

**Title:** Visual working memory is independent of the cortical spacing between memoranda

**Abbreviated title:** Cortical spacing and visual working memory

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1 **Abstract**

2 The sensory recruitment hypothesis states that visual short term memory is maintained in  
3 the same visual cortical areas that initially encode a stimulus' features. Although it is well  
4 established that the distance between features in visual cortex determines their visibility, a  
5 limitation known as crowding, it is unknown whether short term memory is similarly  
6 constrained by the cortical spacing of memory items. Here we investigated whether the  
7 cortical spacing between sequentially presented memoranda affects the fidelity of memory  
8 in humans (of both sexes). In a first experiment, we varied cortical spacing by taking  
9 advantage of the log-scaling of visual cortex with eccentricity, sequentially presenting  
10 memoranda in peripheral vision along either the radial or tangential visual axis with respect  
11 to the fovea. In a second experiment, we sequentially presented memoranda either within  
12 or beyond the critical spacing of visual crowding, a distance within which visual features  
13 cannot be perceptually distinguished due to their nearby cortical representations. In both  
14 experiments and across multiple measures, we found strong evidence that the ability to  
15 maintain visual features in memory is unaffected by cortical spacing. These results indicate  
16 that the neural architecture underpinning working memory has properties inconsistent with  
17 the known behaviour of sensory neurons in visual cortex. Instead, the dissociation between  
18 perceptual and memory representations supports a role of higher cortical areas, such as  
19 posterior parietal or prefrontal regions, or may involve an as yet unspecified mechanism in  
20 visual cortex in which stimulus features are bound to their temporal order.

21

22 **Significance Statement**

23 Although much is known about the resolution with which we can remember visual objects,  
24 the cortical representation of items held in short term memory remains contentious. A  
25 popular hypothesis suggests that memory of visual features is maintained via the

26 recruitment of the same neural architecture in sensory cortex that encodes stimuli. We  
27 investigated this claim by manipulating the spacing in visual cortex between sequentially  
28 presented memoranda such that some items shared cortical representations more than  
29 others, while preventing perceptual interference between stimuli. We found clear evidence  
30 that short term memory is independent of the intra-cortical spacing of memoranda, revealing  
31 a dissociation between perceptual and memory representations. Our data indicate that  
32 working memory relies on different neural mechanisms from sensory perception.

33

### 34 **Introduction**

35 Although a focus of research for decades, the neural basis of working memory storage is  
36 still disputed (Serences, 2016; Xu, 2017). Recent neuro-imaging studies have demonstrated  
37 that items in memory can be decoded from activity in human primary visual cortex (V1).  
38 Whereas the amplitude of the blood-oxygenation-level-dependent (BOLD) signal within V1  
39 is not predictive of a remembered stimulus, patterns of activity across voxels can reliably  
40 predict memoranda (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). For  
41 example, in a study by Harrison and Tong, observers viewed two sequentially presented  
42 oriented gratings and were cued to hold one item in memory so that they could later compare  
43 it with a test grating. These authors found that the remembered stimulus orientation could  
44 be decoded from patterns of activity within V1 during the retention interval. They concluded  
45 that visual cortex retains information about features in working memory. Similar studies have  
46 found that activity patterns within early visual cortex are specific to only the task-relevant  
47 feature of multi-feature objects (Serences et al., 2009) and that the precision of decoding  
48 diminishes with increasing numbers of memoranda (Emrich, Riggall, LaRocque, & Postle,  
49 2013; Sprague, Ester, & Serences, 2014).

50

51 These findings among others have led some researchers to conclude that memory storage  
52 mechanisms are located within the sensory neural systems involved in processing the  
53 stimulus attributes, a proposal termed the *sensory recruitment hypothesis*  
54 (Emrich et al., 2013; Pasternak & Greenlee, 2005; Serences, 2016; Sreenivasan, Curtis, &  
55 D'Esposito, 2014). This hypothesis is appealing in part because visual cortex is thought to  
56 be one of the few brain areas with sufficient processing power to represent objects with the  
57 level of detail observed in short term memory (for a review, see Serences, 2016). However,  
58 it is not clear how visual cortex could maintain memory representations while simultaneously  
59 processing new incoming information, nor how the different perceptual experiences of  
60 seeing versus remembering are accounted for by this hypothesis.

61

62 In contradiction to the sensory recruitment hypothesis, Bettencourt and Xu (2016) found that  
63 target features could not be decoded from early visual cortex when distractors were  
64 presented during the memory retention period, but that such distractors had no impact on  
65 behavioural performance. Bettencourt and Xu could reliably decode activity within a region  
66 of parietal cortex to predict the target stimulus regardless of whether or not a distractor was  
67 presented, suggesting an important role of that area in short term memory. It remains  
68 contentious, therefore, whether visual cortex plays a necessary role in short term memory  
69 maintenance (Xu, 2017).

70

71 In the present study, we tested whether the fidelity with which memoranda are stored is  
72 affected by the neural resources available within early visual cortex, by varying the intra-  
73 cortical spacing of items. When items are presented simultaneously, in the absence of  
74 working memory demands, their intra-cortical spacing is the primary constraint on their  
75 perceptual discriminability. Nearby stimuli “crowd” each other, and the zone of crowding is

