Bestelldat: 23-10-2003-16:49
Bestell-Nr: 2003102304116

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Kunden-/Zugangsnummer
STD03X14309

Verfasser: Gegenfurtner, K. & Kiper, D.
(Aufsatz)
Titel: Contrast detection in luminance and chromatic noise
(Aufsatz)
Seiten: 1880-1888
Titel (Monographie/Zeitschrift)
Journal of the Optical Society of America / A
Washington, DC
Soc.
1084-7529/n

Standort:
ZB 59499 / BBP ZB 59499

Band/ Heft **Jahrgang**
9/ 1992

Lieferform: PDF
Lieferart: E-Mail

Bemerkungen:

Einzelrechnung
Rechnungsanschrift
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LIEFERSCHEIN

Abrechnung über Subito-Zentralregulierung

Lieferbibliothek: BBPhysik / SUB Göttingen
Bearbeitungsdatum: 24.10.03

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Contrast detection in luminance and chromatic noise

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Received September 3, 1991; revised manuscript received May 19, 1992; accepted May 22, 1992

We measured detection thresholds for a vertically oriented 1.2-cycle-per-degree sine-wave grating embedded in spatiotemporal broadband noise. Noise and signal were modulated in different directions in color space around an equal-energy white point. When signal and noise were modulated in the same direction, we observed a linear relationship between noise spectral density and signal energy at threshold. The slope of this function was the same whether the modulation was along a luminance axis or a red–green axis. If the signal was on one axis and the noise was on the other, no masking was observed. These results support the notion of two independent and equally efficient mechanisms tuned to these directions. We then measured threshold elevations for masks with both chromatic and luminance components. When signal and noise were modulated along the same line (for example, bright red and dark green), thresholds were elevated. When we inverted the phase of the chromatic component of the noise relative to the luminance component (bright green and dark red), the masking effect disappeared, even though the amount of noise in the putative luminance and chromatic mechanisms was exactly the same as before. This implies that detection performance is limited by mechanisms sensitive to both luminance and chromatic contrast signals. We characterized these mechanisms by their spectral tuning curves.

1. INTRODUCTION

Since Hering,[1] the idea has been entertained that luminance and chromatic signals travel along at least partially different pathways. This idea received support from anatomical and physiological findings, but there is still much controversy about the extent to which these pathways are nonoverlapping and independent. In this paper we examine the issues of independence and overlap between the two pathways as well as that of the efficiency with which luminance and chromatic information is treated in the visual system.

When the physiological and anatomical evidence for two distinct pathways in the visual system became available,[2–4] it was a natural tendency to test the hypothesis that each pathway is devoted to one of the two types of signal.[5–7] The focus on these two parallel pathways originates in the discovery of the cellular layers of the lateral geniculate nucleus (LGN) in Old World primates. The four dorsal layers contain small cells and are called the parvocellular (P) layers. The two remaining layers are composed of larger neurons and are called the magnocellular (M) layers. There is now considerable evidence that the cells in the P and M layers are driven by different classes of retinal ganglion cells[2–4] and that their outputs remain at least partially segregated at later stages of the visual pathways.[8,9]

The cells in these two types of layer in the LGN differ in several of their physiological properties.[9,10] Cells in the P layers have higher spatial and lower temporal resolutions for luminance variations than those in the M layers. M cells have considerably higher contrast sensitivity and gain than the P cells. In addition to these differences in their responses to purely luminance stimuli, M and P cells also show important differences in their processing of chromatic information. Most neurons in the P layers are color opponent, meaning that their responses to stimuli covering their whole receptive fields are excitatory for a range of wavelengths and inhibitory for another range of wavelengths. On the other hand, magnocellular neurons are typically described as broadband, since the sign of their responses does not vary for a wide range of wavelengths.[11,12] Note, however, that not all the magnocellular neurons are broadband, since approximately half of them show color opponency under certain stimulus conditions.[9]

Because of the differences between these two classes of cells in their responses to chromatic stimuli, the P pathway is often considered to be the color pathway, while the M pathway is described as the luminance pathway. If luminance and chromatic stimuli are processed in these two separate pathways, the results of psychophysical experiments using stimuli that preferentially excite one or the other will reflect the characteristics of that pathway. Therefore any observed difference between the pathway characteristics revealed in experiments using equiluminant chromatic stimuli and those revealed by pure luminance stimuli would support the notion of two separate pathways. Moreover, if there are two separate pathways, there should be no interactions between the processing of luminance and chromatic information.

However, the anatomical and physiological distinction between luminance and chromatic pathways is challenged by several well-documented results. First, it is well established that the P cells respond to both chromatic and luminance signals,[9] thereby providing a possible common physiological substrate for the processing of these two types of information. Moreover, the results of Lennie *et al.*[13] indicate that most cells in the primary visual cortex carry both luminance and chromatic signals. Finally, several psychophysical experiments[9] suggest the presence

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of interactions between luminance and chromatic signals. These results suggest that a double-duty pathway may well exist that carries both luminance and chromatic signals.

To address these issues, a large variety of recent experiments tried to measure the relative performance of the visual system for chromatic and luminance stimuli. These experiments include contrast discrimination,[14,15] vernier acuity,[16,17] orientation and spatial-frequency discrimination,[18] texture segregation,[19] and motion perception.[20] To compare performance between the two systems, one must equate chromatic and luminance inputs. Experimenters often measure contrast-detection thresholds and use this measure as a basic unit. Thresholds in other tasks are then specified as multiples of detection threshold. This assumes that the observer's signal-to-noise ratio is the same for all stimuli (luminance or chromatic) at detection threshold and at equal multiples of threshold.

