

The local and global processing of chromatic Glass patterns

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Glass patterns are a valuable tool to study the cortical stages of form perception. We use circular Glass patterns (cGP) to study the relation between form and color vision. The detection of Glass patterns is thought to be carried out in at least two stages. In the first stage, the local orientation information from the pairs of dots is analyzed. A later stage integrates this local orientation information to yield the global percept of form. Previous work (K. S. Cardinal & D. C. Kiper, 2003) has shown that the second stage is chromatically selective, with a broad tuning in color space. Here we completed our characterization of the integration stage by measuring the size of the spatial integration area. We find that the integration area is similar to the size of V4 receptive fields. Furthermore, we measured the chromatic selectivity and spatial resolution of the first stage mechanisms. First stage mechanisms are more selective for color than the integration stage. Their spatial resolution is consistent with the idea that V1/V2 neurons perform the analysis of the dot pairs' orientation. Our results are consistent with the idea that V1/V2 neurons perform the local analysis, and that spatial integration is achieved at the level of V4.

Keywords: chromatic mechanisms, Glass patterns, psychophysics, form perception

Introduction

Glass patterns (GP) have been used in psychophysical (Dakin, 1997a; Dakin & Bex, 2001, 2002; Kovacs & Julesz, 1992; Wilson, Wilkinson, & Asaad, 1997) and physiological experiments (Smith, Bair, & Movshon, 2002) to investigate the processing of form. GP are made of random dots that are copied, transformed geometrically, and superimposed on the original image (Glass, 1969; Glass & Perez, 1973). If, for example, the transformation is a rotation, observers perceive a circular pattern (see Figure 1).

Several models have been proposed to account for the perception of form in Glass patterns. Some models focus on the analysis of local interactions between the dots forming the pairs (Stevens, 1978; Caelli, 1981; Maloney, Mitchison, & Barlow, 1987). In these, the visual system calculates all possible pairings between dots in the display and analyzes the distribution of the resulting orientations (weighted by the proximity of the dots). Differences in the orientation distributions lead to the percept of structure in the pattern. Other models do not rely on the analysis of neighborhood relations, but on the role of spatial filtering (Wilson et al., 1997; Wilson & Wilkinson, 1998; Barlow & Olshausen, 2004). Dakin (1997b) has compared the performance of these different types of models and showed that filter-based models perform better than those based on the analysis of neighborhood relations.

Although most current models rely on the existence of spatiotemporal filters, their exact nature is still a matter of debate. For example, Wilson and Wilkinson (1998) pro-

posed that the initial stage of filtering is performed by a number of oriented spatial filters, like those commonly used to model the initial stages of cortical visual processing (Smith et al., 2002). The signals from these filters are then rectified and fed to a second stage of analysis, containing other oriented filters at a larger spatial scale. The outputs of the second stage filters are then pooled and summed in a spatially and orientation-specific manner (depending on the type of Glass pattern to analyze). If the summed signals exceed a given threshold, structure determined by the spatial and orientation characteristics of the second stage filters is signaled to subsequent visual-processing stages. This approach relies on filters dedicated to the analysis of structure in visual patterns. It differs from that proposed by Barlow and Olshausen (2004), who invoke a mechanism whose main function is to detect distortions caused by motion in the local power spectrum of visual images. In that scheme, the percept of structure in Glass patterns would thus be a by-product of operations used to analyze optic flow.

Not only the nature of the filters involved but also the operations they perform are currently debated. For example, the rectification following the first stage of filtering in the Wilson and Wilkinson (1998) model has been challenged by results obtained by Wilson, Switkes, and DeValois (2004), who looked at the contrast polarity dependency of the second stage of filtering. Their data show that the second stage of filtering is contrast-polarity sensitive, and thus not consistent with the rectification operation proposed by Wilson and Wilkinson (1998).

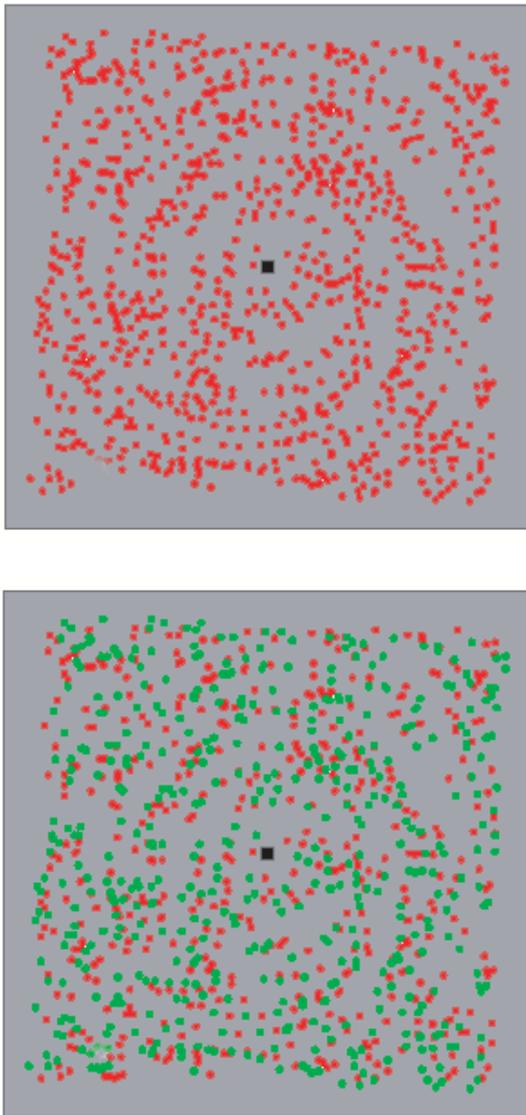


Figure 1. Illustration of the stimuli used in our experiments. Top. A 100% coherent, red Glass pattern, yielding a strong percept of concentric ring. Bottom. The same Glass pattern with dots within each pair having opposite colors. The percept of structure is considerably weaker than in the top panel.

