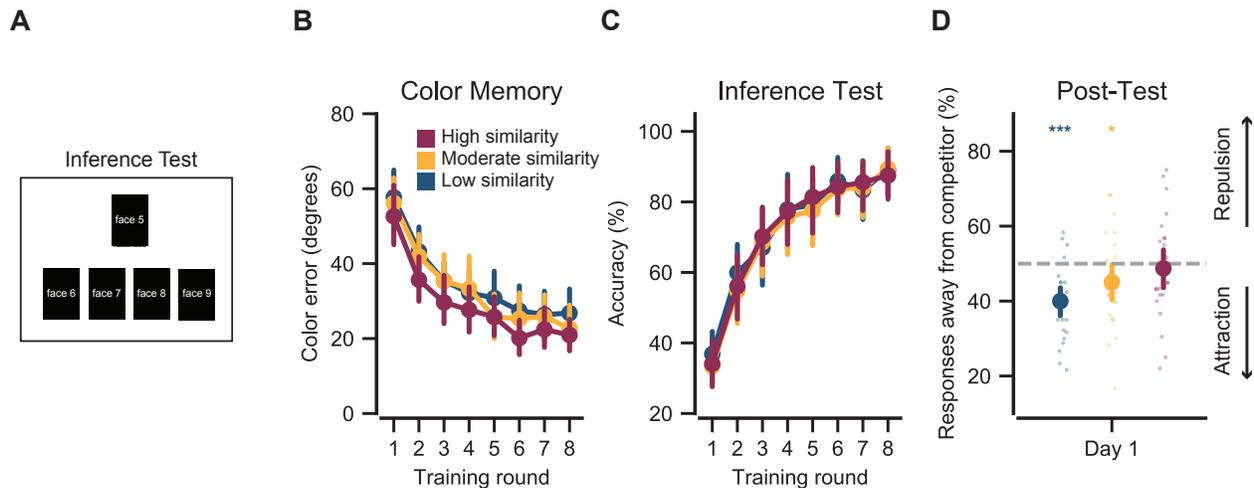
385 **Experiment 4.** In Experiments 1-3, the associative memory task during the training rounds  
386 explicitly required subjects to discriminate between the competing objects. In Experiment 4, we  
387 tested whether this discrimination demand was necessary for inducing repulsion. The critical  
388 difference in Experiment 4, relative to Experiments 1–3, was that we changed the procedures  
389 for the associative memory test in the training rounds so that it now promoted *integration* across  
390 overlapping associations (Richter, Chanales, & Kuhl, 2016; Shohamy & Wagner, 2008;  
391 Zeithamova, Dominick, & Preston, 2012). Specifically, the new associative memory test was an  
392 inference test (Zeithamova et al., 2012) that required subjects to generalize across overlapping  
393 associations. On each trial in the inference test, a face image (probe) was presented at the top  
394 of the screen and subjects had to select a “matching” face, from a set of 4 options presented  
395 below (**Figure 5A**). A “matching” face was defined as a face associated with the same object  
396 category as the probe (ignoring differences in color). For example, two faces would match if  
397 they were each associated with a “backpack,” regardless of whether the backpacks differed in  
398 color. Thus, while the inference test still required associative learning (i.e., object-face learning),  
399 it did not require discriminating between similar objects. However, because color memory was  
400 still tested during the training rounds (as in all prior experiments), color memory remained  
401 relevant and subjects showed robust improvements in color memory across training rounds  
402 (**Figure 5B**).

403 Subjects performed well in the inference task, with above-chance performance in all conditions  
404 by the last round of training ( $P_s < 0.000001$ ; **Figure 5C**). However, in contrast to what we found  
405 in the associative memory tests in Experiments 1–3, color similarity had no effect on  
406 performance in the inference test ( $F_{2,50} = 0.52$ ,  $P = 0.67$ ,  $\eta^2 = 0.006$ ; **Figure 5C**). That is, the  
407 ability to generalize across associations with common object categories was not influenced by  
408 color similarity.

409 As in all of the prior experiments, the percentage of responses away from the competitor during  
410 the color memory Post Test varied by similarity condition ( $F_{2,50} = 5.21$ ,  $P = 0.009$ ,  $\eta^2 = 0.09$ ;  
411 **Figure 5D**). However, for the high similarity condition the percentage of away responses no  
412 long differed from 50% ( $t_{25} = -0.49$ ,  $P = 0.63$ , 95% CI: -6.64 – 4.07, Cohen’s  $d = -0.14$ ).

