Efficient tuning of attention to narrow and broad ranges of task-relevant feature values

Angus F. Chapman^{1*} & Viola S. Störmer^{1,2}

¹Department of Psychology, University of California, San Diego, La Jolla, CA

²Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH

*Currently: Department of Psychological and Brain Sciences, Boston University, Boston, MA

Word Count: 10,964

Please address correspondence to:

Angus Chapman
Department of Psychological and Brain Sciences
Boston University
64 Cummington Mall
Boston, MA 02215
Email: angusc@bu.edu

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RUNNING HEAD: Efficient feature-based tuning

ABSTRACT

Feature-based attention is the ability to select relevant information on the basis of visual features, such as a particular color or motion direction. In contrast to spatial attention, where the attentional focus has been shown to be flexibly adjustable to select small or large regions in space, it is unclear whether feature-based attention can be efficiently tuned to different feature ranges. Here, we establish that the focus of feature-based attention can be adjusted more broadly or narrowly to select currently relevant features. Participants attended to a set of target-colored dots among distractor dots to detect brief decreases in luminance (Experiments 1a, 1b, 2) or bursts of coherent motion (Experiments 3a, 3b, 4). To vary the size of the attentional focus, we manipulated the range of colors that the target dots spanned and found that while participants' performance decreased with larger feature ranges to select, it remained at a relatively high level even at the largest color range, suggesting that broadening the focus of feature-based attention comes only at a small cost and that large feature ranges can be selected relatively efficiently at once. Overall, our findings argue against the idea that feature-based attention is limited to a single feature value at a time and demonstrate that selecting large swaths of feature space is surprisingly efficient. Broadly, these results are consistent with accounts that propose a flexible and generalized set of attentional mechanisms that act across both spatial and feature-based domains.

Keywords: feature-based attention; attentional focus; feature representation; visual organization

Introduction

When navigating and interacting with the world around us, sensory information that is highly salient or relevant to our goals is prioritized by attention (Carrasco, 2011; Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004). Seminal theories have attempted to explain how information processing is shaped by attention, and the resulting perceptual and behavioral outcomes. For example, attention to a particular location in space increases neural processing in cortical regions selective for that location, and improves perception of items that appear there (Kastner, Pisk, De Weerd, Desimone, & Ungerleider, 1999; Pestilli & Carrasco, 2005; Posner, 1980). Likewise, attention can select information based on visual features, such as a particular color or motion direction (Andersen, Hillyard, & Müller, 2008; Sàenz, Buraças, & Boynton, 2003). Several studies have shown that feature-based attention enhances processing of the selected feature (Liu, Larsson, & Carrasco, 2007; Martinez-Trujillo & Treue, 2004; Sàenz et al., 2003; Störmer & Alvarez, 2014; White & Carrasco, 2011), similar to what has been shown for spatial attention. While spatial attention has received a particularly prominent focus in the literature (Eriksen & Yeh, 1985; Itti & Koch, 2000; Lamy & Tsal, 2001; Posner, Snyder, & Davidson, 1980; Treisman & Gelade, 1980; Wolfe, 1994)—often treated as separate and distinct from feature-based attention—it is undetermined whether spatial and feature-based attention rely on largely separate processes or may instead share common processes that act on different mental representations and neural substrates. As such, understanding under what circumstances attentional selection is comparable or different across these modes of attention is necessary for establishing a more general theory of attentional selection.

In research on spatial attention, significant effort has been dedicated to understanding the structure and size of the attentional focus. Many influential models of spatial attention, such as the spotlight (Posner, 1980; Posner et al., 1980), gradient (Downing & Pinker, 1985), zoom lens (Eriksen & St. James, 1986; Eriksen & Yeh, 1985), and normalization model of attention (Reynolds & Heeger, 2009), propose different characteristics of the attentional focus. For example, some have hypothesized that spatial attention exhibits an excitatory peak at the attended location that gradually falls off with increasing distance (e.g., Dori & Henik, 2006; Downing & Pinker, 1985; LaBerge & Brown, 1989; Shulman, Sheehy, & Wilson, 1986), while others have proposed a center-surround profile where locations nearby an attended region are inhibited (Cutzu & Tsotsos, 2003; Hopf et al., 2006; Mounts, 2000; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005). Another important property of the attentional focus is its size: whether it can be adjusted flexibly or is fixed at a particular spatial scale. The zoom-lens model, initially conceived of by Eriksen and St. James (1986), proposes that the size of the attention field can be changed (i.e., one can “zoom in” or “zoom out” to attend to small or big regions in the visual field), but that these changes come at a cost, such that processing efficiency decreases as the size of the attentional focus increases. The more recently developed normalization model of attention also suggests that the attentional field size is a critical component to understand selection (Reynolds & Heeger, 2009). For example, it has been shown that variations in the effects of attention can be explained by different attentional field sizes (Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Itthipuripat, Garcia, Rungratsameetaweemana, Sprague, & Serences, 2014). In sum, seminal models of attention—and spatial attention in particular—have

made explicit assumptions about the flexibility of the attentional focus and how this relates to the pattern of attentional modulations and task performance.

While ample research has investigated the limits of spatial attention, the selection limits of feature-based attention are less well understood. Most research on this topic to date has investigated the concept of attentional templates: the idea that attention is driven by an internal representation of the target stimulus that is separate from the sensory input itself (see Geng & Witkowski, 2019, for a review). This template is a memory representation of the target that provides top-down input to sensory populations, modulating their responses proportional to their selectivity for features associated with the target template. Notably, the template does not need to be a precise representation of the target, but might be broader (because the target feature is vaguely defined, e.g.; Bravo & Farid, 2012; Hout & Goldinger, 2014; Witkowski & Geng, 2022) or asymmetrically tuned (because of a consistent distractor context, e.g.; Geng, Diquattro, & Helm, 2017; Hamblin-Frohman & Becker, 2021; Yu & Geng, 2019). In particular, templates can be defined not only by a specific feature value (e.g., orange) but by a feature relation (e.g., “redder” targets), as demonstrated with behavioral (Becker, Folk, & Remington, 2010, 2013; Becker, Martin, & Hamblin-Frohman, 2019), eye-tracking (Becker, 2010; Becker, Harris, Venini, & Retell, 2014; York, Sewell, & Becker, 2020), and neurophysiological measures (Schönhammer, Grubert, Kerzel, & Becker, 2016). However, these studies generally use a limited but consistent set of stimuli throughout an experiment, to better measure how templates are shaped and optimized through repeated presentations of the target and distractor features. As such, the main factor for attentional selection in these experiments is the similarity between stimuli and the target template held in mind.

In contrast, it is still unknown whether feature-based attention can be allocated towards a range of feature values simultaneously (e.g., colors ranging from red to purple)—changing its width of attentional selection in feature space—or whether attentional allocation to features is limited to select a single or an extremely narrow range of features at one moment in time (i.e., the color red or the motion direction upwards). Indeed, it might be the case that spatial attention is unique in its ability to change its selection window to include smaller or larger regions. Importantly, the question of whether feature-based attention can allocate resources efficiently to different ranges of visual features is separate from the question of how broadly or narrowly attentional templates are tuned: while templates rely on working memory representations and are important to guide selection initially, the question of attentional allocation asks whether attention can support the simultaneous modulation of multiple features. Research investigating the limits of feature-based attention have predominantly focused on examining whether multiple distinct features can be selected at once, with many findings suggesting a stark and fixed limit of feature-based attention. For example, Boolean Map theory (Huang & Pashler, 2007) proposes that attentional selection requires the division of the visual field into regions based on whether a given feature (e.g., the color red) is present or absent at that location, and argues that only a single feature value can be used for selection at a time, while multiple locations can be selected simultaneously. Consistent with this account, studies have shown that cuing two directions of motion (Liu, Becker, & Jigo, 2013) or colors (Liu & Jigo, 2017) benefits perceptual processing less than cuing to a single feature, suggesting a stark selection limit. Furthermore, Liu and Jigo (2017) found evidence to suggest that any

benefits in the two-cue condition could be explained by attention towards a single feature, and proposed that attention can only select a single feature value.

However, previous studies have mostly assessed situations in which feature-based attention is divided between distinct feature values (e.g., the colors red and blue; Andersen, Hillyard, & Müller, 2013; but see Störmer & Alvarez, 2014), but an unanswered question is whether attention can be effectively distributed across a range of feature values (e.g., colors ranging from red to orange); in other words, can feature-based attention change its scope to select broader (or narrower) parts in feature space, similar to how spatial attention can increase its attentional field size to select larger (or smaller) spatial regions? A few studies indirectly speak to this: Herrmann and colleagues (2012) manipulated the uncertainty of a precue in an orientation discrimination task, and found that when precues were highly uncertain (covering 60° of orientation), the behavioral benefit of valid cues was equivalent regardless of the actual orientation of the target stimulus, providing suggestive evidence that participants were distributing their attention across the entire range of potential target orientations during the cue-target interval. Another study using a similar approach found that sensitivity to a motion target decreased as a function of the reliability of the cued motion direction (Ball & Sekuler, 1981), suggesting that spreading attention to larger ranges comes at a behavioral cost. While these studies provide some support for the idea that feature-based attention—like spatial attention—may be relatively flexible in its focus, their manipulation of cue reliability does not require that participants maintain attention to a wide range of features at once, and ultimately the target feature selected was only a single value. Thus, current

research has not directly assessed whether and how multiple feature values can be selected continuously.

If feature-based attention can be flexibly adjusted to select more broad or narrow ranges of feature values, then many models, based predominantly on explaining spatial attention, could incorporate this shared aspect. Some models of attention already assume similar principles for selecting locations and features (Reynolds & Heeger, 2009), predicting that the flexibility of spatial attention should extend to the selection of visual features. Some have even construed spatial dimensions as simply being “features” of the visual world in the same way that colors or orientations are (Maunsell & Treue, 2006), implying that the traditional division between the two modes of attention are unnecessary and that selection for features and spatial locations should follow analogous principles. In this case, the size of the attentional field should not only be able to adjust in location space, as previous work has shown (Castiello & Umiltà, 1990), but should also adjust in feature space, and be thus able to select a range of features with reasonable efficiency. Although there are many differences between spatial and feature-based attention (e.g., Ling, Liu, & Carrasco, 2009; Liu, Stevens, & Carrasco, 2007), they are also highly intertwined. For example, it is well known that the task-relevance of a feature can modulate whether spatial attention is captured and guided to its location (Becker et al., 2010; Folk, Remington, & Johnston, 1992; Grubert & Eimer, 2016; Williams, Brady, & Störmer, 2022). While such studies show that spatial and feature-based attention interact, these domains are often treated as theoretically distinct, with separate mechanisms invoked to account for their findings. However, a major goal of attention research is to characterize general selection mechanisms that bridge across stimulus spaces. Determining the flexibility of

the attentional focus to features is therefore a critical test of whether the mechanisms underlying spatial and feature-based attention are shared or dissociated.

