Integration of differing chromaticities in early and midlevel spatial vision

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Using Glass patterns composed of isoluminant dots we have investigated the segregation and integration of chromatic information by the visual system. By measuring pattern detection when the chromaticities of the two elements forming a dot pair are varied (intradipole variation), we characterize integration at an early level of spatial processing. By measuring pattern detection for dot pairs where the within-pair chromaticity is the same but the among-pair chromaticities are varied (interdipole variation) we characterize integration and segregation for a more global, midlevel, spatial processing mechanism. Using isoluminant patterns in which all dots have the same chromaticity, we find that (i) detection thresholds are similar to those for luminance-defined dots, and (ii) an equivalent-contrast metric approximately equates thresholds for various chromaticities, including those along both the cardinal and the intermediate axes of an opponent-color space. When intradipole chromaticity is varied we observe that (i) the ability of visual mechanisms to extract oriented dot pairs decreases with increasing chromaticity differences, and (ii) average bandwidths are similar for cardinal and intermediate directions. For pattern detection with interdipole chromatic variation the visual system does not segregate noise dot pairs from correlated dot pairs on the basis of chromatic differences alone, and appears to integrate oriented dot pairs of differing chromaticities in forming a global percept, even for large color differences. Isoluminant Glass patterns with translational and concentric correlations give similar results. The results are compared with those obtained for contrast variation in luminance-defined Glass Patterns and are discussed in terms of current multistage models of color processing by the visual system. © 2005 Optical Society of America

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1. INTRODUCTION

An understanding of how the visual system utilizes chromatic information in the perception of scenes requires knowledge of both the basic mechanisms mediating discrimination of one color from another and how local spatial features, once resolved by these mechanisms, are integrated to yield the percept of an object. We report the results of experiments using Glass patterns[1–3] that investigate the ability of the human visual system to integrate elements of differing chromaticities at the early and midlevels of visual processing.

Processing of chromatic information by the visual system is accomplished by neural mechanisms occurring at three or more stages.[4] The first stage, where chromatic selectivity is mediated by three (or more) classes of cone photoreceptors acting as broadly tuned spectral bandpass filters, serves as input for further chromatic processing. More directly relevant to the detection of chromatic patterns are second-stage cone-opponent mechanisms, mediated by retinal ganglion cells and neurons of the lateral geniculate nucleus, and further, third-stage chromatic processing, presumably occurring in the visual cortex. Electrophysiological and psychophysical correlates of second-stage mechanisms have been thoroughly discussed in the literature.[4–7]

Less is known about color processing at higher levels where additional (third-stage and higher) chromatic

mechanisms must account for discrepancies between cone and perceptual opponency[4] as well as mediate the orientationally selective and spatial bandpass processing of isoluminant patterns.[8–19] In area V1, several classes of color-responsive cortical cells have recently been categorized,[20–24] and even at this level it is conceivable that various transformations might apply to differing visual tasks. For instance, the mechanisms employed for color naming may be different from those for color-defined form. Some tasks may be subserved by mechanisms where the second-stage axes are preserved (or where performance is limited by processing at the second stage). This has been shown to be the case for detection,[19] subthreshold summation,[25–27] and in functional magnetic resonance imaging (fMRI) studies.[28] This retention of geniculatelike chromatic selectivity is observed even though detection and subthreshold summation are subserved by bandpass, orientationally selective, and thus cortical, mechanisms.[8,11,29] Second, specific interactions among the outputs of second-stage mechanisms might yield a limited set of third-stage axes with preferred chromatic directions differing from those of the second stage. Such a transformation has been proposed[4] in an effort to resolve the discrepancy between perceptual color opponency proposed by Hering,[30] as measured by hue cancellation[31] and hue scaling,[32,33] and the distinctly different opponency found at the second stage. An additional

feature of the "fourth stage" of this model[4] is that each chromatic pole of the opponent process is independent, as has also been suggested by others.[34] The resulting chromatic mechanisms are unipolar rather than the bipolar mechanisms of traditional second-stage opponent processes. Although this model[4] postulates red and green (and blue and yellow) unipolar mechanisms with symmetrically opposite cone weightings, this is not a required property of discrete, unipolar chromatic processing.[33] A third possibility is that the second-stage outputs are combined with a range of weightings to "tile" color space. Evidence for such a transformation comes from physiological recordings that show that cells in V1 do not show any signs of discrete populations of color-selective cells,[22,24,35–37] as was true at the second stage. The same is true of more central (beyond V1) visual areas.[23,38,39] Such an absence of preferred chromatic axes has also been observed in psychophysical studies involving adaptation and color appearance.[40,41]

Perception of spatial form is also a multistage process. A variety of models have been proposed for the detection of correlations in Glass patterns.[42–46] Although these models differ in details, each requires that initial resolution of local oriented features by Gabor-like filters is followed by integration of these features using midlevel mechanisms. Two recent studies[47,48] demonstrated how manipulations of luminance contrast in Glass patterns had differing effects on pattern perception at an early level, where oriented features are first resolved, and at a midlevel stage where oriented dot pairs are combined to yield global percepts.

To further our understanding of a possible third stage of color processing and its relationship to the perception of form, we employed Glass patterns.[1–3] Glass patterns (see Fig. 1) are constructed by copying and geometrically transforming an array of randomly positioned elements (e.g., dots and Gaussians) and then superimposing the

two arrays. In the experiments reported here, we utilized Glass patterns whose elements were "soft-edged dots." In the majority of the experiments, these dots were isoluminant with the background and were either all of a single chromaticity or, in other cases, selected elements had a second chromaticity. Using isoluminant Glass patterns with elements of a single chromaticity we sought to determine if form processing varies as a function of color and whether, as others have suggested,[49] form vision is degraded for patterns defined solely by chromatic variations. For the experiments utilizing Glass patterns comprised of dots of two chromaticities, the chromatic variations were manipulated in two distinct ways: color differences between the dots composing a dot pair (intradipole variations) and color differences among dot pairs (interdipole variations). Intradipole manipulations allow for the investigation of color processes at the level of an initial combination of features to yield information about orientation, presumably at early levels of the visual cortex. Interdipole variations probe a stage where local oriented features are integrated by more global, midlevel, spatial mechanisms. Additionally, we wanted to determine how these mechanisms may differ when the spatial pattern has global statistical dependences versus strictly local dependences. To this end, we used two different types of patterns, translational and concentric. These patterns have been reported to activate local and more global mechanisms in the visual system, respectively.[2,46,47,50]

