



Effects of Contrast and Temporal Frequency on Orientation Discrimination for Luminance and Isoluminant Stimuli

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Received 29 April 1997; in revised form 25 July 1997

We compared the mechanisms responsible for orientation discrimination of stimuli defined by luminance and red/green isoluminant contrast. A four-alternative forced-choice (4-AFC) paradigm was used to determine thresholds for discriminating 1 cpd sinewave gratings differing in orientation, contrast, or both. When measuring orientation thresholds as a function of stimulus contrast, we found a decrease in thresholds with increasing stimulus contrast. For three temporal frequencies (0, 1, and 8 Hz) the functions relating orientation thresholds to stimulus contrast had similar shapes for luminance and isoluminant gratings, indicating similar processing mechanisms. Thresholds for stationary or slowly moving gratings were consistently lower for isoluminant than for luminance gratings, when contrast was expressed on an absolute RMS-cone-contrast scale. When contrast was defined as multiples of detection thresholds, discrimination was slightly better for luminance gratings. Thresholds for fast moving gratings were similar, irrespective of the definition of contrast. In contrast to previous work, we found a marked “oblique-effect” for both luminance and isoluminant gratings, when measuring discrimination thresholds as a function of standard orientation. Finally, we measured discrimination thresholds for gratings that varied in contrast and orientation simultaneously. The shapes of the resulting two-dimensional threshold contours were similar for luminance and isoluminant gratings, indicating again that these stimuli undergo similar neuronal processing. Performance of the observers could be described by probability summation of the orientation and contrast cues, resulting in an elliptical shape of the two-dimensional threshold contours. In conclusion, our results show similar performance for luminance and isoluminant gratings in several orientation discrimination tasks. The similarity in shape of the different threshold functions presents strong evidence that similar mechanisms underlie orientation discrimination of luminance and isoluminant stimuli. © 1998 Elsevier Science Ltd. All rights reserved.

Form perception Chromatic mechanisms Temporal frequency Contrast

INTRODUCTION

Objects in our visual environment are characterized by numerous attributes, such as form, color, depth, or motion. During the past two decades, research has emphasized the identification of modules that process the different visual attributes separately and in parallel (see Treisman, 1985; Livingstone & Hubel, 1987). This emphasis on parallel processing was at least partially motivated by the finding of independent channels for different stimulus features in the retina and geniculate (Leventhal, Rodieck & Dreher, 1981; Perry, Oehler & Cowey, 1984; Kaplan & Shapley, 1986), in the visual cortex (Livingstone & Hubel, 1984; Hubel & Living-

stone, 1987; DeYoe & Van Essen, 1985; Zeki, 1978) and in higher cortical areas (Ungerleider & Mishkin, 1982). A strict separation of processing streams for visual attributes, however, has come under criticism recently. Many interactions between functional streams have been found anatomically (for a review, see Merigan & Maunsell, 1993) and physiologically (Peterhans & von der Heydt, 1993; Ferrera, Nealey & Maunsell, 1994; Levitt, Kiper & Movshon, 1994; Gegenfurtner, Kiper & Fenstemaker, 1996). In addition, a number of psychophysical studies have presented evidence against a strict separation of color, form and motion (Krauskopf & Farell, 1991; Gegenfurtner & Kiper, 1992; Webster, De Valois & Switkes, 1990; De Valois & Switkes, 1983; Switkes, Bradley & De Valois, 1988; Derrington & Henning, 1993; Metha, Vingrys & Badcock, 1994; Stromeyer, Kronauer, Ryu, Chaparro & Eskew, 1995b; Gegenfurtner & Hawken, 1995; Würger & Landy, 1993; Hawken, Gegenfurtner & Tang, 1994).

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Despite such evidence for interactions, there seems to be strong evidence for independent processing in some cases. For example, the spatial tuning is quite different for stimuli defined by luminance compared with isoluminant stimuli, which are defined by color contrast alone. Whereas the contrast sensitivity function for luminance stimuli is band-pass, it has a low-pass characteristic for isoluminant stimuli and a lower sensitivity at higher spatial frequencies (Kelly, 1983; Mullen, 1985). This implies that some aspects of form perception could be abolished or impaired at isoluminance. The detection of orientation differences is of particular significance, since the extraction of orientation information is considered to be of great importance in the early stages of visual processing (see Marr, 1982).

We therefore compared orientation discrimination as a function of contrast for luminance and isoluminant stimuli. Previous studies have shown that observers are certainly capable of making orientation discrimination judgments at isoluminance (Webster *et al.*, 1990; Würger & Morgan, 1995). However, a direct comparison of the performance for luminance and isoluminant targets is problematic, since there is no canonical way to compare contrasts. Indeed, the results are quite dependent on the metric that is used to compare luminance and isoluminant contrast. Webster *et al.* (1990) determined thresholds for orientation and spatial-frequency discrimination using sinewave gratings defined by either luminance or isoluminant contrast. They found that observers were able to discriminate orientation differences on the basis of isoluminant information, but the thresholds were slightly higher than for luminance defined gratings, when contrast was expressed as multiples of detection threshold. On the other hand, Würger and Morgan (1995) showed that orientation discrimination thresholds were equal for luminance and isoluminant Gabor patches, when contrast was expressed on an absolute root-mean-squared cone contrast scale. The later result is similar to what Krauskopf and Farell (1991) observed earlier in a vernier acuity task, in which performance is assumed to be mediated by orientation-selective mechanisms.

Owing to the lack of a canonical scale for comparing luminance and isoluminant contrast, we focused on qualitative aspects of orientation processing, for example the variation of thresholds under changes of temporal frequency. Temporal frequency is of particular interest, since it is quite likely that different temporal frequency ranges are used for different visual functions. Orientation tuned channels could determine the form of stationary objects, while they might be involved in determining the direction of motion of fast moving objects. Interestingly, temporal frequency turned out to be an important independent variable in several tasks involving isoluminant stimuli (Gegenfurtner & Hawken, 1996a,b).

Another important characteristic of orientation perception is the so-called "oblique-effect". In a variety of visual tasks performance is better for stimuli aligned with the cardinal visual axes, as opposed to obliquely oriented stimuli. We tested whether isoluminant stimuli would

show an "oblique-effect", analogously to what had been observed for luminance defined stimuli (Kelly, 1975; Caelli, Brettel, Rentschler & Hilz, 1983; Orban, Vandenburg & Vogels, 1984). To tap higher level visual processing of orientation, we investigated the combination of simultaneous contrast and orientation differences (Thomas & Olzak, 1990).

Preliminary reports of these data have been presented in Reisbeck and Gegenfurtner (1996).