Here, across five experiments, we examine whether feature-based attention can be flexibly tuned to narrow and broad ranges of colors. We adapted a sustained feature-based attention task (Andersen et al., 2008; Sàenz et al., 2003; Störmer & Alvarez, 2014), where participants attend to a set of target colored dots amongst differently colored distractor dots to detect brief target events (luminance decreases or coherent motion). To assess the efficiency of narrowly and more broadly tuned attention, we varied the range of colors that the target dots spanned from trial to trial, allowing us to measure performance as a function of the distribution of target colors attended. Because the range of relevant colors varied from trial to trial, as well as the region within the feature space those colors were selected from, a consistent attentional template could not be used throughout the experiment. Our findings demonstrate that increasing the size of the attentional focus in feature space results in only a relatively small decrease in processing efficiency, similar to studies of spatial attention. In particular, Experiment 1a (which used a fixed-luminance circular color space) and Experiment 1b (which used a fixed-luminance 2D color space) show that when attention is tuned broadly to a large range of color space, performance decreases only slightly compared to a narrow focus. Experiment 2 demonstrates that this decrease in performance is much lower than would be expected if participants were attending to only a narrow, fixed range of colors. In Experiment 3a and 3b, we confirm that this effect is driven by attentional selection of colors during perception, rather than later decision-related processes by assessing performance on both target and distractor-colored dots. Finally, Experiment 4 demonstrates that attention was

allocated across the entire range of colors relatively uniformly, as participants were just as good at detecting changes at the edges of the color range as those in the center of the range. Together, these experiments demonstrate that feature-based attention can be efficiently adjusted as necessitated by task conditions.

Experiment 1a

Method

Preregistration

We preregistered the predictions and analysis of this experiment on AsPredicted, with a predetermined minimum sample size of 30 (<http://aspredicted.org/blind.php?x=mj2dh7>), providing 80% power to detect a significant effect of $\eta_p^2 > .308$. In comparison, previous studies on this topic have used relatively small sample sizes ($n = 2-12$; Ball & Sekuler, 1981; Liu et al., 2013; Liu & Jigo, 2017; Herrmann et al., 2012).

Open Data

Raw data and analysis code for all experiments are available on the Open Science Framework (<https://osf.io/uf4k6/>).

Participants

Thirty-six undergraduate students from the University of California, San Diego subject pool participated for course credit and gave written informed consent prior to starting the experiment as approved by the Institutional Review Board at UC San Diego. Six participants with an average $d' < 0.5$ across all conditions in the main task were excluded. The remaining 30

participants (24 women, 6 men) were between 18-25 years of age ($M = 19.9 \pm 1.7$ years) and had normal or corrected-to-normal vision.

Stimuli

The experiment was presented on a 22" CRT monitor that was calibrated to linearize RGB output. Participants were seated at approximately 57 cm from the monitor during the experiments. All stimuli were generated using MATLAB (R2016b) with the Psychophysics Toolbox (Brainard, 1997). A centrally presented circular field of dots (5.8° visual angle radius) was presented on a black background (*Figure 1A*). This field contained 200 dots moving independently and randomly at $2.25^\circ/\text{s}$. To prevent participants from tracking single dots, each dot had a limited lifetime and was redrawn at a new random location every 300 ms. A white fixation cross (each bar 0.4° long) was presented in the center of the dot field.

The dot field was separated into two groups: a set of target dots and a set of distractor dots. The target and distractor contained 100 dots each and differed in color. All colors were selected from a set of 360 equally spaced equiluminant colors in the CIELab color space, drawn from a circle with radius 49 units, centered at $L = 54$, $a = 21.5$, $b = 11.5$ (see *Figure 1B*). On each trial, the "center" of the target colors was randomly selected from the color wheel and the distractor was set 180° away, on the opposite side of the color wheel. Across trials, we manipulated the range that the target colors varied in by uniformly drawing colors symmetrically around the "center" target color, such that the width of this range spanned either 10° , 20° , 40° , 60° , 90° , or 120° around the color wheel on each trial (*Figure 1B*). Thus, the target dots had a consistent range within a trial, while the distractor dots were all a single color (see *Figure 1A*, for an example of a 120° range of target colors and a fixed purple distractor

Figure 1. A) Example trial structure for Experiment 1a & 1b. During the pre-trial period (800 ms), only the target dots were presented in color (in this example spanning 120° of the color space), while the distractor dots were shown in grey. Participants then had to attend to the target dots among colored distractor dots throughout the trial to detect a brief (300 ms) decrease in luminance in the target colors. Displays are not shown to scale. B) Circular color space used in Experiment 1a. Target colors were centered at a random position around the space on each trial and spanned 6 ranges as shown by the arc segments (10° , 20° , 40° , 60° , 90° , or 120°). C) 2D color space used in Experiment 1b. Target colors were randomly chosen on each trial and spanned 6 ranges along a line as shown by line segments. The distractor color was at a fixed relative position from this line. For more details on the color spaces, see *Methods*.

color). The colors were selected uniformly from the specified range by creating a sequence of evenly spaced values spanning 100 points in this range, rounded to the nearest whole number, representing the color angle for each target dot. The spatial position of each dot was randomized to avoid any patterns in the layout of the target-colored dots.

Procedure

In the task, participants attended to a set of target-colored dots to detect brief decreases in luminance (*Figure 1A*). On each trial, the dot field was presented for 800 ms during a cueing period, in which the target dots were presented in color, while the distractor dots were presented in a neutral grey (RGB: [100, 100, 100]). This allowed us to present the exact target colors to participants without having to use specific cues or labels to differentiate targets and distractors. After the cueing period, target and distractor dots (now both colored) were presented for 2000 ms, during which participants attended the target dots to detect brief (300 ms) decreases in luminance. The luminance decrease occurred at a random time with the constraint that it could not happen in the 300 ms period at the beginning or end of each trial. At the end of each trial, participants indicated whether this change occurred in the target dots by responding on the keyboard ('m' for a target change, 'n' for no target change). The luminance change could occur in the target dots (50% of trials), the distractor dots (25%), or neither set of dots (25%). Sensitivity (d') was calculated as the normalized hit rate minus normalized false alarm rate (across distractor change and no-change trials). Response criterion (c), where reported, was calculated as $-\frac{1}{2}$ the normalized hit rate plus normalized false alarm rate. Hits and false alarms are also reported in *Table 1*. Participants completed 288 trials of this task (48 per condition).

The magnitude of the luminance decrease was determined for each participant individually at the beginning of the experiment session by a thresholding task. Participants completed 32 trials per thresholding run, in which the luminance decrease was adjusted using a staircasing method: the change became smaller (less detectable) after two consecutive correct responses, and larger (more detectable) after an incorrect response. The luminance decrement was initially set at 40% of the maximum luminance of the dots and was adjusted by 2% with each step. During the thresholding task, all target and distractor dots were colors 180° away from each other on the color wheel (i.e., single colors, no range of colors), and these colors varied randomly from trial-to-trial. Accuracy was fit with a logistic curve using the Palamedes toolbox (Prins & Kingdom, 2009) with a guess rate of 50%, and thresholds were selected as the luminance decrement corresponding to 70% accuracy. Participants completed 1-3 runs of the thresholding task until performance was adequately estimated ($M = 1.87$ runs, $SD = 0.73$).

At the end of the experiment, participants also completed a triad color similarity task, the data from which we do not include here.

Results

Sensitivity (d') to detect the luminance change was computed separately for all color range conditions. To assess how the range of colors present in the target dots affected performance in the task, we conducted a repeated-measures ANOVA on d' across target color range (10°, 20°, 40°, 60°, 90°, or 120° around the color wheel). There was a main effect of target color range, $F(5,145) = 3.42$, $p = .006$, $\eta_p^2 = .106$, such that d' decreased as the range of the target colors increased, further evidenced by a significant linear trend, $F(1,29) = 15.31$, $p < .001$,

Figure 2. A) Results of Experiment 1a. Detection of target luminance changes (d') decreased as the range of target colors increased as a function of the angular distance around the color wheel. B) Results of Experiment 1b. Discrimination decreased as the range of target colors increase as a function of distance in the 2D CIELab color space. Error bars correspond to within-subject SEM.

$\eta_p^2 = .346$, as can be seen in *Figure 2A*. Planned follow-up comparisons (FDR corrected) revealed that this effect was driven by higher d' at the lowest levels of color range (10° & 20°) relative to the highest levels of color range (90° & 120°). Performance at 10° was marginally better than at 90°, $p = .052$, and 120°, $p = .052$, but not different from 20°, 40°, or 60°, $ps > .17$. Performance at 20° was significantly better than at 90°, $p = .026$, and 120°, $p = .005$, marginally better than 40°, $p = .064$, but not different from 60°, $p = .135$. There were no differences in performance between the higher levels of target color range, $ps > .45$. Changes in d' appeared to primarily be driven by a reduction in hit rates (correct detection of target changes) as color range increased, $F(5,145) = 5.75$, $p < .001$, $\eta_p^2 = .165$, as there was no significant effects on false alarms to distractor changes, $F(5,145) = 0.40$, $p = .849$, $\eta_p^2 = .014$, or no-change trials, $F(5,145) = 0.46$, $p = .807$, $\eta_p^2 = .016$ (*Table 1*). These changes are reflected in a significant increase in (i.e., more

conservative) response criterion (c) with higher target color ranges, $F(5,145) = 2.34$, $p = .044$, $\eta_p^2 = .075$.