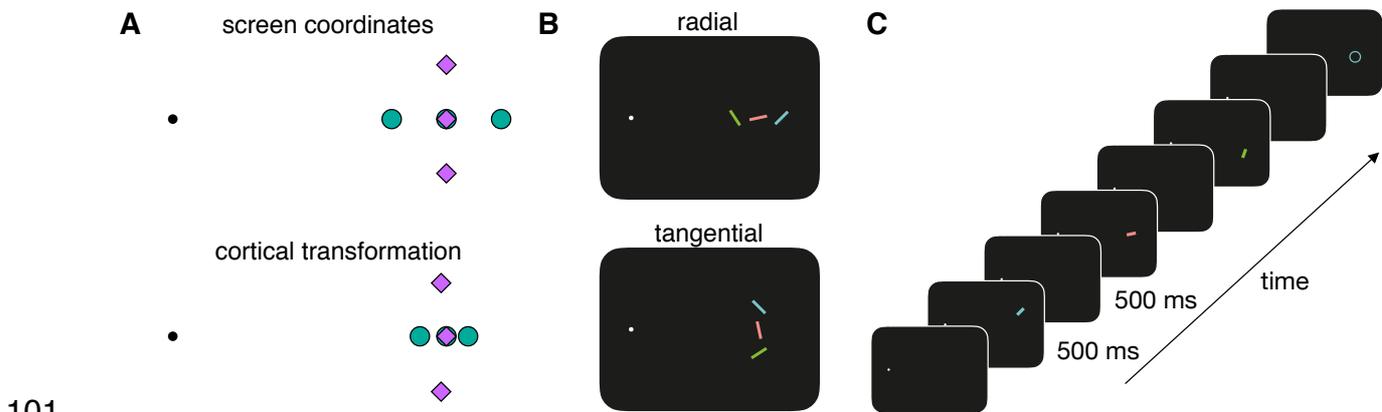
76 determined by the distance between stimuli in retinotopic cortex (Pelli, 2008; Pelli & Tillman,  
77 2008). Visual crowding occurs when the cortical spacing between visual objects prevents a  
78 distinct target representation in early visual cortex (Anderson, Dakin, Schwarzkopf, Rees, &  
79 Greenwood, 2012; J. Chen et al., 2014; Kwon, Bao, Millin, & Tjan, 2014; Pelli, 2008; van  
80 den Berg, Roerdink, & Cornelissen, 2010), or results in pooling of stimulus representations  
81 at later levels of the visual hierarchy (Freeman & Simoncelli, 2011). If short term memory of  
82 items presented in spatial isolation is maintained via the recruitment of the same sensory  
83 areas involved in the encoding of those features, then we should see worse memory  
84 performance for items that are closer together in visual cortex, and therefore share more  
85 neural resources, than for items with greater intra-cortical spacing.

86

## 87 **Materials and Methods**

88 *Experiment 1 Overview.* We investigated whether log-scaling of visual cortex affects short  
89 term memory by having observers remember three items on each trial arranged according  
90 to one of two spatial configurations, and, using a method of adjustment, report the orientation  
91 of the item indicated by a probe. Within a trial, items were aligned along either the tangential  
92 axis or the radial axis, and thus had greater or lesser intra-cortical spacing, respectively (Fig.  
93 1A and 1B). Importantly, in each configuration, one item appeared at 10° eccentricity directly  
94 to the right of fixation, and so targets at this location were matched in all regards except for  
95 the intra-cortical spacing between memoranda within the same trial. We thus focus analyses  
96 only on target items at this location, although all locations were probed equally often so as  
97 to encourage participants to store all items in short term memory. Finally, we ensured our  
98 data were not confounded by perceptual interference (e.g. Yeshurun, Rashal, & Tkacz-

99 Domb, 2015) by presenting items sequentially and with sufficient durations and inter-  
100 stimulus intervals to negate such perceptual effects.



101  
102 Figure 1. Experiment 1 design. A) Differences in cortical spacing in peripheral vision. The top row depicts the  
103 screen coordinates of stimuli in peripheral vision with respect to the point of fixation (black spot). The inter-  
104 item spacing following cortical transformation is shown in the bottom row. Such a cortical representation of  
105 space occurs in V1, which is hypothesised to maintain memory representations. Cortically transformed  
106 coordinates are normalised to the central target position. Green spots and purple diamonds represent radial  
107 and tangential spatial arrangements of stimuli, respectively. Note that, although stimuli are equally spaced in  
108 screen coordinates across conditions, radially arranged stimuli have less intra-cortical spacing than  
109 tangentially arranged stimuli. B) Stimulus design. Memoranda were randomly oriented coloured bars,  
110 presented sequentially along either the radial or tangential axis. Note that the centre stimulus in each condition  
111 occupies the same screen (and therefore cortical) location. C) Example trial sequence. Observers fixated a  
112 white spot while memoranda were presented in sequence. Following a delay after the presentation of the third  
113 item, a probe was shown matching the colour and location of one item chosen at random, cueing observers to  
114 move the mouse to report the remembered orientation of that item. A response bar appeared within the circle  
115 after the first mouse movement was detected, allowing observers to make their response using a method of  
116 adjustment.

117  
118 *Participants.* 10 people participated in Experiment 1 (mean age  $24 \pm 3.07$ ; 5 male, 5 female).  
119 All had typical colour vision and normal or corrected-to-normal acuity and were naïve to the  
120 purposes of the experiment. All observers gave written informed consent and were paid £10

121 per hour for their participation. The study was approved by the University of Cambridge  
122 Psychology Research Ethics Committee.

123

124 *Experimental Setup.* Participants sat in a head and chin rest positioned 57 cm from an ASUS  
125 LCD monitor. The resolution of the monitor was 1920 x 1200 within an area that was 44.8  
126 cm x 28 cm with no pixel interpolation. Stimulus colours were selected after measuring the  
127 luminance of each colour channel of the monitor with a spectrophotometer. Fixation was  
128 monitored online with an EyeLink 1000 (SR Research) recording at 500Hz, calibrated once  
129 before each testing session and re-calibrated as required throughout the experiment (see  
130 below). The experiment was programmed with the Psychophysics Toolbox Version 3  
131 (Brainard, 1997; Pelli, 1997) and EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002) in  
132 MATLAB (MathWorks).

133

134 *Stimuli.* On each trial, three randomly oriented bars ( $2^\circ \times 0.2^\circ$  of visual angle) were presented  
135 sequentially, and each was uniquely coloured red, green, or blue. Colours were matched in  
136 luminance ( $26.2 \text{ cd/m}^2$ ) and the order in which they appeared as well as their screen position  
137 were randomised across trials. A white fixation spot was displayed in the centre of the screen  
138 throughout stimulus presentation and the memory delay period. All stimuli were presented  
139 on a black background (luminance  $< 1 \text{ cd/m}^2$ ).

140

141 Within a trial, stimulus positions were arranged either tangentially or radially with respect to  
142 the point of fixation (Fig. 1B). In both conditions, one item was centred on the horizontal  
143 meridian,  $10^\circ$  right of fixation. In the radial condition, the two other items were positioned  $2^\circ$   
144 left or right of the central item, such that they were arranged along the horizontal meridian.  
145 In the tangential condition, one item was positioned  $2^\circ$  above the central item, and the other

146 was positioned 2° below the central item, such that they were arranged orthogonal to the  
147 horizontal meridian. Although never presented simultaneously, the inter-stimulus spacing  
148 meant that their positions did not overlap. The order in which a stimulus was presented at  
149 each position was randomised across trials.

