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Citation: Rajsic, Jason and Wilson, Daryl E. (2014) Asymmetrical access to color and location in visual working memory. *Attention, Perception, & Psychophysics*, 76 (7). pp. 1902-1913. ISSN 1943-3921

Published by: Springer

URL: <https://doi.org/10.3758/s13414-014-0723-2> <<https://doi.org/10.3758/s13414-014-0723-2>>

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Asymmetrical Access to Color and Location in Visual Working Memory

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Funding for this research was provided by a Discovery grant to Daryl Wilson from the Natural Sciences and Engineering Research Council of Canada.

This paper is published in *Attention, Perception, and Psychophysics*. The final publication is available at Springer via <http://dx.doi.org/10.3758/s13414-014-0723-2>

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Abstract

Models of Visual Working Memory (VWM) have greatly benefitted from the use of the delayed-matching paradigm (Wilken & Ma, 2004). However, in this task, the ability to recall a probed feature is confounded with the ability to maintain the proper binding between the feature that is to be reported and the feature (typically location) that is used to cue a particular item for report. Given that location is typically used as a cue-feature, we used the delayed-estimation paradigm to compare memory for location to memory for color, rotating which feature was used as a cue and which was reported. Our results revealed several novel findings: (1) the likelihood of reporting a probed object's feature was superior when reporting location with a color cue than when reporting color with a location cue, (2) location report errors were composed entirely of swap errors, with little to no random location reports, and (3) both colour and location reports greatly benefitted from the presence of non-probed items at test. This last finding suggests that it is uncertainty over the bindings between locations and colors at memory retrieval that drive swap errors, not at encoding. We interpret our findings as consistent with a representational architecture that nests remembered object features within remembered locations.

Keywords: Visual Working Memory, Precision, Spatial Working Memory

50 Asymmetrical Access to Color and Location in Visual Working Memory

51 When processing sensory information, it is crucial to retain some data regarding what

52 was recently seen in order to minimize the processing of redundant information over time and

53 link visual representations across sudden changes in gaze that result from saccades. Visual

54 working memory (VWM) is the memory system that supports the retention of visual information

55 over time, allowing this visual information to be accessed by higher cognitive functions. A

56 central issue that has received considerable attention in VWM research is the question of

57 representation: what are the units of VWM? An active debate in VWM research is whether

58 information is represented as discrete-units, or as a more graded representation, wherein a

59 continuously variable amount of information may be stored per item. The former position

60 conceptualizes VWM capacity as a limited number of slots available to hold information about

61 remembered objects, whereas the latter considers VWM capacity to be continuously allocable

62 across the objects that are to be remembered. According to slot-based theories (Zhang & Luck,

63 2008; Fukuda, Awh, & Vogel, 2010), VWM stores representations of individuated visual

64 objects, and it is the number of to-be-remembered objects that limits memory capacity. In

65 contrast, continuous-resource theories (Bays, Catalao, & Husain, 2009; van Den Berg et al.,

66 2012) argue that VWM is limited by a continuous resource, and that additional items can be

67 stored in memory at the cost of reduced representational precision. Most critically, continuous-

68 resource theories argue that the number and precision of object representations are not separable:

69 they are inversely related. However, framing the question of VWM representation in this way –

70 as slots versus continuous resources – overlooks the potentially unique contribution of different

71 visual features. In the present study, we compare the representation of a remembered color with a

72 feature that has proven to be “special” in visual cognition: location (Nissen, 1985; Tsal & Lavie,

73 1988; van der Heijden, 1993). First, we review research on the role of location in the traditional
74 measure of VWM performance: the one-shot change detection task.

75 **Location in Delayed-Estimation**

76 In the past several years, a relatively new task has been used to explore the dynamics of
77 VWM. As discussed earlier, the delayed-estimation task (Wilken & Ma, 2004; Zhang & Luck,
78 2008) has been critical in reorienting attention to the issue of whether the information per item in
79 VWM is allocated in a discrete or continuous fashion, as it provides a finer measure of memory
80 performance than the change detection task. Unlike the change detection task, which has been
81 used in the bulk of VWM studies, the delayed estimation task is not a recognition task, but a
82 cued-recall task. In this task, each object presented in the memory sample has two features (e.g.,
83 location and color). For the memory test, participants are cued with one feature (e.g., location)
84 and are tasked with reporting the value of the second feature (i.e., color). Although often
85 discussed as a direct measure of memory for the to-be-reported item, (Zhang & Luck, 2008),
86 performance in such tasks also depends on untested aspects of item memory. This argument has
87 been made by Bays, Catalao & Husain (2009), who were the first to emphasize the difference
88 between responses constituting guesses, where the participant's report reflects complete
89 ignorance, and responses swaps (i.e., binding errors), where the participant's report reflects
90 confusion regarding which information is to be reported.

91 In the delayed-estimation task, because only one of several items is to be reported, the to-
92 be-reported item must be identified based on partial information (usually location, for
93 exceptions, see: Bays, Gorgoraptis, Wee, Marshall, & Husain, 2011, Gorgoraptis, Catalao, Bays,
94 & Husain, 2011) provided by the cue. However, this means that a failure to accurately identify
95 the reported feature of an item may stem from multiple sources. Even in the simple case of

96 colored, homogenously-shaped objects, a successful report hinges on maintaining the memory of
97 an object's color, location, and the binding of these two features. Given recent work showing that
98 memory for an object is not all-or-none, and that partial memory for an item may exist (Fougnie
99 & Alvarez, 2011; Bays, Wu, & Husain, 2011), it seems reasonable then that report failure could
100 actually reflect memory failure for either features or their bindings. Although memory for object
101 locations is clearly a necessary component of successful performance, spatial memory has yet to
102 be evaluated under the same conditions as other object features. Understanding how factors like
103 set size affect VWM for locations is a necessary step in characterizing the sources of
104 performance declines in the delayed-estimation task. In the following section, we review studies
105 of VWM that specifically address the role of location and location-feature bindings in
106 performance.

107 **Location in Change Detection**

108 The bulk of evidence that bears on the question of representation in VWM comes from
109 the one-shot change detection task (Luck & Vogel, 1997). At its core, this is a recognition task,
110 wherein participants are provided with a memory sample, followed by a memory probe. To
111 successfully detect a difference between the memory sample and probe, the probe must be
112 compared with a stored representation of the sample. The most robust finding across change
113 detection studies is that increasing the number of items in a display leads to a reduction in correct
114 recognition (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001; Wheeler & Treisman,
115 2002). However, as noted by Lee and Chun (2001), change detection studies typically confound
116 number of items and number of locations (i.e., each item has its own unique location). By
117 overlaying objects onto the same display locations, Lee and Chun were able to demonstrate that
118 the number of objects, and not the number of locations, primarily limits change detection

119 performance. While the work of Lee and Chun provides support for the claim that information in
120 VWM is stored as objects, other findings demonstrate that spatial information is an important
121 aspect of VWM representation.