This experiment demonstrates that increasing the size of the focus of feature-based attention leads to decreased efficiency in selecting target features, consistent with findings from spatial attention (Castiello & Umiltà, 1990; Maringelli & Umiltà, 1998). The observed decrease in performance, from $d' = 1.76$ at 10° of target color range to $d' = 1.44$ at 120° , is smaller than might be anticipated given the twelve-fold increase in the range of target colors to be attended, as evidenced by the small, yet significant effect size. Specifically, assuming a strict capacity model where only a single color is selected at a time, there should be a steep, linear drop off as the range of target colors to be attended increases. Instead, our findings show that attentional resources are not strictly fixed but flexibly adapt to be allocated almost across large

	Target color range					
	10°	20°	40°	60°	90°	120°
HR	.638 (.173)	.662 (.171)	.589 (.184)	.594 (.181)	.552 (.179)	.557 (.188)
FAR (distractors)	.199 (.153)	.213 (.152)	.227 (.182)	.215 (.157)	.220 (.182)	.236 (.156)
FAR (no-change)	.113 (.126)	.118 (.147)	.116 (.149)	.130 (.134)	.127 (.147)	.130 (.159)

Table 1. Mean (SD) hit rates (HR) and false alarm rates (FAR) as a function of target color range for Experiment 1a. These measures represent the proportion of trials on which participants correctly reported a luminance change in the target dots or incorrectly reported a target change when either the distractor changed (FAR distractors) or neither set of dots changed (FAR no-change).

parts of the feature space. Notably, increasing the target color range affected the rate of hits and not false alarms (see *Table 1*), suggesting that changes in performance were driven primarily by less efficient selection of the target colors as the range increased.

Experiment 1b

Experiment 1a suggests that participants can focus feature-based attention broadly across a range of colors quite efficiently, with relatively small costs in performance. However, one potential alternative explanation for these findings is that the decrease in performance we found is driven not just by the range of target colors, but by the correlated change in target-distractor similarity with different ranges, which affects performance in this type of feature-based attention task (Chapman & Störmer, 2022). Because we used a circular color space, increasing the range of to-be-attended colors necessarily increases the similarity between targets and distractors (as can be seen in *Figure 1B*). At the lowest level of target color range, the distractor color was 175° away from each end of the target distribution, while at the highest level the distractor color was 120° away. To rule out the alternative that (at least some of) the decrease in performance was due to changes in target-distractor similarity across conditions, we conducted a second experiment that ensured that the target color range was not confounded with target-distractor distance. To do this, in Experiment 1b, we chose target and distractor colors from a two-dimensional plane in the CIELab color space (*Figure 1C*). Target colors were selected along a line drawn in this space at a fixed distance from a distractor color; thus, increased color range here actually *decreases* the average distance between target and distractor colors (see *Figure 1C*). It is also worth noting that distractors now differed from

targets in both hue and saturation. While this might complicate a direct comparison between Experiments 1a and 1b, because distractors are more distinct from targets in two feature dimensions, this experiment provides a strong test of the hypothesis that a broad range of feature values can be selected by attention, regardless of distractor similarity.

Method

Preregistration

Just like for Experiment 1a, we preregistered the predictions and analysis of this experiment on AsPredicted, with a predetermined minimum sample size of 30 (<http://aspredicted.org/blind.php?x=24r4aw>), providing 80% power to detect a significant effect of $\eta_p^2 > .308$.

Participants

Thirty-nine undergraduate students participated in this experiment and gave written informed consent as approved by the Institutional Review Board at UC San Diego. Nine participants with an average $d' < 0.5$ across conditions in the main task were excluded. The remaining 30 participants (21 women, 9 men) were between 18-25 years of age ($M = 20.4 \pm 1.9$ years) and had normal or corrected-to-normal vision.

Stimuli

Target and distractor colors were selected from a fixed-luminance 2D-plane in the CIELab color space. For a particular luminance level that was fixed across the experiment ($L = 54$), we generated all colors within the sRGB gamut at steps of 0.25 units along the a and b dimensions. A 'd50' white point was assumed for converting colors from Lab to RGB values. We

selected points in this space such that the distance between target and distractor colors, and between points along the variable target line, were comparable in distance to those selected from the color wheel in Experiment 1a. To generate target and distractor colors, we sampled three points in the color space that formed an equilateral triangle with sides 85 units long. Two points were randomly selected as the maximal ends of the target color line and the remaining point was the distractor color. The midpoint of the target line was the “average” target color, and was restricted to be at least 15 units from the grey point of the color space (Lab = [54, 0, 0]) to avoid target colors that were highly desaturated. Target color range was manipulated by uniformly selecting colors that spanned particular distances along the target line (widths of 7.1, 14.2, 28.3, 42.5, 63.8, and 85 units; these distances correspond to the length of the chords on the color wheel for the angles used in Experiment 1a). This process was repeated until all target and distractor colors fell within the sRGB gamut.

Procedure

The details of the procedure are similar to Experiment 1a. Participants first completed a thresholding task using colors drawn from the 2D color space (target color range = 0; 1-3 runs, $M = 1.60$, $SD = 0.77$). They then completed 336 trials of the main task. Because the colors were slightly less saturated overall, due to the way we selected points in the color space, we lowered the brightness of the baseline grey dots (RGB: [80, 80, 80]). All other parameters were the same.

Results

As in Experiment 1a, we conducted a repeated-measures ANOVA on d' across target color ranges. There was a main effect of target color range, $F(5,145) = 5.03$, $p < .001$, $\eta_p^2 = .148$, such that d' decreased as the target color range increased, as shown in *Figure 2B*. Similar to the previous experiment, there was a highly significant linear trend, $F(1,29) = 17.08$, $p < .001$, $\eta_p^2 = .371$, and planned follow-up comparisons (FDR corrected) revealed that d' was higher at the lowest levels of color range (7.1 and 14.2 units) relative to the highest levels of color range (42.5, 63.8, and 85 units), $ps < .05$. Performance at 28.3 units did not differ from any the other levels, $ps > .063$, nor was there a difference between 7.1 and 14.2 units, $p = .888$, and performance at the highest levels of target color range (42.5, 63.8, and 85 units) did not differ amongst themselves, $ps > .49$. As for Experiment 1a, changes in d' appeared to primarily be driven by a reduction in hit rates as target color range increased, $F(5,145) = 8.90$, $p < .001$, $\eta_p^2 = .235$, as there was no significant effects on false alarms to distractors, $F(5,145) = 1.28$, $p = .275$, $\eta_p^2 = .042$, or no-change trials, $F(5,145) = 0.23$, $p = .948$, $\eta_p^2 = .008$ (*Table 2*). As in Experiment 1a, these changes are reflected in a more conservative response criterion with higher target color ranges, $F(5,145) = 2.31$, $p = .047$, $\eta_p^2 = .074$.

This experiment confirmed that increasing the range of to-be-attended target colors results in decreased performance, even when target-distractor similarity does not concurrently increase. Again, we found that this primarily affected participants' ability to detect changes in the target dots, since only hit rates were affected by the target color range (see *Table 2*). Importantly, the overall decrease in performance for higher ranges of colors is likely not due to factors introduced by the 2D color space. While target colors were less saturated than in

	Target color range (a.u.)					
	7.1	14.2	28.3	42.5	63.8	85
HR	.665 (.175)	.673 (.155)	.637 (.168)	.605 (.139)	.589 (.180)	.575 (.179)
FAR (distractors)	.311 (.177)	.299 (.162)	.346 (.198)	.337 (.157)	.332 (.174)	.377 (.207)
FAR (no-change)	.190 (.143)	.203 (.172)	.189 (.160)	.200 (.183)	.207 (.186)	.225 (.225)

Table 2. Mean (SD) hit rates (HR) and false alarm rates (FAR) as a function of target color range for Experiment 1b. These measures represent the proportion of trials on which participants correctly reported a luminance change in the target dots or incorrectly reported a target change when either the distractor changed (FAR distractors) or neither set of dots changed (FAR no-change).

Experiment 1b, because the 2D space constrained how the target colors could be chosen, colors at the edge of high range targets were further from the distractor and higher saturation on average compared to low target color ranges, demonstrating that attentional selection was similar despite differences between the circular and full 2D CIELab color spaces. However, although the pattern of results was similar across these two experiments, targets and distractors could differ across two dimensions in Experiment 1b (hue and saturation) which may limit the direct comparability of these findings.

Experiment 2

In Experiment 1a and 1b, we demonstrated that participants could attend to a broad range of colors at a relatively low cost. These results appear inconsistent with accounts that assume a strict capacity limit of feature-based attention, for example those that propose only a

single feature value (or a very small range of feature values) can be selected at once (e.g., Huang & Pashler, 2007). According to such accounts, the decrease in performance should be inversely proportional to the number of features attended—and thus much more pronounced than the performance decrease we observed. To directly quantify how strongly performance would decrease if participants only selected a small and fixed feature range across all conditions, in Experiment 2, we directly manipulated the number of target dots and used the observed decrease in performance to predict the range of attended colors in Experiment 1b.

Method

Preregistration

We preregistered the predictions and analysis of this experiment on AsPredicted, with a predetermined minimum sample size of 20 (https://aspredicted.org/Q9S_CDK). Based on pilot experiments, we anticipated a larger effect than in Experiments 1a and 1b, so we estimated fewer participants were needed to detect a significant effect.

Participants

Twenty-four undergraduate students participated in the experiment for course credit. Data from four participants was excluded from the final data set, as their average d' in the main task was below 0.5. The final 20 participants (13 women, 7 men) were between 18-23 years of age ($M = 19.8 \pm 1.2$ years), and had normal or corrected-to-normal color vision.

Stimuli & Procedure

The task proceeded similarly to Experiment 1b, however on each trial the target and distractor colors were fixed at a single value. Thus, participants attended to a single color

among a single distractor color (e.g., just red among blue). To match the colors as closely as possible to those used in Experiment 1b, the colors were initially selected from the same 2D CIELab space used in Experiment 1b assuming a color range of 85 units. However, in the experiment itself, not the entire range was shown but only a single target color that was always selected as the midpoint of this range.