METHODS

Equipment

The stimuli were displayed on a BARCO (CCID 7351B) color television monitor that was driven by a Cambridge Research VSG 2/3 graphics board with a refresh rate of 120 Hz non-interlaced. The images were generated on the monitor by reading through the picture memory in a raster scan and then interpreting the numbers in each location as a color defined in a 256-element color lookup table. Two 8-bit-digital-to-analog converters, which were combined to produce an intensity resolution of 12 bits, were used to control the intensity of each of the three monitor primaries. The luminances of each of the phosphors was measured at various output voltage levels using a Graseby Optronics Model 370 optometer with a model 265 photometric filter. A smooth function was used to interpolate between the measured points and lookup tables were generated to linearize the relationship between voltage output and luminance. All the stimuli in the present experiments had a space-time averaged luminance of 26.25 cd/m². We also made sure that additivity of the three phosphors held over the range of intensities used in these experiments (Brainard, 1989). A Photo Research PR 650 spectroradiometer was used to measure the spectra of the red, green and blue phosphor at their maximum intensity setting. The spectra were multiplied by Judd's 1951 color matching functions to derive *x*, *y* chromaticity coordinates and the luminance *Y* of the phosphors (Irtel, 1992). All further references to luminance and photometric luminance refer to the *V*(λ) curve, as modified by Judd. The matrix equations given by MacLeod and Boynton (1979) were used to calculate cone absorptions (Smith & Pokorny, 1975) from the *X*, *Y*, and *Z* values.

Subjects

Full data-sets were obtained from two subjects, one of which (TR) was the first author. A third subject ran only the first two experiments. All subjects had normal or corrected visual acuity and normal color vision.

Stimuli

The stimuli in all experiments were drifting one-dimensional 1 cpd sinewave gratings of different color, orientation, and temporal frequency (stationary, 1 and 8 Hz). All stimuli were symmetric modulations around a neutral white point (*x*, *y*, *Y* = 0.34, 0.35, 26.25) along a luminance and a red-green axis, which were chosen so

that they would differentially excite the putative L–M and L + M color-opponent mechanisms as defined by Krauskopf, Williams and Heeley (1982). Modulation of the blue–yellow opponent mechanism, S– (L + M), was zero for all stimuli. The maximum stimulation along the L–M axis went from (0.42, 0.31) to (0.22, 0.39) and produced a Weber contrast of 7.96% in the L-cones and 18.29% in the M-cones. For luminance modulations, of course, 100% contrasts can be achieved for both L- and M-cones.

In the first experiment, we used stimuli lying in the plane spanned by the L + M and L–M axes to determine the lines of subjective isoluminance within that plane for each observer separately. In further experiments, red–green variations along these lines of subjective isoluminance were used. In addition, we also used two more settings of the relative luminances of red and green, which were chosen to symmetrically bracket photometric isoluminance (with Judd's correction) and to contain the individual isoluminance setting for a given subject.

To compare the effectiveness of luminance and chromatic stimuli we normalized the contrasts to an absolute cone-contrast scale by calculating the root-mean-squared contrast in the L- and M-cones: $RMS = \sqrt{0.5(l^2 + m^2)}$, where l and m are the Weber contrasts in the L- and M-cones, respectively, calculated using the cone fundamentals proposed by Smith and Pokorny (1975). The maximally achievable RMS-cone-contrast under conditions of photometric isoluminance was 14.1%. For luminance stimuli, the contrast is equal for both cone types and therefore equal to the RMS-cone-contrast.

EXPERIMENT 1: ORIENTATION DISCRIMINATION AND FLICKER PHOTOMETRY

Experiment 1 served a dual purpose. First, to determine whether subjects can make coarse orientation discriminations (horizontal vs vertical) at the detection threshold for these stimuli. Second, to obtain estimates of individual subjective isoluminance for all three observers. Since isoluminance can vary for different tasks (Webster & Mollon, 1993) and temporal frequencies (Stromeyer, Chaparro, Toliás & Kronauer, 1995a), we decided to determine full contours for detection and orientation discrimination in cone contrast space, similarly to what Gegenfurtner & Hawken (1995) and Stromeyer *et al.* (1995b) did for a motion task. The analysis of threshold contours allows us to describe the mechanisms underlying performance in a particular task, orientation discrimination in our case. The individual estimates for isoluminance obtained from the threshold contours were then compared with estimates determined by a more traditional method, flicker photometry.

Methods

Detection. A two-interval forced-choice paradigm was used to determine detection thresholds for 1 cpd vertically oriented sinewave gratings that were presented foveally for 500 msec within a circular aperture subtend-

ing a visual angle of 4 deg. They were stationary or moving at temporal frequencies of 1 or 8 Hz. Stimuli were symmetrically modulated in color along lines with different balances of the L- and M-cones. Contrast was linearly ramped on and off during the first and last 50 msec of the stimulus presentation. Subjects were asked to indicate in which of the two intervals a stimulus was present and an adaptive staircase procedure determined the contrast along a particular direction in color space necessary for detection.

Orientation discrimination. In this experiment we used a two-alternative forced-choice paradigm to determine the minimum contrast for which orientation discrimination of vertically vs horizontally aligned 1 cpd sinewave gratings could be achieved. Stimuli and color directions that were tested were otherwise exactly the same as for detection above. The task of the subjects was to indicate whether the presented grating was vertically or horizontally oriented. An adaptive staircase procedure was used to determine the minimum contrast at which this discrimination could be achieved.

Flicker photometry. In this experiment two uniform fields of light flickered against each other at a temporal frequency of 16 Hz. They were presented foveally and subtended a visual angle of 4 deg. The standard light was modulated along the luminance direction and had a fixed contrast of 12.5%. Test lights with nine different balances of L- and M-cones were used, and the subjects had to adjust the contrast of the test lights until their perception of flicker became minimal. This adjustment process was repeated 10 times for each test stimulus.

Results

Figure 1 shows detection and orientation discrimination contours in cone contrast space for observer TR. The open circles denote detection thresholds and the filled circles the thresholds for orientation discrimination. Since the stimuli were symmetrical modulations around the central white point, each data point is drawn twice. Data for the other two observers look similar, although the individual points of subjective isoluminance varied slightly.

The upper plot shows the results for stationary, the middle for slowly moving (1 Hz) and the lower one for fast moving (8 Hz) stimuli. In all cases thresholds for detection were equal to those for orientation discrimination. For stationary and slowly moving stimuli thresholds were largest in the luminance direction (positive diagonal), as has been found in the case of motion detection earlier (Stromeyer *et al.*, 1995b; Gegenfurtner & Hawken, 1995). Thresholds were lowest along the negative diagonal, indicating that a color-opponent mechanism taking the difference between L- and M-cones was most sensitive. These contours allow a good estimate of how L- and M-cones are weighted by the color-opponent mechanism. Since there is only one data point in the null direction of the color-opponent mechanism, we cannot estimate how L- and M-cones are weighted by the luminance mechanism and thus