Using the above approach, Morgan and Aiba[16] and Krauskopf and Farell[17] showed that vernier acuity was significantly better for luminance stimuli when lines or blurred lines were used. However, Krauskopf and Farell also showed that performance of the two systems could be equated for stimuli without a dc component. They explained this result by the differences in contrast sensitivity to chromatic and luminance stimuli. The luminance contrast-sensitivity function is bandpass, while the chromatic contrast-sensitivity function is low pass.[21,22] Therefore thresholds for the detection of chromatic stimuli containing a dc component will be low relative to the thresholds for luminance stimuli. However, the dc component does not contain any positional information and is therefore irrelevant for the vernier task. When we scale by detection threshold, performance will be worse for chromatic stimuli, simply because the chromatic-detection threshold is lower.

Rather than scaling by detection threshold, one should instead equate the cone contrasts for chromatic and luminance stimuli, because this does not make assumptions about the relationship between detection and the task for which performance is evaluated. However, some assumptions are required if one is to compute a single contrast measure from the three individual cone contrasts. Whereas the contrast for a luminance pattern is the same in the three classes of cones, the situation is different for chromatic stimuli. The excitation of the long-wavelength-sensitive (L) cones is approximately twice as large as the excitation of the middle-wavelength-sensitive (M) cones for a neutral (white) adapting light. For stimuli to be isoluminant, the sum of M- and L-cone excitation must be constant; therefore any increment in the M cones (δM) must be offset by an equally large decrement in the L cones ($-\delta L$), and vice versa. Therefore the contrasts in the individual classes of cones ($\delta M/M$ and $\delta L/L$) will be different for lights in the equiluminant plane, unless $L = M$ for the adapting light, which is generally not the case.

The second question raised in this paper, which concerns interactions between the two systems, is easier to resolve, because the problem of comparing both input contrasts does not arise. The results do vary from task to task. Using a habituation paradigm, Krauskopf *et al.*[23,24] did not find any interactions between the chromatic and luminance systems. On the other hand, Cole *et al.*[15] did find interactions in a color-discrimination experiment. Luminance pedestals of up to two times detection threshold facilitated detection of chromatic tests, and vice versa. For pedestals above that level, thresholds were constant. Similarly, Switkes *et al.*[14] reported facilitation effects for a similar range of pedestal contrasts. In addition, they reported masking of luminance signals by suprathreshold chromatic pedestals but no masking of chromatic signals by luminance pedestals.

To address these two questions, we used the combination of noise masking and ideal-observer-analysis introduced by Pelli.[25] This method measures the efficiency of the visual system for detecting a sine-wave signal in spatiotemporal broadband noise independently of any internal or external scaling of the input. It is therefore suitable for avoidance of the comparison problems described above. By varying the spectral composition of signal and noise independently, we could test for interactions in the processing of luminance and chromatic stimuli. In addition to testing in the pure luminance and pure chromatic directions, we measured performance for stimuli with various combinations of luminance and chromatic components.

2. METHODS

A. Equipment

We used an Adage 3000 raster display processor to generate lights on a Tektronix 690SR color monitor. The monitor extended 27.5 cm vertically and 37 cm horizontally. The display was refreshed at a rate of 120 Hz interlaced. The experiment was controlled by a computer program running on the Adage 68000 processor. We used the three Adage 10-bit color lookup tables to correct for nonlinearities in the voltage versus intensity function. The CIE 1931 (x, y) coordinates of the three monitor phosphors were measured with a Photo Research PR 703A spectrophotometer and were (0.66, 0.32), (0.31, 0.59), and (0.15, 0.06) for red, green, and blue, respectively. The phosphor luminances were measured with a UDT photometer. The mean luminance of the screen was 37 cd/m^2. The stimulus patterns were constrained to a 256×256 pixel square in the center of the screen. At the viewing distance of 160 cm this amounted to 5° of visual angle. The stimuli were surrounded by a white field that extended 10° of visual angle and whose luminance matched the space–time-averaged mean luminance of our stimuli. The display was viewed binocularly through natural pupils in an otherwise dark room.

B. Subjects

We collected data from four subjects. Observer KG (one of the authors) ran all the experiments. Data from observers AB, LS, and DK (the other author) were obtained for some of the experiments. All the observers had normal color vision and normal or corrected-to-normal visual acuity.

C. Description of Lights

We use a subspace of the cardinal direction space introduced by Krauskopf *et al.*[23] to describe our stimuli. Figure 1 shows a schematic diagram of the space. It is a linear transformation of the space of photoreceptor quantum catches. At the origin is an equal-energy white point with CIE (x, y) values of (0.32, 0.33). The space is defined by two axes that go through the white point. The chro-