122 Jiang, Olson, and Chun (2000) investigated the role of spatial and non-spatial feature
123 context in successful recognition. Across a number of studies, participants viewed and encoded
124 displays of colored boxes, or monochromatic shapes. Jiang et al. varied the characteristics of the
125 probe display to determine what information was necessary for correct memory retrieval. The
126 authors discovered that the original spatial configuration of the probe display is very important
127 for correctly detecting the change in the position, color, or shape of an isolated item. Removing
128 the non-tested items from the probe display (i.e., using a partial report display), or scrambling
129 untested items' positions, led to a decrement in change detection performance. Performance on
130 spatial change detection, however, did not suffer when the untested items' colors changed,
131 suggesting that the contextual effect of locations noted previously does not extend to non-spatial
132 features. These results provide compelling evidence that access to VWM for the purposes of
133 recognition is not based on item-based indexing, but that indexing in VWM is at least partially
134 location-based. Olson and Marshuetz (2005) provided further evidence for a location-dependent
135 memory. Participants in this task were required to detect a change in object identity across
136 sample and test arrays. The test arrays were either presented in the same configuration in the
137 same quadrant of the computer monitor, the same configuration in a different quadrant, or in the
138 same quadrant but with a different spatial configuration. Response latencies were consistently
139 slower in the latter condition, showing that VWM for object identity is coded with positional
140 information relative to other items in the array.

141 Treisman and Zhang (2006) further examined the role of location in detection of changes,
142 finding that the appearance of a new feature value was most easily detected when feature-
143 bindings and locations were preserved from sample to test. When objects were presented in new
144 locations at test, binding changes produced a small reduction in performance. However, when the
145 objects occupied the same location at test, a change in feature bindings was often missed,
146 causing a substantial decline in performance. This pattern of findings was also limited to whole
147 display test conditions; performance using a single item probe did not lead to an interaction
148 between binding changes and location changes. Once again, the results implied a special role for
149 location in VWM performance, leading to the suggestion that non-spatial information is bound
150 across features using location as a common index.

151 The finding of location-mediated indexing fits well with the visual architecture postulated
152 by Feature-Integration theory, wherein information regarding the presence of non-spatial features
153 is stored in independent maps that are coordinated by a master-map of locations (Treisman,
154 1998; Quinlan, 2003). This architecture suggests a representational scheme for visual
155 information that exhibits properties similar to those predicted by the object-based and feature-
156 stores theories of VWM representation, with the additional claim that location is a special feature
157 that is critical for indexing and organizing remembered information.

158 **Characterizing Memory for Location in the Delayed-Estimation Paradigm**

159 As is evident from research using change detection, location appears to have unique
160 properties in VWM, and location-feature bindings are a limiting factor. The extent to which the
161 uniqueness of location affects the precision and capacity of VWM is currently unknown.
162 Specifically, the precision of memory for location changes with set size has yet to be quantified.
163 A further unresolved issue is whether in cued-recall it is the loss of bindings, as opposed to lost

164 memory for features or locations, that contributes most to changes in precision and successful
165 retrieval of items . With this in mind, we used the delayed estimation task with a novel twist: at
166 test, the feature used as the memory cue and the feature that is to be reported were changed from
167 trial-to-trial. This allowed us to measure the precision and stability of memory for locations, and
168 provided a means of observing VWM representations from both sides of the task-necessitated
169 binding. On the basis of findings from the change detection literature, we predicted that memory
170 for location would be superior to memory for color; that it would be more easily retrieved and
171 stored. Over three experiments we uncovered three novel insights: (1) the likelihood of retrieving
172 information about a cued object in memory is greater when retrieving location with color than
173 retrieving color with location, (2) errors in cued-recall of location are qualitatively different from
174 those in the cued-recall of color, (3) providing distractor context increased the ability to report a
175 probed location or color, eliminating binding errors entirely.

176 **Experiment 1**

177 The goal of Experiment 1 was to assess the quality of VWM for all aspects of a
178 remembered item by varying the item feature that served as a cue and the feature that was
179 reported during the test portion of a trial. This provided two conditions: Color Report, where
180 item location was used to cue report of a particular remembered item's color; and Location
181 Report, where item color was used to cue report of a particular item's location. For one group of
182 participants, trials for the two report conditions were randomly inter-mixed. As a consequence,
183 participants could not anticipate whether they would be tested on their memory for location or
184 color, and so any differences between these two report conditions cannot be attributed to
185 differing encoding or rehearsal strategies. However, in order to assess the contributions of

186 encoding or rehearsal strategies, we ran a second population of participants: one for whom the
187 two report conditions were blocked.

188 **Method**

189 **Participants.**

190 Eighteen adults participated in this study; nine participated in the Mixed report condition
191 and nine participated in the Blocked report condition. Our aim was to collect at least eight
192 participants for both report conditions, following Zhang and Luck (2008), and we continued with
193 the same number of participants in the following two experiments for consistency. Participants
194 were compensated with course credit or \$10 in cash. All participants reported normal vision and
195 were recruited from a first-year Psychology course and from a list of university students and
196 hospital staff who had expressed interest in Psychology study participation.

197 **Apparatus.**

198 All experiments were conducted on a personal computer in a dimly-lit, sound-attenuated
199 room. Stimuli were presented on a 16" CRT monitor. Participants viewed stimuli from a distance
200 of 50cm, and a chin rest was used to ensure constant viewing distance. Stimuli were created and
201 presented using Matlab version 7.04 and the Psychophysics Toolbox version 3.0.8 (Brainard,
202 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007).

203 **Design and Procedure.**

204 Each trial began with the presentation of a memory sample consisting of a variable
205 number of stimulus items (set sizes 1, 3, 5, or 7). To ensure that we could sample equally from
206 all colors as well as locations while still providing discriminable stimuli, we chose colored rings
207 as memory items. This allowed nearby items to overlap with minimal occlusion (our thanks to
208 Daryl Fougne, personal communication, for this suggestion). Each ring subtended 2° of visual

209 angle. Radial positioning of the centre of each ring was fixed at approximately 6° from fixation
210 and angular positioning was randomized between 0° and 358° in steps of 2° with the restriction
211 that no two rings could be assigned the same angle. Ring colors were determined in a similar
212 manner; a unique angle was chosen for each color between 0° and 358° in steps of 2° . This angle
213 determined which position on an imaginary circle in L^*A^*B color space would be used to
214 generate the item's color. The parameters of the imaginary circle were as follows: centre: [70, 0,
215 0], circle radius: 60, where the plane of the circle was orthogonal to the luminance axis of the
216 color space.

217 After the memory sample had been presented for 100 ms, there was a 900 ms retention
218 interval consisting of a blank screen. Following the retention interval, the memory test was
219 displayed. For Color Report, a location cue (a single ring whose spatial position matched one of
220 the rings presented in the memory sample) was presented, and a 0.5° wide color ring appeared
221 centred at fixation with a radius of 8° . The location ring cue was colored in white at the onset of
222 the test display. The task for participants was to use a computer mouse to adjust the color of this
223 ring by moving the cursor towards the desired color on the color wheel so that the ring matched
224 the color of the memory item that appeared in the cued location earlier in the trial. When the
225 participant clicked the mouse, the response was submitted, and 1000ms of feedback was
226 provided in the form of a small black dot outside the location of the correct color on the color
227 wheel.

