Orientation and spatial-frequency discrimination for luminance and chromatic gratings

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We have examined the accuracy of orientation and spatial-frequency discrimination for sine-wave gratings that vary in either luminance or color. The equiluminant chromatic gratings were modulated along either a tritanopic confusion axis (so that they were detectable on the basis of activity in only the short-wavelength-sensitive cones) or an axis of constant short-wavelength-sensitive cone excitation (so that they could be detected on the basis of opposing activity in only the long- and medium-wavelength-sensitive cones). Grating contrasts ranged from the detection threshold to the highest levels that we could produce; the contrasts of the luminance and color patterns were equated for equal multiples of their respective detection thresholds. Discrimination thresholds for all patterns showed a similar dependence on stimulus contrast, rising sharply at low contrasts and becoming nearly asymptotic at moderate contrasts. However, even at threshold contrasts, observers could still reliably discriminate sufficiently large differences in the orientation or spatial frequency of all patterns, and they could also reliably identify the type of variation (luminance or which color) defining the grating. For most conditions the discrimination thresholds did not differ from the two types of color grating and reached values as low as 1 deg (orientation) or 4% (spatial frequency). Thus observers were able to make accurate spatial judgments on the basis of either type of chromatic information. However, these thresholds were slightly but consistently higher than the thresholds for comparable luminance gratings. This difference in the color and luminance discrimination thresholds may reflect somewhat coarser orientation and spatial-frequency selectivity in the mechanisms encoding the chromatic patterns.

INTRODUCTION

Spatial variations in color are a common and salient feature of most natural scenes. Yet while our perception of spatial information has been extensively studied with stimuli varying in luminance, we know little about the role that comparable chromatic information can play. To examine our ability to use chromatic spatial information, we have compared how accurately subjects can discriminate between different spatial patterns when those patterns are defined by variations in either luminance or color.

The specific tasks that we examined were the discriminations of differences in orientation or spatial frequency for gratings that varied sinusoidally in either luminance or chromaticity. The use of sine-wave gratings as stimuli has the advantage that the gratings permit roughly comparable spatial patterns for luminance and color, despite the large differences in the spatial-contrast-sensitivity functions of the luminance and color systems.[1] For most nonsinusoidal stimuli, such as bars and edges, attenuation by these different functions would produce effectively different patterns depending on whether the stimuli were defined by luminance or color, and this difference would make it more difficult to compare them or to equate contrast appropriately for them.

Human observers are highly sensitive to the orientation and spatial frequency of patterns defined by luminance variations and, for appropriate stimuli, can achieve discrimination thresholds within the hyperacuity range (so that the detected spatial differences are smaller than the diameter of foveal cones[2–4]). Selectivity for orientation and spatial frequency are among the clearest properties of striate cortical cells and of psychophysically defined spatial channels.[5] Such results suggest that something like the stimulus dimensions of orientation and spatial frequency are fundamental to the early visual analysis of form, and it is therefore of interest to examine how accurately these dimensions can be conveyed by color. Moreover, striate cortex cells that are selective for color are often poorly tuned for orientation.[6] If cells with little or no orientation selectivity were principally involved in encoding chromatic patterns, then one might expect correspondingly poor discrimination thresholds for chromatic gratings.

A chromatic grating can be produced by variations along many different chromatic dimensions, and it is possible that these dimensions can lead to different spatial sensitivities. To examine this possibility, we measured discrimination thresholds for two different types of equiluminant color pattern. For one of the gratings, the pattern was defined by chromatic variations along a tritanopic confusion axis. Equiluminant variations along this axis produce constant excitation in the long-wavelength-sensitive (L) and medium-wavelength-sensitive (M) cones. Thus the pattern can be detected by spatial variations in the activity of only the short-wavelength-sensitive (S) cones, and we therefore refer to this pattern as an S grating. In contrast, the second type of grating was defined by equiluminant color variations along an axis of constant S-cone excitation and could there-

