ELSEVIER

Exogenous attention and color perception: Performance and appearance of saturation and hue

Stuart Fuller [a], Marisa Carrasco [a,b,*]

[a] *Department of Psychology, New York University, New York, NY, USA*
[b] *Center for Neural Science, New York University, New York, NY, USA*

Abstract

Exogenous covert attention is an automatic, transient form of attention that can be triggered by sudden changes in the periphery. Here we test for the effects of attention on color perception. We used the methodology developed by Carrasco, Ling, and Read [Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience, 7* (3) 308–313] to explore the effects of exogenous attention on appearance of saturation (Experiment 1) and of hue (Experiment 2). We also tested orientation discrimination performance for single stimuli defined by saturation or hue (Experiment 3). The results indicate that attention increases apparent saturation, but does not change apparent hue, notwithstanding the fact that it improves orientation discrimination for both saturation and hue stimuli.
© 2006 Elsevier Ltd. All rights reserved.

1. Introduction

Visual spatial attention can be separated from the direction of gaze, a dissociation known as covert attention. The endogenous form of covert attention is what is denoted by the phrase "looking out of the corner of one's eye," as we do when watching something peripherally while trying not to be obvious. Endogenous covert attention can be initiated at will, and sustained for an extended time. The automatic form, exogenous covert attention, is what is meant when we say that our attention was "captured" by a sudden flash, abrupt movement, or change in the periphery. A flash of yellow to your side when you step off the curb in New York City may be a speeding taxi, and it triggers a rapid shift in visual attention to its location.

Endogenous covert attention takes a few hundred milliseconds to ramp up, on the order of the time that it takes to execute a saccade, whereas exogenous covert attention peaks around 100 ms and disappears shortly thereafter

(Carrasco, Ling, & Read, 2004a; Carrasco & Yeshurun, 1998; Cheal & Lyon, 1991; Nakayama & Mackeben, 1989). Exogenous attention enhances performance in a variety of visual tasks. It increases sensitivity to luminance contrast (Cameron, Tai, & Carrasco, 2002; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Ling & Carrasco, 2006; Lu & Dosher, 1998, 2000; Pestilli & Carrasco, 2005), spatial resolution (Carrasco, Williams, & Yeshurun, 2002; Yeshurun & Carrasco, 1998, 1999) and speeds information accrual (Carrasco & McElree, 2001; Carrasco, McElree, & Giordano, 2004b). Moreover, it increases the hemodynamic response (an indicator of increased neural activity) to luminance contrast stimuli in early visual areas (Liu, Pestilli, & Carrasco, 2005).

Few studies have investigated possible effects of attention on color perception, and all have used endogenous attention (Blaser, Sperling, & Lu, 1999; Morrone, Denti, & Spinelli, 2004; Prinzmetal, Amiri, Allen, & Edwards, 1998). Prinzmetal et al. (1998) examined hue perception with a dual task paradigm, using a central task to manipulate the locus of attention and a delayed match to sample color task in the periphery. Attention did not affect mean

---

* Corresponding author.
E-mail address: marisa.carrasco@nyu.edu (M. Carrasco).

color-responses but reduced the variability in responses, thus the authors suggested that attention makes hue perception more veridical. Morrone et al. (2004) tested discrimination thresholds of peripheral colored gratings with and without concurrent central tasks. Diverting attention with a concurrent central color task, but not with a central luminance task, impaired performance in the peripheral color task. Similarly, a peripheral luminance task was impaired with a concurrent central luminance task but not a central color task. The authors conclude that the features of luminance and color may draw on independent attentional resources. The single study that examined color saturation and endogenous attention concluded that attention increased the salience of the attended color, but not its apparent saturation (Blaser et al., 1999).

It is known that attention affects performance via different mechanisms. Improvement may result from reduced uncertainty at the level of decision-making (Kinchla, Chen, & Evert, 1995; Palmer, 1994; Pelli, 1985), suppression of external noise (Dosher & Lu, 2000a, 2000b; Lu & Dosher, 2004; Lu, Lesmes, & Dosher, 2002), signal enhancement (Carrasco et al., 2000; Carrasco et al., 2002; Ling & Carrasco, 2006), or both (Cameron et al., 2002; Lu & Dosher, 1998, 2000; Pestilli & Carrasco, 2005). Less is known regarding effects of attention on appearance. The debate over whether attention actually changes our perceptual experience dates to the 19th Century (Helmholtz, 1866; James, 1890). Neither *performance*-based psychophysical measures nor single-cell neurophysiology have addressed the issue. A recently developed methodology quantifies the observer's subjective perception using a task contingent upon a comparative judgment between two stimuli on a particular feature. Studies using this paradigm have demonstrated that exogenous spatial attention (i.e. engaged to a particular location in the visual field) alters observers' subjective experiences of luminance contrast (Carrasco et al., 2004a), spatial frequency (Gobell & Carrasco, 2005), flicker rate (Montagna & Carrasco, 2006), and motion coherence (Liu, Fuller, & Carrasco, in press). Here we examine the effects of exogenous attention on two aspects of color: hue and saturation. In physical terms, hue corresponds to wavelength of a pure color (e.g. the colors of the rainbow). Saturation is the relative purity of a color. A pure monochromatic light is fully saturated; adding white light dilutes it and decreases saturation. A familiar characterization of these dimensions is the color wheel used in many computer programs to select colors for type, etc. Hue varies radially around the wheel, and saturation increases from the center toward the outer boundary. Any spoke of the wheel defines a hue, and position on the spoke defines the intensity or purity of that hue, its saturation.

The three experiments presented here were designed to determine whether exogenous attention affects the appearance of saturation or hue, and whether it improves orientation discrimination for stimuli defined on these dimensions.

2. Experiments

2.1. Apparatus

The experiments were programmed using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and MATLAB 5.2, and run on an Apple G4 computer with a 19-in. Sony Multiscan E 400 color monitor set for 1028×764 pixel resolution at a 75 Hz refresh rate. The monitor was characterized using a Photo Research PR 650 spectrometer at the beginning of Experiment 1 and again before Experiment 3. Following each characterization, the monitor's gamma functions were estimated by non-linear fitting and new color lookup tables were generated. Experiment 3 employed 10-bit color lookup tables and a ATI Radeon 9200 video card to allow finer gradations in color specification.

2.2. Stimuli

All stimuli were ovals subtending 2° of visual angle along the long axis (see Fig. 1). The edges were blurred by a Gaussian envelope clipped to provide a large, uniform internal area of color, while reducing boundary effects (e.g. Mach bands) with the background. The DKL colorspace was used to define chromatic and luminance specifications for all stimuli (see Appendix A). DKL is a spherical colorspace whose chromatic axes correspond to the L–M (red–green) and S (blue–yellow) opponent processes (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, Mandler, & Brown, 1986). The third axis, $L + M + S$, is luminance. Physically equiluminant chromatic planes can readily be defined by setting a constant value for the luminance coordinate (Fig. 2). In the three experiments, we maintained physical equiluminance within sets of colored stimuli, and in Experiment 3 also between stimuli and background. Hue and saturation can be controlled by combination of the remaining two coordinates in Cartesian space, or by converting to a polar system in which azimuth angle controls hue and radius corresponds to saturation.

3. Experiment 1

In this experiment, we investigated whether exogenous attention affects the appearance of saturation.

3.1. Observers

The observers were undergraduate and graduate students in the Psychology Department at New York University. All had normal or corrected to normal vision, and reported normal color vision. Those in doubt were given the Ishihara Test to verify normal color vision. Most observers in the Red and Green conditions performed the experiment for both sets of stimuli in a blocked design, randomly assigned to complete either the Red or the Green
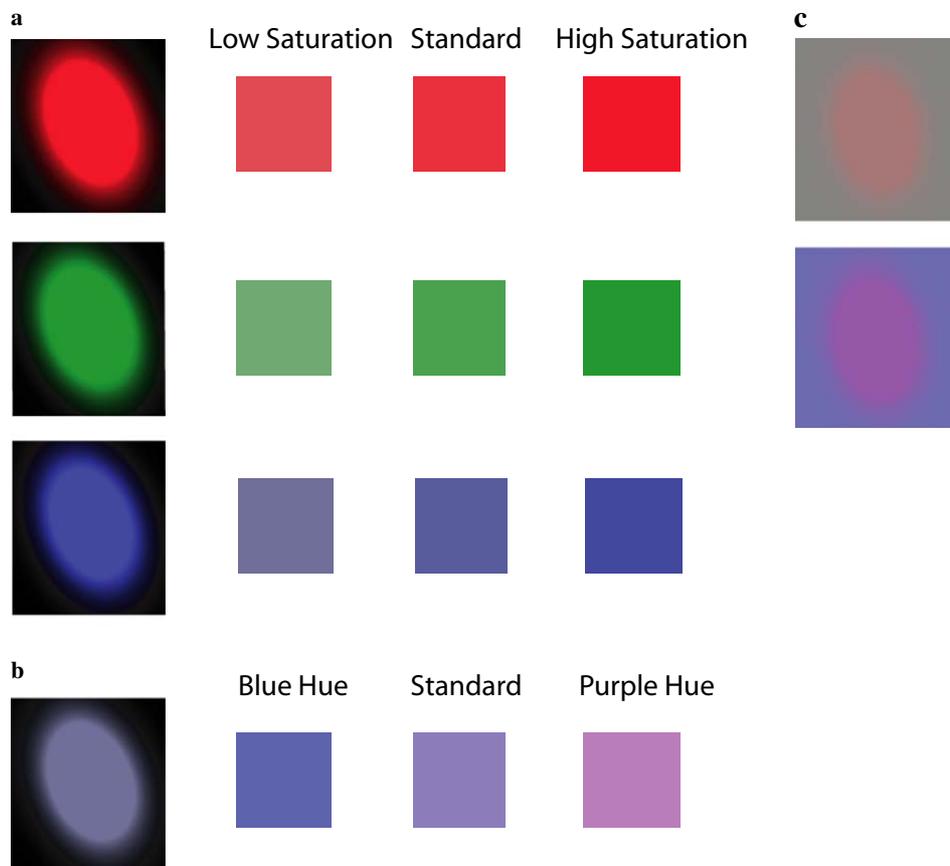
Fig. 1. Color stimuli. (a) Stimuli used in Experiment 1 varied in saturation (in units of radial distance from the white point in DKL space) along three hue vectors in equiluminant planes. Uniform areas of color were wrapped in clipped Gaussian envelopes to blur the edges with the background and minimize border effects. The stimuli subtended 2° of visual angle along the long axis, with a 3:2 aspect ratio. (b) Stimuli for Experiment 2 used the same construction and proportion, but varied in hue along an arc of constant radius in DKL space. (c) Stimuli for Experiment 3 were equiluminant to their backgrounds. Red saturation stimuli were defined on the same red hue vector as in Experiment 1. Hue stimuli were presented on a blue background, from which they differed only in hue, defined along the same arc described in Experiment 2 (see text).

condition first. A separate group performed the task for the Blue condition. The undergraduates were recruited from the NYU Psychology participant pool, and all observers signed an informed consent form approved by the NYU Institutional Review Board. Observers (except an author) were naïve as to the purpose of the experiment.

