Direct Evidence for the Optimal Tuning of Attention

Dirk Kerzel
University of Geneva

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.

Public Significance Statement
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 human observers solve the task may be relevant for applied sciences, such as computer vision.

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

---

In visual search tasks, observers compare the sensory input to a stored representation of the target. Stimuli matching the stored representation are selected for further processing. The collection of features describing the target is referred to as *attentional template* (Bundesen, 1990; Carlisle, Arita, Pardo, & Woodman, 2011; Duncan & Humphreys, 1989; Geng & Witkowski, 2019; Hout & Goldinger, 2015; Liesefeld & Müller, 2020; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Schneider, 2013). The attentional template can be biased by requirements of the search task. For instance, Navalpakkam and Itti (2007) asked observers to search for a target line tilted by 55° among nontarget lines tilted by 50°,

which requires a fine perceptual discrimination. Subsequently, the attentional template underlying the search task was probed by asking observers to find the target line in an array of tilted lines. The results showed that observers most frequently selected an orientation of 60° instead of the true target orientation of 55°, which means that the attentional template was biased by 5° away from the nontargets. Navalpakkam and Itti (2007) argued that shifting the attentional template away from the nontarget feature facilitated search because the signal-to-noise ratio was increased. When target-nontarget similarity is high, similar neural populations are activated by target and nontarget features, resulting in a low signal-to-noise ratio. Shifting the attentional template away from the nontarget feature avoids activation from neural populations responding to the nontarget feature and increases the signal-to-noise ratio. Recent research confirmed shifts of the attentional template and additionally investigated its precision. Geng, DiQuattro, and Helm (2017) found that the precision of the attentional template increased with the frequency of target-similar nontargets. In addition, Yu and Geng (2019) demonstrated that the sharpening was asymmetrical with a

---

Correspondence concerning this article should be addressed to Dirk Kerzel, Department of Psychology, University of Geneva, 40 Boulevard du Pont d'Arve, 1205 Geneva, Switzerland. E-mail: dirk.kerzel@unige.ch

better precision of the attentional template for feature values intermediate between target and nontargets.

No Behavioral Evidence for Optimal Tuning of Attentional Selectivity

While the shift of the attentional template away from nontarget features is a robust finding, there is surprisingly little evidence for a modulation of attentional selectivity by the shift. Typically, it is assumed that voluntary attention is directed at stimuli matching the attentional template, which results in perceptual enhancement of the attended stimuli. For instance, attention may increase the activation of neurons tuned to the target features ("attentional gain," e.g., Reynolds & Chelazzi, 2004), improve perceptual sensitivity for the attended stimuli (e.g., Carrasco, 2011), or reduce reaction times (RTs) to the attended stimuli (e.g., Folk, Remington, & Johnston, 1992). Optimal tuning predicts that perceptual enhancement occurs for target-similar features deviating away from the nontargets. To test this prediction, Scolari and Serences (2009) used a difficult orientation discrimination task similar to Navalpakkam and Itti (2007). The orientation discrimination task was run on most of the trials and required participants to report the location of a target grating deviating by 5° from three nontarget gratings. The orientation of the nontarget gratings and the relative target orientation (i.e., 5° clockwise relative to the nontarget orientation) were cued before onset of the search display. Performance on the search task was never better than 60%, confirming that a fine perceptual discrimination was necessary. The orientation discrimination task was interleaved with attentional probe trials. In Experiment 1, the attentional probe trials consisted of a display with four gratings at various orientations. Participants were asked to select the grating with the cued target orientation. Similar to the results by Navalpakkam and Itti (2007), choices were biased toward gratings with orientations that exaggerated the difference between target and nontargets. In Experiment 2, the attentional probe trials measured perceptual sensitivity to target, nontarget, and surrounding orientations. A single low-contrast Gabor was presented at one of the four locations and participants were asked to indicate its location. The orientation of the low-contrast Gabor was 0°, ±5°, ±10°, ±20°, or ±40° relative to the target orientation. It should be noted that orientations intermediate between target and nontarget were not tested, as target and nontargets were separated by only 5°. A threshold procedure determined the contrast necessary to achieve 75% correct responses at each relative probe orientation. It was expected that thresholds for target-similar orientations deviating away from the nontarget orientation would be enhanced. However, the pattern of results did not support optimal tuning. Instead of the expected one-sided improvement for orientations deviating away from the nontarget orientation, there was improvement on both sides at relative orientations of 10° or 20° (see Figure 4C in Scolari & Serences, 2009). Thus, the shift of the attentional template (Experiment 1) was not accompanied by a corresponding unilateral improvement of perceptual sensitivity (Experiment 2). Rather, the results suggest that attention was tuned bilaterally to off-target orientations. In line with the enhancement on both sides of the target orientation, fMRI recordings of orientation-selective voxels in V1 showed bilateral gain (Scolari & Serences, 2010). However, another study showed unilateral gain for orientations away from both target and distractor, in line with

optimal tuning of attention (Scolari, Byers, & Serences, 2012). The different outcomes of the two fMRI studies may result from different methods, such as differences in task difficulty or the order of stimulus presentation (sequential vs. simultaneous).

It should be noted that the task in Scolari and Serences (2009) and Navalpakkam and Itti (2007) required a fine perceptual discrimination where the target feature was highly similar to the nontarget feature. In contrast, search performance in experiments by Geng and collaborators (Geng et al., 2017; Yu & Geng, 2019) on the shape of the attentional template was much better, with accuracy typically above 90% and chance being at 50% or 25%. In addition, Geng's work focused on color and not orientation. However, similar to behavioral research on orientation discrimination, there was little evidence that attentional selectivity was influenced by the shift of the attentional template. For instance, Geng et al. (2017) demonstrated that it became easier to discriminate the target color when similar nontarget colors were more frequent, but their data do not provide evidence for asymmetric attentional selectivity. The data only confirm that attentional selectivity improved when similar nontarget colors were more frequent, consistent with the observed sharpening of the attentional template. In a similar vein, it has been shown that memory performance for search targets is more precise than for other content of VWM (Rajsic, Ouslis, Wilson, & Pratt, 2017; Rajsic & Woodman, 2020).