150

151 *Procedure.* A typical trial sequence is shown in Figure 1C. At the start of each trial, an  
152 observer had to maintain fixation within a 2° region of the fixation spot for 500 ms for the  
153 trial to proceed. If fixation remained outside this region for more than 2 seconds, the eye  
154 tracker was re-calibrated. Once correct fixation was registered, there was an additional  
155 variable delay between 250 – 750 ms (uniformly distributed). Stimuli were then presented  
156 sequentially in either a tangential or radial arrangement (Fig. 1B). The stimulus duration and  
157 inter-stimulus interval were 500 ms. Following the offset of the third stimulus, there was a  
158 500 ms delay period, after which a probe circle (2° diameter) appeared centred on the  
159 location previously occupied by one of the three items, cueing the observer to report the  
160 orientation of that item using the mouse. Once any movement of the mouse was recorded,  
161 a response bar replaced the probe circle and followed the orientation designated by the  
162 mouse position relative to the bar centre. The response bar had the same dimensions as  
163 the target item, but its orientation was randomised at the start of each response period and  
164 remained on screen until the observer clicked the mouse button to confirm their response.

165

166 During pilot testing with white stimuli, we noted that it was difficult to attribute clearly the  
167 probe circle to one memory item based on location alone, particularly for the radial condition.  
168 This is most likely due to the well-known compression of perceptual space in peripheral  
169 vision (McGraw & Whitaker, 1999; White, Levi, & Aitsebaomo, 1992), and so during  
170 Experiment 1 the probe circle and response bar also matched the colour of the target item.

171 Participants were informed that all items were equally likely to be the target. The target  
172 appeared equally as often across temporal order and location. There were 324 trials,  
173 consisting of 18 repetitions for each target combination (3 target locations for each of 2  
174 spatial arrangements and 3 temporal orders).

175

176 If gaze position deviated by more than  $2^\circ$  from the fixation spot during stimulus presentation,  
177 the inter-stimulus interval, or the delay period, the message, “Don’t look away from the  
178 fixation point until it’s time to respond,” appeared for two seconds, and the trial restarted  
179 with newly randomised stimulus orientations. Each testing session took approximately one  
180 hour. After 50% of trials were completed, the observers were requested to take a short  
181 break, but were also instructed they could rest at other times as they required.

182

183 *Experimental Design and Analyses.* All comparisons in this experiment were within-subjects.  
184 Only trials in which the target item was positioned  $10^\circ$  to the right of fixation were analysed.  
185 For items at this location, we compared memory performance across radial and tangential  
186 conditions with two measures, collapsed across temporal order. We first analysed the  
187 variability of report errors by calculating the circular standard deviation of reports for each  
188 condition for each observer. These values were compared across conditions with a  
189 Bayesian t-test using JASP software (JASP Team, 2017). We used the default Cauchy prior  
190 width of 0.707, but all results reported below were robust to standard alternate prior widths.  
191 Alongside Bayes factors, we provide Student t-test results.

192

193 In a second analysis, we assessed whether there was an influence of intra-cortical spacing  
194 on observers’ reports using a probabilistic model of working memory performance. This was  
195 the “swap” model introduced by Bays et al. (2009), in which observers’ responses are

196 attributed to a mix of noisy reports centred on the target orientation, noisy reports centred  
197 on non-target items, and a uniform lapse rate (see also Zhang & Luck, 2008). The details of  
198 this model have been described extensively elsewhere (for examples, see Bays et al., 2009;  
199 Gorgoraptis, Catalao, Bays, & Husain, 2011). The model has three free parameters:  
200 precision of reports, proportion of swap errors, and proportion of guesses. Parameters were  
201 estimated by maximum likelihood using code available online  
202 (<http://www.paulbays.com/code/JV10>; Bays et al., 2009).

203

204 We compared two versions of the model: a full model in which a separate set of parameters  
205 was used for radial and tangential conditions, and a restricted model in which a single set  
206 of parameters was used for both conditions. To compare which of the two models best  
207 described the data, we used the Akaike Information Criterion (AIC) summed across  
208 participants. To further test whether the models differentially accounted for the data, we  
209 submitted the differences in individuals' AIC scores to Bayesian and Student t-tests.

210

211 *Experiment 2 Overview.* Experiment 2 was designed to ensure the physical spacing between  
212 memoranda would result in competing representations within primary visual cortex. For each  
213 participant in Experiment 2, we first measured the critical spacing of crowding, which is the  
214 area within which crowding occurs (Pelli & Tillman, 2008). We then tested observers'  
215 memory for memoranda presented sequentially within versus beyond their critical spacing.  
216 Moreover, we tested whether there is a correlation between critical spacing and memory  
217 performance, which could arise if working memory is related to individual differences in  
218 cortical surface area (e.g. Schwarzkopf, Song, & Rees, 2011). To increase statistical power  
219 and to assess the correlation between critical spacing and memory performance, we greatly  
220 increased the sample size compared with Experiment 1.

221

222 Each participant first completed a crowding task in which we found the inter-item distance  
223 at which their ability to recognise a target reached threshold level, which we take as the  
224 critical spacing of crowding. A participant's basic task was to identify the orientation of a bar  
225 surrounded by a circle, flanked on either side by distractors (Fig. 3A). Target and distractors  
226 were briefly presented in the upper peripheral visual field, and trial-by-trial variations in inter-  
227 item spacing were controlled by an adaptive procedure. The participant reported the target  
228 orientation by clicking on one of three response options shown around the point of fixation  
229 (a three alternative forced-choice task). After finding their critical spacing, the participant  
230 then completed a memory experiment in which three randomly oriented bars were presented  
231 in sequence in one of two spatial configurations (Fig. 4A). Within each trial, memoranda  
232 were presented across a spatial range equal to either 0.75 or 1.5 times their critical spacing,  
233 corresponding to "crowded" and "uncrowded" conditions, respectively. As in Experiment 1,  
234 there was a common screen position for one item in each condition, and we analysed only  
235 memory performance for this stimulus position. Therefore, any differences in performance  
236 across conditions could only be driven by differences in intra-cortical spacing of memoranda.

237

238 *Participants.* 21 participants took part in Experiment 2 (mean age  $30.14 \pm 8.69$ ; 8 male, 13  
239 female), one had also participated in Experiment 1, and all other details were as per the  
240 previous experiment. Two participants did not complete the experiment due to problems  
241 tracking their eyes, and their data were excluded from analyses, leaving a final sample size  
242 of 19.

243

244 *Experimental Setup.* All details were as per Experiment 1.