To experimentally model conditions where only a small fixed portion of the dots would be selected by attention, as fixed capacity models assume, we manipulated the number of target dots in the display across trials. In our baseline condition, equivalent to previous experiments, there were 100 target dots and 100 distractor dots. Then, across trials, we varied the proportion of target dots relative to this baseline across 6 conditions (100%, 84%, 68%, 52%, 35%, 20%). On trials in which the number of target dots was reduced, the number of distractor dots was increased to maintain 200 dots overall. To allow for comparison across conditions, when the distractor dots changed in luminance this occurred in only 100 dots. Note that with this manipulation, target dots were also spatially more diffuse as the number of dots decreased. This, however, would also be true in Experiments 1a and 1b if participants restricted their attentional focus to a narrow range (e.g., 20°), as the dots falling within that narrow color range would also be spatially more diffuse because colors were randomly distributed across all dot locations. Thus, Experiment 2 allows for a direct comparison with the first experiment. Participants completed 336 trials of the main task, preceded by a luminance thresholding task with equal numbers of target and distractor dots (equivalent to thresholding in Experiment 1b).

Data Analysis

We used this data to predict the range of attended colors in Experiment 1b. To do this, we first extracted the slope of the relationship between the number of target dots in the display and d' from a linear mixed-effects model with 'lmer' from the R package *lme4* (v1.1-26; Bates, Maechler, Bolker, & Walker, 2015). We then inverted this relationship, estimating the change in the proportion of attended target dots based on performance in Experiment 2. To allow an estimate of the attended color range from this relative proportion estimate, we fixed the proportion of attended dots with a color range of 7.1 units to 1.0 (the lowest target color range used in Experiment 1b). Finally, we multiplied the predicted proportion of attended target dots by the width of the target color range, resulting in a measure of the predicted attentional range (e.g., an estimated 0.50 of targets attended from an 85 unit range equals a predicted attentional range of 42.5 units).

Results

We first examined the effect of the number of target dots with a repeated-measures ANOVA, which revealed a significant main effect on performance, $F(5,95) = 14.33$, $p < .001$, $\eta_p^2 = .430$. Similar to previous experiments, there was a significant linear trend downwards in performance as the number of target dots decreased, $F(1,19) = 51.70$, $p < .001$, $\eta_p^2 = .731$. This strong linear effect can be seen in *Figure 3A*. This change in d' was driven by lower hit rates as the proportion of target dots decreased, $F(5,95) = 20.38$, $p < 0.001$, $\eta_p^2 = .517$, while there was no effect on false alarms to distractors, $F(5,95) = 1.05$, $p = .394$, $\eta_p^2 = .052$, or no-change trials, $F(5,95) = 0.19$, $p = .964$, $\eta_p^2 = .010$.

Figure 3. A) Results of Experiment 2. Detection of target luminance changes (d') decreased with fewer target dots presented on the screen. B) Predicted range of feature-based attention in Experiment 1b as a function of the true target color range. Predicted attentional range was based on the slope of the performance in Experiment 1b compared to the slope observed in Experiment 2. Error bars correspond to within-subject SEM. See methods and results for more details.

This data suggests that the results from Experiment 1b cannot be explained by a simple “subsampling” strategy: the target color range increases by 12 times across conditions in Experiment 1b (7.1 to 85 units), while the proportion of target dots in Experiment 2 decreases by only 5 times (100% to 20% of baseline target dots), yet the decrease in performance in Experiment 2 is much greater. To quantify this difference, we used the performance in Experiment 2 to estimate how broadly participants tuned their attention in Experiment 1b. To do this, we first fit a slope to quantify the effect of the number of target dots on performance (Figure 3A), and then used this slope to read out the expected number of target dots attended by participants based on d' in Experiment 1b. For example, d' for the 42.5 unit range in Experiment 1b was roughly 1.20 (see Figure 2B), which maps to a proportion of approximately 0.69 attended dots in Experiment 2 (see Figure 3A), which was then multiplied by the target

color range (42.5) giving a predicted attentional range of 29.4 units. We performed this calculation for each participant and condition in Experiment 1b.

If participants attend to a strictly fixed range of colors, then increasing the target color range (as in Experiment 1b) should be equivalent to decreasing the number of target dots on the display (as in Experiment 2). Thus, we can predict the range of attended colors in Experiment 1b based on how much performance drops in each condition, relative to the observed changes in Experiment 2. As demonstrated in *Figure 3B*, if attention was unlimited to any range of colors, the predicted range would follow the diagonal, while if there was a fixed attentional focus, the predicted range would flatten out once this fixed range was reached. However, we find an intermediate effect, revealing that attention cannot select broader ranges of colors without limits, but that attention is also clearly not strictly fixed in its scope, thus refuting a strong version of the fixed lens model. This analysis assumes that attention inside a fixed range would be all-or-none, and changes in the target color range would map directly onto adding or removing target dots from the display—which is likely not true in practice. Regardless, the much larger decrease in performance in Experiment 2 clearly demonstrates that participants did not attend to a fixed, narrow range of target colors in Experiments 1a and 1b; instead, attentional resources were flexibly allocated across the different color ranges following task demands.

Experiment 3a

In Experiment 1a and 1b, we demonstrated that increasing the range of to-be-attended colors resulted in a decrease in sensitivity for detecting changes in the luminance of target dots.

However, it is possible that participants were not attending to only the target colors, but instead distributed their attention across target and distractor colors to detect *any* luminance change, and only at the end of the trial, when making a response, determined what kind of change it was (target, distractor, or no-change). In this case, decreased performance at larger target color ranges might then be attributable to greater confusability between target and distractor colors. We think such a strategy is unlikely for several reasons. First, we thresholded participants to a performance level where, in our view, it would be difficult to detect luminance changes without focusing attention onto the target colors. Second, across both experiments, we found that increases in the target color range exclusively affected hit rates (detection of changes in the targets) and not false alarm rates (false attribution of distractor changes as target changes). Third, we found a similar pattern of performance in Experiment 1b, despite increases in the target color range increasing the separability of target and distractor colors.

Nonetheless, we sought to get direct evidence to argue against this alternate account. In Experiment 3a, participants performed a task similar to Experiments 1a and 1b, but this time were cued to prioritize the target color to discriminate the direction of a brief interval of coherent motion (either left, right, up, or down), which was more likely to occur in the target dots (80% of changes) relative to distractor dots. However, participants were asked to also report the motion direction when it occurred in the distractor-colored dots. If performance for reporting target changes still decreases as a function of the range of target colors attended, while remaining higher than for reporting distractor changes, this suggests that attentional selection of colors, and not a later decision-making process, is responsible for the effects we observed in Experiment 1. Importantly, because detecting coherent motion requires monitoring

a group of dots (whereas luminance changes used in Experiments 1-2 can be detected in any single dot on the display), the use of coherent motion targets provides stronger evidence in favor of the idea that participants are attending to a broad range of features simultaneously.

Method

Participants

Sixty-two undergraduate students at UC San Diego participated in this experiment for course credit. Sixteen participants were excluded with accuracy below 60% on attention check trials (motion coherence: 100%; target color range: 0°; see *Procedure*). The remaining 46 participants (31 women, 15 men) were between 18-29 years of age ($M = 21.0 \pm 2.4$ years). All participants gave informed consent prior to starting the experiment as approved by the Institutional Review Board at UC San Diego. This sample size provides 80% *a posteriori* power to detect a significant main effect of target color range and interaction with coherent motion color type of $\eta_p^2 > .196$.

Stimuli

This experiment was conducted online, and participants completed the study in a web browser on devices they provided. Stimulus presentation for the experiment was managed using jsPsych (de Leeuw, 2015) with customized plugins based on previous RDK code (Rajananda, Lau, & Odegaard, 2018). A central, circular RDK (400 by 400 px) was presented on a black background and consisted of two sets of 100 independently moving dots (radius 5 px). Each dot had a limited lifetime and was redrawn at a new random location at least once every 500 ms. A white fixation cross (each bar 20 px by 1px) was presented in the center of the dot

field. Target and distractor dot colors were selected from a circular CIELab color space and colors were determined randomly on each trial as in Experiment 1a. The range of target colors was manipulated across trials, spanning either 20°, 40°, 60°, or 120° around the color wheel, similar to Experiment 1a.

Procedure

Trials proceeded similar to Experiment 1a, but with a change from detection of luminance decreases to periods of coherent motion. Because this experiment was conducted online, we had less control over aspects of participants' displays, such as brightness and contrast, so we chose to use a coherent motion event instead of a luminance decrease to minimize this heterogeneity. Pilot experiments suggested this change in tasks produced overall similar patterns of performance as our in-lab studies. First, for 1000 ms, target dots were presented in color alone. Following a 300 ms blank screen, target and distractor dots were presented in color for 500 ms, and participants had to attend both sets of dots for the duration of the trial to detect coherent motion (50% coherence) in one of the cardinal directions (left, right, up, or down) that occurred in either the target or distractor dots. At the end of the trial, participants had to report the correct direction using the arrow keys regardless of which dots moved coherently. Target dots moved coherently on 80% of trials, and participants were instructed to attend to them primarily, while still reporting the direction of the distractor dots if they moved coherently. Participants completed 504 trials of this task, of which 24 had 100% coherent motion in the target dots (which were presented in a single color) and were considered "attention check" trials, to determine whether participants were performing the task as intended. These trials were only used to exclude participants from the main analysis

(see *Participants*) and were excluded from the main data analysis. The remaining 480 trials were distributed evenly across the four target color range conditions (20°, 40°, 60°, or 120°) and coherent motion color type (target or distractor dots, 80%/20% respectively).