413 Interestingly, the percentage of away responses was significantly *lower* than 50% in both the  
414 moderate and low similarity conditions (moderate:  $t_{25} = -2.08$ ,  $P = 0.048$ , 95% CI: -9.83 – -0.04,  
415 Cohen’s  $d = -0.58$ ; low:  $t_{25} = -5.17$ ,  $P = 0.00002$ , 95% CI: -13.99 – -6.02, Cohen’s  $d = -1.43$ ),  
416 suggesting an attraction effect. A direct comparison of the percentage of away responses in the

417 high similarity conditions in Experiment 4 vs. Experiment 1 (which was most closely matched to  
418 Experiment 4) revealed a significant difference ( $t_{47} = 3.33$ ,  $P = 0.002$ , 95% CI: 4.77 – 19.39,  
419 Cohen's  $d = 0.95$ ), confirming that the subtle change in task demands (encouraging integration  
420 as opposed to discrimination) significantly reduced the repulsion effect.



**Figure 5. Task demands influence memory repulsion. (A)** In Experiment 4, all procedures were identical to Experiment 1 except for a subtle change to the associative memory test during the training rounds. Instead of requiring subjects to *discriminate* between competing colors (as in Experiment 1), the associative memory test consisted of an inference test that required subjects to *generalize* across competing objects. On each inference test trial, a probe face was presented and subjects had to select, from a set of four options, which face was associated with the same object as the probe face (irrespective of color). Thus, what was previously the ‘competitor’ face (Experiments 1–3) was now the correct response. Note: Actual faces are not shown here per biorxiv policy. **(B)** Mean color memory error decreased across training rounds (main effect of round:  $F_{1,25} = 101.03$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.63$ ). **(C)** Accuracy on the associative memory tests increased across training rounds (main effect of round:  $F_{1,25} = 225.3$ ,  $P < 0.0000001$ ,  $\eta^2 = 0.79$ ). However, in contrast to the associative memory tests in Experiments 1–3, there was no effect of color similarity on inference accuracy (main effect of similarity:  $F_{2,50} = 0.52$ ,  $P = 0.67$ ,  $\eta^2 = 0.006$ ). **(D)** On the color memory Post Test, the mean percentage of responses away from the competitor varied across similarity conditions, as in Experiments 1–3 (main effect of similarity:  $P = 0.009$ ), but there was no longer a repulsion effect in the high similarity condition ( $P = 0.63$ ). Instead, the mean percentage of responses away from the competitor was significantly below 50% in the moderate and low similarity conditions ( $P$ s  $< 0.05$ ). Small dots reflect data from individual subjects. Notes: Error bars reflect +/- S.E.M.; \*\*\*  $P < 0.001$ ; \*  $P < 0.05$ .

## 421 DISCUSSION

422 While numerous studies have documented the situations and contexts in which interference  
423 between episodic memories produces forgetting, much less is known about how interference  
424 shapes memory for the *features* of events. Using a behavioral paradigm that assessed color  
425 memory on a continuous scale, we show that interference between similar-colored objects

426 induces a repulsion effect wherein the colors of these objects are remembered as being farther  
427 apart than they actually are. This repulsion effect was highly dependent on competition (color  
428 similarity) and was sensitive to task demands. Critically, repulsion was also adaptive in that  
429 greater repulsion was strongly associated with fewer interference-related errors during  
430 associative memory retrieval. These findings provide striking evidence of adaptive memory  
431 distortions that are triggered by competition between highly similar memories.

432 Our study design was modeled after the canonical A-B, A-C interference paradigm (Barnes &  
433 Underwood, 1959). In this paradigm, a single memory cue (A) is paired with two different  
434 associates (B, C). Memory is typically worse for associations in this interference condition  
435 compared to a condition in which a cue is paired with a single associate. In our experiments,  
436 however, overlapping associations had *similar cues* (e.g., two backpacks of different colors) as  
437 opposed to identical cues (the same backpack). This allowed us to parametrically manipulate  
438 the overlap between A-B, A-C associations (conceptually:  $A_1$ -B,  $A_2$ -C). Central to our predictions  
439 was the idea that greater similarity of the cues ( $A_1$ ,  $A_2$ ) should be associated with greater  
440 interference (O'Reilly, 2010). Performance from the associative memory tests clearly confirmed  
441 this prediction (**Supplementary Figure 2**). However, in contrast to classic memory interference  
442 paradigms, overall associative memory accuracy was not our critical dependent measure;  
443 rather, we used this paradigm to measure distortions in how the cues (object colors) were  
444 remembered. If greater similarity between cues leads to greater interference, then we reasoned  
445 that exaggerating the *difference* between the cues would be an adaptive mechanism for  
446 reducing interference. This is precisely what we found.