The most important point to note is that despite these differences, all filter-based models agree on the existence of an initial, local stage of analysis, where the orientation of the dot pairs is analyzed, followed by a more global analysis stage, which pools the orientation signals over a larger area of the visual field. All filter-based models predict that manipulating the contrast or chromatic properties of the dots within a pair, or their spacing, will affect the global percept of form. The effect occurs because the filters performing the initial orientation filtering are sensitive to these manipulations. We thus used such manipulations to characterize the spatiochromatic properties of the initial analysis stage (see [Experiments 2](#) and [3](#)).

The physiological correlates of the analysis stages are also a matter of current research. Wilson et al. (1997, 1998) proposed that the initial filtering and rectification are performed in V1, the second filtering stage in V2, and the global spatial pooling in V4. The latter is supported by reports showing that V4 cells can be more responsive to circular than to linear stimuli (Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Kobatake & Tanaka, 1994; Van Essen & Gallant, 1994). V4 neurons have receptive fields 5-7 times larger than V1 or V2 neurons (Desimone & Schein, 1987; Levitt, Kiper, & Movshon, 1994) and are therefore large enough to detect the form in GPs. Moreover, Tse, Smith, Augath, Trinath, and Logothetis (2002) showed that macaque V4 (but not V1 or V2) responds differentially to different types of Glass patterns.

The notion that the initial stages of analysis are performed in V1/V2 is supported by several observations: V1 and V2 neurons are particularly selective for orientation and their receptive fields' properties allow them to analyze the orientation of individual dot pairs (Smith et al., 2002). Smith et al. (2002) recorded responses from V1 neurons in anesthetized macaques to Glass patterns made of pairs of black dots (same polarity) or black and white dots (opposite polarity, where each pair is made of a black and a white dot) presented on a gray background.

Their results show that although individual V1 (Smith et al., 2002) and V2 neurons (Movshon, Smith, & Kohn, 2003) do not detect the global form in Glass patterns, their properties are consistent with the hypothesis that they perform the initial stages of Glass pattern analysis.

Smith et al. (2002) modeled the spatial receptive field of V1 cells with a linear-oriented filter represented by a Gabor function. They showed that their model reproduced the responses of V1 cells to Glass patterns of same and opposite polarity. For same-polarity patterns, they obtained the best responses when the dot separation was between a quarter and one half the receptive field's spatial period. Psychophysical experiments show that humans (Wilson et al., 1997; Wilson & Wilkinson, 1998) and monkeys (McCollum et al., 2000) detect GP optimally with dot separation of 0.07 to 0.2 deg. This is well within the size of a V1 (or V2) cell-receptive field and in agreement with the physiological data of Smith et al. (2002). In addition, Smith et al. showed that V1 cells respond weakly to opposite-polarity Glass patterns. This observation might explain why observers are often unable to perceive form in these patterns (Dakin, 1997a; Kovacs & Julesz, 1992). Thus, results from both physiological and psychophysical investigations converge to suggest that V1/V2 cells are responsible for the early stage of Glass-pattern processing.

Most data are thus consistent with the notion that V1/V2 cells perform the initial, local analysis of GP, and that the global perception of form is supported by the activity of V4 (and possibly later) cells. These areas represent part of the ventral processing pathway, known to be important for object perception, and where cells are particularly

selective for form and color (Schein & Desimone, 1990; Komatsu, Ideura, Kaji, & Yamane, 1992). Glass patterns are therefore ideal stimuli to study the processing of form signals, and their relation with color.

Cardinal and Kiper (2003) have investigated the color tuning of the integration stage responsible for the detection of GP. Glass patterns were presented simultaneously with background noise, and the colors of the GP and the noise were varied independently. The mechanisms involved in the detection of these GP were found to be color selective, and have a relatively broad tuning in color space. The fact that many V4 neurons are known to have a broad chromatic tuning (Kobatake & Tanaka, 1994; Schein, Marrocco, & de Monasterio, 1982) agrees with the hypothesis that V4 neurons are the late stage of processing of GP. Here we report on new experiments that further characterize the stages of colored GP processing. First, we measured the area over which local chromatic signals are pooled to yield the global percept of form. Comparison of our results with the known receptive field sizes in different cortical areas could indicate where the integration of local signals is performed in the primate brain. Second, we investigated the chromatic tuning and spatial resolution of the mechanisms involved in the local processing of GP. Comparison of these results with the physiological properties of cells in cortical areas should help us locate the initial stage of GP processing.

To measure the size of the integration area, we used colored, circular Glass patterns of different radii. By measuring observers' ability to detect the colored, circular GP as a function of display size, we could obtain an estimate of the integration area.

To study the chromatic properties of the initial stage of GP processing, we varied the color of one dot relative to the other dot in a pair. We found that the tuning of the initial mechanisms involved in Glass pattern detection is relatively narrow in color space.

Finally, to determine the spatial properties of the initial stage of processing, we determined the optimal distance between the dots in each pair. To do so, we used a phenomenon first described by Kovacs and Julesz (1992): Circular GP of opposite polarity are perceived as radial and vice versa. This perceptual phenomenon was explained later by Smith et al. (2002), who showed that the responses of V1 neurons to opposite-polarity GP was maximal when the dot pairs were oriented orthogonal to the cell's preferred orientation (measured with gratings). We therefore measured subjects' ability to discriminate between a circular and a radial GP as a function of dot separation. We found that optimal separation was larger for chromatic than for achromatic patterns. In all cases, the optimal separation is consistent with the size of V1/V2 receptive fields.

Materials and methods

Stimuli were presented in the center of a Sony F500 or a Sony F520R color monitor, controlled by a VSG 2/4

graphics board with gamma-corrected look-up tables (spatial resolution of 800 x 600 pixels, refresh rate of 120 Hz). A computer controlled the presentation of the stimuli and recorded the subject's responses. The subject used a chin rest to stabilize head movement, and viewed the stimuli in a dimly illuminated room; viewing was binocular in all experiments.

