Effects of spatial cues on color-change detection in humans

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Studies of covert spatial attention have largely used motion, orientation, and contrast stimuli as these features are fundamental components of vision. The feature dimension of color is also fundamental to visual perception, particularly for catarrhine primates, and yet very little is known about the effects of spatial attention on color perception. Here we present results using novel dynamic color stimuli in both discrimination and color-change detection tasks. We find that our stimuli yield comparable discrimination thresholds to those obtained with static stimuli. Further, we find that an informative spatial cue improves performance and speeds response time in a color-change detection task compared with an uncued condition, similar to what has been demonstrated for motion, orientation, and contrast stimuli. Our results demonstrate the use of dynamic color stimuli for an established psychophysical task and show that color stimuli are well suited to the study of spatial attention.

Introduction

Primates rely on covert spatial attention to selectively process nonfoveal visual input. The allocation of covert attention is characterized by improved discrimination and detection performance and shorter response times (for a recent review, see Carrasco, 2011). Most studies of visual spatial attention have used the visual feature dimensions of motion, orientation, and contrast; understanding how attention modulates processing in these feature dimensions is of great interest because they are fundamental components of visual perception (Ferster & Miller, 2000; Hildreth & Koch, 1987).

Another stimulus dimension that is fundamental to visual perception is color. The capacity for color vision is furnished by cone photopigments with varied spectral sensitivity. Although primitive mammals possessed at least three cone photopigment genes, their probable nocturnality deemphasized the importance of color vision, thus resulting in the majority of extant mammals having only two such genes (Jacobs, 2009). Among mammals, only the catarrhine primates (old world monkeys, apes, and humans) added a third gene by duplication about 30 million years ago (Jacobs, 2009), consistent with a special importance of trichromatic color vision to this subgroup. In support of this view, there is evidence that trichromacy furnishes advantages over dichromacy in foraging for fruit (Osorio & Vorobyev, 1996) and leaves (Lucas et al., 2003) and in reading social signals from conspecifics (Changizi, Zhang, & Shimojo, 2006).

Despite its importance to visual perception in primates, color has received relatively little scrutiny in the attention literature. The majority of previous work on color and attention has focused on feature-based attention. A human positron emission tomography study found that performance in a color task was weakened by requiring subjects to monitor several feature dimensions simultaneously (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). Human electrophysiological studies have shown enhanced representations of attended color stimuli (Di Russo, Spinelli, & Morrone, 2001; Hillyard & Münte, 1984). Attending selectively to a color can induce motion percepts in ambiguous displays in humans (Blaser, Sperling, & Lu, 1999; Cavanagh, 1992). There are also several electrophysiological studies in monkeys showing feature-based enhancement of color signals (McAdams & Maunsell, 1999; Motter, 1993; Müller, Philiastides, & Newsome, 2005; Saenz, Buraĉas, & Boynton, 2003).

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In contrast, there have been only a handful of articles that have looked at the effects of spatial attention on color processing. Two studies found color task performance decrements when subjects were required to monitor multiple spatial locations rather than a single location (Morrone, Denti, & Spinelli, 2004; Prinzmetal, Amiri, Allen, & Edwards, 1998). Meanwhile, Fuller and Carrasco (2006) found an effect of cueing on perceived saturation but no effect on hue. However, the goal of that work was to determine whether attention alters the subjective experience of color, as it does other properties (Carrasco, 2011), not to determine whether spatial cueing can improve perceptual performance in a color task.

To address this gap in our understanding, we have developed a novel dynamic color stimulus that shares several of the desirable features of the commonly used random dot motion stimulus (Britten, Shadlen, Newsome, & Movshon, 1992). We then used this stimulus in a set of three experiments designed to test the ability of human subjects to detect color changes and to determine how this ability is altered by spatial cues. First, because these color stimuli are new, we first confirmed that they support performance that is comparable to that obtained using more conventional static stimuli (Hansen, Giesel, & Gegenfurtner, 2008; Krauskopf & Gegenfurtner, 1992). We next measured performance in a task design that could accommodate the addition of an informative spatial cue. Finally, we tested how such spatial cues affected color-change detection performance. As in attention tasks using motion, orientation, or contrast, we found that spatial cues can significantly improve detection and reduce response times.

Methods

Visual display

Stimuli were displayed at 1152 × 870 resolution, 60-Hz frame rate on a Sony GDM-C520 CRT (Sony Corp., Tokyo, Japan) controlled by a Mac Mini (Mid 2010 Model; Apple, Cupertino, CA) running Matlab R2012b (The Mathworks, Natick, MA) with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007). Display phosphor luminances and chromaticities were measured with a Tektronix J18 LumaColor II Photometer using the J1803 Luminance Head and J1810 Chromaticity Head, respectively (Tektronix, Inc., Wilsonville, OR).

Color space

Stimulus colors were defined on the Derrington Krauskopf Lennie (DKL) color space (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982). The two chromatic axes of the DKL space correspond to the two categories of cone opponency identified for retinal ganglion cells and neurons in the lateral geniculate nucleus. Values along these axes are combinations of signals from short (S), medium (M), and long (L) wavelength cone types; one axis is termed *constant blue* L – M, and the other *constant red*, S – (L + M). The third achromatic luminance axis is defined as L + M. The two chromatic axes lie in an isoluminant plane, and the intersection of all three axes is termed the *white point*. Following the convention of Hansen and colleagues (2008), we scaled each axis of the DKL space between −1 and +1, with the extremities of this interval reflecting the maximum possible contrast on the display used.

The details of the method used to convert between DKL and RGB coordinates have been given elsewhere (Hansen et al., 2006). In brief, we used the cone fundamentals measured by Smith and Pokorny (1975), along with the coordinates of our display's red, green, and blue phosphors (in CIE space), to construct a rotation matrix allowing us to compute RGB values for any DKL coordinates (in the display's range). We then used individually measured luminance response functions for each phosphor to linearize display output. In practice, our stimuli were restricted to a plane defined by the S – (L + M) and L + M axes (see below). This plane was further restricted to an interval of [–0.15, 0.15] in the L + M "luminance" dimension (corresponding to an interval of [32.6, 42.6] cd/m^2; Figure 1B).

Visual stimuli

We designed novel dynamic color stimuli inspired by the "random dot kinematograms" ubiquitous in the study of vision and attention (Britten et al., 1992). The dynamic color stimuli were circularly windowed checkerboards of 29 × 29 ten-pixel checks (~6.5° diameter, 660 checks; Figure 1A). The color of each check was drawn from a distribution along the S – (L + M) axis of DKL space (Figure 1B): either a Gaussian distribution with fixed variance ($\sigma = 0.15$) and variable mean (μ ranged from −0.4 to +0.4), or a uniform distribution (interval [–0.5, +0.5]). The luminance of the check was then randomly drawn from the interval [–0.15, +0.15] along the L + M axis. This luminance noise was added to prevent individuals from exploiting idiosyncratic spectral sensitivity biases that might cause particular colors to appear lighter or darker. Each check had a lifetime of eight frames (~133 ms) during which its color and luminance values remained static. Once a check reached the end of its lifetime, its frame counter was reset and new color and luminance values