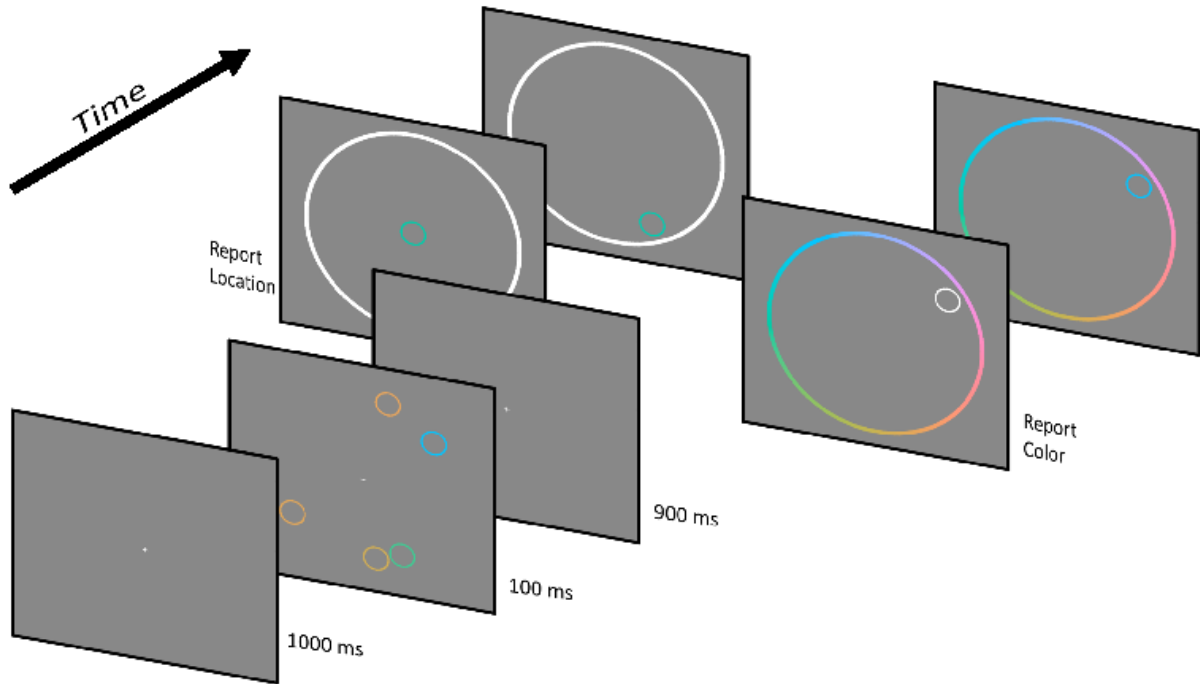
228 For Location Report, the memory test display instead included a blank wheel of identical
229 size and position to the color wheel, but with no color (filled in white). A single colored ring,
230 whose color matched the color of one of the items from the memory sample display (the color
231 cue), was presented in the centre of the screen at the outset of the memory test. The task for

232 participants was to use the mouse to adjust the position of the ring so that it matched the position
233 of the memory item that was cued by color. To equate the Report Location condition with the
234 Report Color condition, the allowable response positions were constrained to possible locations;
235 more specifically, the position of the response ring was always drawn with its distance to fixation
236 fixed at the actual presentation distance. This allowed responses in both report conditions to be
237 measured in angular values only, which were used to compute memory error. Again, after a
238 response was chosen, 1000 ms of feedback was provided in the form of a small black dot
239 appearing adjacent to the cued item's correct location on the empty color wheel before the next
240 trial automatically began. A graphical depiction of our procedure is shown in Figure 1.
241 Participants completed 512 trials in total, spread over eight blocks.

242 **Results**

243 A representative histogram depicting memory performance (response angle – actual
244 angle) for one participant at Set Size 5 is plotted in Figure 2. To determine how memory for each
245 Report condition was affected by set size, we fitted performance for each subject in each
246 condition (eight in total: four set sizes X two report conditions) with the 3-component mixture
247 model developed by Bays, Catalao, & Husain (2009). Briefly, this model uses maximum
248 likelihood estimation to determine the combination of four parameters that maximizes the
249 likelihood of the observed responses. The four parameters returned by the fitting procedure are
250 memory precision (which we express in its inverse: angular standard deviation of the circular
251 normal distribution component of the fitted response distribution, in radians), $p(\text{Target})$,
252 $p(\text{Swap})$, and $p(\text{Guess})$. The latter three parameters refer to the weightings of the three possible
253 distributions, or sources, of responses: a circular normal distribution centered on the cued item's
254 report value, the sum of circular distributions centred on the non-cued items' report values, and a

255 **Figure 1.**



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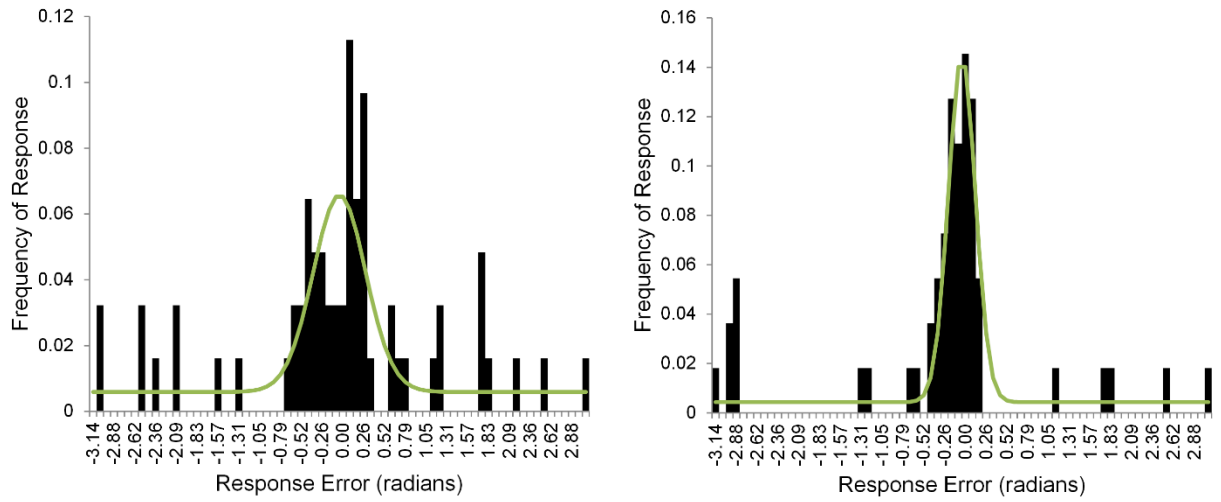
257 A partial depiction of the trial procedure for Experiment 1. Report Condition varied between
 258 trials, with either Location (left) or Color (right). The initial display at test is depicted in front;
 259 behind the initial test display is a depiction of the displays' appearance after a participant had
 260 provided a response. After providing a response, participants received feedback in the form of a
 261 small black dot appearing outside the color wheel at the angular value of the correct response
 262 (not depicted).

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266 **Figure 2.**



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268 Histograms of response error for a sample participant at Set Size five. On the left is performance
269 when color was reported and on the right is performance when location was reported.

