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## Direct evidence for the optimal tuning of attention

KERZEL, Dirk

### Abstract

In search arrays where the target is presented with similar nontarget stimuli, it is advantageous to shift the internal representation of the target features away from the nontarget features. According to optimal tuning theory (Navalpakkam & Itti, 2007), the shift of the attentional template increases the signal-to-noise ratio because the overlap of neural populations representing the target and nontarget features is reduced. While previous research has shown that the internal representation of the target is indeed shifted, there is little evidence in favor of a shift in attentional selectivity. To fill this gap, we used a cue-target paradigm where shorter reaction times (RTs) at cued than at uncued locations indicate attentional capture by the cue. Consistent with previous research, we found that attentional capture decreased with decreasing similarity between cue and target color. Importantly, target-similar cue colors closer to the nontarget colors captured attention less than target-similar cue colors further away from the nontarget colors, suggesting that attentional selectivity was biased away from the nontarget [...]

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4 **Direct evidence for the optimal tuning of attention**

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14 Abstract: 229

15 Main text: 8834

16 Figures: 4

17 Tables: 3

18 Running head: Optimal tuning of attention

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26

**Abstract**

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In search arrays where the target is presented with similar nontarget stimuli, it is advantageous to shift the internal representation of the target features away from the nontarget features. According to optimal tuning theory (Navalpakkam & Itti, 2007), the shift of the attentional template increases the signal-to-noise ratio because the overlap of neural populations representing the target and nontarget features is reduced. While previous research has shown that the internal representation of the target is indeed shifted, there is little evidence in favor of a shift in attentional selectivity. To fill this gap, we used a cue-target paradigm where shorter reaction times (RTs) at cued than at uncued locations indicate attentional capture by the cue. Consistent with previous research, we found that attentional capture decreased with decreasing similarity between cue and target color. Importantly, target-similar cue colors closer to the nontarget colors captured attention less than target-similar cue colors further away from the nontarget colors, suggesting that attentional selectivity was biased away from the nontarget colors. The shift of attentional selectivity matched the shift of the memory representation of the target. Further, the bias in attentional capture was reduced when the nontarget colors were more distinct from the target. We discuss alternative accounts of the data, such as saliency-driven capture and the relational account of attentional capture (Becker, 2010), but conclude that optimal tuning theory provides the best explanation.

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**Keywords**

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visual search, attentional template, attentional selection, feature-based attention, contingent attentional capture, visual memory

**Significance statement**

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We often look for objects that are similar to the surrounding nontarget objects. For instance, the target may have a color that is similar to the other colors present in the display. The visual system operates efficiently in this situation, but the underlying mechanism is poorly understood. Previous research has suggested that observers may slightly modify the search goal in order to optimize performance. Instead of looking for the target, they look for a target that exaggerates the difference between target and nontargets. Understanding how

55 human observers solve the task may be relevant for applied sciences, such as computer  
56 vision.

## 57 **Introduction**

58 In visual search tasks, observers compare the sensory input to a stored  
59 representation of the target. Stimuli matching the stored representation are selected for  
60 further processing. The collection of features describing the target is referred to as  
61 attentional template (Bundesen, 1990; Carlisle, Arita, Pardo, & Woodman, 2011; Duncan &  
62 Humphreys, 1989; Geng & Witkowski, 2019; Hout & Goldinger, 2015; Liesefeld & Müller,  
63 2019; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Schneider, 2013). The attentional  
64 template can be biased by requirements of the search task. For instance, Navalpakkam and  
65 Itti (2007) asked observers to search for a target line tilted by 55° among nontarget lines  
66 tilted by 50°, which requires a fine perceptual discrimination. Subsequently, the attentional  
67 template underlying the search task was probed by asking observers to find the target line in  
68 an array of tilted lines. The results showed that observers most frequently selected an  
69 orientation of 60° instead of the true target orientation of 55°, which means that the  
70 attentional template was biased by 5° away from the nontargets. Navalpakkam and Itti  
71 (2007) argued that shifting the attentional template away from the nontarget feature  
72 facilitated search because the signal-to-noise ratio was increased. When target-nontarget  
73 similarity is high, similar neural populations are activated by target and nontarget features,  
74 resulting in a low signal-to-noise ratio. Shifting the attentional template away from  
75 nontarget feature avoids activation from neural populations responding to the non-target  
76 feature and increases the signal-to-noise ratio. Recent research confirmed shifts of the  
77 attentional template and additionally investigated its precision. Geng, DiQuattro, and Helm  
78 (2017) found that the precision of the attentional template increased with the frequency of  
79 target-similar nontargets. In addition, Yu and Geng (2019) demonstrated that the sharpening  
80 was asymmetrical with a better precision of the attentional template for feature values  
81 intermediate between target and nontargets.

## 82 **No behavioral evidence for optimal tuning of attentional selectivity**

83 While the shift of the attentional template away from nontarget features is a robust  
84 finding, there is surprisingly little evidence for a modulation of attentional selectivity by the  
85 shift. Typically, it is assumed that voluntary attention is directed at stimuli matching the

86 attentional template, which results in perceptual enhancement of the attended stimuli. For  
87 instance, attention may increase the activation of neurons tuned to the target features  
88 ("attentional gain", e.g., Reynolds & Chelazzi, 2004), improve perceptual sensitivity for the  
89 attended stimuli (e.g., Carrasco, 2011), or reduce RTs to the attended stimuli (e.g., Folk,  
90 Remington, & Johnston, 1992). Optimal tuning predicts that perceptual enhancement occurs  
91 for target-similar features deviating away from the nontargets. To test this prediction,  
92 Scolari and Serences (2009) used a difficult orientation discrimination task similar to  
93 Navalpakkam and Itti (2007). The orientation discrimination task was run on most of the  
94 trials and required participants to report the location of a target grating deviating by 5° from  
95 three nontarget gratings. The orientation of the nontarget gratings and the relative target  
96 orientation (i.e., 5° clockwise relative to the nontarget orientation) were cued before onset  
97 of the search display. Performance on the search task was never better than 60%, confirming  
98 that a fine perceptual discrimination was necessary. The orientation discrimination task was  
99 interleaved with attentional probe trials. In Experiment 1, the attentional probe trials  
100 consisted of a display with four gratings at various orientations. Participants were asked to  
101 select the grating with the cued target orientation. Similar to the results by Navalpakkam  
102 and Itti (2007), choices were biased toward gratings with orientations that exaggerated the  
103 difference between target and nontargets. In Experiment 2, the attentional probe trials  
104 measured perceptual sensitivity to target, nontarget and surrounding orientations. A single  
105 low-contrast Gabor was presented at one of the four locations and participants were asked  
106 to indicate its location. The orientation of the low-contrast Gabor was 0°, ±5°, ±10°, ±20°, or  
107 ±40° relative to the target orientation. It should be noted that orientations intermediate  
108 between target and nontarget were not tested, as target and nontargets were separated by  
109 only 5°. A threshold procedure determined the contrast necessary to achieve 75% correct  
110 responses at each relative probe orientation. It was expected that thresholds for target-  
111 similar orientations deviating away from the nontarget orientation would be enhanced.  
112 However, the pattern of results did not support optimal tuning. Instead of the expected one-  
113 sided improvement for orientations deviating away from the nontarget orientation, there  
114 was improvement on both sides at relative orientations of 10° or 20° (see Figure 4C in Scolari  
115 & Serences, 2009). Thus, the shift of the attentional template (Experiment 1) was not  
116 accompanied by a corresponding unilateral improvement of perceptual sensitivity  
117 (Experiment 2). Rather, the results suggest that attention was tuned bilaterally to off-target

118 orientations. In line with the enhancement on both sides of the target orientation, fMRI  
119 recordings of orientation-selective voxels in V1 showed bilateral gain (Scolari & Serences,  
120 2010). However, another study showed unilateral gain for orientations away from both  
121 target and distractor, in line with optimal tuning of attention (Scolari, Byers, & Serences,  
122 2012). The different outcomes of the two fMRI-studies may result from different methods,  
123 such as differences in task difficulty or the order of stimulus presentation (sequential vs.  
124 simultaneous).

125         It should be noted that the task in Scolari and Serences (2009) and Navalpakkam and  
126 Itti (2007) required a fine perceptual discrimination where the target feature was highly  
127 similar to the nontarget feature. In contrast, search performance in experiments by Geng  
128 and collaborators (Geng et al., 2017; Yu & Geng, 2019) on the shape of the attentional  
129 template was much better, with accuracy typically above 90% and chance being at 50% or  
130 25%. In addition, Geng's work focused on color and not orientation. However, similar to  
131 behavioral research on orientation discrimination, there was little evidence that attentional  
132 selectivity was influenced by the shift of the attentional template. For instance, Geng et al.  
133 (2017) demonstrated that it became easier to discriminate the target color when similar  
134 non-target colors were more frequent, but their data do not provide evidence for  
135 asymmetric attentional selectivity. The data only confirm that attentional selectivity  
136 improved when similar nontarget colors were more frequent, consistent with the observed  
137 sharpening of the attentional template. In a similar vein, it has been shown that memory  
138 performance for search targets is more precise than for other content of VWM (Rajsic,  
139 Ouslis, Wilson, & Pratt, 2017; Rajsic & Woodman, 2019).