A Competing Theory: The Relational Account of Attentional Control

In sum, there is little behavioral evidence for optimal tuning of attentional selectivity, which is at odds with the many studies confirming shifts of the attentional template. Further, results consistent with optimal tuning were interpreted as evidence for another theory of attentional control. In Becker, Harris, Venini, and Retell (2014), participants were asked to saccade to a unique color in a square array of four disks around central fixation. Simultaneous with the onset of the disks, a distractor was shown in one of two response-irrelevant locations. In this situation, first saccades land frequently on the distractor when its color is similar to the target color (Becker, Ansorge, & Horstmann, 2009; Born & Kerzel, 2011; Ludwig & Gilchrist, 2002; Mulckhuyse, van Zoest, & Theeuwes, 2008). Building on this effect, Becker et al. (2014) systematically manipulated the deviation of the distractor color from the target color. The distractor color was either equal to the target color, or it deviated toward or away from the nontarget color. For example, if participants were looking for an orange target among yellow nontargets, then red distractors deviate away from the nontarget color, whereas yellow-orange distractors deviate toward the nontarget color (see Figure 1). However, all colors share the same relation with respect to the nontargets as they are all "redder." Becker et al. (2014) observed stronger oculomotor capture by distractor colors deviating away from the nontarget color than for colors deviating toward the nontarget color. The asymmetric distribution of oculomotor capture supports optimal tuning theory because attentional selectivity was biased away from nontargets, presumably to increase the signal-to-noise ratio.

However, Becker et al. (2014) interpreted their results in terms of the relational account of attentional control, which claims that attention is guided by relative, not absolute features (Becker, 2010). The relational account predicts that distractors sharing the
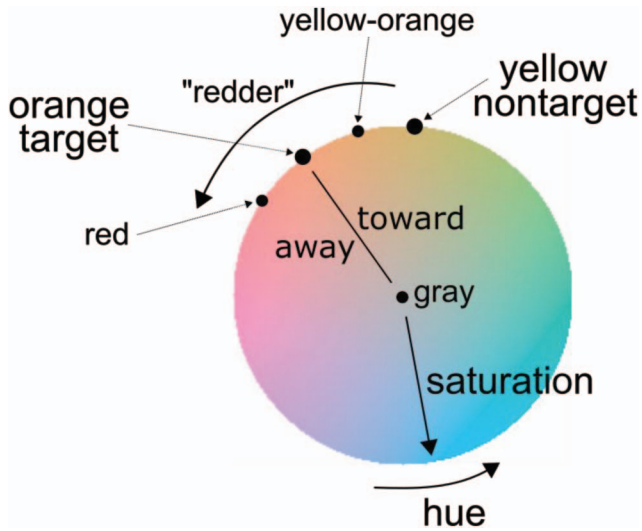
Figure 1. Illustration of a plane in CIELAB-space. Colors are isolumi-nant but vary in hue and saturation. Colors increase in saturation from the gray center to the outside. The saturation is equal for colors at equal radius. Changes in hue correspond to a rotation around gray. The figure shows the coordinates of an orange target with yellow nontargets. Orange in a yellow context is seen as "redder," but neighboring colors share this relation. Yellow-orange is also perceived as "redder" than yellow, but less so than orange because it deviates toward the nontarget color. In contrast, "red" is also perceived as redder, but exaggerates the target–nontarget relation because it deviates away from the nontarget color. Color names only approximate perceived color categories in CIELAB-space. See the online article for the color version of this figure.

target's feature relation to the context will capture attention even if the absolute features are different. For instance, during search for an orange target among yellow nontargets, a red distractor in an orange context would capture attention because the distractor has the same feature relation to the context ("redder," see Figure 1). In contrast, feature-based accounts (e.g., Treue & Martínez Trujillo, 1999) would not predict capture because the absolute target feature differs from the distractor (i.e., the target is orange but the distrac-tor is red). Many experiments using the spatial cueing paradigm by Folk et al. (1992; see below) suggest that cueing effects are robust to changes of the absolute feature values when feature relations are preserved (Becker, 2010; Becker, Folk, & Remington, 2013; Har-ris, Remington, & Becker, 2013; Meeter & Olivers, 2014; Schön-hammer, Becker, & Kerzel, 2017; Schönhammer, Grubert, Kerzel, & Becker, 2016). To account for the asymmetrical oculomotor capture detailed above, Becker et al. (2014) proposed that distrac-tor colors deviating away from the nontargets were "relationally better" than the target, presumably because the distractor colors exaggerated the target–nontarget relation.

In sum, psychophysical experiments testing optimal tuning of attentional selectivity with contrast thresholds provided results conflicting with optimal tuning of attentional selectivity (Scolari & Serences, 2009), but brain imaging results were consistent with optimal tuning (Scolari et al., 2012). Other psychophysical exper-iments using saccadic responses provided evidence in favor of optimal tuning of attentional selectivity, but were used to support an alternative theory (Becker et al., 2014). Thus, behavioral evi-

dence in favor of the optimal tuning of attentional selectivity is scarce. In striking contrast, there is robust evidence for a shift of the memory representation consistent with optimal tuning (Geng et al., 2017; Navalpakkam & Itti, 2007; Scolari & Serences, 2009; Yu & Geng, 2019).

New Evidence From Spatial Cueing

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

Typically, RTs in spatial cueing paradigms are shorter when the cue appears at the same location as the target than when it appears at a different location. However, cueing effects on RTs decrease with increasing color difference between cue and target (Anderson & Folk, 2010; Ansorge & Becker, 2014; Büsel, Pomper, & An-sorge, 2019; Folk & Remington, 1998; Kerzel, 2019). The mod-ulation of cueing effects by cue–target similarity shows that only cues matching the attentional template capture attention. For in-stance, when observers searched for a red target, red cues resulted in cueing effects, whereas green targets did not (Folk & Reming-ton, 1998; Harris, Jacoby, Remington, Travis, & Mattingley, 2019), showing that only colors matching the attentional template for red captured attention.

Spatial cueing effects contingent on the match between features of the cue and the attentional template are thought to be related to feature-based attention (Leonard, Balestreri, & Luck, 2015; Sto-thart, Simons, Boot, & Wright, 2019). In neural measures, feature-based attention is associated with an increased response to the attended feature even at unattended locations (Andersen, Hillyard, & Müller, 2008; Saenz, Buracas, & Boynton, 2002; Treue & Martínez Trujillo, 1999; Zhang & Luck, 2009; but see Moher, Lakshmanan, Egeth, & Ewen, 2014). In behavioral measures, feature-based attention may facilitate performance when partici-pants divide attention across two stimuli sharing the same feature (Sàenz, Buracàs, & Boynton, 2003) or it allows for the spread of adaptation effects to unattended locations (Liu & Mance, 2011). In the context of contingent spatial cueing effects, the idea is that feature-based attention guides attention to the location of the cue, where spatial attention is deployed (Eimer, 2014; Wolfe, Cave, & Franzel, 1989).

Shared and Conflicting Predictions of Optimal Tuning and the Relational Account

Optimal tuning theory suggests that the feature guiding attention is biased away from the nontarget feature when the nontargets are similar to the target. Therefore, target-similar features deviating away from the nontarget colors are expected to produce larger cueing effects than target-similar features deviating toward the nontarget colors. However, regardless of the direction of the de-

viation, cueing effects should be absent for cue colors deviating strongly from the target color (Folk & Remington, 1998; Harris et al., 2019).

