

1           **Contextual cuing survives an interruption from an endogenous cue for attention**

2      Tom Beesley<sup>1</sup>, Louise Earl<sup>1</sup>, Hope Butler<sup>1</sup>, Inez Sharp<sup>1</sup>, Ieva Jaceviciute<sup>1</sup>, and David Luque<sup>2</sup>

3    <sup>1</sup>Lancaster University

4    <sup>2</sup>Universidad de Málaga

5    **Author Note**

6  
7           Tom Beesley  <https://orcid.org/0000-0003-2836-2743>

8           Correspondence concerning this article should be addressed to Tom Beesley, Lancaster  
9 University, Department of Psychology, Lancaster University, UK, LA1 4YD, UK, Email:  
10 t.beesley@lancaster.ac.uk

**Abstract**

11

12 Three experiments explored how the repetition of a visual search display guides search during  
13 contextual cuing under conditions in which the search process is interrupted by an instructional  
14 (endogenous) cue for attention. In Experiment 1, participants readily learnt about repeated  
15 configurations of visual search, before being presented with an endogenous cue for attention  
16 towards the target on every trial. Participants used this cue to improve search times, but the  
17 repeated contexts continued to guide attention. Experiment 2 demonstrated that the presence of  
18 the endogenous cue did not impede the acquisition of contextual cuing. Experiment 3 confirmed  
19 the hypothesis that the contextual cuing effect relies largely on localised distractor contexts,  
20 following the guidance of attention. Together, the experiments point towards an interplay between  
21 two drivers of attention: after the initial guidance of attention, memory representations of the  
22 context continue to guide attention towards the target. This suggests that the early part of visual  
23 search is inconsequential for the development and maintenance of the contextual cuing effect, and  
24 that memory representations are flexibly deployed when the search procedure is dramatically  
25 interrupted.

26

Public significance statement: This study provides a test of how attention is governed by  
27 different aspects of the environment. We examine whether the control of attention by an  
28 instructional stimulus (an arrow that directs attention) will interfere with the way in which  
29 attention is governed by other learnt visual patterns in the environment.

30

*Keywords:* visual search; incidental learning; contextual cuing; attention; endogenous  
31 cuing

### 32 **Contextual cuing survives an interruption from an endogenous cue for attention**

1 It is well established that the process of visual search is guided by past experience. When  
2 we encounter a scene, the extent to which the present stimuli match representations in memory  
3 will determine the effectiveness of the stimulus processing and subsequent search through the  
4 scene. The contextual cuing (CC) task is a common way to study this cognitive process in the lab:  
5 participants typically experience a standard visual search task (i.e., serial processing; slow  
6 search), such as searching for a T amongst L shapes. A set of search configurations is repeated  
7 across trials, and response times to targets are faster compared to those in configurations that do  
8 not repeat. Thus, the repetition of the search configurations leads to the formation of a  
9 representation of the configuration in memory, and future processing of the same configuration  
10 activates this representation, driving more efficient behaviour within that scene.

11 Much work has focused on the nature of the memory and attention processes responsible  
12 for contextual cuing. The effect was initially suggested to be implicit in nature, with repeated  
13 configurations seemingly guiding search unconsciously: typically participants are unable to  
14 articulate their knowledge of the repeated configurations, and show poor ability to recognise  
15 learnt configurations in memory tests (e.g., [Chun & Jiang, 1998](#); [Colagiuri & Livesey, 2016](#)),  
16 although this view of CC has been strongly contested (e.g., [Smyth & Shanks, 2008](#); [Vadillo et al.,](#)  
17 [2016](#)). There are also a number of plausible computational models of how memory  
18 representations of repeated configurations are formed and result in the CC effect (e.g., [Beesley et](#)  
19 [al., 2015](#); [Brady & Chun, 2007](#)). The predominant view is that the memory representations are  
20 best characterised as associative in nature, whereby distractors (or groups of distractors, see  
21 [Beesley et al., 2016](#)) form associations that activate more strongly the contingent target position  
22 within each repeated configuration.

23 The exact nature of how repeated configurations come to facilitate visual search is the  
24 focus of much debate within the literature. Broadly there are two quite distinct theoretical  
25 accounts of why responses are faster for repeated configurations: the early attentional guidance  
26 account, and the late response facilitation account. According to the early account, recognition of

27 the configuration leads to a more efficient search process through the distractor array, such that the  
28 target is localised (fixated) at an earlier time point in search. Perhaps the clearest (and arguably  
29 simplest) evidence in support of this account comes from studies of eye-tracking during CC. For  
30 example, search through repeated configurations results in fewer fixations prior to target  
31 localisation (e.g., [Beesley et al., 2018](#); [Tseng & Li, 2004](#)). According to the late response  
32 facilitation account, the benefit for repeated configurations comes about as a result of enhanced  
33 target processing once it has been localised by attention. One conceptualisation of this process is  
34 that repeated configurations lead to a reduction in the evidence threshold required to ascertain that  
35 the target is present in its location, such that responses can be initiated earlier. Such an account  
36 has been put forward by Sewell et al. ([2018](#)), in order to explain the evidence supporting the late  
37 account from response time modelling of the CC effect.

38 It seems likely that both early and late processes contribute to the overall CC effect (for a  
39 review see [Sisk et al., 2019](#)). The current article focuses on exploration of the early-stage  
40 attentional account of CC. The term “early” here reflects the fact that the CC benefit is present  
41 prior to the detection of the target and the initiation of the response to the target. In fact, the  
42 “early” phase can be further divided. Analysis of eye-movements has shown that serial visual  
43 search can be defined as having two distinct phases: an initial ineffective search in which the  
44 direction of saccades are inconsistent and a secondary effective phase in which each saccade will  
45 draw attention closer to the target. CC appears to result from having more trials with a shorter  
46 ineffective phase.

47 One interpretation of these data is that CC is initially not driven at all by the configuration,  
48 and that the initial distractor processing is not beneficial for the representations that form for  
49 repeated configurations. Supporting evidence for this account comes from Olson and Chun  
50 ([2002](#)), where participants were trained on a CC task in which either all the distractors repeated,  
51 those in the half of the screen containing the target (short-range-context), or those in the half of  
52 the screen that didn't contain the target (long-range-context). CC was observed in the  
53 short-range-context, but not in the long-range-context condition. Thus it would appear that the

54 distractors further from the target are not critical to the generation of a CC effect.

55 Brady and Chun (2007)'s computational account features a mechanism that ensures spatial  
56 constraints are placed on the learning of associations with relation to their proximity to the target.  
57 If the spatial constraints are tuned to modulate learning and restrict associative formations to only  
58 those distractors close to the target, this model can accurately model the data from Olson and  
59 Chun (2002). Since the only consequential mechanism in the model for CC is the associative  
60 weights (and their modulation by spatial constraints), then one prediction that follows from this  
61 account is that the initial phase of search is inconsequential for observing CC.

62 In contrast to the localised facilitation account, it's possible that contextual cuing involves  
63 learning of a procedural template that guides eye-movements in a consistent manner following  
64 experience with the task. A recent study by Seitz et al. (2023) has provided evidence to support  
65 this claim. Participants eye-movements were monitored for repeated and randomly arranged  
66 configurations, and similarity metrics were computed to identify the consistency of scan-paths  
67 over time. Several findings point towards the establishment of a more general type of procedural  
68 learning in CC. Firstly, it was found that scan-path similarity increased over the course of training,  
69 but that the similarity of scan-paths was higher in repeated compared to random configurations.  
70 Secondly, scan-path similarity was higher in the initial half of the search trial compared to the  
71 second half. These data suggest that, in contrast to the earlier characterisations of the initial search  
72 process as "inefficient", this early phase may be an important part of the behavioural response in  
73 CC, potentially involving the development of a generic scanning behaviour.