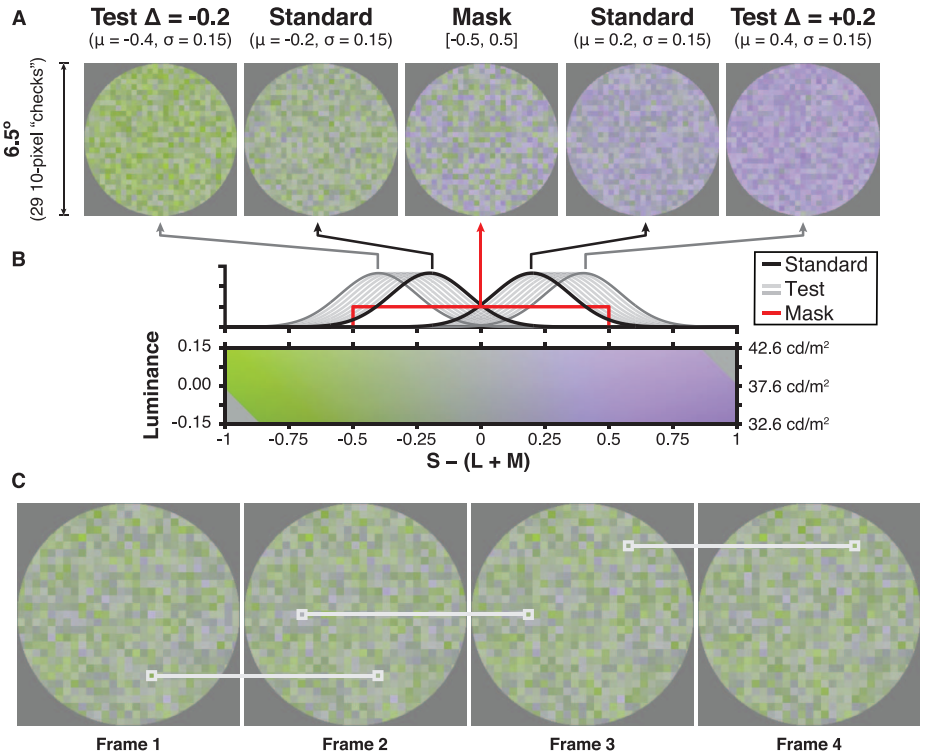


Figure 1. Dynamic color stimuli. (A) Example frames of "standard," "test," and "mask" stimuli. Shown from left to right are example frames of the largest Δ green test stimulus (Δ = −0.2), the green standard stimulus, the mask stimulus, the purple standard stimulus, and the largest Δ purple standard stimulus (Δ = +0.2). Corresponding distributions of each stimulus's check colors are shown below, in B. (B) Subset of Derrington Krauskopf Lennie (DKL) space used for stimulus generation. Stimulus check colors were drawn from the S − (L + M) axis of DKL space, with a luminance axis perturbation in the interval [−0.15, +0.15] (values in cd/m^2 are given on right abscissa). Gray corner regions indicate colors not achievable with our display. Check color distributions on the S − (L + M) axis for standard (black traces), test (gray traces), and mask stimuli (red trace) are depicted on axes above. (C) Schematic of frame-to-frame stimulus dynamics. An example of four consecutive frames of the green, Δ = −0.2, test stimulus, highlighting a single check in each frame reaching maximum lifetime and being reborn with newly drawn color in the next. Checks had a maximum lifetime of eight frames; in each frame, one of eight (~11%) of the 660 checks or ~82 checks were reborn.

were drawn and assigned to it in the subsequent frame (Figure 1C). In the first frame of stimulus presentation, each check's counter value was randomized to an integer between 1 and 8, so a fraction of checks were redrawn in each subsequent frame (on average ⅛ or ~82 checks per frame).

We used three versions of this dynamic color stimulus: standard stimuli, test stimuli, and masks. For standard stimuli, the color of each check was drawn from a Gaussian distribution ($\sigma = 0.15$) along the S – (L + M) axis with a mean value offset from zero ($\mu = -0.2$ or +0.2).

For test stimuli, the saturation was increased relative to the standard stimuli. For each of the two standard stimuli ($\mu = -0.2$ or +0.2), there were eight equally spaced test colors with increasing saturation relative to the standard (Figure 1A, B). Thus, for the $\mu = -0.2$ standard, test colors had mean saturations of {−0.225, −0.25, −0.275, −0.3, −0.325, −0.35, −0.375, −0.4}, and for $\mu = +0.2$, of {+0.225, +0.25, +0.275, +0.3, +0.325, +0.35, +0.375, +0.4}. For simplicity, we will refer to these test stimuli by their Δ values {± 0.025, ± 0.05, ± 0.075, ± 0.1, ± 0.125, ±0.15, ± 0.175, ± 0.2}.

Finally, for masks, the temporal properties were the same as described above for standard and test stimuli, but the check colors were drawn from a uniform distribution [−0.5, +0.5] along the S − (L + M) axis. It is important to note that at the first frame of each stimulus interval, all color and luminance values were redrawn; to eliminate any uncertainty regarding the start of each stimulus interval, there was no blending between mask and stimulus intervals.

Subjects

Eight male subjects between the ages of 28 and 50 years participated in the experiments (S1–S8 in figures and tables). Three were authors (S1, S2, S7), an additional three were members of the lab (S3, S6, S8), and the remaining two were naïve to the purposes of the experiments (S4, S5). All subjects had normal or

corrected-to-normal vision. All subjects were tested with the American Optical Hardy-Rand-Ritter Color Vision Plates, which revealed that seven of eight subjects had normal color vision (S2–S8), whereas the remaining subject was deuteranopic (S1); this type of deficit affects discrimination only along the L – M axis, and indeed, we found S1's performance similar to normal subjects. All subjects gave informed written consent prior to participating in any experimental sessions. Experimental protocols were approved by the institutional review board concerned with the use of human subjects.

All subjects completed Experiment 1 first (two sessions), Experiment 2 second (three sessions), and Experiment 3 third (six sessions), and the order of the sessions was the same for all subjects. In rare cases, one subject (the example subject) ran more than one session per day. In all other cases, at least 24 hr elapsed between sessions. Prior to the first session of each experiment, the subject was given brief (<30 trials) practice sessions with feedback from the experimenter regarding their performance.

Eye movements

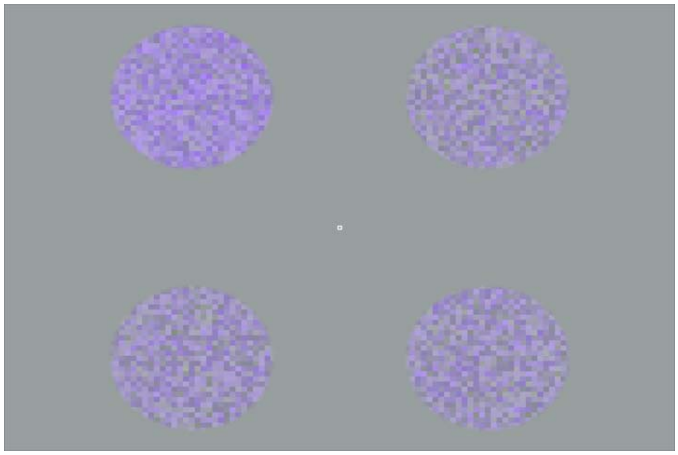
Eye position was monitored at 240 Hz with a video-based eye tracker (Iscan Inc., Woburn, MA); head movements were minimized using a chin rest and forehead band. Subjects were required to keep their gaze within 2° of the central fixation stimulus for the duration of each trial, and eye movement records were automatically examined once each trial ended. If a fixation break was detected, the trial was randomly reshuffled into the remaining trials in the session or the block, as appropriate (see below).

Manual responses

Subjects provided their responses manually using their right hand and a USB numeric keypad (Toshiba, Minato, Tokyo). A soft textured material was affixed to the four corner keys to allow easy identification by touch. In all experiments, response time was unlimited: The trial did not advance until a response was collected. Subjects were given an auditory tone feedback indicating that the response had been detected. This was followed by a 1- to 2-s intertrial interval during which data were saved and stimuli for the next trial were generated.

Experiment 1

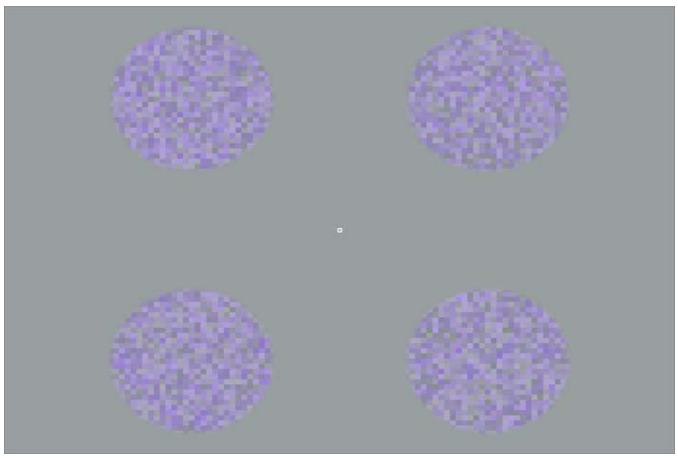
Experiment 1 was a color singleton detection task. Subjects were presented with four stimuli (three