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

Experiment 1

We employed the spatial cueing paradigm developed by Folk et al. (1992) to test whether cueing effects are stronger for target-similar cue colors deviating away from the nontarget colors compared to target-similar cue colors deviating toward the nontarget colors (see Figure 2A). The colors of the nontargets were selected to be similar to the target, but sufficiently different to allow for better than 90% accuracy in the search task. Thus, the task was easy relative to previous experiments on orientation discrimination (Navalpakkam & Itti, 2007; Scolari & Serences, 2009). In fact, target and nontarget colors were sufficiently distinct to allow for the investigation of intermediate color values. The cue was spatially nonpredictive of the target location and preceded the target by about 150 ms (see Figure 2B). The sequence of cue and target presentation did not exceed 200 ms to prevent eye movements. The cue was presented among gray context elements of the same luminance. Therefore, the cue color was not perceived relative to the nontarget colors, which eliminates relational coding. Colors were drawn from CIELAB-space because distances in CIELAB-space reflect perceived color differences (Fairchild, 2005; Witzel & Gegenfurtner, 2015, 2018). To replicate the shift of the attentional template away from nontarget colors reported previously (Geng et al., 2017; Hamblin-Frohman & Becker, 2019; Yu & Geng, 2019), we interspersed trials in which observers were asked to indicate the color of the target on a color wheel. The target color did not change for a given participant. We expect the remembered color to deviate away from the nontarget colors.

Method

Participants. In a previous study, we found cueing effects to decrease with decreasing similarity between target and cue (Kerzel, 2019). We were particularly interested in the difference be-
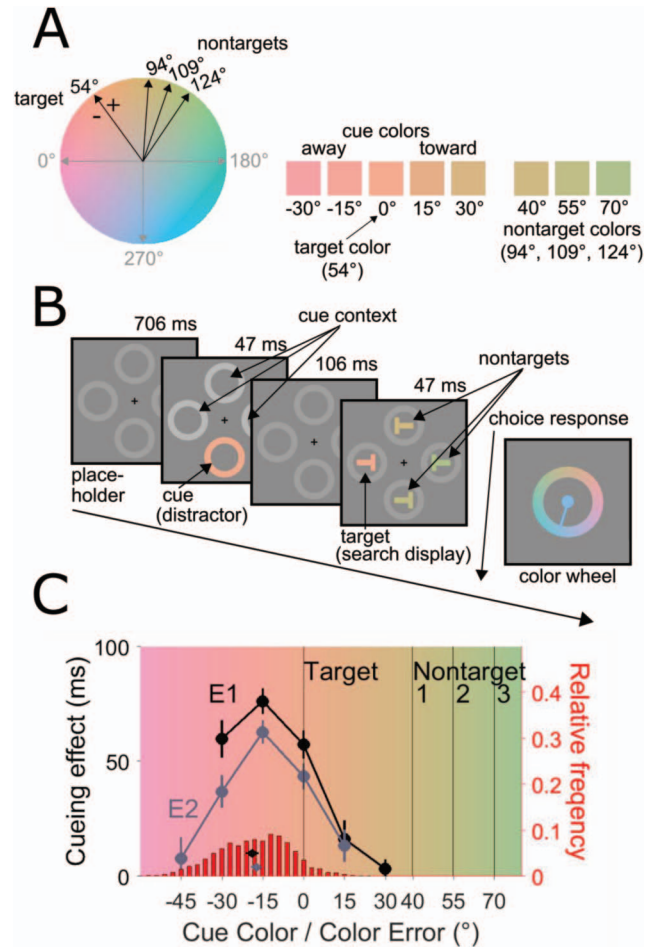

Figure 2. Illustration of experimental stimuli (not drawn to scale) and results from Experiments 1 and 2. Panel A shows the relation between cue, target, and nontarget colors. Orange (54°) is a standard example in the literature but was not shown in the experiments. Positive color differences indicate a deviation from the target color in the direction of the nontarget colors and negative differences indicate a deviation away from the nontarget colors. Panel B shows the sequence of events. Participants discriminated the orientation of the rotated *T* in the target color by mouse click. They were instructed to ignore the cue display. The cue is also referred to as distractor. On some trials, a color wheel appeared, and participants judged the target color. The placeholders were outline rings in the actual experiments but filled rings are shown for clarity. Panel C shows the cueing effect (invalid minus valid condition) in RTs as a function of cue color. Error bars show the between-subjects standard error of the mean. Data from Experiments 1 and 2 are shown in black and light gray, respectively. The relative frequency of color errors, collapsed across Experiments 1 and 2, is indicated by the red (dark gray) bars, which refer to the axis on the right. The estimated memory bias is shown separately for Experiments 1 and 2 by the disks overlaid on the red (dark gray) bars. See the online article for the color version of this figure.

tween cueing effects with a color identical to the target and a color separated by 15° in CIELAB-space. For difficult feature search, the previous study indicated a Cohen's d_z of 0.77, which requires 12 participants with a Type I error probability of .05 and a power of .8. Because we think that even smaller effect sizes are theoret-

ically important, we aimed for a sample size of 22, which would allow us to find significant results with Cohen's d_z as small as 0.55. We collected data from 22 participants but had to eliminate four data sets. Two data sets were eliminated because the assigned target color made the search task too difficult (see below), one participant did not complete the experiment, and another participant was removed because of a high error rate (21%) compared to the remaining participants ($M = 4\%$, $SD = 2\%$). Thus, the final sample size was 18 (2 male, age: $M = 21.8$ years, $SD = 5.2$).

First-year psychology students participated for class credit. All reported normal or corrected-to-normal vision. The study was approved by the ethics committee of the Faculty of Psychology and Educational Sciences and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was given before the experiment started.

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

Stimuli. There was a placeholder, a cue, and a target display for the reaction time (RT) task and a display with a color wheel for the color judgment. The placeholder display was composed of four outline rings, drawn in light gray. The distance from the center of the fixation cross to the center of the outline rings was 3°. The inner and outer borders of the outline rings had a radius of 1.1° and 1.4°, respectively. The linewidth of the borders was 1 pixel or 0.03°. In the cue display, the outline rings were filled. Three rings were filled with the same light gray as the circles and one ring with a color. The colored ring was the cue. In the target display, a T rotated by 90° clockwise or counterclockwise was shown in each placeholder. The bars making up the rotated T were 1° long and 0.3° thick. All four rotated Ts were colored. In each display, two Ts were rotated clockwise and two counterclockwise. A central fixation cross (0.6° diameter) was shown throughout.