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fore be detected only by the (opposing) spatial variations in the activity of the L and M cones. We have therefore labeled this pattern an L–M grating. We chose to examine gratings defined by variations along S and L–M chromatic dimensions primarily because the S cones and the pathways into which they feed seem to differ in a number of ways from the other two cone types.[7] For example, the S-cone system makes little contribution to luminance and is characterized by poor spatial and temporal resolution. These differences have suggested that the S cones may be principally involved in signaling only the chromatic properties of the stimulus, while playing little role in spatial vision. Further, both physiological[8] and psychophysical[9] studies have indicated that, at least at early levels of the visual system, these two types of color variation are encoded by separate opponent color mechanisms. They can therefore be used to examine the spatial capacities of these isolated early opponent pathways.[10]

METHODS

Equipment

The patterns were presented on a 19-in. (48.26-cm) Mitsubishi color monitor with a 60-Hz interlaced raster rate. Photometric luminances and chromaticity coordinates (CIE, 1931) of the monitor phosphors were measured with a Pritchard photometer. These coordinates were (x, y) = (0.580, 0.361) for the red gun, (0.301, 0.592) for the green, and (0.142, 0.066) for blue. The monitor screen was visible through a circular aperture in a surrounding white background (at a slightly lower luminance) and subtended 5 deg at the 3-m viewing distance that was used. To compensate for the longitudinal chromatic aberrations of the eye, subjects viewed the display monocularly through an achromatizing lens[11] and used an adjustable bite bar to maintain alignment.

The monitor was controlled by a Nova 4X computer and a LEXIDATA 3400 graphics system. The LEXIDATA permitted the presentation of any two-dimensional wave form with 8-bit resolution per gun and with 256 color–luminance levels simultaneously displayable. The outputs of each gun were linearized on the basis of calibration files. The dynamic range of the 256 displayable levels could be reduced by additional electronics that attenuated the video outputs. This attenuation made it possible to generate low-contrast patterns without sacrificing high color or luminance resolution.

Stimuli

The patterns were one-dimensional spatial sinusoids of varying orientation, spatial frequency, color, and contrast. Spatial-frequency discrimination was always measured with vertically oriented gratings. For orientation discrimination the spatial frequency was fixed at 2 cycles per degree (c/deg).

The mean luminance (27.4 cd/m^2) and average chromaticity (0.312, 0.331) were the same for all patterns. To produce gratings that varied only in luminance about this average, the relative proportions of the three guns were held constant, while the absolute levels were varied sinusoidally in phase across the screen. The contrast of the luminance variation was defined by the standard Michelson contrast. Gratings that instead varied only in chromatic content were equivalent to two luminance gratings of two different chromaticities and added 180 deg out of phase. In this case 100% contrast was arbitrarily defined as the maximum color difference that we could produce for a given direction in color space (with the restriction that the equiluminant mixture of the two component colors yielded the average chromaticity defined above). In practice, however, we tried to equate the visual effectiveness of the luminance or chromatic patterns by normalizing the contrasts under all conditions in terms of equal multiples of their respective contrast detection thresholds. Switkes *et al.*[12] have shown that this scaling procedure leads to indistinguishable contrast discrimination functions for luminance and chromatic gratings. The contrast thresholds were initially estimated for horizontal gratings by using a temporal two-alternative forced-choice staircase procedure (as described in Ref. 12) and were similar to subsequent estimates based on a simultaneous discrimination–detection procedure (see below).

For individual subjects the photometric luminances that were necessary to equate different colors for the same effective luminance were estimated by using heterochromatic flicker photometry. The measures were made by flickering each of the individual guns against a uniform-field white at 15 Hz. In addition a number of other procedures (described below) were used to ensure that the subject's judgments were based on the chromatic content of the stimuli and not on any unintended residual luminance variations in the color gratings.