With respect to the general issue of form processing in the absence of luminance cues, we find, as have others[51,52] that (i) form processing is not degraded significantly by removal of luminance cues (LM pattern thresholds are identical to luminance pattern thresholds), but (ii) this is not the case for S-defined pattern thresholds, which are slightly elevated relative to LM and luminance patterns. From our experiments addressing color processing at a putative third stage also concerned with form processing,
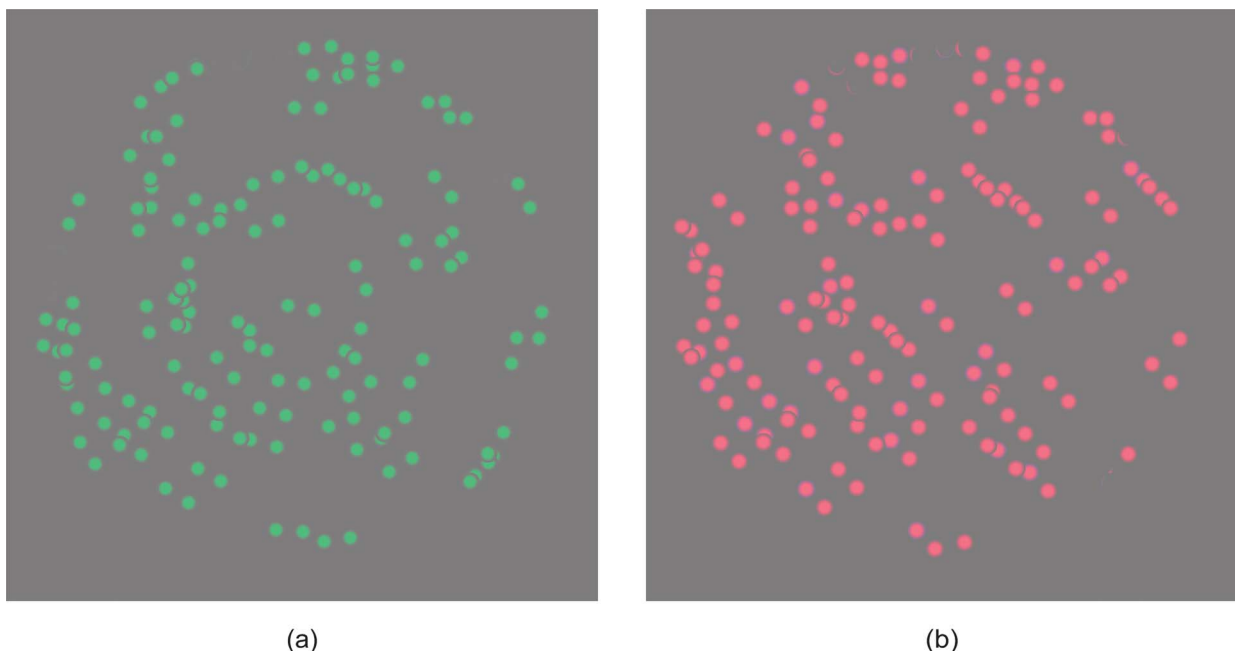

(a)   (b)

Fig. 1.   Chromatic Glass patterns. (a) Concentric pattern in "green" ($\phi \approx 180°$). (b) Translational pattern in "red" ($\phi \approx 0°$).

we (i) confirm that two chromatic mechanisms are insufficient to describe the data, (ii) find that the estimated bandwidth is often narrower than would be predicted by second-stage color processing, and (iii) validate that the upper limit of color integration appears to be less than $90°^{10}$; i.e., chromatic differences larger than 90° in either direction from *any* reference color cannot be integrated to yield pattern perception. With regard to global interactions of color-varying spatial elements (i.e., the interdipole variations), we find that (i) noise of *any* chromaticity can influence detection of a pattern of another color, and (ii) two intermingled patterns of *any* differing chromaticities are integrated to produce thresholds equivalent to that of *one* chromaticity. This suggests that such a process is mediated by color-responsive complex cells that lack color selectivity[53,54] or some other transformation that combines the outputs of a large number of color-selective cells. Finally, in these studies using chromatic Glass patterns we find no preference for pattern configuration (translation or concentric) at any level of processing.

2. EXPERIMENTAL METHODS

A. Stimuli
In these experiments we utilized translational and concentric Glass patterns.[1–3,47] Our pattern elements were circular dots (0.09° diameter plateau) with Gaussian tapered edges (total dot diameter 0.24° of visual angle to e^{-1} contrast). The large element sizes and tapering were used in an effort to minimize chromatic aberrations. The separation of dots within a dot pair was 0.37° for both translational and concentric patterns. The pattern of dot pairs was delimited by a 7.4° circular window containing approximately 140 dots (70 dipoles). The dot pairs were presented on a gray (Illuminant C) background of 37 cd m^{-2}. Stimuli were presented for 750 ms at the selected contrasts with 100 ms up/down ramps.

The chromaticity of the pattern elements was defined in terms of the three-dimensional MacLeod–Boynton–Derrington–Krauskopf–Lennie (MBDKL) opponent color space.[55,56] Our implementation is similar to that of Rabin *et al.*[57] The current studies primarily concern chromaticities in the isoluminant plane. Here chromaticities are defined by excursions relative to the neutral (Illuminant C, 37 cd m^{-2}) background with the parameter ρ describing the magnitude (chromatic contrast) and the angle ϕ the chromaticity ($\phi = 0°$ and 180° correspond to excursions along the $+L-M$ and $+M-L$ axes, respectively; $\phi = 90°$ and 270° along the $+S$ and $-S$ axes, respectively). Luminance pattern elements were achromatic variations above or below the background. The unit vectors used to specify chromaticity of intermediate ϕ corresponded to cone contrasts of L$= \pm 0.073$, M$= \mp 0.141$ along $\phi = 0°$, 180° and S $= \pm 0.821$ along $\phi = 90°$, 270°. In this color space, stimuli having chromaticities along each of the coordinate axes (the "cardinal" axes) selectively activate one of the three classes of second-stage color mechanisms.[55] We further equated the luminances at each chromaticity to reflect individual isoluminance balances for each observer. These were determined using the method of ambiguous motion[58,59] with sinusoidal gratings having a half-cycle of 0.36°, corresponding to the diameter of the Glass dots.

In the Glass patterns, the color of a dot was a unipolar excursion along an axis either in the isoluminant plane or along the luminance axis. How to appropriately scale contrast becomes an issue when comparing results among various color directions. For experiment 1, which compared the detection of Glass pattern along different chromatic axes, we utilized an equivalent contrast metric[60,61] to equate the dot visibilities for various colors. However, our observation that a subject's sensitivity to detection of Glass patterns varies as a function of color contrast[62,63] prompted a different approach for the intradipole and interdipole chromatic variations of experiments 2 and 3. Here we empirically equated color contrast for pattern detection threshold at each color angle by setting a fixed percent dot-pair correlation (that was above the pattern detection threshold at high contrast) and then determining the contrast required for pattern detection at this correlation level (for details see Refs. 62 and 63).

B. Procedures
Pattern detection thresholds were determined by a two-alternative-spatial-forced-choice procedure using the method of constant stimuli. Two Glass patterns were presented side-by-side on the gray background with centers horizontally displaced by 9.7°. Observers were allowed to free-view the patterns. On any given trial one of the paired patterns contained a fraction (randomly varied trial-to-trial among the preselected correlation levels) of dot pairs that were arranged in a manner consistent with concentric or translational structure, and the second contained randomly oriented dot pairs. The observer's task was to select the pattern that contained the correlated dot pairs. Experiments were blocked into runs of 100 trials with a minimum of 400 trials per threshold estimate. Thresholds were estimated via probit analysis[64] at the 75% correct level.

C. Subjects
One of the authors (JAW) and four naïve observers took part in various aspects of these experiments. All had normal or corrected normal 20/20 vision. Observers CT and JAW were well experienced with Glass patterns, while JK, MM, and PW had no prior experience. Subjects were not instructed with regard to strategies for detecting the correlations but only to select the pattern that appeared to have the greater global spatial structure.