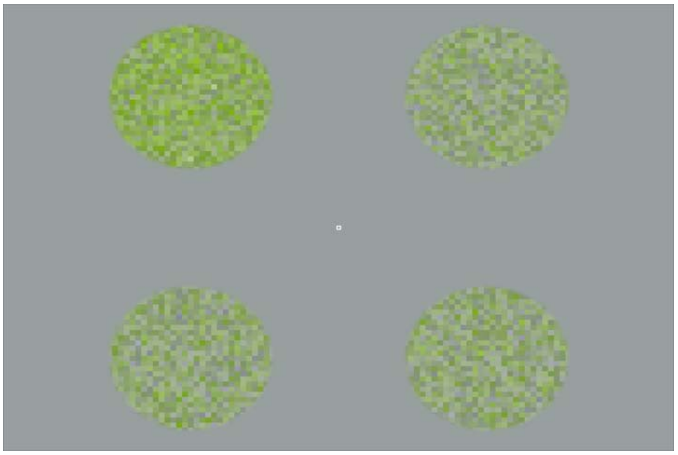
Movie 1. Experiment 1, example trial 1. Purple test stimulus ($\mu = 0.4$, $\Delta = 0.2$) in upper left and purple standard stimuli ($\mu = 0.2$) in upper right, lower left, and lower right. An "upper left" response was considered correct in this trial. Movie is shown at ½ of rate of stimulus presentation during experiment (30 fps vs. 60 fps). Note that stimuli were generated using the Derrington Krauskopf Lennie color space calibrated specifically to display used for experimentation (see the Methods section) and thus appearance will vary accordingly in a device-dependent manner.

standards and one test singleton) and required to indicate the location of the singleton with a button press (Movies 1–4). Subjects were instructed to locate the "more colorful" stimulus patch and were shown examples during brief practice sessions. Subjects were also informed that there was always a singleton present in the display.

A schematic of the trial structure is shown in Figure 2. Each trial began with subjects fixating a small (0.9° diameter) white square (69.4 cd/m^2) on a middle-gray



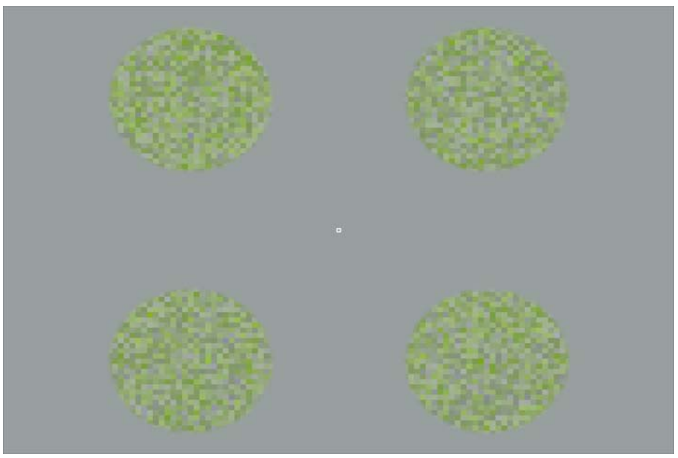
Movie 2. Experiment 1, example trial 2. Purple test stimulus ($\mu = 0.225$, $\Delta = 0.025$) in upper left and purple standard stimuli ($\mu = 0.2$) in upper right, lower left, and lower right. An "upper left" response was considered correct in this trial. Other aspects same as Movie 1.



Movie 3. Experiment 1, example trial 3. Green test stimulus ($\mu =$ 0.4, $\Delta = 0.2$) in upper left and green standard stimuli ($\mu = 0.2$) in upper right, lower left, and lower right. An "upper left" response was considered correct in this trial. Other aspects same as Movie 1.

background (37.6 cd/m^2) for 700 ms; next, four stimulus patches were added to the display for 500 ms (8° eccentricity, one per quadrant). If fixation had been maintained, the fixation stimulus then remained until a response was collected. If fixation was not maintained, the subject was given text feedback on the visual display that the trial would be repeated, pausing the experiment until any button press.

Subjects were instructed to indicate the location of the color singleton by pressing the spatially corresponding textured corner key on the response keypad (e.g., upper left corner key if the singleton was in the upper left of the display). No feedback regarding response accuracy was given.



Movie 4. Experiment 1, example trial 4. Green test stimulus ($\mu =$ 0.225, $\Delta = 0.025$) in upper left and green standard stimuli ($\mu =$ 0.2) in upper right, lower left, and lower right. An "upper left" response was considered correct in this trial. Other aspects same as Movie 1.

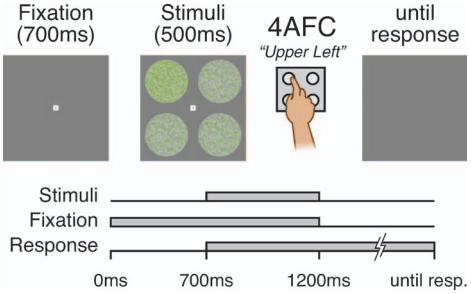


Figure 2. Experiment 1 procedure. In each trial, a fixation stimulus (white square) was presented for 700 ms, followed by four stimulus patches, three "standards" and one "test" for 500 ms. The screen then remained with only the background gray until the subject gave his or her response with a button press. The subject's task was to locate the test stimulus, which had greater saturation than the test stimuli. In this example with green stimuli, the test stimulus is located in the upper-left quadrant of the display, requiring the subject to press the button in the upper left of the response pad.

Trial ordering was pseudorandom but the same across all subjects. For each standard (nonsingletons), each test Δ (singleton) was repeated 10 times at each of the four stimulus locations (40 repetitions). Thus, there were 2 standards $\times$ 8 Δs $\times$ 40 repetitions = 640 trials per subject in Experiment 1. Prior to running any subjects, all 640 trials were mixed and split into two sets of 320 trials. This mixing was done to prevent the singleton from appearing at each location with equal frequency in each session, which might have improved guessing performance on difficult trials. Although randomization of trial order for each subject might have been preferable, there was a small amount of variation in trial ordering from subject to subject because fixation-break trials were randomly reshuffled into the remaining trials. Data were examined for effects of trial ordering on performance, but no pattern was found, and we do not believe that this had any impact on our results.

Experiment 2

Experiment 2 was a two-alternative forced choice (2AFC; yes/no) task. Subjects were presented serially with two color stimulus intervals flanked in time by masks and asked to judge whether the stimulus in the second interval was "more colorful" than that in the first ("yes"), or the same ("no"). Only one of two possible stimulus locations was occupied in a given trial. As in Experiment 1, subjects were shown examples and given the opportunity for a brief practice period.

A schematic of the trial structure is shown in Figure 3. After an initial 700-ms fixation period, a mask

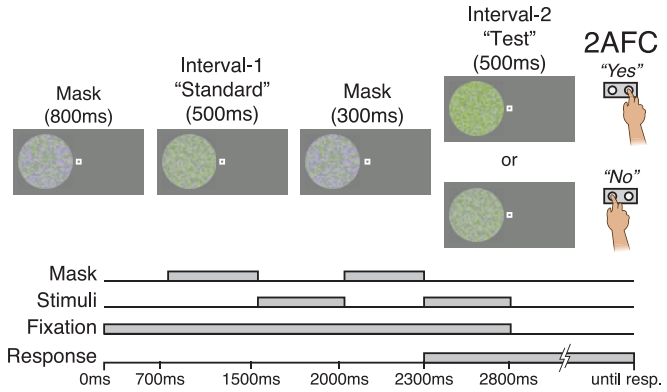


Figure 3. Experiment 2 procedure. In each trial, a fixation stimulus was presented for 700 ms followed by a mask stimulus for 800 ms, then the standard stimulus for 500 ms (Interval 1), then a mask stimulus for 300 ms, and finally the test stimulus for 500 ms (Interval 2). Then only the background luminance remained until the subject gave a response. The subject was required to indicate with a button press whether the test stimulus (Interval 2) was "more colorful" ("yes"; top example at right) than the standard stimulus (Interval 1), or not ("no"; bottom example). In this example, all stimuli were presented on the left; during the experiment, stimuli were presented on the left in 50% of trials and on the right in 50%.

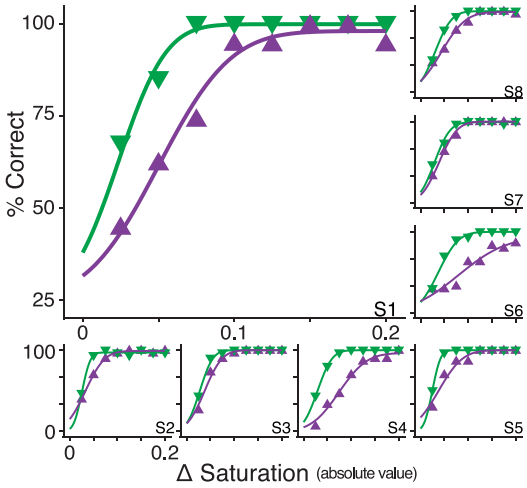


Figure 4. Experiment 1 discrimination performance. Enlarged plot is presented as an example (S1). Small plots have identical axis limits and tick-mark placement as large example (S2–S8). Data points (filled triangles) are percentage correct values for each Δ saturation plotted against the absolute value of Δ to allow for comparison of performance between green and purple stimuli. Green and purple traces are cumulative Gaussian fits to data. Associated threshold values are given in Table 1.

stimulus was shown for 800 ms (8° eccentricity) and then replaced by a standard stimulus lasting 500 ms (Interval 1). A second, 300-ms mask stimulus was then shown, followed by the 500-ms test stimulus (Interval 2; i.e., "change" – non-zero Δ, or "no change" – zero Δ, equivalent to a repetition of the standard).