We use the DKL color space (Derrington, Krauskopf, & Lennie, 1984) to describe our stimuli (Figure 2). This space is based on the cone-excitation spectra, and is centered on an equal energy white point. The colors of the Glass patterns and the background on which they were presented were chosen on the isoluminant plane. In other words, unless specified otherwise, background and dots always had the same photometric luminance of 17 cd/m² (calibrated with a Tektronix J1800 photometer, based on the CIE 1924 photometric standard observer).

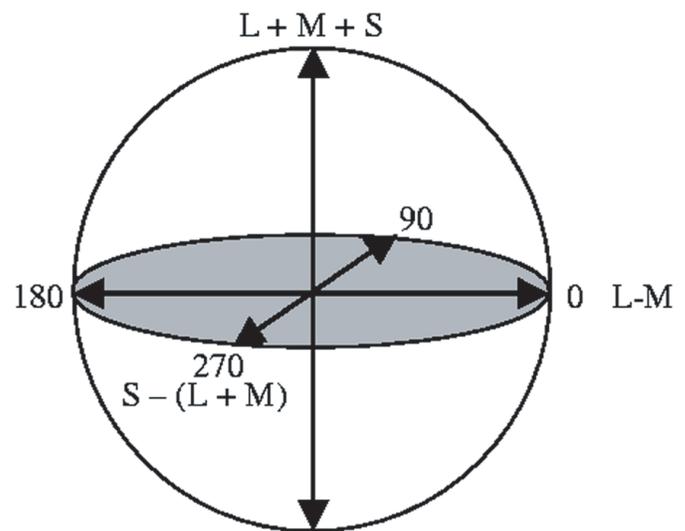


Figure 2. The Derrington, Krauskopf, and Lennie (DKL) color space. The center of this space corresponds to the equal energy white point. There are two chromatic axes [L-M and S- (L+M)], as well as a luminance axis orthogonal to these. The two chromatic axes define an isoluminant plane (gray area). Modulation along the L-M axis leaves the excitation of the S-cones constant, and the excitation of the L- and M-cones covary to keep their sum constant. Along the S-(L+M) axis, only the S-cones' excitation changes. Along the luminance axis, the excitations of all three cones vary in proportion to their values at the white point. A stimulus in this space can be represented by a vector and can be defined by three coordinates. Its *azimuth* is defined as the angle formed by its projection on the isoluminant plane and the L-M axis. Its *elevation* is defined as the angle it forms with its projection onto the isoluminant plane, which determines the component of luminance. Its *amplitude* is represented by the vector's length. The chromatic axes were scaled in proportion to the subject's detection thresholds (see text).

All subjects except one had normal color vision (as determined by the Farnsworth-Munsell color test and the Ishihara color plates) and normal or corrected-to-normal vision. One subject who participated only in the second experiment with black and white GP had a red-green deficiency. All procedures conformed to the Declaration of Helsinki.

Preliminary experiment: Detection thresholds

In DKL space, the scaling of the axes is arbitrary. To equate the visibility of stimuli across color directions and subjects, we scaled them to their detection threshold. We carried out a two-interval forced-choice task (2IFC): In one interval no stimuli were presented, and in the other interval patches of 500 randomly oriented pairs of a particular chromatic azimuth were presented (the stimulus size was fixed at 28 deg; all other parameters as in [Experiment 1](#) below). The subject had to indicate in which interval the stimuli were presented by pressing the appropriate key on the computer's keyboard. An incorrect response was indicated by a sound and the saturation of the stimuli was increased by 0.1 log unit. Three correct successive responses induced a decrease in the saturation of the stimuli by 0.1 log unit. Each staircase terminated after 12 reversals, and the threshold was calculated as an average of the reversals' values. For each chromatic azimuth the threshold measurement was carried out twice. For all subsequent experiments with GP, the dot saturation (or intensity for black and white patterns) was set for each subject at 5 times its detection threshold. This low multiple of threshold was chosen to minimize potential luminance artifacts and to ensure that equally visible stimuli could be used in all directions of color space: Some subjects' detection thresholds in some color directions were high (particularly for the azimuth of 90-deg condition) and did not allow us to generate stimuli at more than 5 times the detection threshold.

Experiment I: Integration size of the global processing stage

Five subjects participated in this experiment. Viewing distance was 100 cm for four subjects and 50 cm for one subject. We investigated the size of the summation area that enabled the global processing of circular Glass patterns (cGP). Each subject was presented with a cGP of different azimuth: 0°, 90°, 180°, 270° isoluminant to the background or of different luminance (black: elevation -90°, or white: +90°) relative to the background. We used a 2IFC protocol: Each trial consisted of two presentations in random order, one consisting of randomly positioned and oriented dot pairs presented in a circular aperture, the other consisting of a cGP (of varying coherence level, see below) presented in a circular aperture of the same size. The subject had to indicate in which presentation was the cGP. We measured the threshold coherence level yielding reliable

detection of the pattern, as a function of aperture diameter. Coherence is defined as the percentage of dot pairs contributing to the pattern. For example, a 50% coherent cGP with 1000 dot pairs is made of 500 pairs oriented along circles, and 500 randomly oriented pairs.

Each presentation was preceded by a tone, and an incorrect response was indicated by a tone. An incorrect response led to an increase in the coherence level of the signal by 0.1 log unit, and three successive correct responses decreased the level of coherence of the signal by 0.1 log unit. Each staircase terminated after 18 reversals (or 12 for the aperture diameters larger than 252 min), and threshold was calculated as an average of the reversal values.

A single session measured threshold for three sizes presented in random order. Each session was repeated twice. Each subject did two sets of experiments, with two different azimuths or elevations.

The aperture diameters varied from 0.6 to 13.7°. The cGP were of constant density (4%). The distance between the dots of a pair was of 13.4 min or 26.8 min (at 50 cm). The dot size was 8.25 min (16.5 at 50 cm). The dot size is greater than in other experiments with GP (Kovacs & Julesz, 1992; Smith et al., 2002; Wilson et al., 1997; Wilson & Wilkinson, 1998) to reduce the effects of chromatic aberrations (Cardinal & Kiper, 2003). The stimulus was presented for 166 ms and the interval between each presentation depended on the size of the Glass pattern presented. In between presentations the center of the screen was a neutral gray. The time between two trials depended of the subject's response.