245

246 *Stimuli.* Stimuli were bars ( $0.85^\circ \times 0.04^\circ$ ) centred in a circle with a diameter matching the  
247 bar length, and a width of  $0.04^\circ$  (Fig. 3A and 4A). Three of such stimuli were displayed in  
248 each trial of both the crowding experiment and the memory experiment, and were uniquely  
249 coloured. We chose three colours equally spaced in CIE  $L^*a^*b^*$  colour space, approximating  
250 red ( $L^* = 74, a^* = 34.6, b^* = 20$ ), green ( $L^* = 74, a^* = -28.3, b^* = 28.3$ ), and blue ( $L^* = 74, a^*$   
251  $= -28.3, b^* = -28.3$ ) hues. Colours were randomly assigned to the three stimuli on each trial.  
252 A white fixation spot was displayed in the centre of the screen throughout stimulus  
253 presentation and the memory delay period. All stimuli were presented on a black  
254 background.

255

256 In the crowding task, three oriented stimuli were presented simultaneously on each trial (Fig.  
257 3A). The target orientation was random, while the distractors' orientations were selected  
258 randomly from a uniform distribution that excluded orientations within  $22.5^\circ$  of the target  
259 orientation. Stimuli were centred  $8.5^\circ$  above fixation, and arranged tangentially relative to  
260 fixation. The centre stimulus was the target, and the others were distractors. As described  
261 below, the target-distractor distance was controlled via a staircase. Response stimuli were  
262 target and distractors in a neutral hue (grey), appearing in random positions but equally  
263 spaced on the border of an imaginary circle (radius =  $1.7^\circ$ ) around the screen centre (Fig.  
264 3A). When response stimuli were on screen, observers could move a standard mouse arrow  
265 that appeared in the screen centre. In the memory experiment, memoranda were of the  
266 same dimensions as the target and distractors in the crowding experiment, were each  
267 randomly assigned the colours described above, but were presented sequentially in random  
268 order. Stimulus orientations in the memory experiment were randomised with no restrictions.

269

270 *Procedure.* A typical trial sequence of the crowding task is shown in Fig. 3A. Each trial began  
271 following fixation compliance as per Experiment 1. Target and distractors appeared for  
272 500ms. Following a 500ms delay, response stimuli and the response arrow appeared  
273 centered at fixation, and observers moved the arrow with the mouse and clicked on which  
274 stimulus they thought matched the target orientation. Observers were instructed that the  
275 target was always the central item on every trial, and that one response item matched its  
276 orientation exactly. No other instruction was explicitly given regarding the distractor  
277 response items, but if a participant asked about them, the experimenter told them that one  
278 item matched the target, and the other two response items matched the distractors. The  
279 next trial immediately followed each mouse click that fell within the border of a stimulus, and  
280 that stimulus was taken as their response.

281

282 The distance between the target and each distractor was controlled on each trial via an  
283 adaptive procedure, QUEST (Watson & Pelli, 1983), set to find the target-distractor spacing  
284 at which performance reached 67% accuracy (the midpoint of the psychometric function for  
285 a 3AFC task). We ran two randomly interleaved staircases of 36 trials each. For each  
286 QUEST procedure, we set the initial midpoint of the psychometric function ( $\mu$ , see below) to  
287 two different levels to probe the asymptotes of the fitted function. These values, based on  
288 pilot observations, were set to 3.4° and 1.7°. These different QUEST parameters have the  
289 added advantage that the participant initially experiences relatively difficult and easy trials  
290 early on during testing. Furthermore, we allowed the target-distractor distance to vary only  
291 in steps of 0.21° during this threshold task. The procedure took approximately 7 minutes.  
292 Note that, while there was inevitably a working memory component to the crowding task,  
293 only the central element needed to be held in memory, therefore performance in this task

294 indexes crowding occurring in sensory processing, due to the simultaneously presented  
295 flankers, rather than in memory.

296

297 The memory experiment was conducted in the same session as the crowding task, and is  
298 shown in Fig. 4A. Fixation compliance was performed, as above, and then each memory  
299 item was shown in random order, with a duration, inter-stimulus interval, and delay period  
300 of 500ms. Memoranda were shown in one of two spatial configurations, either spaced to fall  
301 within or beyond the critical spacing of crowding, as measured during the preceding task.  
302 After the delay period, a circle (diameter =  $0.85^\circ$ , width =  $0.04^\circ$ ) matching the colour and  
303 location of one memory item was displayed, indicating to the observer to report that item's  
304 orientation using the mouse. After the first mouse movement was registered, a response  
305 bar appeared within the circle so that the entire response stimulus matched the target  
306 dimensions. Observers then reported the target orientation as per Experiment 1 and the  
307 next trial began. Fixation errors and breaks were dealt with as described for Experiment 1.  
308 The crowding task and memory experiment took between 1 – 1.5 hours per observer. The  
309 number of trials per stimulus combination was as described in Experiment 1.

310

311 *Experimental Design and Statistical Analyses.* We pooled data across staircases in the  
312 crowded task and used the least-squares method to fit the Weibull function specified by  
313 Watson and Pelli (1983 see Fig. 3B). We modified the function to have three free  
314 parameters:  $\mu$ ,  $\sigma$ , and  $g$ , corresponding to the midpoint of the psychometric function, the  
315 slope, and the lapse rate, respectively. We took an observer's critical spacing to be  $\mu$ , which  
316 was bound between  $0.85^\circ$  and  $8.5^\circ$ , the lower of which ensured incomplete overlap of  
317 stimulus positions in the memory experiment for participants with very small crowding zones.  
318 Note that the lower bound was reached by only 2 out of 19 participants, while none reached

319 the upper bound (Fig. 3C), and so this restriction is unlikely to have affected the results. The  
320 slope,  $\sigma$ , was bound between 0 and infinity, and lapse rate  $g$  was bound between 0 and 0.05  
321 as recommended by Watson and Pelli (see also, Wichmann & Hill, 2001).

322

323 All comparisons in the memory experiment were within-subjects. We performed the same  
324 analyses of report variability and model fitting as per Experiment 1, but now with the  
325 conditions “crowded” and “uncrowded” to indicate trials in which memoranda were  
326 presented within or beyond the critical spacing of crowding, respectively. Importantly, these  
327 analyses were restricted to only memory items presented at the same screen position in  
328 both conditions so performance was matched in all aspects except for the spatial  
329 arrangement of memoranda. We further tested for a relationship between cortical spacing  
330 and short term memory with correlational analyses. We performed both a Bayesian Pearson  
331 Correlation and linear regression using JASP to test if memory performance, regardless of  
332 crowding level, could be predicted by critical spacing. We again restricted data to only trials  
333 in which the memory item was presented directly above fixation. For the Bayesian  
334 correlation, we used the default stretched beta prior width of 1, but results of this analysis  
335 were robust to various prior widths.