3. RESULTS

A. Experiment 1: Chromatically Homogeneous Pattern Elements
The first experiment addressed whether form vision is degraded when the elements of a Glass pattern are isoluminant rather than luminance-defined. We also wanted to compare the ability of the visual system to detect form along various directions in color space. Pattern correlation thresholds were determined for patterns having unipolar chromatic excursions at 22.5° (ϕ) intervals in color space. To equate the chromatic contrast for differing chromaticities and for luminance contrast, we utilized a contrast metric based on perceptual contrast matching.[60] In
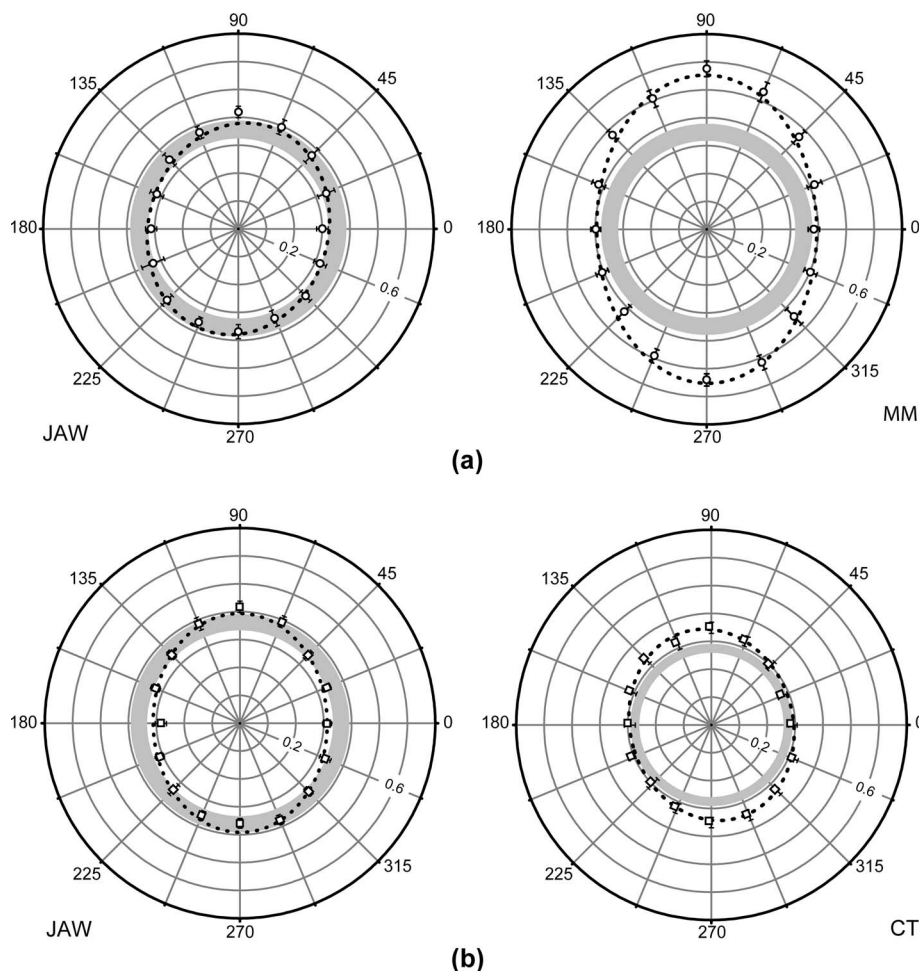
Fig. 2. Pattern detection as a function of dot chromaticity (experiment 1). Thresholds (±1 standard deviation) for (a) concentric patterns (open circles) and (b) translational patterns (open squares). The dotted curves are least-squares fits of ellipses to the data. Each observer's average detection threshold for luminance increments and decrements (±1 standard deviation) is indicated by the grey circular area.

the isoluminant plane, equally salient contrasts correlate well with an ideal-observer-based, equivalent-contrast metric.[65–67]

Figures 2(a) and 2(b) show the results of these experiments for concentric patterns (observers JAW and MM) and translational patterns (observers JAW and CT). Thresholds (radius) are plotted as a function of color angle (ϕ) and are shown as open circles (concentric correlations) or open squares (translational correlations), ±1 standard deviation. The dotted curves are least-squares fits to an ellipse centered at the origin; for comparison, the gray ring indicates the average threshold for luminance increments and decrements, ±1 standard deviation (at luminance contrasts above 10%, Glass pattern detection thresholds are relatively insensitive to contrast level when all dots have identical contrast).[47] Data for translational correlations for subject MM (not shown) are similar to those of JAW in Fig. 2(b).

These results indicate that form, as generated by Glass pattern correlations, can be detected in the absence of luminance information. For observer JAW, the equivalent contrast metric[60] yields patterns that have roughly equal correlation thresholds at all chromaticities. However, even with this contrast normalization, all observers show relatively higher thresholds at chromaticities near the S

axis. Thresholds for stimuli defined by LM variations are not significantly different from those measured with achromatic patterns (gray ring). In fact, observer JAW's thresholds for isoluminant LM patterns were *lower* than those for achromatic patterns for both concentric and translational configurations. Additionally we find that most observers are no less sensitive to form variations along intermediate color directions than they are along the cardinal directions, implying an important role for third-stage color mechanisms in form vision. Thresholds along opposing ends of chromatic axes are similar, suggesting the absence of unipolar mechanisms with greatly differing sensitivities.

B. Experiment 2: Intradipole Color Manipulations of Glass Pattern Elements

In this second series of experiments we wanted to determine the extent to which observers can integrate differing chromaticities to yield an oriented element that can then be used in building a global percept of form. To accomplish this, we specified eight reference colors in the MB-DKL isoluminant plane ($\phi_r = 0°$ through $315°$ in $45°$ steps) for one dot in each dot pair and systematically varied the test color ϕ_t of the other dot in $±22.5°$ (or $±15°$) steps from the reference. For example, if the reference color were

$45°$, we estimated pattern detection thresholds for dots with $\phi_r = 45°$ paired with dots having $\phi_t = 45°$, $22.5°$, $67.5°$, $0°$, $90°$,... [see Fig. 3(a)]. This manipulation allowed us to estimate the chromatic integration bandwidth of the mechanisms involved in the initial resolution of paired dots into oriented features. Since detection thresholds for Glass patterns with luminance-varying elements are sensitive to the relative contrast of the paired dots,[47,68,69] we took some care in selecting the chromatic contrasts used in experiment 2. For the various ϕ, relative color contrasts were equalized by measuring, as a function of contrast, detection thresholds for a Glass pattern having elements of a single chromaticity and a fixed correlation level (chosen to be suprathreshold at high contrasts). The contrasts used in experiment 2 (and experiment 3) were those required to give a correlation threshold of 0.35 at each chromaticity [however, note that the data of Fig. 5(a) corresponded to an early experiment which utilized CT's contrasts derived for correlation thresholds of 0.5].

The results for translational patterns and for concentric patterns are shown in Figs. 4 and 5, respectively. The data indicate that when the two dots within a pair have chromaticities that differ by $\delta\phi \approx 90°$ (e.g., when one lies along $L+M-$ and the second $+S$, or one at $45°$ and the second at $135°$) subjects are no longer able to distinguish a fully correlated pattern from one with randomly oriented dipoles [also see example in Fig. 3(a)]. This is true regardless of the reference color and regardless of whether the reference axis is along a second-stage opponent direction [Figs. 4(a) and 5(a)] or along an intermediate direction [Figs. 4(b) and 5(c)]. The solid curves in Fig. 4 and 5 are fits of cosine functions to the data from which we estimated bandwidths. For reference chromaticities along the cardinal axes [Figs. 4(a), 5(a), and 5(b)] the average bandwidths (half-width at half-height) were $51.13°$ (CT, translation), $47.75°$ (CT, concentric), $53.5°$ (JK, concentric), and $36.13°$ (JAW, concentric, not shown) using a default cardinal axis weighting.[56] Averaged bandwidths for reference chromaticities lying between the canonical directions

[Figs. 4(b) and 5(c)] were $52.5°$ (CT, translation) and $49.5°$ (JK, concentric). Although slightly broader than bandwidths for cardinal axis reference colors, these data support the notion that two orthogonal color axes are insufficient to describe third-stage color mechanisms (see Discussion, Section 4). Furthermore, we find no differences between concentric and translational configurations, suggesting that this is a strictly local, early-level process.