Experiment II: Chromatic selectivity of the first stage mechanisms

Nine subjects participated in this experiment. Three subjects were aware of the aim of the experiment. Their results did not differ from those of the naive subjects. Viewing was at a distance of 50 cm. The number of pairs of dots in the stimuli remained constant ($n = 500$). The stimuli subtended a viewing angle of 28°. All other parameters were as in [Experiment 1](#).

We investigated the subjects' ability to detect cGP when the dots within each pair had different colors. Each trial consisted of two presentations in random order: one consisting of 500 randomly positioned and oriented dot pairs, and one consisting of a circular Glass pattern of varying coherence. The subject had to indicate in which presentation was the cGP. For each session, the stimuli consisted of dot pairs for which one dot color was fixed, and the other was varied around the isoluminant plane. The fixed dot direction was either along one of the axes (azimuth of 0, 90, 180, or 270 deg) or in the 45- or 315-deg directions. The cGP and the random pattern always had the same number of dots of each color: If the glass pattern was made of red and green dots, the random dots' presentation was

made of 500 green dots and 500 red dots of the same color as the cGP dots. We measured each subject's coherence threshold as a function of the difference in color between the two dots forming a pair.

Six subjects were tested for the chromatic azimuth 0. Other azimuths were studied with two subjects each. Experimental procedures were as in [Experiment 1](#).

Experiment III: Spatial resolution of the first stage mechanisms

Five subjects participated in this experiment. For each interval either a circular or a radial pattern was presented randomly in two successive intervals. The patterns could be of same polarity or opposite polarity within the same session. The subject had to indicate in which interval the circular GP was presented.

Viewing distance was 50 cm. We measured the subjects' ability to distinguish the circular from the radial pattern as a function of dot pair separation (which varied from 16.25 to 55.25 min, using the method of constant stimuli). We used dot colors along the cardinal direction of DKL space (azimuths of 0, 90, 180, and 270 deg) as well as black or white dots. For example, the patterns could be of directions 0° for the two sets of dots or of 0° and 180° for each set of dots within one session. Each presentation was preceded by a tone, but, unlike for [Experiments 1 and 2](#), no feedback was given about whether the response was correct or incorrect. The presentations were repeated 15 times and

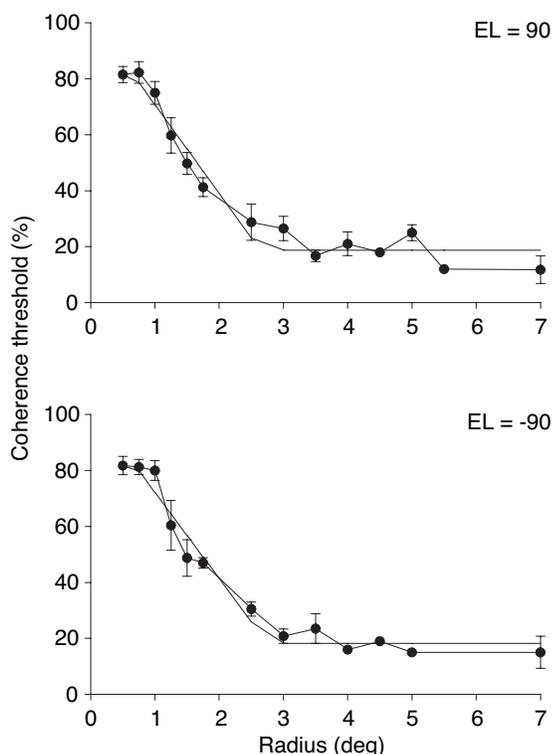


Figure 3. Coherence threshold as a function of the window size (radius) for white (EL = 90) and black (EL = -90) circular Glass patterns.

the percentage of correct responses was taken. The duration of the presentation was of 166 ms, and the interval between the two presentations was 100 ms. Each session was repeated twice.

Results

Experiment I: Integration size of the global processing stage

We measured subjects' ability to detect cGP as a function of aperture size in different directions of DKL space.

[Figure 3](#) shows the average of two subjects' data for black (elevation -90) and white cGP (elevation 90) on a gray background. Each point corresponds to the mean over the two sets of data for the two subjects, and the error bars are standard deviations. The thresholds decreased steeply between 0.6° and 2.6° of radius for both types of presentation and reach a minimum at 2.69° for the black cGP and 2.55° for the white cGP. The solid lines represent least-squares linear fits to each of a maximum of three data segments: one or two initial segments to the monotonically decreasing part of the data and one horizontal segment to fit the asymptotic performance.

To determine the summation area over which the chromatic patterns are processed, we repeated the same experiment with colored cGPs. The results are shown in [Figure 4](#). There was variation in the radii for which minimal thresholds were reached. We found integration areas of from 2.94° for az = 0, 2.51° for az = 180, 3.4° for az = 90, and 4.2° for az = 270. The difference between the integration areas for red (az = 0) and green (az = 180) GP was not statistically significant (*t* test, $p = .5$), neither was that between yellow (az = 90) and blue (az = 270) GP. The difference between red or green and blue or yellow patterns, however, was significant (*t* test, $p < .05$).

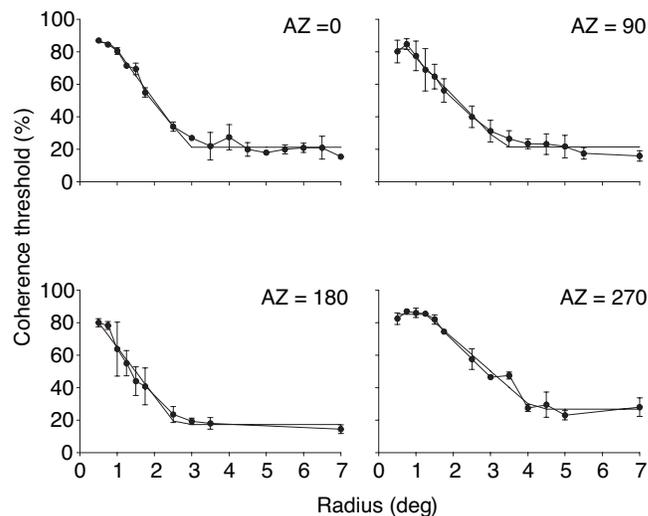


Figure 4. Changes in coherence thresholds as a function of the size (radius) of the Glass patterns for azimuths 0, 90, 180, and 270. The lines show linear segments fitted to the data (see text).