The chromatic variations defining either the S or L–M axes were determined empirically for the two principal subjects (author MW and a highly trained, paid observer SW) by using a modified version of the two-color threshold technique used by Stiles.[13] Contrast detection thresholds for a range of different equiluminant color gratings (defined by different directions of chromatic variation about the same average chromaticity[9]) were measured in the presence or absence of a short-wavelength (430-nm) adapting background (from a monochromator with a xenon source superimposed upon the display with a beam splitter). This background was chosen to elevate detection thresholds selectively for the S cones and thus should have produced the largest threshold change for the chromatic grating closest to the S axis. In turn, adaptation to a long wavelength (580 nm) was used to desensitize the L and M cones and thus should have produced the largest threshold elevation for a grating that was defined by the L–M axis. The threshold changes produced by these two adapting conditions are shown for subject MW in Fig. 1, in which we have plotted the log change in contrast threshold as a function of both the approximate dominant wavelength of the color variation and the corresponding color direction (or angle) in an equiluminant color space proposed by MacLeod and Boynton.[14] [In this space an angle of 0 deg corresponds to an axis of +L- (or −M-) cone excitation, while that of 90 deg corresponds to an axis of S-cone excitation. The relative scaling of the two axes in this space is arbitrary and is such that we needed to sample much finer angular increments in the area of 0 deg than in the area of 90 deg.] For both tested subjects the S and L–M axes defined in this way were similar but differed slightly from the standard observer. (The same axes were also used for a third subject, AL, whose individual axes were not tested.)