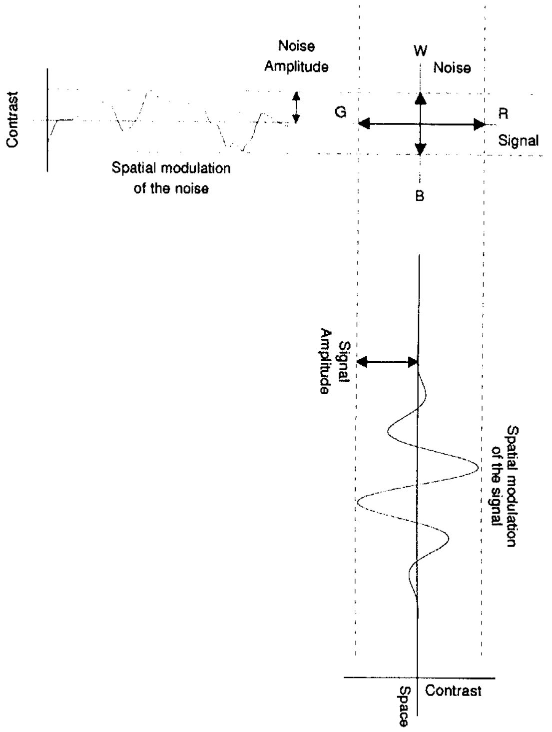


Fig. 1. Spectral and spatial properties of our stimuli. We specify the color of the stimuli by using the color space in the upper right-hand corner. At its origin is an equal-energy white. The luminance axis stretches from black (B) to white (W). The chromatic axis has red (R) and green (G) at its end points. The signal was a sine wave modulated symmetrically around the white point. It was also multiplied by a Gaussian function of space and time. The noise pixels were chosen from a uniform distribution of colors along a line symmetric around the white point.

matic axis goes from a red of (0.41, 0.29) to a green of (0.23, 0.38). Along that axis the excitations of the L and M cones (computed according to Smith and Pokorny[26]) are varied in such a way that their sum remains constant. Only their relative excitations change. For changes along the other axis, the luminance of the lights is varied. To increase the luminance, we add white; to decrease it, we subtract white. The scaling of both axes relative to each other is arbitrary. It is important to note that the results presented in Section 3 below do not depend in any way on the choice of scale factor.

D. Stimuli

On every trial the stimulus appeared in the middle of the screen. It consisted of a signal and a noise component. We added signal and noise by interleaving alternate frames on the monitor, thus reducing the effective refresh rate to 60 Hz. The spatial, temporal, and chromatic properties of signal and noise could be varied independently. The schematic diagram in Fig. 1 illustrates the spatial properties of the stimuli.

The signal was a three-dimensional Gabor patch. It consisted of a vertically oriented sine wave that was modulated between two colors D^+ and D^- chosen to lie symmetrically around the origin (white point) of the color space. The sine wave was vignetted by a three-dimensional Gaussian. The signal S is defined by

$$S(x, y, t) = G\left(\frac{x}{\sigma_x}\right)G\left(\frac{y}{\sigma_y}\right)G\left(\frac{t}{\sigma_t}\right)C_S \sin(\omega_x x)D^+, \qquad (1)$$

where $G(z)$ is the one-dimensional Gaussian probability-density function

$$G(z) = (2\pi)^{-1/2} \exp(-z^2/2) \qquad (2)$$

and C_S specifies the contrast of the signal. For luminance signals, D^+ was a white color at twice the luminance of the white point, and the resulting contrast measure is equivalent to the Michelson contrast. For targets modulated along the chromatic axis only, D^+ was arbitrarily chosen to be the largest excursion in the red direction that we could produce on our monitor. Because of the frame interleave we could produce contrasts only between 0 and 0.5. The energy (i.e., variance) of S is proportional to the square of the contrast C_S.

We used a value of 1.2 cycles per degree (cpd) for ω_x in all the experiments. Several control experiments run at other spatial frequencies indicated no significant influence of spatial frequency over a range of frequencies from 1 to 4 cpd. The space constants σ_x and σ_y of the Gaussian were both set to 0.8° visual angle, and the time constant σ_t was 170 ms.

The noise was three-dimensional spatiotemporal broadband noise. The color of the noise pixels was drawn from a uniform distribution along a line in color space. The end points of the line, $C_N D^+$ and $C_N D^-$, were chosen to be symmetric around the white point. C_N specifies the maximum noise contrast. In addition, the noise pixels were scaled so that the average color, computed for each noise frame and over the whole field, was equal to the white adapting field presented between stimulus presentations. The noise spectrum was flat up to a spatial frequency of 12 cpd and a temporal frequency of 15 Hz. Because the noise intensities followed a uniform distribution, the noise energy was proportional to the square of the contrast ($\sigma^2 = \frac{1}{3}C_N^2$ for a uniform distribution).

E. Procedure

Each trial consisted of two intervals marked by a tone. In one of the intervals, randomly chosen, only the noise pattern was presented. The other interval contained the sum of the signal and noise patterns. The observer's task was to indicate which interval contained the signal. Audible feedback was given to indicate incorrect responses. For each noise level we first measured a preliminary threshold, using a binary search procedure. These preliminary thresholds were used as the starting values for two interleaved staircases. Staircases for the different noise levels were also interleaved. An incorrect response led to an increase of the signal contrast on the next trial, and a series of three correct responses led to a decrease. The staircase thus converged to a level where the probability of a correct response was 0.79. After six reversals were reached for each staircase, the mean of the turning points was used as a threshold estimate.

3. RESULTS

A. Signal and Noise on the Same Axis

When both signal and noise vary on the luminance axis, a linear relationship between signal energy at threshold and

