The detection of colored Glass patterns

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The detection of many chromatic stimuli is mediated by mechanisms that sum their inputs linearly. As a result, these mechanisms have a broad range of selectivity in color space, as do the majority of cells in the early stages of visual processing. In extrastriate cortex, there are cells with a narrow tuning in color space. The function of these cells is not fully understood: they could be involved in color categorization, or could mediate the detection of stimuli such as Glass patterns, whose properties make them undetectable by early stages of processing. We measured the tuning properties of the mechanisms responsible for the detection of colored Glass patterns and found that they have a broad tuning in color space. Our results suggest that Glass patterns are detected by a multitude of mechanisms that sum their inputs linearly.

Keywords: Glass patterns, color vision, object perception, psychophysics

Introduction

To understand color perception, researchers have studied the properties of the mechanisms underlying performance in color vision tasks. In most cases, mechanisms were characterized by their number, preferred color, and tuning in color space. The last, in particular, has been a matter of some debate.

Psychophysical experiments have shown that performance in various color detection or discrimination tasks is mediated by a small number of broadly-tuned color-opponent mechanisms (Krauskopf, Williams, and Heeley, 1982; Krauskopf & Gegenfurtner, 1992). One mechanism prefers color modulations along the red-green (R/G) direction, another along blue-yellow (B/Y), and the third preferentially encodes luminance. These three broad, "cardinal" mechanisms explain a surprisingly large amount of psychophysical data (see Wandell, 1995, or Boynton, 1992, for reviews).

More recent studies have reported the existence of additional, "higher-order" color mechanisms (Krauskopf, Williams, Mandler, & Brown, 1986; Gegenfurtner & Kiper, 1992; Webster & Mollon, 1991, Krauskopf, Wu, & Farell, 1996; but see Sankeralli & Mullen, 1997 for a different view). Studying the detection of colored targets embedded in two-dimensional, dynamic white noise, Gegenfurtner and Kiper (1992) revealed the existence of additional mechanisms whose preferred directions in color space do not always lie along the cardinal directions. Moreover, these mechanisms appeared to have a spectral bandwidth significantly narrower than those described previously. The existence of narrowly-tuned detection mechanisms, however, has been challenged.

D'Zmura and Knoblauch (1998) showed that the results of Gegenfurtner and Kiper could be explained without narrowly-tuned mechanisms. Instead, the subjects performing the detection task did not always use the broadly-tuned mechanism best suited to detect a particular target, but one less affected by the noise present in the stimulus, a strategy known as "off-axis" looking. This strategy results in data that can be interpreted as revealing narrowly tuned mechanisms. If this strategy is prevented by adding more chromatic noise directions to the stimulus, the detection mechanisms appear broadly tuned. D'Zmura and Knoblauch's results were later confirmed by Gegenfurtner (personal communication).

The existence of broadly tuned color-opponent mechanisms has been supported by physiological findings. The properties of the cardinal mechanisms correspond, albeit incompletely (Abramov, 1997), to those of individual ganglion cells in the retina and parvocellular neurons of the lateral geniculate nucleus (pLGN). Retinal ganglion (Lee, 1996) and pLGN cells (Derrington et al., 1984) cluster into three distinct classes, whose preferred modulations lie along the cardinal directions of color space. These cells have a broad tuning, consistent with the notion that they sum their inputs in a linear fashion (Derrington, Krauskopf, & Lennie, 1984). A red-green cell, for example, would simply subtract the signals it receives from middle-wavelength sensitive (M) cones from those originating in long-wavelength sensitive (L) cones, or vice-versa.

Higher-order color mechanisms are thought to lie in the cortex. Lennie, Krauskopf, and Sclar, (1990) showed that in the primary visual cortex (V1) of macaques, individual neurons often prefer colors that lie in intermediate directions of color space. The majority of V1 cells sum their inputs linearly, resulting in a broad tuning

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in color space (Lennie et al., 1990). However, cells with a narrow tuning in color space do exist in the cortex. Although not totally absent in V1 (Cottaris & DeValois, 1998), narrowly-tuned cells are found in significant numbers in area V2 (Kiper, Fenstemaker, & Gegenfurtner, 1997), and in subsequent stages of the ventral processing stream. Zeki (1980) reported the existence of narrowly-tuned cells in V4, an area known for its involvement in color processing. However, as in V2, most V4 cells show a chromatic tuning that is not narrower than that in the retina or LGN (Schein, Marrocco, & de Monasterio, 1982). Finally, narrowly-tuned color selective cells appear to be numerous in Infero-Temporal (IT) cortex (Komatsu, Ideura, Kaji, & Yamane, 1992).

The functional role of the narrowly-tuned cells found in V2 and beyond remains mysterious. It is possible that these cells are not directly involved in the detection and discrimination of colored targets, but play a role only in color categorization. Humans naturally categorize colors into 9 to 11 universal categories (Berlin & Kay, 1969), each comprising a narrow part of the color spectrum. Indeed, a role in color categorization has been proposed by Komatsu for cells in IT cortex (Komatsu, 1997). On the other hand, it is also possible that the involvement of narrowly-tuned cells in target detection has been missed, because the stimuli used in most studies could be detected by broadly-tuned cells located before, or in, V1. In the present study, we use stimuli that can be detected only by cells located in higher areas of the visual pathways.