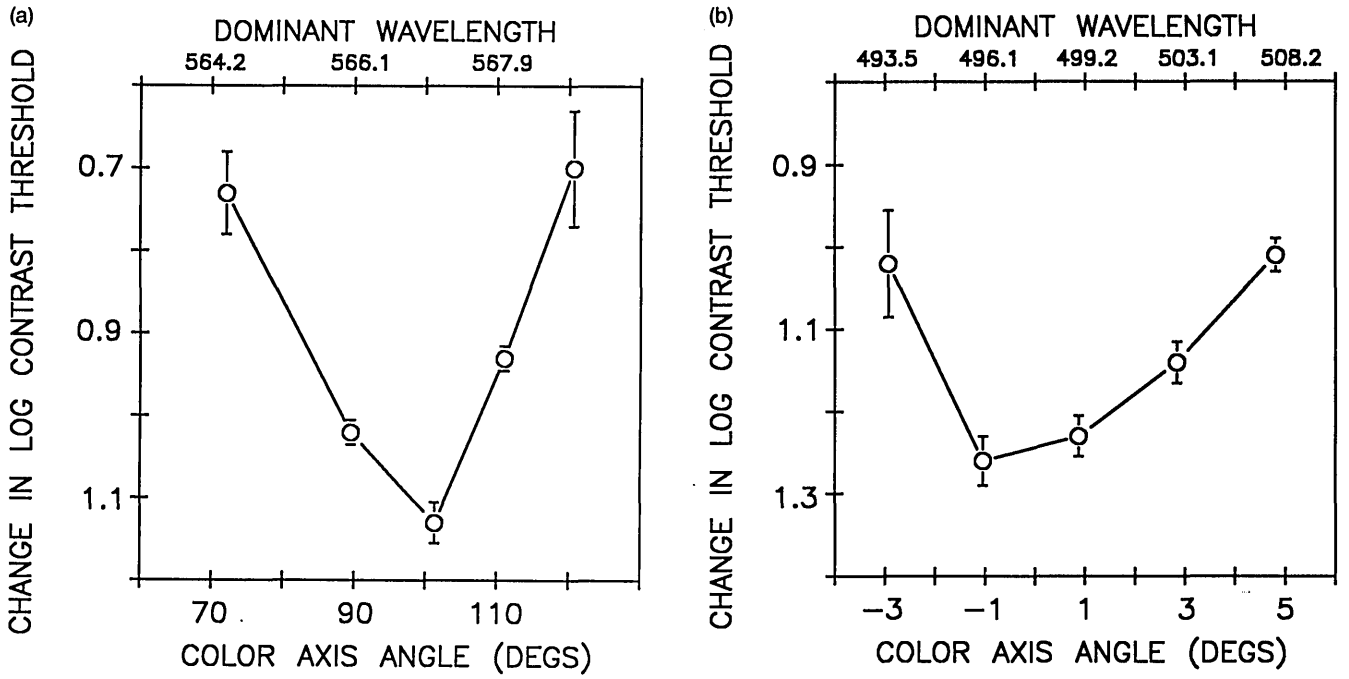

Fig. 1. Estimates of the chromatic directions corresponding to the S and L–M axes passing through our average chromaticity. The change in grating contrast threshold owing to the presence of an adapting background is plotted for gratings defined by color variations along different chromatic axes. The angle of the color axis corresponds to the angle of color variation in the MacLeod–Boynton[14] color diagram: (a) 430-nm background chosen to desensitize the S cones, (b) 580-nm background chosen to desensitize the L and M cones. The observer was MW.

Figure 2 shows the CIE coordinates of the resulting color axes used to define the chromatic gratings for all subjects.

Procedure

Orientation and spatial-frequency discrimination thresholds were measured by using the method of constant stimuli. On each trial, a single grating was presented at one of two possible orientations (randomly chosen from symmetrical clockwise or counterclockwise offsets from vertical) or frequencies (usually an equal percentage greater or less than 2 c/deg). We chose to display only one of the gratings on each trial so that similar procedures were used for measuring discrimination at both threshold and suprathreshold contrasts. However, additional measures for spatial-frequency discrimination between two gratings that were both presented on a single trial yielded similar results (see below). To avoid the potential use of local spatial cues, we randomly varied the phase of the gratings across trials. In addition, for frequency discrimination the mean contrasts of the gratings were randomly varied over a range of ±0.075 log unit, so that the discriminations could not be based on possible differences in the apparent contrast of the two gratings. The gratings were displayed at maximum contrast for 200 msec and ramped on and off with 130-msec Gaussian ramps. Tones marked the start of the trial and the presence of the pattern and provided feedback for incorrect responses.

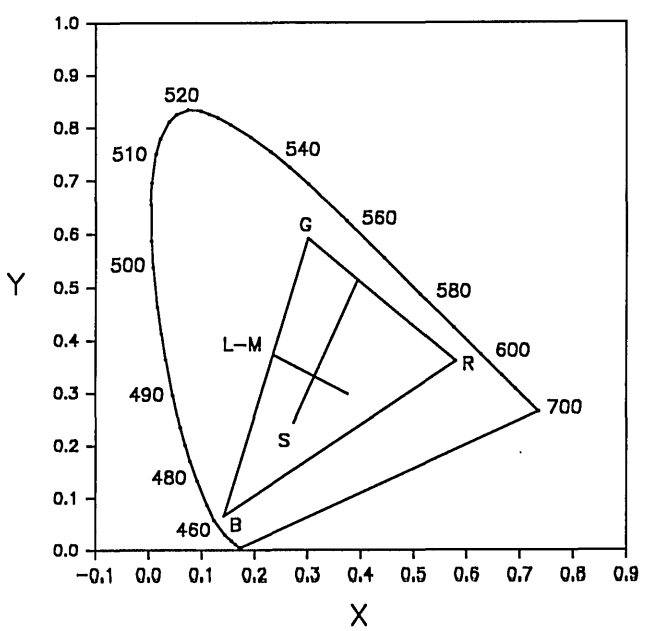

Fig. 2. CIE coordinates of the monitor phosphors and of the chromatic variations used to define the L–M and S chromatic gratings.

A single run consisted of 10 practice trials followed by 80–100 trials during which responses were recorded. During each run only one pair of orientations or frequencies was presented. A set of 4–6 possible pairs, which were chosen on the basis of preliminary measures to bracket the discrimination threshold, was run in random order. In each session discrimination thresholds were estimated for the luminance grating and for each chromatic grating at the same multiple of threshold contrast with the order of the patterns and different contrasts roughly counterbalanced across different sessions. Subjects received extensive practice on all conditions before the reported data were collected.