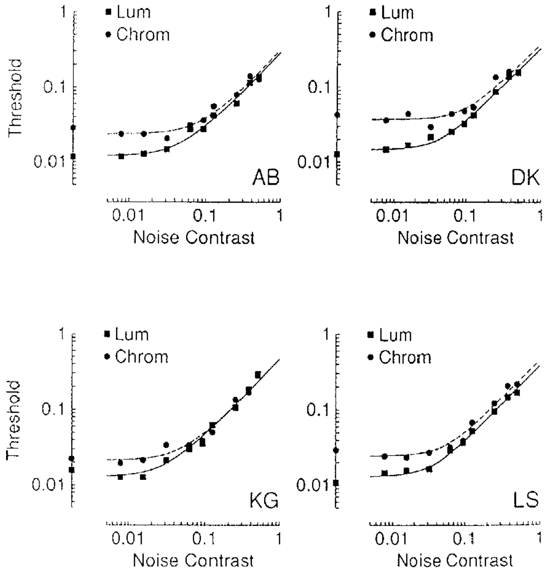


Fig. 2. Signal contrast at threshold plotted as a function of noise contrast on log axes. Signal and noise vary on the same line in color space. The circles are for chromatic signal and noise, and the squares are for luminance signal and noise. The solid curves show the best-fitting curve [Eq. (4)] for luminance signal and noise, and the dashed curves show the same for chromatic signal and noise. The parameters are given in Table 1.

noise energy is observed. This relationship was described in detail by Pelli[25] and Legge *et al.*[27] The square symbols in Fig. 2 show the data. If we denote signal energy at threshold by E_t and noise energy by N, then

$$E_t = E_{\text{intr}} + kN, \tag{3}$$

where E_{intr} is the signal energy necessary for detection when no noise is added externally. We assume that the noise internal to the visual system (often referred to as intrinsic noise) limits performance in this case. Taking logs on both sides results in

$$\log(E_t) = \log(E_{\text{intr}} + kN). \tag{4}$$

When the external noise is small relative to the intrinsic noise, the second term on the right-hand side of Eq. (4) becomes negligible, and threshold is constant. This is described by the horizontal parts of the curves in Fig. 2. As the external noise becomes larger, the second term of Eq. (4) dominates E_t:

$$\log(E_t) = \log(k) + \log(N). \tag{5}$$

We observe a diagonal line of slope 1 and intercept log(k). At the point where the two lines intersect, the internal noise and the external noise have the same effect on threshold. The threshold at that point is therefore twice the threshold with the internal noise alone. The amount of external noise necessary to achieve this is called equivalent noise (N_{eq}), because it is equivalent to the noise internal to the system.

It is not surprising that thresholds in our task increase when we increase the amplitude of the noise. The task becomes harder. Ideal-observer analysis is a way to specify how much of a given change in threshold can be attributed to the change in the difficulty of the task. An observer is defined to be ideal if its decision is based on the ratio of the likelihood of the stimulus given signal and noise to the likelihood of the stimulus given noise alone, or on a monotone function of this likelihood ratio. Green and Swets[28] computed the ideal observer for the detection of a sine-wave signal with known amplitude and phase in broadband noise. They showed that performance d' for a cross correlator at a certain criterion for detectability is given by

$$d' = (E_t/N)^{1/2}, \tag{6}$$

the signal-to-noise ratio of the input. Because $N_{\text{eq}} = 0$ for the ideal observer, it follows that the constant k in Eq. (4) is equal to d'^2. We can now define the sampling efficiency J for a human observer as the ratio of the ideal observer's level of performance at a certain signal-to-noise ratio to the human observer's, which is given by k from Eq. (4):

$$J = d'^2/k. \tag{7}$$

We were not concerned with the absolute level of performance and therefore did not compute J. Our goal was to compare the efficiency for processing luminance and chromatic stimuli. Because signal and noise were the same except for a change in direction in color space, d'^2 for the ideal observer was the same for both kinds of stimulus. Therefore we could directly compare values of k for the different stimuli without computing d' for the ideal observer.

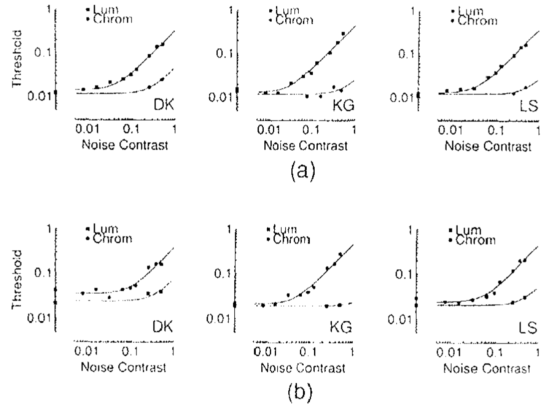
The circles in Fig. 2 show results for signal and noise varying along the chromatic axis. We observed a curve similar to the luminance data, illustrating the linearity of the relationship between signal energy at threshold and noise energy. As we mentioned in Subsection 2.C above, the scaling of the chromatic contrast is arbitrary. It is important to note that, because the efficiency parameter is a unitless quantity, this scaling factor does not have any effect on the lateral position of the diagonal line. This permitted us to compare the data for the two conditions directly. Even though the absolute thresholds cannot be compared, Fig. 2 shows that the limiting performance for large noise contrasts was the same.

The solid and dashed curves in Fig. 2 show the best fit of the linear model given in Eq. (3). Because the variances at each point were approximately equal on a logarithmic scale, we fitted Eq. (4) directly to the data, rather than the simpler linear regression of Eq. (3). Table 1 summarizes the parameter estimates. C_t estimates the contrast threshold in the absence of noise. It is proportional to the square root of the observer's intrinsic noise E_{intr}. For subject KG the efficiency was equal for luminance and chromatic stimuli. For the other subjects there

Table 1. Best-Fitting Parameters from Eq. (3)[a]

	Luminance		Chromatic	
Observer	C_t	k	C_t	k
AB	0.012	0.083	0.023	0.098
DK	0.014	0.113	0.037	0.147
KG	0.013	0.216	0.021	0.212
LS	0.013	0.143	0.024	0.203

[a] C_t gives the estimate of the observer's contrast threshold, which is proportional to the square root of the observer's intrinsic noise E_{intr}. k is inversely proportional to the efficiency of the observer.