#### 140 **A competing theory: The relational account of attentional control**

141         In sum, there is little behavioral evidence for optimal tuning of attentional selectivity,  
142 which is at odds with the many studies confirming shifts of the attentional template. Further,  
143 results consistent with optimal tuning were interpreted as evidence for another theory of  
144 attentional control. In Becker, Harris, Venini, and Retell (2014), participants were asked to  
145 saccade to a unique color in a square array of four disks around central fixation.  
146 Simultaneous with the onset of the disks, a distractor was shown in one of two response-  
147 irrelevant locations. In this situation, first saccades land frequently on the distractor when its  
148 color is similar to the target color (Becker, Ansorge, & Horstmann, 2009; Born & Kerzel,  
149 2011; Ludwig & Gilchrist, 2002; Mulckhuyse, van Zoest, & Theeuwes, 2008). Building on this

150 effect, Becker et al. (2014) systematically manipulated the deviation of the distractor color  
151 from the target color. The distractor color was either equal to the target color, or it deviated  
152 toward or away from the nontarget color. For example, if participants were looking for an  
153 orange target among yellow nontargets, then red distractors deviate away from the  
154 nontarget color, whereas yellow-orange distractors deviate toward the nontarget color (see  
155 Figure 1). However, all colors share the same relation with respect to the nontargets as they  
156 are all "redder". Becker et al. (2014) observed stronger oculomotor capture by distractor  
157 colors deviating away from the nontarget color than for colors deviating toward the  
158 nontarget color. The asymmetric distribution of oculomotor capture supports optimal tuning  
159 theory because attentional selectivity was biased away from nontargets, presumably to  
160 increase the signal-to-noise ratio.

161         However, Becker et al. (2014) interpreted their results in terms of the relational  
162 account of attentional control, which claims that attention is guided by relative, not absolute  
163 features (Becker, 2010). The relational account predicts that distractors sharing the target's  
164 feature relation to the context will capture attention even if the absolute features are  
165 different. For instance, during search for an orange target among yellow nontargets, a red  
166 distractor in an orange context would capture attention because the distractor has the same  
167 feature relation to the context ("redder", see Figure 1). In contrast, feature-based accounts  
168 (e.g., Treue & Martinez Trujillo, 1999) would not predict capture because the absolute target  
169 feature differs from the distractor (i.e., the target is orange but the distractor is red). Many  
170 experiments using the spatial cueing paradigm by Folk et al. (1992; see below) suggest that  
171 cueing effects are robust to changes of the absolute feature values when feature relations  
172 are preserved (Becker, 2010; Becker, Folk, & Remington, 2013; Harris, Remington, & Becker,  
173 2013; Meeter & Olivers, 2014; Schönhammer, Becker, & Kerzel, 2017; Schönhammer,  
174 Grubert, Kerzel, & Becker, 2016). To account for the asymmetrical oculomotor capture  
175 detailed above, Becker et al. (2014) proposed that distractor colors deviating away from the  
176 nontargets were "relationally better" than the target, presumably because the distractor  
177 colors exaggerated the target-nontarget relation.

178         In sum, psychophysical experiments testing optimal tuning of attentional selectivity  
179 with contrast thresholds provided results conflicting with optimal tuning of attentional  
180 selectivity (Scolari & Serences, 2009), but brain imaging results were consistent with optimal  
181 tuning (Scolari et al., 2012). Other psychophysical experiments using saccadic responses



182 provided evidence in favor of optimal tuning of attentional selectivity, but were used to  
183 support an alternative theory (Becker et al., 2014). Thus, behavioral evidence in favor of the  
184 optimal tuning of attentional selectivity is scarce. In striking contrast, there is robust  
185 evidence for a shift of the memory representation consistent with optimal tuning (Geng et  
186 al., 2017; Navalpakkam & Itti, 2007; Scolari & Serences, 2009; Yu & Geng, 2019).

### 187 **New evidence from spatial cueing**

188         The first goal of the present study was to provide more compelling evidence for  
189 asymmetric attentional selectivity in a situation that promoted a biased attentional  
190 template. We focused on search for color targets and used displays which allowed for  
191 accuracy better than 90%. Importantly, we temporally separated the search display from the  
192 distractor event used to measure attentional selectivity. In a variant of the spatial cueing  
193 paradigm developed by Folk et al. (1992, reviews by Burnham, 2010; Büsel, Voracek, &  
194 Ansorge, 2018), the distracting cue preceded the target display by 150 ms. Temporal  
195 separation of cue and target display allowed for independent manipulation of cue and target  
196 context.

197         Typically, RTs in spatial cueing paradigms are shorter when the cue appears at the  
198 same location as the target than when it appears at a different location. However, cueing  
199 effects on RTs decrease with increasing color difference between cue and target (Anderson  
200 & Folk, 2010; Ansorge & Becker, 2014; Büsel, Pomper, & Ansorge, 2018; Folk & Remington,  
201 1998; Kerzel, 2019). The modulation of cueing effects by cue-target similarity shows that  
202 only cues matching the attentional template capture attention. For instance, when  
203 observers searched for a red target, red cues resulted in cueing effects, whereas green  
204 targets did not (Folk & Remington, 1998; Harris, Jacoby, Remington, Travis, & Mattingley,  
205 2019), showing that only colors matching the attentional template for red captured  
206 attention.

207         Spatial cueing effects contingent on the match between features of the cue and the  
208 attentional template are thought to be related to feature-based attention (Leonard,  
209 Balestreri, & Luck, 2015; Stothart, Simons, Boot, & Wright, 2019). In neural measures,  
210 feature-based attention is associated with an increased response to the attended feature  
211 even at unattended locations (Andersen, Hillyard, & Müller, 2008; Saenz, Buracas, &  
212 Boynton, 2002; Treue & Martinez Trujillo, 1999; Zhang & Luck, 2009) (but see Moher,  
213 Lakshmanan, Egeth, & Ewen, 2014). In behavioral measures, feature-based attention may

214 facilitate performance when participants divide attention across two stimuli sharing the  
215 same feature (Sàenz, Buraças, & Boynton, 2003) or it allows for the spread of adaptation  
216 effects to unattended locations (Liu & Mance, 2011). In the context of contingent spatial  
217 cueing effects, the idea is that feature-based attention guides attention to the location of  
218 the cue, where spatial attention is deployed (Eimer, 2014; Wolfe, Cave, & Franzel, 1989).

### 219 **Shared and conflicting predictions of optimal tuning and the relational account**

220 Optimal tuning theory suggests that the feature guiding attention is biased away  
221 from the nontarget feature when the nontargets are similar to the target. Therefore, target-  
222 similar features deviating away from the nontarget colors are expected to produce larger  
223 cueing effects than target-similar features deviating towards the nontarget colors. However,  
224 regardless of the direction of the deviation, cueing effects should be absent for cue colors  
225 deviating strongly from the target color (Folk & Remington, 1998; Harris et al., 2019).

226 While these predictions of optimal tuning (Navalpakkam & Itti, 2007) overlap with  
227 the relational account (Becker et al., 2014), there is an important limitation in the relational  
228 account. Cueing effects are only predicted when the relation between target and nontargets  
229 is the same as between cue and cue context. When the feature relations differ, the  
230 relational account does not apply. Therefore, work on the relational account presented the  
231 distracting cue in a colored context so that both cue and target were characterized by  
232 differences in hue relative to the surrounding stimuli. In the current experiments, we  
233 presented the cue in the context of gray stimuli, while the target was presented among  
234 colored nontargets. In other words, the cue differed from the context by its larger  
235 saturation, whereas the target had a different hue compared to the target context (see  
236 Figure 1). Further, we tested the memory representation of the target without showing the  
237 nontarget elements, which avoided perceptual biases (e.g., Ekroll, Faul, Niederee, & Richter,  
238 2002). Thus, both perception of the cue colors and the memory judgments were absolute  
239 (i.e., relative to gray) and not relative to the nontarget stimuli. Shifts in attentional selectivity  
240 therefore support optimal tuning but are not predicted by the relational account.

### 241 **Experiment 1**

242 We employed the spatial cueing paradigm developed by Folk et al. (1992) to test  
243 whether cueing effects are stronger for target-similar cue colors deviating away from the  
244 nontarget colors compared to target-similar cue colors deviating toward the nontarget  
245 colors (see Figure 2A). The colors of the nontargets were selected to be similar to the target,

246 but sufficiently different to allow for better than 90% accuracy in the search task. Thus, the  
247 task was easy relative to previous experiments on orientation discrimination (Navalpakkam  
248 & Itti, 2007; Scolari & Serences, 2009). In fact, target and nontarget colors were sufficiently  
249 distinct to allow for the investigation of intermediate color values. The cue was spatially non-  
250 predictive of the target location and preceded the target by about 150 ms (see Figure 2B).  
251 The sequence of cue and target presentation did not exceed 200 ms to prevent eye  
252 movements. The cue was presented among gray context elements of the same luminance.  
253 Therefore, the cue color was not perceived relative to the nontarget colors, which eliminates  
254 relational coding. Colors were drawn from CIELAB-space because distances in CIELAB-space  
255 reflect perceived color differences (Fairchild, 2005; Witzel & Gegenfurtner, 2015, 2018). To  
256 replicate the shift of the attentional template away from nontarget colors reported  
257 previously (Geng et al., 2017; Hamblin-Frohman & Becker, 2019; Yu & Geng, 2019), we  
258 interspersed trials in which observers were asked to indicate the color of the target on a  
259 color wheel. The target color did not change for a given participant. We expect the  
260 remembered color to deviate away from the nontarget colors.