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

The hue of the target was fixed for each participant and counterbalanced across participants. The hue of the cue was selected randomly among deviations of 0°, ±15° and ±30° from the target color. The hues of the three nontargets were the same on each trial and deviated by 40°, 55°, and 70° from the target hue. In the context of the present study, "color" is synonymous with "hue" because neither saturation nor lightness varied.

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

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

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

Procedure. A trial started with the presentation of the placeholder display for 706 ms. Then, the cue display was shown for 47 ms, followed by the placeholder display for 106 ms and the target display for 47 ms. The resulting cue–target stimulus onset asynchrony (SOA) was 153 ms. After target offset, the placeholder display remained visible until a response was registered.

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

On trials with a color judgment, the color wheel was preceded by a 1.5-s message saying that the color of the target had to be indicated and that responses should be as precise as possible. Participants were informed that the target color was always the same. Participants confirmed their color judgments with a mouse click. The individual median RT for the mouse click was between

2,719 and 7,324 ms (M = 4,225 ms) from the onset of the color wheel. After the click, the static color wheel remained on the screen for another 300 ms before a blank screen was shown for 500 ms.

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

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

Results

Cues presented at the target location are referred to as valid cues, whereas cues presented at a nontarget location are referred to as invalid cues. Mean RTs and error rates as a function of cue validity and cue color are shown in Table 1. We subtracted performance on valid trials from performance on invalid trials to obtain cueing effects. Average cueing effects are shown in Table 1 and Figure 2C. In addition, Table 1 shows the significance of one-sample t tests against zero for each cueing effect. Further, we calculated the color error as the difference between true and judged target color. The red (dark gray) bars in Figure 2C show the distribution of color errors in 3° bins. Because there were no differences between Experiments 1 and 2, the distribution in Figure 2C shows the combined data. The data from all experiments are available in the open science framework at: https://osf.io/6jeax/?view_only=88951708ce254b139d7f884a897624d3.

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

We conducted a 4 (cue color relative to target color: difference of −30°, −15°, 0°, 15°, and 30°) × 2 (cue validity: valid, invalid) ANOVA on individual mean RTs. The main effect of cue validity, $F(1, 17)$ = 76, $p < .001$, η_p^2 = .816, showed that RTs were shorter

with valid than invalid cues (500 vs. 542 ms). Further, there was a main effect of cue color, $F(4, 68)$ = 4.81, p = .002, η_p^2 = .22, and a significant interaction of cue color and cue validity, $F(4, 68)$ = 42.11, $p < .001$, η_p^2 = .592. As shown in Table 1 and Figure 2C, the cueing effect decreased with increasing separation of cue and target color, but the decrease was not symmetric around the target color. By paired t test, the mean cueing effect for the −30° cue color was larger than for the 30° cue color (60 vs. 3 ms), $t(17)$ = 6.19, $p < .001$, Cohen's d_z = 1.46. Similarly, the cueing effect for the −15° cue color was larger than for the 15° cue color (76 vs. 16 ms), $t(17)$ = 7.79, $p < .001$, Cohen's d_z = 1.84. Overall, the distribution of cueing effects shows a shift away from the nontarget colors with a peak around −15°. While the current cue colors capture the right side of the distribution adequately, the left side is only represented by a single cue color (−30°). Nonetheless, the difference between −30° and −15° was significant by paired t test (60 vs. 76 ms), $t(17)$ = 2.68, p = .016, Cohen's d_z = 0.63.

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

Memory bias. Color errors were fit with the mixture model proposed by Zhang and Luck (2008) with an additional bias parameter. The model provides an estimate of the standard deviation of the distribution of the memory error, an estimate of the guess rate, and an estimate of the bias of the distribution. Fits were performed by the MemToolbox (Suchow, Brady, Fougnie, & Alvarez, 2013). Here, we focus on the bias parameter to evaluate whether the memory representation was shifted toward or away from the context colors. The mean memory bias is illustrated by the black disk with horizontal error bars overlaid on the distribution of color errors in Figure 2C. By one-sample t test, the mean bias parameter was −19° and significantly smaller than zero, $t(17)$ = 8.15, $p < .001$, Cohen's d_z = 1.92. The direction and magnitude of the bias fits well with the shifted distribution of cueing effects.

Discussion

We found cueing effects for target-similar colors to be asymmetrically distributed. Cueing effects were larger for target-similar cue colors shifted away from the nontarget colors than for cue colors shifted toward the nontarget colors. At the same time, there was a bias in the judged target color in the same direction. Participants remembered the target color to be further away from the nontarget colors than it actually was. The magnitude of the shift in the attentional template (color judgments) agreed with the shift in attentional selectivity (cueing effects) and amounted to about −19° in CIELAB-space.

Experiment 2

Similar to results by Becker et al. (2014), the results from Experiment 1 did not show a return to baseline for target-similar colors deviating away from the nontarget colors. Thus, it may be

Table 1

Reaction Times (ms) and Choice Errors (%) as a Function of Cue Color and Cue Validity in Experiment 1

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)	

Note. The cueing effect (CE) is the difference between invalid and valid cue conditions. The standard error of the mean (*SEM*) is indicated in parentheses. Cueing effects were significant if the *p*-value of the respective one-sample *t* test was smaller than .01 (Bonferroni correction for five tests). Significant cueing effects are marked by an asterisk.

possible that attentional selectivity was biased toward the largest color difference. While the cue was presented in a context of gray elements, one may argue that its saliency was calculated across the temporal average of cue and target displays. If cue and target displays are collapsed, then cue colors deviating away from the nontarget colors are more salient. Possibly, their larger saliency accounts for the larger capture and the asymmetric distribution. Many studies have suggested a link between saliency and attentional capture (e.g., Burnham & Neely, 2008; Feldmann-Wüstefeld, Miyakoshi, Petilli, Schubö, & Makeig, 2017; Liesefeld, Liesefeld, Müller, & Rangelov, 2017; Theeuwes, 1991; Töllner, Zehetleitner, Gramann, & Müller, 2011; van Zoest, Donk, & Theeuwes, 2004; reviewed by Theeuwes, 2019). To rule out effects of saliency, we included cue colors that deviated more strongly from the nontarget colors. Stronger deviations increase the saliency in the averaged displays, but they also decrease the similarity with respect to the target color. Decreased similarity between cue and target color, in turn, is known to reduce attentional capture (e.g., Kerzel, 2019). Thus, a saliency-based explanation of the cueing effects in Experiment 1 predicts reliable cueing effects with increasing distance from the nontarget color, while asymmetrical attentional selectivity predicts a return to baseline with large differences between cue and target colors. To measure the full distribution of cueing effects, we shifted the cue colors from Experiment 1 by $-15°$.