336

## 337 **Results**

338 *Experiment 1.* Perceptual resolution in peripheral vision is constrained by the distance  
339 between objects in primary visual cortex. As visual eccentricity increases, fewer visual  
340 neurons are available to process a constantly sized input, and this relationship is  
341 approximately logarithmic (Duncan & Boynton, 2003; Pelli, 2008). This log-scaling of visual  
342 cortex causes greater perceptual interference when multiple items are presented along a  
343 radial axis from the fovea compared with a tangential axis (Pelli & Tillman, 2008; Toet &

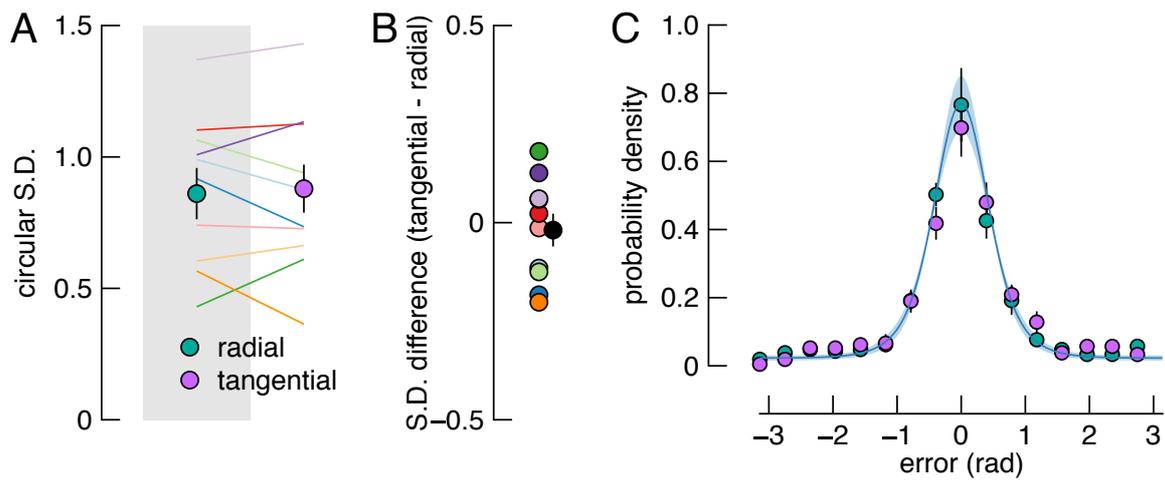
344 Levi, 1992). In Experiment 1, we tested whether working memory is similarly influenced by  
345 the cortical spacing between memoranda (Fig. 1A). Observers were required to remember  
346 three sequentially presented randomly oriented bars arranged either radially or tangentially  
347 relative to the point of fixation (Fig. 1B). At the end of each sequence, observers' memory  
348 of orientation was tested for a single item indicated by a location and colour probe (Fig. 1C),  
349 and responses were made by manually adjusting a response bar to match the cued item.  
350 To control for non-memory related differences across conditions, such as visual acuity, we  
351 analysed memory performance only for targets positioned at 10° to the right of fixation in  
352 each condition. These stimuli were matched in all regards except their spatial context.

353

354 Figure 2 summarises observers' report errors for memoranda presented within a radial or  
355 tangential spatial configuration. As shown in Figure 2A, the circular standard deviation did  
356 not consistently differ between configurations. Indeed, a Bayesian paired-samples t-test  
357 found weak-to-moderate evidence in favour of there being no difference between conditions  
358 ( $B_{01} = 2.97$ ;  $t(9) = 0.45$ ,  $p = 0.66$ ). These data provide evidence against the hypothesis that  
359 short term memory is worse when memoranda are more closely spaced in visual cortex.

360

361



362

363 Figure 2. Results of Experiment 1. A) Report variability for each condition. Filled circles show the mean circular  
 364 standard deviation of reports for radial (green) and tangential (purple) configurations. Coloured lines show  
 365 individual participants' data. Error bars indicate  $\pm 1$  SE. B) Differences in report variability across conditions.  
 366 The black datum shows the mean difference and the coloured data show individual difference scores, with  
 367 colours corresponding to lines in (A). C) Error distributions and model fit. Frequency of errors for the radial and  
 368 tangential conditions are expressed as probability densities, with colours as in (A). Data are shown for 16  
 369 equally spaced bins, in the range  $[-\pi, \pi]$ . The solid blue line shows predictions of the best-fitting model, in  
 370 which we assume memory is independent of the configuration of stimuli (shaded area indicates  $\pm 1$  SE).

371

372 Figure 2C shows the distribution of errors in each condition. The solid line shows the fit of a  
 373 model in which we assumed memory performance factors are independent of the  
 374 arrangement of stimuli. This model was a better fit to the data than the model in which  
 375 cortical spacing could influence memory performance (summed  $\Delta AIC = 29.5$ ; 8 out of 10  
 376 participants; Bayesian paired-samples t-test:  $B_{10} = 3.60$ ;  $t(9) = 2.83$ ,  $p = 0.02$ ; maximum  
 377 likelihood (ML) parameter values, mean (SE): precision = 5.21 (0.25); swaps = 0.10 (0.01);  
 378 guesses = 0.14 (0.02)). This analysis further supports a dissociation between intra-cortical  
 379 spacing and memory performance.

380

381 Finally, we ruled out the possibility that, although memory for the central item was  
 382 unaffected, cortical spacing may have influenced the flanking memoranda which were

383 excluded from the preceding analyses. We therefore repeated the above analyses, but  
384 included only trials in which the probed item was not in the central position. We first collated  
385 data across the remaining probe locations for each condition. We again found that there  
386 was no difference in circular standard deviation between radial and tangential conditions  
387 ( $B_{01} = 2.89$ ;  $t(9) = 0.52$ ,  $p = 0.62$ ). The model in which we assume working memory is  
388 independent of cortical spacing was also the superior model (summed  $\Delta AIC = 34.4$ ; 9 out of  
389 10 participants).