Results

To assess the effect of target color range and attention (coherent motion in attended vs. unattended color) on performance, we performed a repeated-measures ANOVA on participants' accuracy in reporting the direction of the coherent motion. This revealed a main effect of attention, $F(1,45) = 65.65$, $p < .001$, $\eta_p^2 = .593$, such that participants were on average more accurate at reporting coherent motion in the target dots than the distractor dots, suggesting that attention was primarily focused on the target dots as instructed. There was also a main effect of target color range, $F(3,135) = 3.11$, $p = .028$, $\eta_p^2 = .065$, such that accuracy decreased as the range of target colors increased, replicating the findings from Experiment 1a and 1b. There was no interaction between these factors, $F(3,135) = 0.09$, $p = .967$, $\eta_p^2 = .002$, however when assessing the effect of target color range for each set of dots separately, we did find that the range of target colors had a detrimental effect on accuracy for coherent motion in the target dots, $F(3,135) = 5.87$, $p < .001$, $\eta_p^2 = .115$, but not distractor dots, $F(3,135) = 1.00$, $p = .354$, $\eta_p^2 = .022$. Follow-up pairwise comparisons (FDR corrected) revealed that accuracy was generally lower for coherent motion in the target dots at 120° compared to smaller target color ranges (20° vs 120°, $p < .001$; 40° vs 120°, $p = .061$; 60° vs 120°, $p = .003$), while there was no difference in accuracy among the lower target color ranges ($\leq 60^\circ$; $ps > .2$).

Figure 4. A) Results of Experiment 3a. Accuracy in reporting the direction of coherent motion was higher for target than distractor dots. Further, a small but reliable decrease in accuracy was observed as a function of the range of target colors. B) Results of Experiment 3b with two presentation windows. Accuracy for coherent motion direction was higher for target than distractor dots. There was a significant decrease in accuracy at higher target color ranges, but only for coherent motion in the target dots. Error bars are within-subjects SEM.

Additionally, there were no differences in accuracy for coherent motion in the distractor dots for any levels of target color range (all p s > .4). For all levels of target color range, coherent motion was detected better in the target dots compared to distractor dots (p s < .001). These patterns are summarized in *Figure 4A*. These results indicate that the effects of increasing the range of target colors are driven by attentional selection during perceptual processing, as participants were worse in detecting changes in the distractor color compared to the target color. Furthermore, they show a small performance decrease as the target color range increases, replicating the pattern observed in Experiment 1.

Experiment 3b

The findings of Experiment 3a suggest that the decrease in performance for broader target color ranges is not driven by decision processes at the end of the trial, but are due to continuous attentional allocation to the target dots. In Experiment 3b, we attempted to replicate the basic findings of Experiment 3a in an alternate version of the task that instead used two presentations windows. Specifically, participants were presented with two consecutive 500 ms windows with only one window containing the coherent motion. They were instructed to attend to both consecutive displays to detect motion in one window or the other. Because coherent motion was present in only one window, increasing uncertainty in the stimulus display (as was true for the luminance changes in Experiment 1a, 1b, and 2), we expected this might exaggerate the magnitude of the attention effects observed in Experiment 3a.

Method

Participants

Sixty-eight undergraduate students at UC San Diego participated in this experiment for course credit. Eight participants were excluded with accuracy below 60% on attention check trials (motion coherence: 100%; target color range: 0°; see *Procedure*). The remaining 60 participants (45 women, 11 men, one non-binary, 3 did not report their gender) were between 18-32 years of age ($M = 20.14 \pm 2.2$ years). This sample size provides 80% *a posteriori* power to detect a significant main effect of target color range and interaction with coherent motion color type of $\eta_p^2 > .119$.

Stimuli & Procedure

Trials proceeded similar to Experiment 3a, but with the presentation of two stimulus windows. First, the target dots were presented alone for 1000 ms to cue participants which colors to attend to. Following a 300 ms blank screen, participants were presented with two consecutive 500 ms displays consisting of target and distractor dots—separated by a 300 ms blank screen—and had to attend to both sets of dots in both windows to detect coherent motion (50% coherence). The coherent motion could occur in either the target or distractor dots, in either the first or second presentation window, and in one of the cardinal directions (left, right, up, or down). At the end of the trial, participants had to report which window the motion was present in (responding with ‘1’ or ‘2’) as well as the direction of the motion (using the arrow keys), regardless of which dots moved coherently. Target dots moved coherently on 80% of trials, and participants were instructed to attend to them primarily, while still reporting the direction of the distractor dots if they moved coherently. Participants completed 264 trials of this task, including 24 “attention check” trials which had 100% coherent motion in the target dots in one window and all target dots were presented in a single color. The remaining 240 trials were distributed evenly across the two target color range conditions (20° or 120°) and coherent motion color type (target or distractor dots, 80%/20% respectively).

Results

To assess the effect of target color range (20° vs. 120°) and attention (coherent motion in the target vs. distractor dots) on performance, we performed a repeated-measures ANOVA on participants’ accuracy in reporting the direction of the coherent motion. There was a

significant effect of attention, $F(1,59) = 47.41$, $p < .001$, $\eta_p^2 = .446$, as participants had higher accuracy for reporting the direction of coherent motion in target dots relative to distractors, consistent with attention being primarily focused on the target dots. There was no main effect of target color range, $F(1,59) = 2.56$, $p = .115$, $\eta_p^2 = .042$, however there was a significant interaction, $F(1,59) = 5.37$, $p = .024$, $\eta_p^2 = .083$. Follow-up analyses revealed that accuracy for detecting the target motion was significantly lower for target color ranges of 120° relative to 20° , $t(59) = 4.23$, $p < .001$, $d_z = 0.55$. In contrast, accuracy for detecting distractor motion was not affected by the target color range, $t(59) = 0.26$, $p = .793$, $d_z = 0.03$. These patterns are summarized in *Figure 4B*.

Overall, the findings from Experiments 3a and 3b indicate that the effects of increasing the range of target colors are driven by attentional selection during perceptual processing and not later decision-related processing. Even when participants reported changes that occurred in either set of dots, they still had lower performance as the target color range increased, suggesting that selection of the target colors was less efficient as the size of their attentional focus increased. Despite this, performance was still relatively high overall, consistent with the interpretation that feature-based attention can be tuned relatively efficiently to a wide range of colors. Additionally, because participants attended to targets within relatively short presentation windows in both experiments, these findings cannot straightforwardly be attributed to strategic shifts of attention throughout the range of target colors during the trial. Further, these experiments argue against the idea that participants were attending to a limited range of dots on any given trial, since coherent motion (as opposed to luminance changes) are dependent on a simultaneous global percept across many dots in the display.

Experiment 4

Thus far, our data are consistent with the interpretation that participants can adjust the size of the focus of feature-based attention according to task demands, with only small costs in performance. This interpretation is similar to results in spatial attention where studies have shown that participants adjust the size of their spatial focus of attention in response to different cues (Castiello & Umiltà, 1990; Eriksen & St. James, 1986). However, the decrease in performance we observed is also consistent with an account in which the size of the attentional focus is fixed and relatively narrow, in which case lower performance at wider ranges could simply be driven by the fact that participants only attend to a subset of target colors, effectively not processing colors outside of this narrow focus to the same extent. Because the target events in our experiments (i.e., luminance decreases or coherent motion) occur throughout the entire range of colors, signals occurring outside the scope of a fixed focus would be much weaker, resulting in overall lower performance as the range of target colors increases. While Experiment 2 rules out a strong version of such fixed capacity models, which would predict a much stronger decrease in performance than the one we find, we aimed to test more directly how attention is distributed across broad ranges of color in Experiment 4.

We instructed participants to attend to broad ranges of feature values (120° around the color wheel), while coherent motion events occurred either for the 50% of target dots in the center of the color distribution ($\pm 30^\circ$ of the central target color) or at the edges of this color distribution (outer 50%; i.e., colors 30-60° either side of the target range; see *Figure 5A*). If participants attend primarily to a narrow range of colors in the center of the color distribution, we expect performance to be higher for trials in which the motion coherence appeared in the

center, relative to at the edges, of the distribution. Alternatively, if attention is tuned broadly and uniformly across the entire color range, we would expect no difference in performance between these conditions.

Method

Participants

Forty-six undergraduate students at UC San Diego participated in this experiment for course credit and gave informed consent prior to starting the experiment as approved by the Institutional Review Board at UC San Diego. Six participants were excluded with accuracy below 60% on attention check trials (motion coherence: 100%). The remaining 40 participants (31 women, 8 men, 1 did not report their gender) were between 18-30 years of age ($M = 20.5 \pm 2.0$ years). This sample size provides 80% *a posteriori* power to detect a significant main effect of $\eta_p^2 > .200$ and significant paired-comparisons of $d_z > 0.45$.

Stimuli & Procedure

The experiment was presented similarly to Experiment 3a with a single stimulus presentation window, however on each trial the range of target colors was 120°. Participants completed 264 trials of the task, divided into 3 main conditions determined by which dots moved coherently: distractor events (48 trials), central target events (96 trials), and edge target events (96 trials). On distractor trials, a random 50% of the distractor-colored dots moved coherently; on central target trials, the 50% of dots at the center of the target color range ($\pm 30^\circ$ of the mean color) moved coherently; on edge target trials, the 50% of dots outside the center of the target color range (30-60° clockwise and counter-clockwise from the mean color, see

Figure 5A) moved coherently. Distractor trials made up 20% of the main trials of the experiment, as in Experiment 3a. The remaining 24 trials were attention check trials, in which 100% of the target dots moved coherently. Just like in Experiment 3a, these trials only served the purpose to exclude data from participants that were not doing the task as instructed and were not used in the main analysis. As in Experiment 3a and 3b, participants reported the direction of coherent motion that occurred in either the target or distractor dots (up, down, left, or right).

Results

The effect of the color type (target-center, target-edge, distractor) revealed that performance was significantly affected by which dots moved coherently, $F(2,78) = 19.05$, $p < .001$, $\eta_p^2 = .328$. Comparisons between the conditions showed that performance was significantly lower for coherent motion in the distractor dots compared to either of the target conditions (target-center: $t(39) = 4.70$, $p < .001$, $d_z = 0.74$; target-edge: $t(39) = 4.36$, $p < .001$, $d_z = 0.69$), indicating that participant attended to the target colors primarily. However, performance did not differ between motion coherence probed at the center or the edge of the target dot range, $t(39) = 0.04$, $p = .972$, $d_z = 0.01$, and Bayesian analysis revealed support for a null effect, $BF_{01} = 5.86$ (JZS prior, with scale $r = .707$; Rouder, Speckman, Sun, Morey, & Iverson, 2009). That is, participants detected coherent motion just as accurately when it occurred in colors at the edge of the target color range—split across two segments of the range—as when it occurred in the center of the target color range. Given that participants were instructed to attend to the entire target color range, and the center and edge probes were not predictable and occurred briefly and at a random time during the trial, these findings suggest that

Figure 5. A) Example of trial conditions in Experiment 4. The target colors always spanned a range of 120° (black line), but the coherent motion occurred in only 50% of the dots: either the dots in the central 60° of the target range ($\pm 30^\circ$ from the target mean, blue line), or the dots at the edge of the target range (30-60° either side of the target mean, red line). B) Results of Experiment 4. Accuracy in reporting the direction of coherent motion was just as high for coherence in the center of the range as at the edge of the target color range. However, accuracy was higher for both compared to coherence in the distractor dots.

participants selected all colors relatively uniformly rather than a subset of the target colors.