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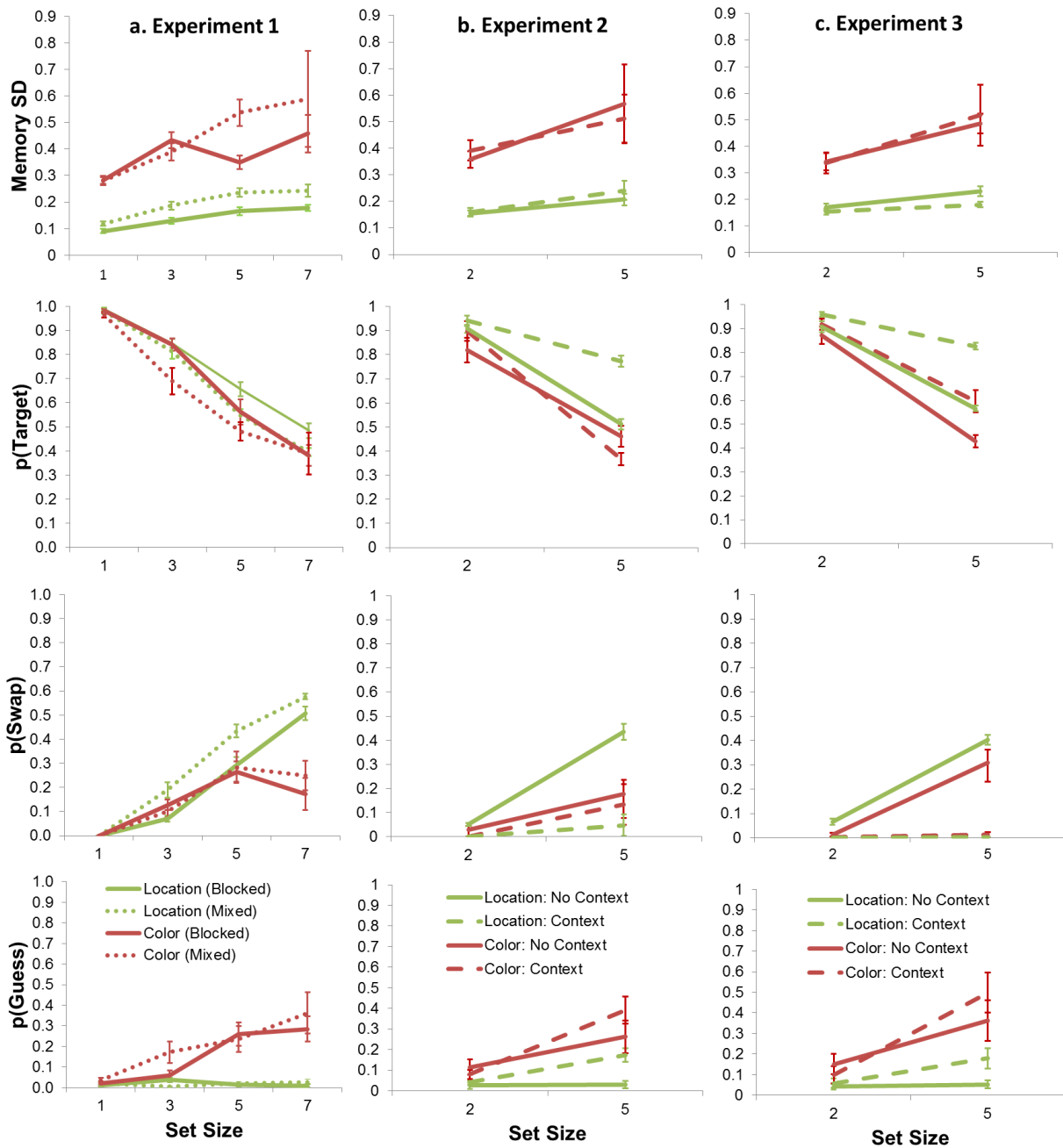
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282 uniform distribution. The values of these three parameters reflect the likelihood of each type of
283 response in a particular condition, and since the three sources are mutually exclusive, the values
284 of these three parameters must sum to one for a particular fit. For a more detailed explanation of
285 the model, see Bays, Catalao, & Husain, 2009. Our analyses were concerned with determining
286 which, if any, of these markers of memory performance differed between report conditions.

287 As can be seen in Figure 3a, performance differed in two notable ways: when reporting
288 location with color, the probability of a target response was overall greater, and only swap errors
289 were made, with no random guessing. To assess the reliability of differences in performance for
290 the two Report conditions, we performed a three-way, mixed model ANOVA for each parameter
291 value returned by the fitting procedure detailed above. The ANOVA's factors were
292 Randomization Condition (Mixed or Blocked: Between-Subjects), Report Condition (Color
293 Report or Location Report: Within-Subjects), and Set Size (1, 3, 5, or 7: Within-Subjects). The
294 ANOVA showed a main effect of Randomization Condition for $p(\text{Target})$, $F(1, 16) = 4.61$, $p =$
295 $.048$, $MSE = 0.004$, such that the likelihood of correctly reporting the tested item's feature value
296 was slightly higher in the blocked condition (see Figure 3a). This increase in $p(\text{Target})$ was
297 accompanied by a marginal increase in memory precision, $F(1, 16) = 3.71$, $p = .07$, $MSE = 0.005$,
298 suggesting that $p(\text{Target})$ performance in the blocked condition did not increase because of a
299 trade-off between quantity and quality of item representations in VWM. In addition, a marginal
300 interaction was found between Set Size and Randomization condition on $p(\text{Swap})$, $F(3, 48) =$
301 2.47 , $p = .07$, such that swaps were more likely in the Mixed condition, with this trend being
302 most prominent at higher set sizes. In summary, advance knowledge of the reported feature
303 (Blocked condition) did lead to a slight increase in performance. We suggest that this may reflect
304 preferential VWM resource allocation to the feature to be reported.

305 **Figure 3.**



306

307 Estimated memory parameters in Experiment 1 (a), Experiment 2 (b), and Experiment 3 (c) as a
 308 function of Memory Set Size (x-axis), Report Condition (location, color), and Randomization
 309 Condition (blocked, mixed). The first row depicts the mean estimated circular standard deviation
 310 of the fitted target distributions, the second depicts mean estimated p(Target), the third depicts

311 mean estimated $p(\text{Swap})$, and the fourth mean estimated $p(\text{Guess})$. Error bars reflect one within-
312 subjects standard error of the mean.

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333 Set Size exhibited an expected main effect for all memory parameters, all $F_s(3, 45) >$
334 $8.78, p_s < .001$. For both Report conditions, increasing the number of to-be-remembered items
335 led to a decrease in precision, as well as a decrease in $p(\text{Target})$ and an increase in the $p(\text{Swap})$
336 and $p(\text{Guess})$. There was also a main effect of Report condition on all memory parameters,
337 $F_s(1, 16) > 7.58, p_s \leq .01$. Precision differed considerably between location reports and color
338 reports, although given that these are different features, comparison of absolute angular precision
339 is uninformative. When expressed as percent changes in precision between set sizes, Report
340 condition no longer reached significance, $F(1, 16) = 0.82, p = .38$, suggesting that increasing set
341 size modulated precision similarly regardless of the reported feature. When it came to $p(\text{Target})$,
342 however, the main effect of Report condition demonstrated that participants were more likely to
343 correctly report an object's location given its color than they were to report an object's color
344 given its location. The $p(\text{Swap})$ was overall higher when locations were reported, likely as a
345 consequence of the striking absence of guesses at all set sizes when location was reported (see
346 Figure 3a).