Subjects were informed that they could respond any time after the onset of Interval 2. Subjects indicated a "yes" response by pressing the lower-right (textured) corner key on the response keypad and "no" by the lower-left key. No feedback regarding response accuracy was given. As described above, responses were not collected after fixation breaks; these trials were shuffled into those remaining in the session for later repetition.

The proportion of "change" and "no-change" trials was adjusted to minimize guessing. The task of the subjects was to respond "yes" to "change" trials and "no" to "no-change" trials, rather than locating the color singleton as in Experiment 1. Thus, in addition to nonzero Δ values, Experiment 2 included "no-change" ($\Delta = 0$) trials in which the test stimulus (Interval 2) had the same mean as the standard. We again repeated each of the eight nonzero Δs 40 times (20 per side) = 640 trials and included an additional 320 $\Delta = 0$ catch trials, for a total of 960 trials. We chose this quantity of no-change trials to avoid increasing the guess rate: A roughly equal number of change and no-change trials might have encouraged more guessing both in no-change and in difficult-change trials. We mixed all 960 trials and partitioned the experiment into three sessions prior to running subjects, to minimize guessing.

Experiment 3

Experiment 3 was a 2AFC (yes/no) task like Experiment 2, but with two stimuli presented simultaneously at different locations. This was designed to test how performance might be degraded by asking subjects to monitor two stimulus locations simultaneously and whether performance might improve when valid spatial cues were provided (Movies 5–7).

Each trial (Figure 5) began with a fixation period (700 ms) followed by the presentation of a pair of masks (8° left and right). In cued blocks, one mask was surrounded (for 500 ms) by a circular white cue-ring offset by ~0.23° (thickness ~0.14°) indicating which of the two locations might show the upcoming color change. In uncued blocks, no information was provided to the subject about which of the two locations might show the color change. After 800 ms, the masks were replaced with one of each standard stimulus (Interval 1) for 500 ms, then a pair of 300-ms duration masks, and finally by a pair of test stimuli for 500 ms (Interval 2).

In each trial, either one or neither of the test stimuli in Interval 2 had a nonzero Δ. In cued blocks, only the cued location might have a test stimulus in Interval 2 with nonzero Δ (100% valid cue), and the subjects' task was to respond "yes" if they detected this difference and "no" if no difference was detected. In uncued

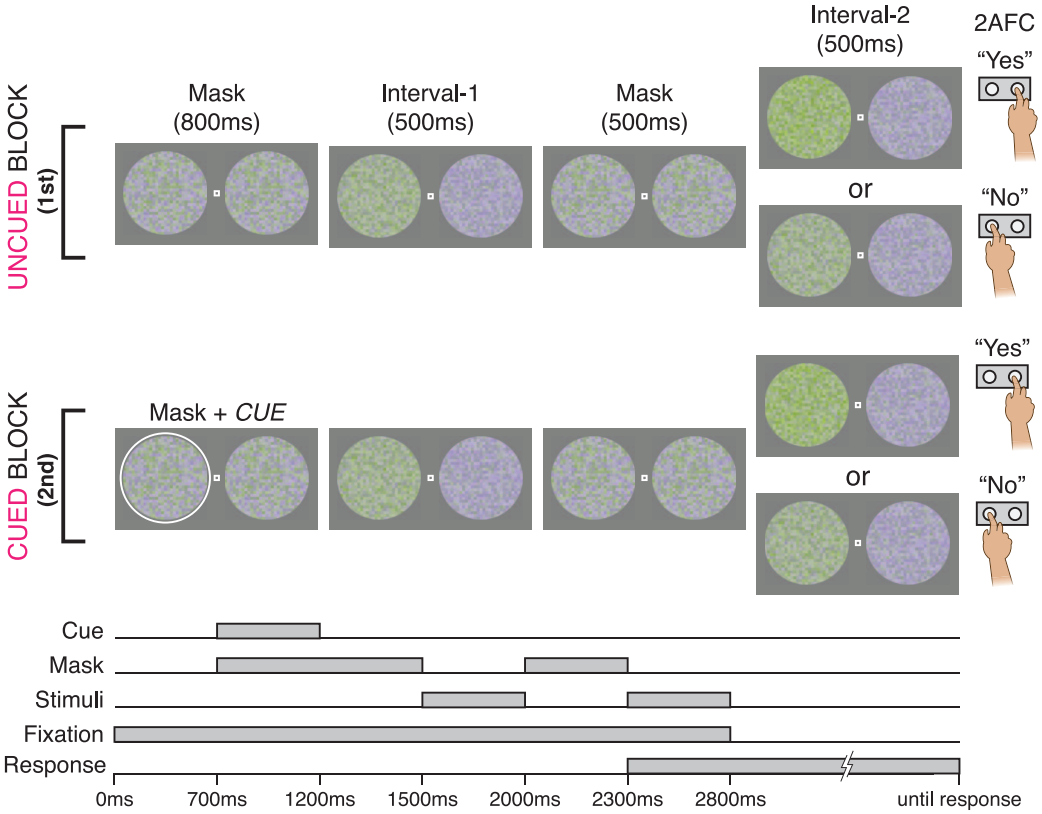
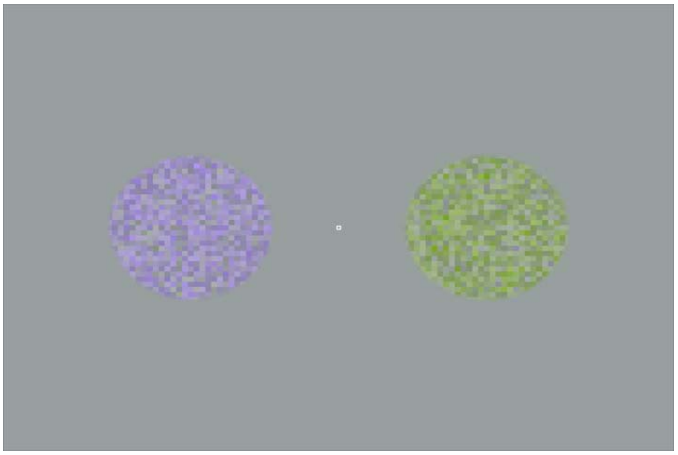
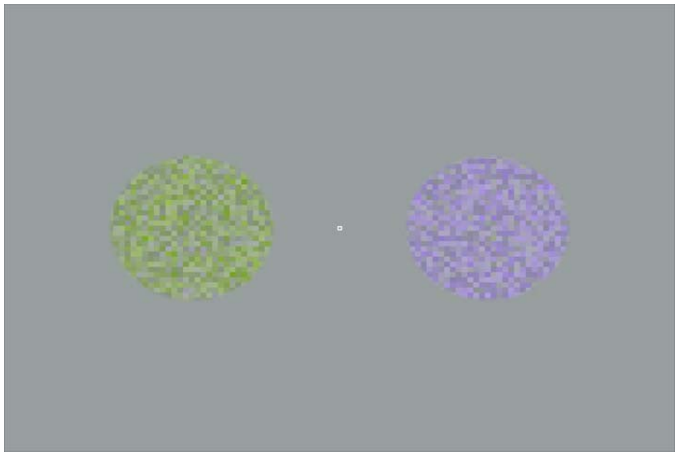