The results of this experiment could potentially be biased by the fact that we used stimuli at only 5 times the detection threshold. Because chromatic sensitivity declines with retinal eccentricity (Abramov & Gordon, 1977), peripheral dots are less visible than central ones, and this could lead to an underestimation of the integration area. To control for this possibility, we performed experiments with two additional subjects (both with corrected-to-normal vision) who had low saturation thresholds for the detection of the 500 randomly oriented pairs. Their low initial threshold allowed us to perform measures with stimuli at 5 times the detection threshold (as with the other subjects), and to repeat them with stimuli at 12 times detection threshold. All other parameters and procedures were as described above. The results of this experiment are shown in Figure 5.

It is apparent that increasing the visibility of the stimuli did not result in a significant change in performance. For subject DK, with stimuli having an azimuth of 180 deg, the integration area estimates were 2.3 (5 times threshold) and 2.7 (12 times threshold). For JN, the stimuli had azimuth 0 deg, and the integration estimates were 1.9 deg at 5 times threshold and 1.8 at 12 times threshold. The estimates are not significantly different for either of the two subjects. This result corroborates with reports of previous subjects who said the stimuli at 5 times detection thresholds were always clearly visible in their entirety. We found that the mechanisms responsible for the integration of local signals along the S-(L+M) axes have larger integration areas than those tuned to the L-M axis.

Experiment II: Chromatic tuning of the first stage mechanisms

To investigate the chromatic tuning of the local analysis stage, we varied the color of one dot within each pair while the other dot color was kept constant. We measured the threshold coherence level as a function of dot color difference in the four cardinal directions of DKL space (Figure 2). Each datum in Figure 6 corresponds to the mean over all subjects for each azimuth; the error bars are standard deviations. For all subjects, the coherence level was increased significantly when the difference between the two dots' color was more than 45°. It was getting harder for the subject to actually perceive the pattern. For patterns with a fixed dot azimuth of 0, 180, and 270 deg, the absolute thresholds did not differ significantly. They ranged from 18% coherence, when the dots were of identical color, to 94% when they had a difference of 180 deg. For patterns with one dot at a fixed azimuth of 90 deg, coherence thresholds were slightly higher, ranging from 24% to 100% coherence. These values are similar to those reported previously for the detection of colored Glass patterns (Cardinal & Kiper, 2003).

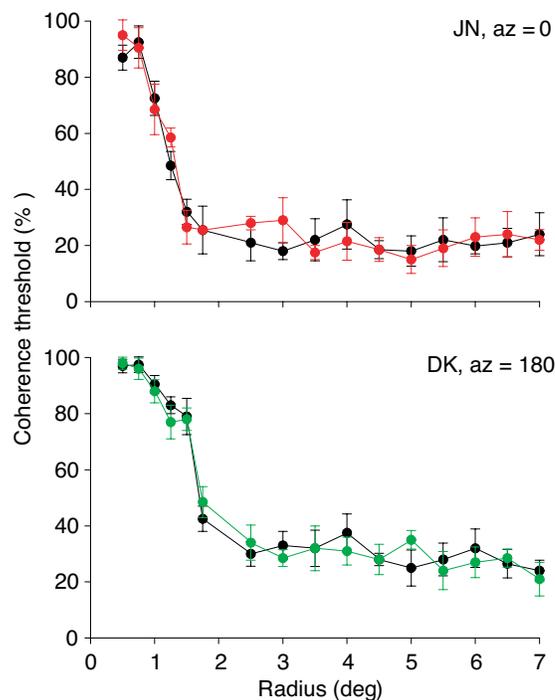


Figure 5. Comparison of the results obtained with stimuli at 5 times detection threshold (black symbols and lines) and 12 times detection threshold (colored symbols and lines) for two subjects. The integration area estimates do not vary significantly between the two conditions.

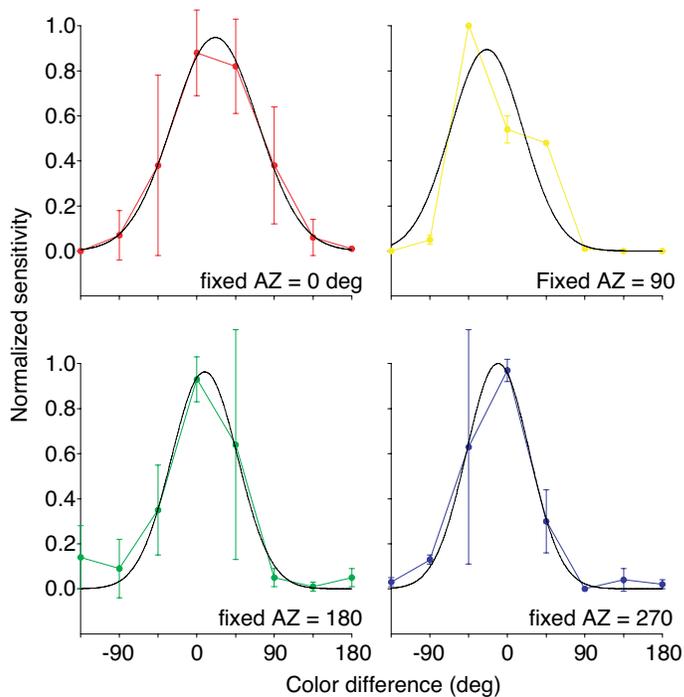


Figure 6. Cardinal directions: average threshold coherence as a function of the difference between the constant azimuth of one dot (dot 1) and the changing azimuth of the other dot (dot 2) of each pair. Error bars are the standard deviation of the means. The curve corresponds to the best-fitting Gaussian function to the data (see text).