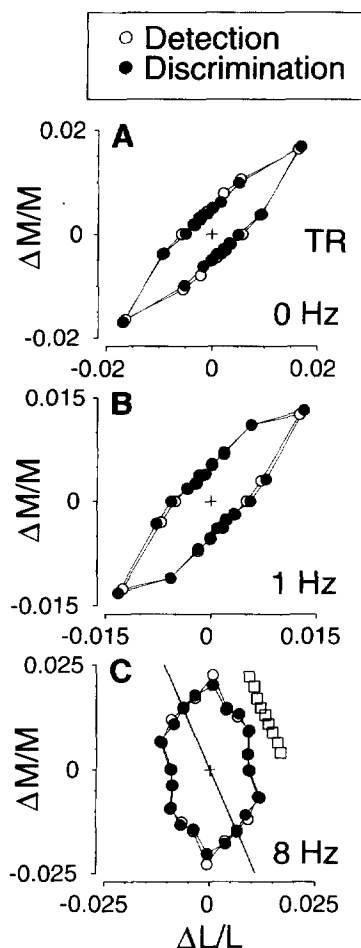


FIGURE 1. Threshold contours for the detection (open circles) and orientation discrimination (filled circles) of a foveally presented 1 cpd sine-wave grating that was either stationary (A) or moved with temporal frequencies of 1 Hz (B) or 8 Hz (C) for subject TR. The abscissas denote contrast of the L-cones and the ordinates plot M-cone contrasts. Half of the contour was determined and thresholds subsequently reflected around the origin (cross). In addition, the lower plot (8 Hz) shows flicker photometry measurements (open squares). For better comparison, the contrast of the flicker data was scaled by a factor of 10. The solid line with negative slope denotes the direction of photometric isoluminance. Note the different scaling.

determine isoluminance. However, it should be clear that the sensitivity of the luminance mechanism is much lower than that of the color-opponent mechanism. For example, if we use photometric isoluminance and assume that subjective luminance is determined by the L-cones only, contrast along the isoluminant direction would still have to be more than 10-times above threshold to be detected by the luminance mechanism.

At higher temporal frequencies (8 Hz), sensitivity in the luminance direction became greater, while sensitivity to isoluminant stimuli decreased, as can be seen in Fig. 1(C). The data points neighboring the luminance direction all fall close to a line in color space, and allow an estimate of the relative weights of L- and M-cones for luminance. For observer TR, this is very close to photometric luminance (solid line).

We compared this estimate of isoluminance to an estimate obtained using flicker photometry at 16 Hz. The

open squares in Fig. 1(C) show the results. For better visibility the contrasts have all been scaled by a factor of 10 (the standard luminance stimulus had 12.5% contrast). The points fall close to a line ($r^2 = 0.995$) that parallels the long flanks of the detection contour.

Discussion

We found no significant differences in thresholds for detection and orientation discrimination for any of the observers in the above tasks. This shows that coarse orientation discriminations are possible at detection threshold for all L- and M-cone balances. We used the above measures to define subjective isoluminance for all three observers. The estimates of subjective isoluminance obtained with flicker photometry and through the analysis of the detection contours at 8 Hz show remarkable agreement for all three observers, even though individual estimates deviated slightly from photometric isoluminance. For low temporal frequencies flicker photometry is not possible. The analysis of detection contours also fails, since the sensitivity in the luminance direction is rather poor compared with that in the isoluminant direction. However, for the very same reason we can safely exclude a big effect of a luminance-based mechanism on the orientation discrimination of isoluminant stimuli up to levels of at least 10 times detection threshold.

EXPERIMENT 2: ORIENTATION THRESHOLDS AS A FUNCTION OF STIMULUS CONTRAST

Our second experiment is a variation of the experiments performed by Webster *et al.* (1990) and Würger and Morgan (1995). In addition to varying the contrast of stationary stimuli, as was done in those studies, we also looked at different temporal frequencies. At high temporal frequencies moving luminance gratings are detected by directionally selective mechanisms (Stromeyer, Madsen, Klein & Zeevi, 1978; Watson, Thompson, Murphy & Nachmias, 1980). Therefore, the orientation information might in this case be used to extract the direction in which an object is moving, rather than just to indicate the orientation of an object border. It has been suggested that the motion of fast moving isoluminant stimuli might actually be signaled by a luminance-based mechanism (Gegenfurtner & Hawken, 1996b), in which case we might be able to observe differences between fast moving and slowly moving isoluminant stimuli.

Methods

Procedure. Subjects were seated at a distance of 172 cm from the monitor, which subtended 12 deg \times 12 deg of visual angle. A black fixation square of 8 min side length was displayed at the center of the screen. The stimuli were presented on an uniform gray background of mean luminance (26.25 cd/m²), extending over the whole monitor screen. They consisted of four discs, each 1 deg in diameter. The centers of the discs were located 0.75 deg eccentric on the corners of an imaginary square

that was symmetrically arranged around the fixation spot. Presentation time was 500 msec and stimulus contrast was ramped on and off during the first and last 50 msec. During each presentation, three of the discs showed the same sinewave gratings (standard stimuli) and the fourth showed a grating that differed in orientation (test stimulus). The spatial frequency of all gratings was 1 cpd and the spatial phase was randomly chosen for each grating. We used a low spatial frequency of 1 cpd to avoid chromatic aberration artifacts for our isoluminant gratings (Cavanagh & Anstis, 1991; Flitcroft, 1989; Marimont & Wandell, 1994). Since we did not smoothen the edges of the stimulus patches, chromatic aberration artifacts along the circumference of the discs are quite possible. However, note that any such aberration artifacts do not contain orientation information. The subjects had to determine which of the discs was different from the others. They did so by pressing one of four keypad buttons representing the locations of the discs on the screen. In Experiments 2 and 3 a staircase procedure was used to control the magnitude of the orientation difference between standard and test stimuli. In Experiment 4, a method of constant stimuli was used to determine thresholds.

In this experiment we measured orientation thresholds for stationary (0 Hz), slowly (1 Hz) and fast (8 Hz) moving 1 cpd sinewave gratings as a function of stimulus contrast. The standard stimuli were oriented vertically and the test stimulus had a randomly chosen clockwise or counterclockwise offset from the vertical orientation. A staircase procedure was used to determine the thresholds for the test stimuli at different contrasts and for each of the three drift rates. An up-down method (Levitt, 1971) controlled the magnitude of the orientation difference between standard and test stimuli. The difference between the test and standard stimuli was decreased after three consecutive correct responses and increased after an incorrect one. Threshold estimates were then determined from the mean of the six reversal points of the staircase. Two independent runs for each stimulus were interleaved, and the procedure was repeated six times. The average value of these 12 measurements was used as the final estimate for the threshold. We compared the thresholds of luminance gratings with the thresholds for isoluminant gratings modulated along the L-M axis. Stimulus contrast was expressed on an absolute RMS-cone-contrast scale. For comparison, the contrasts were also expressed as being multiples of their respective contrast detection threshold. For the measurement of detection thresholds, only one patch was shown, and the observer had to indicate in which of the four possible locations it appeared. We calculated the ratio between the detection thresholds for luminance and isoluminant gratings and multiplied the contrasts of the isoluminant stimuli by this factor. Since thresholds for isoluminant stimuli are generally lower in cone-contrast space, the effect of this normalization was a rightward shift of the isoluminant function. The relative position of both functions is the same as it would be when scaling

the original functions with the respective detection thresholds.

Isoluminance. Stimuli in this experiment were modulated along the luminance axis and along three or four slightly different red-green axes. One corresponded to photometric isoluminance, taking into account Judd's correction. The other two were chosen symmetrically around photometric isoluminance. For these stimuli, the luminance of the most saturated red or green differed from the luminance at the white point by ± 0.8 cd/m². One of them (red darker) corresponded to individual isoluminance for two observers (KL, DU). The fourth axis corresponded to individual isoluminance of the third observer (TR), for whom the luminance of the most saturated red was 0.4 cd/m² darker than at the photometric setting.