RESULTS

Orientation Discrimination at Suprathreshold Contrasts

If the mechanisms underlying orientation or spatial-frequency discrimination are functionally similar for lumi-

nance and color, then we might expect the discrimination thresholds for the luminance and chromatic patterns to show a similar dependence on stimulus contrast. To examine this possibility, we measured the thresholds over a wide range of contrasts. This examination was also necessary because it was not obvious how best to equate the contrasts of luminance and chromatic patterns in our particular task. Measures of the discrimination thresholds at a single contrast would not permit us to distinguish possible differences in the spatial sensitivities of the color and luminance systems from possible contrast-dependent effects on the discriminations.

Examples of orientation discrimination thresholds obtained for gratings at two different contrasts are shown in Fig. 3, in which the percentage of correct responses has been plotted as a function of the difference in orientation. The filled symbols show the results for luminance gratings, while the open symbols correspond to the different chromatic gratings. Each of the points shown is based on 300 trials collected over 3 different sessions.

Figure 3(a) shows the results for trials in which the contrasts of the gratings were all at four times their respective detection thresholds. For the luminance gratings, this value corresponded to a Michelson contrast of only 1.4% for the observer. Clearly, at each of the orientation differences tested, the difference was more reliably discriminated when it was defined by a variation in luminance than by either type of chromatic variation, while the results for the two color gratings did not differ significantly from each other. Figure 3(b) shows analogous results for gratings at 16 times their threshold contrasts. At this contrast level, the ability to discriminate the orientation improved for all three types of stimuli, and the absolute difference between the luminance and chromatic patterns was smaller. Nevertheless performance was still consistently better for the luminance gratings with the ratio of the luminance to color discrimination thresholds approximately the same at both contrasts.

From the probability-of-seeing curves obtained for each condition, the orientation difference necessary to discriminate between the patterns 75% of the time was estimated by using probit analysis.[15] These thresholds are plotted as a function of the multiple of threshold contrast in Fig. 4 for the two subjects. The points shown represent the mean of the thresholds obtained from three or four different sessions. The error bars correspond to ±1 standard error of the mean and are shown except when they are smaller than the data symbols. Note that the scale of the orientation axis is different for the two subjects, owing to the much higher thresholds of subject SW at low contrasts.

To a first approximation, the discrimination thresholds for the luminance and chromatic patterns show a similar dependence on stimulus contrast. In each case performance tends to become asymptotic at moderately low contrasts, so that there is little improvement in discrimination at higher contrasts, but falls rapidly for contrasts near the detection threshold (a pattern more clearly emphasized in the insets of Fig. 4, which replot the thresholds on linear axes). This pattern of results is generally similar to a number of previous measures of orientation discrimination for luminance gratings (though the multiple of threshold contrasts at which optimal performance is reached tends to be higher than previously reported values[16–18]). The orientation thresholds for the two types of chromatic grating do not significantly differ (except perhaps for SW at the lowest contrasts) but are consistently higher than the thresholds for comparable luminance gratings. At the higher contrasts these thresholds averaged for both subjects are 0.65 deg for luminance and 0.99 deg for color. For subject MW the ratio of the color to luminance thresholds is fairly constant across the range of contrasts tested, though it becomes progressively larger for subject SW at lower contrasts. (Subject SW's substantially higher discrimination thresholds for color at low contrasts and the consequent increase in her color–luminance ratio might have resulted from small errors in her