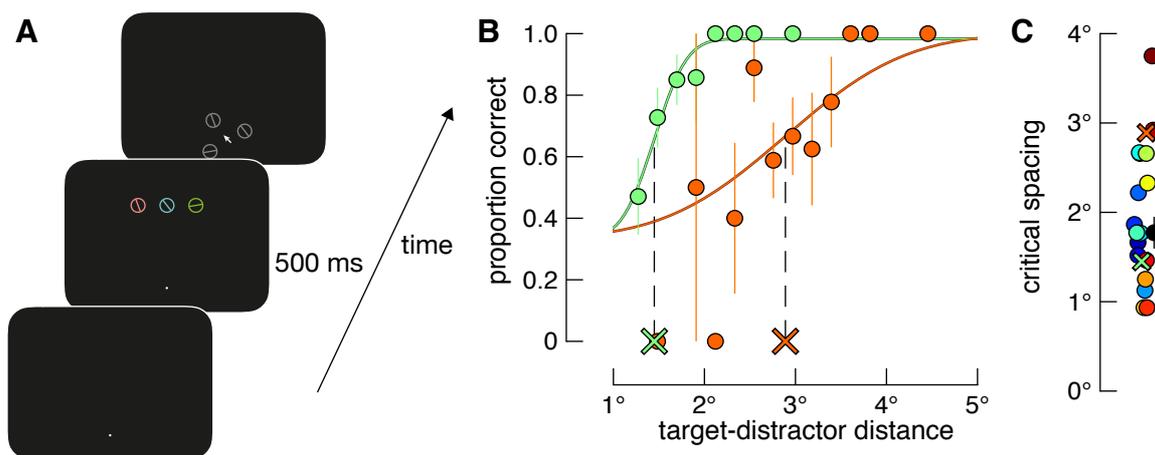
390

391 *Experiment 2.* In Experiment 1 we manipulated intra-cortical spacing of memoranda by  
392 presenting items along a radial or tangential visual axis relative to fixation. We found positive  
393 evidence that performance was the same across conditions (Fig. 2A). These results suggest  
394 that visual short term memory does not have the properties of visual crowding that  
395 characterize retinotopic sensory areas that encode features. It is possible, however, that the  
396 stimulus arrangements we selected were not appropriately scaled to produce overlapping  
397 cortical mnemonic representations. To address this possibility, we conducted a second  
398 experiment in which we used a psychophysical approach to tailor intra-cortical spacing of  
399 memoranda individually for each participant.

400

401 We tested whether the cortical spacing of memoranda affects short term memory by  
402 sequentially presenting items either within or beyond the critical spacing of crowding. Critical  
403 spacing was found for each participant in a perceptual crowding task in which we used an  
404 adaptive staircase to find the target-distractor distance at which they could identify a target  
405 orientation at threshold level (Fig. 3A). Results from two example participants who  
406 performed differently at this task are shown in Figure 3B. Figure 3C shows the critical  
407 spacing estimates for all observers and the median for the group. Critical spacing estimates

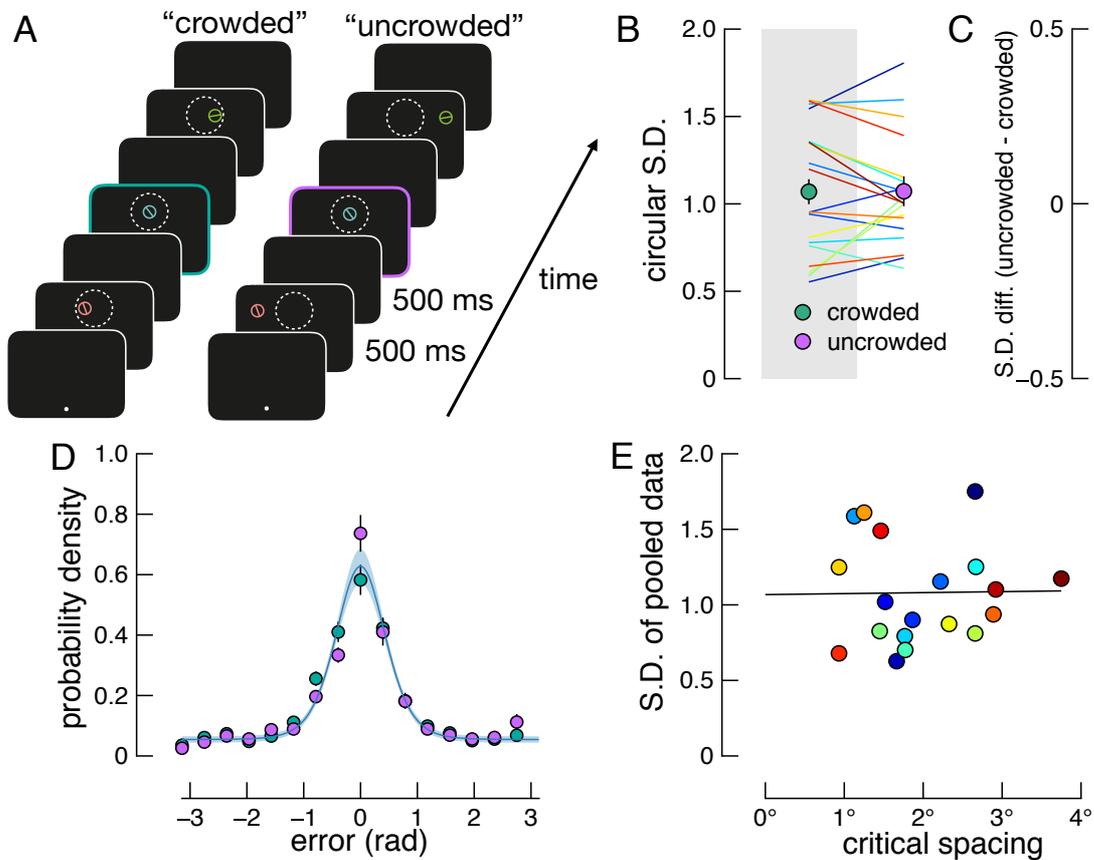
408 span an almost-fourfold range, and such between-subjects variability has been reported  
 409 previously (Greenwood, Szinte, Sayim, & Cavanagh, 2017; Petrov & Meleshkevich, 2011).  
 410 To control for between-subjects crowding variability in the memory experiment, and  
 411 therefore control for cortical spacing variability across participants, we adjusted the spatial  
 412 range of memoranda in the memory experiment to be either 0.75 times (“crowded”) or 1.5  
 413 times (“uncrowded”) an observer’s critical spacing.