Results

The results of three different subjects for the three temporal frequencies are shown in Figs 2-4. Figure 2 shows orientation discrimination thresholds for all three subjects for stationary gratings (0 Hz), Fig. 3 for slowly moving (1 Hz) and Fig. 4 for fast moving (8 Hz) gratings. In each figure the abscissa denotes contrast on an absolute RMS-cone-contrast scale. The ordinate represents the orientation thresholds. For each temporal frequency and subject, detection thresholds are indicated as arrows on the abscissa. In general, orientation thresholds decreased with increasing stimulus contrast. Diamonds show thresholds for red-green stimuli at individual isoluminance. The filled circles denote thresholds for photometric isoluminance, whereas upward and downward pointing triangles indicate thresholds when red was slightly brighter or darker than the neutral white, respectively. The solid lines without markers indicate orientation thresholds for the isoluminant gratings when their contrast is expressed in multiples of detection threshold. For all temporal frequencies, the function relating orientation thresholds to stimulus contrasts was similar for luminance and isoluminant stimuli. Detection thresholds for the different drift rates were similar for different observers. At low temporal frequencies, detection thresholds were lower for isoluminant stimuli, owing to the low-pass characteristic of the isoluminant contrast sensitivity function (Kelly, 1983). At higher temporal frequencies, thresholds for luminance and isoluminant stimuli were almost equal.

For stationary and slowly moving stimuli, thresholds for isoluminant gratings were consistently lower on an RMS cone-contrast scale, as can be seen in Figs 2 and 3. However, when stimulus contrast was expressed as multiples of detection threshold, performance was slightly better for luminance gratings (Figs 2 and 3, solid lines). This contrast normalization procedure leads to a rightward shift of the curves for isoluminant stimuli, since their detection thresholds are lower. The shift is larger for stationary and slowly moving stimuli (1 Hz) because the difference in detection thresholds is higher. This results in a better performance for luminance-

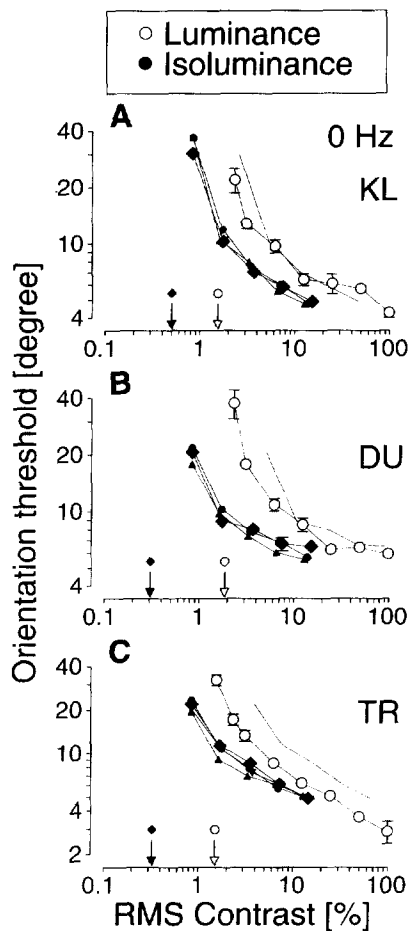


FIGURE 2. Effect of stimulus contrast on orientation thresholds for three subjects. Stimuli were stationary 1 cpd sinusoidal gratings defined by either luminance (open circles) or red-green chromatic contrast (filled symbols). Thresholds have been determined for four slightly different red-green (L-M) axes. Filled circles correspond to photometric isoluminance. Diamonds correspond to the individual isoluminance points for each subject. Two other axes (upward and downward pointing triangles) were chosen symmetrically around photometric isoluminance. In each graph the abscissa denotes stimulus contrast as an absolute RMS-cone-contrast and the ordinate represents orientation thresholds. Arrows on the abscissa represent detection thresholds for luminance (open arrowheads) and isoluminant stimuli (filled arrowheads). Solid lines represent contrast of the isoluminant gratings as multiples of detection threshold. Subjects are identified by their initials in the upper right-hand corner of each graph. Note the different scaling for subject TR.

defined test stimuli than for isoluminant stimuli. However, thresholds for the largest possible luminance and isoluminant contrasts were quite similar for two of our three subjects. Only one subject (TR) had significantly lower thresholds for luminance stimuli.

For fast (8 Hz) moving gratings, thresholds are similar, irrespective of the definition of stimulus contrast (Fig. 4). Only for the lowest stimulus contrasts was performance better for the luminance gratings. The difference in detection thresholds is small and results in a smaller rightward shift of the isoluminant data when contrasts are normalized to detection threshold. At fast drift rates, it does not make much of a difference if contrast is expressed on an absolute RMS-cone-contrast scale or as multiples of detection threshold. Since thresholds once

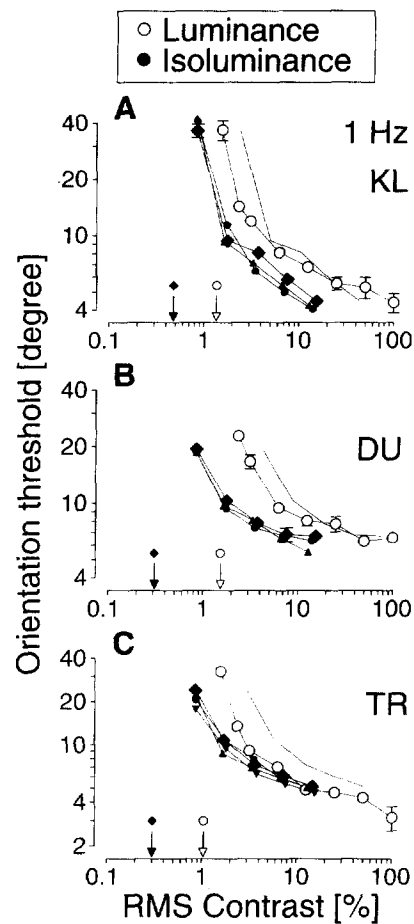


FIGURE 3. Effect of stimulus contrast on orientation thresholds for three subjects. Stimuli were 1 cpd slowly moving (1 Hz) sinusoidal gratings defined by either luminance (open circles) or red-green chromatic contrast (filled symbols). All other details as in Fig. 2.

again decreased with increasing contrast, and since the maximum contrast that we could achieve at isoluminance was approx. one-tenth of the maximum possible luminance contrast, this implies that asymptotic thresholds were lower for luminance gratings under this condition. In none of the conditions did we observe any significant differences for the different settings of isoluminance.