C. Experiment 3: Inter Dipole Color Manipulations of Glass Pattern Elements

In the third series of experiments, we investigated the role of color in segmentation and integration at higher levels of color and form processing. To accomplish this, we kept the color of the dots within a dipole the same while we varied the color *among* dipoles. During any given run, half the dipoles had one chromaticity while the remainder had a second chromaticity. Thus the full pattern was a combination of two interleaved subpatterns that could be controlled independently. In these experiments, one of the subpatterns had a fixed color angle of $\phi_r = 0°(L+M-)$ and the color (ϕ_t) of the second subpattern was fixed within a run but was varied between runs using color angle step sizes of $45°$. We empirically equated color contrast as in experiment 2.

In one set of these interdipole experiments we attempted to determine how a "signal" subpattern is segmented from a "noise" subpattern when the two subpatterns differ in chromaticity. In this experiment, the first subpattern (signal) contained a proportion of oriented dipoles that was varied within a run and the second subpattern (noise) contained only randomly oriented dipoles. A second set of experiments addressed integration of form from dipoles that differed in chromaticity. Here we used the same paradigm of interleaving two subpatterns, except *both* subpatterns contained a fraction of properly oriented dipoles that were co-varied to determine pattern de-
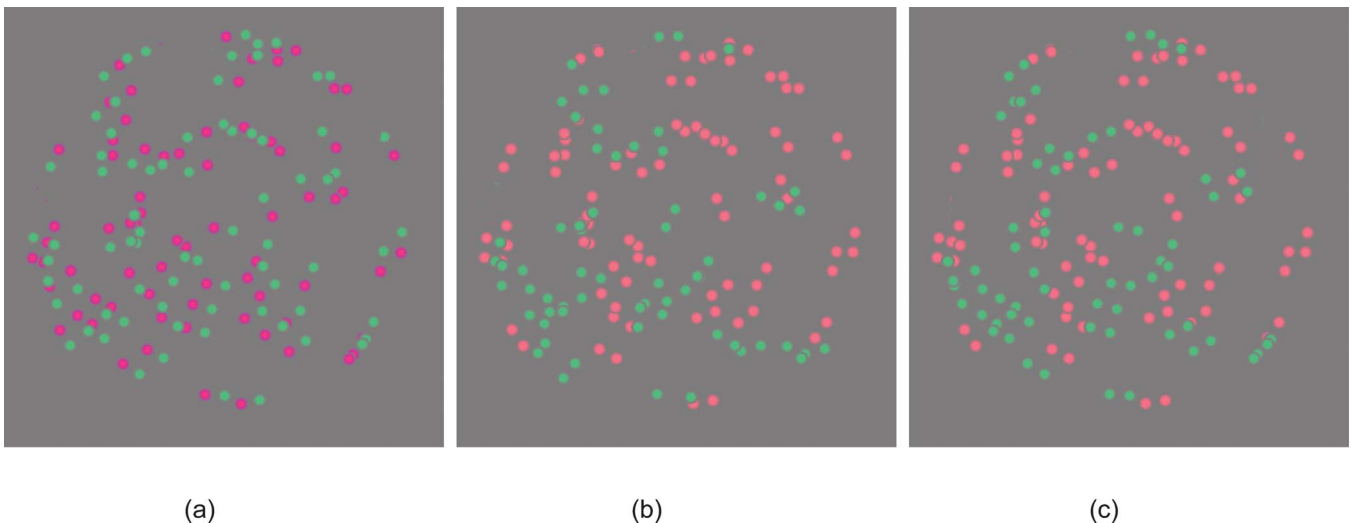

(a)   (b)   (c)

Fig. 3. Examples of concentric Glass patterns with intradipole and interdipole chromatic variations. (a) Intradipole variation with "violet" ($\phi_t \approx 90°$) and "green" ($\phi_t \approx 180°$) paired dots having 1.0 correlation (all dot pairs in concentric orientations); (b) interdipole variation with "red" signal ($\phi_r \approx 0°$, 1.0 correlation) and "green" noise ($\phi_t \approx 180°$; 0.0 correlation); (c) interdipole variation with "red" signal ($\phi_r \approx 0°$, 1.0 correlation) and "green" signal ($\phi_t \approx 180°$; 1.0 correlation).
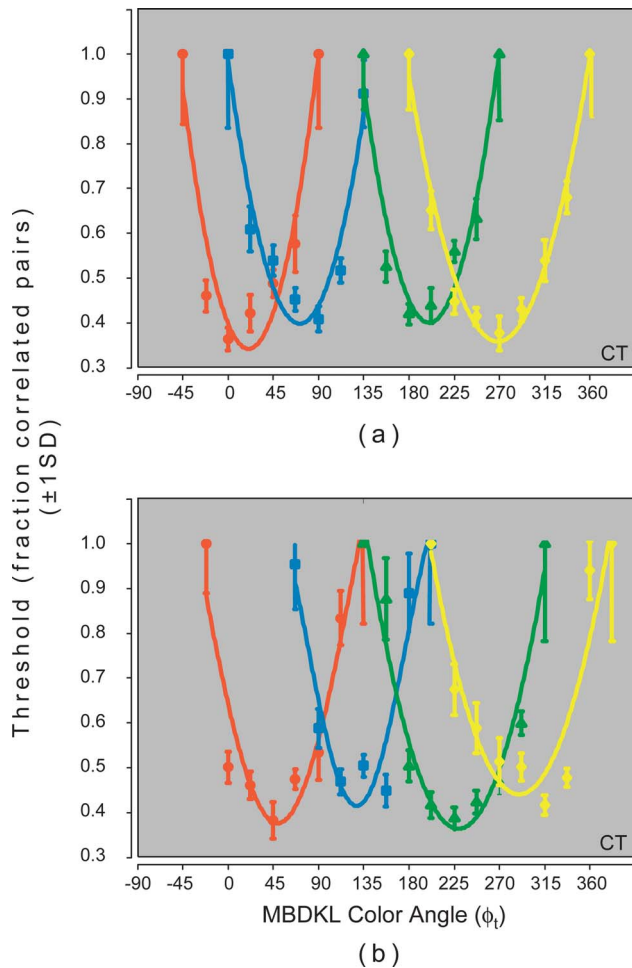
(a)

(b)

Fig. 4.   Pattern detection thresholds for intradipole color variations in translational Glass patterns (experiment 2). (a) Thresholds for observer CT at four reference angles along canonical color axes: red circles, $\phi_r=0°$; blue squares, $\phi_r=90°$; green triangles, $\phi_r=180°$; and yellow diamonds, $\phi_r=270°$. (b) Thresholds for observer CT at four reference angles for chromaticities along intermediate color axes: red circles, $\phi_r=45°$; blue squares, $\phi_r=135°$; green triangles, $\phi_r=225°$; and yellow diamonds, $\phi_r=315°$. The solid lines show least-squares fit of an $[A\cos(\phi_0-\phi)]^n$ function to the data.

reference-subpattern-only conditions are indicated by star-in-circle (concentric patterns) and star-in-square (translational patterns) symbols. To facilitate comparison with other data, the gray annular regions indicate thresholds (± 1 standard deviation) for these reference subpatterns in the absence of a second subpattern. Thresholds for the signal+noise condition are shown as filled circles (concentric) and solid squares (translations). Thresholds for the signal+signal are indicated by open circles (concentric patterns) and open squares (translational pat-

tection thresholds. Figure 3 includes examples of each of these manipulations. Figure 3(b) is a pattern representative of signal+noise with the signal dots (correlation 1.0) in red ($\phi_r \approx 0°$) and the noise dots in green ($\phi_t \approx 180°$). Figure 3(c) is an example of the signal+signal conditions; in this case both subpatterns have a correlation of 1.0. To determine the magnitude of segmentation for the signal +noise conditions or integration for the signal+signal conditions we compared the pattern detection thresholds from the interdipole conditions to those obtained from a homogeneously colored subpattern in the absence of a second subpattern (i.e., a condition similar to experiment 1, but with half the number of dot pairs).