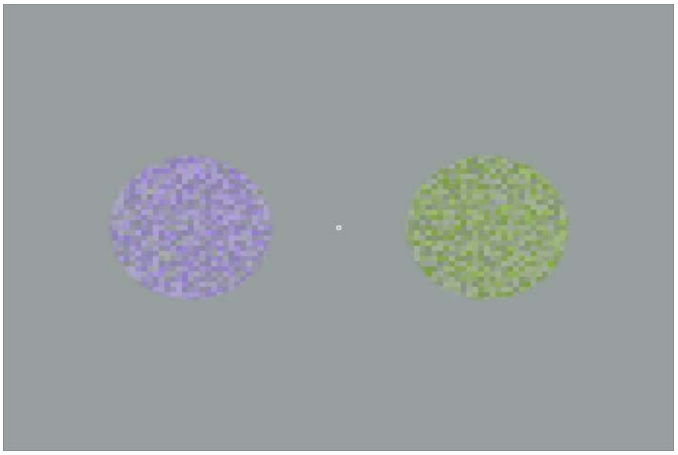
Figure 5. Experiment 3 procedure. In each trial of the uncued block (top image sequence), a fixation stimulus was presented for 700 ms followed by a mask stimulus for 800 ms, then one green and one purple standard stimulus for 500 ms (Interval 1), then two mask stimuli for 300 ms, and finally one green and one purple test stimulus for 500 ms (Interval 2). Then only background illumination remained until the subject gave a response. Trials in the cued block were the same, save for the addition of a cue-ring surrounding one of the two initial mask stimuli for 500 ms. In half of each subject's sessions, the uncued block was completed first and the cued block second, with this order reversed in the remaining sessions. In the uncued block, the subject's task was to respond "yes" if either of the stimuli in Interval 2 was more saturated than those in Interval 1 or "no" if neither was. In the cued block, the subject was to respond "yes" if the test stimulus in the cued location was more saturated or "no" if it was not.



Movie 5. Experiment 3, example trial 1. Cued-block trial with purple ($\mu = -0.2$) and green standards ($\mu = 0.2$) on the left and right, respectively, in Interval 1 and purple standard on left ($\mu = -0.2$), green test ($\mu = 0.4$, $\Delta = 0.2$) on right in Interval 2. A "yes" response was considered correct in this trial. Other aspects same as Movie 1.



Movie 6. Experiment 3, example trial 2. Cued-block trial with green ($\mu = 0.2$) and purple standards ($\mu = -0.2$) on the left and right (respectively) in Interval 1 and green standard on left ($\mu = 0.2$), purple test ($\mu = -0.4$, $\Delta = -0.2$) on right in Interval 2. A "yes" response was considered correct in this trial. Other aspects same as Movie 1.



Movie 7. Experiment 3, example trial 1. Cued-block trial with purple ($\mu = -0.2$) and green standards ($\mu = 0.2$) on the left and right (respectively) in Interval 1 and purple standard on left ($\mu = -0.2$), green test ($\mu = 0.2$, $\Delta = 0$) on right in Interval 2. A "no" response was considered correct in this trial. Other aspects same as Movie 1.

blocks, either stimulus location (but not both) might have a test stimulus in Interval 2 with nonzero Δ, and the subjects' task was again to respond "yes" or "no" depending on whether or not they detected a difference. As in Experiment 2, the lower-right corner key was used for "yes" responses and lower-left key for "no." Also, subjects were again shown examples and given the opportunity for a brief practice period prior to the session.

Both standards ($\mu = -0.2$ and $+0.2$) were presented in each trial. On half the trials (as in Figure 5), the $\mu = -0.2$ "green" standard was presented on the left and the $\mu = +0.2$ "purple" standard was presented on the right; on the other half, this pattern was reversed. A test stimulus was always presented in the appropriate spatial location for its standard, for example, if $\Delta = -0.025$, the test stimulus with $\mu = -0.225$ was always presented (in Interval 2) in the same location occupied by the $\mu = -0.2$ standard in Interval 1 (Movies 5–7).

Each of the six sessions of Experiment 3 had a cued and an uncued block. In total, Experiment 3 comprised 1,920 trials (960 cued, and 960 uncued); as in Experiment 2, those 960 trials were a combination of 640 nonzero Δ and 320 $\Delta = 0$ trials. Importantly, in the cued condition, cue presentation was balanced across location, standard color, and Δ value. Prior to running any subjects, cued and uncued trials were mixed separately, split into six 160-trial sets, and paired to make six 320-trial sessions. To avoid the impact of any during-session learning on performance in a particular type of block, in Sessions 1, 3, and 5, the uncued block was first, and in Sessions 2, 4, and 6, the cued block was first.

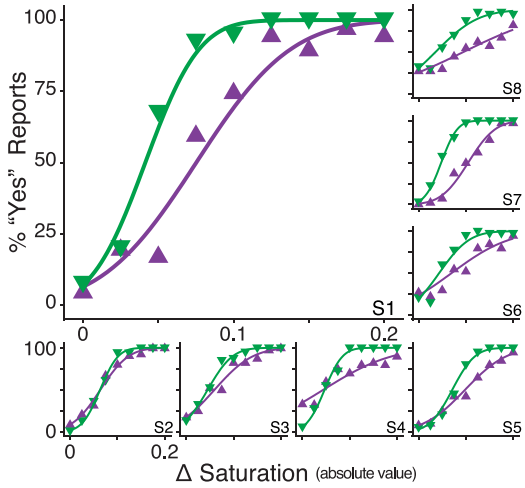


Figure 6. Experiment 2 detection performance. Enlarged plot presents example subject's data (S1). As previously, small plots have identical axis limits and tick-mark placement as large example (S2–S8). Data points (filled triangles) are percentage "yes" report values for each Δ saturation, plotted against the absolute value of Δ to allow for comparison of performance between green and purple stimuli. The percentage "yes" report values correspond to percentage correct for nonzero Δ (as in Figure 4) and to the false-alarm rate for $\Delta = 0$. Green and purple traces are cumulative Gaussian fits to data. Associated threshold values are given in Table 2.

Data analysis

Before pooling performance data across stimulus location for fitting, data sets were examined for irregularity. Hits were calculated for Experiments 1, 2, and 3, and correct rejections were calculated for Experiments 2 and 3. In Experiment 1, a hit was defined as a correct localization of the singleton; in Experiments 2 and 3, hits were defined as "yes" answers in response to nonzero Δ tests. Correct rejections were defined as "no" responses to $\Delta = 0$ tests. We calculated hits, correct rejections, and total trials separately for each standard and each location by subject (and cued/uncued conditions in Experiment 3), and a χ^2 proportion test was used to compare performance across locations for each subject and standard (and for each condition in Experiment 3). This test compares two or more proportions under the null hypothesis that the proportions are the same (Fleiss et al., 2013). We found no significant variations in the proportions of hits (Experiments 1, 2, and 3) or correct rejections (Experiments 2 and 3) by stimulus location (all $p > 0.1$; Experiment 1: $df = 3$, error $df = 636$, all $\chi^2 < 6$; Experiment 2: $df = 1$, error $df = 958$, all $\chi^2 < 3$; Experiment 3: $df = 1$, error $df = 1918$, all $\chi^2 < 3$).

Cumulative Gaussian functions were fit to individual subject performance data separately for each standard (and for cued/uncued in Experiment 3). Psychometric

functions were fitted using the psignifit toolbox version 2.5.6 for MATLAB (see http://bootstrap-software.org/psignifit/), which implements the maximum-likelihood method described by Wichmann and Hill (2001). The general form of the function Y we used was $Y(x; \alpha, \beta, \gamma, \lambda) = \gamma + (1 - \gamma - \lambda)$ x $F(x; \alpha, \beta)$, where x was the absolute value of Δ and F was a cumulative Gaussian function. The γ parameter is referred to as the "guess rate" and λ the "miss rate" or "lapse rate" (the former in "yes"/"no" and latter in n-AFC tasks). In the case of the cumulative Gaussian, the α and β parameters are the mean (μ) and standard deviation (σ) of the underlying distribution, respectively. Threshold performance was chosen to be the Δ yielding a value of 80% correct for a given psychometric function, and confidence intervals were computed by a bootstrapping procedure. Although arbitrary, the 80% level is one of several that have typically been used in previous studies.

We used a Monte Carlo method for comparison of individual subject performance between data sets. This procedure, which we refer to as a "Monte Carlo parameter test," tested the difference in fit parameters μ and σ between two data sets under the null hypothesis that the same psychometric function gave rise to both: a simulated joint distribution ($n = 10{,}000$) of differences, $P(\mu 1 - \mu 2, \sigma 1 - \sigma 2)$, between two data sets was generated by pooling and resampling, then the likelihood (p value) of the actual difference was calculated by comparison with this distribution. Because of differences in design between Experiment 1 and Experiments 2 and 3, this procedure allowed us to compare performance within Experiment 1 and between Experiments 2 and 3 but not between Experiment 1 and 2 or 3.