## 261 **Methods**

262 **Participants.** In a previous study, we found cueing effects to decrease with  
263 decreasing similarity between target and cue (Kerzel, 2019). We were particularly interested  
264 in the difference between cueing effects with a color identical to the target and a color  
265 separated by  $15^\circ$  in CIELAB-space. For difficult feature search, the previous study indicated a  
266 Cohen's  $d_z$  of 0.77, which requires 12 participants with a type 1 error probability of .05 and a  
267 power of .8. Because we think that even smaller effect sizes are theoretically important, we  
268 aimed for a sample size of 22, which would allow us to find significant results with Cohen's  $d_z$   
269 as small as 0.55. We collected data from 22 participants but had to eliminate four datasets.  
270 Two datasets were eliminated because the assigned target color made the search task too  
271 difficult (see below), one participant did not complete the experiment, and another  
272 participant was removed because of a high error rate (21%) compared to the remaining  
273 participants ( $M = 4\%$ ,  $SD = 2\%$ ). Thus, the final sample size was 18 (2 male, age:  $M = 21.8$   
274 years,  $SD = 5.2$ ).

275 First-year psychology students participated for class credit. All reported normal or  
276 corrected-to-normal vision. The study was approved by the ethics committee of the Faculty  
277 of Psychology and Educational Sciences and was carried out in accordance with the Code of

278 Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was  
279 given before the experiment started.

280 **Apparatus.** Stimuli were displayed on a 21-inch CRT monitor (Mitsubishi Diamond Pro  
281 2070) with a refresh rate of 85 Hz and a pixel resolution of 1,280 × 1,024 (horizontal ×  
282 vertical), driven by an ATI Radeon HD 3450 graphics card with a colour resolution of eight  
283 bits per channel. CIE1931 chromaticity coordinates and luminance ( $xyY$  with  $Y$  in  $\text{cd}/\text{m}^2$ ) of  
284 the monitor primaries were  $R = (0.630, 0.340, 18.5)$ ,  $G = (0.293, 0.610, 60.9)$ , and  $B = (0.152,$   
285  $0.069, 9.9)$ . The Psychtoolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) was used to  
286 run the experiment. Observers viewed the screen at 64 cm. Head position was stabilized  
287 with a chin/forehead rest.

288 **Stimuli.** There was a placeholder, a cue, and a target display for the RT task and a  
289 display with a color wheel for the color judgment. The placeholder display was composed of  
290 four outline rings, drawn in light gray. The distance from the center of the fixation cross to  
291 the center of the outline rings was  $3^\circ$ . The inner and outer borders of the outline rings had a  
292 radius of  $1.1^\circ$  and  $1.4^\circ$ , respectively. The linewidth of the borders was 1 pixel or  $0.03^\circ$ . In the  
293 cue display, the outline rings were filled. Three rings were filled with the same light gray as  
294 the circles and one ring with a color. The colored ring was the cue. In the target display, a T  
295 rotated by  $90^\circ$  clockwise or counter-clockwise was shown in each placeholder. The bars  
296 making up the rotated T were  $1^\circ$  long and  $0.3^\circ$  thick. All four rotated Ts were colored. In each  
297 display, two Ts were rotated clockwise and two counter-clockwise. A central fixation cross  
298 ( $0.6^\circ$  diameter) was shown throughout.

299 The difference in hue between cue and target, and between target and nontargets  
300 was quantified in CIELAB-space. The white-point of CIELAB was  $xyY = (0.29, 0.30, 89.27)$ .  
301 Stimuli were presented on a grey background with the chromaticities of the white-point and  
302 a lightness of  $L^* = 55$ , which corresponded to a luminance of  $20.5 \text{ cd}/\text{m}^2$ . The fixation cross,  
303 the placeholders, the achromatic cues and the borders of the rotated Ts were light gray ( $L^* =$   
304  $73$  or  $40.3 \text{ cd}/\text{m}^2$ ). The colors that served as cue, target and nontarget colors were sampled  
305 along a hue circle at a lightness of  $L^* = 73$  and a saturation (chroma) of 34.

306 The hue of the target was fixed for each participant and counterbalanced across  
307 participants. The hue of the cue was selected randomly among deviations of  $0^\circ$ ,  $\pm 15^\circ$  and  
308  $\pm 30^\circ$  from the target color. The hues of the three nontargets were the same on each trial

309 and deviated by 40°, 55°, and 70° from the target hue. In the context of the present study,  
310 “color” is synonymous with “hue” because neither saturation nor lightness varied.

311 The color wheel represented an isoluminant hue circle with the same lightness and  
312 saturation as the cue and target colors. The radius of the color wheel was 1.2° (inner edge)  
313 and the line width was 0.6°. To cancel motor biases and to avoid response repetition, the  
314 spatial orientation of the zero hue angle was randomized between trials. By turning the  
315 mouse around the initial mouse position on the desk, participants were able to rotate the  
316 line cursor. The color pointed to by the line cursor was used to draw the cursor line and a  
317 central disk with 0.3° radius shown inside the color wheel.

318 **Design.** The 160 combinations of 4 cue positions, 4 target positions, 5 cue colors (-  
319 30°, -15°, 0°, +15°, +30°), and 2 responses (left, right) were presented once in random order  
320 in a trial block. Positive deviations of the cue colors (i.e., +15°, +30°) indicate that the cue  
321 color deviated from the target color towards the nontarget colors, whereas negative  
322 deviations (i.e., -15°, -30°) indicate deviations away from the nontarget colors. Participants  
323 completed 5 blocks of 160 trials for a total of 800 trials on the RT task. The color task was  
324 run on every 16<sup>th</sup> trial for 50 color judgments. Target color was varied across participants by  
325 assigning one of eight equally spaced colors from CIELAB color space to each participant  
326 (23°, 68°, 113°, 158°, 203°, 248°, 293°, and 338°). In addition, we counterbalanced the  
327 direction of the difference between target and nontarget colors across participants. For  
328 instance, the nontarget colors for a 113° target color were at 113° plus 40°, 55°, and 60° (i.e.,  
329 at 153°, 168°, and 173°), but another participant would be shown nontarget colors at 113°  
330 minus 40°, 55°, and 60° (i.e., at 73°, 58°, and 53°). We expect color flipping to cancel biases in  
331 color perception. The color and orientation of nontargets were selected randomly without  
332 replacement from the available values.

333 During data collection, we noticed that our rendition of CIELAB-space lacked  
334 resolution around the 248° target color (blue). Visual inspection and the high error rates of  
335 one participant showed that it was more difficult to discriminate the 248° target color from  
336 the nontargets. We therefore removed the datasets of the two participants who had been  
337 presented with the 248° target and eliminated the 248° color from the set of available target  
338 colors for the remaining participants. Low precision for blue compared to other colors in  
339 CIELAB-space has been reported before (see Figure 7 in Bae, Olkkonen, Allred, & Flombaum,  
340 2015).

341           **Procedure.** A trial started with the presentation of the placeholder display for 706  
342 ms. Then, the cue display was shown for 47 ms, followed by the placeholder display for 106  
343 ms and the target display for 47 ms. The resulting cue-target SOA was 153 ms. After target  
344 offset, the placeholder display remained visible until a response was registered.

345           Participants responded to the orientation of the letter T by mouse click (T rotated  
346 counter-clockwise: left button, T rotated clockwise: right button). They were instructed to  
347 respond as rapidly as possible while keeping the error rate below 10%. They were also  
348 instructed to ignore the cue display.

349           On trials with a color judgment, the color wheel was preceded by a 1.5 s-message  
350 saying that the color of the target had to be indicated and that responses should be as  
351 precise as possible. Participants were informed that the target color was always the same.  
352 Participants confirmed their color judgments with a mouse click. The individual median RT  
353 for the mouse click was between 2,719 and 7,324 ms ( $M = 4,225$  ms) from the onset of the  
354 color wheel. After the click, the static color wheel remained on the screen for another 300  
355 ms before a blank screen was shown for 500 ms.

356           Participants were first trained on the color judgment task, then on the RT task, and  
357 finally completed five blocks of the combined task. To avoid effects of color category, the  
358 target color was not named during practice, but was shown among gray nontargets in the  
359 first set of practice trials.

360           Visual feedback informed participants about choice errors, anticipations ( $RTs < 0.2$  s)  
361 and late trials ( $RTs > 1.5$  s). Anticipations were extremely rare and will not be reported. Every  
362 80 trials, visual feedback about the proportion of correct responses, median RTs and median  
363 color error were displayed for at least 5 s, forcing participants to take a short break.