The results of experiments with interdipole chromatic variation are shown in Fig. 6. In this figure we report thresholds (radius) as a function of color angle from two naïve observers (JAW's data, not shown, were similar) for concentric patterns [Figure 6(a)] and for translational patterns [Figure 6(b)]. Thresholds for the $\phi_r=0°$
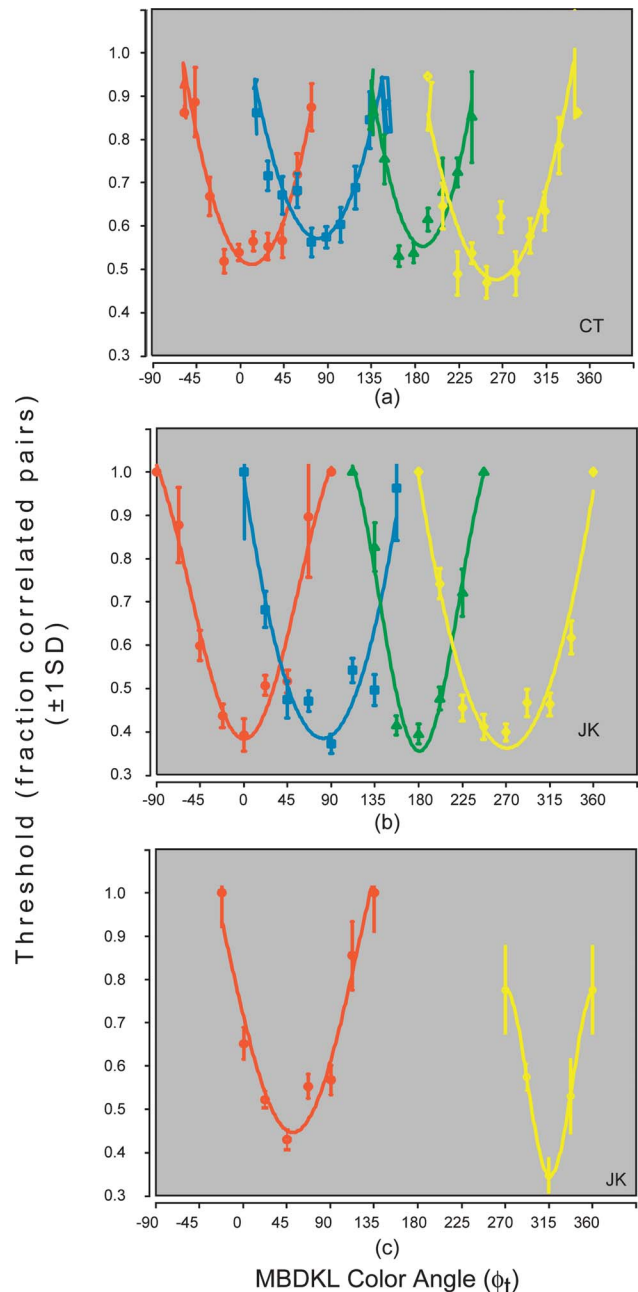

(a)

(b)

(c)

Fig. 5.   Pattern detection thresholds for intradipole color variations in concentric Glass patterns (experiment 2). Thresholds for observer (a) CT and (b) JK at four reference angles along canonical color axes. (c) Thresholds for observer JK at two reference angles for chromaticities along intermediate color axes $\phi_r=45°$ and 315°. Symbols and colors as in Fig. 4.
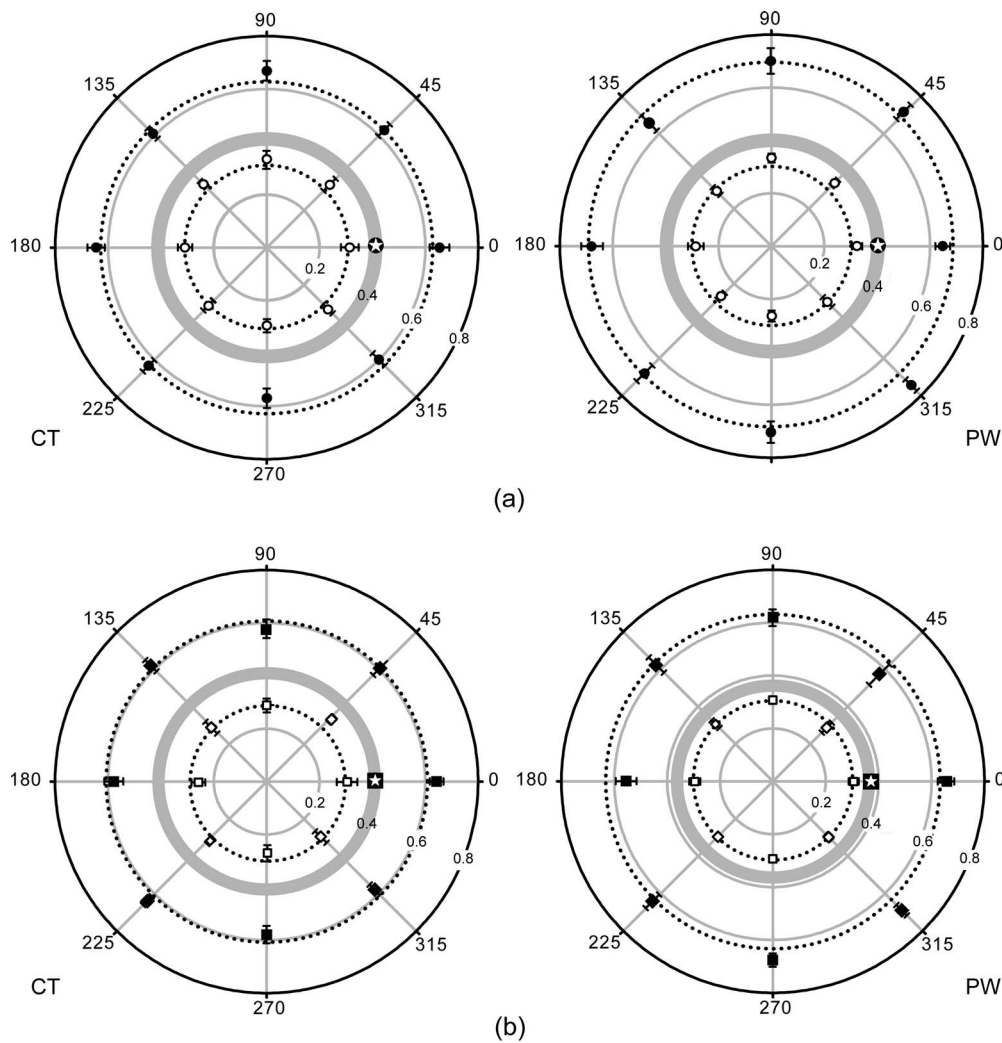
Fig. 6. Pattern detection thresholds for interdipole chromatic variations (experiment 3). (a) Concentric Glass patterns: The symbol star-in-circle is the threshold for the $\phi_r=0°$ reference "signal" subpattern in the absence of a second subpattern; this subpattern was a component of all stimuli employed in experiment 3. To facilitate comparison with other data, the gray annular region also indicates this threshold (±1 standard deviation). Filled circles indicate the thresholds when "noise" subpatterns of various chromaticities (ϕ_t) were added to the reference subpattern. Open circles indicate the threshold when "signal" subpatterns of various chromaticities (ϕ_t) were added to the reference subpattern. Error bars give ±1 standard deviation. (b) Translational Glass patterns: The symbols star-in-square, filled squares, and open squares refer to thresholds for the reference "signal" subpattern alone, the "signal+noise" condition, and the "signal+signal" condition [as in (a)]. In all cases the thresholds correspond to the fraction of correlated dot pairs in the reference "signal" subpattern required for pattern detection.