We normalized our data and fitted them with a Gaussian function (black curve) to obtain estimates of chromatic tuning. The Gaussian fits capture the data well: The fit accounts for 77% of the variance for the azimuth of 90°, and more than 90% of the variance for the other azimuths. The tuning bandwidth of the mechanisms, given by the standard deviation of the best-fitting Gaussian, varied from 26° at azimuth 270°, 38.32° at azimuth 180°, 41.92° at azimuth 90°, and 49° at azimuth 0°.

For intermediate directions in DKL space (azimuth of 45 and 315), similar results were observed (Figure 7). The Gaussian fits account for 98% and 94% of the variance respectively and the tuning widths were 39.4° and 32.8°.

Therefore, the mechanisms involved in the local analysis of cGP appear similarly tuned in all directions of DKL color space.

If the mechanisms involved in the detection of cGP were summing their inputs linearly, the detection threshold would vary as a function of the angle (α) between the azi-

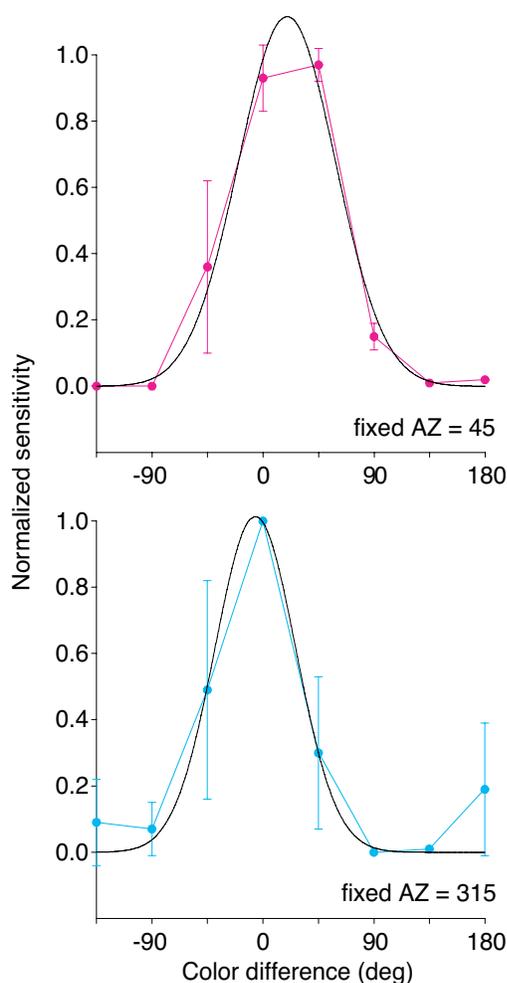


Figure 7. Intermediate directions: threshold coherence as a function of the difference in color between the two dots for intermediate directions in color space. Conventions as in Figure 6.

imuth of one dot and that of the second dot in each pair. The threshold would then be well fitted by a cosine function (Derrington et al., 1984). This was not the case. Figure 8 shows the data averaged over all subjects and color directions, along with their best-fitting Gaussian (continuous curve) and cosine (dotted line). The Gaussian accounts for 99% of the variance in the data, whereas the cosine accounts for 64%. The standard deviation of the best-fitting Gaussian is 46°.

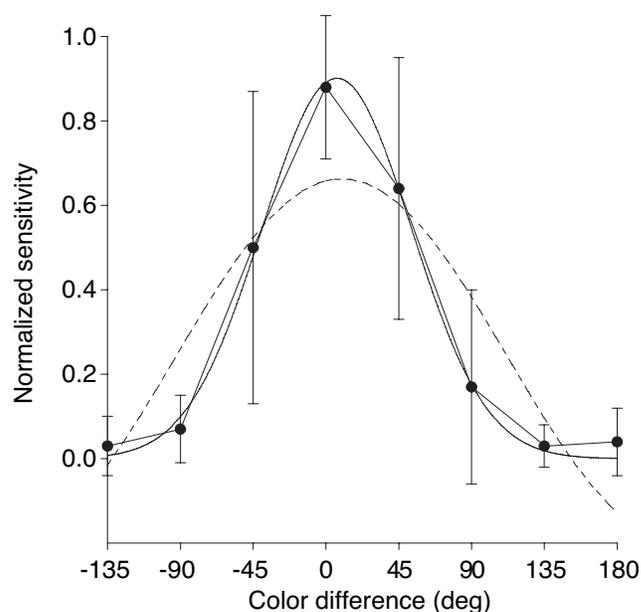


Figure 8. Average over all color azimuths: threshold coherence as a function of the difference between the constant azimuth of one dot (dot 1) and the changing azimuth of the other dot (dot 2). The data were well fitted by a Gaussian function, but not by the cosine (dotted curve) that would result from linear combination of the inputs (see text).

Our results thus indicate that the mechanisms responsible for the local analysis of GP do not combine their inputs linearly, and have a relatively narrow selectivity in color space.

During this experiment, we thus observed that when the colors of the two dots were of opposite polarity, the detection of the circular pattern was severely impaired. In addition, subsequent casual observations of the stimuli suggested that if the interdot distance was reduced, a radial pattern could be perceived. This phenomenon has been observed and investigated in the luminance domain (Kovacs & Julesz, 1992; Smith et al., 2002; Glass & Switkes, 1976). This dependence of perception on interdot distance provides a useful mean to measure the size of the mechanisms responsible for the local analysis of Glass patterns. We therefore quantified this phenomenon, as described below.

Experiment III: Spatial resolution of the first stage mechanisms

In this experiment we varied the distance between the dots of each pair forming the GP and presented GP of same or opposite polarity. One interval contained a circular GP, the other a radial one. The subjects' task was to indicate the interval containing the *circular* GP. Results are shown in Figure 9. When subjects were presented with same-polarity GP, the percentage of correct responses was equal or close to 100% (i.e., the subjects had no difficulty in detecting in which interval the circular GP was presented). It was somewhat harder for the maximum distance between the dots of 55.25 min of arc with chromatic GP of azimuth 0°.