## 364 **Results**

365           Cues presented at the target location are referred to as valid cues, whereas cues  
366 presented at a non-target location are referred to as invalid cues. Mean RTs and error rates  
367 as a function of cue validity and cue color are shown in Table 1. We subtracted performance  
368 on valid trials from performance on invalid trials to obtain cueing effects. Average cueing  
369 effects are shown in Table 1 and Figure 2C. In addition, Table 1 shows the significance of  
370 one-sample t-tests against zero for each cueing effect. Further, we calculated the color error  
371 as the difference between true and judged target color. The red bars in Figure 2C show the  
372 distribution of color errors in  $3^\circ$  bins. Because there were no differences between

373 Experiments 1 and 2, the distribution in Figure 2C shows the combined data. The data from  
 374 all experiments are available in the open science framework at the link  
 375 [https://osf.io/6jeax/?view\\_only=88951708ce254b139d7f884a897624d3](https://osf.io/6jeax/?view_only=88951708ce254b139d7f884a897624d3)

376 **RTs.** We considered responses with RTs outside the response window of 1.5 s as late  
 377 and excluded these trials from analysis (0.2%). We also excluded trials with choice errors  
 378 (3.7%) and trials with RTs that were 2.5 standard deviations above the respective condition  
 379 mean (1.2%).

380 We conducted a 4 (cue color relative to target color: difference of  $-30^\circ$ ,  $-15^\circ$ ,  $0^\circ$ ,  $15^\circ$ ,  
 381 and  $30^\circ$ )  $\times$  2 (cue validity: valid, invalid) ANOVA on individual mean RTs. The main effect of  
 382 cue validity,  $F(1, 17) = 76$ ,  $p < .001$ ,  $\eta_p^2 = .816$ , showed that RTs were shorter with valid than  
 383 invalid cues (500 vs. 542 ms). Further, there was a main effect of cue color,  $F(4, 68) = 4.81$ ,  $p$   
 384  $= .002$ ,  $\eta_p^2 = .22$ , and a significant interaction of cue color and cue validity,  $F(4, 68) = 42.11$ ,  $p$   
 385  $< .001$ ,  $\eta_p^2 = .592$ . As shown in Table 1 and Figure 2C, the cueing effect decreased with  
 386 increasing separation of cue and target color, but the decrease was not symmetric around  
 387 the target color. By paired t-test, the mean cueing effect for the  $-30^\circ$  cue color was larger  
 388 than for the  $30^\circ$  cue color (60 vs. 3 ms),  $t(17) = 6.19$ ,  $p < .001$ , Cohen's  $d_z = 1.46$ . Similarly, the  
 389 cueing effect for the  $-15^\circ$  cue color was larger than for the  $15^\circ$  cue color (76 vs. 16 ms),  $t(17)$   
 390  $= 7.79$ ,  $p < .001$ , Cohen's  $d_z = 1.84$ . Overall, the distribution of cueing effects shows a shift  
 391 away from the nontarget colors with a peak around  $-15^\circ$ . While the current cue colors  
 392 capture the right side of the distribution adequately, the left side is only represented by a  
 393 single cue color ( $-30^\circ$ ). Nonetheless, the difference between  $-30^\circ$  and  $-15^\circ$  was significant by  
 394 paired t-test (60 vs. 76 ms),  $t(17) = 2.68$ ,  $p = .016$ , Cohen's  $d_z = 0.63$ .

395 **Choice Errors.** Individual percentages of choice errors were submitted to the same  
 396 ANOVA as above. The main effect of cue validity,  $F(1, 17) = 24.36$ ,  $p < .001$ ,  $\eta_p^2 = .589$ , was  
 397 modulated by the interaction of cue color and cue validity,  $F(4, 68) = 7.06$ ,  $p < .001$ ,  $\eta_p^2 =$   
 398  $.293$ . Inspection of Table 1 shows that the difference between valid and invalid trials was  
 399 larger for cue colors away from the context colors than for cue colors towards the context  
 400 colors, which is in accord with the RT data.

401 **Memory Bias.** Color errors were fit with the mixture model proposed by Zhang and  
 402 Luck (2008) with an additional bias parameter. The model provides an estimate of the  
 403 standard deviation of the distribution of the memory error, an estimate of the guess rate,  
 404 and an estimate of the bias of the distribution. Fits were performed by the MemToolbox

405 (Suchow, Brady, Fournie, & Alvarez, 2013). Here, we focus on the bias parameter to evaluate  
406 whether the memory representation was shifted towards or away from the context colors.  
407 The mean memory bias is illustrated by the black disk with horizontal error bars overlaid on  
408 the distribution of color errors in Figure 2C. By one-sample t-test, the mean bias parameter  
409 was  $-19^\circ$  and significantly smaller than zero,  $t(17) = 8.15$ ,  $p < .001$ , Cohen's  $d_z = 1.92$ . The  
410 direction and magnitude of the bias fits well with the shifted distribution of cueing effects.

#### 411 **Discussion**

412 We found cueing effects for target-similar colors to be asymmetrically distributed.  
413 Cueing effects were larger for target-similar cue colors shifted away from the nontarget  
414 colors than for cue colors shifted toward the nontarget colors. At the same time, there was a  
415 bias in the judged target color in the same direction. Participants remembered the target  
416 color to be further away from the nontarget colors than it actually was. The magnitude of  
417 the shift in the attentional template (color judgments) agreed with the shift in attentional  
418 selectivity (cueing effects) and amounted to about  $-18^\circ$  in CIELAB-space.

#### 419 **Experiment 2**

420 Similar to results by Becker et al. (2014), the results from Experiment 1 did not show  
421 a return to baseline for target-similar colors deviating away from the nontarget colors. Thus,  
422 it may be possible that attentional selectivity was biased toward the largest color difference.  
423 While the cue was presented in a context of gray elements, one may argue that its saliency  
424 was calculated across the temporal average of cue and target displays. If cue and target  
425 displays are collapsed, then cue colors deviating away from the nontarget colors are more  
426 salient. Possibly, their larger saliency accounts for the larger capture and the asymmetric  
427 distribution. Many studies have suggested a link between saliency and attentional capture  
428 (e.g., Burnham & Neely, 2008; Feldmann-Wüstefeld, Miyakoshi, Petilli, Schubö, & Makeig,  
429 2017; Liesefeld, Liesefeld, Müller, & Rangelov, 2017; Theeuwes, 1991; Töllner, Zehetleitner,  
430 Gramann, & Müller, 2011; van Zoest, Donk, & Theeuwes, 2004; reviewed by Theeuwes,  
431 2019). To rule out effects of saliency, we included cue colors that deviated more strongly  
432 from the nontarget colors. Stronger deviations increase the saliency in the averaged  
433 displays, but they also decrease the similarity with respect to the target color. Decreased  
434 similarity between cue and target color, in turn, is known to reduce attentional capture (e.g.,  
435 Kerzel, 2019). Thus, a saliency-based explanation of the cueing effects in Experiment 1  
436 predicts reliable cueing effects with increasing distance from the nontarget color, while



437 asymmetrical attentional selectivity predicts a return to baseline with large differences  
 438 between cue and target colors. To measure the full distribution of cueing effects, we shifted  
 439 the cue colors from Experiment 1 by  $-15^\circ$ .

#### 440 **Methods**

441 The methods were the same as in Experiment 1 with the exception that the cue color  
 442 deviated by  $-45^\circ$ ,  $-30^\circ$ ,  $-15^\circ$ ,  $0^\circ$ , or  $15^\circ$  from the target color. Twenty-two new students  
 443 participated, but one dataset had to be excluded because of excessive errors (51.4% vs. 4.2%  
 444 in the remaining sample). The mean age of the included participants was 21 years with  $SD =$   
 445 2.2. There were two men in the final sample.

#### 446 **Results**

447 **RTs.** We excluded choice errors (3%), late trials (0.1%) and outliers (1.4%) before  
 448 calculating individual mean RTs. We conducted a 4 (cue color:  $-45^\circ$ ,  $-30^\circ$ ,  $-15^\circ$ ,  $0^\circ$ , and  $15^\circ$ )  $\times$   
 449 2 (cue validity: valid, invalid) ANOVA on individual mean RTs. The main effects of cue validity,  
 450  $F(1, 20) = 48.66$ ,  $p < .001$ ,  $\eta_p^2 = .71$ , and cue color,  $F(4, 80) = 8.65$ ,  $p < .001$ ,  $\eta_p^2 = .3$ , were  
 451 modulated by a significant interaction of cue color and cue validity,  $F(4, 80) = 14.94$ ,  $p < .001$ ,  
 452  $\eta_p^2 = .428$ . Inspection of the gray symbols in Figure 2C shows that the peak of the  
 453 distribution of cueing effects was on  $-15^\circ$  and that cueing effects decreased symmetrically  
 454 around this peak. To confirm the decrease on both sides, we compared neighboring cue  
 455 colors ( $-45^\circ$  vs.  $-30^\circ$ ,  $-30^\circ$  vs.  $-15^\circ$ , etc.). By paired t-test with Bonferroni correction for four  
 456 tests (critical  $p$  of .0125), all differences were significant,  $ts(20) > 3.45$ ,  $ps < .003$ , Cohen's  $d_z >$   
 457 0.75. To provide further evidence for the symmetry of the decrease, we also compared the -  
 458  $45^\circ$  and  $15^\circ$  cue color, and the  $-30^\circ$  and  $0^\circ$  cue color, because these cue colors were on  
 459 mirror locations in the distribution of cueing effects. None of these differences were  
 460 significant,  $ps > .28$ , suggesting that the decrease was symmetrical around the peak.