Observers were assigned to a main condition or a control condition defined by different task instructions (see Procedure). The numbers of observers used in the analysis were: 21 in the Red condition (11 main instruction condition, 10 control condition), 19 in the Green condition (9 main instruction, 10 control), and 19 in the Blue condition (10 main instruction, 9 control). For each color and instruction condition one observer was non-naive (an author), and the rest were naïve to the purpose of the experiment. Data for three observers (2 Green control, 1 Blue control), out of 62, were discarded for failure to follow instructions or inability to perform the task at a preset overall orientation performance level (905%).

3.2. Stimuli

The stimuli were specified along three vectors emanating from the central white point, in hue directions that are commonly called red, green, and blue. In DKL space, the blue and green vectors were close to the S cone axis, and the red vector was intermediate to the L–M and S axes. Having the same hue angle and different distances from the white point, the stimuli in each set shared common hue and luminance but had different saturations. Red stimuli were in an equiluminant plane of $20\,cd/m^2$, green stimuli were $35\,cd/m^2$, and blue stimuli were $15\,cd/m^2$. All were presented on an achromatic background at the monitor's white point and $3\,cd/m^2$. For each of the three stimulus hues, 11 saturations were selected, such that the highest and lowest saturations could be reliably discriminated from the midpoint saturation by observers (see Appendix A for stimuli DKL color coordinates). Pairs of stimuli were created at each saturation value, with the long axis of the oval tilted 20° to the right or left of vertical. By design, the suprathreshold visibility of the stimuli coupled with this tilt made orientation discrimination relatively easy. Given that our interest was the subjective comparison of apparent saturation, we used discrimination performance during training trials as an indication that observers were able to perform the task (i.e. correct response $\geqslant 90\%$).
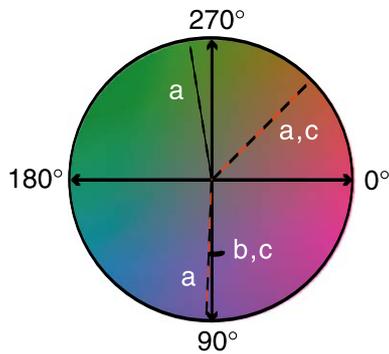
Fig. 2. Schematic of stimuli in DKL colorspace. (a) Saturation stimuli for Experiment 1 were sampled along the vectors emanating from the white point, with constant hue and different saturations. Luminances were blue 15 cd/m², red 20 cd/m², and green 35 cd/m². (b) Stimuli for Experiment 2 varied in hue, but not saturation, at luminance of 15 cd/m² along an arc denoted here by a line segment intersecting the blue saturation vector. (c) Experiment 3 used red stimuli along the same hue vector shown above for Experiment 1 at 20 cd/m², and hue stimuli located on the same arc as used in Experiment 2 at 15 cd/m². Red saturation stimuli were presented on an equiluminant gray background. Hue stimuli were presented on an equiluminant blue background corresponding to blue endpoint of the hue arc.

3.3. Procedure

Observers were seated 57 cm from the monitor in a darkened room. A chinrest was used to set distance from the monitor and head orientation. Fig. 3 shows a schematic of an individual trial. Observers were instructed to maintain fixation on the cross at the center of the screen throughout the experiment. Stimulus onset was preceded by a 67 ms cue

(white, 100 cd/m²) subtending 0.3° of visual angle in one of three randomized locations on the screen: at the location of the central fixation point (the Neutral cue), or 5.5° to the left or right of fixation along the horizontal meridian. The cue was followed by the gray background with only the fixation cross for an interstimulus interval (ISI) of 53 ms. A pair of stimuli were presented simultaneously for 40 ms, at 4° eccentricity on either side of the fixation point along the horizontal meridian. Following stimulus offset, observers had unlimited time to respond but were encouraged to do so within 1–2 s to complete the experiment within approximately 1 h. The next trial started 500 ms after response.

In each trial, one of the two stimuli presented had the middle (i.e. sixth in the sequence of eleven) saturation among the stimulus set (the Standard stimulus, see Appendix A for DKL values). The other in the pair (the Test stimulus) was randomly selected from among the 11 saturations in the set. Location of the Standard stimulus to the right or left of fixation was randomized across trials, and the orientations of the two stimuli (right or left tilt) were random and independent. As cue location was also randomized, the cue was non-predictive of the locations and orientations of the Test and Standard stimuli. Observers were explicitly told that the cue was non-informative for the task, and therefore they could disregard it. They were informed that all cues would provide information about the temporal onset of the stimuli. Observers were shown the locations in which the stimuli would appear. The task was a contingent orientation discrimination task. In the main experiment, observers were instructed to report "the orientation of the stimulus that is more colorful" (e.g. "redder," "greener," "bluer"). In the control condition,
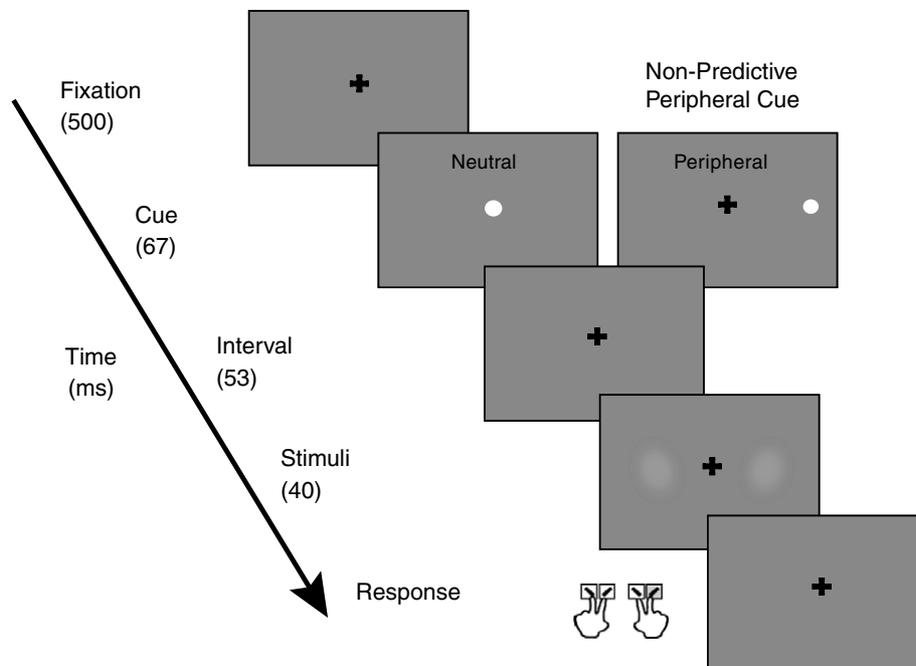

Fig. 3. Trial sequence for Experiment 1. Observers maintain fixation at the central cross throughout the experiment. A white cue subtending 0.3° visual angle appears at fixation, or 1.5° eccentric to where the right and left stimuli will be presented. Following an ISI, stimulus presentation occurs 120 ms after onset of the cue. Observers report the orientation of the stimulus that is more (less) colorful using one of four keys on the computer keyboard (see text).

observers performed the task under the reversed instructions; i.e., report "the orientation of the stimulus that is less colorful." The target to the left of fixation was represented by the "z" and "x" keys for left and right orientation, respectively. Responses for the right target used the "," and "/" keys. The compound nature of the task allowed collection of data on the comparative judgment of the appearance of the two stimuli, which was our primary interest, while shifting the observers' focus to the goal of correctly reporting the orientation of the stimulus they selected. Observers performed a practice block of 100 trials to learn the task. The experiment consisted of 10 blocks of 100 trials.

3.4. Results and discussion

For analysis, the trials for each observer were grouped into three conditions: those in which the cue was near the Test stimulus location (Test cue), the Standard stimulus location (Standard cue), or at the central fixation point (the Neutral cue). Psychometric functions of the probability of choosing the Test stimulus as a function of Test stimulus saturation were fit to each cue condition, using maximum likelihood estimation of two-parameter Weibull functions (threshold and slope). The point of subjective equality (PSE) was calculated for each fit by inverting the Weibull function to find the Test stimulus saturation at which observers chose the Test at chance (50%).

Demonstrations of the expected psychometric functions and possible results are shown in Fig. 4. For both the main and control instructions, the PSE for the Neutral cue condition should approximately equal the Standard saturation; i.e. at the point of objective equality (POE). In all six comparisons (three colors, two instructions), the PSE deviated

by $\leqslant 1\%$ from the POE. If exogenous attention increased apparent saturation, the psychometric functions for the Test cue and Standard cue conditions would shift to the left and to the right, respectively (Fig. 4a). When the Test is cued, a less saturated Test stimulus would be indistinguishable from the Standard. When the Standard is cued, the Test would have to be more saturated to be equivalent. If the pattern in Fig. 4a were due to an increase in apparent saturation, then the functions should shift in the same directions for the control instructions, when the observer is asked to report the *less* colorful stimulus in the pair, as shown in Fig. 4b. If the shifts in the functions were simply due to response bias to the cue, then we would expect the shifts to be in opposite directions when the instructions were reversed, yielding the pattern in Fig. 4c. Absent cue bias or any effect of attention, the expected functions for the three cue conditions would be identical and overlap.