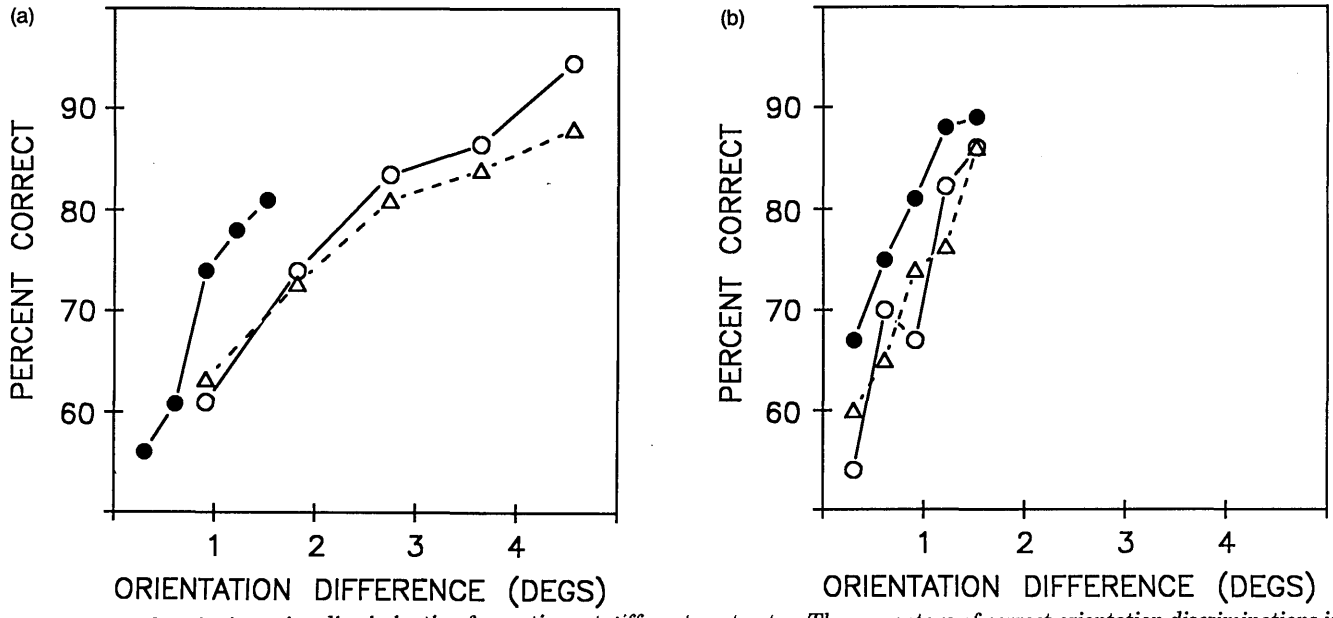

Fig. 3. Examples of orientation discrimination for gratings at different contrasts. The percentage of correct orientation discriminations is plotted as a function of the difference in orientation between the two gratings: (a) 4 times threshold contrast; (b) 16 times threshold contrast. Filled circles are luminance gratings; open circles are L–M gratings; open triangles are S gratings. The observer was MW.