(a)

(b)

Fig. 3. (a) Thresholds for detecting a luminance signal in chromatic noise (circles) or luminance noise (squares). (b) Thresholds for detecting a chromatic signal in chromatic noise (circles) or luminance noise (squares).

was an advantage of luminance over chromatic stimuli, but this difference was small.

We therefore conclude from our data that the visual system is equally efficient in detecting chromatic and luminance signals in these experiments.

B. Interactions between Luminance and Chromatic Mechanisms

The directions in color space that we chose for the above experiments were motivated by the habituation experiments of Krauskopf *et al.*[23] They measured detection thresholds for temporal modulations of a uniform 2° field after exposure to a sinusoidal temporal modulation of the field. The habituation color and the signal color were chosen independently to be on either the luminance axis or one of the two chromatic axes of cardinal direction space. Habituation along one axis did not change the thresholds for stimuli along the other axes, whereas it elevated thresholds for stimuli along the same axis. Little selective habituation was found for intermediate directions in color space. For example, thresholds for luminance stimuli depended mostly on the luminance component of the habituation stimulus and were independent of the chromatic component. Their results strongly support the idea that detection is mediated by three independent mechanisms, each tuned to one of the cardinal directions.

In order to examine whether the cardinal directions show independence in our paradigm, we selected signal and noise to be in different cardinal directions. The circles in Fig. 3(a) show the results for a luminance signal and chromatic noise. The thresholds remained constant for all the noise contrasts. For comparison the effects of luminance noise on the detection of the luminance signal are shown by the squares. These are the same data as those in Fig. 2. The squares in Fig. 3(b) show thresholds for the detection of a chromatic signal at different levels of luminance noise. Again there is little elevation of threshold with an increase in noise energy. The leftmost data pair of each graph was measured in the absence of noise. Because the physical stimuli were identical, thresholds should be the same in both cases. Any difference between them is the result of day-to-day variation in threshold. This result confirms the results of Krauskopf *et al.*[23] and is consistent with the notion that mechanisms in the cardinal directions are independent.

C. Intermediate Directions

While the above results are consistent with the notion of independent mechanisms tuned to the cardinal directions of color space, they do not permit us to determine whether there exist additional mechanisms tuned to other directions. Our next experiment was designed to test this hypothesis. We used stimuli that contain both luminance and chromatic information, such as a signal made of bright red and dark green stripes and a noise made of bright red and dark green dots. These stimuli simultaneously excite the luminance and chromatic mechanisms. The square symbols in Fig. 4 show the results for signal and noise made of bright red and dark green elements. The masking function is similar to those shown in Fig. 2 above: noise of sufficient energy increased the detection thresholds for the signal.

The diagram in Fig. 5(a) shows that this is what the two-mechanism hypothesis would predict. Both the chromatic and the luminance channels are excited by the signal and the noise. Thus the mechanisms that mediate the detection of the signal in this case, whether it be the luminance, the chromatic, or a combination of the two mecha-

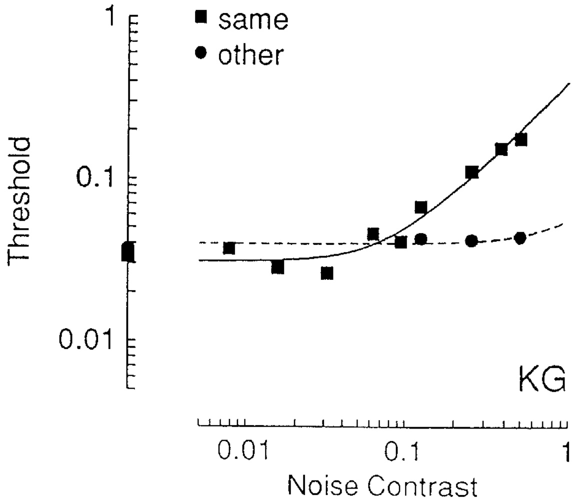
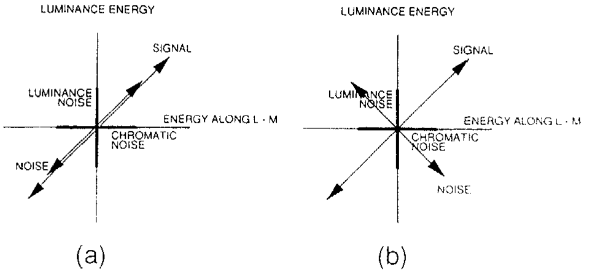


Fig. 4. Thresholds for detecting a signal consisting of bright red and dark green components. The mask had either bright red and dark green components (squares) or bright green and dark red components (circles).



(a)

(b)

Fig. 5. (a) Signal and noise vary along the same line in color space. The noise in the assumed luminance and chromatic mechanisms is also identical. (b) Signal and noise are on different diagonals. The amount of noise in the assumed luminance and chromatic mechanisms is still the same.

nisms, will also be affected by the noise and show elevated thresholds for high noise contrasts.

Figure 5(b) shows another stimulus that would excite these two mechanisms in exactly the same way. If the signal is left unchanged (bright red and dark green stripes) and the noise is made of bright green and dark red dots, the noise energy for both luminance and chromatic mechanisms is the same as that above [Fig. 5(b)]. The outputs of the putative luminance and chromatic mechanisms are not affected by the change in the polarity of the noise. Therefore, if these are the only mechanisms present, we should observe the same masking effect in the two stimulus conditions outlined in Fig. 5. If there exist other mechanisms, we predict a different result: when signal and noise lie in different directions, mechanisms tuned to the direction of the signal will be able to mediate detection but will be less or even not at all affected by the noise. In that case we should observe a decrease or a total disappearance of the masking.