To illustrate why the comparison of results for the main and control instructions differentiate a consistent attentional effect from cue bias, the subjective comparisons between the Standard and each Test saturation can be stated in simple equations. On each trial, observers evaluate the relative saturations of Test (T) and Standard (S). Absent any attentional effect or bias to influence the comparison, the PSE should occur when T = S; i.e. at the POE. This is the expectation for the neutral cue condition in Figs. 4a–c.

First, consider the situation if attention, engaged by the peripheral cue, *increases* apparent saturation for whichever stimulus is cued by an amount (A). When the Test is cued, the PSE will be at (T + A) = S, and when the Standard is cued it will be at T = (S + A). That is, the physical saturation of the Test at PSE will be lower than the Standard when the Test is cued and higher than the Standard when the Standard is
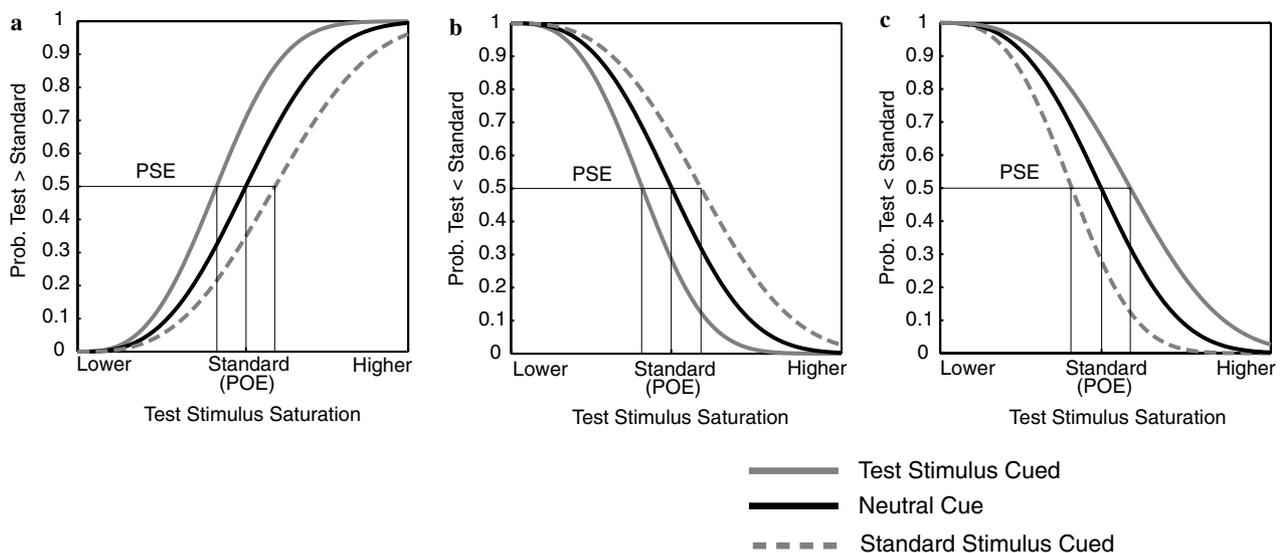

Fig. 4. Hypothetical results for saturation appearance (Experiment 1). At the point of subjective equality (PSE), observer selects test stimulus on 50% of trials (chance). If attention increases apparent saturation, the PSE will shift to the left when the Test stimulus is cued and to the right when the Standard is cued, under both sets of instructions (a and b). If the observer is biased by the cue to more often select the cued stimulus, we expect the same results in (a) when the observer selects the more 'colorful' stimulus, but the results in (c) under the reversed instructions. The PSEs will shift in opposite directions if there is cue bias but no effect of attention. Absent cue bias, if there is no effect of attention, the psychometric functions for all three cue conditions should be identical.
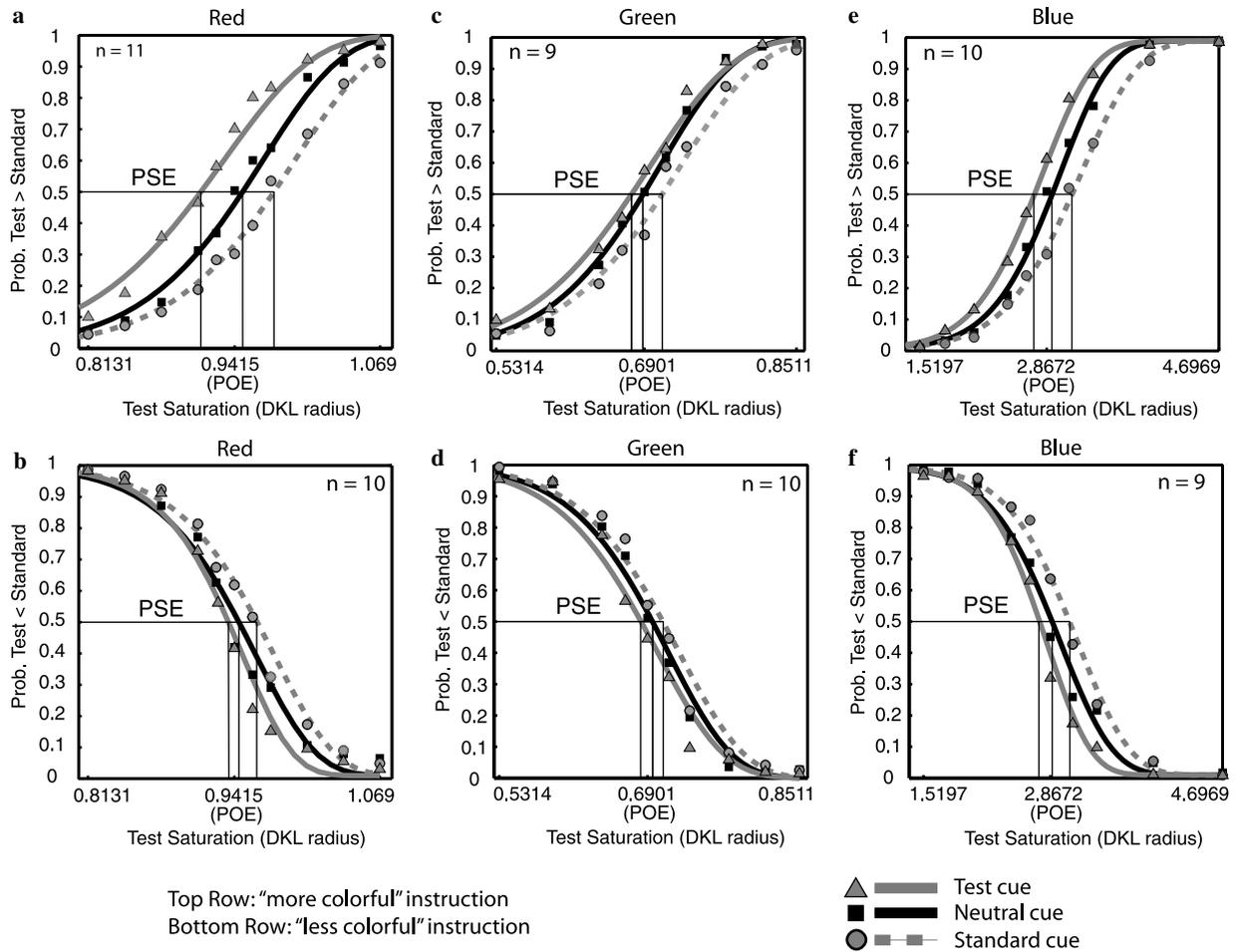
Fig. 5. Psychometric functions of saturation appearance (Experiment 1). Data for all observers per color and instruction condition were combined and fitted with Weibull functions. Data points are marked with symbols, fitted functions with lines. Stimulus color is on columns [red stimuli, (a and b); green stimuli, (c and d); blue stimuli, (e and f)]. Top row is main instructions ["select stimulus that is more colorful" (a, c, and e)], bottom row is control instructions ["select stimulus that is less colorful" (b, d, and f)]. Horizontal axes represent Test stimulus saturation distances in DKL colorspace from the achromatic point, increasing saturation runs left to right, and Standard stimulus saturations (POEs) correspond to the center labeled values on the horizontal axes. Vertical axes are percent of trials for which the Test was selected as more colorful (top row, main instructions) or the Test was selected as less colorful (bottom row, reversed instructions). Points of Subjective Equality (PSEs) consistently shift to the left for the Test cue condition (triangles, solid gray lines), indicating that with exogenous attention a physically less saturated Test stimulus appears equal to a more saturated Standard. Correspondingly, when the Standard is cued (circles, dashed gray lines), the Test must be physically more saturated to appear equal to the Standard. Neutral cue condition is indicated by black squares and solid black lines.

cued. Note that this formulation is independent of the "polarity" of the instructions, leading to the expectation that a consistent attentional increase in apparent saturation will yield the patterns of results depicted in Fig. 4a (main instructions—'more colorful' instructions) and Fig. 4b (control or reversed instructions—'less colorful' instructions).

Next, consider the situation of cue bias (B). For the main instruction ('more colorful') when the Test is cued, the bias would lead to more frequent Test responses, as if observers were overestimating T. Thus, the PSE will be at $T + B = S$, i.e. the function would shift towards lower Test saturations (Fig. 4a). The critical difference for the control, reversed instructions ('less colorful') is that when the Test is cued, again there would be more frequent Test responses, but in this case it would be as if observers were underestimating T, because the instruction is to report the less saturated stimulus. Thus, the PSE will be at $T - B = S$, i.e. the function would shift towards higher Test saturations (Fig. 4c).

The results collapsed across observers for each of the three stimulus hues and two sets of observer instructions are shown in Figs. 5a–f. They match the expected results from Figs. 4a and b. The PSEs shift in the same directions for both sets of instructions, ruling out response bias to the cue as the cause of the differences by cue condition. When the Test stimulus was cued, the PSE shifted to the left, indicating that an attended, but physically less saturated Test stimulus is indistinguishable from the Standard stimulus. Note that the figures for Green and Blue stimuli (Figs. 5c–f) depict ten of the eleven Test values actually used in the experiment and the analysis, in order to better show the dynamic ranges of the psychometric functions. The point omitted from each figure was well outside the dynamic range. The central labeled saturation values on the horizontal denote the Standard value for each set of stimuli.