414  
 415 Figure 3. Design and results of the crowding task. A) Example trial sequence. After fixating a white spot, three  
 416 stimuli were presented in the upper visual field. An observer’s task was to identify the orientation of the centre  
 417 stimulus, and report its orientation by clicking on the matching stimulus in grey in the subsequent display. The  
 418 distance between target and distractors on each trial was controlled via an adaptive procedure. B) Example  
 419 results and psychometric functions. Differently coloured data show results for two differently performing  
 420 observers. Solid lines show Weibull functions fit to each dataset. Dashed black lines and coloured X symbols  
 421 show the midpoint of the function and corresponding critical spacing estimates, respectively, for each  
 422 participant. C) Estimated critical spacing for 19 observers. The median critical spacing is shown as the black  
 423 datum, while individual participants’ values are shown in various colours. Estimates corresponding to the  
 424 psychometric functions in (B) are shown as X symbols. Data have been randomly jittered on the x-axis to  
 425 minimise overlap. Error bars in all panels show  $\pm 1$  SE.

426  
 427 Results from the memory experiment are shown in Figure 4B-E. We first compared  
 428 observers’ report variability for the crowded and uncrowded conditions (Fig. 4B). These data  
 429 are summarised as difference scores in Figure 4C. Rather than finding an effect of crowding

430 on response standard deviation, a Bayesian paired-samples t-test found moderate evidence  
 431 in favour of there being no difference between conditions ( $BF_{01} = 4.21$ ;  $t(18) = 0.051$ ,  $p =$   
 432  $0.96$ ).



433  
 434 Figure 4. Experiment 2 design and results. A) Example trials of the crowded and uncrowded conditions.  
 435 Observers fixated a white spot and viewed a sequence of randomly orientated memoranda that appeared  
 436 within (crowded condition) or beyond (uncrowded condition) the critical spacing of their upper visual field, as  
 437 indicated by the white dotted circle (shown for illustration only). After the final delay period, a probe appeared  
 438 at one of the memorandum locations, and observers reported the target orientation at this location using a  
 439 method of adjustment (see Methods). B) Report variability for each condition. Data are shown as in Fig. 2A.  
 440 Coloured lines indicating each observer's performance match colours in Figure 3C. C) Differences in report  
 441 variability across conditions. Data are shown as in Fig. 2B. D) Error distributions and model fit. Green and  
 442 purple points show crowded and uncrowded conditions, respectively. Data are shown as described in Fig. 2C.  
 443 The model assuming memory performance is independent of cortical spacing (blue line) was again a better fit  
 444 to the data than the model assuming an influence of cortical spacing, which has been omitted to increase  
 445 visibility. E) Relationship between critical spacing and memory performance. We found no correlation between  
 446 report variability pooled across conditions and critical spacing. Solid line indicates regression line of best fit.

447

448 Figure 4D shows the distribution of report errors averaged across observers, with green and  
449 purple data showing crowded and uncrowded conditions, respectively. We tested whether  
450 memory performance across conditions is better described by a model in which cortical  
451 spacing influences performance, or a model in which working memory is independent of  
452 cortical spacing of memoranda. The blue line in Figure 4D shows the model that is  
453 independent of cortical spacing, which was a better fit than the alternate model (summed  
454  $\Delta\text{AIC} = 52.46$ ; 16 out of 19 participants; Bayesian paired-samples t-test:  $B_{10} = 150.2$ ;  $t(18)$   
455  $= 2.83$ ,  $p < 0.001$ ; ML parameter values, mean (SE): precision = 5.62 (0.16); swaps = 0.04  
456 (0.002); guesses = 0.34 (0.01)). Note that, although there is a higher probability density of  
457 uncrowded trials than crowded trials in the central bin (Fig. 4D;  $\text{BF}_{10} = 6.61$ ), 16 bins were  
458 arbitrarily chosen for display purposes, and there would have been evidence against such  
459 a difference between conditions had we selected, for example, 15 bins ( $\text{BF}_{10} = 0.43$ ). The  
460 analysis of variability and model fitting above are based on raw (unbinned) data so are not  
461 influenced by arbitrary designation of bin size.

462

463 Figure 4E shows the results of the correlational analysis in which we investigated whether  
464 there was a relationship between observers' critical spacing and memory performance. A  
465 Bayesian Correlation Pairs test found moderate evidence that there is no relationship ( $r =$   
466  $0.015$ ,  $\text{BF}_{01} = 3.52$ ). Similarly, a linear regression that uses critical spacing to predict report  
467 error found a slope of only 0.007 ( $t = 0.062$ ,  $p = 0.951$ ), indicating that there is no relationship  
468 between critical spacing and working memory performance.

469

470 As with Experiment 1, we again ruled out the possibility that cortical spacing may have  
471 influenced the flanking memoranda which were excluded from the preceding analyses. We

472 repeated the above analyses including only trials in which the probed item was not in the  
473 central position, collapsing data across the remaining probe locations for each condition. In  
474 support of the results above, we found that there was no difference in circular standard  
475 deviation between crowded and uncrowded conditions ( $B_{01} = 4.08$ ;  $t(18) = 0.27$ ,  $p = 0.79$ ).  
476 Finally, the model in which we assume working memory is independent of cortical spacing  
477 was superior (summed  $\Delta AIC = 51.86$ ; 16 out of 19 participants).

478

## 479 **Discussion**

480 We investigated whether the cortical spacing between sequentially presented memoranda  
481 affects observers' ability to hold those items in memory. In Experiment 1, we manipulated  
482 intra-cortical spacing by arranging memoranda either radially or tangentially relative to the  
483 fovea (Fig. 1). In Experiment 2, we tailored the intra-cortical spacing of memoranda to each  
484 observer by first quantifying their critical spacing of crowding (Fig. 3), and we then presented  
485 memory items within or beyond this region (Fig. 4). Across both experiments, we found  
486 positive evidence that working memory performance is independent of the cortical distance  
487 between memoranda. Although the strength of evidence in each experiment was only  
488 moderate, the combined evidence across experiments is assessed by the product of the  
489 individual Bayes Factors, i.e. 12.5, which is substantial.

490

491 Our study provides clear evidence of a dissociation between perceptual coding and memory  
492 coding within a very short period after stimulus offset. Cortical distance in retinotopically  
493 organised visual cortex can account for a wide variety of perceptual phenomena, such as  
494 visual acuity (Duncan & Boynton, 2003), shape perception (Michel, Chen, Geisler, &  
495 Seidemann, 2013), subjective experience of size (Schwarzkopf et al., 2011), and visual  
496 crowding (Pelli, 2008). In the present study, however, we have shown that memory

497 representations of non-spatial features are independent of their V1 sensory representations.  
498 We know from our data that the emergence of dissociated representations occurs within the  
499 timeframe of the target duration and inter-stimulus interval (1 s). This time-course thus  
500 places an upper bound on the transfer of retinotopic sensory representations to other neural  
501 systems involved in working memory.