Discussion

Our results are in agreement with previous experiments by Webster *et al.* (1990) and Würger & Morgan (1995). When expressed as multiples of detection thresholds, orientation discrimination thresholds are indeed lower for luminance gratings than for isoluminant gratings, just as Webster *et al.* (1990) found. However, when contrast is expressed as an absolute RMS-cone-contrast, thresholds are equal or lower for isoluminant gratings, which is what Würger & Morgan (1995) found. Overall, thresholds were higher in our experiments than in both of the above-mentioned studies, where subjects had to judge whether a single, foveally presented grating was oriented clockwise or counterclockwise from vertical. In our 4-AFC experiments, the grating patches were slightly off-center (0.75 deg eccentricity), and observers had to integrate

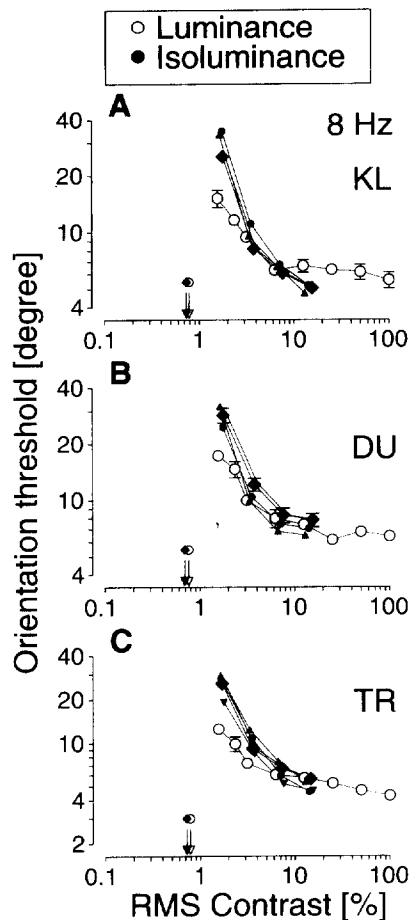


FIGURE 4. Effect of stimulus contrast on orientation thresholds for three subjects. Stimuli were 1 cpd fast moving (8 Hz) sinusoidal gratings defined by either luminance (open circles) or red-green chromatic contrast (filled symbols). All other details as in Fig. 2.

information about four different parafoveal locations in the visual field, rather than compare one foveated grating to an internal standard. This is similar to texture segmentation tasks and the magnitude of the thresholds we obtained is comparable with what other investigators have found in more complex tasks (Nothdurft, 1985; Landy & Bergen, 1991; Foster & Westland, 1995).

One question implied by these results is whether any method for normalizing contrast is better than any other one. The goal in all these normalizing procedures is to achieve an equal signal to noise ratio at the stage in the visual system that is responsible for the task that is being investigated. Using multiples of detection threshold assumes that the signal to noise ratio is equal at detection threshold, and that any other mechanisms receive and use the same signals as the detection mechanism. This might not always be the case, as was pointed out by Krauskopf and Farell (1991). Whereas all stimulus energy can be used for detection, there might be stimulus features that cannot be used for other tasks. In Krauskopf and Farell's (1991) experiment, vernier thresholds for even-symmetric Gabor patches, the mean color or luminance of which differed from the background, were lower for luminance targets than for isoluminant targets, when

contrast was expressed as multiples of detection threshold. This was not the case for odd-symmetric Gabor patches, without a change in mean color or luminance, where thresholds were equal for both types of stimuli. Whereas the change in mean color or luminance can be used for detection, and certainly is used by the low-pass chromatic system, it conveys no useful positional information and therefore cannot be used in the vernier acuity task.

To summarize, there are several assumptions underlying all contrast normalization procedures. If possible, measures for comparing luminance and isoluminance should be used that are independent of contrast. Our further experiments were, therefore, aimed to see whether we could find a qualitative difference in the orientation discrimination of luminance and isoluminant stimuli.

EXPERIMENT 3: "OBLIQUE-EFFECT"

One characteristic of contrast detection and orientation discrimination for luminance stimuli is the "oblique-effect". Thresholds are lowest when stimuli are either horizontally or vertically oriented, and higher for oblique orientations (Campbell, Kulikowski & Levinson, 1966; Kelly, 1975; Caelli *et al.*, 1983; Orban *et al.*, 1984; Regan & Price, 1986; Foster & Westland, 1995). We investigated whether there is an "oblique-effect" for the orientation discrimination of isoluminant gratings and whether this effect is of similar magnitude to the one observed for luminance gratings.

Methods

In this experiment, orientations of the standard gratings were varied clockwise in 30-deg steps (0, 30, 60, 90, 120, 150 deg) and the respective orientation thresholds determined by a staircase procedure. Measurements for all orientations were interleaved. Gratings were stationary. Contrast was 6.25% for luminance stimuli and 7.05% RMS-cone-contrast for isoluminant stimuli. Each observer's individual estimate of isoluminance was used.

Results

The results for two observers are shown in Fig. 5. The abscissa denotes the orientation of the standard stimulus and the ordinate specifies orientation threshold. For the luminance and isoluminant gratings we observed minimal thresholds when standard gratings were aligned with the main visual axes and significant higher thresholds for the oblique orientations. Overall, thresholds were slightly higher in this experiment, since measurements for the different orientations were interleaved. The shape of the functions relating orientation thresholds to standard orientation are similar. Both observers show a 2–4-fold increase in thresholds at the oblique orientations, irrespective of the chromatic content of the stimulus.

Discussion

Our results show a marked "oblique-effect" for the orientation discrimination of isoluminant gratings. Earlier results on detection thresholds were not conclusive.

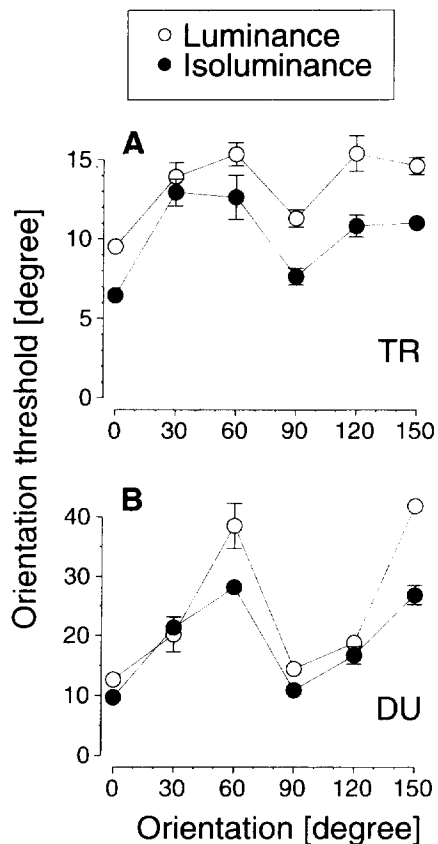


FIGURE 5. Orientation of the standard gratings and its effect on orientation thresholds for two observers. Orientation of the stationary 1 cpd standard grating, defined by 6.25% luminance (open circles) or 7.05% isoluminant contrast (filled circles), varied between 0 and 150 deg. The abscissa denotes orientation of the standard grating and the ordinate represents orientation thresholds. Subjects are identified by their initials in the lower right-hand corner of each graph. Note the different scaling of the ordinate for observer DU.