Two-way ANOVAs were conducted for each of the three stimulus hue conditions (three cue conditions within-subjects × two observer instructions between-sub-
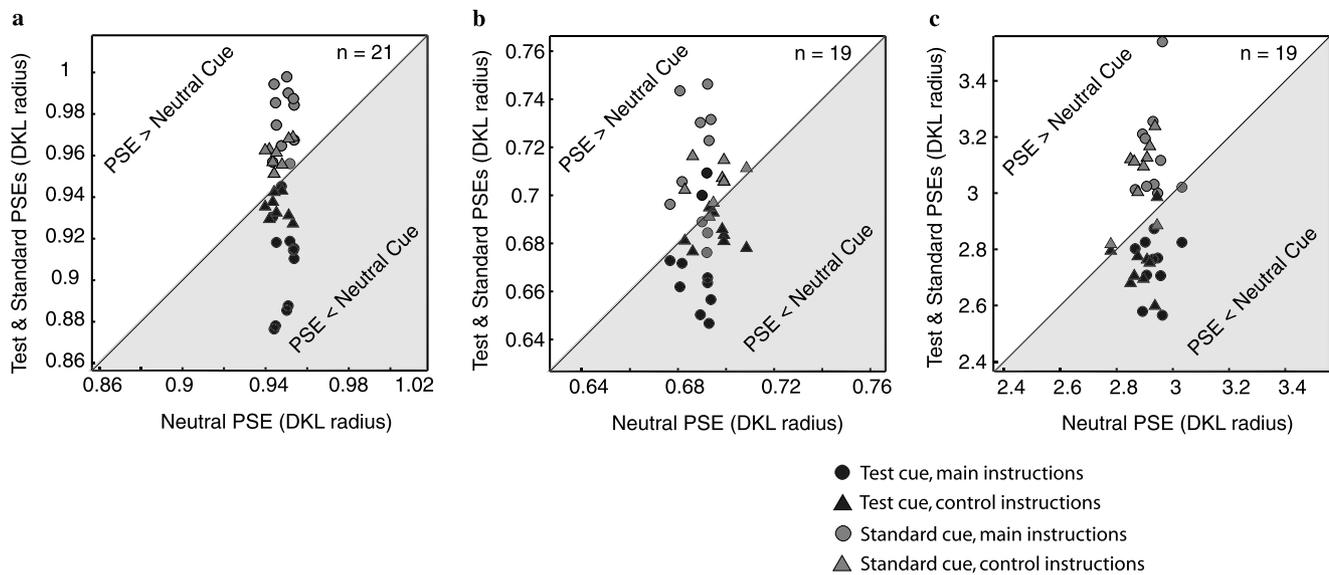
Fig. 6. Individual observers, PSE shifts for saturation appearance (Experiment 1). (a) Red stimuli; (b) green stimuli; (c) blue stimuli. Horizontal axes represent the fitted PSEs for the Neutral cue condition, in DKL distance from the achromatic point. PSEs for the Test and Standard cue conditions are plotted on the vertical axes, in the same units. If there is no effect of the peripheral cues, all points are expected to cluster randomly in the centers of the plots close to the diagonal lines. PSEs consistently shift negative in the Test cue condition (black symbols) and positive in the Standard cue condition (gray symbols), for both the main (circles) and control instructions (triangles), indicating that attention increases the apparent saturation of the stimulus that is cued. Simply responding more often to the stimulus that was cued (cue bias) would cause opposite shifts for the two instruction conditions, mixing black circles with gray triangles, and gray circles with black triangles.

jects) on the individual observers' PSEs (the 50% thresholds from the Weibull fits). For observers of the *red* saturation stimuli, we found a significant main effect of the cue ($F(2,36) = 55.5$, $p < .001$, $\eta^2 = .76$) and a significant interaction effect of cue $\times$ instruction ($F(2,36) = 14.0$, $p < .005$, $\eta^2 = .44$). The main effect of instruction was not significant ($F(1,18) = 1.5$, $p > .1$, $\eta^2 = .08$). All factor contrasts of cue condition were significant ($p < .001$), confirming that the PSE for the Test cue condition was lower than the Neutral cue and the Standard cue was higher than the Neutral cue. Because the PSEs shifted in the same directions for both the main and control instructions, response bias is ruled out as an explanation for the results. The interaction of cue and instruction emerged because the magnitude of the shifts was larger for the main instructions ("choose the more colorful stimulus") than for the control, reversed instructions ("choose the less colorful stimulus"). This magnitude difference may correspond to the fact that several of the observers who participated in both instruction conditions reported that the task felt easier or "more natural" under the main instructions. This asymmetry is reminiscent of those reported in visual search by Treisman and colleagues (Treisman & Gormican, 1988; Treisman & Souther, 1985).[1] However, the analogy is limited because in a search condition a target

appears amidst various distracters, whereas in this study there are always two stimuli, they only vary in their saturation level, and more importantly, each observer decides in each trial which stimulus to respond to; i.e., there is not a predetermined target.

The ANOVA for *green* stimuli yielded a significant main effect of cue type ($F(2,36) = 17.0$, $p < .001$, $\eta^2 = .50$), but no main effect of instructions or interaction of cue $\times$ instructions. All factor contrasts for cue condition were significant ($p < .001$), with a lower PSE for the Test cue condition and a higher PSE for the Standard cue condition. The ANOVA for *blue* stimuli yielded a significant main effect of cue type ($F(2,36) = 39.0$, $p < .001$, $\eta^2 = .70$), but no main effect of instructions or interaction of cue $\times$ instructions. As with the red and green stimuli, all factor contrasts for cue condition were significant ($p < .001$), with a lower PSE for the Test cue condition and a higher PSE for the Standard cue condition.

The PSE shifts revealed by the ANOVAs were consistent for individual observers, as shown in Figs. 6a–c. The PSEs for Test cue and Standard cue conditions are plotted on the vertical axes, versus the PSE for the neutral cue condition on the horizontal axes. Were there no effect of attention, the points would be expected to cluster around the diagonal line. They fall close to the Standard saturation values on the horizontal axis, indicating that the PSE estimates for the Neutral cue occurred at approximately equal physical saturation for Test and Standard. The results are skewed along the vertical axes, with negative shifts in PSE for the Test cue and positive shifts for the Standard cue.

The PSE analysis showed that attention affects apparent saturation. Another possible effect of attention may be to

---

[1] These authors argued that there are different demands in visual search for deviating values and for standard values in terms of attended vs. non-attended processing. They stated that asymmetries emerge because features 'standard' to the system activate only a prototypical 'channel' whereas 'deviating' features activate both they prototypical channel and their own channel. These authors proposed that the direction of the search asymmetry can be considered as a diagnostic tool to identify the 'primitives' of the visual system.

improve observers' ability to differentiate between two saturation stimuli, increasing sensitivity to saturation *differences*. The steepness of the psychometric function reflects this sensitivity, represented by the slope parameter (β) in the Weibull fits. A shallow slope means that relatively large stimulus differences are needed to reliably make the comparative judgment, whereas a steep slope indicates smaller saturation differences will suffice. We performed within-subjects ANOVAs across the three cue conditions on the beta parameters for each stimulus color and main and control instructions. In all cases, the ANOVAs were not significant (Red, main instructions $F(2,20) = 1.9$, $p > .1$, $\eta^2 = .16$; Red, control instructions $F(2,16) = 2.9$, $p > .05$, $\eta^2 = .27$; Green, main instructions $F(2,18) < 1$; Green, control instructions $F(2,16) = 2.0$, $p > .1$, $\eta^2 = .20$; Blue, main instructions $F(2,18) = 1.1$, $p > .1$, $\eta^2 = .11$; Blue, control instructions $F(2,18) = <1$).

In sum, adapting a paradigm developed to investigate the effect of exogenous attention on contrast appearance (Carrasco et al., 2004a) enabled us to investigate whether attention alters perceived saturation. Observers reported the orientation of a stimulus contingent upon a judgment of the relative saturation of two stimuli presented simultaneously. The results of Experiment 1 are consistent across three widely separated hues (red, green, blue) and two opposing sets of observer instructions ('more colorful' and 'less colorful'). They indicate that attention increases the apparent saturation of a colored stimulus relative to a neutral condition and to an unattended stimulus (PSE). The control conditions, in which we reversed the instructions to the observers, allow us to rule out a cue-bias explanation of the data. We have used similar control experiments in studies investigating the effects of exogenous attention on contrast sensitivity (Carrasco et al., 2004a) and flicker rate (Montagna & Carrasco, 2006). The finding that attention increases perceived saturation, in conjunction with the finding that attention increases perceived contrast (Carrasco et al., 2004a), suggests that attention alters appearance in situations when it may also benefit discrimination.

4. Experiment 2

So far, we know that attention alters appearance in two of the three dimensions of color space, i.e. luminance (Carrasco et al., 2004a) and saturation (Experiment 1). In this experiment, we investigated whether attention affects the appearance of the third dimension—hue.

4.1. Observers

The observers were twelve graduate and undergraduate students, eight of whom participated in both instruction conditions (counterbalanced order). Four observers had participated in Experiment 1. Eleven were naive to the purpose of the experiment, and one was an author. Recruiting and vision requirements were the same as in Experiment 1.

4.2. Stimuli

The stimuli were defined along an arc in DKL space orthogonal to the blue vector shown in Fig. 1, and thus varied in hue (from 'blue' to 'purple') but not saturation or physical luminance. We used 9 hues at $15 \, \text{cd/m}^2$ for all observers, such that the ends of the range could reliably be distinguished from the middle stimulus, presented on a $3 \, \text{cd/m}^2$ gray background (refer Appendix A for DKL parameters). Stimuli orientations were 20° to the right or left of vertical.