447 Notably, our core predictions concerning memory repulsion effects were directly inspired by  
448 recent evidence of repulsion effects in human hippocampal activity patterns (Ballard et al., 2019;  
449 Chanales et al., 2017; Favila et al., 2016; Hulbert & Norman, 2015; Schapiro et al., 2012).  
450 Indeed, there are a number of striking parallels between these prior neuroimaging findings and  
451 the current behavioral findings. First, a critical finding from prior studies is that hippocampal  
452 repulsion is *triggered by* event similarity (Chanales et al., 2017; Favila et al., 2016; Hulbert &  
453 Norman, 2015; Schapiro et al., 2012). For example, Chanales et al. (2017) found that  
454 hippocampal repulsion was greatest for the segments of spatial routes that were most difficult to  
455 discriminate. Similarly, Schapiro et al. (2012) found that hippocampal repulsion selectively  
456 occurred for abstract images that had high levels of visual similarity. Here, in Experiments 1-3  
457 we found robust and selective evidence of behavioral memory repulsion when color similarity

458 was high (24 degrees apart). Second, hippocampal repulsion is thought to be a gradual,  
459 learning-related process (Chanales et al., 2017; Favila et al., 2016; Hulbert & Norman, 2015;  
460 Schlichting et al., 2015). Indeed, during initial stages of learning, there may be attraction  
461 between hippocampal representations of similar events, with this attraction only ‘flipping’ to  
462 repulsion with extended training (Chanales et al., 2017; Favila et al., 2016; Schlichting et al.,  
463 2015). Likewise, repulsion effects in the current study only emerged after extensive training;  
464 during initial color memory tests (during the training rounds), subjects’ color memories tended to  
465 be biased *toward* the competing object’s color (**Supplementary Figure 1**). Finally, hippocampal  
466 repulsion is thought to be adaptive in that it is associated with reduced interference  
467 (confusability) between highly similar memories (Colgin et al., 2008; Favila et al., 2016; Hulbert  
468 & Norman, 2015). Here, we show that the repulsion effect in color memory was,  
469 overwhelmingly, more pronounced in those subjects that suffered the fewest interference errors  
470 during the associative memory test. When specifically considering high similarity trials with  
471 ‘correct’ color memory (defined as +/- 11 degrees of the target), the difference between subjects  
472 with high vs. low rates of interference errors was striking: subjects that had more interference  
473 errors had response distributions that were centered on the *veridical color value*; in contrast,  
474 subjects with fewer interference errors exhibited a response distribution that was *shifted away*  
475 *from the color of competing object*. Thus, the current behavioral findings strongly parallel  
476 previously-described properties of hippocampal repulsion.

477 In order to induce a repulsion effect in color memory, we deliberately developed a training  
478 procedure that involved alternation between study and competitive retrieval (Experiments 1–3).  
479 This procedure was inspired by evidence that study/retrieval alternation is very effective in  
480 creating distinct representations of overlapping memories (Hulbert & Norman, 2015; Storm,  
481 Bjork, & Bjork, 2008) and in inducing differentiation of hippocampal activity patterns (Hulbert &  
482 Norman, 2015; Kim, Norman, & Turk-Browne, 2017). These dynamics have also been detailed  
483 in computational models that address how episodic memory interference is resolved (Norman,  
484 Newman, Detre, & Polyn, 2006; Norman, Newman, & Detre, 2007). More generally, our results  
485 build on evidence that competitive remembering triggers active mechanisms that reshape the  
486 memory landscape in order to reduce interference (Anderson, 2003; Anderson, Bjork, & Bjork,  
487 1994; Kim et al., 2017; Levy, 2002; Norman et al., 2006, 2007; Wimber, Alink, Charest,  
488 Kriegeskorte, & Anderson, 2015).