Kelly (1975) measured detection sensitivity to flickering isoluminant and luminance gratings at two spatial frequencies (6 and 2 cpd) and a range of temporal frequencies. For luminance gratings, the "oblique-effect" was stronger at the higher spatial frequency and present at all temporal frequencies. For isoluminant gratings an "oblique-effect" was present only at the higher spatial frequency at low temporal frequencies (<10 Hz). Kelly attributed this effect to potential luminance intrusions. Murasugi and Cavanagh (1988) found an anisotropy for drifting isoluminant gratings (2 Hz) at high spatial frequencies, but their data suggest that horizontal gratings are detected better than vertical. Generally, the problem is that the "oblique-effect" for detection is pronounced only at high spatial frequencies, where the sensitivity of the color system is lower (Kelly, 1983; Mullen, 1985) and where it is difficult to generate isoluminant stimuli without chromatic aberration (Marimont & Wandell, 1994). The "oblique-effect" reported for orientation discrimination (Foster & Westland, 1995) is much more pronounced than for simple contrast detection. Our data show a marked "oblique-effect" for orientation discrimination at isoluminance, adding to the evidence that orientation perception for luminance and

isoluminant stimuli is done by similar neural mechanisms. Interestingly, Rabin, Switkes, Crognale, Schneck and Adams (1994) recently showed that VEP latency exhibits a clear "oblique-effect" for low spatial frequency (1 cpd) high contrast isoluminant gratings.

EXPERIMENT 4: THRESHOLD CONTOURS

In the previous two experiments, the test stimulus patches differed only in orientation on each trial, except for the differences in phases, which were randomized in all four patches. Therefore, discriminations were based on orientation-selective mechanisms. We were interested in the question of whether differences in other visual attributes could be combined by the visual system with the orientation differences to achieve higher performance. One attribute that is known to have an effect on discrimination is contrast. As shown in Experiment 2, higher contrasts in all four stimulus patches lead to lower orientation discrimination thresholds. Thus, it seems possible that combined differences in contrast and orientation could provide even better performance than the differences in the single attributes. Thomas and Olzak (1990) have shown Euclidean summation between orientation and contrast for luminance gratings. Their conclusions were based on measurements of orientation and contrast discriminability, and the subsequent determination of performance for a single compound stimulus. Instead, we chose to test various combinations of orientation and contrast differences to trace out a complete two-dimensional discrimination contour. Comparing the resulting contours for luminance and isoluminant stimuli provides a further test of whether the processing mechanisms for these two classes of stimuli are qualitatively different.

Methods

Methods were identical to the ones used in Experiment 2, except for the following variations. Standard stimuli were stationary 1 cpd sinewave gratings of vertical orientation and a fixed contrast of 6.25% for luminance stimuli and 7.05% RMS-cone-contrast for isoluminant stimuli. The gratings were chosen to be well above detection threshold and to produce orientation thresholds of similar magnitude. The test stimuli varied simultaneously in orientation and contrast, except for the test directions coinciding with the orientation and contrast axes. We chose eight or ten different test directions, which differed by the proportion of change in orientation and contrast. The sign of the orientation change (clockwise or counterclockwise) was randomly varied from trial to trial. Therefore, only one half of the orientation-contrast plane was measured. Since we were interested in the exact shape of the psychometric function in this experiment, we used a method of constant stimuli. Psychometric functions were obtained by fitting the observed data with a Weibull function:

$$P_c(C) = P_{\text{guess}} + [(1 - P_{\text{guess}})(1 - \exp(-(C/\alpha)^\beta))],$$

where $P_c(C)$ is the probability of obtaining a correct

response when the magnitude of the difference along a particular test direction is C . P_{guess} is the probability of correctly guessing, which was set to 0.25. α and β are parameters identifying the slope and position of the psychometric curve. Threshold was defined as the point where $C = \alpha$, and where as a consequence $P_c(C) = 0.72$. Performances for simultaneous differences in orientation and contrast were compared with the prediction of probability summation from the psychometric functions for contrast and orientation alone. Thereby the predicted proportion correct (not corrected for guessing) due to probability summation for a contrast C and an orientation O is given by the probability of getting either one correct:

$$\begin{aligned} PS(O, C) &= 1 - (1 - P_c(O))(1 - P_c(C)) \\ &= 1 - [\exp(-(O/\alpha_o)^{\beta_o})\exp(-(C/\alpha_c)^{\beta_c})], \end{aligned}$$

where α_o , α_c , β_o and β_c are the parameters of the psychometric functions for contrast and orientation alone. It is not obvious how probability summation would work in such a task, and indeed it would fail if the two channels would signify two different patches as different in a single trial. No mechanism exists to break such ties. However, the same problem arises, for example, in two-interval forced-choice tasks, where the two channels could similarly disagree. A popular way to resolve this problem has been the assumption of high thresholds (see Graham, 1989). It is assumed that a mechanism never gets activated above threshold when a stimulus is not presented. This way a mechanism would never produce a "false alarm" and the problem of ties does not arise.

As an alternative combination rule, we tested whether the threshold contours could be described by a Minkowski-metric. The threshold $T(O, C)$ for an orientation difference O and a contrast difference C is given by:

$$T(O, C) = [O^p + C^p]^{1/p},$$

where the exponent p is characteristic for the particular Minkowski-metric. An exponent of 1 results in simple linear summation, an exponent of 2 indicates a Euclidean summation rule, and very large exponents indicate a city-block summation, where the dimension with the larger difference is chosen. The Euclidean metric is often interpreted as an optimal combination of information under the constraint that the information comes from independent pathways. The resulting discrimination contour in that case is elliptical.

Results

Figure 6 shows psychometric functions for luminance defined stimuli for differences in contrast alone [Fig. 6(A), triangles], and in orientation alone [Fig. 6(B), circles]. The two thin curves show the respective psychometric functions for these two conditions. Performance for the combined contrast and orientation differences (diamonds) are also shown in each graph. The heavy curve shows the prediction of probability summation, taking into account contrast and orientation differences. For the particular test directions shown in

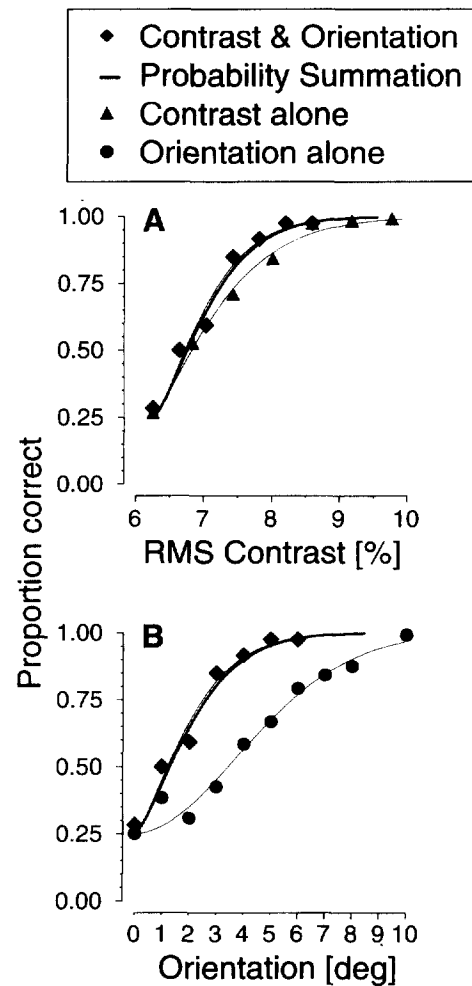


FIGURE 6. Psychometric functions showing the performance of subject TR for luminance-defined test stimuli. The proportions of correct responses are plotted as a function of stimulus contrast (A) and orientation (B). Standard stimuli were vertically oriented 1 cpd sinewave gratings of 6.25% RMS-cone-contrast. Performance for test stimuli varying in contrast (A: triangles) or orientation (B: circles) alone is compared with the performance for test differing simultaneously in contrast and orientation from the standard stimulus (A and B: diamonds). In these combined stimuli the proportional change in contrast and orientation was held constant. In the plane spanned by contrast and orientation this corresponds to a specific direction away from the standard stimulus (see Fig. 8). Performance was better for test stimuli varying simultaneously in contrast and orientation (diamonds) as compared with test stimuli defined by contrast (triangles) or orientation (circles) alone. In addition, the thick lines indicate the predicted performance of the observer for the combined stimuli on the basis of probability summation.