4.3. Procedure

The procedure was the same as for Experiment 1, using stimuli that varied in hue (but not saturation or luminance). We used 9 stimulus hue values. Under one set of instructions, observers were instructed to report "the orientation of the stimulus that is more blue." In the control condition observers were given reversed instructions, they reported "the orientation of the stimulus that is more purple." The order of the instructions was randomized for observers participating in both conditions. Observers performed 900 trials per instruction condition, yielding 33 trials at each combination of Test stimulus value and cue condition.

4.4. Results and discussion

The Weibull-fitted data collapsed across observers are shown in Fig. 7. Individual observers' functions followed the pattern shown in the collapsed results. Fig. 7a shows the results for the instructions to "report the orientation of the stimulus that is more *blue*," and Fig. 7b corresponds to instructions to "report the orientation of the stimulus that is more *purple*."

A two-way ANOVA (three cue conditions within-subjects × two instruction conditions between-subjects) was conducted on the individual observers' PSEs. There were no significant main effects for cue ($F(2,26) = 1.9$, $p > .05$, $\eta^2 = .09$) or instructions ($F(1,18) < 1$), but there was a significant interaction effect of cue and instructions ($F(2,36) = 3.6$, $p < .05$, $\eta^2 = .17$). A one-way ANOVA for the *blue* instructions revealed no significant effect of cue condition ($F(2,18) < 1$), indicating no change in relative hue appearance. However, the one-way ANOVA for the *purple* instructions indicated a significant cue effect ($F(2,18) = 7.5$, $p < .01$, $\eta^2 = .45$). Paired comparisons showed that the PSE for the Test cue was significantly lower than the Standard cue ($t(9) = 3.4$, $p < .01$) and the Neutral cue ($t(9) = 2.5$, $p < .05$), i.e. shifted in the purple direction, but the PSEs for Standard and Neutral cues did not differ ($t(9) = 1.3$, $p > .1$). In contrast to the results of Experiment 1, in which PSE shifts were significant and in the same direction for main and reversed instructions, only one pair-wise comparison was significant for one set of instructions. If cueing a stimulus had a reliable effect on hue, making it appear more purple as the statistical test suggests, then it should have been
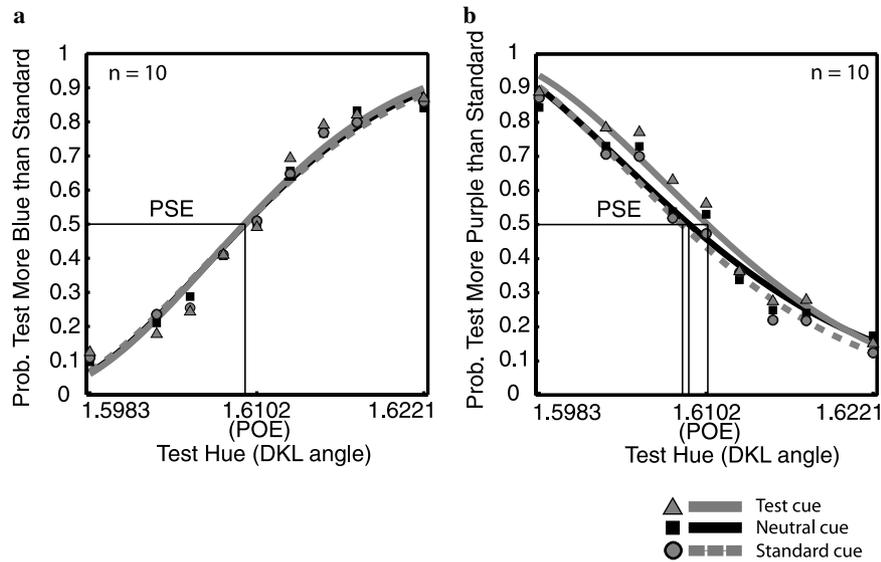
Fig. 7. Psychometric function of hue appearance (Experiment 2). Data for all observers by instruction condition were combined and fit with Weibull functions for each cue condition (Test cue: triangles, solid gray lines; Neutral cue: squares, solid black lines; Standard cue: circles, dashed gray lines). (a) Instructions were to report orientation of the bluer stimulus of the each pair and (b) instructions were to report on the more purple of the pair. The hue of the Test stimulus is plotted on the horizontal axes in DKL azimuth (radians), with the blue end of the stimulus range at left and the purple end at right. Vertical axes indicate the proportion of trials in which observers selected the Test stimulus. When selecting the bluer stimulus, the fits are identical for all three cue conditions, indicating no change in appearance. The small differences in (b) between the Test cue and the other two conditions are attributed to a slight response bias in favor of the cued stimulus.
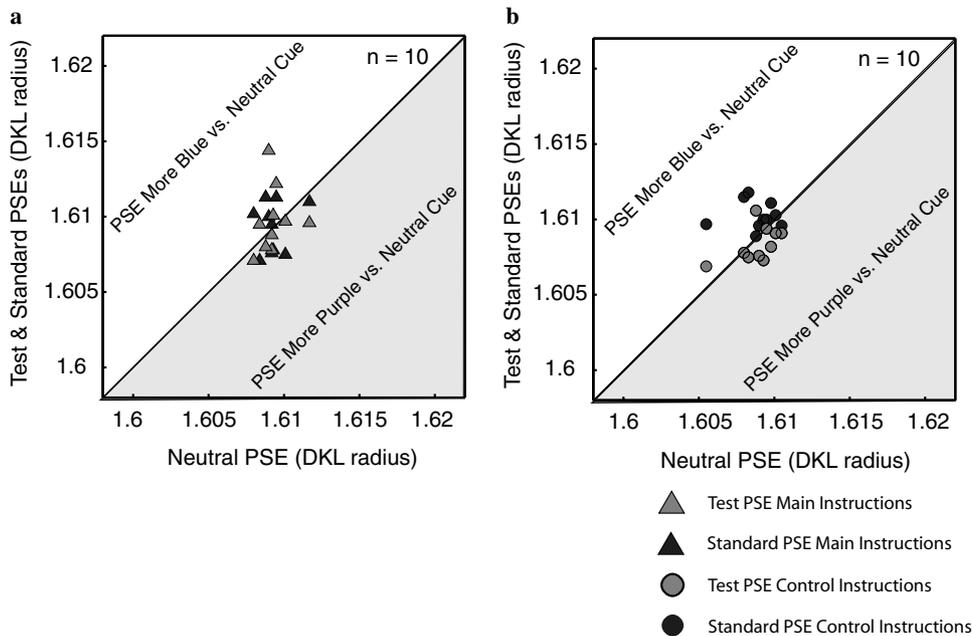

Fig. 8. Individual observers, PSEs for hue appearance (Experiment 2). PSEs for all observers by instruction conditions [(a) select "more blue" stimulus; (b) select "more purple" stimulus]. Horizontal axis is the PSE for the Neutral cue condition, in units of radial angle in the DKL equiluminant plane (lower values are more "purple," higher values more "blue"). Vertical axes are the PSE for the Test (gray symbols) and Standard cue conditions (black symbols). In contrast to the saturation results in Experiment 1 (see Fig. 6), the data are clustered around the diagonal line that represents equality of Test and Standard PSE with the Neutral PSE. The PSEs for the Test and Standard cue conditions are more intermixed, particularly in (a). The slight separation in (b) is attributed to a slight response bias in favor of the cued stimulus.

manifested in comparable PSE shifts under both sets of instructions. Therefore, we cannot conclude that attention changes the appearance of hue.

The individual PSEs are plotted in Figs. 8a and b. The PSE for the Test cue and Standard cue conditions are plot-

ted on the vertical axis, versus the PSE for the Neutral cue condition on the horizontal axis. The points on the two figures fall close to the hue value of the Standard on the horizontal axis, indicating that the PSE estimates for the Neutral cue occurred at approximately equal physical hues

for Test and Standard. For both the main and control instructions, the PSE deviated by $\leqslant 0.2\%$ from the POE.

Fig. 8a, corresponding to the instructions to "report the orientation of the stimulus that is more blue," shows no systematic effect of attention on apparent hue among individual observers; the PSEs for Test and Standard cue conditions are randomly intermixed near the Neutral PSE. Fig. 8b shows the small but significant shifts in Test and Standard PSEs from the ANOVA analysis when observers were instructed to select the "stimulus that is more purple." For six observers, the Test PSE was shifted toward purple relative to the Neutral and the Standard PSE was shifted toward blue. One observer had shifts in the opposite directions, and for the remaining three observers both Test and Standard deviated from Neutral in the same direction.

In this experiment, the slope of the psychometric functions (β parameters) can be interpreted as a measure of ability to discriminate between the hues of the Test and Standard stimuli. To test for changes in sensitivity to hue differences, we performed a two way ANOVA on the Weibull rate parameters for the individual observers, with cue condition as a within-subjects factor and instructions as a between-subjects factor. There were no significant main effects of cue ($F(2, 36) < 1$) or instructions ($F(1, 18) < 1$), and no significant interaction of cue × instructions ($F(2, 36) < 1$). We find no evidence to suggest that cueing attention to one of the two stimuli had any effect on observers' ability to differentiate between hues at the two locations.

In short, this experiment indicates that exogenous attention does not alter hue appearance. This result is noteworthy given that attention does change the appearance of the two other dimensions of the color space–saturation (Experiment 1) and luminance contrast (Carrasco et al., 2004a). Moreover, this result indicates that the effect of attention on saturation appearance (Experiment 1) cannot be attributed to cue bias. The finding that hue is unaffected by attention may be due to the fact that hue comparisons entail qualitative differences, whereas contrast and saturation comparisons entail quantitative differences within a particular dimension (we discuss this possibility in Section 6). In the next experiment, we evaluate effects of attention on performance mediated by either saturation or hue differences.