74 Importantly, Seitz et al. (2023) suggest that CC is best characterised as involving the  
75 acquisition of this generic procedural scanning response, and a configuration-specific facilitation.  
76 These behaviours occur in the early and late period of oculomotor guidance, respectively. The  
77 question remains as to how critical the early activation of procedural knowledge is to the  
78 development of CC. The current article examines this by significantly interrupting the search  
79 process with an endogenous cue for attention. In all experiments participants complete a  
80 contextual cuing visual search task but are also presented with an arrow that signals the side of the

81 screen on which the target will appear. Thus, this cue disrupts the natural search process,  
82 considerably reducing the operation of the generic scanning response in the early phase of search.  
83 The experiments therefore examine whether this initial part of the search process is  
84 inconsequential for the observation of the CC effect, or whether the development and maintenance  
85 of the generic scanning behaviour contributes substantially to the CC effect.

86 In the current experiments we explored how CC is affected by the interruption of the  
87 search process by a clear direction of attention from an endogenous cue. In Experiment 1 we  
88 examine whether a learnt pattern of behaviour is disrupted due to the onset of the endogenous cue,  
89 while in Experiment 2 we seek to establish whether the CC effect is weaker under these  
90 conditions. Experiment 3 explores the underlying drivers of the CC effect, in terms of the  
91 distractor-target associations, during these procedures.

### 92 **Experiment 1**

93 Experiment 1 sought to examine whether the learnt attentional behaviour that develops  
94 during contextual cuing is still expressed when participants are directed by an endogenous  
95 (instructional) cue to search in a particular region of the visual scene, hindering the operation of  
96 early-stage visual search processes. Participants were first trained with a set of four repeating  
97 configurations in phase 1 across 5 epochs of 32 trials each. Then prior to phase 2, participants  
98 were told that an arrow would appear before every trial indicating the side of the screen on which  
99 the target would be located. This arrow was valid on every trial. In phase 2, the repeating  
100 configurations were presented in two forms: “consistent”, where the target appeared in the same  
101 position as it has appeared for that configuration in phase 1; and “inconsistent”, where the target  
102 appeared in a position in the opposite quadrant of the screen from where it had appeared in phase  
103 1. Random configurations were also presented in this phase. The inclusion of the inconsistent  
104 trials in this phase provides a test of whether the distractors processed in the early stages of search  
105 continue to guide attention in the presence of the endogenous cue. If this is the case, we would  
106 also expect that the contextual cues would guide attention *away* from the (new) target quadrant on  
107 inconsistent trials, and so response times should be slower on these trials compared to those on

108 random trials.

## 109 **Method**

### 110 *Participants*

111 Thirty-one undergraduate students from Lancaster University were recruited (mean age =  
112 20.1, SD = 1.1; 17 identified as female and 14 as male) via the Psychology Research Participation  
113 System in the Department of Psychology at Lancaster University, in return for the opportunity to  
114 use the recruitment system for their own research in future years. Analysis of the current  
115 experiments was performed with Bayesian methods, seeking support for either the null or  
116 alternative hypothesis on critical tests. As such we aimed for the maximum sample size that could  
117 be achieved by the resources of the experimenter (approximately 30). These sample sizes were  
118 similar to much of our previous lab work with contextual cuing tasks.

### 119 *Materials*

120 Participants were tested individually in a quiet room with a Dell laptop with a 15.6”  
121 screen, a screen resolution of 1920 x 1080, and a full size external keyboard for participants to use  
122 to respond to the task. Participants sat approximately 50 cm from the screen. Stimulus  
123 presentation was controlled by MATLAB using the Psychophysics Toolbox extensions (Brainard,  
124 1997; Kleiner, Brainard & Pelli, 2007; Pelli, 1997). Responses to the target stimulus were made  
125 by pressing the ‘c’ or ‘n’ key on a standard keyboard. All experimental materials are available at  
126 the github repository for this study.

127 Distractor stimuli were an ‘L’ shape (rotated 0°, 90°, 180°, or 270°) while the target  
128 stimulus was a ‘T’ shape (rotated at either 90° or 270°). Stimuli were 8 mm square and arranged  
129 in a square grid of 144 evenly spaced cells (12 x 12) which was positioned centrally on the screen  
130 and was 170 mm square. The grid itself was invisible to participants. The fixation cross  
131 (displayed centrally before each trial) was 4 mm square. The background of the screen was grey  
132 (RGB: .6, .6, .6) and the stimuli were presented in black (RGB: 1, 1, 1). There was a small offset  
133 in the vertical line of the ‘L’ distractors, which increased the similarity between the ‘L’ distractors  
134 and the target ‘T’, making the search task more difficult (Duncan & Humphreys, 1989).

135 *Design*

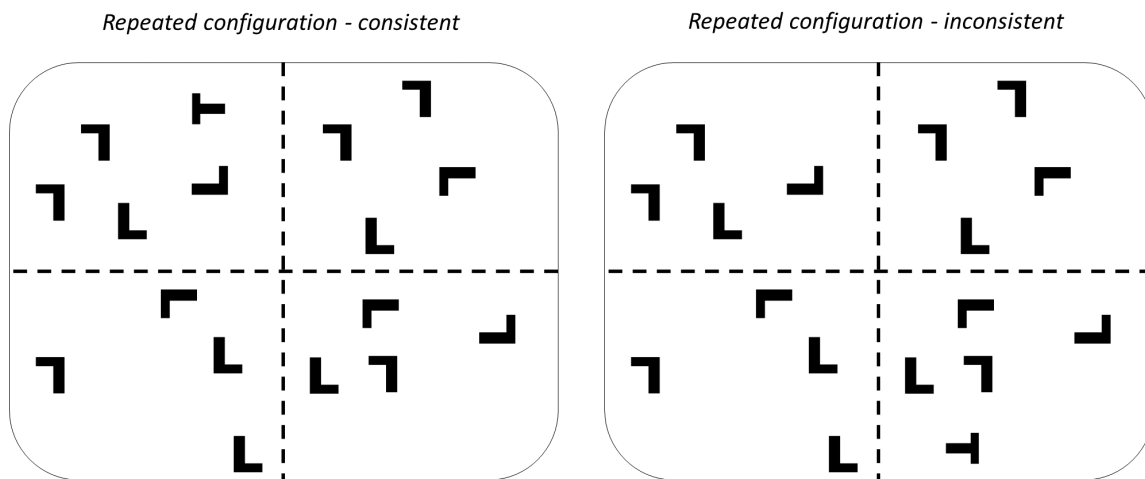
136 Phase 1 employed a within-subjects design with factors of epoch (1-5) and configuration  
137 (repeated and random). All configurations contained 16 distractors, equally divided between the  
138 four quadrants of the display, and one target. Four repeated configurations were trained<sup>1</sup>. Four  
139 target locations were used, with one from each quadrant assigned to each of the repeated  
140 configurations. These same four target positions were used for the random configurations  
141 throughout the task. Each of these four target positions was chosen at random from one of five  
142 locations within each quadrant, that were approximately equidistant from the center of the screen.  
143 Distractors could not appear in these target locations.

144 Phase 2 employed a within-subjects design with factors of epoch (6-10) and configuration  
145 (repeated: consistent; repeated: inconsistent; random: consistent; random:inconsistent). On each  
146 trial, there was a .5 probability that an “inconsistent” version of the configuration would be  
147 presented. This meant that the target was relocated to a diametrically opposed target position such  
148 as to maximise the displacement from the trained target position (see Figure 1). This could occur  
149 for both the repeated and random configurations, hence creating four unique trial types for this  
150 phase. While random configurations did not have a “trained”, associated, target position, it is  
151 necessary to divide the random trials into consistent and inconsistent trial types in this way in  
152 order to assess any target frequency effects that may occur, since the inconsistent target locations  
153 used in this phase were novel.

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<sup>1</sup> Though CC experiments may frequently train 8 or 12 repeated configurations, it has been established that participants typically learn only a subset of these (Smyth & Shanks, 2008). In order to avoid simply adding unnecessary noise to our measure of CC, our lab typically trains just 4 repeated configurations in our CC procedures.





**Figure 1**

*Schematic of the manipulation of target position in consistent and inconsistent trials of phase 2. The dashed lines show the division of the stimuli into quadrants, but were not present in the task procedure.*

154 **Procedure**

155 Participants were tested individually in a quiet testing room. They were given instructions  
156 on how to complete the task, including the presentation of an example of a search trial.