Fig. 6, threshold increments in the orientation direction were balanced by threshold increments in the contrast direction. Figure 7 shows the analogous graphs for isoluminant stimuli.

For both luminance and isoluminant stimuli, the proportion of correct discriminations is higher when both attributes vary than when only one attribute is different. However, performance for the combined differences is well approximated by the prediction from probability summation over the whole range of the psychometric curve. Independent detection of differences in contrast and orientation, followed by a stage that

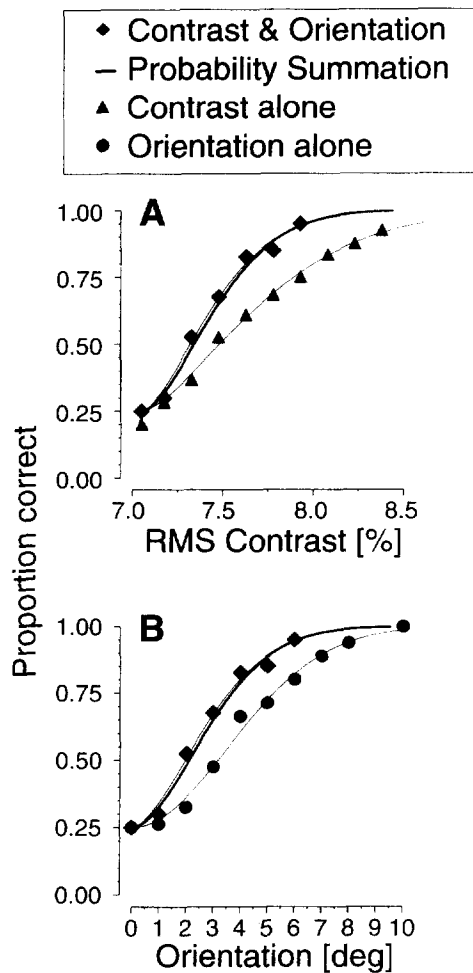


FIGURE 7. Psychometric functions showing the performance of subject TR for isoluminant test stimuli. The proportions of correct responses are plotted as a function of stimulus contrast (A) and orientation (B). Standard stimuli were vertically oriented 1 cpd red-green sinewave gratings of 7.05% RMS-cone-contrast. Performance for test stimuli varying in contrast (A: triangles) or orientation (B: circles) alone is compared with the performance for test differing simultaneously in contrast and orientation (A and B: diamonds) from the standard stimulus. In these combined stimuli the proportional change in contrast and orientation was held constant. In the plane spanned by contrast and orientation this corresponds to a specific direction away from the standard stimulus (see Fig. 8). In addition, the thick lines indicate the predicted performance of the observer for the combined stimuli on the basis of probability summation.

signals a difference when either input channel signals such a difference, can therefore explain the improvement in performance for combinations. Figure 8 shows performance for other weighted combinations of orientation and contrast differences, together with the predictions from probability summation. Over the whole two-dimensional discrimination contour, probability summation predicts performance quite well. Furthermore, a comparison of luminance stimuli [Fig. 8(A)] and isoluminant stimuli [Fig. 8(B)] shows no systematic differences. Both luminance and chromatic orientation discrimination mechanisms follow probability summation rules.

The fits of different Minkowski-metrics to the

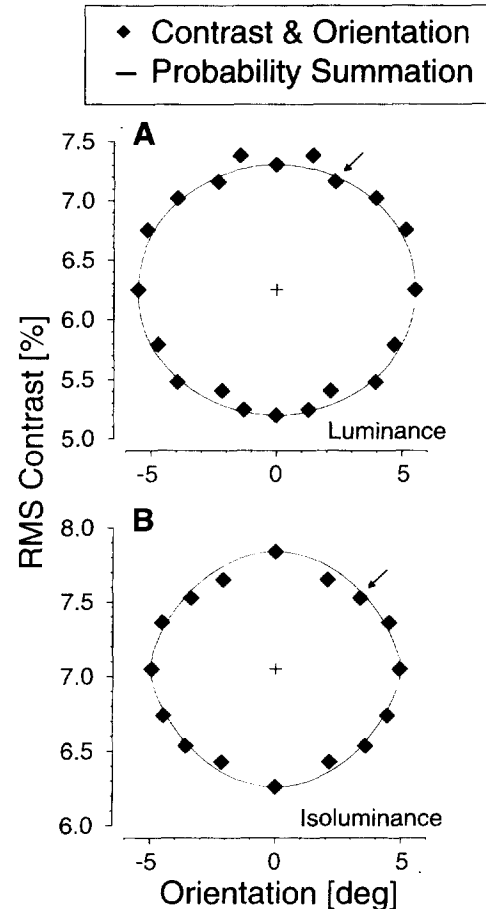


FIGURE 8. Threshold contours showing the performance of observer TR for stimuli varying simultaneously in contrast and orientation, as compared with the standard stimuli. The x -axis denotes changes in orientation and the y -axis represents changes in contrast on an absolute RMS-cone-contrast scale. Results are shown for stimuli defined by luminance (A) and isoluminant (B) contrast. Standard stimuli were vertically oriented 1 cpd sinewave gratings with contrasts of 6.25% for the luminance and 7.05% for the isoluminant gratings. They are indicated by the crosses in the center of each plot. Thresholds for the test stimuli (diamonds) were determined from psychometric functions for different directions away from the standard stimulus. The arrows indicate the thresholds determined from Figs 6 and 7. The solid ellipses represent threshold predictions on the basis of probability summation.

discrimination contours support this analysis. For luminance, the best-fitting exponent was 2.01, indicating Euclidean summation of contrast and orientation differences. For isoluminance, we found a best-fitting exponent of 1.72, which is within measurement error of Euclidean summation, indicating an optimal summation of independent channels coding orientation and contrast. For subject DU, whose data are not shown here, the best-fitting exponents were also close to a value of 2 (2.34 for luminance and 2.19 for isoluminance).