5. Experiment 3

We have demonstrated changes in apparent saturation (Experiment 1) but not in apparent hue (Experiment 2) with exogenous spatial attention. Given the absence of an effect in Experiment 2, it remains to be shown that the cue used in both experiments successfully engaged exogenous attention but did not alter hue appearance. Recent research has shown that attention changes appearance of luminance contrast (Carrasco et al., 2004a), spatial resolution (Gobell & Carrasco, 2005), and motion coherence (Liu et al., in press). Importantly, attention also changes *performance-based* measures in these visual dimensions: contrast (Carrasco et al., 2000; Ling & Carrasco, 2006; Lu & Dosher, 1998), spatial

resolution (Carrasco et al., 2002; Yeshurun & Carrasco, 1998, 1999), and motion coherence (Liu et al., in press). Indeed, in previous studies we have obtained both an effect on appearance and a corresponding effect on some performance-based measure (e.g. orientation discrimination, etc.). In this experiment, we validated the effectiveness of the cueing procedure by testing whether the type of cue used in Experiments 1 and 2 can improve orientation discrimination of colored stimuli that are differentiated from the background by saturation (Condition 1) or by hue (Condition 2).

5.1. Observers

Nineteen graduate and undergraduate students participated in the experiment. Ten observers participated in the saturation condition, and ten participated in the hue condition (an author participated in both conditions). Three observers had participated in Experiment 1 and two in Experiment 2. All observers, except an author, were naïve as to the purpose of the experiment.

5.2. Stimuli

There were two types of stimuli. Condition 1: The *saturation* stimuli lay along the same red vector used in Experiment 1 and were presented on a equiluminant ($20 \, cd/m^2$) gray background. A range of stimuli at small saturation increments were used, tilted 10° to the right or left of vertical. The saturation value for each observer was determined by staircase procedure (PEST), estimating the saturation corresponding to 75% correct orientation discrimination. Condition 2: The *hue* stimuli lay along the same hue arc in DKL colorspace as in Experiment 2, presented on an equiluminant ($15 \, cd/m2$), isosaturated blue background. Orientations were 10° to the right or left of vertical. See Appendix A for DKL saturation and hue parameters used.

5.3. Procedure

Viewing conditions and timing parameters were the same as in Experiments 1 and 2. A single stimulus was presented in each trial, 4° to the right or left of fixation along the horizontal meridian. Stimulus location was randomly varied, as were cue location (at fixation, or 1.5° eccentric to the right or left stimulus locations) and stimulus orientation (right 10° tilt or left 10° tilt). The design thus had three cue conditions: Neutral, when the cue appeared on the center of the display; Valid-cue when the cue appeared on the same side of fixation as the stimulus; Invalid-cue when the cue appeared on the opposite side of the stimulus.[2]

---

[2] We tested orientation discrimination this way because with the oval, low spatial-frequency stimuli in Experiments 1 and 2, the Test saturation and hue ranges needed to estimate a full psychometric function for appearance rendered orientation discrimination nearly a step function. Conversely, the use of larger tilt angles required the stimuli to have small differences in saturation or hue from the background, which were incompatible with the appearance task.
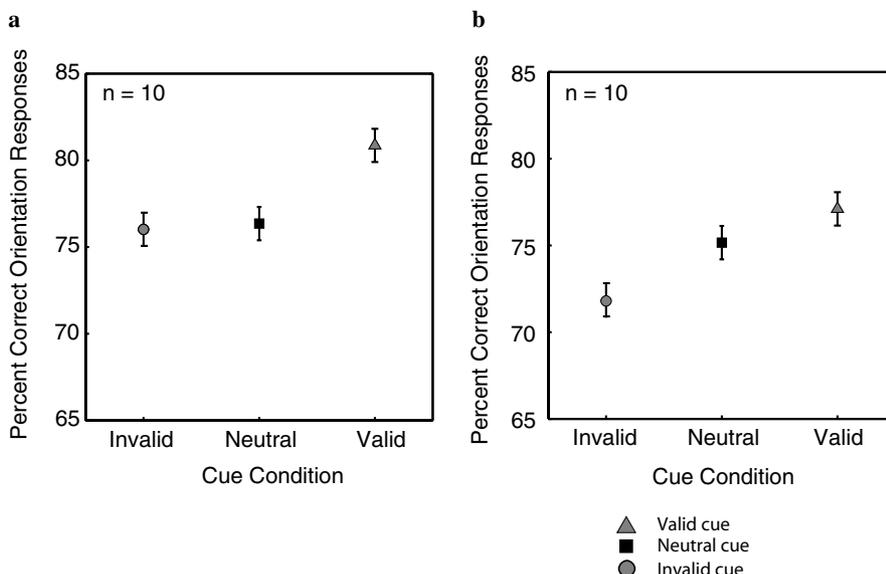
Fig. 9. Results of Experiment 3 on orientation discrimination. Mean percent correct orientation responses across observers for red saturation stimulus (a) and hue stimulus (b). In the Valid cue condition, a cue appeared 1.5° eccentric to the stimulus location along the horizontal meridian. The cue appeared at fixation in the Neutral condition, and 5.5° eccentric to fixation on the opposite side of the stimulus in the Invalid cue condition. All stimuli were supra-threshold for hue or saturation, and equiluminant to the background. Stimulus values were calibrated for each observer to correspond to a 75% correct orientation performance threshold in the Neutral condition. For saturation (a), performance for the Valid cue condition was significantly better than both Neutral and Invalid conditions. For hue (b), the Valid and Invalid conditions were significantly different. Error bars are standard ±1 SE.

Prior to the main experiment, observers performed 10 PEST staircases in which the cue always appeared at fixation, and the saturation or hue was varied to estimate the 75% performance threshold for correct orientation discrimination. In the main experiment, the stimulus saturation (or hue) was fixed at the mean value of the PEST estimates, and cue location was randomized as described above. Observers performed 10 blocks of 100 trials each.

5.4. Results and discussion

Mean performance levels (percent correct orientation responses) are shown in Figs. 9a–b. Separate one-way within-subjects ANOVAs were performed for the saturation and hue stimuli, with arc sine square root transformed percent correct responses as the dependent variable and the three cue conditions as the independent variable. The cue effect was significant for both the saturation stimuli ($F(2, 18) = 7.6$, $p < .01$, $\eta^2 = .47$) and the hue stimuli ($F(2, 18) = 7.3$, $p < .01$, $\eta^2 = .45$).

For the saturation stimuli, orientation discrimination performance was significantly improved by the Valid cue compared to the Neutral cue ($t(9) = 3.2$, $p < .01$) and the Invalid cue ($t(9) = 3.5$, $p < .005$), after Bonferroni correction. For the hue stimuli, the Valid cue improved performance relative to the Invalid cue ($t(9) = 4.8$, $p < .001$); the neutral cue did not differ significantly from the other two cues.

In summary, Experiment 3 demonstrated that exogenous attention improves orientation discrimination performance for both saturation and hue targets that are equiluminant with the background. These results not only validated the effectiveness of the peripheral cue we used to

manipulate transient attention, but they also revealed a dissociation of attentional effects on appearance from effects on orientation discrimination: It is possible for attention to alter performance with stimulus defined be a given dimension without affecting the appearance of such a dimension.

6. General discussion

In this study, we investigated the effects of exogenous covert attention, a transient, automatic, and stimulus-driven form of attention, on color perception. We found that exogenous spatial attention changes apparent color saturation but does not change apparent hue, whereas it improves orientation discrimination performance for both hue and saturation stimuli. The presence of an attentional enhancement of behavioral performance does not lead to, or require, a corresponding change or enhancement in appearance.

Carrasco et al. (2004a) developed a paradigm to investigate the effect of exogenous attention on apparent contrasts, in which observers reported the orientation of a stimulus contingent upon a judgment of the relative contrast of two stimuli presented simultaneously. The initial implementation of this paradigm showed that exogenous attention increases apparent contrast. This study built on earlier results demonstrating that exogenous attention improves orientation discrimination for contrast Gabor stimuli (Cameron et al., 2002; Carrasco et al., 2000; Pestilli & Carrasco, 2005), bridging the gap between modulation of contrast sensitivity and visual awareness (Luck, 2004; Treue, 2004). A subsequent study employing the same paradigm showed that exogenous attention increases apparent

spatial frequency (Gobell & Carrasco, 2005). Two recent studies have shown that exogenous attention also alters the appearance of dynamic stimuli: It increases both apparent flicker rate (Montagna & Carrasco, 2006) and apparent motion coherence (Liu et al., 2006).

The present study, the first to investigate the effects of exogenous attention on color perception, furthers these results by demonstrating that exogenous attention alters the subjective perception of color saturation (Experiment 1). The effect was consistent for three widely separated, equiluminant regions of color space, and was robust to the reversal of observer instructions used in the control experiment. An equally important finding is that the same paradigm revealed no effect on apparent hue in Experiment 2. The null effect of cueing on hue appearance indicates that the effect of cueing on saturation appearance cannot be explained by cue bias. The dissociation of the appearance of saturation and hue is particularly notable in light of our Experiment 3, which showed that exogenous attention improves orientation discrimination for both hue and saturation stimuli. Moreover, this experiment validated the effectiveness of the cueing procedure used in all three experiments.

In a psychophysical study investigating mechanisms of suprathreshold chromatic discrimination, Sankeralli and Mullen (1999) found that hue discrimination regions in cone color space are wedge shaped, i.e. a function of the azimuth angle between hues. Two hues at the discrimination threshold do not become more discriminable if their physical saturations are increased proportionately while their hues are held fixed. In other words, our perceptions of hue and saturation are independent. This finding helps explain the results of our first two experiments. Experiment 1 showed an increase in apparent saturation with attention, an increase that would likely have been caused by attention in Experiment 2. However, the comparative judgment we instructed observers to make in Experiment 2 was based on relative hue, not a composite difference of hue and saturation. If we consider the change in apparent saturation as if it were equivalent to a change in physical saturation, the azimuth angle separating the two stimuli in colorspace, and the difference in appearance on the task-relevant dimension, remains unchanged. Thus, there is no change in apparent hue even when apparent saturation changes.