Method

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

Results

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

Choice errors. Table 2 reports average error rates. Individual percentage of choice errors was submitted to the same ANOVA as

Table 2

Reaction Times (ms) and Choice Errors (%) as a Function of Cue Color and Cue Validity in Experiment 2

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)

Note. The cueing effect (CE) is the difference between invalid and valid cue conditions. The standard error of the mean (*SEM*) is indicated in parentheses. Cueing effects were significant if the p-value of the respective one-sample t test was smaller than .01 (Bonferroni correction for five tests). Significant cueing effects are marked by an asterisk.

above. The main effect of cue validity, $F(1, 20) = 3.46$, $p = .078$, $\eta_p^2 = .15$, and the interaction of cue color and cue validity, $F(4, 80) = 2.49$, $p = .05$, $\eta_p^2 = .11$, approached significance, reflecting more choice errors for cue colors deviating away from the nontarget color.

Memory bias. The mean memory bias is illustrated by the light gray disk with horizontal error bars overlaid on the distribution of color errors in Figure 2C. By one-sample t test, the mean bias parameter was $-17°$ and significantly different from zero, $t(20) = 8.6$, $p < .001$, Cohen's $d_z = 1.88$. The direction and magnitude of the bias were very similar to Experiment 1.

Discussion

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

Experiment 3

To provide further evidence for optimal tuning and to better describe the scope of the relational account, we manipulated the
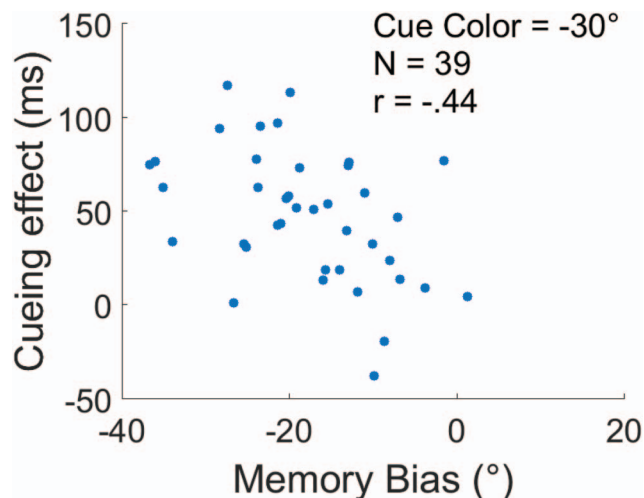
Figure 3. Correlation between the individual cueing effects for the −30° cue color and individual memory biases. Data were collapsed across Experiments 1 and 2. See the online article for the color version of this figure.

similarity between target and nontarget colors. Optimal tuning predicts that the similarity between target and nontargets determines the shift of the attentional template. When target and nontargets are similar, the attentional template is shifted away from the nontargets to optimize the signal-to-noise ratio. However, when target and nontargets are dissimilar, no shift of the attentional template should occur. The reason is that the overlap in the neural distributions activated by target and nontargets is reduced, so that a shift of the attentional template is no longer beneficial. Thus, we expect the asymmetry in the distribution of cueing effects and the shift of the attentional template to be reduced when the nontargets are more distinct from the target. We measured cueing effects for the −15° and 15° cue colors with two different nontarget contexts. The "close" nontarget colors were the same as in the previous Experiments. The "far" nontarget colors were 30° further away (see Figure 4).

Method

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

Results

The first and second block after initial training served to familiarize participants with the two sets of nontarget colors and were

not analyzed, reducing the number of available trials from 768 to 512 with 32 color judgments.

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

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

Memory bias. The mean memory bias for close and far nontarget colors is illustrated by the black and light gray symbols, respectively, overlaid on the distribution of color errors in Figure 4. The fit was performed on 16 color judgments per condition. By one-sample t test, the mean bias parameter was significantly dif-
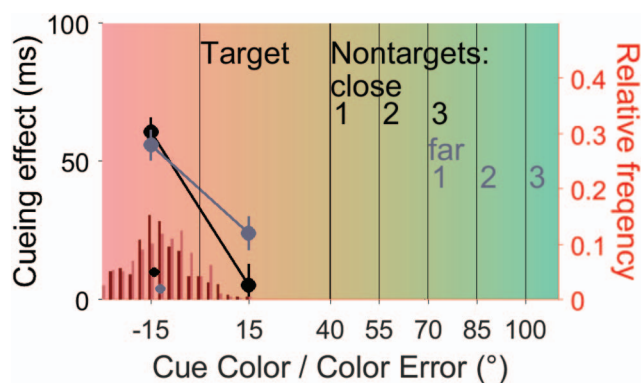

Figure 4. Results from Experiment 3. The cueing effects for cue colors of −15° and 15° are shown as a function of nontarget color. Data from the condition with close nontarget colors (40°, 55°, and 70°) are shown in black and data from the condition with far nontarget colors (70°, 85°, and 100°) are shown in light gray. The distribution of color errors for the close and far nontargets is shown by the dark and light bars, respectively. The center of the distribution of color errors, as indicated by the mixture model, is shown by the disks overlaid on the bars. See the online article for color version of this figure.

Table 3

Reaction Times (ms) and Choice Errors (%) as a Function of Cue Color and Cue Validity in Experiment 3

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)

Note. The cueing effect (CE) is the difference between invalid and valid cue conditions. The standard error of the mean (*SEM*) is indicated in parentheses. Cueing effects were significant if the *p*-value of the respective one-sample *t* test was smaller than .01 (Bonferroni correction for five tests). Significant cueing effects are marked by an asterisk.

ferent from zero with close (−14°) and far (−12°) nontarget colors, ts(21) > 7.57, ps < .001, Cohen's d_z > 1.61. The small difference between far and close of 2° was significant, t(21) = 2.17, p = .042, Cohen's d_z = 0.46, suggesting that the memory bias away from the nontarget colors was reduced when the nontarget colors were far.

Discussion

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

Further, the effect of nontarget color is outside the scope of relational theory (Becker, 2010). Changes of the nontarget color concerned the relative hue in the target display. In contrast, the saturation of the cue relative to its context was unchanged. Because the cue–context relation did not match the target–nontarget relation, relational theory does not apply. Further, the relational account describes distractor colors away from the nontarget colors as relationally better (Becker et al., 2014). However, the relational account does not specify the exact feature distance of "relationally best" distractor colors. It could be that all colors exaggerating the target–nontarget relation capture more strongly than the target, but without difference among the exaggerated colors. Results from Experiments 1–3 refute the idea of a uniform increase in capture across all cue colors deviating away from the nontarget color. Rather, there was a peak of the cueing effects at −15° (Experiments 1–2) and a reduction of the cueing effects when the nontarget color was more distinct (Experiment 3).