157 Participants were shown the two correct responses for the two possible orientations of targets.

158 Each trial commenced with a fixation cross presented in the center of the screen for 500  
159 ms, which was then replaced immediately by the search configuration. Participants searched for  
160 the target stimulus and responded with a left or right response depending on its orientation.

161 Reaction times (RTs) were recorded from the onset of the search configuration. Following a valid  
162 response (c or n), the configuration was removed from the screen. The ITI was 1000 ms. If  
163 participants made an incorrect response to the target orientation, "INCORRECT RESPONSE"  
164 appeared in red in the center of the screen for 3000 ms, prior to the ITI. If participants did not  
165 respond within 6000 ms, "TIMEOUT - TOO SLOW" appeared in red in the center of the screen  
166 for 3000 ms, prior to the ITI.

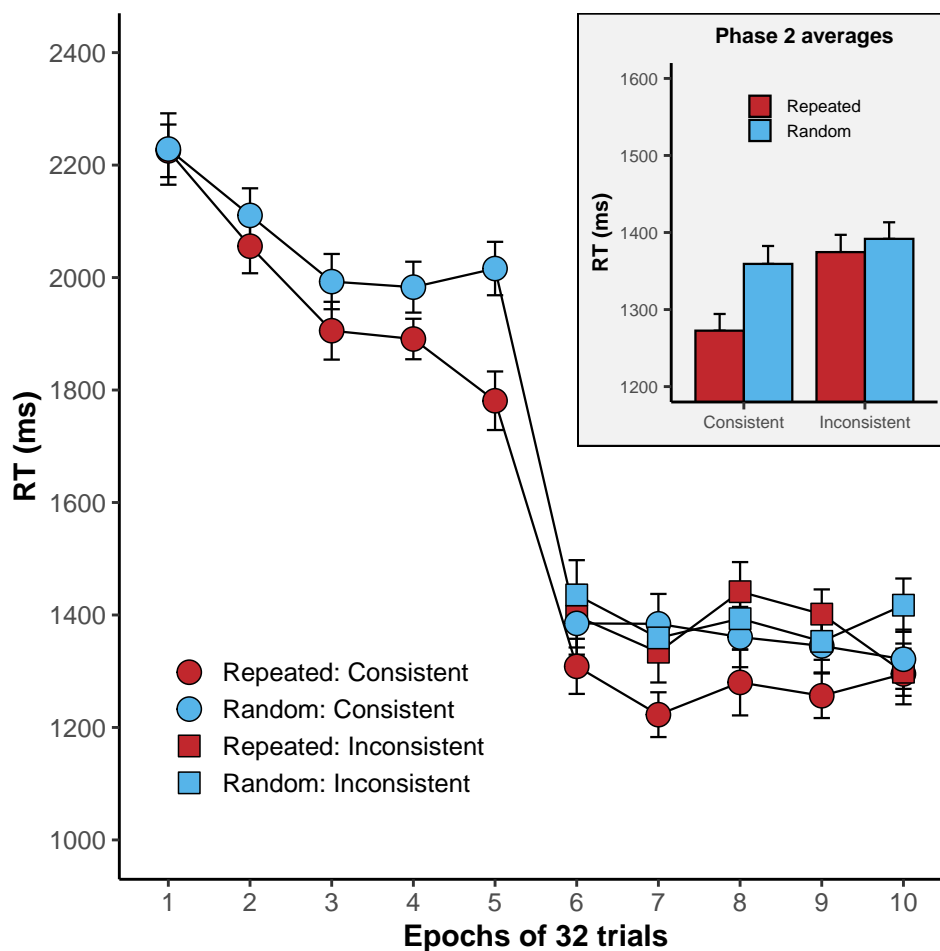
167 Each block of eight trials contained each of the four different repeated configurations and  
168 four random configurations. These eight configurations could appear in any order with the  
169 constraint that the position of the target did not repeat across trials or across consecutive blocks.

170 A rest break of 30 seconds was given every 80 trials. Trials started automatically after  
171 these breaks.

172 After 160 trials, prior to phase 2, participants were given an instruction screen which  
173 detailed the arrow that would appear on the screen prior to the configuration. They were able to  
174 ask any questions they had at this stage and then proceeded to phase 2. The arrow appeared for  
175 1000ms following the fixation cross, before the presentation of the search configuration. The task  
176 was otherwise identical to that used in phase 1.

## 177 **Results**

178 Our criterion for removing outlier data, at both the participant level and the trial level, was  
179 2.5 standard deviations above or below the mean of the sample. On average, trials ended with a  
180 timeout on 1.97% of trials (SD = 2.53). Two participants had an unusually high proportion of  
181 timeouts and were removed from the analysis. The mean accuracy of participants (not including  
182 timeout trials) was 98.10% (SD = 1.65%). One participant had an unusually low proportion of  
183 accurate trials and was also removed. The only participant deemed to be an outlier in terms of  
184 mean response time (hereafter RT) was also excluded on the basis of the timeout criterion, noted  
185 above. For the remaining twenty-eight participants we removed trials with a timeout and  
186 inaccurate trials, before removing outliers from the RT data. On average, the proportion of  
187 outliers removed was 3.03% (SD = 0.79%). Zero participants had an unusual proportion of trials  
188 removed as outlier RTs (greater than 2.5 SDs above the mean).



**Figure 2**

*RT data for Experiment 1. The phase 2 averages across the four trial types are shown inset.*

*Within-subject error bars were computed by a process of normalising the RT data for the sample (Cousineau, 2005).*

189            Figure 2 shows the RT data across the 10 epochs of the experiment. In phase 1 (epochs  
 190 1-5) a contextual cuing effect emerged, with faster responses to repeated over random  
 191 configurations. In phase 2, the presence of the guiding arrow led to a clear reduction in the  
 192 response times. For all participants, the mean RT across epochs 4 and 5 was higher than the mean  
 193 RTs across epochs 6 and 7. Despite the clear evidence for the processing of the endogenous cue,  
 194 the underlying search configuration continued to play a role in the guidance of attention, with

195 faster response times for (consistent) repeated configurations compared to random configurations.

196 These data were analysed with a Bayesian ANOVA<sup>2</sup>, using the *BayesFactor::anovaBF()*  
197 function in R (version 4.4.0; R Core Team (2024)). All analyses in this study used the default  
198 parameters for the priors, which “places mass in reason-able ranges [of effect sizes] without being  
199 overcommitted to any one point” (Rouder et al., 2017, p. 317). First taking the data from phase 1  
200 (epochs 1-5), there was strong support for the model containing the factors of epoch and  
201 configuration (repeated vs. random),  $BF_{10} = 2.1 \times 10^{12} \pm 0.54\%$ . The addition of the interaction  
202 term did not improve the model fit,  $BF = 0.45 \pm 0.85\%$ , though there was no evidence for the  
203 absence of the interaction. The best fitting model was a better fit than the two models containing  
204 only one of the factors, smallest  $BF = 35.09 \pm 0.96\%$ , providing strong support for both the effects  
205 of configuration and epoch. Partial eta-squared ( $n_p^2$ ) effect sizes were calculated using  
206 *effectsize::eta\_squared*, giving values of: 0.22 for the effect of configuration; 0.39 for the effect of  
207 epoch; and 0.1 for the interaction effect.