Glass patterns (Glass, 1969; Glass & Perez, 1973) are stimuli that cannot be detected by cells located in or before V1. These patterns are made by superimposing two identical arrays of random dots and performing a transformation, such as a shift, rotation, or expansion, to one of them (see Figure 2). Patterns of this type are ideal stimuli for isolating late stages of processing because their perception requires integration of information over a large area of the visual field. They are not "seen" by V1 cells, whose receptive fields are too small to allow for such an integration (Maloney, Mitchison, & Barlow, 1987; Wilson & Wilkinson, 1998; Smith, Bair, & Movshon, 2002). Indeed, it is only in areas as late as V4 that the existence of cells responding to similar patterns has been reported (Gallant, Braun, & Van Essen, 1993). Therefore, we studied the chromatic properties of the mechanisms underlying the detection of Glass patterns. We then compared these data to those of a color categorization experiment, known to reveal narrowly-tuned mechanisms (Komatsu, 1997).

Our results show that the late mechanisms responsible for the detection of Glass patterns are not restricted to the R/G, B/Y, and Luminance directions in color space, and that their tuning in color space is broad. These data were already presented in preliminary form (Cardinal & Kiper, 2000).

Methods

We collected data from 6 subjects for the Glass pattern experiment. Two subjects (DK and KC) were aware of the purpose of the experiments. Their results did not differ from those of the other, naïve subjects. All subjects had normal or corrected-to-normal visual acuity, and normal color vision as determined by the Farnsworth-Munsell color test and Ishihara color plates. All subjects were informed of the nature of the experiments, and the procedures conformed to the declaration of Helsinki.

Stimuli

The stimuli were displayed on a Sony F500 color monitor, controlled by a VSG 2/4 graphics board with Gamma corrected look-up tables. A personal computer controlled the experiment and recorded the subjects' responses. Subjects used a chin rest to stabilize head movements and viewed the stimulus in a dimly illuminated room. Viewing was binocular, at a distance of 70 cm.

We use the color space introduced by Derrington, Krauskopf, & Lennie (1984) (DKL color space) to define our stimuli, as illustrated in Figure 1. This space is a linear transformation of the space of photoreceptor quantum catches. At the origin is an equal energy white point. In the horizontal plane, there are two chromatic axes (L-M and S-(L+M)), as well as a luminance axis orthogonal to these. The four color directions defined by these two axes are often called "cardinal" directions. The two chromatic axes define an isoluminant plane. Modulation along the L-M axis leaves the excitation of the S-cones constant, and the excitation of the L- and M-cones covary as 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

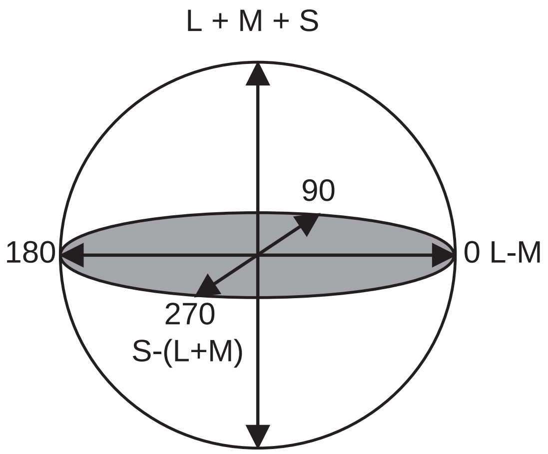

Figure 1: Derrington-Krauskopf-Lennie color space (see text for a complete description). The chromaticities of our stimuli were all located in the isoluminant plane (shaded area).

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, which determines the component of hue. 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 relative scaling of the axes is arbitrary. We chose to scale the axes so that the largest excursion possible in any direction on our display monitor corresponds to a contrast of 1. Pilot experiments were used to determine the subjects' thresholds for the detection of 250 randomly oriented dot pairs as a function of the dot color intensity. The intensities of the signal and noise dots used in the experiments were chosen, for each subject, to be equal multiples of the detection threshold. The azimuths of 0 deg/180 deg correspond to the L-M axis, and 270 deg/90 deg to the S-(L+M) axis, respectively. In the following, we qualify for simplicity, the 0 deg direction as red, 180 deg as green, 90 deg as yellow and 270 deg as blue, although these directions do not correspond to the perceptual unique hues (Abramov,1997).

Experiment I: Glass Pattern Detection

We tested the ability of trained human observers to reliably detect circular, static Glass patterns embedded in noise. We used a two-interval forced choice task. In each trial, one interval consisted of the Glass pattern (signal) embedded in noise, while the other contained noise only. The subject's task was to indicate the interval containing the signal (see Figure 2). The chromatic content of the signal and noise could be varied independently. We measured thresholds for the detection of Glass patterns in various combinations of signal and noise colors. Two randomly interleaved noise azimuths were used per session and were chosen to be symmetric (in DKL color space) around the azimuth of the signal. For example, in one session, half the trials presented a signal with an azimuth of 0 deg embedded in noise dots of 30 deg, while in the other half the signal was embedded in noise of 330 deg.

Each trial started with the brief presentation (160 ms) of a fixation point (a 1.6 x 1.6 min white dot) at the center of the display, followed by the two intervals. The fixation point remained visible throughout the trial. Interval onsets were signaled by a short beep. Each interval's duration was 100 ms, as was the time between them. The time between two trials was variable, as it was contingent on the subject's response.