terns). The dotted curves are least-squares fits of circles to the data. Error bars correspond to ±1 standard deviation.

For the signal+noise condition (filled circles and solid squares) we find that (i) as expected, addition of a subpattern of randomly oriented dot pairs having the same chromaticity ($\phi_t=0°$) as the reference pattern raises detection threshold (from ~40% to ~60%), (ii) of greater interest, the effect of the added noise is virtually independent of its chromaticity (i.e., random dot pairs of any color are equally effective in raising the threshold of the $\phi_r=0°$ reference sub-pattern), and (iii) similar effects are observed for translational and concentric patterns. These signal+noise results show that midlevel mechanisms responsible for pattern segregation are not color-selective, as

there is uniform elevation of thresholds relative to our reference subpattern (i.e., detection of the signal pattern is *not* blind to noise of differing chromaticity).

Results for the signal+signal condition (open circles and open squares) indicate that (i) the addition of a second signal sub-pattern having the same chromaticity ($\phi_t=0°$) as the reference pattern reduces detection threshold (from ~40% to ~30%; i.e., lower fractional threshold with increased density of dot pairs), (ii) the effect of the added signal is virtually independent of its chromaticity, and (iii) similar effects are observed for translational and concentric patterns. These results suggest that midlevels of the visual system integrate information about form irrespective of color. Furthermore, these results show complete integration of all chromaticities given that thresh-

olds for the mixed subpattern are not significantly different from those of homogeneously colored, full-density patterns.

4. DISCUSSION

There were four major goals of these studies. One was to ascertain how joint spatial–chromatic variations, in the absence of luminance cues, are used in the perception of form. A second was to determine how these mechanisms might be preferentially selective to global versus local spatial statistics.[46,47,50] A third goal was to test whether detection of Glass patterns might involve unique or previously suggested third-stage mechanisms, and if so to measure the nature and bandwidth of these mechanisms. Finally, we wanted to determine how color information may be utilized by processes beyond a third stage.

A. Color and Form

1. Homogeneous Color versus Luminance
In early discussions of color and form vision, some researchers asserted that color-selective cells in the cortex are insensitive to orientation and that color information "is not important in form perception" (Ref. 70, p. 3420). However, there is also a wealth of physiological and psychophysical information showing that a significant population of cells in V1 respond to isoluminant patterns with bandpass spatial frequency and orientation tuning[20,21,23,37,54] and that, in detection and discrimination tasks for isoluminant gratings, human observers exhibit bandpass spatial frequency and orientation selectivity.[8–11,13–17] There is also evidence that subsequent stages of form processing that integrate the outputs of early levels can operate with isoluminant patterns.[51,52,62,63]

For detection of Glass patterns, we have confirmed the conclusions of these previous studies by demonstrating that the visual system is capable of integrating isoluminant elements across space to resolve global pattern configurations. Detection thresholds for isoluminant Glass patterns are similar to those for patterns constructed from elements defined by luminance increments or decrements. Although all observers have somewhat higher thresholds at $\phi=90°$ and 270° (Fig. 2), for two of the three observers pattern detection thresholds are similar, irrespective of chromaticity, when chromatic contrasts are equated by an ideal-observer contrast metric. This is in accord with the studies of "contour integration" by Mullen *et al.*[51] and McIlhagga and Mullen[52] who find color performance is on par with luminance. However, for other aspects of form perception various studies reach differing conclusions regarding performance with achromatic versus isoluminant patterns. For example, measuring an observer's ability to detect deviations from circularity, Mullen and Beaudot[49] conclude that there is a general deficit for two-dimensional form perception at isoluminance (along both the LM and the S axes).

2. Early versus Midlevel Form Processing
The intradipole and interdipole chromatic variations (experiments 2 and 3) give one an opportunity to probe the

integration of differing chromaticities at early-level and midlevel stages of form resolution. For luminance-defined Glass patterns it is assumed that the first step in form detection is the resolution of oriented features by Gabor-like filters in V1.[47,71] If such a mechanism is applicable to isoluminant Glass patterns, the results of experiment 2 imply that these filters are optimally activated by dot pairs having similar chromaticity. Orientationally selective V1 neurons that respond to isoluminant stimuli, originally observed by Thorell *et al.*[54] and more recently categorized as "color–luminance" neurons,[20–24] are prime candidates for such early-processing filters. Since neurons of this type display peak chromatic preferences that tile the isoluminant plane,[22,35–37] one might expect that a dot pair constructed with intradipole chromatic variation would activate a chromatically selective filter with preferred chromaticity intermediate to that of the individual dots and thus support form detection (the filter effectively averaging or blurring the chromaticity of the dots). However, the averaged chromatic contrast of a dot pair of identical chromaticity (e.g., $\phi_r = \phi_t = 45°$; $\phi_{avg} = 45°$) is greater than that of a dot pair with differing intradipole chromaticity (e.g., $\phi_r = 0°$, $\phi_t = 90°$; $\phi_{avg} = 45°$). Thus activation of color-luminance neurons would be most effective with homochromatic dot pairs ($\phi_r = \phi_t$) and would fall off with increasing chromatic difference.

Alternatively the early-level processing of form may differ for Glass patterns defined by color and those having luminance elements. Differences in the spatial properties of V1 receptive fields responding to color and luminance gratings have been recently reported.[24] Resolution of individual dot elements by the subpopulation of nonoriented "color" neurons in V1[20–24,72] could be followed, at a later stage, by combination of the paired dots to yield an oriented feature. The results of experiment 2 indicate that such integration would have to be color specific.

Less is known regarding the physiological mechanisms that would provide the basis for midlevel integration of oriented units. Several electrophysiological studies report cells with receptive fields that are preferably activated by circular stimuli, both in V1 and V2[73] and in V4.[74,75] In addition, Wilson *et al.*[50] have, based on psychophysical experiments, postulated the existence of neurons in V4 that integrate local dipoles arranged in a circular manner. Our data from experiment 3 indicate that the chromatic selectivity of integration at this level is quite different from that of early visual processing: Midlevel integration of oriented features is virtually "colorblind" (i.e., unselective for color but not "blind" to the presence of dot pairs of differing chromaticity) while early-level integration of individual dots is color specific. Below we further discuss the relationship of early-level and midlevel form processing to the various stages in the transformation of chromatic visual information.