208 A Bayesian ANOVA on the data from phase 2 (epochs 6-10) found strong support for the  
209 model containing the factors of configuration (repeated vs. random) and target position (consistent  
210 vs. inconsistent),  $BF_{10} = 45.85 \pm 0.85\%$ . The next best fitting model contained these two factors  
211 and the interaction term, and was not a substantially worse fit to the data,  $BF = 0.56 \pm 2.05\%$ . The  
212 best fitting model (with factors of configuration and target position, but no interaction) was a  
213 substantially better fit to the data than the model containing only the factor of configuration  $BF =$   
214  $20.45 \pm 1.19\%$  providing evidence that RTs were faster on consistent than inconsistent trials.  
215 There was no evidence for a difference between the best fitting model and the model containing  
216 only the factor of target position,  $BF = 2.34 \pm 1.12\%$ . The relevant effect sizes ( $n_p^2$ ) were: 0.14 for

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<sup>2</sup> The Bayesian analyses here follow the process outlined in Rouder et al. (2017). Briefly, we present the best fitting model evaluated against the null model, and then compare this fit to that of other models. Where the comparison of two models (i.e., A against B) reveals a Bayes Factor of greater than 3, this is taken as support for the components of model A that are not present in model B. Bayes Factors of less than 0.33 are taken as evidence in support of the equivalence of two models. Following Wetzels et al. (2011) we use the terms “substantial” ( $BF > 3$ ;  $BF < 1/3$ ), and “strong” ( $BF > 10$ ;  $BF < 1/10$ ) to reflect the levels of support for the results of the model comparisons.

217 the effect of configuration; 0.22 for the effect of target position; and 0.14 for the interaction of  
218 these two factors.

219 To further explore responses to the different trial types in phase 2, Bayesian t-tests were  
220 run using *BayesFactor::ttestBF* (using the default Cauchy prior) for comparisons between the  
221 repeated and random configurations, across the two target position conditions (consistent and  
222 inconsistent). This revealed substantial support for a difference between the response times on  
223 “repeated: consistent” trials and those on the respective random trials (random: consistent),  $BF_{10}$   
224 =  $4.14 \pm 0\%$ . There was also substantial evidence to suggest there was no meaningful difference  
225 between the response times for the “repeated: inconsistent” trials and the respective random trials,  
226  $BF_{10} = 0.24 \pm 0.03\%$ .

227 To compare the size of the CC effect across phases 1 and 2, we calculated a “CC effect  
228 score” by subtracting the RT on consistent repeated trials from the RT on consistent random trials.  
229 Positive values reflect a CC effect. There was a CC effect score of 142.72 ms (SD = 202.68) for  
230 the end of phase 1 (epochs 3-5) and a CC effect score of 106.76 ms (SD = 176.12) for the start of  
231 phase 2 (epochs 6-8). A Bayesian t-test of the effect of phase on CC effect found moderate support  
232 for the null result,  $BF = 0.25$ , suggesting that the CC effect was not attenuated in the second phase.

## 233 Discussion

234 In Experiment 1 we established a contextual cuing effect in the first phase, before  
235 introducing an endogenous cue for attention that directed the participants consistently towards the  
236 side of the screen on which the target was presented. Unsurprisingly, this had a dramatic effect on  
237 reducing RTs in all participants, but there remained a significant contextual cuing effect in this  
238 second phase. Thus, disrupting a substantial part of the early search process did not appear to  
239 affect the performance of the contextual cuing that had been established: notably there was  
240 evidence to suggest that the contextual cuing effect in phase 2 was of a similar magnitude to that  
241 which was observed in phase 1. On some repeated trials in phase 2, we positioned the target in a  
242 diametrically opposed location on the screen. On these trials there was no impact of the repeated  
243 configuration on performance.

244 These findings together support a view of contextual cuing in which the initial process of  
245 search is inefficient, not being guided in any way by the repeated context. Only when attention  
246 lands within a region of space approaching the target does the repeated configuration take over to  
247 guide search efficiently towards the target. It should be acknowledged that the variable search  
248 behaviour that participants would exhibit during the early part of the search process would  
249 naturally lead them to search the area around the target on many trials. As such, on trials without  
250 the endogenous cue, the termination of the inefficient phase of search will occur earlier on some  
251 trials compared to others. The cuing of attention by the valid arrow cue ensures this termination  
252 happens on every cued trial, eliminating the inefficient phase of search.

253 The maintenance of a robust contextual cuing effect in phase 2, in the presence of the  
254 endogenous cue, suggests that CC is a robust and flexible behaviour. The apparent ability to  
255 entirely disrupt and negate the early part of the search process, whilst maintaining an intact CC  
256 effect, is at odds with the “general procedural learning” that has been suggested to occur in CC  
257 (Seitz et al., 2023). According to this account, “...what may look an ineffective phase [of search]  
258 actually constitutes an important period during which procedural learning of a general scanning  
259 scheme becomes functional.” (Seitz et al., 2023, p. 9). The present data suggest that this aspect of  
260 search can be eliminated at no cost to CC.

## 261 **Experiment 2**

262 In Experiment 1 we demonstrated that an established effect of contextual cuing is  
263 maintained even when attention is being guided by the presence of a valid endogenous cue. That  
264 is, we found that the *performance* of an established search behaviour in contextual cuing is not  
265 disrupted by the guidance of attention. In Experiment 2 we wanted to explore whether the  
266 *learning* of the contextual cue itself was affected by the presence of a valid endogenous cue. That  
267 is, does the presence of a valid endogenous cue, which leads to a controlled command of  
268 attention, limit the development of a contextual cuing effect. To do this, we trained each  
269 participant on two sets of repeating configurations. One of these sets was always presented in the  
270 presence of a valid endogenous cue, while the other set was always presented in the absence of the

271 endogenous cue. The extent to which there is a “cue-competition” effect between the endogenous  
272 cue and the contextual cues can be examined by comparing the contextual cuing effect we observe  
273 for the two sets of configurations. Given the clear difference in RTs we observed in Experiment 1  
274 between the trials with the endogenous cue present and the cue being absent, we anticipated the  
275 same difference in responding in Experiment 2. Therefore we also included a second phase of  
276 Experiment 2 in which we removed the endogenous cue entirely from the task. This second phase  
277 therefore allowed us to directly compare the contextual cuing for the two sets of configurations  
278 when RTs were at a comparable level.

279         Given the results of Experiment 1, we would anticipate that the size of the CC effect would  
280 be comparable in the two conditions. That is, Experiment 1 suggests that the CC effect is  
281 unaffected by the presence of the endogeneous cue, and therefore that the effect is reliant on the  
282 cuing that occurs by distractors later in the search process. Removal of the inefficient period of  
283 search should not dramatically affect the development of CC.

## 284 **Method**

### 285 *Participants*

286         Thirty-four undergraduate students from Lancaster University were recruited (mean age =  
287 20.74, SD = 5.29; 28 identified as female and 6 as male) via the Psychology Research  
288 Participation System in the Department of Psychology at Lancaster University, in return for the  
289 opportunity to use the recruitment system for their own research in future years.

### 290 *Materials*

291         Participants were tested in a quiet laboratory testing cubicle, with a standard PC and a 24”  
292 monitor set at a resolution of 1920 x 1080 pixels. Since the monitor was larger for this  
293 experiment, the dimensions of the presented stimuli had a proportional increase in size: Distractor  
294 stimuli were 11 mm square; the search grid was 240 mm square; the fixation cross was 6 mm  
295 square. In all other respects, the materials were the same as those detailed in Experiment 1.

## 296 *Design*

297 Four repeated configurations were created in an identical manner to those used in  
298 Experiment 1. For each participant, two of these configurations were used for the condition in  
299 which the arrow cue was presented before the configuration, while two were used for the “control”  
300 condition (no arrow presented). As in Experiment 1, the four repeated configurations were paired  
301 with unique target positions from each of the four quadrants. We counterbalanced the use of the  
302 target quadrants across the factors of configuration type (repeated and random) and cue condition  
303 (arrow vs. no-arrow). For half of the participants, targets in the top left and bottom right were  
304 used for the repeated configurations presented with the arrow (cue-competition) condition, with  
305 targets in the top right and bottom left used for repeated configurations in the no-arrow (control)  
306 condition. For these participants, random configurations presented with the arrow had targets in  
307 the top right and bottom left, and random configurations without the arrow had targets in the top  
308 left and bottom right. For the other half of the participants these assignments were reversed  
309 (repeated-arrow: top-right and bottom-left; repeated-no arrow: top-left and bottom-right;  
310 random-arrow: top-left and bottom-right; random-no arrow: top-right and bottom-left).