The stimuli were made of dot pairs presented on a grey background with a luminance of 17 cd/m^2. The separation between dots in a pair was 9.8 min. At the viewing distance we used, the stimulus subtended 20.5 deg of visual angle. To minimize the possible contamination of our data by luminance artifacts induced by chromatic aberrations, we used a relatively large dot size (6.9 x 6.9 min visual angle). The luminance of the dots was equal to that of the background. Furthermore, we also ran experiments where the luminance of each dot was randomized. Randomization of the dots' luminance had no effect on the pattern of results. This confirms the subjects' phenomenological reports that they always looked for a pattern defined by color, not brightness, and could always correctly identify the colors of both signal and noise dots.

The number of signal and noise dots remained constant between trials (500 and 1000 respectively), but the proportion of signal pairs contributing to the Glass pattern could vary from trial to trial. For example, a 50% coherent stimulus would consist of 250 dot pairs making

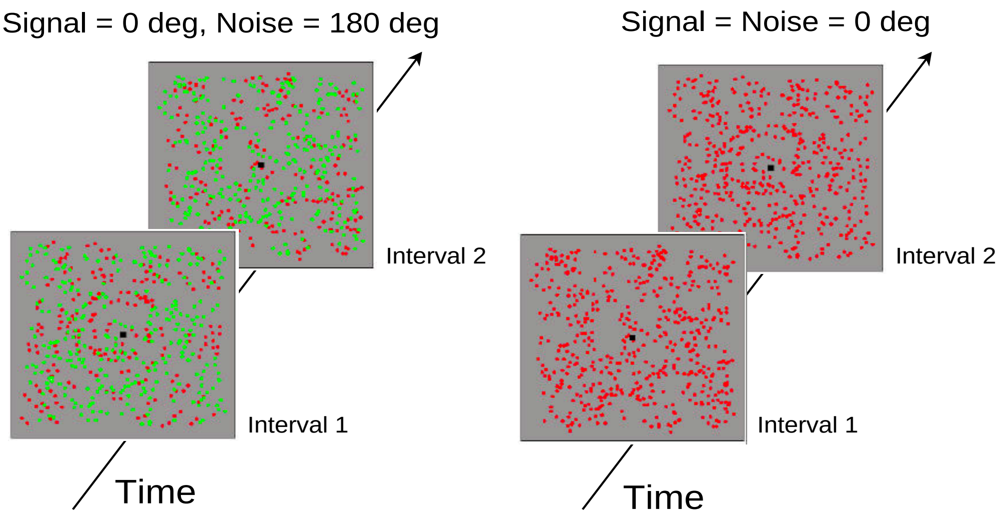

Figure 2: Schematic representation of the stimuli. The trial on the left (with signal in interval 1) shows an example of noise and signal having opposite azimuths, while that on the right has equal azimuths (signal in interval 2).

the signal pattern (i.e. signal-colored dot pairs), 250 randomly-oriented dot pairs having the same color as the signal pattern (i.e. signal-colored noise dot pairs), and 1000 randomly-oriented noise pairs. To minimize the intrinsic variability in the visibility of Glass patterns (see Discussion), dot pairs were distributed in a pseudorandom fashion, so that the numbers of signal- and noise-colored dot pairs were equal in each quadrant of the display. Schematic representations of the stimuli are shown in Figure 2. We measured the threshold coherence of the signal pairs as a function of the noise color. A given experimental session started with a coarse preliminary estimate of threshold. Upon its completion, a low tone indicated the start of the data collection proper. We used two randomly interleaved staircases, with 3 correct responses resulting in a 0.1 log unit decrease in the coherence of the signal in the next trial, and one error resulting in a 0.1 log unit increase. Errors were signaled by a tone. Each staircase terminated after 6 reversals, and threshold was taken as the average of the reversal values.

In a few early experiments, we used the method described by Maloney et al. (1987) and Wilson and Wilkinson (1998) [1]. We measured the maximal number of noise dots that could be added to a signal made of a fixed number (80 pairs) of dots. The noise consisted of randomly-positioned single dots (noise dots). The interval that did not contain the signal consisted of 80 randomly-positioned and oriented dot pairs (noise pairs), having the same color as the signal and embedded in individual noise dots, as in the interval containing the signal. All noise dots had the same color in a given trial. The two methods yielded results that are qualitatively identical and will not be further distinguished.

Experiment II: Color Categorization

To serve as a comparison to the tuning widths of the Glass pattern detection mechanisms (see below), we ran additional experiments using a traditional color categorization task: single-hue scaling (Miller & Wooten, 1992). In a given session, subjects were shown four series of 24 presentations of a disk (area = 1 deg^2, presentation duration 416 msec, luminance 41 cd/m^2) whose color was randomly modulated in 15 deg steps throughout the full 360 degrees of azimuth in DKL space. The disks were presented on an equiluminant grey background. Interstimulus intervals were variable, depending on the response times of the subjects. In a given series, subjects were instructed to state what percentage of the disk's color was either red, blue, yellow, or green. Each series was run twice and the results averaged.

Results

Example results from Exp. I are shown in Figure 3. These graphs show data obtained for the detection of Glass patterns in each of the four cardinal directions. We plot the minimal signal coherence necessary to detect the Glass pattern reliably, as a function of noise azimuth.