489 Across our experiments, we identify several boundary conditions for the repulsion effect. First,

490 as noted above, we consistently observed repulsion in the high similarity condition (24 degrees)  
491 but not in the moderate/low similarity conditions (48, 72 degrees). However, with even higher  
492 similarity (6 degrees), the repulsion effect was no longer significant. Thus, the relationship  
493 between similarity and the repulsion effect followed an inverted u-shape function, suggesting a  
494 'sweet spot' at which repulsion occurs. This finding is consistent with theoretical perspectives on  
495 the relationship between memory competition and memory plasticity (Ritvo et al., 2019).  
496 Specifically, memory representations are thought to be most susceptible to plasticity (weakening  
497 or distortion) at particular levels of competition. If memory representations are *too similar* or *too*  
498 *dissimilar*, then plasticity is not expected to occur. This theoretical perspective is supported by  
499 several examples of non-monotonic relationships between neural measures of competition and  
500 memory/plasticity (Chanales et al., 2017; Detre, Natarajan, Gershman, & Norman, 2013; Lewis-  
501 Peacock & Norman, 2014; Newman & Norman, 2010).

502 Another boundary condition to the repulsion effect that we identify relates to task demands.  
503 Namely, the repulsion effect was not observed when task demands explicitly encouraged  
504 integration (instead of discrimination) of similar objects (Experiment 4). Interestingly, this  
505 integration demand led to an 'attraction effect' for the low and moderate similarity conditions, but  
506 not for the high similarity condition. On the one hand, storing a single 'averaged' color value for  
507 each object pair (i.e., attraction) would seemingly be an efficient strategy when task demands  
508 require integration (Gluck & Myers, 1993; Richards et al., 2014). However, it is possible—  
509 though speculative—that event similarity triggers some degree of repulsion regardless of task  
510 demands (Favila et al., 2016) and that, in Experiment 4, results in the high similarity condition  
511 reflect offsetting effects of integration and repulsion. While detailed consideration of this point is  
512 beyond the scope of the present manuscript, our findings establish that task demands are an  
513 important factor, along with event similarity, but additional research will be required to map out  
514 exactly how and when repulsion effects are influenced by task demands.

515 Although our findings were specifically motivated by empirical phenomena and theoretical  
516 perspectives in the field of episodic memory, they contribute to a broader literature documenting  
517 adaptive exaggeration in cognitive processes. For example, similar biases have previously been  
518 documented in visual working memory (Bae & Luck, 2017; Rademaker, Bloem, De Weerd, &  
519 Sack, 2015), estimates of temporal duration (Ezzyat & Davachi, 2014), and judgments of social  
520 categories (Förster, Liberman, & Kuschel, 2008; Krueger & Rothbart, 1990; Wilder & Thompson,  
521 1988). This raises the question of whether the repulsion effect we observed is, fundamentally, a

522 bias in episodic memory or whether the bias might occur during another cognitive processing  
523 stage. In particular, it is possible that the bias occurred during perception and this bias was then  
524 reinstated during memory retrieval. This framing is not incompatible with our claims. That said, it  
525 is important to emphasize that any bias during perception would still be dependent on long-term  
526 memory in that a perceptual bias could only occur to the extent that a *remembered stimulus*  
527 exerted an influence on a currently perceived stimulus (Teng & Kravitz, 2019). Moreover, it is  
528 interesting to note that damage to the hippocampus (a structure critical for episodic memory  
529 formation) is also associated with impairments in fine-grained perceptual discriminations (Aly,  
530 Ranganath, & Yonelinas, 2013), suggesting that the distinction between memory and perception  
531 may not be categorical (Aly & Turk-Browne, 2018). Ultimately, while it is an interesting question  
532 whether the repulsion effect reported here also occurred during perception, the critical points  
533 are that the repulsion effect we report (a) was induced by long-term memory, (b) it was  
534 remarkably stable over time (e.g., it persisted ~24 hours in Experiment 1), and (c) it strongly  
535 predicted associative interference errors in a canonical episodic memory paradigm.

536 Collectively, our results robustly establish that similarity between long-term memories triggers a  
537 repulsion in remembered feature values and that this exaggeration of remembered features is  
538 highly adaptive. These findings strongly support the idea that memory distortions generally  
539 reflect the operation of an adaptive memory system (Schacter, 1999), while providing specific,  
540 new evidence of how such distortions can mitigate memory interference.

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