## 311 *Procedure*

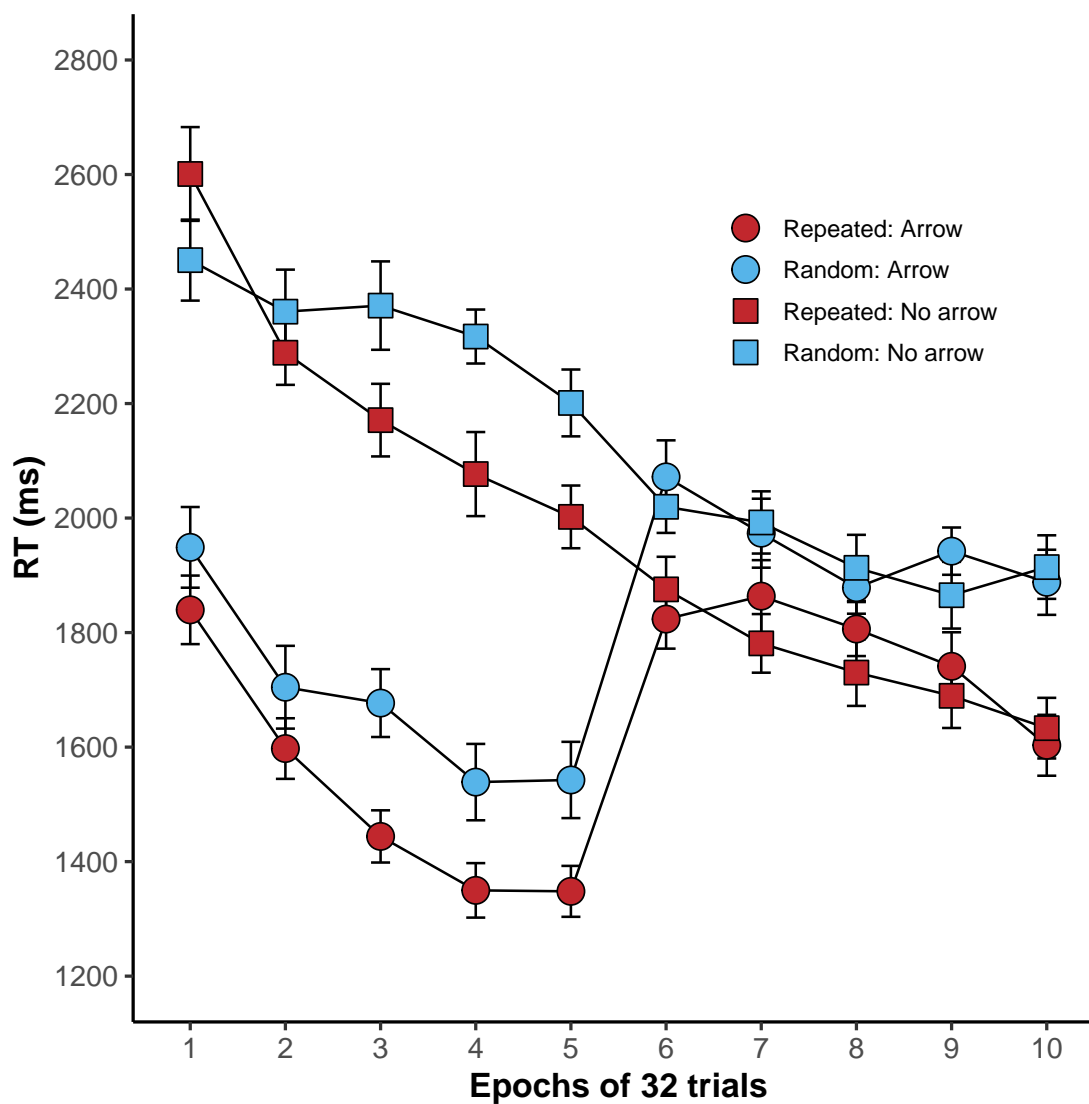
312 The procedure was the same as Experiment 1 with the following differences. Participants  
313 received 320 trials in total. For the first 160 trials, the arrow was presented for the relevant  
314 conditions. For the final 160 trials, the arrow was never presented. Rest breaks were given every  
315 60 trials.

## 316 **Results**

317 Our criteria for removing outlier data were identical to Experiment 1. On average, trials  
318 ended with a timeout on 2.13% of trials ( $SD = 1.83$ ). Zero participants had an unusually high  
319 proportion of timeouts. The mean accuracy of participants (not including timeout trials) was  
320 95.85% ( $SD = 6.10\%$ ). One participant had an unusually low proportion of accurate trials and  
321 were removed from the sample. Zero participants were deemed to be an outlier in terms of mean  
322 RT.



323 For the remaining thirty-three participants we removed trials with a timeout and inaccurate  
 324 trials, before removing outliers from the RT data. On average, the proportion of outliers removed  
 325 was 2.81% (SD = 1.04%). One participant had an unusual proportion of trials removed as outlier  
 326 RTs and was not included in the final analysis.



**Figure 3**

*RT data for Experiment 2. Error bars show standard error of the mean on normalised data.*

327 Figure 3 shows the RT data across the 10 epochs of the experiment. Contextual cuing  
 328 emerged rapidly in both the arrow and no-arrow conditions, with little suggestion that the CC

329 effect was different in the two conditions. The phase 1 data were explored with a Bayesian  
330 ANOVA, which revealed that the best fitting model contained the factors of epoch, configuration  
331 (repeated vs. random), and endogenous cue (arrow present vs. arrow absent), with no interaction  
332 terms,  $BF_{10} = 7.3 \times 10^{100} \pm 1.87\%$ . The next best fitting model contained all three factors and the  
333 interaction of epoch and configuration,  $BF_{10} = 5.5 \times 10^{100} \pm 4.71\%$ , and this model was not a  
334 substantially worse fit to the data,  $BF = 0.76 \pm 5.07\%$ . All other models were substantially worse  
335 fits than the best fitting model, largest  $BF = 0.25 \pm 5.12\%$ . Importantly, the interaction term  
336 between the factors of endogenous cue and configuration did not improve the fit of the model,  
337 providing substantial support for the absence of this interaction,  $BF = 0.19 \pm 2.74\%$ . The relevant  
338 effect sizes ( $n_p^2$ ) were: 0.44 for the effect of epoch; 0.4 for the effect of configuration; 0.85 for the  
339 effect of endogenous cue; 0.12 for the interaction effect between configuration and epoch; and  
340 0.02 for the interaction between configuration and endogenous cue.

341 When the endogenous cue was removed in the second half of the experiment, RTs were  
342 equivalent across the two conditions. An effect of configuration was seen for both cuing  
343 conditions, with little discernible difference between the size of the cuing effects. We conducted a  
344 Bayesian ANOVA with factors of epoch, configuration and endogenous cue condition (arrow  
345 vs. no-arrow). The best fitting model was that with just the factors of epoch and configuration with  
346 no interaction between the factors,  $BF_{10} = 9.6 \times 10^{14} \pm 0.88\%$ . There was substantial support for  
347 this model over the next best fitting model,  $BF = 9.13 \pm 1.28\%$ . To examine the interaction of the  
348 configuration and endogenous cue factors, we compared the model containing those two factors to  
349 the model containing the two factors plus the interaction of configuration and endogenous cue,  
350 which revealed substantial support for the absence of an interaction,  $BF = 0.12 \pm 2.24\%$ . The  
351 relevant effect sizes ( $n_p^2$ ) were: 0.62 for the effect of configuration; and 0.25 for the effect of epoch.

352 To provide further support for the absence of the interaction between the factors of  
353 configuration type and endogenous cue, the data from across the experiment (epochs 1-10) were  
354 analysed with a Bayesian ANOVA with only the factors of configuration and endogenous cue. The  
355 best fitting model was that with the two factors and no interaction,  $BF_{10} = 3.9 \times 10^{51} \pm 6.41\%$ .