The data obtained from this experiment show a characteristic pattern. In all cases, the detection of the Glass pattern is modulated as a function of the noise

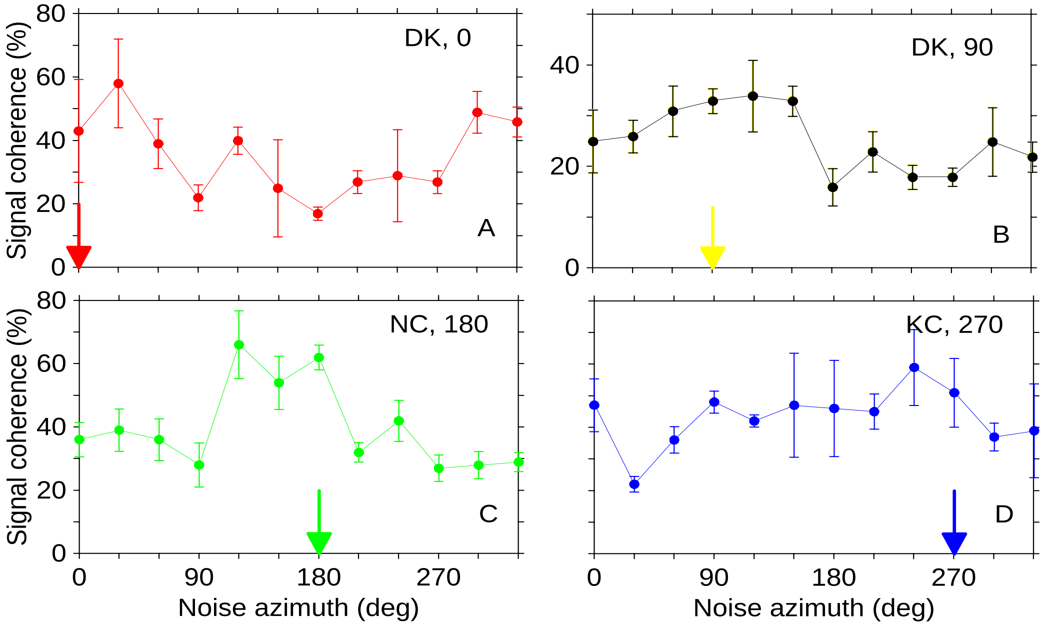

Figure 3: Representative examples of the results obtained in Exp. I, in each of the cardinal direction of DKL space (0 deg in A, 90 in B, 180 in C, and 270 in D), for subjects DK, NC, and KC. Each graph plots the threshold signal coherence as a function of the noise azimuth. The arrow indicates the azimuth of the signal. Error bars are the standard error of the threshold estimates. Note the different scale on the ordinate of B.

color. Thresholds are highest when noise azimuth is equal or near to that of the signal azimuth. In other words, the visibility of the Glass pattern is most impaired when the noise is of the same color as the pattern. When signal and noise have different colors, thresholds decrease as the difference between signal and noise colors increases.

For example, a green pattern (180 deg azimuth, Figure 3C) is more difficult to detect among other green dots than among red ones. In many cases (Figure 3A for example), the lowest threshold was obtained when the noise color maximally differed from that of the signal, i.e. when their azimuths differed by 180 deg. The selectivity of a detecting mechanism can be evaluated by analyzing the variation in the detection threshold of a given Glass pattern as a function of the noise azimuth. If the detecting mechanism sums its inputs linearly, the detection thresholds for various noise directions must be determined by the angle between the noise direction and that of the mechanism's highest sensitivity. Specifically, the detection threshold will then be proportional to the cosine of the angle between the signal and the noise direction. To determine whether this is the case, we normalized our data and fitted them with a cosine.

In most cases, the selectivity of the mechanisms detecting the Glass patterns is consistent with the hypothesis that they sum their inputs linearly. Representative examples of this analysis are shown in Figure 4.

The abscissa indicates the difference between noise and signal azimuths, and the ordinate plots the detection thresholds normalized to their minimum and maximum. The dotted curves show one cycle of the best- fitting cosine, whose amplitude and phase were free to vary.

To assess the overall quality of the cosine fits, we performed the same analysis on the data averaged across subjects. Figure 5 shows the averaged data for each cardinal direction of DKL space and the best-fitting cosine for each data set. The cosine fit accounts for 87% of the variance for the 0 deg signal, 82% for the 90 deg and 180 deg signals, and 86% for the 270 deg signal. Thus, the cosine provides a good description of the results. Although occasional individual data sets are not well- described by the cosine (see Figure 3D for ex.), this is likely due to the large variability observed in our data (see Discussion).

For Glass patterns whose colors lie between the cardinal directions of DKL space, the pattern of results is the same. Figure 6 shows two such examples, for patterns with azimuths of 135 deg and 225 deg, respectively.

As seen with the cardinal directions, these detection thresholds are most impaired by noise dots having an azimuth equal to that of the signal. We found no difference between the data obtained with Glass patterns lying in intermediate directions compared to those in the cardinal directions.