The paradigm used in Experiment 1 is incapable of determining whether the attended stimulus increases in apparent saturation or the unattended stimulus decreases, or both, because it employs a relative judgment and the observer chooses the stimulus on which to report. Pestilli and Carrasco (2005) used a similar methodology to the one used here, with two simultaneously presented contrast stimuli to investigate the effect of attention on performance (rather than appearance) in an orientation discrimination task. Attention increased contrast sensitivity at the attended location whereas it decreased sensitivity at the unattended location as compared to the Neutral condition. Similarly, the results of Experiment 1 are consis-

tent with attention both increasing the apparent saturation of the attended stimulus and reducing the apparent saturation of the unattended stimulus as compared to the Neutral condition. The results of Experiment 3 are also consistent with Pestilli and Carrasco (2005), finding evidence of a performance benefit at the attended location in Experiment 3a and a cost at the unattended location in Experiment 3b. Unlike Pestilli and Carrasco (2005), who measured sensitivity in the three cue conditions dynamically via a staircase method, we fixed the stimulus intensity for each observer based on a prior estimation of threshold. Estimation errors for our initial thresholds could have led to floor and ceiling effects for individual observers, explaining the asymmetric patterns of significance in our results.

6.1. Prothetic vs. metathetic dimensions

The pattern of results indicates that exogenous attention does not change subjective appearance on all visual dimensions, suggesting that neural processing of hue is different from that of contrast, spatial frequency, and saturation in some critical way. One potentially useful idea in this context is that of metathetic versus prothetic perceptual dimensions (Stevens & Galanter, 1957). Saturation, contrast, and spatial frequency are prothetic dimensions, having meaningful zero values and inherent directionality. It is reasonable to think in terms of "more" and "less" in the range between totally unsaturated (i.e. achromatic) and fully saturated, monochromatic colors. Hue, or what we commonly mean by the word "color," is metathetic. Our percepts of red and blue are qualitatively different. We often describe hues intermediate to our basic color categories by combining names, e.g. red-orange, but indicate by this a mixing of colors for which we have categorical names. There is no objective "less-to-more" gradient in hue; red-orange can be described as more orange compared to red and more red compared to orange. Attention has a consistent directional effect on apparent saturation, contrast, motion coherence, flicker rate, and spatial frequency. It is reasonable to speculate why attention increases the appearance of these dimensions; for instance, increased contrast and saturation facilitate the discrimination of the features of the signal, and make it easier to discriminate the signal from the background. By comparison, there is no a priori reason why attention should affect apparent hue in one direction or another.

6.2. Endogenous attention and color

Endogenous attention differs from exogenous attention in several important respects, including time course, sustainability and voluntary control. In addition, endogenous attention can be allocated at will to global visual features, such as color, shape, and orientation. Given these differences, it does not necessarily follow that exogenous and endogenous attention should have similar effects on all dimensions of visual perception.

In a study dealing with color saturation and feature-based attention, Blaser et al. (1999) asked observers to attend to a particular color when presented with an ambiguous motion stimulus consisting of red and green bars on a yellow background, alternated temporally with contrast-modulated achromatic noise. Each successive presentation of bars and noise was phase shifted 90°. One way to resolve the ambiguity is to increase the physical saturation of one of the colors, yielding a consistent direction of apparent motion. The authors found that endogenous attention to one of the colors also resolved the motion ambiguity, with the direction of motion corresponding to the attended color. They concluded that endogenous attention increased the salience of the attended color, but did not change apparent saturation. Clearly, attention changed observers' perception of the motion in the stimuli. The results are inconclusive regarding the subjective experience or appearance of the colors because observers reported only on the direction of motion; there was no direct measurement of apparent saturation.

Prinzmetal et al. (1998) examined the effects of endogenous attention on hue perception in a delayed match to sample task, manipulating attention via a dual task at a separate spatial location. The mean hue responses did not differ between attention conditions, but the standard deviation of responses was smaller in the attended condition. This led the authors to conclude that endogenous attention does not change the fundamental hue that is perceived, but makes hue perception more veridical or truer to the objective hue of the stimulus. The similarity between Prinzmetal et al.'s (1998) conclusions and those of the current study is suggestive that the perception of hue is robust to both exogenous and endogenous attention. However, methodological limitations of Prinzmetal et al. (1998) study (Carrasco et al., 2004a; Treue, 2004) and differences between that study and the present one make such an assertion merely speculative.

6.3. Neurophysiology of color and attention

How might our results be interpreted in terms of the physiological mechanisms of color processing and attention?

A progression of neuronal preferences for color has been identified from retinal receptors through several areas of visual cortex. In V1, V2, and V4, electrophysiology has revealed cells with preferences for hues intermediate to the red–green and blue–yellow signals that arise at the ganglion cells (Yoshioka, Dow, & Vautin, 1996). Corresponding psychophysical evidence indicates that the preferences may become more broadly distributed away from the cardinal cone axes at higher levels, resulting in spectrally tuned, broadband channels for color (D'Zmura & Knoblauch, 1998).

A critical cortical area for awareness of color is in the vicinity of the lingual gyrus and collateral sulcus, identified as V4/V8 (Beauchamp, Haxby, Jennings, & DeYoe, 1999; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990;

Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; McKee-fry & Zeki, 1997). This area is more activated in fMRI by color stimuli than by luminance stimuli (Beauchamp et al., 1999). Interestingly, there is evidence of modulation in the collateral sulcus by endogenous attention when attending to color (Corbetta et al., 1990). At the single-unit level, attention modulates neuronal activity in visual cortex across several areas of visual cortex, including V4, and stimulus features, such as contrast, orientation and motion (Cook & Maunsell, 2002; Cook & Maunsell, 2004; Martinez-Trujillo & Treue, 2004; McAdams & Maunsell, 1999; McAdams & Maunsell, 2000; Reynolds, Pasternak, & Desimone, 2000; Treue & Martinez Trujillo, 1999). This modulation is consistent with contrast gain (for a review see Reynolds & Chelazzi, 2004).

Consider first the possible effect of attention on hue. Hue discrimination has been modeled as a computation of ratios between chromatic signals. According to Guth's (1991) A.T.D. model, such a computation could be performed on transformed opponent process signals, explaining the presence in striate cortex of neurons with hue preferences intermediate to the cardinal cone axes. The model signifies the two cone-opponent signals by T and D, which in an equiluminant plane of color space can be envisioned as the axes of an x, y coordinate system. Any ratio of the two signals defines a line outward from the achromatic point, specifying a particular hue. The points on that line all share the same signal ratio, but differ in the combined strength of the chromatic signals (saturation). Sankeralli and Mullen (1999) confirmed psychophysically that hue discrimination is mediated by ratio-based mechanisms, which predict the radial discrimination regions in cone color space found in their study.

Psychophysically, there is evidence that both endogenous and exogenous attention affect contrast gain (Dosher & Lu, 2000a; Huang & Dobkins, 2005; Ling & Carrasco, 2006). Assuming multiplicative modulation by attention, operating on ratio-based, tuned hue detectors (or channels), modulation of the *input signals* to such channels would not change their relative activations. Were this also the case throughout visual cortex, we would expect the appearance of hue to be insensitive to attention just as found in Experiment 2. The *outputs* of such hue detectors, however, would be increased by multiplicative modulation in proportion to their sensitivities to the particular ratio of inputs received. Thus, exogenous attention would increase the overall strength, but not the relative contributions, of color signals, leading to a stronger sensation of perceived saturation.

Information from color is combined with other dimensions in early vision (Gegenfurtner, 2003). For instance, electrophysiological studies show that color and spatial frequency are combined as early as V1 (Johnson, Hawken, & Shapley, 2001; Shapley & Hawken, 2002), and psychophysical studies indicate orientation tuning in color channels (Clifford, Spehar, Solomon, Martin, & Zaidi, 2003; Vimal, 1997; Webster, De Valois, & Switkes, 1990). Thus, attention could modulate sensitivity to color boundaries and orientation of colored stimuli, analogous to its effects on lumi-

nance contrast. Populations of neurons (channels) will respond to a tilted color stimulus according to the match between the stimulus and their preferences. The dominance of the activation in one channel relative to the others determines the discriminability of the stimulus orientation. With attention modulating the activation of all channels multiplicatively, activity in the stimulus-preferring channel will increase by a greater absolute margin than the other channels. Competition between channels would be more easily resolved, resulting in a stronger orientation signal, and improved discrimination performance.

To answer a question posed long ago regarding whether attention affects subjective experience (Helmholtz, 1866; James, 1890), we recently implemented a paradigm to study effects of attention on appearance (Carrasco et al., 2004a; Gobell & Carrasco, 2005; Liu et al., in press; Montagna & Carrasco, 2006). This study has assessed the effects of exogenous attention on orientation discrimination and appearance in the color domain. We show that attention improves orientation discrimination mediated by hue and saturation stimuli, and that whereas it increases the appearance of saturation it does not affect that of hue stimuli. Attention not only affects how we perform in a visual task, but on some prothetic visual dimensions, it also affects what we see.

Appendix A

DKL is a spherical colorspace defined by three orthogonal axes representing two opponent chromatic cone dimensions $(L - M$ and $S)$ and one luminance dimension $(L + M + S)$. Specifying coordinates in DKL requires selection of a reference cone activation vector, usually derived from the background of the visual display and representing the adaptation state. To simplify the calculations for these experiments, we chose cone values corresponding to the achromatic (white) points at the desired luminance for each set of colored stimuli.

Cone values	15 cd (blue stimuli)	20 cd (red stimuli)	35 cd (green stimuli)
	9.6356	12.8474	22.483
	5.3644	7.1526	12.517
	0.2673	0.3564	0.6237
CIE XYZ	13.1133	17.4844	30.5976
	15	20	35
	16.5961	22.1282	38.7243

DKL values were initially expressed in spherical coordinates. Luminance corresponded to elevation angle, which was zero in each case due to our selection of cone values. Azimuth angles controlled hue, with the zero azimuth representing activation along the $L - M$ axis in the direction of positive $L - M$ values. Following the convention of Derrington et al. (1984), positive angles rotated clockwise and negative angles rotated counterclockwise from zero azimuth. Radius controlled distance from the white point, or

saturation. For a given cone background and constant azimuth, varying the radius allowed specification of different saturations for a fixed luminance and hue. Fixing cone background and radius, varying the azimuth over small ranges determined equiluminant points of equal saturation at different hues.

DKL values for the stimuli used in Experiments 1 and 2 appear in the tables below. Shown here are the endpoint values (i.e. the ends of the ranges for each stimulus set) and the values of the Standard stimuli.