356 The addition of the interaction term did not strengthen the model, with substantial evidence for  
357 the absence of the interaction,  $BF = 0.09 \pm 6.53\%$ . The relevant effect sizes ( $n_p^2$ ) were: 0.77 for  
358 the effect of the endogenous cue; and 0.61 for the effect of configuration.

## 359 Discussion

360 Experiment 2 sought to examine whether the presence of a valid endogenous cue would  
361 impair the acquisition of a contextual cuing effect. In the first phase, two sets of configurations  
362 were trained, one of which was always presented in the presence of the endogenous cue, and one  
363 set which was presented without the endogenous cue. Overall there was considerable evidence  
364 that the cue was processed and acted upon, as response times to the target were much faster on  
365 cued trials. However, there was no evidence to suggest that the instructed guidance of attention  
366 impaired the acquisition of the configurations on those trials. Furthermore, when the endogenous  
367 cue was never presented in the final phase of the experiment, the size of the contextual cuing  
368 effect was equivalent between the two sets of configurations; the Bayesian analyses found support  
369 for the equivalence of these CC effects.

370 The data from Experiment 2 are consistent with the findings of Experiment 1: the early  
371 phase of search is inconsequential for the development of contextual cuing. The equivalence of  
372 the CC effects across the two groups (cued and uncued) would suggest that the guidance by the  
373 context was driven entirely by the distractors that appear close to the target. The longer search  
374 times in the uncued condition clearly indicate that a far greater number of distractors are  
375 processed in this condition, but that the enhancement of attentional guidance by the repeated  
376 distractors is limited to the later part of the search process, and therefore those nearer to the target.  
377 Alternatively, it is at least possible that the repeated distractors are processed rapidly at the onset  
378 of the trial, before the effects of the endogenous cue on attention are observed. If this is the case,  
379 then those repeated distractors that influence search (producing the CC effect) need not be  
380 localised around the target. Experiment 3 provides a test of these two possible accounts.

### Experiment 3

381

382 As noted earlier, the analysis of eye-movements during contextual cuing tasks (Beesley et  
383 al., 2018; Tseng & Li, 2004) has revealed a characteristic scanning pattern comprising two phases:  
384 search initially occurs in an inefficient manner, as the eyes move between distractors in the central  
385 region of the distractor field, before then moving in a more directed manner towards the target  
386 position. Contextual cuing appears to result from a cessation of the inefficient search phase at an  
387 earlier time point in the entire search process, such that processing of repeated distractors will, on  
388 average, result in fewer fixations. With respect to the current study, in Experiments 1 and 2 we  
389 have initially directed attention towards the side of the screen that contains the target on cued  
390 trials. This will bring about an early cessation of the first phase of the search process. From here,  
391 however, it seems that search is still facilitated by the repetition of the context.

392 To test this characterisation of the interaction between the endogenous cue and the  
393 repeated context, we exposed participants to the same procedure as used in phase 1 of Experiment  
394 1, which establishes a contextual cuing effect prior to the use of the endogenous cue. In a second  
395 phase we then presented the endogenous cue on every trial (as in Experiment 1), but we  
396 manipulated the presence of the repeated distractors within the configurations. For each repeated  
397 configuration we created two variations: in the “proximal” configurations, only the distractors in  
398 the quadrant containing the target match those from the full repeated configuration, while the  
399 distractors in the other three quadrants were randomly arranged on each trial; in the “distal”  
400 configurations, the distractors closest to the target were randomised, while the distractors in the  
401 other three quadrants were the same as those in the full repeated configuration. During this phase  
402 we also presented fully repeated configurations and fully randomised configurations. Comparison  
403 of the response times across these four trial types will allow us to determine the contribution of  
404 proximal and distal distractors to the CC effect when attention is cued endogenously.

## 405 **Method**

### 406 *Participants*

407           Forty-two undergraduate students from Lancaster University were recruited (mean age =  
408 18.64, SD = 2.84; 28 identified as female and 14 as male) via the Psychology Research  
409 Participation System in the Department of Psychology at Lancaster University, in return for the  
410 opportunity to use the recruitment system for their own research in future years.

### 411 *Materials*

412           All materials, including stimuli and testing environment were identical to Experiment 2.

### 413 *Design*

414           The design of phase 1 was identical to Experiment 1, with four repeated configurations  
415 created and presented with random configurations during this phase. For phase 2, each of the four  
416 configurations was manipulated to create two alternative conditions. In the “Repeated distal”  
417 condition, the four distractors in the target quadrant were randomly arranged on each trial, while  
418 the 12 distractors in the other three quadrants were presented in the same positions as had been  
419 trained in phase 1. Thus, slower response times for this condition (compared to the fully repeated  
420 configurations) would indicate the extent to which participants CC was governed by the  
421 distractors closest to the target. For the “Repeated proximal” condition, the four distractors in the  
422 target quadrant were presented in the same positions as had been trained in phase 1, while the 12  
423 distractors in the other three quadrants were randomly arranged on each trial. Thus, slower  
424 response times for this condition (compared to the fully repeated configurations) would indicate  
425 the extent to which CC was governed by the distractors further from the target. Comparison of the  
426 RTs for these different configurations with those of the random configurations would allow for the  
427 assessment of whether these subsets of distractors had *any* contribution to the CC effect that had  
428 developed during phase 1.

### 429 *Procedure*

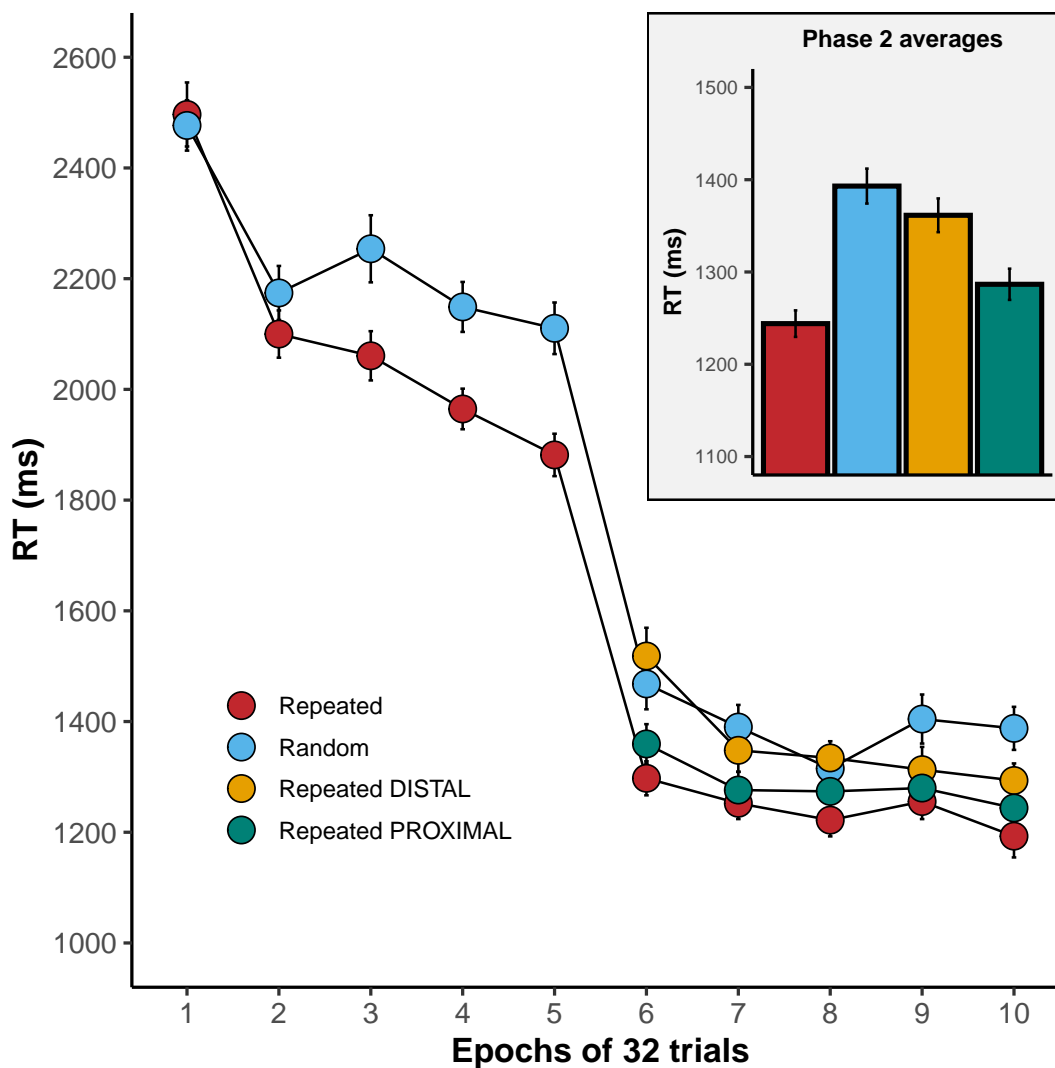
430           The procedure was identical to Experiment 1.