Response time data were also subjected to regularity tests prior to pooling across locations. Separately for each subject and standard color, response times grouped by stimulus location were compared using a Kruskal-Wallis nonparametric analysis of variance (ANOVA) and found to be indistinguishable (all $p > 0.15$; Experiment 1: $df = 3$, all $\chi^2 < 5$; Experiments 2 and 3: $df = 1$, all $\chi^2 < 1.5$). Confidence intervals on medians for a given sample of data were calculated by the formula $x \pm 1.57*(Q3 - Q1)/\mathrm{sqrt}(n)$, where x is the median, Q1 is the first quartile, Q3 is the third quartile, and n is the number of data points in the sample.

Results

We used our novel color stimulus in a series of three experiments leading up to a test of spatial attention on color-change detection. The aim of the first experiment was to compare color discrimination using our dynamic color stimuli to the performance obtained in previous studies using static colored disks. The second experiment tested the ability of subjects to detect differences in color across time, rather than across spatial locations. Finally, in the third experiment, we manipulated spatial attention during color-change detection by adding a distracter stimulus and measuring how spatial cueing changes performance. The series of three experiments was conducted in a total of eight human subjects, including two (S4, S5) who were naïve about the experimental aims.

Experiment 1: Color discrimination across spatial locations

To validate the use of dynamic color stimuli, we first used them in a protocol that emulated a previously established color discrimination procedure. In each trial, the subject was required to fixate a white square on a gray background while four circular stimulus patches were presented in the periphery (Figure 2). Three of the patches had one of two possible "standard" colors (green or purple), and the fourth "test" patch had the same hue but increased saturation relative to the standard (Figure 1A). The subject was instructed to indicate the location of the more colorful singleton patch by pressing one of four possible buttons.

We limited our color discrimination measurements to specific portions of DKL space. The standards' mean colors were ± 0.2 away from the adaptation point (the achromatic background), along the $S - (L + M)$ or blue-yellow axis (Figure 1A, B). For both the green and purple standard, there were eight possible mean test saturation values increasing away from the adaptation point in increments of 0.025 to a maximum test saturation of ± 0.4 (Δ of ± 0.2; Figure 1B). Thus, we always measured sensitivity to increasing saturation, away from the adaptation point, along the blue-yellow axis.

We calculated hits (correct localizations) and total trials for each of the four possible test stimulus locations and the two color standards. Observing no significant differences in performance depending on test location (see the Methods section), we pooled data across the four test locations for each subject, separately for the green and purple standards.

To summarize performance, we constructed psychometric functions and calculated psychophysical thresholds. We plotted performance (percentage correct) as a function of the difference in saturation between standard and test (Δ) and fit the data with cumulative Gaussian functions. We used the fitted functions to calculate 80% correct threshold values and

	Green (threshold and 95% CI)	Purple (threshold and 95% CI)
S1	0.04 [0.03, 0.05]	0.06 [0.05, 0.07]
S2	0.04 [0.04, 0.05]	0.06 [0.05, 0.07]
S3	0.05 [0.04, 0.06]	0.11 [0.10, 0.13]
S4	0.04 [0.03, 0.05]	0.07 [0.06, 0.08]
S5	0.06 [0.05, 0.08]	0.15 [0.11, 0.18]
S6	0.05 [0.04, 0.06]	0.06 [0.05, 0.08]
S7	0.05 [0.04, 0.06]	0.08 [0.06, 0.09]
S8	0.04 [0.03, 0.05]	0.08 [0.07, 0.10]

Table 1. Experiment 1 threshold performance values by subject. *Notes:* Threshold performance values (80% correct) for each subject (S1–S8) in Experiment 1, along with 95% confidence intervals in square brackets. Values rounded to nearest hundredth. Subjects S4 and S5 were naïve to the purposes of this experiment. Subjects S7, S2, and S1 are the first, second, and third author, respectively.

a bootstrapping procedure to estimate the associated confidence intervals (see the Methods section).

The pattern of discrimination results we observed was consistent across subjects (Figure 4). An example subject's data (S1; Figure 4, large panel) is representative of the pattern exhibited by the other seven subjects (S2-S8; Figure 4, small panels). Individuals reliably identified the location of the test stimulus above chance level (25%) for all saturation differences, for both standards. Across the eight subjects, the discrimination thresholds obtained with the green standard (0.04–0.06) were lower and less variable than those obtained with the purple standard (0.06–0.15; Table 1). This difference in discrimination threshold between green and purple standards was corroborated by a statistically significant difference in performance in each subject (Monte Carlo parameter test; all $p < 0.01$; see the Methods section).

These findings are consistent with previous studies of color discrimination. The range of threshold values we found with dynamic color stimuli is comparable to what has been previously found using static stimuli (Hansen et al., 2008; Krauskopf & Gegenfurtner, 1992). Moreover, the difference in discrimination thresholds that we observed between green and purple standards is also corroborated by the results from those studies.

Having established that our color stimuli yield results consistent with earlier work, we next evaluated a task design that would accommodate the addition of a spatial cue.

Experiment 2: Color-change detection

In our second experiment, we probed color-change detection in a single spatial location across two temporal intervals. Subjects fixated as in Experiment 1 and were presented with a single stimulus patch, either to the left or right of fixation (Figure 3). Colored stimuli were presented in two intervals—standard in Interval 1 followed by test in Interval 2—and each colored stimulus was preceded by a noise mask. The noise mask was gray on average but contained a range of green through gray to purple checks (Figure 1). The standard colors were as in Experiment 1, either green or purple, whereas the test color could either be more saturated than the standard or have the same saturation as the standard. The task of the subject was to indicate with a button press whether or not the stimulus in Interval 2 was more colorful (i.e., more saturated) than Interval 1 ("yes" or "no").

This choice of experimental design reflected our plan to test color perception while manipulating spatial attention (Experiment 3). The discriminations in Experiment 1 involved comparison across spatial locations—this is a well-established method for testing color discrimination but poorly suited for tests of spatial attention because stimuli at multiple spatial locations must be processed to perform the task. To examine how spatial cueing affects color perception, it was necessary to first establish baseline performance for stimuli presented at a single location.

Our performance metric was calculated as the proportion of "yes" reports for zero and nonzero Δs (difference in saturation between test and standard), for each of the two stimulus locations. Again, observing no significant differences in performance depending on test locations (see the Methods section), we combined the data within subjects, separately for the green and purple standards.

The pattern of results from this 2AFC task (Figure 6) was generally similar to what we obtained in Experiment 1. All subjects showed an orderly increase in "yes" reports with increasing Δ (Figure 6, filled symbols) over the same range of values used in Experiment 1. Also as in Experiment 1, individual detection thresholds were higher for saturation increases from the purple standard, compared with the green standard (Table 2), again corroborated by significant differences in performance (Monte Carlo parameter tests; all $p < 0.04$). In contrast to Experiment 1, most subjects displayed a small tendency to falsely report a saturation increase when none had occurred ($\Delta = 0$), reflecting a response bias.

Despite this one difference, the similarity of the outcomes between Experiments 1 and 2 demonstrates that these dynamic stimuli were effective for testing color judgments in a range of experimental designs. The results of Experiment 2 also provided a point of comparison for measuring performance under the more demanding conditions of our third experiment, in which we introduced spatial cues.

	Green (threshold and 95% CI)	Purple (threshold and 95% CI)
S1	0.09 [0.08, 0.10]	0.10 [0.10, 0.11]
S2	0.08 [0.07, 0.09]	0.11 [0.10, 0.13]
S3	0.07 [0.07, 0.08]	0.14 [0.12, 0.17]
S4	0.10 [0.10, 0.11]	0.16 [0.14, 0.17]
S5	0.09 [0.08, 0.10]	0.15 [0.13, 0.17]
S6	0.07 [0.06, 0.08]	0.14 [0.13, 0.15]
S7	0.10 [0.08, 0.11]	0.22 [0.19, 0.27]
S8	0.07 [0.06, 0.07]	0.12 [0.11, 0.13]

Table 2. Experiment 2 threshold performance values by subject. *Notes:* Threshold performance values (80% "yes" reports) for each subject (S1–S8) for Experiment 2, along with 95% confidence intervals in square brackets. Values rounded to the nearest hundredth.

Experiment 3: Effects of spatial cues on color-change detection

The goal of our final experiment was to determine whether spatial cueing provided any performance benefit in a color-change detection task. To that end, we increased spatial uncertainty by adding a second stimulus patch for subjects to monitor for possible color changes and a spatial cue that indicated which of the two stimuli might change.