461 **Choice Errors.** Table 2 reports average error rates. Individual percentage of choice  
 462 errors was submitted to the same ANOVA as above. The main effect of cue validity,  $F(1, 20) =$   
 463  $3.46$ ,  $p = .078$ ,  $\eta_p^2 = .15$ , and the interaction of cue color and cue validity,  $F(4, 80) = 2.49$ ,  $p =$   
 464  $.05$ ,  $\eta_p^2 = .11$ , approached significance, reflecting more choice errors for cue colors deviating  
 465 away from the nontarget color.

466 **Memory Bias.** The mean memory bias is illustrated by the gray disk with horizontal  
 467 error bars overlaid on the distribution of color errors in Figure 2C. By one-sample t-test, the

468 mean bias parameter was  $-17^\circ$  and significantly different from zero,  $t(20) = 8.6$ ,  $p < .001$ ,  
469 Cohen's  $d_z = 1.88$ . The direction and magnitude of the bias were very similar to Experiment 1.

#### 470 **Discussion**

471 Experiment 2 mapped the distribution of cueing effects and showed a symmetrical  
472 decrease of cueing effects around the peak, which was located at approximately  $-15^\circ$ . The  
473 cueing effect returned to baseline on both sides of the distribution (see Table 2 for  $t$ -tests  
474 against zero). Consistent with optimal tuning, both attentional selectivity and the attentional  
475 template were shifted away from the nontarget colors. In contrast, the results are  
476 inconsistent with the idea of saliency-driven capture. Large differences between cue and  
477 nontargets did not result in more attentional capture, even though cue saliency increased in  
478 the combined cue-target display. To substantiate the idea that the pattern of cueing effects  
479 was driven by the biased memory representation of the target, we correlated individual  
480 cueing effects for each cue color with individual shifts of the attentional template. To  
481 increase power, we collapsed across Experiments 1 and 2 and analyzed only the cue colors  
482 that were common to both Experiments. As shown in Figure 3, there was a significant  
483 correlation for the  $-30^\circ$  cue color,  $r(37) = -.44$ ,  $p = .005$ . The remaining correlations were not  
484 significant,  $ps > .22$ , suggesting that large memory biases only promoted cueing effects for  
485 cue colors that deviated strongly away from the nontarget color. Further, the correlation  
486 suggests that our measures of attentional selectivity and attentional template reflect the  
487 same underlying representation.

#### 488 **Experiment 3**

489 To provide further evidence for optimal tuning and to better describe the scope of  
490 the relational account, we manipulated the similarity between target and nontarget colors.  
491 Optimal tuning predicts that the similarity between target and nontargets determines the  
492 shift of the attentional template. When target and nontargets are similar, the attentional  
493 template is shifted away from the nontargets to optimize the signal-to-noise ratio. However,  
494 when target and nontargets are dissimilar, no shift of the attentional template should occur.  
495 The reason is that the overlap in the neural distributions activated by target and nontargets  
496 is reduced, so that a shift of the attentional template is no longer beneficial. Thus, we expect  
497 the asymmetry in the distribution of cueing effects and the shift of the attentional template  
498 to be reduced when the nontargets are more distinct from the target. We measured cueing  
499 effects for the  $-15^\circ$  and  $15^\circ$  cue colors with two different nontarget contexts. The "close"

500 nontarget colors were the same as in the previous Experiments. The "far" nontarget colors  
 501 were 30° further away (see Figure 4).

## 502 **Methods**

503 The methods were as in Experiment 1 with the following exceptions. Only the -15°  
 504 and 15° cue colors were shown. The 64 combinations of 4 cue positions, 4 target positions, 2  
 505 cue colors (-15°, +15°), and 2 responses (left, right) were presented twice in a block of 128  
 506 trials. The nontarget colors changed between blocks. The close nontarget colors were at 40°,  
 507 55°, and 70° from the target and the far nontarget colors were at 70°, 85°, and 100°. Blocks  
 508 with close and far nontargets alternated and the nontarget colors in the first block were  
 509 counterbalanced across participants. Twenty-two new students participated (5 men, age:  $M$   
 510 = 20.4,  $SD = 2$ ) and performed 6 blocks of 128 trials for a total of 768 trials with 48 color  
 511 judgments.

## 512 **Results**

513 The first and second block after initial training served to familiarize participants with  
 514 the two sets of nontarget colors and were not analyzed, reducing the number of available  
 515 trials from 768 to 512 with 32 color judgments.

516 **RTs.** We excluded choice errors (4.6%), late trials (0.2%) and outliers (2.2%) before  
 517 calculating individual means. We conducted a 2 (nontarget colors: close, far) x 2 (cue color: -  
 518 15°, 15°) x 2 (cue validity: valid, invalid) ANOVA on individual mean RTs. The main effects of  
 519 cue validity,  $F(1, 21) = 79.99, p < .001, \eta_p^2 = .79$ , cue color,  $F(1, 21) = 15.19, p = .001, \eta_p^2 =$   
 520  $.42$ , nontarget colors,  $F(1, 21) = 9.22, p = .006, \eta_p^2 = .31$ , as well as the two-way interactions  
 521 of nontarget colors and cue color,  $F(1, 21) = 12.56, p = .002, \eta_p^2 = .37$ , and cue color and  
 522 validity,  $F(1, 21) = 38.31, p < .001, \eta_p^2 = .65$ , were significant. Importantly, all these effects  
 523 were modulated by a significant three-way interaction,  $F(1, 21) = 6.73, p = .017, \eta_p^2 = .24$ . As  
 524 shown in Figure 4, the cueing effect decreased from the -15° to the 15° cue color, but this  
 525 decrease was smaller with far than with close nontarget colors. More precisely, the cueing  
 526 effect decreased from 61 ms to 5 ms with the close nontarget colors, but only from 56 ms to  
 527 24 ms with the far nontarget colors. The reduction of the difference was mainly caused by  
 528 the 15° cue color. That is, the cueing effects were significantly different between close and  
 529 far nontarget colors for the 15° cue color (5 vs. 24 ms),  $t(21) = 3.45, p = .002$ , Cohen's  $d_z =$   
 530  $0.74$ , but not for the -15° cue colors (61 vs. 56 ms),  $p = .511$ .

531 **Choice Errors.** Individual percentages of choice errors were submitted to the same  
 532 ANOVA as above. The main effect of cue validity,  $F(1, 21) = 27.14$ ,  $p < .001$ ,  $\eta_p^2 = .56$ , and the  
 533 interaction of cue color and cue validity,  $F(1, 21) = 9.93$ ,  $p = .005$ ,  $\eta_p^2 = .32$ , reached  
 534 significance. Inspection of Table 3 showed no sign of speed-accuracy tradeoff.

535 **Memory Bias.** The mean memory bias for close and far nontarget colors is illustrated  
 536 by the black and gray symbols, respectively, overlaid on the distribution of color errors in  
 537 Figure 4. The fit was performed on 16 color judgments per condition. By one-sample t-test,  
 538 the mean bias parameter was significantly different from zero with close ( $-14^\circ$ ) and far ( $-12^\circ$ )  
 539 nontarget colors,  $ts(21) > 7.57$ ,  $ps < .001$ , Cohen's  $d_z > 1.61$ . The small difference between far  
 540 and close of  $2^\circ$  was significant,  $t(21) = 2.17$ ,  $p = .042$ , Cohen's  $d_z = 0.46$ , suggesting that the  
 541 memory bias away from the nontarget colors was reduced when the nontarget colors were  
 542 far.

#### 543 Discussion

544 We evaluated effects of target-nontarget similarity by changing the nontarget colors.  
 545 Consistent with optimal tuning, we observed that asymmetric attentional selectivity was  
 546 reduced when the nontarget colors were less similar to the target. According to optimal  
 547 tuning theory, the reduction of the asymmetry reflects that neural populations activated by  
 548 target and nontarget colors were more distinct, which reduced the advantage of shifting the  
 549 attentional template away from the nontarget colors. Further, the experiment shows that  
 550 optimal tuning was adjusted rapidly as the nontarget colors alternated between blocks of  
 551 trials. Finally, there was also a small change in the remembered target color consistent with  
 552 the reduced bias in attentional selectivity. Because of its small size, however, the reduction  
 553 should be interpreted with care. Nonetheless, it is surprising that the remembered target  
 554 color changed at all given that the true target color was invariable across trial blocks.

555 Further, the effect of nontarget color is outside the scope of relational theory  
 556 (Becker, 2010). Changes of the nontarget color concerned the relative hue in the target  
 557 display. In contrast, the saturation of the cue relative to its context was unchanged. Because  
 558 the cue-context relation did not match the target-nontarget relation, relational theory does  
 559 not apply. Further, the relational account describes distractor colors away from the  
 560 nontarget colors as relationally better (Becker et al., 2014). However, the relational account  
 561 does not specify the exact feature distance of “relationally best” distractor colors. It could be  
 562 that all colors exaggerating the target-nontarget relation capture more strongly than the

563 target, but without difference among the exaggerated colors. Results from Experiments 1-3  
564 refute the idea of a uniform increase in capture across all cue colors deviating away from the  
565 nontarget color. Rather, there was a peak of the cueing effects at  $-15^\circ$  (Experiments 1-2) and  
566 a reduction of the cueing effects when the nontarget color was more distinct (Experiment 3).