## 431 Results

432 Our criteria for removing outlier data were identical to Experiment 1. On average, trials  
433 ended with a timeout on 2.81% (SD = 2.25) of trials. Two participants had an unusually high  
434 proportion of timeouts and were removed from the sample. The mean accuracy of participants  
435 (not including timeout trials) was 96.09% (SD = 8.57%). Two participants that had an unusually  
436 low proportion of accurate trials and were also removed. Zero participants were deemed to be an  
437 outlier in terms of mean RT.

438 For the remaining thirty-eight participants we removed trials with a timeout and inaccurate  
439 trials, before removing outliers from the RT data. On average, the proportion of outliers removed  
440 was 3.17% (SD = 0.71%). Zero participants had an unusual proportion of trials removed as outlier  
441 RTs.

442 Figure 4 (main panel) shows the RT data across the 10 epochs of Experiment 3. As in  
443 Experiment 1, contextual cuing was readily established in phase 1. These data were subjected to a  
444 Bayesian ANOVA which revealed that the best fitting model contained the factors of configuration  
445 (repeated vs. random) and epoch, and an interaction between those factors,  $BF_{10} = 5.3 \times 10^{24} \pm$   
446  $0.79\%$ . However, the model without the interaction provided a strong fit to the data,  $BF_{10} = 5.2 \times$   
447  $10^{24} \pm 1.18\%$ , and a comparison between the two models did not find any evidence in support of  
448 the interaction term,  $BF = 0.97 \pm 1.42\%$ . There was strong support for the best fitting model over  
449 the remaining models, smallest  $BF = 3900.29 \pm 0.84\%$ , providing strong support for the factors of  
450 epoch and configuration. The relevant effect sizes ( $n_p^2$ ) were: 0.38 for the effect of the epoch; and  
451 0.47 for the effect of configuration; and 0.08 for the interaction of these two factors.



**Figure 4**

*RT data for Experiment 3. Error bars show standard error of the mean on normalised data.*

452 The response times decreased significantly with the presentation of the valid endogenous  
 453 cue in phase 2. Response times to the fully repeated configurations were somewhat comparable to  
 454 those when just the proximal repeated distractors were present. Response times for the distal  
 455 repeated distractors appeared to be slower and comparable to the fully random configurations.  
 456 The phase 2 data were subjected to a Bayesian ANOVA which found that the best fitting model  
 457 contained the factors of configuration and epoch but no interaction between the factors,  $BF_{10} =$

458  $1.4 \times 10^{14} \pm 0.45\%$ . This model provided a superior fit to the data compared to the next best  
459 fitting model that included the two factors and the interaction term,  $BF = 121.25 \pm 1.08\%$ ,  
460 providing strong support for the contribution of the two factors and the absence of an interaction  
461 between the two factors. The relevant effect sizes ( $n_p^2$ ) were: 0.37 for the effect of configuration;  
462 and 0.16 for the effect of epoch.

463 The inset graph in Figure Figure 4 shows the mean RTs to the four types of configuration,  
464 averaged across the 5 epochs of phase 2. To explore the differences in response times, Bayesian  
465 t-tests were run for all pairwise comparisons. The response times to repeated and  
466 repeated-proximal configurations were both faster than those to random configurations, smallest  
467  $BF_{10} = 10313.81 \pm 0\%$ . In contrast, there was no evidence that the response times to  
468 repeated-distal configurations were different from those to random configurations,  $BF_{10} = 0.39 \pm$   
469  $0.04\%$ . Response times to repeated configurations were faster than those to repeated-proximal  
470 configurations,  $BF_{10} = 4.67 \pm 0\%$ . Response times to repeated-proximal configurations were  
471 faster than those to repeated-distal configurations,  $BF_{10} = 31.88 \pm 0\%$ .

## 472 Discussion

473 Experiment 3 explored the localisation of the distractors driving contextual cuing when  
474 attention is guided by an endogenous cue. As expected, there was substantial evidence that  
475 contextual cuing was present when the distractors close to the target were maintained, but not  
476 when these distractors were randomly arranged. These data appear to confirm a clear order to the  
477 interplay between the two drivers of attention: initially attention is guided by the endogenous cue  
478 towards one half of the screen, and then search is refined by the presence of the valid configural  
479 cues (the repeated distractors). Like in Experiment 1, the phase 2 data demonstrate the resilience  
480 of the CC effect to changes in the search process. Despite visual search never commencing in a  
481 cued manner during the initial acquisition period of phase 1, a CC effect was readily observed in  
482 phase 2. Thus it seems that the stored representations of configurations surrounding target  
483 positions are flexibly deployed in visual search, despite changing demands on controlled  
484 attentional processes. Notably the fully repeated configurations exerted more of a benefit on



485 search than those containing only the proximal distractors, suggesting that the repeating  
486 distractors beyond the target quadrant have some (but possibly lesser) influence on search (Brady  
487 & Chun, 2007).

488 These data lend support to the notion that the effect of the repeated configuration is a late  
489 process within visual search, and that each trial commences with an inefficient search process that  
490 is not guided by the repeated configuration (Beesley et al., 2018; Tseng & Li, 2004). In some  
491 ways, these findings represent a paradox of CC: the cuing effect occurs almost at the point at  
492 which target detection has been made. One interpretation would be that this demonstrates the  
493 importance of spatial contiguity in the formation of visual associations (Renaux et al., 2017).  
494 Alternatively, it provides support for the proposed “decision threshold” accounts of CC (Kunar et  
495 al., 2007; Sewell et al., 2018), which posit that the repeated distractors close to the target ensure a  
496 reduced threshold for target detection, resulting in faster response times.

#### 497 **General Discussion**

498 Three experiments explored the impact of a central endogenous cue of attention on the  
499 contextual cuing of visual search. In Experiment 1, having established a contextual cuing effect,  
500 each trial was preceded by a central endogenous cue of attention in the form of an arrow, directing  
501 attention towards the side of the screen in which the target was positioned (this arrow cue was  
502 always valid, as was the case in each of the three experiments). Despite participants clearly using  
503 this cue, visual search was still facilitated by the presence of the repeating pattern of visual search.  
504 This experiment demonstrated that, once acquired, the activation of the memory representation  
505 and its impact on performance of visual search remains intact in the presence of a top-down  
506 instruction to guide attention. Experiment 2 examined the storage of these contextual  
507 representations, and whether this process was impaired by an endogenous cue guiding search. We  
508 found equivalent levels of contextual cuing for configurations trained with the endogenous cue and  
509 those trained in its absence. Together, these two experiments suggest a seamless interplay between  
510 these two factors governing attention in visual search: the endogenous cue initially guides  
511 attention and the repeated configuration continues to refine and guide attention towards a fixation

512 on the target. In Experiment 3 we therefore explored whether the localised distractors around the  
513 target were sufficient to generate CC following the guidance by the endogenous cue. Indeed, there  
514 was a significant CC effect in the case of the proximal distractors, but repeated configurations that  
515 did not contain the proximal distractors failed to generate a CC effect, suggesting that the proximal  
516 distractors play a crucial role in search following the guidance of attention by the endogenous cue.