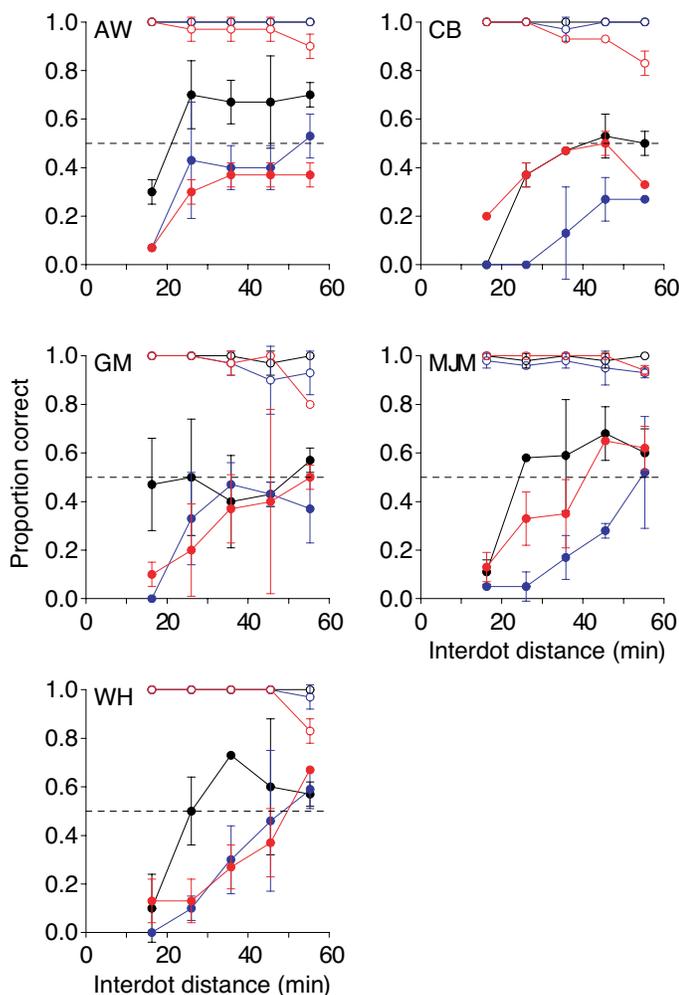


Figure 9. Percentages of correct responses as a function of the distance between the dots of each pair (in pixels) for five different subjects. Open symbols show data for the same polarity patterns, whose detection was easy for most interdot distances tested. Filled symbols show data for opposite polarity patterns. Black is for achromatic patterns, red for the red-green patterns, and blue for the blue-yellow patterns. At short interdot distances, an opposite-polarity, circular GP is perceived as radial.

When presented with opposite-polarity GP with the shortest interdot distance, in all except one condition (one subject with black and white GP) the percentage of correct responses was close to 0%. Performance increased as the distance between the dot pairs increased up to an average of 60%. This indicates that at the smallest distance, the subjects almost always saw a circular GP when a radial GP was presented. (Subjects informal reports indicate that for small interdot distances, the circular pattern was perceived as radial.) As the distance increased, subjects' performance approximated chance level (50%).

There were important variations between subjects in this task. In most cases, the curve for the achromatic GP is above those for colored GP, which were similar to one another. This is best seen in Figure 10, which shows the average of all subjects. To quantify the results, we fitted each set of data with the integral of a Gaussian, and obtained the value at which the curve crosses the 25% correct level. We take this median (or mean) value as an estimate of the spatial resolution of the mechanisms responsible for the local analysis of GP.

The median for the achromatic mechanism was 16.57 arcmin with (± 1.22). The median for the blue-yellow mechanism was 33.46 (± 12.79) min and 25.74 (± 14.86) min for the red-green direction. The medians for the red-green and blue-yellow GP are not significantly different (t test, $p = .8$), but both are different from that of the achromatic patterns (t test, $p = < .05$ in both cases). This shows that the first stage mechanisms responsible for the analysis of achromatic dot pairs have a higher spatial resolution than those analyzing chromatic patterns.

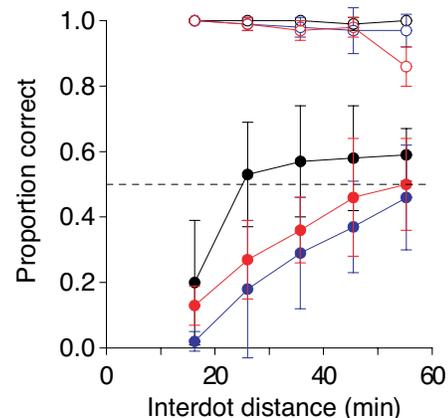


Figure 10. Percentage of correct responses as a function of the distances between the dots of each pair. Average over five subjects' data.

Conclusion

The present experiments extend our previous studies on the mechanisms involved in the detection of cGP. Cardinal and Kiper (2003) had shown that the spatial integration stage is performed by chromatically selective mecha-

nisms. The selectivity of these mechanisms is well described by a cosine, indicating that they combine their inputs linearly. We postulated that V4 neurons broadly tuned in color space could be the physiological substrate for the integration stage. The present results support this idea. Measuring the extent of the integration area ([Experiment 1](#)), we found that form in chromatic Glass patterns is extracted by mechanisms with an integration area that ranged from 2.51° to 4.2° . This is considerably larger than the foveal receptive fields of V1 (Snodderly & Gur, 1995) or V2 (Levitt et al., 1994) neurons, but similar to those reported in V4 (Schein et al., 1982; Schein & Desimone, 1990). For achromatic patterns, we found integration areas with a radius of approximately 2.5° . This value is slightly higher than that reported by Wilson et al. (1997) ($\sim 1.6^\circ$). This difference is likely due to differences in the stimuli, in particular the dot density: Wilson et al. used a density of 6%, 50% higher than ours.