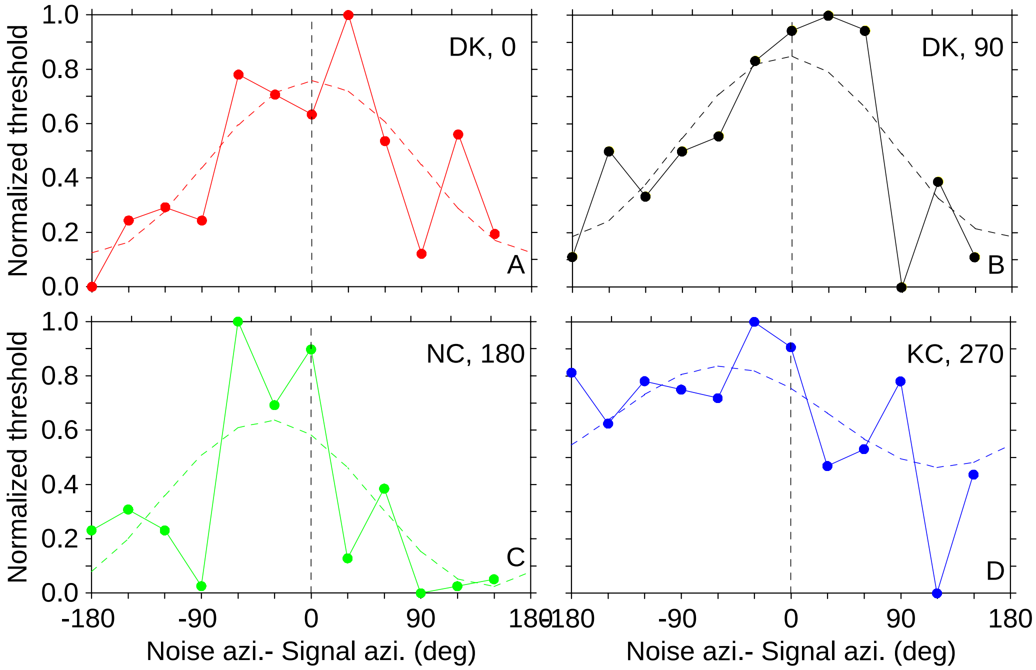

Figure 4: Examples of normalized data from Exp. I (same signal directions and subjects as in Figure 3). The abscissa shows the difference between noise and signal azimuths, the ordinate the coherence threshold normalized to its minimum and maximum. The dashed curve shows the best fitting cosine to each set of data.

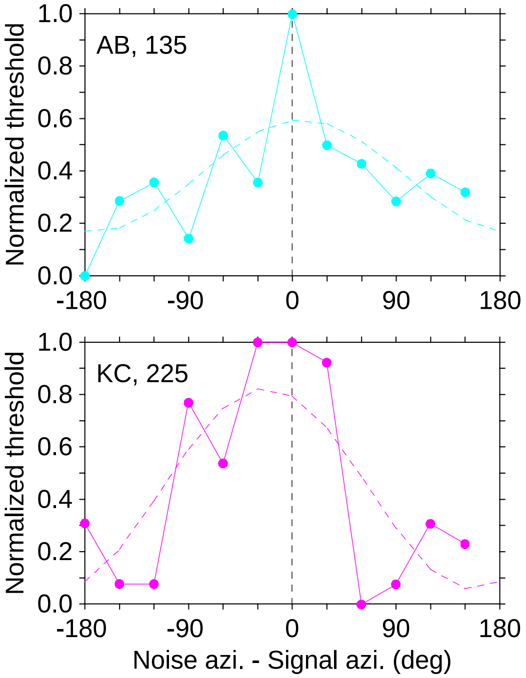

Figure 5: Examples of data obtained using signals in intermediate directions (135 deg, top; 225 deg, bottom) of DKL space.

Similar results were obtained for signals in the 45 deg and 315 deg directions. Note that due to the subjects' limited availability, they were not each tested for all signal directions. Each intermediate direction was tested in two to four subjects only.

These results suggest that the detection of Glass patterns is mediated by a multitude of mechanisms, whose preferred directions in DKL space are not restricted to the cardinal directions.

Figure 7 summarizes our data. It shows the normalized data averaged across all subjects and conditions. The dotted curve in Figure 7 is the best fitting cosine to the averaged data. The cosine provides a good description, accounting for 89% of the variance in the data. Statistical analysis revealed that the data do not differ significantly from the cosine (χ^2 goodness-of-fit (df = 13): 2.08, α = 0.01). So far the conclusions drawn from this analysis rely on the model's prediction, yet would be strengthened by a direct comparison with mechanisms involved in other tasks. For this reason, we decided to compare the tuning of the Glass pattern mechanisms to that of other mechanisms known to have a narrow tuning in color space.

To further characterize the selectivity of the Glass pattern detecting mechanisms in color space, we compared their selectivity to that of the mechanisms involved in color categorization. Color categorization is known to be mediated by a limited number of mechanisms whose bandwidth is narrow (Sternheim & Boynton, 1966; Komatsu, 1997). Two examples of the results obtained in our color categorization task are shown in Figure 8. Each curve plots the proportion of a given color (red, yellow, green, or blue), estimated by a human observer for colored disks whose azimuths spanned the isoluminant plane.