Additionally, the lack of a difference in performance for center and edge probes suggests that category boundaries have a limited effect on broadly tuning attention to color, since the colors in the edge condition were more likely to come from different color categories relative to the center probe condition (see *Figure 5A*, e.g.).

Discussion

A critical question for models of attention is whether selection operates in a similar way across different domains, such as location and feature spaces, or whether selection relies on distinct mechanisms—and exhibits distinct limits—depending on the nature of the domain in question. Here, we tested if one proposed characteristic of spatial attention generalizes to the feature domain: whether the attentional focus can be adjusted in size and be flexibly tuned more narrowly or broadly to select different ranges of target features. We used a task which required participants to attend to sets of dots in particular colors to detect brief changes in their luminance or motion direction and varied the range of target colors to assess the efficiency of concurrent attentional selection for multiple colors. We found that as target color ranges increased, performance decreased, as would be expected if selection of multiple colors was less efficient; however, this performance decrease was rather small and participants still performed well above chance at the highest levels of target color range in all experiments, even when target colors spanned 120° of a circular color space (e.g., from greens through to reds; see *Figure 1B*). Interestingly, we found little-to-no cost in efficiency for attending colors spanning approximately 20° in color space, suggesting that this might be the default span of attention focus in this feature space. Experiment 3a and 3b confirmed that the effects of color range on performance were driven by changes in the efficiency of target selection, rather than by later decision-related processes that might be based on the distractors as well. Finally, Experiment 4 showed that attention was distributed across the entire range of target colors, suggesting that selection of a range of colors seems to occur relatively uniformly, given that participants were just as good at detecting a change when it happened to colors within the

center of the distribution as when it happened for perceptually more distinct colors at the edge of the color distribution (see *Figure 5A*).

Feature-based attention can be tuned broadly during continuous selection

Our findings are inconsistent with theories that assume strict capacity limits where only a fixed, narrow range of features can be selected at once—in the extreme, just a single color value. Under such accounts, as the target color range increases, fewer target dots would fall inside this fixed attentional range, resulting in a steep, linear decrease in performance like we observed in Experiment 2 where we decreased the number of target dots presented. Instead, our results suggest that feature-based attentional resources are not strictly fixed, but can instead be allocated relatively flexibly across large ranges of feature values as required by the task at hand. This finding is consistent with the previously reported flexibility of attentional templates. Notably, theories argue that the flexibility of such templates is dependent on knowledge of the likely target features: when targets are well specified, precise templates can guide efficient selection, while broader templates capture uncertainty when information about the target is less well known (Geng & Witkowski, 2019). In contrast, our study demonstrates that attention can be tuned to a broad range of features when that entire range is relevant to the task. In our experiments, the to-be-attended features ("template") were specified by the full range of target colors shown on a given trial, and the exact colors and their range varied across trials. Thus, if participants attended broadly, this was not due to uncertainty about the relevance of the features, but driven by the stimulus itself. Additionally, the attentional focus would necessarily change from trial-to-trial, and participants could not prepare ahead of time

what to tune their attention to since the target features were not known in advance. Future work could build on this by further dissociating the range and predictiveness of the target features, such as by having consistent features within a given range be more or less relevant than others. More recently, it has been proposed that templates may differ for attentional selection (i.e., guidance of attention towards the features similar to the target held in mind) and perceptual decision-making (i.e., matching a possible target to the target features held in mind), suggesting that there may be different types of “tuning” possible at each of these processing stages (Hamblin-Frohman & Becker, 2021; Yu, Hanks, & Geng, 2022; Yu, Johal, & Geng, 2022). Under this framework, our task design most closely appears to align with attentional selection, since participants were required to maintain attention to the range of currently relevant colors to perform well in the task. Additionally, the results of Experiment 3a and 3b, where no “match” decision was required, argue against the idea that our findings are due to decision-making processes.

Selection of multiple distinct features vs. contiguous ranges of features

Previous research has shown a restricted focus of attention when multiple discrete and categorically distinct features are selected (e.g., blue and red, Liu & Jigo, 2017). How then, in our study, do participants select large ranges of color values spanning distinct color categories relatively efficiently? Cueing multiple distinct features as in previous work (Liu et al., 2013; Liu & Jigo, 2017) likely does not affect attention field size, but instead appears more comparable to manipulations assessing “multi-focal” attention, similar to what has been done in spatial attention (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000; Castiello & Umiltà, 1992; McMains

& Somers, 2004). In our experiments we always cued entire ranges of colors, and these colors were always chosen from contiguous regions in feature space. Thus, it could be the case that selecting perceptually contiguous color values is easier than selecting two distinct colors. That is, intermediate colors may help span disconnected regions of the feature space, allowing attention to “bridge the gap” between distinct parts—and thus categorically different colors—of the feature space. Recent work of ours is consistent with this interpretation. By manipulating the similarity between target and distractor items, we found that attentional selection was equally and maximally effective for distractors beyond approximately 40-50° from a target color (Chapman & Störmer, 2022), suggesting that such colors can be easily ignored by the visual system when irrelevant for a task. Compared to the current study, where colors spanning up to 120° of color space were efficiently selected, and previous research arguing that distinct targets could not be jointly selected (Liu et al., 2013; Liu & Jigo, 2017), these findings collectively suggest that a contiguous set of target features can provide a scaffold that aids attentional selection. Additionally, in addition to enhancing target features, downweighing the non-target feature may also aid performance, especially since in our experiments there was a single distractor color. Importantly, a strategy of just ignoring the distractor would not explain the performance decrease with changes in the target range we observe here. Nonetheless, future work could investigate the role of distractor processing more directly. One important factor would be how efficiently targets and distractors can be discriminated (Chapman & Störmer, 2022), meaning that manipulations that affect the similarity between these features or that increased the range of the distractor features may provide further insight into the flexibility of attentional focus (Duncan & Humphreys, 1989; Geng & Witkowski, 2019).

Other accounts have suggested that attentional selection can be defined by feature relations (e.g., that targets are “redder” than distractors), rather than feature values (Becker et al., 2010, 2013, 2019). In these studies, although targets were defined by a specific feature value (e.g., orange) it was found that attention was often guided towards a range of non-target features that matched the relationship between the target and distractor features (e.g., to all items “redder” than the yellow distractors). A relational coding account of our findings seems unlikely for several reasons. While it is possible to divide the representation of the 2-D color spaces we used into separate “target” and “distractor” regions, such a template is equally applicable to any target color range, and thus would not predict the variation in performance that we observe in our study. Thus, attending to a feature relation alone could not explain our findings. Indeed, for many conditions in our task there is no single relation that captures the distinction between targets and distractors (e.g., *Figure 1A* where targets are “redder”, “yellower”, and “greener” than the distractors).

Relation between feature- and location-based models of attention

Our results indicate that feature-based attention can select broad ranges of feature values relatively efficiently. This is in agreement with previous studies that showed that participants could prepare for an upcoming target feature even when cues were unreliable (e.g., spanning a range of possible target orientation), suggesting that attention was broadly tuned (Ball & Sekuler, 1981; Herrmann et al., 2012). In one study, Herrmann and colleagues (2012) argued in support of the normalization model of attention, in which increasing the attentional field size (i.e., the range of features that are enhanced by attention) resulted in

enhancement of relevant feature values, despite a decrease in the overall response of populations tuned to those values. This is consistent with the results of the current study, where wider ranges of target colors lead to overall worse performance, though target colors were still enhanced relative to distractors. Notably, the normalization model does not have separate mechanisms for features and spatial dimensions but treats them as fundamentally similar (Reynolds & Heeger, 2009), and thus allows for both dimensions to have a flexible focus. That is, the differences between feature-based and spatial modes of selection might not be driven by different mechanisms, but simply by the properties of the stimulus space under investigation. Importantly, the normalization model distinguishes between changes in the stimulation field size (i.e., how broad the stimulus is in location or feature space) and changes in the attentional field size, which allows the model to account for a wide range of experimental findings. While Herrmann and colleagues (2012) kept the stimulus field fixed (e.g., the target was only a single feature value), within the context of the normalization model, our experiments varied the stimulus field by manipulating the range of the target colors and assumed that participants adjusted their attentional focus accordingly. Further investigations that comprehensively manipulate the size of the stimulation and attention fields separately will be necessary to directly test the predictions of the normalization model within different feature spaces.

Models of spatial attention take advantage of the known map-like structure of spatial representations. For example, neighboring spatial positions in the visual field are represented nearby each other in visual cortex, while positions further apart are represented at larger cortical distances (Gardner, Merriam, Movshon, & Heeger, 2008; Mountcastle, 1997).