3. Translations versus Concentric
Wilson and co-workers[46,50] have suggested that detection of translational and rotational Glass patterns may involve differing mechanisms, i.e., that these configurations activate local and more global mechanisms, respectively. We have further applied this idea in modeling the effects of the size of sampled patches on the detection of transla-

tional and concentric correlations.[47] This model demonstrates that, since detection of concentric (and hyperbolic) patterns requires comparison of the orientations of adjacent dipoles while detection of translation involves only the absolute orientation of individual dipoles, concentric patterns will require a larger region of global integration. We have used this model to explain why opposite-polarity, interdipole achromatic noise had a differing effect on the detection of translational and concentric patterns. With this background as motivation, we used both translational and concentric patterns in each experimental condition.

In each of our experiments isoluminant translational and concentric Glass patterns gave similar results. For our dot-size and dot-density parameters, translational and concentric isoluminant patterns of homogeneous chromaticity have similar detection thresholds (experiment 1). Translational and concentric patterns show the same reduced detectability with increasing differences in intrapair chromaticity (experiment 2). As was the case for achromatic patterns, the visual system cannot integrate the dots to give an oriented feature when elements within a pair have opposite polarities (chromaticities at the opposite ends of a color axis). For both translational and concentric Glass patterns we found that observers were able to integrate signal from dot pairs differing in chromaticity, with performance being independent of the color differences (experiment 3) and were unable to segregate signal from noise irrespective of the interpair color differences (experiment 3). This latter situation differs from that found for achromatic patterns, where the detection threshold of a Glass pattern of oriented white (luminance increment) dot pairs is raised by the addition of black (luminance decrement) noise dot pairs for translational correlations (similar to the color results) but is unaffected for concentric correlations (differing from the color results).

Little is known about the chromatic signature of midlevel mechanisms for extracting form. This observation of complete "colorblindness" in experiment 3 implies that, for these patterns, differing chromaticity plays no role in integrating signal or segregating signal from noise.

B. Transformations of Chromatic Information

1. Third-Stage Color Mechanisms

As suggested in the Introduction, a possible role of a third stage (V1) of color processing is to combine the outputs of the second-stage lateral geniculate nucleus (LGN) system with different weightings. Among the candidates for third-stage color processing mechanisms are (i) retention of the two second-stage (LGN) cardinal color axes, (ii) transformations that create a set of third-stage color axes along a limited number of chromatic directions, and (iii) interactions among LGN mechanisms that yield cortical neurons having preferred chromaticities fully tiling color space. Furthermore, subpopulations of cortical neurons could represent several of these possibilities, and such subpopulations might be utilized in various perceptual tasks.

There is now considerable physiological[20–24,35–37,39] and psychophysical[6,32,40,41,76–79] evidence for higher-level color mechanisms tuned to directions intermediate to the gen-

iculate LM and S axes. The physiological studies identify V1 and V2 neurons having peak chromatic sensitivities throughout color space, although two of the studies[35,36] comment that the observed distribution exhibits biases, as would be required for models with a limited number of preferred third-stage color axes.[4]

Somewhat distinct subpopulations of cells that respond to isoluminant stimuli have also been characterized.[20–24] The psychophysical studies demonstrate that two orthogonal chromatic channels with fixed peak sensitivity are insufficient to explain data from experiments based on adaptation, motion integration, or color appearance. However, the actual number and distribution of chromatic channels cannot always be resolved by psychophysical experiments. Hue scaling data[32,33] have been analyzed in terms of four bipolar chromatic mechanisms (two chromatic axes, plus mirror images) with color specificities that are rotated versions of the second-stage LGN mechanisms.[4] Using color appearance following adaptation, Webster and Mollon[41] proposed a large number of overlapping chromatic channels tiling the chromatic plane. Lennie[38] argued that four to eight color channels would be sufficient to account for their results. However this is essentially a lower bound and does not necessarily indicate that there are actually only four to eight mechanisms contributing to this task.

Our results extend previous experiments concerned with third-stage color mechanisms into the realm of spatiochromatic integration. In the current studies we have shown that, for patterns at intermediate color directions, mechanisms exist that can resolve information about orientation and support the detection of global form. Previous studies of orientation discrimination have concentrated only on LM-, S-, and luminance-varying gratings[15] or Gabors in the LM/luminance plane.[16] Experiment 1 shows that observers are equally capable in resolving form composed of chromatic stimuli at intermediate color angles. In general, this result is not surprising, given that it has been shown that orientation discrimination is quite good for isoluminant gratings[15] and may even be better than luminance orientation discrimination at lower frequencies when each is equated for spatial frequency and rms cone contrast.[16] Our results are consistent with this; our pattern elements were large and Gaussian-tapered to constrain information to the lower spatial frequencies and were equated for equivalent color contrast at various color angles.

The variation of intradipole chromaticity, experiment 2, allows us to further characterize these intermediate mechanisms. In agreement with Lennie,[38] our estimates of third-stage color bandwidths (half-width at half-height) suggest that four bipolar (eight unipolar) mechanisms may be a reasonable *minimal* number and thus inconsistent with the retention of LGN second-stage axes. The observed bandwidths for degradation of pattern detection with increasing intradipole color difference are similar along the cardinal and intermediate directions (Figs. 4 and 5) and somewhat narrower than those for second-stage mechanisms (60° in LGN versus 47.1° for the average cardinal axis references across three observers). This narrowing of color tuning is consistent with the narrowing of color tuning found in V1 versus LGN cells.[35]

The intradipole results at the intermediate color directions place further limitations on the nature of third-stage color processing. If the cardinal axes of the LGN were maintained, then one would expect a dot of intermediate chromaticity to activate both $L-M$ and $S-(L+M)$ mechanisms [for example, at $\phi=45°$ both $+L-M$ and $+S-(L+M)$ would be activated]. Thus thresholds for homochromatic Glass patterns would be mediated by a combination of form detection in the individual LM and $S-(L+M)$ channels. However in the heterochromatic, intradipole case, one would expect a pair of dots having chromaticities $\phi_r=+45°$ and $\phi_t=-45°$ to each activate both cardinal mechanisms [$+L-M$, $+S-(L+M)$ at $\phi=45°$ versus $+L-M$, $-S+(L+M)$ at $\phi=-45°$] and provide a basis for form detection. Thus for both the bipolar and unipolar cortical versions of the second-stage cardinal mechanisms, one would expect detection bandwidths to extend well beyond $90°$ for oblique chromatic reference axes. The bandwidths observed for these axes (Figs. 4 and 5) are considerably narrower.

One of the issues with utilizing the MBDKL color space is how appropriately to weight unit vectors along the cardinal axes, weights that determine the actual chromaticity at intermediate angles. The results in Figs. 2 and 3 are reported with the default MacLeod and Boynton[56] values. We have also computed chromaticity bandwidths for LM and S unit vectors having contrasts obtained for equal detection thresholds along the cardinal directions for each observer.[62,63] The values of ϕ for intermediate chromaticities were obtained by trigonometric combinations of these perceptually based vectors. Bandwidths with this alternative weighting showed modest changes, but the general trend is further narrowing of the bandwidths by $0.75°$–$1.25°$ for the cardinal axis references (mean$=46.91°$). This was also true of the oblique axis references for JK (MacLeod and Boynton weighting, $54°$; perceptual weighting, $51°$), but not for CT (MacLeod and Boynton weighting, $55.25°$; perceptual weighting, $55.9°$).