347 Set Size and Report condition interacted as well, but only for $p(\text{Swap})$ and $p(\text{Guess})$,
348 $F_s(3, 48) > 10.92, p < .001$. For $p(\text{Guess})$, this interaction shows that for reporting color, guesses
349 increased with set size, but for location report, there were few guesses regardless of set size. In
350 contrast, for $p(\text{Swap})$, the interaction shows that swaps increase with set size more for location
351 reports than for color reports.

352 Discussion

353 Experiment 1 revealed two interesting findings. First, the likelihood of a correct response,
354 $p(\text{Target})$, was overall higher when locations were reported given color than when colors were
355 reported given a location. Intuitively, the $p(\text{Target})$ should be identical if item memory is a

356 simple bundle of features (location and color) that has a probabilistic failure rate, determined in
357 part by set size, as a correct response requires the maintenance of both features as well as their
358 binding. It is unclear whether this difference should be attributed to color's superiority as a cue
359 or locations superiority as a reported feature. A full assessment of this issue is beyond the
360 intended scope of this paper; our goal is to stress that VWM performance departs from what
361 would be expected if the representation of an item in VWM consisted of two components:
362 feature values, and a uniform "binding" (or "bindings") between them. Rather, our results
363 suggest that alternatives must be considered (see General Discussion).

364 The second finding of interest was a substantial difference in the types of incorrect
365 responses observed between Report conditions. When participants were reporting color, errors
366 were best modelled as a mixture of swaps and guesses. However, when reporting location,
367 participants never guessed a random location – errors were always swap errors. We have
368 reported this finding earlier (Rajic & Wilson, 2012, see also: Pertzov, Dong, Peich, & Husain,
369 2012), and believe it to be a robust effect reflecting fundamental differences in memory for
370 location and color. The difference in these two conditions cannot be attributed to an effect of
371 location clustering, as our previous work showed the same distinct difference in types of errors
372 while imposing a 30° buffer between the color and location values selected for memory displays.
373 The results of this experiment, however, leave unclear whether participants have a higher
374 capacity for locations, and their performance was limited by their ability to use color to report
375 the correct location, or if participants simply guess locations that they remember instead of
376 choosing random locations when they do not know which to report. To resolve this ambiguity,
377 we designed a second experiment which included a new condition; a distractor-context
378 condition. In this condition, participants were again cued to recall a location given a color, or a

379 color given a location, but the test display included the non-tested, or distractor, items from the
380 memory sample display. We reasoned that these displays would provide participants additional
381 cues as to the tested information, providing a superior index of the amount of information stored
382 regarding the tested item.

383 **Experiment 2**

384 **Methods**

385 Stimulus presentation was identical to the Mixed condition of Experiment 1 with two
386 differences. First, only two set sizes were used to allow a sufficient number of observations per
387 condition to be collected: set sizes two and five. Second, one additional type of memory test
388 display was added; the distractors-present display. The distractors-present displays were identical
389 to the stimulus displays used in the previous experiment, except that the un-tested items were
390 drawn in their original positions and colors, while the tested item was either drawn as a white
391 ring in its original location (to be filled in with its remembered color) for the Color Report
392 condition, or drawn as a colored-in ring in the centre of the screen (to be positioned in its
393 remembered location) for the Location Report condition. Participants ($n = 9$) again completed
394 512 trials over eight blocks.

395 **Results**

396 The results, plotted in Figure 3b, show a strong effect of context on location reports,
397 greatly increasing $p(\text{Target})$, and eliminating swap errors in favor of guessing, but no such
398 change occurred for color. Participant responses were again fit to the 3-component mixture
399 model developed by Bays et al. (2009). These estimated parameter values were each submitted to
400 a 3-way repeated measures ANOVA with the following factors: Context (No Context or
401 Distractors-Present), Set Size (2 or 5), and Report Condition (Color Report or Location Report).

402 Three-way interactions between Context, Set Size, and Report Condition on $p(\text{Target})$ and
403 $p(\text{Swap})$, $F_s > 10.32$, $p_s < .02$, demonstrated that the Context and Set Size conditions had
404 different effects on memory performance for the two Report conditions. As such, we examined
405 the effects of Context and Set Size for the two Report Conditions separately (see Figure 3b).

406 When color was reported, Set Size did not modulate precision, $F(1, 8) = 2.73$, $p = .14$, but
407 affected all other memory parameters, $F_s(1, 8) = 7.77$, $p < .03$, reducing $p(\text{Target})$ and increasing
408 both types of errors. Context showed no main effects, $F_s(1, 8) < 1.82$, $p_s > .22$. However,
409 Context interacted with Set Size for $p(\text{Target})$ and $p(\text{Guess})$, $F_s(1, 8) > 7.01$, $p_s < .03$, suggesting
410 that the presence of distractors affected the success of item retrieval. At Set Size 2, the presence
411 of distractors led to an increase in $p(\text{Target})$ of 8%, but at Set Size 5, distractors caused a
412 decrease in $p(\text{Target})$ of 9%. It appears that providing distractor context was helpful in providing
413 access to additional information when only two items were remembered, but at larger set sizes,
414 the additional information impaired performance.

415 When location was reported, qualitatively different results were obtained again. Set Size
416 showed a main effect on all memory parameters, $F_s(1, 8) > 11.64$, $p_s < .01$, as expected. In
417 contrast to when color was reported, there was a main effect of Context for $p(\text{Target})$, $p(\text{Swap})$,
418 and $p(\text{Guess})$, $F_s(1, 8) > 8.63$, $p_s < .02$, and Context interacted with Set Size on the same three
419 memory parameters, $F_s(1, 8) > 9.98$, $p_s < .02$. As can be seen in Figure 3b, these interactions
420 came in the form of difference amplification; the impact of Distractor Context was greater in all
421 cases as Set Size increased. Overall, the presence of Distractor Context led to an increase in
422 $p(\text{Target})$, a decrease in $p(\text{Swap})$, and an increase in $p(\text{Guess})$. Especially noteworthy was the
423 near elimination of swap errors when Distractor Context was presented ($M_{\text{Set} = 2} = 0.0002$, $SE_{\text{Set} = 2}$
424 $= 0.0002$; $M_{\text{Set} = 5} = 0.05$, $SE_{\text{Set} = 5} = 0.04$) compared to when it was not ($M_{\text{Set} = 2} = 0.04$, $SE_{\text{Set} = 2}$

425 = 0.007; $M_{\text{Set} = 5} = 0.43$, $SE_{\text{Set} = 5} = 0.03$), and the emergence of random guesses when location
426 was reported.

427 To determine if the asymmetry in navigating color-location bindings at retrieval found in
428 Experiment 1 was replicated, we compared the $p(\text{Target})$ between Report Conditions by
429 conducting a repeated Measures ANOVA on Set Size and Report Condition only for trials in
430 which context was not provided at test. A main effect of Set Size was present, $F(1, 24) = 47.41$, p
431 $< .01$, as well as a marginal main effect of Report Condition, $F(1, 24) = 3.20$, $p = .09$, both of
432 which were qualified by an interaction, $F(1, 24) = 47.64$, $p < .01$. Follow up t -tests revealed that
433 at Set Size 2, Reporting Location given color was superior to Reporting Color given Location,
434 $F(1,24) = 5.15$, $p = .03$, but at Set Size 5, the difference was not reliable, $F(1, 24) = 1.72$, $p = .20$.
435 Experiment 2, therefore, provided a partial replication of the retrieval asymmetry uncovered in
436 Experiment 1.