Experiment 1: constant luminance and hue, variable saturation

	El. (radians)	Az. (radians)	Rad.
Red 20 cd			
High saturation	0	5.2697	1.0690
Standard	0	5.2697	0.9415
Low saturation	0	5.2697	0.8131
Blue 15 cd			
High saturation	0	1.6220	5.6262
Standard	0	1.6220	2.8672
Low saturation	0	1.6220	1.5197
Green 35 cd			
High saturation	0	4.5966	0.8511
Standard	0	4.5966	0.6901
Low saturation	0	4.5966	0.4726

Experiment 2: constant luminance and saturation, variable hue

Lum 15 cd	El. (radians)	Az. (radians)	Rad.
"Bluer" hue	0	1.6221	1.8925
Standard hue	0	1.6102	1.8925
"Purpler" hue	0	1.5983	1.8925

In Experiment 3, we constructed ranges of stimuli and used the PEST procedure to estimate 75% performance (orientation discrimination) thresholds for each observer, then fixed the stimulus values for the main experiment. The minimum and maximum available values are shown below. The step size indicates the azimuth (radius) difference between stimuli used in the PEST estimations.

Experiment 3: ranges for variable hue stimuli (blue) and variable saturation stimuli (red)

Blue hue 15 cd	El. (radians)	Az. (radians)	Rad.	Azimuth step
	0	1.6221	1.8925	0.0005
	0	1.5471	1.8925	
Red sat. 20 cd	El. (radians)	Az. (radians)	Rad.	Radius step
	0	5.2697	0	0.0017
	0	5.2697	.25	

The stimuli were ovals of uniform color as defined in the tables above, graded at the edges into the display background by applying a clipped bivariate Gaussian function (see Section 2.2). The calculations for the stimulus images were performed in radial DKL coordinates, and transformed into Cartesian DKL coordinates before the final linear transformations into CIE and the monitor RGB values. The transformations from DKL to RGB followed the method described by Brainard (1996).

References

Beauchamp, M. S., Haxby, J. V., Jennings, J. E., & DeYoe, E. A. (1999). An fMRI version of the Farnsworth–Munsell 100-Hue test reveals multiple color-selective areas in human ventral occipitotemporal cortex. *Cerebral Cortex, 9*(3), 257–263.

Blaser, E., Sperling, G., & Lu, Z. L. (1999). Measuring the amplification of attention. *Proceedings of the National Academy of Sciences of the United States of America, 96*(20), 11681–11686.

Brainard, D. H. (1996). Cone contrast and opponent modulation color spaces. In P. K. Kaiser & R. M. Boynton (Eds.), *Human Color Vision* (pp. 563–579). Washington, DC: Optical Society of America.

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

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research, 42*(8), 949–967.

Carrasco, M., Ling, S., & Read, S. (2004a). Attention alters appearance. *Nature Neuroscience, 7*(3), 308–313.

Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 5363–5367.

Carrasco, M., McElree, B., & Giordano, A. M. (2004b). Temporal performance fields: visual and attentional factors. *Vision Research, 44*, 1351–1365.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Research, 40*, 1203–1215.

Carrasco, M., Williams, P. E., & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: support for signal enhancement. *Journal of Vision, 2*(6), 467–479.

Carrasco, M., & Yeshurun, Y. (1998). The contribution of covert attention to the set-size and eccentricity effects in visual search. *Journal of Experimental Psychology: Human Perception and Performance, 24*(2), 673–692.

Cheal, M., & Lyon, D. R. (1991). Central and peripheral precuing of forced-choice discrimination. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 43 A*(4), 859–880.

Clifford, C. W., Spehar, B., Solomon, S. G., Martin, P. R., & Zaidi, Q. (2003). Interactions between color and luminance in the perception of orientation. *Journal of Vision, 3*(2), 106–115.

Cook, E. P., & Maunsell, J. H. (2002). Attentional modulation of behavioral performance and neuronal responses in middle temporal and ventral intraparietal areas of macaque monkey. *Journal of Neuroscience, 22*(5), 1994–2004.

Cook, E. P., & Maunsell, J. H. (2004). Attentional modulation of motion integration of individual neurons in the middle temporal visual area. *Journal of Neuroscience, 24*(36), 7964–7977.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science, 248*(4962), 1556–1559.

D'Zmura, M., & Knoblauch, K. (1998). Spectral bandwidths for the detection of color. *Vision Research, 38*(20), 3117–3128.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology, 357*, 241–265.

Dosher, B. A., & Lu, Z. L. (2000a). Noise exclusion in spatial attention. *Psychological Science, 11*(2), 139–146.

Dosher, B., & Lu, Z. L. (2000b). Mechanisms of perceptual attention in precuing of location. *Vision Research, 40*, 1269–1292.

Gegenfurtner, K. R. (2003). Cortical mechanisms of color vision. *Nature Reviews Neuroscience, 4*, 563–572.

Gobell, J., & Carrasco, M. (2005). Attention alters the appearance of spatial frequency and gap size. *Psychological Science, 16*(8), 644–651.

Guth, S. L. (1991). Model for color vision and light adaptation. *Journal of the Optical Society of America A, 8*(6), 976–993.

Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. (1998). Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience, 1*(3), 235–241.

Helmholtz, H. V. (1866). In J. P. Southall (Ed.), *Treatise on Physiological Optics* (Vols. 2 and 3, 3rd ed.). Rochester, NY: Optical Society of America.

Huang, L., & Dobkins, K. R. (2005). Attentional effects on contrast discrimination in humans: evidence for both contrast gain and response gain. *Vision Research, 45*(9), 1201–1212.

James, W. (1890). *The principles of psychology*. New York: Henry Holt.

Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience, 4*(4), 409–416.

Kinchla, R. A., Chen, Z., & Evert, D. (1995). Precue effects in visual search: data or resource limited. *Perception & Psychophysics, 57*, 441–450.

Krauskopf, J., Williams, D. R., Mandler, M. B., & Brown, A. M. (1986). Higher order color mechanisms. *Vision Research, 26*(1), 23–32.

Ling, S., & Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research, 46*, 1210–1220.

Liu, T., Fuller, S. & Carrasco, M. (in press). Attention alters the appearance of motion coherence. *Psychonomic Bulletin & Review*.

Liu, T., Pestilli, F., & Carrasco, M. (2005). Transient attention enhances perceptual performance and fMRI response in human visual cortex. *Neuron, 45*(3), 469–477.

Lu, Z. L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38*, 1183–1198.

Lu, Z. L., & Dosher, B. A. (2000). Spatial attention: different mechanisms for central and peripheral temporal precues? *Journal of Experimental Psychology: Human Perception and Performance, 26*, 1534–1548.

Lu, Z. L., & Dosher, B. A. (2004). Spatial attention excludes external noise without changing the spatial frequency tuning of the perceptual template. *Journal of Vision, 4*(10), 955–966.

Lu, Z. L., Lesmes, L. A., & Dosher, B. A. (2002). Spatial attention excludes external noise at the target location. *Journal of Vision, 2*(4), 312–323.

Luck, S. J. (2004). Understanding awareness: one step closer. *Nature Neuroscience, 7*, 208–209.

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.

McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience, 19*(1), 431–441.

McAdams, C. J., & Maunsell, J. H. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. *Journal of Neurophysiology, 83*(3), 1751–1755.

McKeefry, D. J., & Zeki, S. (1997). The position and topography of the human colour centre as revealed by functional magnetic resonance imaging. *Brain, 120*(Pt 12), 2229–2242.

Montagna, B., & Carrasco, M. (2006). Transient covert attention and the perceived rate of flicker. *Journal of Vision, 6*(9), 955–965.

Morrone, M. C., Denti, V., & Spinelli, D. (2004). Different attentional resources modulate the gain mechanisms for color and luminance contrast. *Vision Research, 44*(12), 1389–1401.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research, 29*(11), 1631–1647.

Palmer, J. (1994). Set-size effects in visual search: the effect of attention is independent of the stimulus for simple tasks. *Vision Research, 34*, 1703–1721.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A, 2*(9), 1508–1532.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Pestilli, F., & Carrasco, M. (2005). Contrast sensitivity is enhanced at cued and impaired at uncued locations. *Vision Research, 45*, 1867–1875.

Prinzmetal, W., Amiri, H., Allen, K., & Edwards, T. (1998). Phenomenology of attention: I. Color, location, orientation, and spatial frequency. *Journal of Experimental Psychology: Human Perception and Performance, 24*(1), 261–282.

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience, 21*, 611–647.

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron, 26*(3), 703–714.

Sankeralli, M. J., & Mullen, K. T. (1999). Ratio model for suprathreshold hue-increment detection. *Journal of the Optical Society of America A, 16*(11), 2625–2637.

Shapley, R., & Hawken, M. (2002). Neural mechanisms for color perception in the primary visual cortex. *Current Opinion in Neurobiology, 12*(4), 426–432.

Stevens, S. S., & Galanter, E. H. (1957). Ratio scales and category scales on a dozen perceptual continua. *Journal of Experimental Psychology, 54*, 377–411.

Treisman, A., & Gormican, S. (1988). Feature analysis in early vision: evidence from search asymmetries. *Psychological Review, 95*(1), 15–48.

Treisman, A., & Souther, J. (1985). Search asymmetry: a diagnostic for pre-attentive processing of separable features. *Journal of Experimental Psychology: General, 114*, 285–310.

Treue, S. (2004). Perceptual enhancement of contrast by attention. *Trends in Cognitive Sciences, 8*(10), 435–437.

Treue, S., & Martinez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature, 399*(6736), 575–579.

Vimal, R. L. P. (1997). Orientation tuning of the spatial-frequency-tuned mechanisms of the Red-Green channnel. *Journal of the Optical Society of America A, 14*(10), 2622–2632.

Webster, M. A., De Valois, K. K., & Switkes, E. (1990). Orientation and spatial-frequency discrimination for luminance and chromatic gratings. *Journal of the Optical Society of America A, 7*(6), 1034–1049.

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature, 396*(6706), 72–75.

Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research, 39*(2), 293–306.

Yoshioka, T., Dow, B. M., & Vautin, R. G. (1996). Neuronal mechanisms of color categorization in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioral Brain Research, 76*(1–2), 51–70.