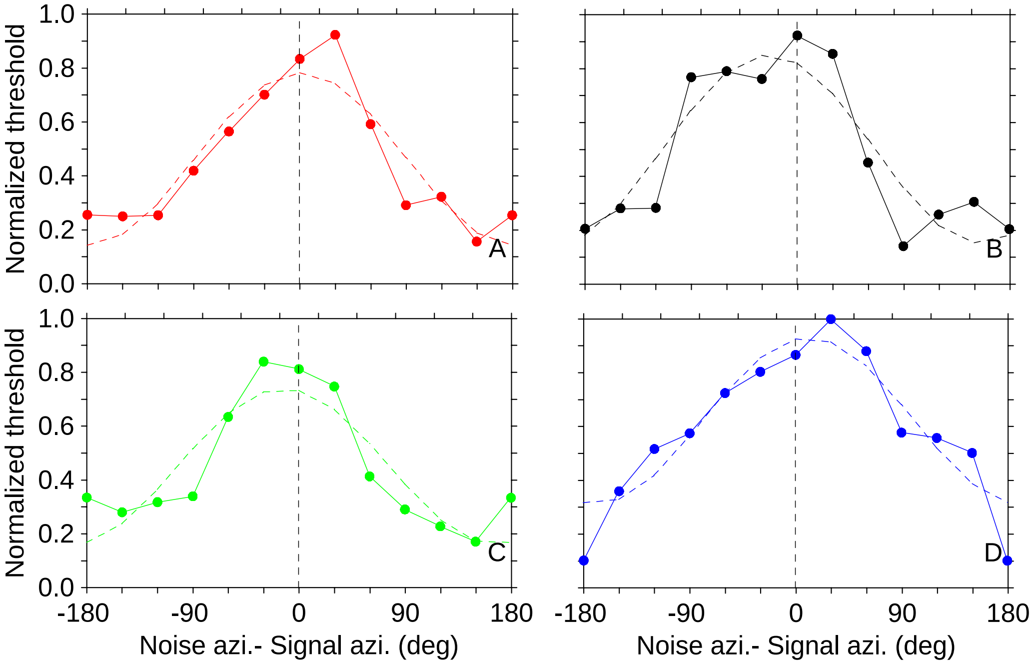

Figure 6: Normalized data for the 0 (A), 90 (B), 180 (C) and 270 deg (D) signals, averaged across all subjects. The dashed curves show the best fitting cosine for each data set. The cosine fit accounts for more than 80% of the variance in all signal directions.

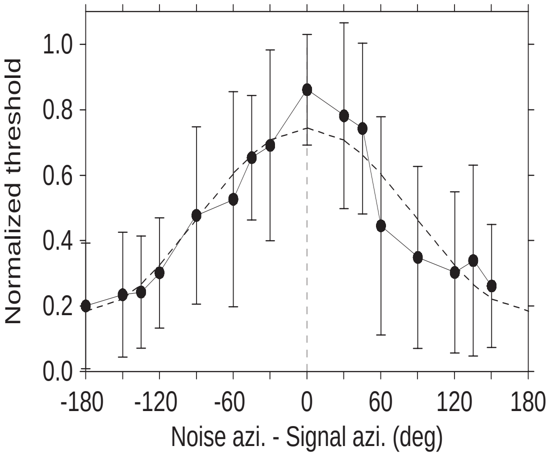

Figure 7: Normalized data averaged across all subjects and directions of DKL space (N = 27 [2]). The error bars show the standard deviations. The best fitting cosine (dashed curve) accounts for 89% of the variance in the data.

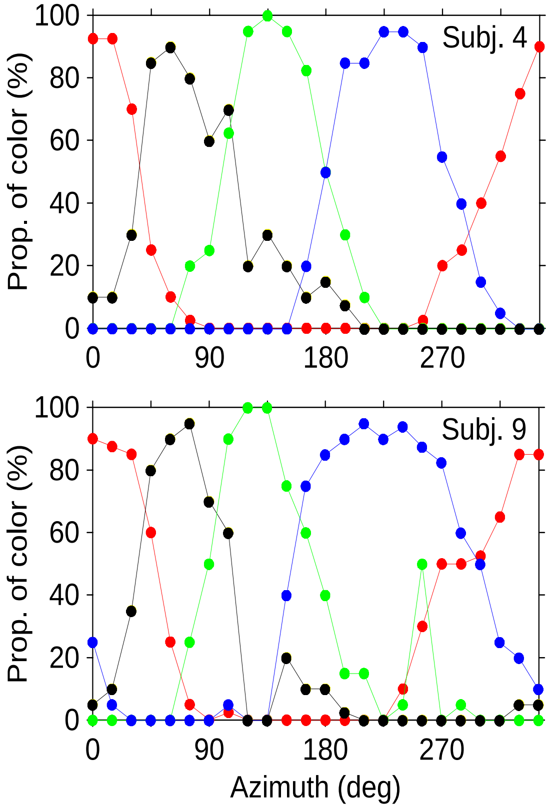

Figure 8: Examples of color categorization for two subjects. Each curve shows the estimated percentage of the colors red, yellow, green, or yellow (from left to right) as a function of the stimulus azimuth.

To determine the tuning bandwidth of the mechanisms involved in color categorization, we fitted each set of data with a Gaussian curve. The standard deviation of the best-fitting Gaussian was taken as our bandwidth estimate. We repeated the same procedure for our Glass pattern detection data. The distribution of bandwidths for these two experiments is shown in Figure 9. The two distributions are different. The median of the categorization mechanisms' distribution is 38.9, while it is 89.2 for the Glass pattern detection mechanisms (p<0.001, test of two medians, Welkowitz, Ewen, & Cohen, 1982, p. 311).