437 **Discussion**

438 Experiment 2 demonstrated an additional way in which memory for location differed
439 from memory for color. When reporting location, Distractor Context had no impact on memory
440 for Set Size 2 but substantially improved memory for Set Size 5. In contrast, when reporting
441 color, Distractor Context produced a small memory improvement only for Set Size 2 and seemed
442 to actually impair memory performance for Set Size 5. It is possible that, instead of reflecting
443 differences in the ability to use location and color information to access VWM, the effect of
444 context at retrieval was constrained by our brief sample presentation (100ms). Specifically,
445 participants may have encoded and maintained too few colors for context to have improved color
446 recall. With this in mind, we ran a third experiment where the sample presentation was extended
447 to 600ms.

448

Experiment 3

449 **Methods**

450 An additional nine adults participated in an experiment that was identical to Experiment
451 2, with the sole adjustment of an increase in the sample duration from 100ms to 600ms.

452 **Results**

453 The results of Experiment 3, shown in Figure 3c, demonstrate that a longer encoding time
454 led to an effect of context for color reports as well as location report. Data from Experiment 3
455 was analysed in the same fashion as in Experiment 2; fitted parameters were submitted to a 2
456 (Context) x 2 (Set Size) x 2 (Report Condition) repeated-measures ANOVA. Figure 3c depicts
457 the fitted parameters for each of the Report Conditions, Set Sizes, and Contexts. For memory
458 precision, a main effect of Report Condition, $F(1, 56) = 65.38, p < .01$, and of Set Size, $F(1, 56)$
459 $= 12.37, p < .01$, were present, indicating that precision was overall higher for location than
460 color, and that increasing Set Size overall decreased precision. Report Condition and Set Size
461 also interacted, $F(1, 56) = 4.06, p = .049$, such that the slopes relating Set Size to precision were
462 not equal across the Report Conditions. This finding is not terribly consequential, however, given
463 that increasing Set Size would not add a constant decrement in precision, but produce a
464 multiplicative change. When expressed as percent changes in precision across set size, Report
465 Condition did not significantly affect the reduction in precision caused by Set Size, $F(1, 8) =$
466 $3.21, p = .11$.

467 When it came to $p(\text{Target})$, the critical three-way interaction from Experiment 2 no
468 longer held, $F(1, 56) = 0.54, p = .47$. As is visible in Figure 3c, both Color and Location
469 benefitted from the presence of Context when a longer sample duration was provided. Main
470 effects of Set Size, Report Condition, and Context, were found, $F(1, 64)s > 14.28, ps < .01$. In

471 addition, 2 two-way interactions were present – between Report Condition and Set Size, $F(1, 64)$
472 $= 6.22$, $p = 0.02$, and between Set Size and Context, $F(1, 64) = 7.97$, $p < .01$. The former
473 indicated that Set Size reduced $p(\text{Target})$ when reporting color more than when reporting
474 location, $t(8) = 2.75$, $p = 0.03$. The latter indicated that the effect of Context was far greater at
475 Set Size 5 than at Set Size 2, $t(8) = 6.26$, $p < .01$.

476 The most dramatic change occurred for $p(\text{Swap})$. There was a main effect of Set Size,
477 $F(1, 56) = 30.31$, $p < .01$, demonstrating that swaps increased when more items were present in
478 the memory sample display, and a main effect of Context, $F(1, 56) = 43.80$, $p < .01$, such that
479 swaps decreased when context was provided at retrieval. Inspecting Figure 3c, it appears that
480 swaps never occurred at all when context was provided. One-tailed, one-sample t -tests confirmed
481 that, for location and color both, $p(\text{Swap})$ was statistically indistinguishable from zero when
482 context was provided, $t(8)s < 1.00$, $ps > .17$. A two-way interaction was also present, $F(1, 56) =$
483 28.20 , $p < .01$, between Set Size and Context, such that the reduction in swaps was larger at Set
484 Size 5, $t(8) = 11.57$, $p < .01$. Finally, $p(\text{Guess})$ showed the same main effects and interactions as
485 $p(\text{Target})$, consistent with the conclusion that Context, by eliminating swap errors, led to
486 memory reports being either correct reports or guesses.

487 As in Experiment 2, we endeavoured to determine whether the retrieval asymmetry found
488 in Experiment 1 would replicate. To do this, we again ran a 2-way repeated measures ANOVA
489 using only No Context trials. The resulting main effects of Set Size and Report Condition were
490 both significant, $F(1, 24)s > 12.96$, $ps < .01$, but were qualified by an interaction, $F(1, 24) =$
491 138.67 , $p < .01$. To determine the nature of this interaction, we compared $p(\text{Target})$ between
492 Report Color and Report Location separately for both set sizes. At Set Size 2, the $p(\text{Target})$ did
493 not differ between the two, $F(1, 24) = 2.10$, $p = 0.16$, but at Set Size 5, $p(\text{Target})$ was

494 significantly greater for Report Location, $F(1, 24) = 33.06$, $p < .01$. These results demonstrate
495 that the retrieval asymmetry again appeared, even when the sample duration was increased.

496 **Discussion**

497 When given sufficient time to encode color information, Context was also able to
498 improve color memory performance. For both features, $p(\text{Target})$ increased substantially when
499 context was provided, and $p(\text{Swap})$ was eliminated. Providing context at retrieval increased
500 $p(\text{Target})$ for colors from 0.43 (+/- 0.06, 95% WS CI) to 0.60 (+/- 0.11, 95% WS CI), and
501 $p(\text{Target})$ for locations from 0.57 (+/- 0.03, 95% WS CI) to 0.83 (+/- 0.03, 95% WS CI). These
502 results strongly suggest that swap responses in the delayed estimation task are largely due to
503 uncertainty regarding feature bindings at memory retrieval, not illusory conjunctions at
504 encoding. In other words, swap errors could be considered “educated guesses” as opposed to
505 mistaken beliefs. It is also noteworthy that, even with the longer sample duration – a duration
506 long enough to eliminate all swap errors for both features – capacity for locations still exceed
507 that of colors. In addition, the $p(\text{Target})$ for location reports was overall higher than that of color
508 reports even when context was not provided, replicating the retrieval asymmetry from
509 Experiment 1.

510 **General Discussion**

511 **Summary of results**

512 Across three experiments we demonstrated notable differences in memory performance
513 depending on whether the color or locations of items was reported. When color was reported, a
514 mixture of guessing and swapping errors emerged as set size increased, replicating previous
515 findings (Bays, Catalao, & Husain, 2009). However, when locations were retrieved with color,
516 virtually no guess errors were present and only swap errors were made. Experiment 2 compared

517 distractor context with no context at test. When location was reported, context had no impact on
518 memory for set size 2 but greatly improved memory for set size 5. When color was reported,
519 context improved memory at set size 2, but actually hurt memory at set size 5. After increasing
520 the sample duration to 600ms in Experiment 3, context at retrieval benefitted memory not just for
521 location but also for color report, and led to an elimination of swap responses. Again, it should
522 be stressed that during encoding the participant did not know which feature would be tested so
523 that both color and location needed to be encoded regardless of which was to be reported.