The results are indicated by the circles in Fig. 4. There was no masking for the condition in which signal and noise were in different directions. The bright green and dark red dots did not mask the bright red and dark green stripes. A performance difference under these conditions cannot be accounted for by the luminance and chromatic mechanisms alone. We found the same results when the polarity of signal and noise was reversed. Therefore we conclude that more than the luminance and chromatic red–green mechanisms are involved in this detection task.

While our first two experiments confirmed the existence of two independent mechanisms tuned to the cardinal directions described by Krauskopf *et al.*,[23] this last result demonstrates that performance in this task not only is limited by the putative luminance and chromatic mechanisms but involves mechanisms that combine luminance and chromatic information.

D. Chromatic Tuning Curves

Our next step was to characterize the sensitivity of the mechanisms revealed in the above experiments to stimuli in different directions of color space. In those experiments we observed that thresholds for detecting luminance signals increased when we added noise in the luminance direction. The mechanism underlying detection in that case is therefore highly sensitive to luminance stimuli. On the other hand, noise varying along the purely chromatic direction hardly affected its threshold. Therefore the detecting mechanism is not especially sensitive to chromatic noise. We can now generalize this procedure and use noise in several directions of color space to measure the sensitivity of a mechanism in these directions. If we repeat these measurements for a given signal and a variety of different noise directions, we can specify the chromatic tuning curve for any mechanism. This will give us an idea of how many mechanisms there are, how narrowly or widely tuned they are, and whether there are interactions between different mechanisms.

In each experimental session the direction of the signal was held constant and different noise directions were interleaved in separate staircases. Once again we measured the signal contrast necessary to make the signal just detectable in the noise. The noise vectors were chosen to be of equal length according to a scaling determined by the detection thresholds for the signal in the absence of noise. Note, however, that this arbitrarily chosen scaling does not affect the tuning curves as long as the noise vectors are of equal length in the chosen space. For example, for subject KG the thresholds for detecting the luminance signal were approximately 75% as high as the thresholds for detecting the chromatic signal. Therefore the contrast was set at 28% for the luminance noise and at 38% for the chromatic noise, reflecting the same ratio. This led to a threshold elevation by a factor of approximately 8 in both directions.

Figure 6(a) shows the results for the signal in the luminance direction. The thick, straight lines illustrate the signal used in this particular experiment. The filled circles indicate the measured thresholds. The angle that each data point forms with the abscissa represents the direction of the noise vector in color space. The distance from the origin indicates the signal contrast necessary to make the signal just visible in the noise. Because both signal and noise were symmetric modulations around the white point, each data point is shown twice in the graph, reflected around the origin. To facilitate comparisons among the graphs, we scaled them so that the maximum threshold was of unit value. The small circle in the middle of each graph represents the detection threshold for the signal in the absence of noise. Thresholds for noise orthogonal to the signal are close to the unmasked thresholds, confirming our result above that chromatic noise does not mask luminance signals.

Figure 6 shows the results for different signals. In all the graphs the largest masking is for a noise in a direction close to the signal. In general, we would expect the masking to be largest in the direction to which the mechanism responsible for detection is most sensitive. This direction is not necessarily the direction arbitrarily chosen by us as our signal. We performed experiments using signals other than the ones shown in Fig. 6, for example, bright green and dark red stripes. The tuning curves were similar to the ones shown in Fig. 6, in that the tuning appeared narrow and the masking was largest in a direction close to the signal. This suggests that there may be more than the three mechanisms revealed in Fig. 6.

If the mechanism responses were strictly proportional to the stimulus energy, they should vary in proportion to the cosine of the angle between the noise vector and the direction to which the mechanism is tuned. Thus, as long as we chose our noise vectors to be of equal length in a given space, the threshold elevation should be proportional to that cosine. The curves in Fig. 6 show the predictions. Note that, because these graphs plot signal contrast as opposed to signal energy, the cosine-rule predictions do not appear as circles. All the data points fell within the predicted curves. This means that the threshold elevations were smaller than expected. Since we know from our experiments above that the mechanisms are linear with respect to noise energy, it is likely that these results are due to interactions between neighboring mechanisms rather than to nonlinearities in the individual mechanisms.

To summarize, there seems to be a multitude of mechanisms tuned to different directions in color space. Their tuning is narrower than expected from a model based on independent linear mechanisms. Because we have already