Presumably, this retinotopic organization allows attention to modulate visual processing in a targeted way across different parts of the cortical map, for example enhancing smaller or larger contiguous regions within the map, which directly correspond to small and large regions in the external world. Indeed, researchers have argued that this organizing principle can explain cognitive capacity limits, such as those found in attention and working memory (Franconeri, Alvarez, & Cavanagh, 2013). Such map-like structures also exist for visual features: for example, motion direction is organized by similarity in MT (Albright, Desimone, & Gross, 1984), and color maps that are based on perceptual similarity have been found in regions of the ventral processing stream such as V4 (Bohon, Hermann, Hansen, & Conway, 2016; Brouwer & Heeger, 2009; Conway & Tsao, 2009). At a representational level, these maps could allow attention to spread to relevant features that are similar to one another (i.e., represented nearby each other in the feature map), which would allow attention to utilize similar operations across different feature spaces. Thus, there may be a fundamental similarity in how attention selects ranges of features within these feature maps and locations within retinotopically-organized spatial maps. Together, this would suggest that separate mechanisms for feature-based and spatial attention are not necessary (as in Boolean Map theory, Huang & Pashler, 2007, e.g.); instead, a general set of attentional mechanisms can be used across any representations that are appropriately organized. Therefore, we might anticipate that any stimulus space that has a map-like organizational structure would follow similar principles and allow for flexibility in the focus of attention. Possible examples include shape (Tanaka, 1996, 2003), motion direction (Albright et al., 1984), and sound frequency (Merzenich & Brugge, 1973; Moerel, De Martino, & Formisano, 2012). On the other hand, while relational information in some contexts may affect selection of

specific features, it remains unclear whether and how relations may impact spatial attention, suggesting some potential differences between selection in these domains that remain unresolved as of yet.

Conclusion

Overall, our study demonstrates that feature-based attention is not as restricted as some previous research has suggested, and that attention can be relatively efficiently tuned more broadly or narrowly as required by the range of currently relevant feature values. This seems appropriate for an adaptive visual system, given that the quality of visual input is rarely constant over time. For color in particular, viewing and lighting conditions can dramatically impact perception (Brainard et al., 2006; Lafer-Sousa, Hermann, & Conway, 2015; McDermott, Malkoc, Mulligan, & Webster, 2010), and so flexibility in the attentional system can allow for some stability across these possible changes.

As we have argued, our results mirror previous research in spatial attention, where a flexible size of the attentional focus is a core aspect of many models. Our study thus adds to the evidence suggesting that similar selection principles underlie spatial and feature-based attention. For example, it has recently been shown that feature-based attention elicits surround-suppression in feature space (Navalpakkam & Itti, 2007; Störmer & Alvarez, 2014; Wang, Miller, & Liu, 2015), similar to the selection profile of spatial attention (Hopf et al., 2006; Larsson, Solomon, & Kohn, 2016; Müller et al., 2005). Our results demonstrate that attention can select more narrow or broad parts of feature space, analogous to selecting small or large spatial regions, consistent with theories that argue in favor of flexible selection mechanisms

(Becker et al., 2014; Eriksen & St. James, 1986). Broadly, these findings demonstrate that at least some of the mechanisms underlying spatial and feature-based attention may be shared, indicating that more effort should be given to understanding the intersection of these two modes of attention.

References

- Albright, T. D., Desimone, R., & Gross, C. G. (1984). Columnar organization of directionally selective cells in visual area MT of the macaque. *Journal of Neurophysiology*, 51(1), 16–31.
<https://doi.org/10.1152/jn.1984.51.1.16>
- Alvarez, G. A., & Cavanagh, P. (2005). Independent Resources for Attentional Tracking in the Left and Right Visual Hemifields. *Psychological Science*, 16(8), 637–643.
<https://doi.org/10.1111/j.1467-9280.2005.01587.x>
- Andersen, S. K., Hillyard, S. A., & Müller, M. M. (2008). Attention Facilitates Multiple Stimulus Features in Parallel in Human Visual Cortex. *Current Biology*, 18(13), 1006–1009.
<https://doi.org/10.1016/j.cub.2008.06.030>
- Andersen, S. K., Hillyard, S. A., & Müller, M. M. (2013). Global Facilitation of Attended Features Is Obligatory and Restricts Divided Attention. *Journal of Neuroscience*, 33(46), 18200–18207. <https://doi.org/10.1523/JNEUROSCI.1913-13.2013>
- Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 834–846.
<https://doi.org/10.1037/0096-1523.26.2.834>
- Ball, K., & Sekuler, R. (1981). Cues reduce direction uncertainty and enhance motion detection. *Perception & Psychophysics*, 30(2), 119–128. <https://doi.org/10.3758/BF03204469>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
<https://doi.org/10.18637/jss.v067.i01>
- 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(2), 247–265.

<https://doi.org/10.1037/a0018808>

Becker, S. I., Folk, C. L., & Remington, R. W. (2010). The Role of Relational Information in Contingent Capture. *Journal of Experimental Psychology: Human Perception and Performance*, 36(6), 1460–1476. <https://doi.org/10.1037/a0020370>

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(5), 634–647. <https://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(1), 264–291. <https://doi.org/10.1037/a0033489>

Becker, S. I., Martin, A., & Hamblin-Frohman, Z. (2019). Target templates in singleton search vs. feature-based search modes. *Visual Cognition*, 27(5–8), 502–517. <https://doi.org/10.1080/13506285.2019.1676352>

Bohon, K. S., Hermann, K. L., Hansen, T., & Conway, B. R. (2016). Representation of perceptual color space in macaque posterior inferior temporal cortex (The V4 complex). *ENeuro*, 3(4). <https://doi.org/10.1523/ENEURO.0039-16.2016>

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436.

Brainard, D. H., Longère, P., Delahunt, P. B., Freeman, W. T., Kraft, J. M., & Xiao, B. (2006). Bayesian model of human color constancy. *Journal of Vision*, 6, 1267–1281. <https://doi.org/10.1167/6.11.10>

Bravo, M. J., & Farid, H. (2012). Task demands determine the specificity of the search template.

Attention, Perception, and Psychophysics, 74(1), 124–131.

<https://doi.org/10.3758/s13414-011-0224-5>

Brouwer, G. J., & Heeger, D. J. (2009). Decoding and Reconstructing Color from Responses in

Human Visual Cortex. *Journal of Neuroscience*, 29(44), 13992–14003.

<https://doi.org/10.1523/JNEUROSCI.3577-09.2009>

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, 51(13), 1484–1525.

<https://doi.org/10.1016/j.visres.2011.04.012>

Castiello, U., & Umiltà, C. (1990). Size of the attentional focus and efficiency of processing. *Acta*

Psychologica, 73(3), 195–209. [https://doi.org/10.1016/0001-6918\(90\)90022-8](https://doi.org/10.1016/0001-6918(90)90022-8)

Castiello, U., & Umiltà, C. (1992). Splitting Focal Attention. *Journal of Experimental Psychology:*

Human Perception and Performance, 18(3), 837–848. [https://doi.org/10.1037/0096-](https://doi.org/10.1037/0096-1523.18.3.837)

[1523.18.3.837](https://doi.org/10.1037/0096-1523.18.3.837)

Chapman, A. F., & Störmer, V. S. (2022). Feature similarity is non-linearly related to attentional

selection: evidence from visual search and sustained attention tasks. *Journal of Vision*,

22(8), 4. <https://doi.org/10.1167/jov.22.8.4>

Conway, B. R., & Tsao, D. Y. (2009). Color-tuned neurons are spatially clustered according to

color preference within alert macaque posterior inferior temporal cortex. *Proceedings of*

the National Academy of Sciences of the United States of America, 106(42), 18034–18039.

<https://doi.org/10.1073/pnas.0810943106>

Cutzu, F., & Tsotsos, J. K. (2003). The selective tuning model of attention: psychophysical

evidence for a suppressive annulus around an attended item. *Vision Research*, 43(2), 205–

219. [https://doi.org/10.1016/S0042-6989\(02\)00491-1](https://doi.org/10.1016/S0042-6989(02)00491-1)
- de Leeuw, J. R. (2015). jsPsych: A JavaScript library for creating behavioral experiments in a Web browser. *Behavior Research Methods*, 47(1), 1–12. <https://doi.org/10.3758/s13428-014-0458-y>
- Desimone, R., & Duncan, J. (1995). Neural Mechanisms of Selective Visual Attention. *Annual Review of Neuroscience*, 18(1), 193–222.
<https://doi.org/10.1146/annurev.ne.18.030195.001205>
- Dori, H., & Henik, A. (2006). *Indications for two attentional gradients in endogenous visual-spatial attention. Visual Cognition* (Vol. 13). <https://doi.org/10.1080/13506280500277504>
- Downing, C. J., & Pinker, S. (1985). The spatial structure of visual attention. In M. I. Posner & O. S. M. Marin (Eds.), *Attention and Performance XI*. Routledge.
- Duncan, J., & Humphreys, G. W. (1989). Visual Search and Stimulus Similarity. *Psychological Review*, 96(3), 433–458. <https://doi.org/10.1037/0033-295X.96.3.433>
- Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention. *Perception & Psychophysics*, 40(4), 225–240.
- Eriksen, C. W., & Yeh, Y. Y. (1985). Allocation of Attention in the Visual Field. *Journal of Experimental Psychology: Human Perception and Performance*, 11(5), 583–597.
<https://doi.org/10.1037/0096-1523.11.5.583>
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control. *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 1030–1044. <https://doi.org/10.1037/0096-1523.18.4.1030>
- Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources: Competitive

content maps for attention and memory. *Trends in Cognitive Sciences*, 17(3), 134–141.

<https://doi.org/10.1016/j.tics.2013.01.010>

Gardner, J. L., Merriam, E. P., Movshon, J. A., & Heeger, D. J. (2008). Maps of visual space in human occipital cortex are retinotopic, not spatiotopic. *Journal of Neuroscience*, 28(15), 3988–3999. <https://doi.org/10.1523/JNEUROSCI.5476-07.2008>

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(12), 1993–2007. <https://doi.org/10.1037/xhp0000430.supp>

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

Grubert, A., & Eimer, M. (2016). All set, indeed! N2PC components reveal simultaneous attentional control settings for multiple target colors. *Journal of Experimental Psychology: Human Perception and Performance*, 42(8), 1215–1230. <https://doi.org/10.1037/xhp0000221>

Hamblin-Frohman, Z., & Becker, S. I. (2021). The attentional template in high and low similarity search: Optimal tuning or tuning to relations? *Cognition*, 212(April), 104732. <https://doi.org/10.1016/j.cognition.2021.104732>

Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., & Heeger, D. J. (2010). When size matters: Attention affects performance by contrast or response gain. *Nature Neuroscience*, 13(12), 1554–1561. <https://doi.org/10.1038/nn.2669>

Hopf, J.-M. M., Boehler, C. N., Luck, S. J., Tsotsos, J. K., Heinze, H.-J. J., & Schoenfeld, M. A.