517 Our data are consistent with previous theoretical (Brady & Chun, 2007) and empirical  
518 (Olson & Chun, 2002) work that has highlighted the influence of distractor configurations  
519 localised to the target. Experiment 2 in particular demonstrates that acquisition of effective  
520 representations is equivalent if search is limited to one half of the display from the outset. In  
521 Experiment 3 the CC effect was observed only when fully repeated and proximal-repeated  
522 configurations were presented. Interestingly the CC effect was substantially weaker in the case of  
523 configurations with only proximal-repeated distractors. This must reflect a generalisation  
524 decrement between the stored representation and the available cues for the target. Our  
525 manipulation of the influence of repeated distractors was based on disrupting the repeating  
526 configurations on a quadrant basis: those inside the quadrant retained their positions, while those  
527 outside were randomised. This somewhat crude manipulation will not perfectly capture the  
528 impact of all distractors: it is likely that the influence of distractors at increasing distances from  
529 the target will have a gradually reducing influence on driving a CC effect.

530 The current data reveal that the influence of repeated contexts has a relatively late control  
531 on behaviour in visual search. Previous analysis of eye-movements during CC (Beesley et al.,  
532 2018; Tseng & Li, 2004) has shown that contextual cuing (and visual search more generally) has  
533 two characteristic components. The first of these is an inefficient search process where search fails  
534 to move towards the target in trials with more fixations. This is followed by a phase in which  
535 monotonic, positive increments are made toward the target position in the final 3 to 4 fixations.  
536 CC reduces the frequency of trials with the initial search period (there are more of such trials for  
537 random configurations and fewer for repeated configurations). Search behaviour under CC  
538 conditions is necessarily variable, however, and each time a configuration is encountered, the

539 pattern of eye-movements will inevitably be driven by a range of factors that lead to variation in  
540 the scan path taken. What is clear is that it is the final few fixations and saccades that are crucial to  
541 the search behaviour that facilitates CC, and this period will follow a variable length of ineffective  
542 search. Thus, the effect of the endogenous central cue in the current study is to eliminate, or  
543 considerably reduce, the engagement with this first phase of the search process. The results of this  
544 study strongly imply that the positive associative information in the repeating configurations is  
545 extracted in the final stages of search and is localised around the target. This is true both in terms  
546 of the performance of an acquired configuration (Experiments 1 and 3) and the acquisition of the  
547 representation for that configuration (Experiment 2).

548         Recently, work by Seitz et al. (2023) has suggested that CC is made up of both  
549 configuration-specific learning, and eye-movements that reflect "...procedural learning of a  
550 general scanning scheme..." [p. 9]. This latter aspect of the acquired CC behaviour was suggested  
551 to occur within the earlier period of inefficient search. If such a behaviour developed in our CC  
552 task, it is clear that this behaviour is not critical to the performance of the CC effect (in Exp 1 and  
553 Exp 3), or to the development of the learned behaviour that drives the CC effect (Exp 2). Contrary  
554 to the suggestion by Seitz et al. (2023), it's at least possible that such general procedural learning  
555 has some influence over the later stages of search. However, such an account would have to  
556 assume that this learnt behaviour is flexible enough to survive the curtailment of a considerable  
557 portion of the pattern of eye-movements. We would argue it is simpler to account for the present  
558 data by assuming the expression of a pattern-specific sequence of eye-movements that occurs late  
559 on in the search process, following the period of ineffective search.

560         The current data are also consistent with a late-stage "response threshold" account of CC  
561 (Sewell et al., 2018). According to this perspective, the facilitation for repeated configurations  
562 occurs because the target is more readily detected amongst the surrounding distractors. Analysis  
563 of ERPs has revealed enhanced contra-lateral delay activity (CDA) for repeated over random  
564 configurations. This is thought to reflect "postselective (focal-attentional) processing of items  
565 held in working memory" (Chen et al., 2022). In the present tasks, such a mechanism would not

566 be affected by the onset of the endogenous cue and the curtailing of the period of ineffective  
567 search. Taken together, the results here point towards the possibility of three components to the  
568 behaviour in CC: an early ineffective search, followed by enhanced localisation and increased  
569 perceptual discrimination of the target, driven by the distractors closest to the target.

570 The effect of CC on visual search has frequently been characterised as an automatic  
571 influence on behaviour (e.g., [Chun & Jiang, 1998](#); [Chun & Nakayama, 2000](#); [Geyer et al., 2021](#)).  
572 This characterisation of CC comes from multiple aspects of the observed effect. Updating of the  
573 associations is somewhat slow and seemingly inflexible to changes in the acquired associations  
574 ([Makovski & Jiang, 2011](#); [Manginelli & Pollmann, 2009](#); e.g., [Zellin et al., 2013](#)), and therefore  
575 perhaps reflects a habitual form of behaviour. In addition, contextual cuing has frequently been  
576 observed in the absence of above-chance recognition memory for the repeating search  
577 configurations (e.g., [Colagiuri & Livesey, 2016](#)), which suggests a non-conscious, automatically  
578 evoked form of behaviour. Despite this persistent characterisation, the automaticity (or  
579 controllability) of CC has rarely been directly tested in the literature. To our knowledge, only the  
580 experiments of Luque and colleagues ([Luque et al., 2017](#); [Luque et al., 2021](#)) have directly  
581 assessed this aspect of CC, by placing the influence of the configuration in competition with  
582 top-down goals in the task. Their findings supported the conclusion that CC performance can be  
583 controlled and will not guide search for the target when another aspect of the task governs  
584 attentional control. In the current study, the repeated configurations continued to have an  
585 influence on search performance even when attention had been guided by the endogenous cue. In  
586 this respect, it might be suggested that these results are somewhat at odds with the conclusions of  
587 Luque and colleagues ([Luque et al., 2017](#); [Luque et al., 2021](#)).

588 To what extent is this behaviour best characterised as “automatic” in nature? Arguably the  
589 clearest demonstration of an automatic effect of a stimulus on behaviour is when the associated  
590 behaviour is elicited even when it is counter-productive to the current goals ([Moors & De Houwer,](#)  
591 [2006](#)). We could argue that such a test was constructed in the repeated inconsistent trials of  
592 Experiment 1, in which the repeated configuration was associated with a target that was

593 previously located in a position on the opposite side of the screen to the direction indicated by the  
594 endogenous cue. If the repeated configuration had an effect on behaviour on these trials, we would  
595 have expected to see slower response times compared to random trials. This was not the case:  
596 response times were equivalent in these two conditions. As such it is hard to claim here that the  
597 configuration is having an *automatic* effect on behaviour, according to this strict characterisation  
598 of such an effect. Nevertheless, the experiments here reveal a flexible interplay between top-down  
599 drivers of attention and configuration-driven effects of attention in CC.

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## Declarations

604

### *Funding*

605

Not applicable

606

### *Conflicts of interest/Competing interests*

607

Not applicable

608

### *Ethics approval*

609

Ethical approval was granted by the Department of Psychology Ethics Committee, Lancaster University, conforming to the British Psychological Society Code of Ethics and Conduct.

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### *Consent to participate*

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All participants gave informed consent to participate in the study. All data was stored anonymously at the point of collection.

614

615

### *Consent for publication*

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All participants gave informed consent for their (anonymised) data to be used in publication.

617

618

### *Availability of data and materials*

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The raw data and experimental materials are freely available at the project repository [http://github.com/tombeesley/CC\\_EC](http://github.com/tombeesley/CC_EC)

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621

### *Code availability*

622

The data analysis scripts and the manuscript source files are available at [http://github.com/tombeesley/CC\\_EC](http://github.com/tombeesley/CC_EC). The analyses reported in this manuscript are computationally reproducible from the manuscript source files (using R v4.4.0).

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### *Authors' contributions*

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T.B. Designed the experiments; programmed the experiments; conducted the statistical analyses; wrote the manuscript. D.L. Designed the experiments; contributed to the writing of the

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629 manuscript. L.E., H.B., I.S., I.J., contributed to the design of the experiments; collected the data;  
630 approved the final manuscript version.



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