The present experiments also support the notion that the initial analysis of cGP is performed by V1/V2 neurons. We found that the early stage mechanisms code for the orientation of dot pairs over a distance of 16.5 min for achromatic patterns, and about 30 min for the chromatic ones. This is consistent with the size of V1 (Snodderly & Gur, 1995) and V2 receptive fields (Levitt et al., 1994). Moreover, we found that these mechanisms, on average, have a tuning in color space more narrow than predicted by a linear combination of their inputs. This is exactly the kind of tuning one expects if the underlying neuronal population comprises a mixture of relatively broadly tuned neurons, and some more narrowly tuned ones, as is the case in primate V1 (Lennie, Krauskopf, & Sclar, 1990; Cottaris & DeValois, 1998; Wachtler, Sejnowski, & Albright, 2003) and in V2 (Kiper, Fenstemaker, & Gegenfurtner, 1997). Similar results have been reported by Switkes (2002), who also manipulated the chromaticity of dots making circular and translational Glass patterns. Moreover, the chromatic selectivity we measured in [Experiment 2](#) appears very similar to the results of Clifford, Spehar, Solomon, Martin, and Zaidi (2003), who measured the colored selectivity of the tilt illusion. Their measurements are particularly relevant because the tilt illusion is dependent on the activity of the same orientation-selective cells that we think are responsible for the initial analysis of Glass patterns. In their study, Clifford et al. report selectivities that range from 20.3 deg to 44.4 deg in DKL space (half width at half height). Here, our estimates range from 26 deg to 49 deg. Moreover, both studies also agree that selectivity along the cardinal directions of DKL space does not differ from that along intermediate directions. Thus, our results are in good agreement with a number of physiological as well as psychophysical results on the selectivity of V1 and V2 chromatic mechanisms.

Together, our previous and present characterization of the mechanisms involved in the processing of colored cGP strongly supports the hypothesis that initial analysis of GP

is performed by V1 and V2 neurons, and that the global integration stage relies primarily on the activity of V4 cells.

Our results show that form and color are not treated by segregated, distinct neuronal circuits. Based on a number of physiological and anatomical observations, several authors had proposed that these two visual attributes are analyzed by separate neuronal populations (Shipp & Zeki, 1985; Livingstone & Hubel, 1988; Zeki & Bartels, 1998). This notion is controversial, several studies suggesting that individual cortical neurons can simultaneously code for form and color (Leventhal, Thompson, Liu, Zhou, & Ault, 1995; Gegenfurtner, Kiper, & Fenstemaker, 1996; Friedman, Zhou, & von der Heydt, 2003). Our results on the perception of colored Glass pattern show that both the initial, local analysis and the integration of signals across space are performed by mechanisms that are simultaneously chromatically and form selective. Orientation-selective mechanisms are necessary to code the orientation of dot pairs, and the experiments presented here show that these mechanisms are color selective as well. Moreover, our previous data (Cardinal & Kiper, 2003) show that the analysis of more complex forms (i.e., the concentric circles seen in cGP) is also performed by chromatically selective mechanisms. In other words, we show that in several stages of the form-selective cortical pathway, form-specific signals are treated by color-selective mechanisms.

This conclusion differs from that reached by Kovacs and Julesz (1992), and more recently by Clifford, Holcombe, and Pearson (2004). In both of these studies, albeit using very different experimental protocols, the authors conclude that the mechanisms responsible for the perception of structure in Glass patterns are not color selective. We believe that this difference comes mostly from the fact that in their studies, regardless of their color, the Glass patterns were made of dots whose luminance differed significantly from the background. In other words, the Glass patterns were best detected by mechanisms sensitive to luminance, but not color, variations. Here, by having the dot luminance equal to that of the background, we specifically target mechanisms that must be chromatically selective. Note however that results reported in abstract form (Switkes, 2002) are at odds with ours. Switkes also used Glass patterns made of colored dots isoluminant with the background, and varied the color of dot pairs independently. His results show that the global analysis stage in the processing of Glass patterns seems to be color insensitive. The origin of difference in these results and ours is not clear, and might come from the very different experimental protocols and stimulus parameters used in our respective studies.

The latter point is of interest because it imposes constraints on the models developed to account for the perception of Glass patterns. Indeed, the rectification following the initial filtering in the Wilson models (Wilson et al., 1997; Wilson & Wilkinson, 1998) implies that the second

stage of processing should be blind to contrast polarity. As mentioned above, experiments manipulating luminance contrast in Glass patterns suggest that this might not be the case (Wilson et al., 2004; Badcock, Clifford, & Khuu, 2005). Similarly, our results in the color domain imply that no rectification of the chromatic signals occurs between the initial and global processing stages. Further experiments are necessary to resolve this issue. In particular, we believe that recording the activity of form-selective neurons in extrastriate cortex will reveal whether they are sensitive to contrast and chromatic polarity.

Two additional aspects of our data are noteworthy. First, Experiment 3 suggests that the spatial resolution of the early, local mechanisms is lower for chromatic than for achromatic stimuli. This result agrees with previous physiological (Thorell, De Valois, & Albrecht, 1984) and psychophysical (Granger & Heurtley, 1973) reports showing a lower acuity for chromatic versus achromatic stimuli. However, we also found that the spatial resolution along the S-(L+M) direction is comparable to that along the L-M direction. This contradicts previous reports that the L-M system has higher spatial resolution than the S-(L+M) system (van der Horst & Bouman, 1969; Granger & Heurtley, 1973), but agrees with the results of Mullen (1985). In fact, Mullen showed that the acuity difference between the two systems could be attributed to chromatic aberrations, not to a difference in resolution proper. Our data thus support the notion that the L-M and the S-(L+M) systems have comparable spatial resolution.

Second, the results obtained in the first experiment show a significant difference in integration area between patterns along the L-M and those along the S-(L+M) axes. The physiological basis for this difference is not clear, but may be related to the coarser sampling of the visual image performed by the S-cone system (Calkins, 2001). Indeed, to obtain a signal of equivalent strength, it might be necessary for S-(L+M) mechanisms to sample a larger area of the visual field than for L-M mechanisms. Precise physiological measures of the spatial resolution of cells tuned to these color directions will be necessary to settle this issue.

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