Discussion

Simultaneous differences in orientation and contrast certainly present a more complex challenge to the visual system. Most neurons in primary visual cortex (V1) are selective to the orientation of stimuli (Hubel & Wiesel, 1968), and they are also sensitive to changes in contrast

(Barlow, Kaushal, Hawken & Parker, 1987). However, single neurons in V1 do confound contrast and orientation. Increases in contrast and changes towards the neuron's preferred orientation would both be accompanied by the same increase in neuronal response. Mechanisms allowing simultaneous discrimination of contrast and orientation are therefore most likely situated in higher cortical areas, combining information about contrast and orientation differences from separate populations of neurons. In agreement with Thomas and Olzak (1990) we found Euclidean summation of independent mechanisms for contrast and orientation differences. Our observation of identical summation rules for luminance and isoluminant stimuli strengthens the view that at higher stages these stimuli are processed by analogous mechanisms.

GENERAL DISCUSSION

Our experiments provide evidence that orientation discrimination, an important requirement for form perception, is not impaired under conditions of isoluminance. Furthermore, we did not find any qualitative differences in the processing of orientation differences for luminance and isoluminant stimuli. This is the case for simple orientation discrimination, as well as for complex discrimination of simultaneous differences in orientation and contrast. This finding does not make any statement about whether a single common mechanism processes both luminance and isoluminance, or whether two separate mechanisms have evolved the same processing strategies, based on similar task requirements. However, measurements of orientation-specific adaptation (Bradley, Switkes & De Valois, 1988) and the tilt after-effect (Flanagan, Cavanagh & Eizner Favreau, 1990) have convincingly shown that there are separate mechanisms for luminance and red-green isoluminance. In a similar way, detection mechanisms for luminance and isoluminance were also shown to be independent (Cole, Stromeyer & Kronauer, 1990; Switkes *et al.*, 1988; Gegenfurtner & Kiper, 1992; Mullen & Losada, 1994).

The results of our first experiment show quite clearly that even the most sensitive chromatic mechanisms can make orientation discriminations for low spatial frequency targets. Thresholds for detection and coarse horizontal vs vertical orientation discriminations were identical in all directions of the plane in color space spanned by L- and M-cones. Furthermore, the contours make it quite clear that the sensitivity to chromatic contrast is much higher than to luminance contrast for such low spatial frequency stationary stimuli, suggesting that most coarse orientation judgments at a low spatial scale are made by a color-opponent mechanism.

The results of Experiment 2 confirm previous findings by Webster *et al.* (1990) and Würger and Morgan (1995). For stationary or slowly moving gratings, orientation discrimination thresholds for isoluminant gratings were equal or lower than thresholds for luminance gratings, when contrast was expressed on an absolute cone-contrast scale. Due to the high sensitivity for detection

of chromatic patterns, when contrast was expressed as multiples of detection thresholds, the orientation discrimination thresholds were slightly higher for isoluminant gratings. This agrees with earlier results by Webster *et al.* (1990) and is probably due to a larger orientation bandwidth at isoluminance (Bradley *et al.*, 1988).

Of course all our claims are valid only for the low spatial frequencies we have investigated here (1 cpd). At higher spatial frequencies, above 4 cpd, chromatic aberration might play an important role. As pointed out by Marimont and Wandell (1994) and by Flitcroft (1989), the chromatic part of such stimuli is already severely attenuated on the retina. This makes it very difficult first of all to investigate responses to such stimuli without introducing chromatic aberration artifacts (but see Mullen, 1985; Williams, Sekiguchi & Brainard, 1993). But, more importantly, it would contradict certain optimality principles if the human brain would have high sensitivity to stimuli that it never has to face in the environment. In fact, results by Würger and Morgan (1995) indicate that orientation discrimination for isoluminant stimuli becomes worse relative to luminance stimuli as spatial frequency increases.

Since all absolute comparisons of luminance and isoluminant stimuli are based on strong assumptions about the underlying mechanisms, we rather chose to investigate in more detail qualitative characteristics of the underlying processing mechanisms. The "oblique-effect" reported for luminance-defined stimuli is such a characteristic. Orientation discrimination for the main visual axes (vertical and horizontal) is remarkably higher than that for the oblique axes (Westheimer, 1979). The resulting meridional anisotropy has been described in detail by many investigators (Caelli *et al.*, 1983; Orban *et al.*, 1984; Regan & Price, 1986; Heeley & Timney, 1988). The basis of this effect is not yet clear, even though physiological experiments revealed a relative under-representation of neurons in monkey visual cortex tuned to oblique orientations (Mansfield, 1974; Mansfield & Ronner, 1978). On the other hand, Heeley and Timney (1988) pointed out that if this were the case, other high precision tasks in the spatial domain would be affected. They showed that orientation bandwidths and sampling density of the differently tuned orientation filters is the same for all directions. Further mechanisms have been proposed for this effect, namely the influence of external information input from body posture or vestibular information that act in concordance with the main visual axes and lower orientation thresholds (Heeley & Buchanan-Smith, 1990). In all these experiments luminance-defined stimuli have been used, except for Kelly (1975), who presented evidence that detection of isoluminant stimuli does not exhibit the "oblique-effect". Our results show a strong "oblique-effect" for orientation discrimination of isoluminant gratings, and the effect is of the same order of magnitude as for luminance gratings (Fig. 5). The difference in results is probably caused by different task requirements. In detection tasks, such as used by Kelly (1975), the

“oblique-effect” is pronounced only under conditions of high spatial frequencies, to which the chromatic system is not very sensitive. A larger “oblique-effect” can be seen in orientation discrimination (Foster & Westland, 1995). In our data the magnitude of the effect is comparable for luminance and isoluminant stimuli, supporting the notion of identical processing strategies for both types of stimuli.

The results of our fourth experiment, using stimuli varying in contrast and orientation simultaneously, agree with this notion. We found evidence for probability summation of contrast and orientation differences, irrespective of whether stimuli were defined by chromatic or by luminance contrast. Probability summation in this case accounted not only for threshold performance, but also for the slopes of the psychometric functions for the combined orientation-contrast stimuli. Probability summation is in agreement with a model that postulates initial independent detection of orientation and contrast differences, which are then combined statistically at a later stage (see Graham, 1989). This is an efficient way to improve discrimination behavior. If information from the chromatic channel was regarded as less salient for the visual system, we would expect this stimulus aspect to be de-emphasized, and discrimination contours to be different.

Rivest and Cavanagh (1996) had previously found summation of different visual attributes for localizing a contour. They combined up to three stimulus attributes (luminance, texture and color) and showed that precision of contour localization increases when the test contour is defined by two or more stimulus attributes in comparison with test contours defined by only one attribute. They concluded that the different stimulus attributes are equally weighted by the visual system to increase the precision of localization. Their localization task does not lend itself to an analysis in terms of probability summation in any straightforward way. However, they successfully predicted combined performance using a model statistically summing the uncertainties from several independent channels. This is similar to the optimal combination of independent channels that fits our data well.

In conclusion, our results present strong evidence that, at least for low spatial frequencies, the same processing strategies for orientation discrimination are employed by the luminance and chromatic channels.

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Acknowledgements—We would like to thank Patrick Cavanagh for critically reviewing this article and making numerous helpful suggestions. We are grateful to Mike Hawken and John Krauskopf for valuable discussions, and to Doris Braun and Ted Sharpe for comments on an earlier version of this manuscript. KRG was supported by a Habilitationsstipendium from the German Research Council (DFG Ge 879/2-1).