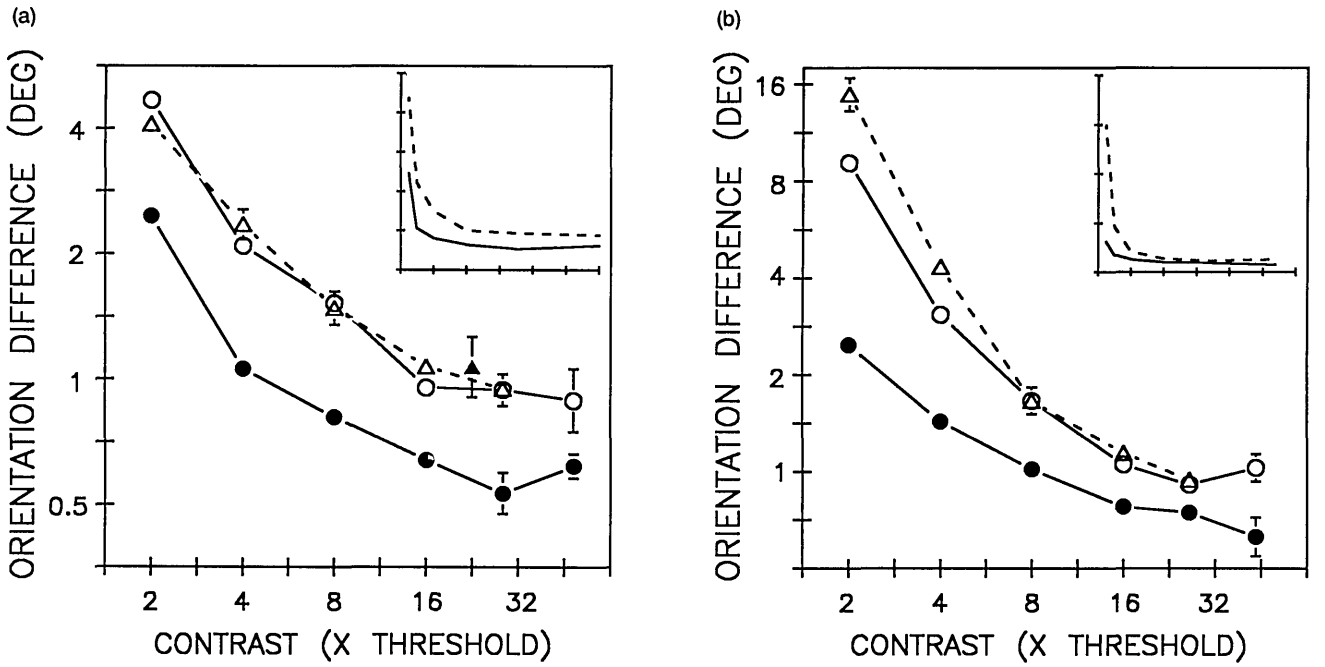

Fig. 4. Orientation discrimination thresholds for the luminance (filled circles), L–M (open circles), and S (open triangles) gratings as a function of the multiple of threshold contrast: (a) results for subject MW, (b) results for subject SW. (Note that the orientation axis is scaled differently for the two.) The insets show the thresholds replotted on linear axes. In (a), the filled triangle indicates the thresholds for the S gratings remeasured in the presence of a long-wavelength adapting background that was added to increase isolation of the S cones.

estimated detection thresholds. However, these thresholds were consistent with separate experiments in which the contrast thresholds for discrimination and detection were measured simultaneously; see below.)

To the extent that the lowest orientation discrimination thresholds reach different asymptotic levels for the luminance and chromatic gratings, the differences that we found between luminance and color cannot be due to a failure to equate the effective contrasts of the different patterns. Instead, they must reflect an actual difference in the visual processing of luminance and chromatic stimuli. On the other hand, scaling the contrasts relative to their respective detection thresholds does appear to be an appropriate metric for equating the luminance and chromatic stimuli in this task because, again, it results in a similar contrast dependence for all three patterns. As we noted, contrast discrimination thresholds have also been found to be similar for luminance and color when the luminance and chromatic contrasts are normalized according to their detection thresholds.[12]

The tendency of the orientation discrimination thresholds to reach asymptotic values at moderately low contrasts also argues against the possibility that the orientation thresholds for the nominally chromatic patterns are in reality based on a luminance artifact in the chromatic gratings. An error in the balance of the two colors in the color grating that was constant across the extent of the display (for example, an error due to incorrect flicker photometric settings) would produce a residual luminance variation in the chromatic grating with a contrast that was a constant proportion of the chromatic contrast. If this artifact determined the discrimination thresholds for the color gratings, then these thresholds should resemble the thresholds for the actual luminance grating at a contrast equivalent to the artifact. Consequently, the curve describing the contrast dependence of the orientation thresholds for color should be the same shape as the luminance curve but shifted *horizontally* to the right along the contrast axis (with the amount of the shift equal to the ratio of the real contrast to the artifactual contrast) and should eventually be asymptotic at the same orientation threshold. However, the actual results for the color gratings are much better fitted by a *vertical* displacement of the luminance curve. For subject MW's data, the best-fitting horizontal displacements would require a luminance artifact in the color gratings that was 50% of the contrast of the luminance gratings and would describe the color data poorly. Alternatively, the best-fitting vertical shift of the luminance curve (74% increase in thresholds) leaves an rms residual error of only 5% in the predicted orientation thresholds for color.