524 Our results suggest that memory for an item's location is encoded more quickly than an
525 item's color. This can be most simply seen by comparing the data of Experiment 2 and 3. In
526 Experiment 2, for Location report, multiplying $p(\text{Target})$ from the Distractor Context condition
527 by the number of items at set size five provides an average capacity estimate of $k = 3.87$ (+/-
528 0.025: 95% WS CI), notably larger than the estimate provided by the No Context condition ($k =$
529 2.56, +/- 0.025: 95% WS CI) or for the average capacity for color report in either the Context (k
530 = 1.84, +/- 0.30: 95% WS CI) or No Context ($k = 2.31$, +/- 0.50: 95% WS CI) conditions. In
531 Experiment 3, this was still true – the k estimate for color when context was present (2.98 +/-
532 0.53, 95% WS CI) was lower than for location (4.13 +/- 0.17, 95% WS CI).

533 We suggest that the Distractor Context conditions reflect the capacity for unbound
534 features (i.e., color and location), whereas the No Context conditions reflect the capacity for
535 color-location bindings, which are necessary for successful performance when no distractors are
536 present. When distractors are present, participants are able to adopt the strategy of simply
537 reporting the feature that is missing from their memory of the sample display, and do not need to
538 rely on the cue feature at all. That this additional strategic possibility led to improved
539 performance suggests that the features of remembered items are represented in a common space

540 that allows for the comparison of the remembered features of multiple items to improve
541 performance. In the multiple-object tracking literature, a higher capacity for locations than for
542 feature-location bindings has also been reported (Pylyshyn, 2004), lending support to the
543 conclusion the capacity for bindings is poorer than the capacity for maintaining unbound
544 features.

545 **Representation**

546 One can interpret these findings in terms of the representational architecture of spatial
547 and non-spatial visual (or object) working memory. Fractionation of the visual buffer in
548 Baddeley's (1992) model of working memory has been suggested (Logie & Pearson, 1997), and
549 the present data may be used to inform differences between these two postulated stores. Our
550 results would imply that the capacity of spatial working memory exceeds that of visual working
551 memory (at least in so far as our context manipulation can successfully isolate the ability to
552 report unbound features). Furthermore, the cued-recall task places an additional burden of having
553 to maintain temporary cooperation between the stores, binding object representations to their
554 location for report, and that this is also a capacity-limited ability.

555 However, we suggest that considering these two types of memory as completely separate
556 is not necessary. Instead, spatial memory may benefit from a greater capacity if the architecture
557 of VWM is like that described by an alternate version of FIT in which each feature map also
558 codes the locations of its coded features (Johnston & Pashler, 1990). This conceptualization of
559 VWM suggests that instead of storing free-floating item representations, VWM codes
560 information in a map-like format, where location is coded across multiple maps, unlike many
561 other non-spatial features (see Franconeri, Alvarez, and Cavanagh, 2013, for a discussion of
562 map-based representations in cognition). This representational format is inspired by the coding

563 properties of the visual cortex, where receptive fields represent various non-spatial properties,
564 but include some degree of spatial tuning (Van Essen & Maunsell, 1983). If visual working
565 memory representations are grounded in the cortical machinery that codes the remembered
566 information in perception, as suggested by Postle (2006, see also: Fuster, 1997), then a location-
567 based representational format is a natural by-product of the visual system's coding scheme. A
568 number of studies have provided support for this hypothesis using human fMRI, showing that
569 information about remembered items is present in early visual areas during the retention interval
570 of a visual memory test (Harrison & Tong, 2009; Ester, Anderson, Serences, & Awh, 2013;
571 Emrich, Riggall, LaRocque, & Postle, 2013).

572 Our asymmetrical retrieval results may be accounted for by such an architecture, as
573 binding in this format would not be a simple connection between two features. If memories in
574 VWM exist in visual maps, there are numerous spatial codes available, and so retrieval of
575 location could be augmented by tuning a retrieved memory trace from one map with the memory
576 traces for location available on other maps. The same advantage could not be extended to
577 features like color if fewer redundant codes are available, or if co-registration across maps must
578 be mediated by location.

579 This architecture is also compatible with findings from change detection. As noted
580 earlier, Jiang et al. (2000) showed that change detection is considerably poorer when spatial
581 context is scrambled than when color context is scrambled. A map-based architecture easily
582 accommodates this result, as this representational format requires that comparing remembered
583 colors to the colors presented in a probe display must be mediated by location. While a dual-
584 stores account could account for our data by suggesting that object-location bindings are required
585 by the task, and so produce localized object representations held in VWM as a consequence, the

586 data of Jiang et al. suggest otherwise. In their task, location was unnecessary for change
587 detection, yet it still appeared to be intimately bound to the object representations that supported
588 performance.

589 In addition, this architecture provides a mechanism for the now well-established retro-cue
590 effect (Makowski, Sussman, & Jiang, 2008; Sligte, Scholte, & Lamme, 2008; Murray, Nobre,
591 Clark, Cravo, & Stokes, 2013). The location signalled by the retro cue can be used to attend to
592 the cued-location, allowing resources to be devoted to the item information specified by the cued
593 location. Pertzov et al. have argued that the ability to focus attention within VWM using a retro
594 cue may rely on spatial memory, in which case a spatial code is necessary for VWM to be
595 attentively accessed (2013). Indeed, a recent study by Lara and Wallis (2014) showed that
596 neurons in the prefrontal cortex show spatial selectivity when multiple items are being
597 remembered, even when non-spatial information is being maintained in working memory.
598 Finally, this representational format aligns nicely with the recent findings of Pertzov and Husain,
599 (2013) who showed that colors and orientations are mis-bound more often when items are
600 presented in the same location than when they are presented in different locations. In the former,
601 a particular location must coordinate feature-bindings for multiple items, leading to increased
602 interference.

603 Finally, an attractive feature of this representational format is that it provides a basis for
604 retrieval mechanisms within VWM. As noted earlier, the map architecture suggested for VWM
605 storage bears a strong resemblance to certain versions of FIT, which were designed to account
606 for visual search performance. What emerges, then, is the possibility that VWM retrieval
607 operates by analogy to visual search; representations are accessed in a similar fashion to how
608 search may be guided to items in a visual search display. Indeed, Hyun et al. (2009) have shown

609 that comparison of test displays with remembered displays operates similarly to the inspection of
610 a display during visual search: detection of differences is more efficient than the detection of
611 similarity, attention is oriented quickly to the location of a difference, and differences can be
612 detected in a pop-out like fashion.

613 **Conclusion**

614 By varying the reported feature in a delayed-estimation memory paradigm, and by
615 varying the presence of non-tested items at test, we have shown that the ability to report
616 remembered features is improved when non-tested items are presented. In addition, for the no
617 context conditions, when participants reported a location that did not correspond to the tested
618 item's location, they consistently erred by reporting another item's location, never guessing at
619 random, unlike when color memory was tested. Finally, we reliably found an asymmetry in
620 cued-retrieval such that retrieving location with a color cue tended to be more effective than
621 retrieving color with a location cue. We suggest that our results are best accommodated by a
622 map-like representational format wherein non-spatial features are coded with some degree of
623 spatial information, much like what is suggested by Feature-Integration Theory. This format
624 would allow for the binding of non-spatial features, mediated by a common location index, and
625 provide a mechanism for retrieving information.