The procedure used in Experiment 3 was an extension of the two-interval task used in Experiment 2. Uncued and cued trials were presented in separate blocks to avoid possible task-switching costs. In each uncued trial, either of the two stimuli might increase in saturation (Figure 5). In cued trials, a cue-ring was briefly presented surrounding one of the stimulus locations, and an increase in color saturation was possible only at the cued location (100% valid cue). Subjects were instructed to respond "yes" for an increase in saturation from Interval 1 to Interval 2 and "no" if there was no change in saturation. Subjects were also explicitly informed about the predictive value of the cue and thus knew that increases in saturation could occur in either patch during uncued blocks but occurred only in the cued patch during cued blocks. In addition to response valence ("yes" or "no"), we also measured response time. Subjects were informed that response collection would begin at the onset of Interval 2 (Figure 5) and that they had unlimited time to respond.

The spatial uncertainty caused by adding the second patch in the uncued trials dramatically impaired detection performance and increased response times. Performance in uncued blocks of Experiment 3 exhibited a high incidence of false alarms and little change in "yes" response rate with increasing Δ (Figure 7). In fact, in 7 of 16 cases, the estimated saturation change thresholds were larger than the radius of our DKL space (>1; Table 3). By comparison with the results from the single-patch conditions (Experiment 2), uncued-block response times were slowed by several hundred milliseconds (1069 ms vs. 741 ms in median across subjects; Figure 8). Response times also showed little variation with increasing Δ. These findings document the enormous difficulty subjects had in

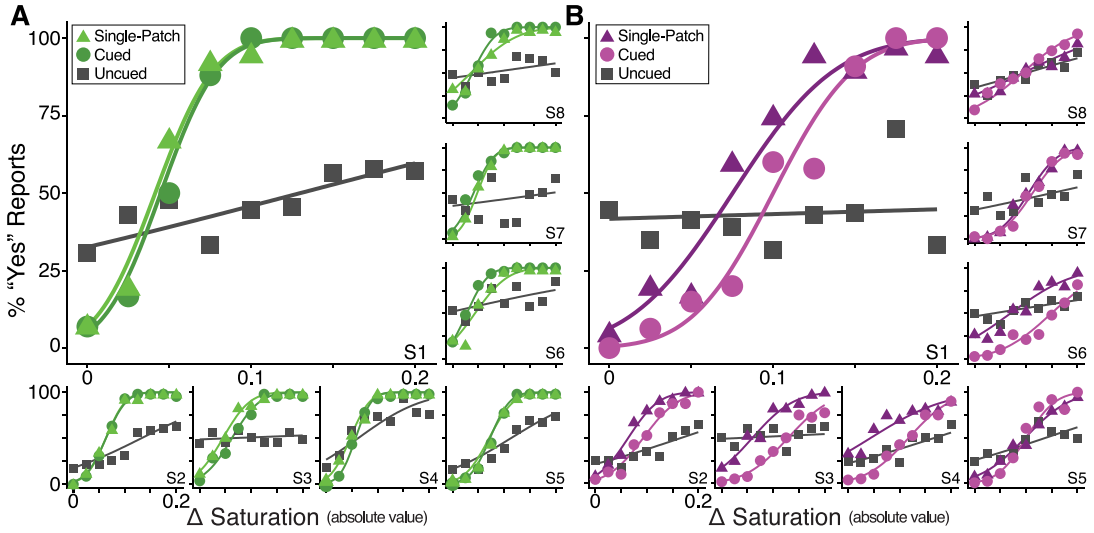


Figure 7. Experiment 3 detection performance. Enlarged plots present example subject's data (S1); small plots have identical axis limits and tick-marks (S2–S8). Plotting conventions as in Figure 6. Associated threshold values are given in Table 3. (A) Detection performance with green standard: percentage of trials on which a saturation increase was reported for each Δ. Gray-filled symbols and traces correspond to uncued performance data, dark green to cued, and light green to single patch (from Experiment 2). (B) Detection performance with purple standard. Gray-filled symbols and traces are uncued data, dark purple are cued, and lighter purple are single patch (from Experiment 2).

	Green-cued (threshold and 95% CI)	Green-uncued (threshold and 95% CI)	Purple-cued (threshold and 95% CI)	Purple-uncued (threshold and 95% CI)
S1	0.09 [0.08, 0.1]	0.25 [0.22, 0.31]	0.14 [0.13, 0.15]	0.34 [0.27, 0.49]
S2	0.10 [0.09, 0.11]	>1	0.18 [0.17, 0.2]	>1
S3	0.08 [0.07, 0.09]	0.15 [0.13, 0.17]	0.17 [0.16, 0.19]	0.35 [0.28, 0.51]
S4	0.10 [0.09, 0.11]	0.21 [0.19, 0.25]	0.14 [0.13, 0.15]	0.32 [0.25, 0.45]
S5	0.06 [0.05, 0.07]	0.24 [0.17, 0.55]	0.21 [0.19, 0.25]	>1
S6	0.07 [0.06, 0.08]	>1	0.15 [0.14, 0.18]	>1
S7	0.07 [0.06, 0.08]	>1	0.16 [0.14, 0.19]	0.3 [0.23, 0.51]
S8	0.07 [0.06, 0.08]	0.37 [0.25, 0.91]	0.13 [0.12, 0.15]	>1

Table 3. Experiment 3 threshold performance values by subject. *Notes:* Uncued and cued threshold performance values (80% "yes" reports) for each subject (S1–S8) in Experiment 3, along with 95% confidence intervals in square brackets. Values rounded to nearest hundredth. Entries of ">1" indicate cases in which thresholds would lie outside the limits of our Derrington Krauskopf Lennie color space.

monitoring multiple stimulus locations for saturation increases, even for larger Δs that were easily discriminated when presented in single stimulus patches.

Cueing restored individual performance to levels resembling the single-stimulus condition. This restoration of performance to single-patch levels was stronger for the green standard (Figure 7A) than for the purple (Figure 7B). In all cases, cued block performance was significantly different from uncued (Monte Carlo parameter tests; all $p \ll 0.01$). For the green standard, cued-block performance was indistinguishable from single-patch in five of eight subjects (S1, S2, S4, S5, S7; Monte Carlo parameter tests; smallest $p = 0.148$), whereas in three of eight subjects, restoration was incomplete (S3, S6, S8; all $p < 0.03$). For the purple standard, restoration was more variable: For two of eight subjects, cued-block performance was the same as single-patch performance (S5, S7; $p = 0.13, 0.52$), one of eight subjects had better cued-block performance (S8; $p = 0.043$), and five of eight subjects had better single-patch performance (S1, S2, S3, S4, S6; all $p < 0.05$). Overall, cued-block performance closely matched the baseline performance observed in the single-patch condition (Experiment 2), despite the presence of an additional salient stimulus. These findings suggest that the spatial cue helped subjects base their decisions almost exclusively on the stimulus at the cued location.

Performance was improved during cued blocks compared with uncued blocks at the population level as well. In an ANOVA on individual thresholds with three

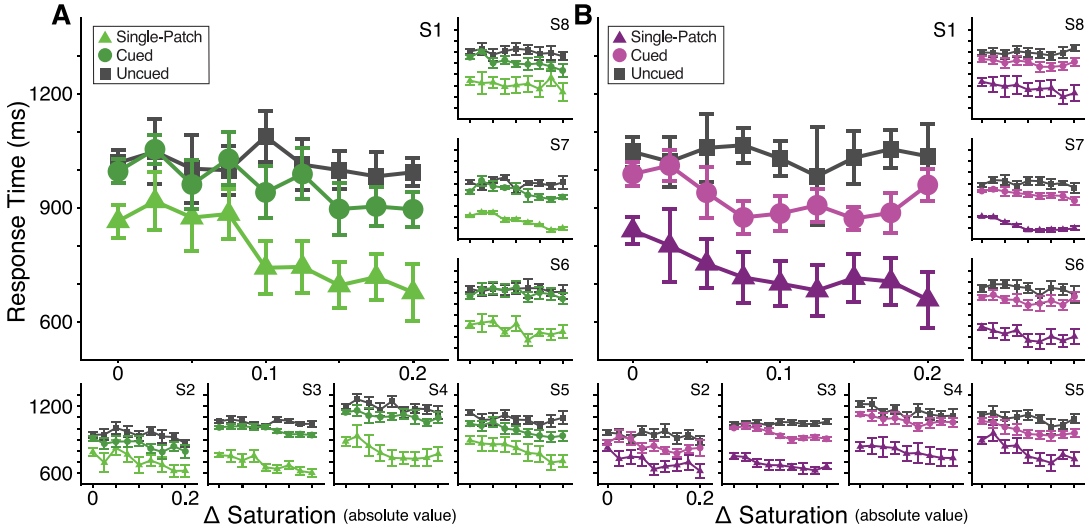


Figure 8. Experiment 3 response time data. Enlarged plots present example subject's data; small plots have identical axis limits and tick-marks. Median response time of "yes" reports only (±95% confidence interval; see the Methods section) is plotted against the absolute value of Δ saturation. (A) Saturation increase detection response times from green standard. Dark gray–filled symbols and traces are uncued response data, dark green are cued, and light green are single patch (from Experiment 2). (B) Saturation increase detection response times from purple standard. Dark gray–filled symbols and traces are uncued response data, dark purple are cued, and lighter purple are single patch (from Experiment 2).