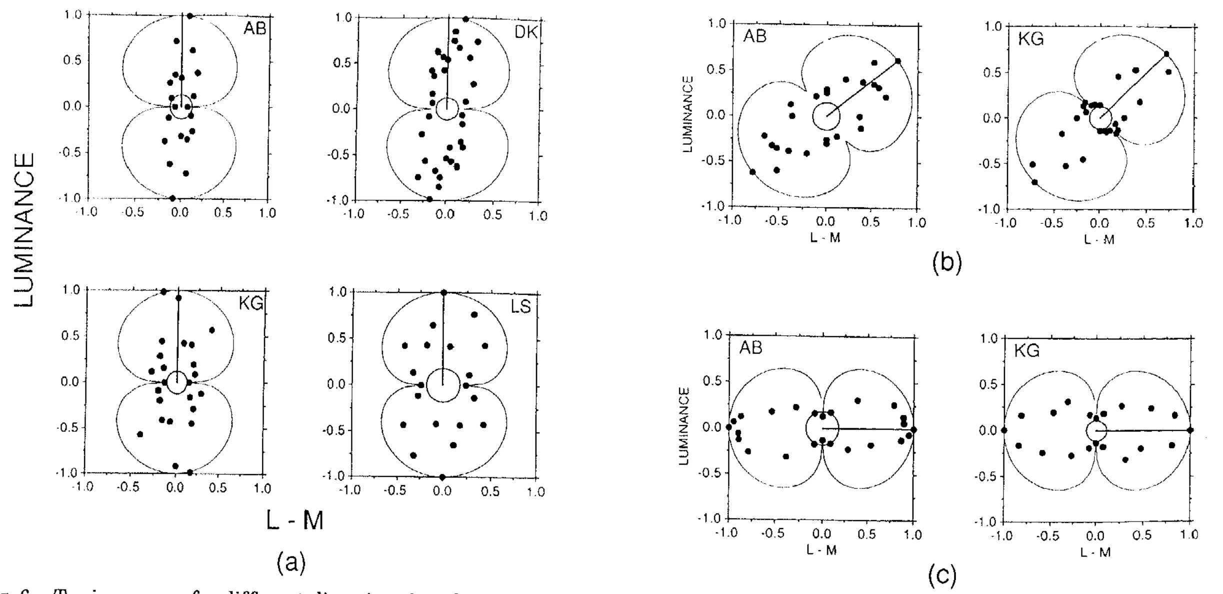
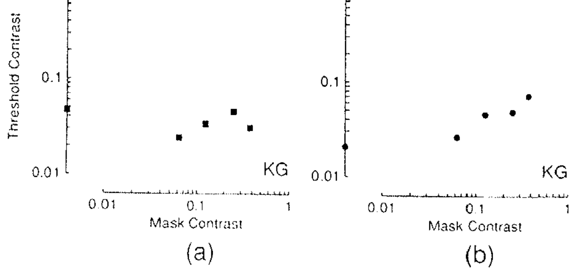


Fig. 6. Tuning curves for different directions in color space. The signal is indicated by the thick, straight lines. The distance of each dot from the origin represents the threshold for detecting the signal, where we use a noise along a line in the direction of the dot. The small circles in the middle indicate the unmasked threshold. The thin curves give the predictions of the cosine rule. (a) Signal in the luminance direction. (b) Signal with bright red and dark green components. (c) Signal in the isoluminant plane.

established the linearity of the individual mechanisms, we conclude that there must be interactions between the mechanisms.

E. Contrast Discrimination

Switkes *et al.*[14] carried out experiments on contrast discrimination with chromatic and luminance stimuli. They used a sine-wave pattern to mask a sine-wave signal. Stimuli were modulated along a yellow–black luminance axis and a red–green chromatic axis. They found that suprathreshold luminance masks increased thresholds for detecting luminance signals. In the same way chromatic masks increased thresholds for detecting chromatic signals. Once contrasts were normalized by the unmasked (detection) thresholds, the two masking curves fell one on top of the other. Luminance masks did not increase thresholds for detecting a chromatic signal. However, chromatic masks of sufficiently high contrast (above 16%) lead to a threshold elevation for detecting the luminance signal. Switkes *et al.*[14] interpret their results with a two-channel model with various interactions between the luminance and chromatic channels. We replicated their experiments and extended them to intermediate directions in color space to see whether discrimination in that case can indeed be described by only two independent mechanisms.



(a) (b)

Fig. 7. Results for sinusoidal stimuli. (a) Thresholds for detecting a chromatic sine wave masked by a luminance sine wave of varying contrast. (b) Reversed case of detecting a luminance grating masked by a chromatic grating.

As in our main experiments, we used a 1.2-cpd sine wave as the signal. The mask had the same spatiotemporal properties as the signal but was 90° out of phase.[29] The observer had to judge which interval contained the sum of signal and mask. Figure 7 shows the results for one of our observers. As in Ref. 14, a luminance mask did not raise the threshold for detecting a chromatic signal, whereas the chromatic mask did elevate thresholds for detecting luminance signals.

In addition, we performed the same experiment for signal and mask each containing both chromatic and luminance information. The mask contrasts in the intermediate directions were the same as those in the tuning curve experiments described in Subsection 3.D (for observer KG a mask of 38% chromatic contrast and 28% luminance contrast was used). Table 2 gives the threshold elevations for different combinations of signal and mask. We observed the same basic finding as with the random noise masks: there was a substantially higher elevation of threshold when signal and mask were on the same diagonal. This indicates that indeed more than two mechanisms are necessary in this contrast-discrimination task.

F. Spatial Properties

The above experiments lead us to conclude that performance in these tasks was mediated by a set of linear mechanisms tuned to a variety of directions in color space. Moreover, the narrow tuning of these mechanisms suggests that they are not independent. These conclusions are different from those of Krauskopf *et al.*,[23] who proposed the existence of two independent linear mechanisms. A possible explanation for this discrepancy is that our stimuli had different spatial characteristics from those used in the study of Krauskopf *et al.* While we used a signal whose chromaticity was spatially modulated, Krauskopf *et al.* used stimuli of uniform chromaticity. We therefore ran a new series of experiments, using stimuli similar to those that they used. These experiments are also similar to those reported by D'Zmura,[30] who performed masking experiments with isoluminant stimuli.

In these new experiments the signal was a square subtending 2° of visual angle whose color was varied by a Gaussian in time along a vector originating at the white point. For example, if the signal direction were chosen along the chromatic axis in the red direction, the square's would be white, become progressively more red until it reached its peak contrast, and then progressively return to white. At any given time the square was of a uniform chromaticity.