502

503 This result sheds light on previous psychophysical studies that have found errors in working  
504 memory due to spatially proximal memoranda. Pertzov et al (2014) and Ahmad et al (2017)  
505 found that memory for non-spatial features was worse when memoranda were presented  
506 sequentially at overlapping or similar screen locations than when memoranda were  
507 presented at spatially separate screen locations. However, the timing used in these  
508 experiments would have likely produced perceptual interference sometimes referred to as  
509 “temporal crowding” (Yeshurun et al., 2015). Such perceptual interference would degrade  
510 the encoding of memoranda due to their persistent overlapping cortical representations.  
511 Indeed, the nature of errors in these previous studies of working memory are consistent with  
512 those in visual crowding paradigms with minimal working memory demands (Ester, Klee, &  
513 Awh, 2014; Harrison & Bex, 2015; 2017). The combination of target duration and inter-  
514 stimulus interval used by Pertzov et al. (500 ms) thus sets a lower bound on the time required  
515 to transform a sensory signal into a memory representation.

516

517 Our results raise several important challenges for the hypothesis that working memory  
518 representations are maintained via the same sensory neurons that encoded the features of  
519 memoranda (Serences, 2016). Previous studies in which a remembered feature is decoded  
520 from activity within V1 typically analyse activity within voxels corresponding to the spatial  
521 location of the memory item (e.g. Harrison & Tong, 2009; Serences et al., 2009). Because

522 our data reveal that sensory representations are independent of memory representations,  
523 these decoding analyses must either be decoding non-sensory neurons that are  
524 nonetheless tuned to the memoranda feature dimension, which we think is unlikely, or reflect  
525 an influence from other areas. Other brain regions implicated in memory maintenance  
526 include prefrontal cortex and posterior parietal cortex (Bettencourt & Xu, 2016; Christophel,  
527 Hebart, & Haynes, 2012; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Todd &  
528 Marois, 2004). In prefrontal cortex in particular, neurons display activity during memory  
529 delays that encodes stimulus locations and features (Goldman-Rakic, 1995; Mendoza-  
530 Halliday & Martinez-Trujillo, 2017; Murray et al., 2017; Wimmer, Nykamp, Constantinidis, &  
531 Compte, 2014) (but see Lara & Wallis, 2014). These areas are part of a distributed network  
532 involved in working memory, and the role of V1 in this network remains to be fully understood  
533 (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017; D'Esposito, 2007; D'Esposito &  
534 Postle, 2015).

535

536 Another alternative is that working memory is maintained via the recruitment of sensory  
537 neurons well beyond the initial sensory representation (Ester, Serences, & Awh, 2009).  
538 According to this *neural outsourcing* proposal, the memory representation of a stimulus  
539 might be shifted to neurons that normally encode sensory stimulation in some other part of  
540 the visual field. However, it is yet to be clarified how visual features with overlapping sensory  
541 representations are allocated to other sensory regions in a way that prevents memory  
542 interference, nor how a mapping is maintained between outsourced representations and  
543 their original locations in the visual field.

544

545 Bays (2014) recently proposed a neural resource model of working memory, based on  
546 population coding, that can account for changes in memory precision as a function of the

547 number of memoranda. A key feature of this model is that a fixed amount of neural activity  
548 (i.e. spiking) must be shared amongst all memory items. Increasing set size, therefore,  
549 decreases the neural resource available for each item, resulting in a loss of memory  
550 precision. The property of maintaining a fixed level of population activity is termed  
551 normalisation: it has been described as a canonical neural computation, implemented in  
552 many different neural systems using varied mechanisms (Carandini & Heeger, 2012). To  
553 accurately reproduce observed effects of set size, the normalisation in the model must  
554 operate globally, i.e. not limited to particular regions of the visual field or particular stimulus  
555 feature values (Bays, 2015). The present results are in agreement with this, in that they  
556 confirm there is no cost of spatial proximity of memoranda as might be expected from a  
557 purely local form of normalisation.

558

559 Neurophysiological evidence consistent with global normalisation has been found in  
560 prefrontal and posterior parietal cortices, areas which have been implicated as playing an  
561 important role in working memory maintenance (for a review, see Bays, 2015). Although  
562 inspired by properties of visual neurons, the neural resource model is agnostic as to the  
563 neural locus of working memory representations, as population coding is a common  
564 mechanism of representation observed throughout the brain (Pouget, Dayan, & Zemel,  
565 2000), including prefrontal cortex (Murray et al., 2017; Wimmer et al., 2014). Nonetheless,  
566 one possible interpretation, consistent with the present findings, is that, in the case of visual  
567 working memory representations, normalisation occurs within networks in which neurons  
568 are not strictly topographically organised.

569

570 Although neural models of short term memory can account for a broad range of human  
571 performance, we are not aware of any model that can account for our result. In a recent

572 study, Schneegans and Bays (2017) presented strong evidence in favour of a model in  
573 which non-spatial features are combined with spatial location via a conjunctive population  
574 code. This extension of the neural resource model correctly predicted their empirical  
575 observation that, when memoranda are presented simultaneously, observers were more  
576 likely to confuse items in working memory (“swap” errors) when the cued memory item was  
577 close to distractors than when distractors were relatively distant from the cued item.

578

579 This model is also consistent with the results of Tamber-Rosenau et al (2015), who found  
580 that the frequency of swap errors for simultaneously presented memoranda depends on the  
581 degree of perceptual crowding. Because visual crowding increases positional uncertainty  
582 (Harrison & Bex, 2017), a conjunctive code that binds spatial location with orientation will  
583 produce more swap errors under strongly-crowded conditions than weakly-crowded  
584 conditions, as was observed by Tamber-Rosenau et al. Schneegans and Bays’ (2017)  
585 model therefore suggests an important role of location in binding non-spatial features when  
586 items are presented simultaneously, but leaves open the question of how to account for the  
587 present findings with sequentially presented memoranda. It is possible that non-spatial  
588 features can be bound according to a conjunctive code that links features with their temporal  
589 order, but neurophysiological evidence for such a model is scarce. Accounting for the lack  
590 of spatial interactions between sequentially presented memoranda represents a challenge  
591 for future modelling efforts.

592

### 593 **Author Contributions**

594 W.J.H. and P.M.B. designed research; W.J.H. performed research; W.J.H analysed data;

595 W.J.H. and P.M.B. wrote the paper.

596

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