General Discussion

The current research pursued two goals. First, we provide missing behavioral evidence for changes in attentional selectivity predicted by optimal tuning of attention (Navalpakkam & Itti, 2007). Previous research confirmed that the memory representation of the search target (i.e., the attentional template) was biased away from nontarget features (Geng et al., 2017; Hamblin-Frohman & Becker, 2019; Navalpakkam & Itti, 2007; Scolari & Serences, 2009; Yu & Geng, 2019). However, there is little behavioral evidence to suggest that the shifted attentional template affected attentional selectivity. The current study filled this gap by showing that cueing effects are asymmetrically distributed around the target color. In general, cueing effects are large when the cue color corresponds to the target color and decrease continuously with increasing difference between cue and target colors (Anderson & Folk, 2010; Ansorge & Becker, 2014; Büsel et al., 2019; Folk & Remington, 1998; Kerzel, 2019). In the current investigation, we found that the distribution of cueing effects was not symmetric around the target color but was shifted away from the nontarget colors. Thus, an important conclusion from the current study is that cueing effects may not be maximal for cues in the target color, but for target-similar cue colors deviating away from the nontarget colors. Classical research was based on the assumption that the attentional template corresponds to the target feature (Folk & Remington, 1998; Folk et al., 1992), but this assumption holds only true when the target is sufficiently distinct from the nontarget colors. For instance, the colors red and green used in Folk and Remington (1998) would correspond to a distance of 180° in CIELAB-space. It is unlikely that nontarget colors as distinct as 180° in CIELAB-space bias attentional selectivity. However, we show that distances as large as 70° in CIELAB-space may be sufficient (cf. Experiment 3). Further, we measured memory for the target color and replicated the bias away from the nontarget colors. The magnitude of the bias corresponded to the shift in the distribution of cueing effects. As predicted by optimal tuning, the bias in the memory representation decreased when the nontarget colors were more distinct from the target color. The reduction was small, which may be due to the alternating trial blocks with close and far nontarget colors. Manipulating nontarget colors in a between-subjects design may yield larger effects.

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

Previous Failures to Provide Evidence for Optimal Tuning

The results of the present research contrast with those of a previous study by Scolari and Serences (2009). However, target and nontarget features in Scolari and Serences (2009) were similar to the point where the accuracy of target localization was never better than 60%. If the current sign conventions are adopted (which are opposite to Scolari & Serences, 2009), the nontarget orientation in Scolari and Serences (2009) was at +5° relative to the target at 0°. Consistent with the current study, contrast thresholds improved for relative orientations of −10° or −20° (their Figure 4C), which deviated away from the nontarget. However, there was also improvement for the nontarget orientation and an orientation deviating in the same direction as the nontargets, but more strongly (i.e., +10°). The bilateral improvement suggested off-channel gain to Scolari and Serences (2009; see also Scolari & Serences, 2010), but was considered incompatible with optimal tuning. Because target and nontargets were more distinct in the current study, it is difficult to compare the present results to those of Scolari and Serences (2009). In a more comparable study, the nontargets would be at +5° in CIELAB-space (as for instance in Yu & Geng, 2019) so that colors away from the nontarget (−15°, −30°, and −45°) and beyond the nontarget (+15°, +30°, +45°) could be investigated. It seems likely that the peak of the cueing effects would be biased away from the nontarget color, similar to the

current study (i.e., at −15°). However, it seems unlikely that another peak of cueing effects would be observed beyond the nontarget color (i.e., at +30°). The reason is that cueing effects decrease rapidly with increasing distance between cue color and attentional template (see also Kerzel, 2019). In the current study, the memory representation of the target was at −18° so that cue colors at +15° already resulted in close-to-zero cueing effects, which makes it unlikely that another peak would occur at even larger distances (i.e., +30° or beyond). However, a definitive answer would require new experiments with a fine color discrimination task.

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

Precision of Attention and Memory

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

In light of the low precision of attentional selectivity, it may be understandable that relatively distinct nontarget colors resulted in

a shift of the attentional template. The closest nontarget color in Experiments 1 and 2 was at 40° from the target color. This color difference is highly discriminable from the target color, given that the *SD* of memory errors was only 9° and a color category in CIELAB-space can be as small as 36° (estimated from Figure 7 in Bae et al., 2015). The high discriminability is also visible in the low error rates of less than 5%. It would be interesting to know how much the neural populations representing target and nontarget stimuli overlapped for colors this far apart. It seems safe to conclude that the overlap was less than in the experiments by Navalpakkam and Itti (2007), where task difficulty was much higher. Despite the much smaller overlap, we found evidence in line with optimal tuning. Possibly, attentional tuning to color is less precise than attentional tuning to orientation, so that effects of optimal tuning are present even with large perceptual differences, whereas they would be absent for orientation, where attentional tuning is better. Future research should study the relation between perceptual precision and attentional selectivity in more detail.

Same Location Costs

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

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

References

Andersen, S. K., Hillyard, S. A., & Müller, M. M. (2008). Attention facilitates multiple stimulus features in parallel in human visual cortex. *Current Biology, 18,* 1006–1009. http://dx.doi.org/10.1016/j.cub.2008.06.030

Anderson, B. A., & Folk, C. L. (2010). Variations in the magnitude of attentional capture: Testing a two-process model. *Attention, Perception, & Psychophysics, 72,* 342–352. http://dx.doi.org/10.3758/APP.72.2.342

Ansorge, U., & Becker, S. I. (2014). Contingent capture in cueing: The role of color search templates and cue-target color relations. *Psychological Research, 78,* 209–221. http://dx.doi.org/10.1007/s00426-013-0497-5

Bae, G. Y., Olkkonen, M., Allred, S. R., & Flombaum, J. I. (2015). Why some colors appear more memorable than others: A model combining categories and particulars in color working memory. *Journal of Experimental Psychology: General, 144,* 744–763. http://dx.doi.org/10.1037/xge0000076

Becker, S. I. (2010). The role of target–distractor relationships in guiding attention and the eyes in visual search. *Journal of Experimental Psychology: General, 139,* 247–265. http://dx.doi.org/10.1037/a0018808

Becker, S. I., Ansorge, U., & Horstmann, G. (2009). Can intertrial priming account for the similarity effect in visual search? *Vision Research, 49,* 1738–1756. http://dx.doi.org/10.1016/j.visres.2009.04.001

Becker, S. I., Folk, C. L., & Remington, R. W. (2013). Attentional capture does not depend on feature similarity, but on target–nontarget relations. *Psychological Science, 24,* 634–647. http://dx.doi.org/10.1177/0956797612458528

Becker, S. I., Harris, A. M., Venini, D., & Retell, J. D. (2014). Visual search for color and shape: When is the gaze guided by feature relationships, when by feature values? *Journal of Experimental Psychology: Human Perception and Performance, 40,* 264–291. http://dx.doi.org/10.1037/a0033489

Born, S., & Kerzel, D. (2011). Time-course of feature-based top-down control in saccadic distractor effects. *Journal of Experimental Psychology: Human Perception and Performance, 37,* 1689–1699. http://dx.doi.org/10.1037/a0024282