### 567 **General Discussion**

568 The current research pursued two goals. First, we provide missing behavioral  
569 evidence for changes in attentional selectivity predicted by optimal tuning of attention  
570 (Navalpakkam & Itti, 2007). Previous research confirmed that the memory representation of  
571 the search target (i.e., the attentional template) was biased away from nontarget features  
572 (Geng et al., 2017; Hamblin-Frohman & Becker, 2019; Navalpakkam & Itti, 2007; Scolarì &  
573 Serences, 2009; Yu & Geng, 2019). However, there is little behavioral evidence to suggest  
574 that the shifted attentional template affected attentional selectivity. The current study filled  
575 this gap by showing that cueing effects are asymmetrically distributed around the target  
576 color. In general, cueing effects are large when the cue color corresponds to the target color  
577 and decrease continuously with increasing difference between cue and target colors  
578 (Anderson & Folk, 2010; Ansorge & Becker, 2014; Büsel, Pomper, et al., 2018; Folk &  
579 Remington, 1998; Kerzel, 2019). In the current investigation, we found that the distribution  
580 of cueing effects was not symmetric around the target color but was shifted away from the  
581 nontarget colors. Thus, an important conclusion from the current study is that cueing effects  
582 may not be maximal for cues in the target color, but for target-similar cue colors deviating  
583 away from the nontarget colors. Classical research was based on the assumption that the  
584 attentional template corresponds to the target feature (Folk & Remington, 1998; Folk et al.,  
585 1992), but this assumption holds only true when the target is sufficiently distinct from the  
586 nontarget colors. For instance, the colors red and green used in Folk and Remington (1998)  
587 would correspond to a distance of  $180^\circ$  in CIELAB-space. It is unlikely that nontarget colors  
588 as distinct as  $180^\circ$  in CIELAB-space bias attentional selectivity. However, we show that  
589 distances as large as  $70^\circ$  in CIELAB-space may be sufficient (cf. Experiment 3). Further, we  
590 measured memory for the target color and replicated the bias away from the nontarget  
591 colors. The magnitude of the bias corresponded to the shift in the distribution of cueing  
592 effects. As predicted by optimal tuning, the bias in the memory representation decreased  
593 when the nontarget colors were more distinct from the target color. The reduction was

594 small, which may be due to the alternating trial blocks with close and far nontarget colors.  
595 Manipulating nontarget colors in a between-subject design may yield larger effects.

596 A second goal of the present investigation was to contrast the optimal tuning account  
597 with the relational account proposed by Becker and colleagues (Becker, 2010; Becker et al.,  
598 2013; Becker et al., 2014). The account states that the visual system does not code distractor  
599 and target features in an absolute manner, but relative to the surrounding context. To  
600 account for larger oculomotor capture by target-similar colors deviating away from the  
601 nontargets, Becker et al. (2014) suggested that these colors were "relationally better". The  
602 notion that exaggerated feature relations attract attention more strongly makes similar  
603 predictions as the optimal tuning account. To disentangle the two accounts, we presented  
604 the distracting cue color with gray context elements and the target color with colored  
605 nontargets. Thus, the cue-context relation was entirely different from the target-nontarget  
606 relation. That is, the cue was more colorful than the gray cue context whereas target and  
607 nontargets were both colored but differed in hue. Because the relative cue feature did not  
608 match the relative target feature, the relational account does not apply. In contrast, the  
609 optimal tuning account refers to absolute feature values and does not depend on feature  
610 relations. Therefore, our results can be easily accommodated by optimal tuning, but are  
611 outside the scope of the relational account. Also, it is unclear how the relational account  
612 would handle the effects of decreased target-nontarget similarity in Experiment 3. The  
613 decrease of target-nontarget similarity did not change the direction of the difference  
614 between target and nontarget colors in CIELAB-space but changed the feature distance.  
615 Optimal tuning nicely accommodates the smaller attentional asymmetry with a larger  
616 feature distance by stating that the reduced overlap in neural activations obliterates the  
617 need to shift the attentional template away from the nontargets. In contrast, the relational  
618 account does not consider distances in feature space as much as directions, but the two  
619 components are necessary to account for the present data.

### 620 **Previous failures to provide evidence for optimal tuning**

621 The results of the present research contrast with those of a previous study by Scolari  
622 and Serences (2009). However, target and nontarget features in Scolari and Serences (2009)  
623 were similar to the point where the accuracy of target localization was never better than  
624 60%. If the current sign conventions are adopted (which are opposite to Scolari and  
625 Serences, 2009), the nontarget orientation in Scolari and Serences (2009) was at +5° relative

626 to the target at 0°. Consistent with the current study, contrast thresholds improved for  
627 relative orientations of -10° or -20° (their Figure 4C), which deviated away from the  
628 nontarget. However, there was also improvement for the nontarget orientation and an  
629 orientation deviating in the same direction as the nontargets, but more strongly (i.e., +10°).  
630 The bilateral improvement suggested off-channel gain to Scolari and Serences (2009; see  
631 also Scolari & Serences, 2010), but was considered incompatible with optimal tuning.  
632 Because target and nontargets were more distinct in the current study, it is difficult to  
633 compare the present results to those of Scolari and Serences (2009). In a more comparable  
634 study, the nontargets would be at +5° in CIELAB-space (as for instance in Yu & Geng, 2019)  
635 so that colors away from the nontarget (-15°, -30°, and -45°) and beyond the nontarget  
636 (+15°, +30°, +45°) could be investigated. It seems likely that the peak of the cueing effects  
637 would be biased away from the nontarget color, similar to the current study (i.e., at -15°).  
638 However, it seems unlikely that another peak of cueing effects would be observed beyond  
639 the nontarget color (i.e., at +30°). The reason is that cueing effects decrease rapidly with  
640 increasing distance between cue color and attentional template (see also Kerzel, 2019). In  
641 the current study, the memory representation of the target was at -18° so that cue colors at  
642 +15° already resulted in close-to-zero cueing effects, which makes it unlikely that another  
643 peak would occur at even larger distances (i.e., +30° or beyond). However, a definitive  
644 answer would require new experiments with a fine color discrimination task.

645 Other differences between the current study and Scolari and Serences (2009)  
646 complicate a comparison. Scolari and Serences (2009) used a difficult orientation search  
647 where accuracy was the primary dependent variable. In contrast, we used a relatively easy  
648 color search where RT was the primary dependent variable. In some previous studies, it was  
649 noted that involuntary effects of attention were easier to observe in RT than in accuracy  
650 measures (Kerzel, Zarian, & Souto, 2009; Prinzmetal, McCool, & Park, 2005). Further, target  
651 and nontargets were fixed in the current experiments, whereas they changed from trial to  
652 trial in Scolari and Serences (2009). However, previous research has demonstrated that  
653 electrophysiological and behavioral measures of attentional selectivity did not change  
654 between fixed and variable targets (Grubert, Carlisle, & Eimer, 2016; Kerzel & Witzel, 2019).  
655 Therefore, we believe that this methodological difference is unlikely to contribute to the  
656 different results.

**657 Precision of attention and memory**

658           In a previous publication, Kerzel (2019) demonstrated in a very similar experimental  
659 paradigm that the precision of attentional selectivity was far worse than the precision of the  
660 underlying memory representation. The previous publication focused on the variability of  
661 memory judgments and the width of the distribution of cueing effects with carefully  
662 balanced nontarget stimuli in the target display. In contrast, the current study had biased  
663 nontarget stimuli to examine shifts of attentional selectivity. Nonetheless, it is interesting to  
664 evaluate the precision of memory and attention in the present study. In Experiments 1 and  
665 2, the average *SD* of color judgments was 9° after removing outliers (i.e., color judgments  
666 deviating by more than 2.5 *SD*). The mean error of the color judgments was -18°, collapsed  
667 across Experiments 1 and 2. To evaluate how likely it was that participants confounded one  
668 of the cue colors with the remembered target color, it is revealing to express the distance  
669 between remembered target color and cue color in terms of the standard deviation of the  
670 memory error. According to this calculation, the 0° cue color was 2 *SD* distant from the  
671 remembered target color and the -30° cue color was 1.3 *SD* distant. Thus, it was rather  
672 unlikely that participants confused the 0° or -30° cue colors with the remembered target  
673 color. However, there was substantial attentional capture by these cue colors (see Tables 1  
674 and 2). Thus, colors that participants were able to reject as different from the target color in  
675 their memory judgments nonetheless captured their attention, confirming the earlier  
676 conclusion that attentional selectivity is far worse than the precision of the underlying  
677 memory representation.