factors (Cued/Uncued × Standard Color × Subject), there was a significant effect for cued/uncued ($df = 1$, $F = 11.14$, prob $> F = 0.0125$). The interaction of Cued/Uncued × Standard Color was not significant ($df = 1$, F $= 0.4$, prob $> F = 0.5491$), suggesting that the effect of spatial cueing did not depend on whether the standard was green or purple. Also, individual ANOVAs on psychometric function parameters (μ, σ; fit to individual data) revealed a significant effect of cued/uncued on σ ($df = 1$, $F = 13.06$, prob $> F = 0.0086$) and of standard color on μ ($df = 1$, $F = 6.47$, prob $> F = 0.0385$).

Cueing also improved response time. Cued-block response times were significantly faster than uncued-block response times (paired t test on individual median response times, $df = 7$, $t = -4.0034$, $p = 0.0052$; Figure 8). However, cued-block response times were significantly slower than single-patch response times (paired t test on individual subject median response times, $df = 7$, $t = 2.8147$, $p = 0.026$). To determine whether the dependence of response time on Δ saturation differed in cued-block versus single-patch trials, we conducted a one-way analysis of covariance. We found that the slope of the relationship between response time and Δ saturation differed significantly between cued-block and single-patch trials ($df = 1$, $F = 34.6$, $p < 0.01$). These findings suggest that although the ability to discriminate saturation increases was largely restored to single-stimulus levels by cueing, other aspects of the decision-making process remained affected by the presence of the additional competing stimulus.

Discussion

The primary goal of this work was to measure the effects of spatial cueing on performance in a color perception task. To that end, we developed novel dynamic color stimuli inspired by dot motion stimuli and used them in three psychophysical tasks. In the first experiment, we sought to validate our stimuli by using them to measure color discrimination thresholds in a previously established experimental design. Finding thresholds comparable to those obtained with static stimuli (Hansen et al., 2008; Krauskopf & Gegenfurtner, 1992), we concluded that our stimuli were well suited for spatial cueing experiments. The second experiment, which measured subjects' abilities to discriminate a color change over time at a single location, served principally as a performance baseline for the subsequent cueing experiment. The third experiment assessed the effects of spatial cueing by comparing color-change detection performance in uncued to cued conditions. Our findings indicate that spatial cueing improves detection of color saturation increases and speeds the responses to such changes.

A novel dynamic stimulus for studying color

The development of our stimulus was motivated by the need for flexible control, allowing for wide applicability. As mentioned previously, we drew inspiration from random-dot motion stimuli, which have been used extensively in behavioral and physiological studies (Britten et al., 1992; Dobkins & Bosworth, 2001; Zaksas & Pasternak, 2006). One reason random-dot motion stimuli have been so widely used is that they can be varied in myriad ways to accommodate task demands: percentage coherence, dot density, contrast, dot color, and so on. Similarly, flexible control of our stimuli relies on several variable aspects: (a) the distribution of check colors (its shape and parameters), (b) the distribution of check luminances (again, both shape and parameters), (c) the number of checks (or equivalently their size), and (d) check lifetime. For example, modulating task difficulty in Experiment 1 could be afforded by increasing the variance in check colors, by increasing check lifetime, or by reducing the number of checks.

Previous researchers have also recognized advantages in using a dynamic color stimulus. Seo, Lee, and Averbeck (2012) required monkeys to judge the dominant color in a dynamic color stimulus consisting of a mixture of blue and red pixels. Some pixels changed color in each frame, but the average red/blue composition remained fixed. In that work, they relied on the dynamic nature of the stimulus to extend the time required for the animal to judge the more common pixel color.

Importantly, our dynamic color stimulus gives answers that are consistent with more traditional methods of studying color perception. Previous studies found color discrimination thresholds comparable to those reported here using a 4AFC design with static, solid-colored discs (Hansen et al., 2008; Krauskopf & Gegenfurtner, 1992) and with static noise patches (Hansen et al., 2008). Much as we report, those studies also show elevated saturation discrimination thresholds in the positive direction along the S + (L − M) axis (increasingly "purple"), compared with the negative direction (increasingly "green"). At present, the reason for this asymmetry is unclear.

Effects of spatial cueing on color perception

Cueing dramatically improved performance in our saturation change detection task. As has been shown for motion (Dobkins & Bosworth, 2001), orientation (Lu & Dosher, 1998), and contrast stimuli (Carrasco, Penpeci-Talgar, & Eckstein, 2000), we find that valid spatial cues improve performance and speed response times in a color-change detection task. The mechanisms

underlying performance improvement in this type of cued versus uncued paradigm are as yet unresolved (see Carrasco, 2011, for a recent review). Our view is that the phenomenon of spatial attention may be a consequence of the ongoing effort to weight sensory data appropriately for motor and nonmotor decision making (Krauzlis, Bollimunta, Arcizet, & Wang, 2014).

Previous work has established that spatial cueing affects color perception, but ours is the first to demonstrate performance enhancement in a color task. Fuller and Carrasco (2006) found that an uninformative spatial cue increased apparent saturation but did not alter perception of hue. A cue-induced increase in perceived saturation does not, however, account for our finding. Such an increase would leave the amplitudes of color changes (Δs) identical in uncued and cued blocks and thus cannot account for the performance differences we observe between those conditions. Rather than altering perceived saturation, our result suggests that spatial cueing improves change-detection performance by aiding spatial selection. This difference between our own finding and that of Fuller and Carrasco (2006) is likely attributable to task structure: (a) our own task emphasized spatial selection whereas theirs emphasized spatial comparison; (b) their cue-onset asynchrony was 50 ms, ideal for engaging exogenous attention, whereas ours was 800 ms, likely engaging endogenous attention; and (c) our cue was completely informative, whereas theirs was completely uninformative.

The importance of spatial selection for performance in color tasks has been demonstrated previously. Two studies have found that color processing is affected by tasks requiring subjects to monitor multiple spatial locations. Prinzmetal, Presti, and Posner (1986) found that stimulus hue identification accuracy is decreased when performing a simultaneous letter identification task. Meanwhile, Morrone and colleagues (2004) found that concurrent monitoring of two stimulus locations for color processing degrades color-contrast detection performance relative to monitoring a single location. Both studies are in keeping with our finding that monitoring multiple stimulus locations (as in our uncued condition) leads to performance decrements.

A more expansive experimental design might have provided a better handle on mechanisms but carried the risk of confounds. A design such as one in which either interval could contain the test stimulus ("which interval was more colorful") or in which saturation might increase or decrease ("was the test stimulus more or less colorful"?) were both options that might have provided insight into what aspects of color perception are affected by spatial cueing but also might present difficulties. For example, detection of saturation decrements might show a different sensitivity from detection of saturation increments. Although we purposely used a mask to control adaptation state, it is possible that the classic two-interval forced choice design might have produced asymmetries in detection performance depending on the order of presentation. Because our experimental goal was to test the effect of spatial cueing on color-change detection, we decided to hold the other experimental variables constant to minimize these possible confounds. We are hopeful that our results will serve as a starting point for further work that might examine the interaction between spatial cueing and color-perception more fully.

Conclusions

We developed a novel dynamic color stimulus to examine how the perceptual processing of color is affected by the allocation of spatial attention. We find that spatial cues can significantly improve detection and reduce response times and can restore performance to levels similar to those obtained with single stimuli in the absence of distracters. Our findings demonstrate the feasibility of using color stimuli, of particular importance for primates in natural environments, more broadly in studies of spatial attention.

Keywords: spatial attention, color, change detection

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