- (2006). Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proceedings of the National Academy of Sciences*, 103(4), 1053–1058. <https://doi.org/10.1073/pnas.0507746103>
- Hout, M. C., & Goldinger, S. D. (2014). Target templates: the precision of mental representations affects attentional guidance and decision-making in visual search. *Attention, Perception, and Psychophysics*, 77(1), 128–149. <https://doi.org/10.3758/s13414-014-0764-6>
- Huang, L., & Pashler, H. (2007). A Boolean Map Theory of Visual Attention. *Psychological Review*, 114(3), 599–631. <https://doi.org/10.1037/0033-295X.114.3.599>
- Itthipuripat, S., Garcia, J. O., Rungratsameetaweemana, N., Sprague, T. C., & Serences, J. T. (2014). Changing the spatial scope of attention alters patterns of neural gain in human cortex. *Journal of Neuroscience*, 34(1), 112–123. <https://doi.org/10.1523/JNEUROSCI.3943-13.2014>
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40(10–12), 1489–1506. [https://doi.org/10.1016/S0042-6989\(99\)00163-7](https://doi.org/10.1016/S0042-6989(99)00163-7)
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased Activity in Human Visual Cortex during Directed Attention in the Absence of Visual Stimulation. *Neuron*, 22, 751–761. [https://doi.org/10.1016/S0896-6273\(00\)80734-5](https://doi.org/10.1016/S0896-6273(00)80734-5)
- LaBerge, D., & Brown, V. (1989). Theory of Attentional Operations in Shape Identification. *Psychological Review*, 96(1), 101–124. <https://doi.org/10.1037/0033-295X.96.1.101>
- Lafer-Sousa, R., Hermann, K. L., & Conway, B. R. (2015). Striking individual differences in color

perception uncovered by “the dress” photograph. *Current Biology*, 25(13), R545–R546.

<https://doi.org/10.1016/j.cub.2015.04.053>

Lamy, D., & Tsal, Y. (2001). On the status of location in visual attention. *European Journal of Cognitive Psychology*, 13(3), 305–342. <https://doi.org/10.1080/09541440125789>

Larsson, J., Solomon, S. G., & Kohn, A. (2016). fMRI adaptation revisited. *Cortex*, 80, 154–160.

<https://doi.org/10.1016/j.cortex.2015.10.026>

Ling, S., Liu, T., & Carrasco, M. (2009). How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Research*, 49(10), 1194–1204.

<https://doi.org/10.1016/j.visres.2008.05.025>

Liu, T., Becker, M. W., & Jigo, M. (2013). Limited featured-based attention to multiple features.

Vision Research, 85, 36–44. <https://doi.org/10.1016/j.visres.2012.09.001>

Liu, T., & Jigo, M. (2017). Limits in feature-based attention to multiple colors. *Attention, Perception, and Psychophysics*, 79(8), 2327–2337. <https://doi.org/10.3758/s13414-017-1390-x>

Liu, T., Larsson, J., & Carrasco, M. (2007). Feature-Based Attention Modulates Orientation-Selective Responses in Human Visual Cortex. *Neuron*, 55(2), 313–323.

<https://doi.org/10.1016/j.neuron.2007.06.030>

Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research*, 47(1), 108–113.

<https://doi.org/10.1016/j.visres.2006.09.017>

Maringelli, F., & Umiltà, C. (1998). The control of the attentional focus. *European Journal of Cognitive Psychology*, 10(3), 225–246. <https://doi.org/10.1080/713752276>

- Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, 14(9), 744–751.
<https://doi.org/10.1016/j.cub.2004.04.028>
- Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, 29(6), 317–322. <https://doi.org/10.1016/j.tins.2006.04.001>
- McDermott, K. C., Malkoc, G., Mulligan, J. B., & Webster, M. A. (2010). Adaptation and visual salience. *Journal of Vision*, 10(13), 1–32. <https://doi.org/10.1167/10.13.17>
- McMains, S. A., & Somers, D. C. (2004). Multiple Spotlights of Attentional Selection in Human Visual Cortex. *Neuron*, 42, 677–686. [https://doi.org/10.1016/S0896-6273\(04\)00263-6](https://doi.org/10.1016/S0896-6273(04)00263-6)
- Merzenich, M. M., & Brugge, J. F. (1973). Representation of the cochlear partition on the superior temporal plane of the macaque monkey. *Brain Research*, 50(2), 275–296.
[https://doi.org/10.1016/0006-8993\(73\)90731-2](https://doi.org/10.1016/0006-8993(73)90731-2)
- Moerel, M., De Martino, F., & Formisano, E. (2012). Processing of natural sounds in human auditory cortex: Tonotopy, spectral tuning, and relation to voice sensitivity. *Journal of Neuroscience*, 32(41), 14205–14216. <https://doi.org/10.1523/JNEUROSCI.1388-12.2012>
- Mountcastle, V. B. (1997). The columnar organization of the neocortex. *Brain*, 120(4), 701–722.
<https://doi.org/10.1093/brain/120.4.701>
- Mounts, J. R. W. (2000). Attentional capture by abrupt onsets and feature singletons produces inhibitory surrounds. *Perception & Psychophysics*, 62(7), 1485–1493.
<https://doi.org/10.3758/BF03212148>
- Müller, N. G., Mollenhauer, M., Rösler, A., & Kleinschmidt, A. (2005). The attentional field has a Mexican hat distribution. *Vision Research*, 45(9), 1129–1137.

<https://doi.org/10.1016/j.visres.2004.11.003>

Navalpakkam, V., & Itti, L. (2007). Search Goal Tunes Visual Features Optimally. *Neuron*, 53(4), 605–617. <https://doi.org/10.1016/j.neuron.2007.01.018>

Pestilli, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research*, 45(14), 1867–1875.

<https://doi.org/10.1016/j.visres.2005.01.019>

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32(1), 3–25. <https://doi.org/10.1080/00335558008248231>

Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109(2), 160–174.

<https://doi.org/10.1037/0096-3445.109.2.160>

Prins, N., & Kingdom, F. A. A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. Retrieved from <http://www.palamedestoolbox.org>

Rajananda, S., Lau, H., & Odegaard, B. (2018). A random-dot kinematogram for web-based vision research. *Journal of Open Research Software*, 6(1). <https://doi.org/10.5334/jors.194>

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, 27, 611–647.

<https://doi.org/10.1146/annurev.neuro.26.041002.131039>

Reynolds, J. H., & Heeger, D. J. (2009). The Normalization Model of Attention. *Neuron*, 61(2), 168–185. <https://doi.org/10.1016/j.neuron.2009.01.002>

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin and Review*, 16(2), 225–

237. <https://doi.org/10.3758/PBR.16.2.225>

Sàenz, M., Buraças, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research*, 43(6), 629–637. [https://doi.org/10.1016/S0042-](https://doi.org/10.1016/S0042-6989(02)00595-3)

6989(02)00595-3

Schönhammer, J. G., Grubert, A., Kerzel, D., & Becker, S. I. (2016). Attentional guidance by relative features: Behavioral and electrophysiological evidence. *Psychophysiology*, 53(7), 1074–1083. <https://doi.org/10.1111/psyp.12645>

Shulman, G. L., Sheehy, J. B., & Wilson, J. (1986). Gradients of spatial attention. *Acta Psychologica*, 61, 167–181. [https://doi.org/10.1016/0001-6918\(86\)90029-6](https://doi.org/10.1016/0001-6918(86)90029-6)

Störmer, V. S., & Alvarez, G. A. (2014). Feature-based attention elicits surround suppression in feature space. *Current Biology*, 24(17), 1985–1988.

<https://doi.org/10.1016/j.cub.2014.07.030>

Tanaka, K. (1996). Inferotemporal Cortex and Object Vision. *Annual Review of Neuroscience*, 19, 109–139. <https://doi.org/10.1146/annurev.neuro.19.1.109>

Tanaka, K. (2003). Columns for complex visual object features in the inferotemporal cortex: Clustering of cells with similar but slightly different stimulus selectivities. *Cerebral Cortex*, 13(1), 90–99. <https://doi.org/10.1093/cercor/13.1.90>

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12, 97–136. [https://doi.org/10.1016/0010-0285\(80\)90005-5](https://doi.org/10.1016/0010-0285(80)90005-5)

Wang, Y., Miller, J., & Liu, T. (2015). Suppression effects in feature-based attention. *Journal of Vision*, 15(5), 1–16. <https://doi.org/10.1167/15.5.15>

White, A. L., & Carrasco, M. (2011). Feature-based attention involuntarily and simultaneously

improves visual performance across locations. *Journal of Vision*, 11(6), 1–10.

<https://doi.org/10.1167/11.6.15>

Williams, J. R., Brady, T. F., & Störmer, V. S. (2022). Guidance of Attention by Working Memory Is a Matter of Representational Fidelity. *Journal of Experimental Psychology: Human Perception and Performance*, 48(3), 202–231. <https://doi.org/10.1037/xhp0000985>

Witkowski, P. P., & Geng, J. J. (2022). Attentional Priority Is Determined by Predicted Feature Distributions. *Journal of Experimental Psychology: Human Perception and Performance*. <https://doi.org/10.1037/xhp0001041>

Wolfe, J. M. (1994). Guided Search 2.0 A revised model of visual search. *Psychonomic Bulletin & Review*, 1(2), 202–238. <https://doi.org/10.3758/BF03200774>

York, A. A., Sewell, D. K., & Becker, S. I. (2020). Dual target search: Attention tuned to relative features, both within and across feature dimensions. *Journal of Experimental Psychology: Human Perception and Performance*, 46(11), 1368–1386. <https://doi.org/10.1037/xhp0000851>

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(3), 336–353. <https://doi.org/10.1037/xhp0000609>

Yu, X., Hanks, T. D., & Geng, J. J. (2022). Attentional Guidance and Match Decisions Rely on Different Template Information During Visual Search. *Psychological Science*, 33(1), 105–120. <https://doi.org/10.1177/09567976211032225>

Yu, X., Johal, S. K., & Geng, J. J. (2022). Visual search guidance uses coarser template

information than target-match decisions. *Attention, Perception, and Psychophysics*, 1432–1445. <https://doi.org/10.3758/s13414-022-02478-3>