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10,* 433–436. http://dx.doi.org/10.1163/156856897X00357

Bundesen, C. (1990). A theory of visual attention. *Psychological Review, 97,* 523–547. http://dx.doi.org/10.1037/0033-295X.97.4.523

Burnham, B. R. (2010). Cognitive load modulates attentional capture by color singletons during effortful visual search. *Acta Psychologica, 135,* 50–58. http://dx.doi.org/10.1016/j.actpsy.2010.05.003

Burnham, B. R., & Neely, J. H. (2008). A static color discontinuity can capture spatial attention when the target is an abrupt-onset singleton. *Journal of Experimental Psychology: Human Perception and Performance, 34,* 831–841. http://dx.doi.org/10.1037/0096-1523.34.4.831

Büsel, C., Pomper, U., & Ansorge, U. (2019). Capture of attention by target-similar cues during dual-color search reflects reactive control among top-down selected attentional control settings. *Psychonomic Bulletin & Review, 26,* 531–537. http://dx.doi.org/10.3758/s13423-018-1543-5

Büsel, C., Voracek, M., & Ansorge, U. (2018). A meta-analysis of contingent-capture effects. *Psychological Research.* Advance online publication. http://dx.doi.org/10.1007/s00426-018-1087-3

Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011). Attentional templates in visual working memory. *The Journal of Neuroscience, 31,* 9315–9322. http://dx.doi.org/10.1523/JNEUROSCI.1097-11.2011

Carmel, T., & Lamy, D. (2014). The same-location cost is unrelated to attentional settings: An object-updating account. *Journal of Experimental Psychology: Human Perception and Performance, 40,* 1465–1478. http://dx.doi.org/10.1037/a0036383

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research, 51,* 1484–1525. http://dx.doi.org/10.1016/j.visres.2011.04.012

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96,* 433–458. http://dx.doi.org/10.1037/0033-295X.96.3.433

Eimer, M. (2014). The neural basis of attentional control in visual search. *Trends in Cognitive Sciences, 18,* 526–535. http://dx.doi.org/10.1016/j.tics.2014.05.005

Ekroll, V., Faul, F., Niederée, R., & Richter, E. (2002). The natural center of chromaticity space is not always achromatic: A new look at color induction. *Proceedings of the National Academy of Sciences of the United States of America, 99,* 13352–13356. http://dx.doi.org/10.1073/pnas.192216699

Fairchild, M. D. (2005). *Color appearance models.* Hoboken, NJ: Wiley.

Feldmann-Wüstefeld, T., Miyakoshi, M., Petilli, M. A., Schubö, A., & Makeig, S. (2017). Reduced visual attention in heterogeneous textures is reflected in occipital alpha and theta band activity. *PLoS ONE, 12,* e0187763. http://dx.doi.org/10.1371/journal.pone.0187763

Folk, C. L., & Remington, R. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 847–858. http://dx.doi.org/10.1037/0096-1523.24.3.847

Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 1030–1044. http://dx.doi.org/10.1037/0096-1523.18.4.1030

Geng, J. J., DiQuattro, N. E., & Helm, J. (2017). Distractor probability changes the shape of the attentional template. *Journal of Experimental Psychology: Human Perception and Performance, 43,* 1993–2007. http://dx.doi.org/10.1037/xhp0000430

Geng, J. J., & Witkowski, P. (2019). Template-to-distractor distinctiveness regulates visual search efficiency. *Current Opinion in Psychology, 29,* 119–125. http://dx.doi.org/10.1016/j.copsyc.2019.01.003

Grubert, A., Carlisle, N. B., & Eimer, M. (2016). The control of single-color and multiple-color visual search by attentional templates in working memory and in long-term memory. *Journal of Cognitive Neuroscience, 28,* 1947–1963. http://dx.doi.org/10.1162/jocn_a_01020

Hamblin-Frohman, Z., & Becker, S. I. (2019, May). *Contrasting relational and optimal tuning accounts in attentional and perceptual selection.* Paper presented at the annual meeting of the Vision Sciences Society, St. Petersburg, FL.

Harris, A. M., Jacoby, O., Remington, R. W., Travis, S. L., & Mattingley, J. B. (2019). Taking a closer look at visual search: Just how feature-agnostic is singleton detection mode? *Attention, Perception, & Psychophysics, 81,* 654–665. http://dx.doi.org/10.3758/s13414-018-01642-y

Harris, A. M., Remington, R. W., & Becker, S. I. (2013). Feature specificity in attentional capture by size and color. *Journal of Vision, 13*(3) 12. http://dx.doi.org/10.1167/13.3.12

Hout, M. C., & Goldinger, S. D. (2015). Target templates: The precision of mental representations affects attentional guidance and decision-making in visual search. *Attention, Perception, & Psychophysics, 77,* 128–149. http://dx.doi.org/10.3758/s13414-014-0764-6

Kerzel, D. (2019). The precision of attentional selection is far worse than the precision of the underlying memory representation. *Cognition, 186,* 20–31. http://dx.doi.org/10.1016/j.cognition.2019.02.001

Kerzel, D., & Witzel, C. (2019). The allocation of resources in visual working memory and multiple attentional templates. *Journal of Experimental Psychology: Human Perception and Performance, 45,* 645–658. http://dx.doi.org/10.1037/xhp0000637

Kerzel, D., Zarian, L., & Souto, D. (2009). Involuntary cueing effects on accuracy measures: Stimulus and task dependence. *Journal of Vision, 9*(11), 16. http://dx.doi.org/10.1167/9.11.16

Kleiner, M., Brainard, D. H., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3? *Perception, 36*(14), 1–16.

Lamy, D., Leber, A., & Egeth, H. E. (2004). Effects of task relevance and stimulus-driven salience in feature-search mode. *Journal of Experimental Psychology: Human Perception and Performance, 30,* 1019–1031. http://dx.doi.org/10.1037/0096-1523.30.6.1019

Leonard, C. J., Balestreri, A., & Luck, S. J. (2015). Interactions between space-based and feature-based attention. *Journal of Experimental Psychology: Human Perception and Performance, 41,* 11–16. http://dx.doi.org/10.1037/xhp0000011

Liesefeld, H. R., Liesefeld, A. M., Müller, H. J., & Rangelov, D. (2017). Saliency maps for finding changes in visual scenes? *Attention, Perception, & Psychophysics, 79,* 2190–2201. http://dx.doi.org/10.3758/s13414-017-1383-9

Liesefeld, H. R., & Müller, H. J. (2020). A theoretical attempt to revive the serial/parallel-search dichotomy. *Attention, Perception, & Psychophysics, 82,* 228–245. http://dx.doi.org/10.3758/s13414-019-01819-z