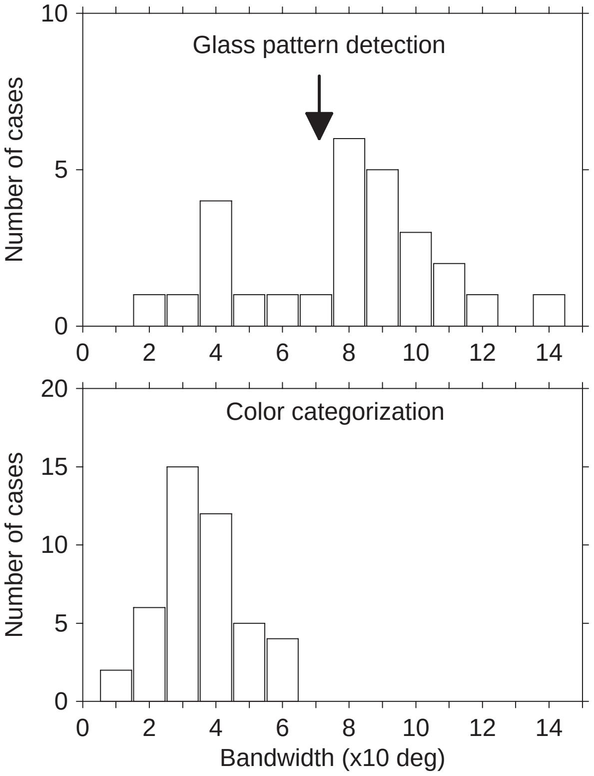

Figure 9: Distribution of tuning widths of the Glass pattern detection mechanisms (top), and of those responsible for color categorization (bottom). The bandwidths were derived from Gaussian curves fitted to each set of data. The arrow in the top panel indicates the bandwidth expected for a linear mechanism.

The median of the Glass pattern distribution is close to the value of 71.5 deg [3], indicated by the arrow in Figure 9, which is that predicted if the mechanisms combined their inputs linearly (i.e. it corresponds to the value obtained by fitting a Gaussian curve to one cycle of a cosine). Although the range of Glass pattern mechanism bandwidths is quite large (see Discussion), this result shows that the mechanisms detecting Glass patterns have a broader tuning in DKL space than those underlying color categorization. Their selectivity is consistent with the hypothesis that they combine their inputs linearly. Note that linear combination of the inputs results in a broad selectivity, but a broad selectivity does not imply a linear combination of the inputs. Our data only show that the mechanisms' selectivity does not allow us to reject this hypothesis.

Discussion

The results of our experiments suggest that the mechanisms responsible for the detection of chromatic, circular Glass patterns have a broad tuning in color space, relative to those of the mechanisms underlying color categorization. The tuning is consistent with the hypothesis that they combine their inputs linearly. In that respect, they do not differ from the early level mechanisms involved in the detection or discrimination of spatially localized targets (Krauskopf et al., 1982; Krauskopf & Gegenfurtner, 1992; D'Zmura & Knoblauch, 1998). The broad tuning of these mechanisms is particularly evident when compared to that of the mechanisms involved in color categorization, as shown in Figure 9. The human visual system thus seems to rely primarily on relatively broad mechanisms for the detection of a variety of chromatic visual targets. In contrast, for the more cognitive operation of categorization, the mechanisms involved are more selective.

A possible alternative interpretation of our results from Exp. I is that we did not measure the chromatic tuning of the mechanisms responsible for the detection of the Glass patterns. Rather, it is possible that the subjects selectively attended to only one color at a time, namely that of the signal. This was a possible strategy since the signal color remained the same within an entire given session. In other words, an attention mechanism could have "filtered out" the noise color, letting only the signals forming the Glass pattern through. These signals would then be integrated by a color-insensitive Glass pattern mechanism. If that were the case, our first experiment would have measured the chromatic selectivity of this attention mechanism, not of the Glass pattern detection mechanism per se. This was unlikely to be the case for two reasons. First, we observed that the absolute thresholds differed for the different signal directions. In Figure 3, note that the coherence thresholds for the yellow signal (panel B) are lower than for the other signal directions (A, C and D) approximately by a factor of 2. This is not consistent with the notion that all signals are detected by a single, chromatically-insensitive mechanism.

Second, we performed a control experiment in which each dot pair could have one of two maximally different colors, for example red or green. In half of the trials (the "segregated" condition) the signal pairs were all of the same color, randomly chosen to be red or green in a given trial, and the noise pairs all had the other color. In the other trials (the "mixed" condition), half of the signal pairs were red, the other half green, and the noise pairs were also equally divided between red and green. In such a session, attending to only one color would not provide any benefit. If the thresholds for the detection of the patterns in the segregated and mixed conditions were the same, we would then conclude that the subjects had indeed used an attention mechanism whose output was analyzed by a Glass detection mechanism that is not tuned for color. On the other hand, if detection was solely mediated by a chromatically- tuned Glass pattern mechanism, we would expect the "mixed" thresholds to be significantly higher than the "segregated" thresholds, approximately by a factor of 2. We performed this control experiment in three subjects, using the same psychophysical procedures as described in the methods section. We tested each subject with combinations of red or green pairs (0 deg or 180 deg), and with yellow or blue pairs (90 deg or 270 deg). The results are shown in Figure 10. The data show that in all conditions, the thresholds for the "mixed" condition are significantly higher than for the "segregated" condition. On average, the "mixed" is higher than the "segregated" threshold by a factor of 1.85, close to the value of 2 expected if detection was mediated by a chromatically tuned Glass pattern mechanism. We therefore conclude that our first experiment revealed the chromatic tuning of such mechanisms.