678           In light of the low precision of attentional selectivity, it may be understandable that  
679 relatively distinct nontarget colors resulted in a shift of the attentional template. The closest  
680 nontarget color in Experiments 1 and 2 was at 40° from the target color. This color  
681 difference is highly discriminable from the target color, given that the *SD* of memory errors  
682 was only 9° and a color category in CIELAB-space can be as small as 36° (estimated from  
683 Figure 7 in Bae et al., 2015). The high discriminability is also visible in the low error rates of  
684 less than 5%. It would be interesting to know how much the neural populations representing  
685 target and nontarget stimuli overlapped for colors this far apart. It seems safe to conclude  
686 that the overlap was less than in the experiments by Navalpakkam and Itti (2007) where task  
687 difficulty was much higher. Despite the much smaller overlap, we found evidence in line with  
688 optimal tuning. Possibly, attentional tuning to color is less precise than attentional tuning to



689 orientation, so that effects of optimal tuning are present even with large perceptual  
690 differences, whereas they would be absent for orientation, where attentional tuning is  
691 better. Future research should study the relation between perceptual precision and  
692 attentional selectivity in more detail.

### 693 **Same location costs**

694 Finally, it is interesting to note that the current set of experiments yielded either  
695 positive or no cueing effects, but no negative cueing effects. Negative cueing effects are  
696 often referred to as same location costs and correspond to worse performance at cued  
697 compared to uncued locations. In previous research, same location costs were observed  
698 when the search display was heterogeneous and search for a particular feature was required  
699 (Carmel & Lamy, 2014; Kerzel, 2019; Lamy, Leber, & Egeth, 2004; Schoeberl, Ditye, &  
700 Ansoerge, 2018). In the current experiments, the search displays were somewhat  
701 heterogeneous, but the variability in color was moderate compared to previous studies.  
702 Nontargets in the current study were 15° to 30° apart (i.e., nontarget colors were 40°, 55,  
703 70° or 70°, 85°, 100°), whereas nontargets in previous studies varied by (estimated) 90° to  
704 180° (Carmel & Lamy, 2014; Kerzel, 2019; Lamy et al., 2004). Besides the more  
705 homogeneous nontarget colors, it may be that the cue colors were not sufficiently dissimilar  
706 from the target color to yield same-location costs. In a search task of comparable difficulty,  
707 Kerzel (2019) observed same locations costs with cue colors of 60°, whereas the maximal cue  
708 color was 45° in the current experiments. Thus, it is possible that same location costs  
709 emerge with more dissimilar cue colors or with a more heterogeneous target context.

710 In sum, we provide direct evidence for the optimal tuning of attention. Attentional  
711 capture was larger for target-similar cues that exaggerated the difference to the nontargets,  
712 suggesting that attentional selectivity was biased away from the nontargets. Replicating  
713 previous research, we found the memory representation of the target to be biased in the  
714 same direction. The current results cannot be accommodated by the relational account of  
715 attentional capture and provide solid support for optimal tuning.

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- 906

907 **Table 1.** Reaction times (ms) and choice errors (%) as a function of cue color and cue validity  
 908 in Experiment 1. The cueing effect (CE) is the difference between invalid and valid cue  
 909 conditions. The standard error of the mean (SEM) is indicated in parenthesis. Cueing effects  
 910 were significant if the *p*-value of the respective one-sample t-test was smaller than .01  
 911 (Bonferroni correction for five tests). Significant cueing effects are marked by an asterisk.  
 912

Cue Color	Reaction Times (ms)			Choice Errors (%)		
	invalid	valid	CE (SEM)	invalid	valid	CE (SEM)
-30°	552	492	60* (8)	5.7	1.3	4.4* (0.8)
-15°	553	477	76* (6)	5.1	2.5	2.6* (0.9)
0°	544	487	57* (6)	4.7	2.1	2.6* (0.6)
+15°	532	516	16 (8)	3.9	3.6	0.3 (0.7)
+30°	529	526	3 (4)	3.8	4	-0.2 (0.7)

913

914



915 **Table 2.** Reaction times (ms) and choice errors (%) as a function of cue color and cue validity  
 916 in Experiment 2. The cueing effect (CE) is the difference between invalid and valid cue  
 917 conditions. The standard error of the mean (SEM) is indicated in parenthesis. Cueing effects  
 918 were significant if the *p*-value of the respective one-sample t-test was smaller than .01  
 919 (Bonferroni correction for five tests). Significant cueing effects are marked by an asterisk.  
 920

Cue Color	Reaction Times (ms)			Choice Errors (%)		
	invalid	valid	CE (SEM)	invalid	valid	CE (SEM)
-45°	519	511	8 (9)	3.8	4.2	-0.3 (0.8)
-30°	526	489	37* (7)	5.1	2.5	2.6* (0.8)
-15°	526	464	63* (5)	4.2	3.7	0.5 (0.8)
0°	522	478	44* (6)	4.2	3	1.3 (0.8)
+15°	514	501	14 (7)	3.9	3.9	0.0 (0.8)

921

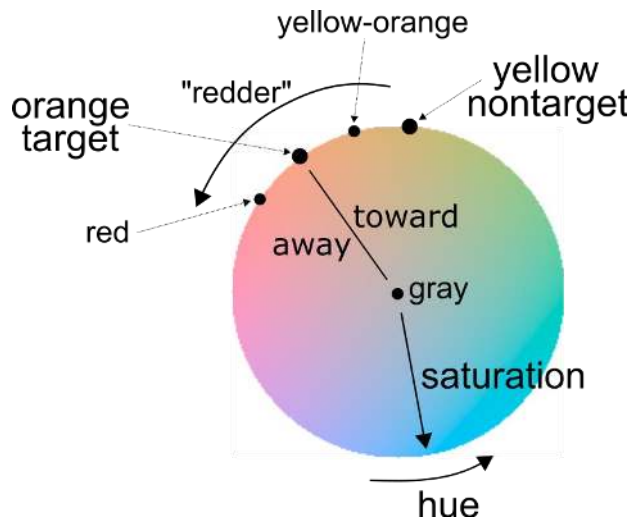
922

923 **Table 3.** Reaction times (ms) and choice errors (%) as a function of cue color and cue validity  
 924 in Experiment 3. The cueing effect (CE) is the difference between invalid and valid cue  
 925 conditions. The standard error of the mean (SEM) is indicated in parenthesis. Cueing effects  
 926 were significant if the  $p$ -value of the respective one-sample t-test was smaller than .01  
 927 (Bonferroni correction for five tests). Significant cueing effects are marked by an asterisk.  
 928

context	Cue Color	Reaction Times (ms)			Choice Errors (%)		
		invalid	valid	CE (SEM)	invalid	valid	CE (SEM)
close	-15°	512	451	61* (2)	6.9	2.7	4.1* (0.8)
	+15°	500	495	5 (8)	5.6	4.6	1 (0.8)
far	-15°	505	449	56* (6)	6.6	1.7	4.9* (0.9)
	+15°	490	466	24* (6)	5.6	3	2.6 (1)

929

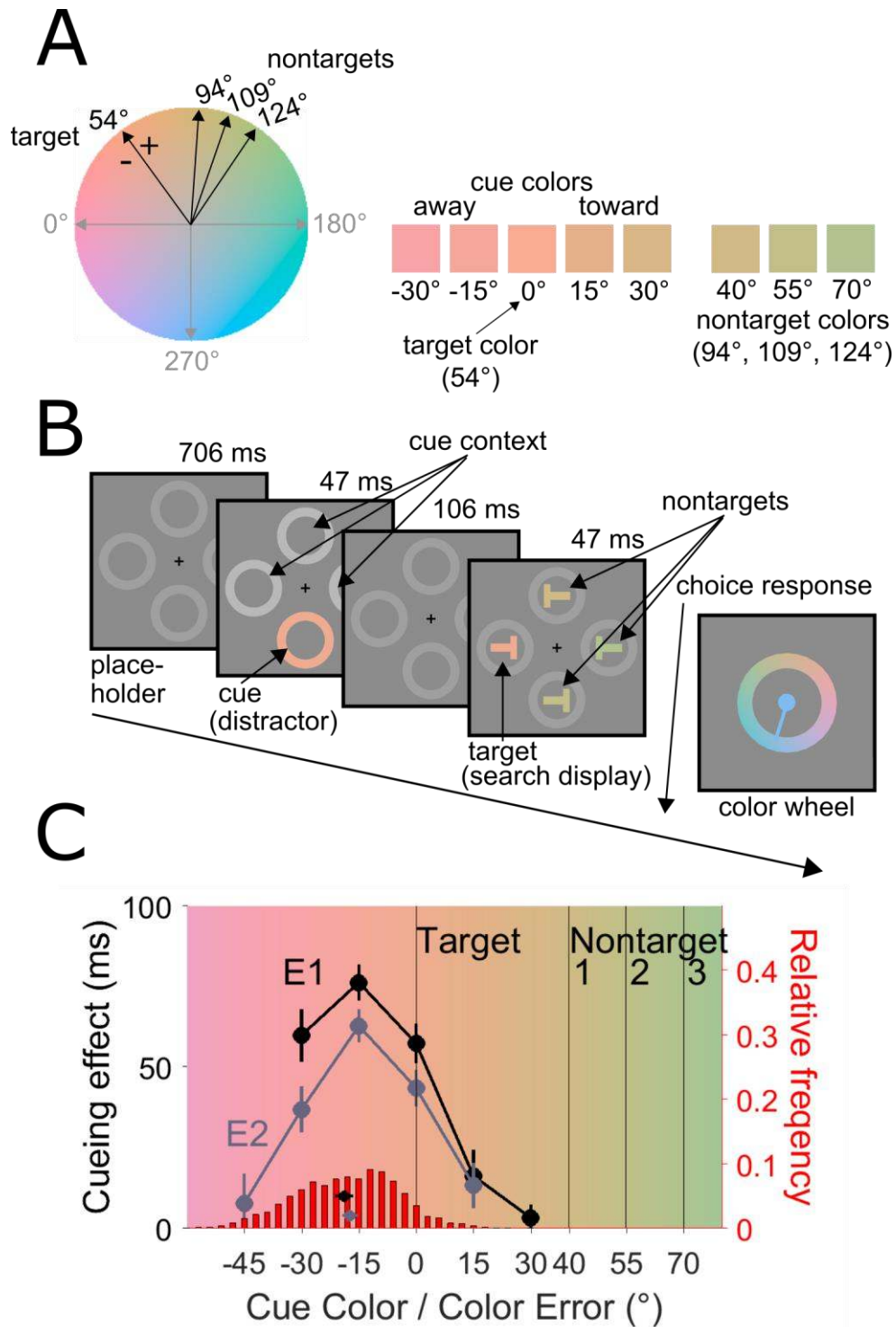
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932