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References

- 632
- 633 Baddeley, A. (1992). Working Memory. *Science*, 255(5044), 556-559.
- 634 Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working
635 memory is set by allocation of a shared resource. *Journal of Vision*, 9(10):7, 1-11.
- 636 Bays, P. M., Gorgoraptis, N., Wee, N., Marshall, L., & Husain, M. (20011). Temporal
637 dynamics of encoding, storage, and reallocation of visual working memory. *Journal of Vision*,
638 11(10): 6, 1-15.
- 639 Bays, P. M., Wu, E. Y., & Husain, M. (2011). Storage and binding of object features in
640 visual working memory. *Neuropsychologia*, 49(6), 1622-1631.
- 641 Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433-436.
- 642 Emrich, S. M., Riggall, A. C., LaRocque, J. J., & Postle, B. R. (2013). Distributed
643 patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual
644 short-term memory. *The Journal of Neuroscience*, 33(15), 6516-6523.
- 645 Ester, E. F., Anderson, D. E., Serences, J. T., & Awh, E. (2013). A neural measure of
646 precision in visual working memory. *Journal of Cognitive Neuroscience*, 25(5), 754-761.
- 647 Fougnie, D. & Alvarez, G. A. (2011). Object features fail independently in visual
648 working memory: Evidence for a probabilistic feature-store model. *Journal of Vision*, 11(12):3,
649 1-12.
- 650 Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources:
651 competitive content maps for attention and memory. *Trends in Cognitive Science*, 17(3), 134-
652 141.
- 653 Fukuda, K., Awh, E., & Vogel, E. K. (2010). Discrete capacity limits in visual working
654 memory. *Cognitive Neuroscience*, 20(2), 177-182.

- 655 Fuster, J. M. (1997). Network memory. *Trends in Neurosciences*, *20*(10), 451-459.
- 656 Gorgoraptis, N., Catalao, R. F. G., Bays, P. M., & Husain, M. (2011). Dynamic updating
657 of working memory resources for visual objects. *The Journal of Neuroscience*, *31*(23), 8502-
658 8511.
- 659 Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working
660 memory in early visual areas. *Nature*, *458*(7238), 632-635.
- 661 Hyun, J., Woodman, G. F., Vogel, E. K., Hollingworth, A., & Luck, S. J. (2009). The
662 comparison of visual working memory representations with perceptual inputs. *Journal of*
663 *Experimental Psychology: Human Perception and Performance*, *35*(4), 1140-1160.
- 664 Jiang, Y., Olson, I. R., & Chun, M. M. (2000). Organization of visual short-term
665 memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*(3), 683-
666 702.
- 667 Johnston, J. C., & Pashler, H. (1990). Close binding of identity and location in visual
668 feature perception. *Journal of Experimental Psychology: Human Perception and Performance*,
669 *16*(4), 843-856.
- 670 Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007).
671 What's new in Psychtoolbox-3. *Perception*, *36*(14), 1-1.
- 672 Lara, A. H. & Wallis, J. D. (2014). Executive control processes underlying multi-item
673 working memory. *Nature Neuroscience*,. Advance online publication. doi: 10.1038/nn.3702
- 674 Lee, D., & Chun, M. M. (2001). What are the units of visual short-term memory, objects
675 or spatial locations?. *Perception & Psychophysics*, *63*(2), 253-257.

676 H. Logie, R., & Pearson, D. G. (1997). The inner eye and the inner scribe of visuo-spatial
677 working memory: Evidence from developmental fractionation. *European Journal of Cognitive*
678 *Psychology*, 9(3), 241-257.

679 Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features
680 and conjunctions. *Nature*, 390(6657), 279-281.

681 Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working
682 memory reduces interference from memory probes. *Journal of Experimental Psychology:*
683 *Learning, Memory, and Cognition*, 34(2), 369.

684 Murray, A. M., Nobre, A. C., Clark, I. A., Cravo, A. M., & Stokes, M. G. (2013).
685 Attention Restores Discrete Items to Visual Short-Term Memory. *Psychological science*, 24(4),
686 550-556.

687 Nissen, M. I. (1985). Accessing features and objects: Is location special? In M. I. Posner
688 & O. S. M. Marin (Eds.), *Attention and performance XI* (pp. 205–219). Hillsdale, NJ: Erlbaum.

689 Olson, I. R., & Marshuetz, C. (2005). Remembering “what” brings along “where” in
690 visual working memory. *Perception & Psychophysics*, 67(2), 185-194.

691 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming
692 numbers into movies. *Spatial vision*, 10(4), 437-442.

693 Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2012). Rapid Forgetting Prevented by
694 Retrospective Attention Cues. *Journal of Experimental Psychology: Human Perception and*
695 *Performance*, (39(5), 1224-1231.

696 Pertzov, Y., & Husain, M. (2013). The privileged role of location in visual working
697 memory. *Attention, Perception, & Psychophysics*, 1-11.

- 698 Pertzov, Y., Dong, M. Y., Peich, M. C., & Husain, M. (2012). Forgetting What Was
699 Where: The Fragility of Object-Location Binding. *PloS one*, 7(10), e48214.
- 700 Postle, B. R. (2006). Working memory as an emergent property of the mind and brain.
701 *Neuroscience*, 139(1), 23-38.
- 702 Pylyshyn, Z. (2004). Some puzzling findings in multiple object tracking: I. Tracking
703 without keeping track of object identities. *Visual cognition*, 11(7), 801-822.
- 704 Quinlan, P. T. (2003). Visual feature integration theory: past, present, and future.
705 *Psychological bulletin*, 129(5), 643.
- 706 Rajsic, J., & Wilson, D. E. (2012). Remembering where: Estimated memory for visual
707 objects is better when retrieving location with colour. *Visual Cognition*, 20(9), 1036-1039.
- 708 Sligte, I. G., Scholte, H. S., & Lamme, V. A. (2008). Are there multiple visual short-term
709 memory stores?. *PLOS one*, 3(2), e1699.
- 710 Treisman, A., & Zhang, W. (2006). Location and binding in visual working memory.
711 *Memory & cognition*, 34(8), 1704-1719.
- 712 Treisman, A. (1998). Feature binding, attention and object perception. *Philosophical*
713 *Transactions of the Royal Society of London. Series B: Biological Sciences*, 353(1373), 1295-
714 1306.
- 715 Lavie, N., & Tsal, Y. (1994). Perceptual load as a major determinant of the locus of
716 selection in visual attention. *Perception & Psychophysics*, 56(2), 183-197.
- 717 van den Berg, R., Shin, H., Chou, W. C., George, R., & Ma, W. J. (2012). Variability in
718 encoding precision accounts for visual short-term memory limitations. *Proceedings of the*
719 *National Academy of Sciences*, 109(22), 8780-8785.

- 720 Van der Heijden, A. H. C. (1993). The role of position in object selection in vision.
721 *Psychological Research*, 56(1), 44-58.
- 722 Maunsell, J. H., & van Essen, D. C. (1983). The connections of the middle temporal
723 visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *The*
724 *Journal of neuroscience*, 3(12), 2563-2586.
- 725 Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions,
726 and objects in visual working memory. *Journal of Experimental Psychology: Human Perception*
727 *and Performance*, 27(1), 92.
- 728 Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory.
729 *Journal of Experimental Psychology: General*, 131(1), 48.
- 730 Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal*
731 *of Vision*, 4(12).
- 732 Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual
733 working memory. *Nature*, 453(7192), 233-235.
- 734