Before discussing the relationship between these results and the chromatic tuning of individual neurons, we address the issue of the variability observed in our data. As described in the results section, fits to individual data sets were sometimes poor, improving only after several additional sessions of data collection. We believe that this high variability is mostly due to the intrinsic variability of the Glass patterns themselves. Although we constrained the number of signal and noise dots to be the same in the four quadrants of our stimuli, the spatial arrangement of the signal dot pairs within a quadrant still influences the visibility of the pattern. If the signal pairs are mostly located close to the central fixation point and are evenly spread, detection of the pattern is easier than if the pairs are more peripheral and located in independent clusters. Measuring the detection threshold for these patterns therefore requires a large number of stimulus repetitions, and limits the number of color directions that can be measured in a single subject. The intrinsic variability in the visibility of Glass patterns is probably also responsible for the long training necessary to obtain stable, reliable thresholds.

While the properties of Glass patterns make them valuable stimuli for the psychophysical study of object perception, they unfortunately introduce noise in the results. Nonetheless, comparison with the results of the color categorization experiment show convincingly that the chromatic tuning of the mechanisms underlying Glass pattern detection is broader than that of the color categorization mechanisms.

Our results indicate that Glass patterns are detected by a population of cells having large receptive fields and a relatively broad chromatic selectivity. These properties are consistent with those of V4 cells. At corresponding eccentricities, V4 neurons have linear dimensions 6-7 times larger than V1 neurons (Desimone & Schein, 1987). Moreover, the majority of color-selective V4 cells

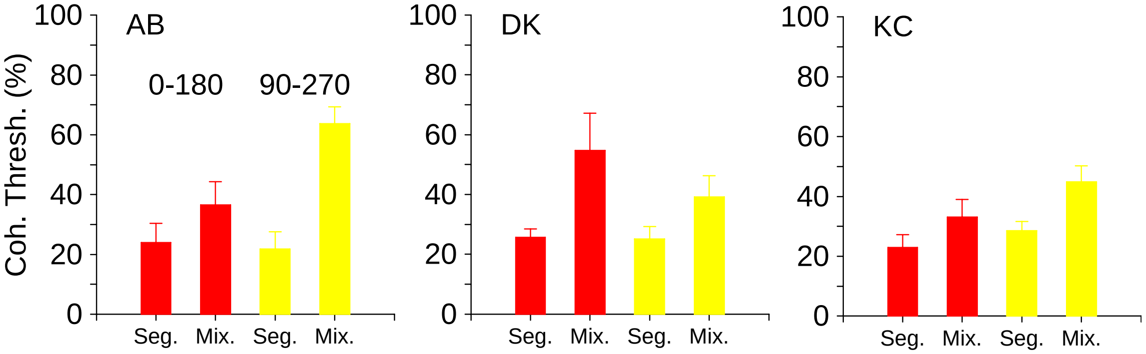

Figure 10: Results of the control experiment using the "segregated" and "mixed" conditions (see text). Data from three subjects (AB, DK and KC), each tested with red-green and yellow-blue combinations (abscissa). In all cases, the coherence threshold (ordinate) is significantly higher in the "mixed" than in the "segregated" condition. Error bars show the standard errors of the threshold estimates.

have a broad color selectivity, indistinguishable from that of neurons at earlier level (Schein et al., 1982). These spatial and chromatic properties, in addition to the report that some V4 neurons are specifically tuned to circular, concentric stimuli (Gallant et al., 1993), make them ideal candidates to underlie the detection of circular Glass patterns. Recent results using functional magnetic resonance imaging in humans and in anaesthetized monkeys seem to confirm this hypothesis. Indeed, Tse, Smith, Augath, Trinath, Logothetis, and Movshon (2002) reported that in addition to areas V1 and V2, anterior extrastriate areas including V4 are activated by the presentation of Glass patterns. Moreover, the difference in activity due to circular, compared to other (radial and translational) Glass patterns was most marked in area V4, suggesting that this area contains neurons preferentially tuned to circular patterns. The higher activity induced by circular Glass patterns could explain the observation that they are processed more efficiently than other Glass patterns (Wilson, Wilkinson, & Asaad, 1997).

Conclusions

We conclude that chromatic, circular Glass patterns are detected by a population of neurons with a broad tuning in color space relative to those involved in color categorization, and with relatively large receptive fields. These neuronal properties are consistent with those of the color selective cells of area V4. The visual system thus relies on mechanisms having a relatively broad selectivity, even while detecting complex objects whose perception requires the integration of signals within large areas of the visual field. Because the tuning properties of the mechanisms revealed in our experiments do not correspond to those of the narrowly-tuned color selective cells observed in several extrastriate areas, the role of these cells in visual perception remains unknown.

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Footnotes

[1] To determine whether our subjects, stimuli, and experimental setup were comparable to those previously described in the literature, we tested the ability of three subjects to detect achromatic Glass patterns using the additive noise method introduced by Maloney et al. (1987). Each dot was white, with a luminance of 82 cd/m^2 and the background was dark (2 cd/m^2). Our three subjects could tolerate 740, 602 and 545 noise dots respectively, giving an average of 629. This is very similar to the results published by Maloney et al. who found an average of 700 tolerated noise dots for patterns made of 100 pairs.

[2] Because of the limited subjects' availability, they were not tested for all signal directions. Each subject was tested in 3-4 cardinal and 1-2 intermediate directions.

[3] The median value of the Glass mechanism distribution (89.2) is not significantly different from 71.5, sign test, $\alpha = 0.05$

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