The signal was superimposed upon the center of a square twice its horizontal and vertical extent whose color was also spatially uniform but randomly modulated in time along a vector originating at the white point.[31] The observer's task was to indicate which of the two intervals contained the sum of signal and mask.

We again used signals and masks containing simultaneously luminance and chromatic components. These directions and the mask contrasts were the same as those described in Subsection 3.E above. We measured the minimum signal contrast necessary to make it just detectable. In one condition, both signal and mask were modulated along the same vector in color space, while in the other condition the mask direction was 90° away from the signal's.

Table 3 shows the results. For a given signal the mask raised the threshold by the same amount whether it was in the same direction as that of the signal or in the other. Threshold elevations in this condition are thus consistent with the predictions of a model based on the mechanisms proposed by Krauskopf *et al.*[23] Mechanisms tuned to intermediate directions do not contribute to performance.

4. DISCUSSION

Our aim in this paper was to determine whether luminance and equiluminant chromatic inputs are processed by one or several channels. In particular, we measured the efficiency with which the visual system processes luminance and chromatic information and determined whether there are interaction effects when both types of input are presented simultaneously.

The results shown above in Fig. 2 indicate that the efficiency is the same for luminance and chromatic inputs. Mechanisms tuned only to these two directions, however, are not sufficient to explain the results obtained with stimuli in intermediate directions of color space. When we measured the characteristics of these additional mechanisms, we found that their efficiency was the same as that observed by us earlier in the luminance and chromatic directions. We also found that they are narrowly tuned in color space, which we interpret as the result of interactions between neighboring mechanisms. We did not find interactions between mechanisms tuned to directions orthogonal to each other, for example, the luminance and chromatic directions.

The question is then at what level in the visual pathway are these mechanisms located. The fact that we obtained different results when we changed our stimuli from Gabor patches to small squares of uniform chromaticity may shed some light on that issue. While the two types of stimuli greatly differ in their frequency spectra, because the square patch contains a dc component as well as higher spatial frequencies, it is difficult to determine how these differences could account for the difference in performance. One possibility is that the presence of the dc component leads these stimuli to be processed at different stages of the visual system. Support for this view comes from the report that cells in the LGN usually respond well to stimuli covering their whole receptive field,[10] while those in the cortex do not (at least in the luminance domain[13,31]). We therefore speculate that the spatially uni-

Table 2. Thresholds for Detecting a Sine-Wave Signal in the Presence of a Sine-Wave Pedestal[a]

	Signal			
	Signal and Noise in the Same Direction		Signal and Noise in Different Directions	
Observer	Bright Red, Dark Green	Bright Green, Dark Red	Bright Red, Dark Green	Bright Green, Dark Red
AB	6.97	7.46	2.05	2.14
DK	9.04	6.44	1.66	1.67
KG	5.96	5.71	3.3	3.12

[a] Thresholds are given as multiples of the unmasked thresholds for the same signal.

Table 3. Thresholds for the Detection of a Uniform 2° Field in the Presence of a 4° Flickering Noise field[a]

	Signal			
	Signal and Noise in the Same Direction		Signal and Noise in Different Directions	
Observer	Bright Red	Bright Green	Bright Red	Bright Green
AB	1.96	1.5	2.19	1.68
DK	2.80	2.42	2.64	3.03
KG	2.30	2.32	2.53	2.29

[a] Thresholds are given as multiples of the unmasked thresholds.

form 2° square was a more effective stimulus for LGN than for cortical cells.[32]

If tasks using Gabor patches indeed tap a different stage of processing than those using more uniform targets, then it is not surprising that our results lead to conclusions different from the habituation results of Krauskopf *et al.*[23] It would be quite interesting to see whether the habituation results of Krauskopf *et al.* change with the use of sine-wave gratings as stimuli.

Switkes *et al.*[14] found that suprathreshold chromatic pedestals had a strong masking effect on luminance test stimuli, whereas luminance masks even of high contrast levels did not significantly increase thresholds for the detection of a chromatic target. This was confirmed by our replication of their results. However, our data using random noise masks did not show any sign of masking under either condition. This is most likely because our random noise masks had their energy spread evenly across the spectrum and therefore had only a limited amount of energy in the spatial-frequency band of the channel mediating detection. The sine-wave masks used by Switkes *et al.* had all their energy concentrated at the frequency of the detecting channel. It is therefore likely that higher levels of noise energy would have increased thresholds in our experiments as well.

In conclusion, our results show that it is incorrect to assume that psychophysical performance is always determined by the activity of just a luminance and a chromatic mechanism. We demonstrated the existence of additional mechanisms that determine performance in the detection task that we used. The possible involvement of these mechanisms must be considered when one interprets the results of other visual tasks.

ACKNOWLEDGMENTS

The authors thank Mike Hawken, John Krauskopf, and the two anonymous reviewers for their many helpful comments. This study was supported by National Eye Institute grant EY 02017 to J. Anthony Movshon and by U.S. Air Force grant AFOSR-89-0429 to John Krauskopf.

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29. As was pointed out by one of the reviewers, the 90° phase shift leads to a different phase relationship between the chromatic and luminance components of the composite grating when signal and mask are on different diagonals. This might serve as a cue to facilitate performance. However, data obtained with a 0° phase shift showed the same pattern of results, suggesting that this cue is not used by the subjects.
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32. It could be argued that the stimulus contains an edge separating the signal (small square) from the mask (larger square), which would stimulate cortical neurons as well. In that case a performance difference between the same/other diagonal conditions would be predicted.