Liu, T., & Mance, I. (2011). Constant spread of feature-based attention across the visual field. *Vision Research, 51,* 26–33. http://dx.doi.org/10.1016/j.visres.2010.09.023

Ludwig, C. J., & Gilchrist, I. D. (2002). Stimulus-driven and goal-driven control over visual selection. *Journal of Experimental Psychology: Human Perception and Performance, 28,* 902–912. http://dx.doi.org/10.1037/0096-1523.28.4.902

Meeter, M., & Olivers, C. N. (2014). Target features and target–distractor relation are both primed in visual search. *Attention, Perception, & Psychophysics, 76,* 682–694. http://dx.doi.org/10.3758/s13414-013-0611-1

Moher, J., Lakshmanan, B. M., Egeth, H. E., & Ewen, J. B. (2014). Inhibition drives early feature-based attention. *Psychological Science, 25,* 315–324. http://dx.doi.org/10.1177/0956797613511257

Mulckhuyse, M., van Zoest, W., & Theeuwes, J. (2008). Capture of the eyes by relevant and irrelevant onsets. *Experimental Brain Research, 186,* 225–235. http://dx.doi.org/10.1007/s00221-007-1226-3

Navalpakkam, V., & Itti, L. (2007). Search goal tunes visual features optimally. *Neuron, 53,* 605–617. http://dx.doi.org/10.1016/j.neuron.2007.01.018

Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences, 15,* 327–334. http://dx.doi.org/10.1016/j.tics.2011.05.004

Prinzmetal, W., McCool, C., & Park, S. (2005). Attention: Reaction time and accuracy reveal different mechanisms. *Journal of Experimental Psychology: General, 134,* 73–92. http://dx.doi.org/10.1037/0096-3445.134.1.73

Rajsic, J., Ouslis, N. E., Wilson, D. E., & Pratt, J. (2017). Looking sharp: Becoming a search template boosts precision and stability in visual working memory. *Attention, Perception, & Psychophysics, 79,* 1643–1651. http://dx.doi.org/10.3758/s13414-017-1342-5

Rajsic, J., & Woodman, G. F. (2020). Do we remember templates better so that we can reject distractors better? *Attention, Perception, & Psychophysics, 82,* 269–279. http://dx.doi.org/10.3758/s13414-019-01721-8

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience, 27,* 611–647. http://dx.doi.org/10.1146/annurev.neuro.26.041002.131039

Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience, 5,* 631–632. http://dx.doi.org/10.1038/nn876

Sàenz, M., Burâcas, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research, 43,* 629–637. http://dx.doi.org/10.1016/S0042-6989(02)00595-3

Schneider, W. X. (2013). Selective visual processing across competition episodes: A theory of task-driven visual attention and working memory. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 368,* 20130060. http://dx.doi.org/10.1098/rstb.2013.0060

Schoeberl, T., Ditye, T., & Ansorge, U. (2018). Same-location costs in peripheral cueing: The role of cue awareness and feature changes. *Journal of Experimental Psychology: Human Perception and Performance, 44,* 433–451. http://dx.doi.org/10.1037/xhp0000470

Schönhammer, J. G., Becker, S. I., & Kerzel, D. (2017). Which kind of attention is captured by cues with the relative target color? *Visual Cognition, 25,* 703–714. http://dx.doi.org/10.1080/13506285.2017.1323811

Schönhammer, J. G., Grubert, A., Kerzel, D., & Becker, S. I. (2016). Attentional guidance by relative features: Behavioral and electrophysiological evidence. *Psychophysiology, 53,* 1074–1083. http://dx.doi.org/10.1111/psyp.12645

Scolari, M., Byers, A., & Serences, J. T. (2012). Optimal deployment of attentional gain during fine discriminations. *The Journal of Neuroscience, 32,* 7723–7733. http://dx.doi.org/10.1523/JNEUROSCI.5558-11.2012

Scolari, M., & Serences, J. T. (2009). Adaptive allocation of attentional gain. *The Journal of Neuroscience, 29,* 11933–11942. http://dx.doi.org/10.1523/JNEUROSCI.5642-08.2009

Scolari, M., & Serences, J. T. (2010). Basing perceptual decisions on the most informative sensory neurons. *Journal of Neurophysiology, 104,* 2266–2273. http://dx.doi.org/10.1152/jn.00273.2010

Stothart, C., Simons, D. J., Boot, W. R., & Wright, T. J. (2019). What to where: The right attention set for the wrong location. *Perception, 48,* 602–615. http://dx.doi.org/10.1177/0301006619854302

Suchow, J. W., Brady, T. F., Fougnie, D., & Alvarez, G. A. (2013). Modeling visual working memory with the MemToolbox. *Journal of Vision, 13*(10), 9. http://dx.doi.org/10.1167/13.10.9

Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & Psychophysics, 50,* 184–193. http://dx.doi.org/10.3758/BF03212219

Theeuwes, J. (2019). Goal-driven, stimulus-driven, and history-driven selection. *Current Opinion in Psychology, 29,* 97–101. http://dx.doi.org/10.1016/j.copsyc.2018.12.024

Töllner, T., Zehetleitner, M., Gramann, K., & Müller, H. J. (2011). Stimulus saliency modulates pre-attentive processing speed in human visual cortex. *PLoS ONE, 6,* e16276. http://dx.doi.org/10.1371/journal.pone.0016276

Treue, S., & Martínez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature, 399,* 575–579. http://dx.doi.org/10.1038/21176

van Zoest, W., Donk, M., & Theeuwes, J. (2004). The role of stimulus-driven and goal-driven control in saccadic visual selection. *Journal of Experimental Psychology: Human Perception and Performance, 30,* 746–759. http://dx.doi.org/10.1037/0096-1523.30.4.749

Witzel, C., & Gegenfurtner, K. R. (2015). Chromatic contrast sensitivity. In R. Luo (Ed.), *Encyclopedia of color science and technology* (pp. 1–7). Heidelberg, Germany: Springer. http://dx.doi.org/10.1007/978-3-642-27851-8_17-1

Witzel, C., & Gegenfurtner, K. R. (2018). Color perception: Objects, constancy, and categories. *Annual Review of Vision Science, 4,* 475–499. http://dx.doi.org/10.1146/annurev-vision-091517-034231

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 419–433. http://dx.doi.org/10.1037/0096-1523.15.3.419

Yu, X., & Geng, J. J. (2019). The attentional template is shifted and asymmetrically sharpened by distractor context. *Journal of Experimental Psychology: Human Perception and Performance, 45,* 336–353. http://dx.doi.org/10.1037/xhp0000609

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 453,* 233–235. http://dx.doi.org/10.1038/nature06860

Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience, 12,* 24–25. http://dx.doi.org/10.1038/nn.2223