933 **Figure 1.** Illustration of a plane in CIELAB-space. Colors are isoluminant but vary in hue and  
 934 saturation. Colors increase in saturation from the gray center to the outside. The saturation  
 935 is equal for colors at equal radius. Changes in hue correspond to a rotation around gray. The  
 936 figure shows the coordinates of an orange target with yellow nontargets. Orange in a yellow  
 937 context is seen as "redder", but neighboring colors share this relation. Yellow-orange is also  
 938 perceived as "redder" than yellow, but less so than orange because it deviates toward the  
 939 nontarget color. In contrast, "red" is also perceived as redder, but exaggerates the target-  
 940 nontarget relation because it deviates away from the nontarget color. Color names only  
 941 approximate perceived color categories in CIELAB-space.

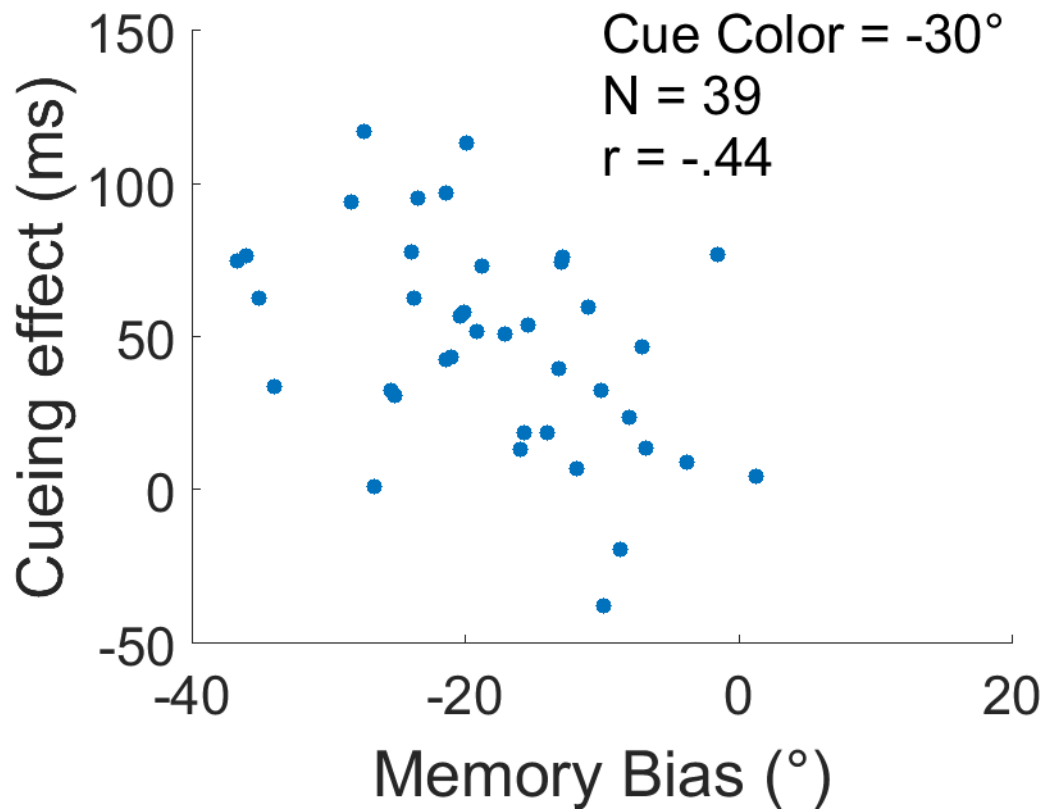


942

943

944 **Figure 2.** Illustration of experimental stimuli (not drawn to scale) and results from  
 945 Experiments 1 and 2. **Panel A** shows the relation between cue, target and nontarget colors.  
 946 Orange (54°) is a standard example in the literature but was not shown in the experiments.  
 947 Positive color differences indicate a deviation from the target color in the direction of the  
 948 nontarget colors and negative differences indicate a deviation away from the nontarget

949 colors. **Panel B** shows the sequence of events. Participants discriminated the orientation of  
950 the rotated T in the target color by mouse click. They were instructed to ignore the cue  
951 display. The cue is also referred to as distractor. On some trials, a color wheel appeared, and  
952 participants judged the target color. The placeholders were outline rings in the actual  
953 experiments but filled rings are shown for clarity. **Panel C** shows the cueing effect (invalid  
954 minus valid condition) in reaction times as a function of cue color. Error bars show the  
955 between-subject standard error of the mean. Data from Experiments 1 and 2 are shown in  
956 black and gray, respectively. The relative frequency of color errors, collapsed across  
957 Experiments 1 and 2, is indicated by the red bars, which refer to the axis on the right. The  
958 estimated memory bias is shown separately for Experiments 1 and 2 by the disks overlaid on  
959 the red bars.  
960

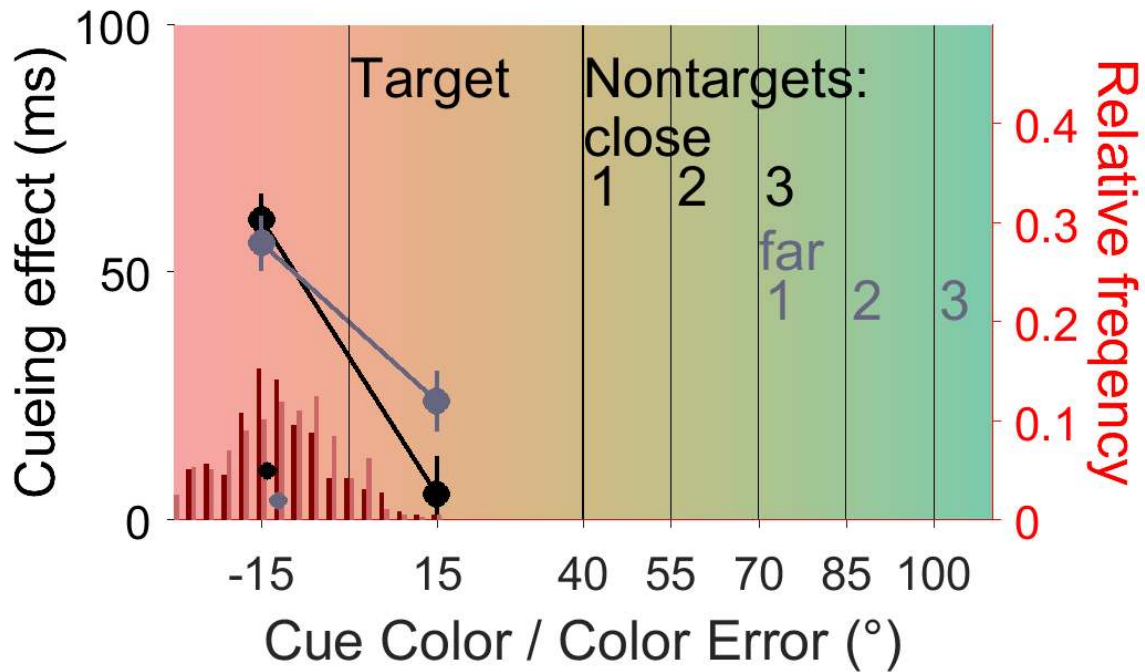


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963 **Figure 3.** Correlation between the individual cueing effects for the  $-30^\circ$  cue color and  
964 individual memory biases. Data were collapsed across Experiments 1 and 2.

965



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967

968 **Figure 4.** Results from Experiment 3. The cueing effects for cue colors of  $-15^\circ$  and  $15^\circ$  are  
 969 shown as a function of nontarget color. Data from the condition with close nontarget colors  
 970 ( $40^\circ$ ,  $55^\circ$ , and  $70^\circ$ ) are shown in black and data from the condition with far nontarget colors  
 971 ( $70^\circ$ ,  $85^\circ$ , and  $100^\circ$ ) are shown in gray. The distribution of color errors for the close and far  
 972 nontargets is shown by the dark and light bars, respectively. The center of the distribution of  
 973 color errors, as indicated by the mixture model, is shown by the disks overlaid on the bars.

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