2. Beyond the Third-Stage Color Mechanisms
A discussion of further color processing in the detection of form in Glass patterns involves two issues: (i) Are there additional features of the color transformations involved in resolution of the oriented segments (dot pairs), and (ii) what is the nature of chromatic selectivity of the midlevel processes effecting the integration of individual oriented segments? The first of these involves a possible transformation of bipolar opponent mechanisms to unipolar mechanisms. De Valois and De Valois[4] have modeled such a transformation as a "fourth stage" of color processing, and Sankeralli and Mullen[34] demonstrated unipolar effects in chromatic masking. Although unipolar versus opponent mechanisms are somewhat difficult to distinguish by strictly psychophysical means, two aspects of our results address this issue. First, in experiment 1 the observed detection thresholds are nearly identical for unipolar chromaticities at opposing ends of a color axis (Fig. 2). Thus if a transformation to unipolar or rectified mechanism has occurred, the sensitivities of the independent mechanisms' mediating either end of a color axis must be similar.[4] Second, in experiment 2, we find that two dots with chromaticities at opposite ends of a bipolar axis cannot be integrated to give the percept of an oriented segment. This could originate from cancellation in an opponent mechanism, the lack of interaction of unipolar mechanisms with large $\delta\phi$, or spatial averaging of the chromaticities of the two dots by orientationally selective V1 color-luminance neurons.

In contrast to the intradipole (early-level processing) results, experiment 3 indicates that the midlevel processes that mediate global integration and segregation of dot pairs from throughout the pattern are "colorblind," i.e., pooling occurs but appears to be insensitive to the differing chromaticities of the oriented elements. V1 complex cells that respond robustly to isoluminant stimuli but lack color-selectivity have been observed[54] and could serve as a neural substrate for this "colorblind" pooling. In that little is known about the binding of color and form at levels beyond V1, our results pose an interesting finding that future electrophysiological, imaging, and psychophysical studies must address. The relationship of these results to other studies of segmentation and integration is discussed in Section 5.

5. CONCLUSIONS AND COMPARISON WITH OTHER STUDIES

In these experiments, we have examined a number of ideas concerning the joint processing of color and form: (i) we investigated the role of pure color information in form vision; (ii) we also examined whether these mechanisms are preferentially more or less sensitive to translational versus rotational patterns; (iii) we clarified whether observers are sensitive to pattern arrangements when the elements are derived from intermediate directions in color space; (iv) we determined the bandwidth of postulated third-stage color mechanisms concerned with processing form; and (v) we established how color information may be utilized by segmentation and integration processes beyond early cortical processing. In experiment 1, we showed that observers' sensitivities to isoluminant LM Glass patterns are on par with those for achromatic patterns. In addition, observers' sensitivities did not change for pattern type—translational versus rotational. We also showed that observers are just as sensitive to patterns composed of elements from intermediate color directions as they are to cardinal axis and achromatic patterns. In experiment 2, we estimated the bandwidth of postulated third-stage mechanisms and determined that our data are in accord with physiological data that show a narrowing of color tuning. Also, we estimated the upper limit of color integration at this third stage and found that it is less than $90°$, irrespective of the reference color. Finally, in experiment 3, we measured the extent to which midlevel spatial mechanisms will integrate or segregate pattern elements based on color. We found that higher levels of joint color–spatial processing are color responsive, but lack color selectivity.

In an experiment exploiting the "orthogonal flow" often observed when Glass patterns have paired elements with opposite contrast polarities,[2,3] Kovacs and Julsez[80] utilized translationally correlated patterns to demonstrate that color cues could not reverse the effects of luminance polarity in judgments of static flow. This is somewhat sur-

prising in light of the results of robust detection of isoluminant Glass patterns in experiment 1. Although masking studies reveal interactions between color and luminance contrast,[11] the more dominant interaction, color-masks-luminance, would not provide an explanation of the static flow appearance.

Studies of intrapair chromatic integration in Glass patterns have been previously reported.[63,81] Using the tilt illusion, Clifford *et al.*[82] investigated interactions among gratings of differing orientations and chromaticities. They found that these interactions decrease with increasing chromatic difference and their measured bandwidths ($\approx 50°$ full width) are similar to those we obtained in experiment 2 (Fig. 4). From their data they conclude that "the cardinal chromatic axes have no special status at the level(s) of visual cortex at which the tilt illusion is mediated," consistent with our interpretations based on experiment 2. Although the tilt illusion arises from interactions among orientationally tuned mechanisms while experiment 2 probes activation within orientation filters, it is not unreasonable to speculate that they may both occur at an early level of visual processing, pehaps in V1.[82] This would be in contrast to the nonselective chromatic processing we observe in the global integration of oriented pairs, presumably by higher level processes.

Cardinal and Kiper[83] have recently reported results of Glass pattern detection experiments with stimuli similar to some of those in our experiment 3 (interdipole chromatic variation for concentric patterns, with $\phi_r = 0°$, in the signal+noise condition). Although in the two studies the experimental conditions differed significantly, the studies concur somewhat in reporting broad[83] or no (current study) chromatic tuning for the effects of signal and noise dot pairs of differing chromaticity. Cardinal and Kiper[83] also report that dot pairs at 0° and 180° are integrated differently in an experiment similar to the signal+signal condition of experiment 3. However, we find that additional oriented red or green dot pairs are equally effective in enhancing the detection of a half-pattern of red dot pairs (Fig. 6). We believe that these differing observations may arise from the differences in experimental protocols in the two studies, including density of displayed dots, possible luminance artifacts (size and shape of individual dots, separation of paired dots, and individual versus standard observer isoluminance), differing temporal presentation, and differences in the selection and control of dot contrast at various chromaticities. Although Cardinal and Kiper[83] report "randomization of the dot's luminance had no effect on the pattern of results," we found that the relative contrast (i.e., saturation) used at differing chromaticities had a significant effect on detection threshold, as might be expected from studies with achromatic patterns.[47] This motivated us to employ perceptually equivalent contrasts in experiments 2 and 3. In addition, the similar results we obtain for translational and concentric patterns lead us to believe that the privileged processing suggested for concentric patterns in the color area V4[83,84] is not responsible for the broad (non)spectral tuning.

The lack of color specificity among oriented elements in the midlevel processing of form in Glass patterns was a surprising result to us; we expected differing chromaticity

to provide a potent clue to integration and segregation of form in images. Li and Lennie[85] demonstrated that first-order variations in chromaticity provide a strong clue to surface segmentation, but that second-order variations were less robust. They attributed this finding to mechanisms that sum chromaticity over large regions. Such integration over regions of slowly varying chromaticity would be relevant to segmentation of objects in natural images. However Glass patterns composed of punctuate dots and oriented virtual segments that are separated by a neutral background pose an artificial situation for segmentation based on regions of similar chromaticities.

The binding of color and orientation in temporally varying stimuli has been investigated for simple gratings[86] and for Glass patterns.[87] These two studies indicate that, for stimuli presented at moderate temporal frequencies, color remains bound to form in early-level processing but global pattern detection loses color specificity in midlevel processing. Although our stimuli are presented at rates where both form and color are evident, we also observe color specificity in local form integration (experiment 2) but loss of color specificity in global integrations (experiment 3).

Mullen *et al.*[51] found that contour integration appears to be mediated by a process common to all postreceptoral chromatic mechanisms. However they found that this process was not "colorblind," in that the intercession of a yellow–blue element disrupted an observer's ability to detect a path defined by red–green elements. We have suggested[47] that, like contour integration, midlevel processing of concentric (but not translational) Glass patterns requires comparison of the orientation of neighboring elements. However the processes involved in Glass pattern detection are more global and statistical[47] in nature than those in the contour integration task, reflecting the differences between a texture and a path. That we find segregation and integration in both translational and concentric chromatic Glass pattern to be "colorblind" may reflect the differing perceptual requirements of these tasks.

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