However, the observed results might still be consistent with the possibility that the chromatic orientation discrimination thresholds are due to spatially nonuniform luminance artifacts in the color gratings (which might have become asymptotic at slightly higher thresholds than the actual luminance grating, for example, because they were more spatially delimited or restricted to the periphery). In fact, because we used spatially extended patterns, some nonuniform residual luminance contrast in the chromatic gratings was inevitable owing to such factors as the inhomogeneities of the retina and the fact that we did not correct for the lateral chromatic aberration of the eye. To control against the possibility that these potential artifacts contributed to the performance with the chromatic gratings, the orientation thresholds for the S grating were remeasured in the presence of a long-wavelength (>590-nm) uniform background (Wratten #26), which was chosen to desensitize the L and M cones. This background reduced the sensitivity to

both the luminance and L–M gratings by more than 0.7 log unit but had little effect on the S grating thresholds. The combination of the nominally equiluminant tritanopic color pair and the adapting background should therefore have been much more effective at isolating the S-cone pathways (which appear to make little contribution to luminance[19]) and at reducing the contrast of any potential luminance variation. Nevertheless, as indicated by the filled triangle in Fig. 4(a), the discrimination thresholds remained similar, suggesting that the observed thresholds for the color gratings are in fact based on the chromatic information in the stimulus.

Spatial-Frequency Discrimination at Suprathreshold Contrasts

In Fig. 5 comparable measures of spatial-frequency discrimination as a function of grating contrast (again expressed as multiples of threshold) have been plotted for both subjects. The average frequency of the gratings was 2 c/deg. Each point shown is again based on the average of threshold estimates from three or more separate sessions. Clearly, both the relative discrimination thresholds for luminance and color and the way in which they vary with contrast are similar to the results that we found for orientation discrimination and are also similar to a number of previous measures of spatial-frequency discrimination for luminance gratings.[16,18,20,21] Thus these results again show that observers can make accurate spatial discriminations on the basis of chromatic information and suggest that the spatial processes underlying these discriminations are functionally similar for luminance and chromatic contrast. In fact, in the present measures the differences between the discrimination thresholds for color and luminance tend to be smaller than those found for orientation discrimination, averaging only 35–40% at the higher contrasts. Moreover the estimates of the frequency thresholds were more variable than the comparable threshold estimates for orientation discrimination (owing in part to long-term-practice effects), so that many of the differences at higher stimulus contrasts are not significant.

The average differences that we found between the frequency discrimination thresholds for color and luminance at 2 c/deg are comparable in magnitude with differences that have been reported for luminance frequency discrimination thresholds at different base frequencies[4,22] (though others have reported constant Weber fractions for frequency discrimination[23]). To examine whether the differences between color and luminance depended on the specific reference frequency used, we measured discrimination thresholds for both the luminance and chromatic gratings at a range of average frequencies from 0.5 to 4 c/deg.[24] For these measures the field size was increased from 5 to 9 deg (to accommodate the lower average frequencies). We also modified the procedure by presenting both gratings from a given pair on each trial, so that observers could more directly compare the two stimuli to be discriminated (though this did not clearly improve performance beyond the final practiced thresholds for the previous experiment).

In this case the average contrasts of all the gratings were fixed at a 20 times threshold (close to the highest that we could produce for the L–M grating at 4 c/deg), so that the physical contrasts varied with both the spatial frequency and the type of variation (luminance or chromatic) defining the pattern. As before, the average contrast was randomly varied by ±0.075 log unit on different trials. An example of the nominal contrast thresholds on which this scaling was based is shown in Fig. 6, in which the luminance or chromatic contrast sensitivities (or reciprocals of the thresholds for nominal contrast, as defined in the Methods section) have been plotted as a function of spatial frequency. For techni-

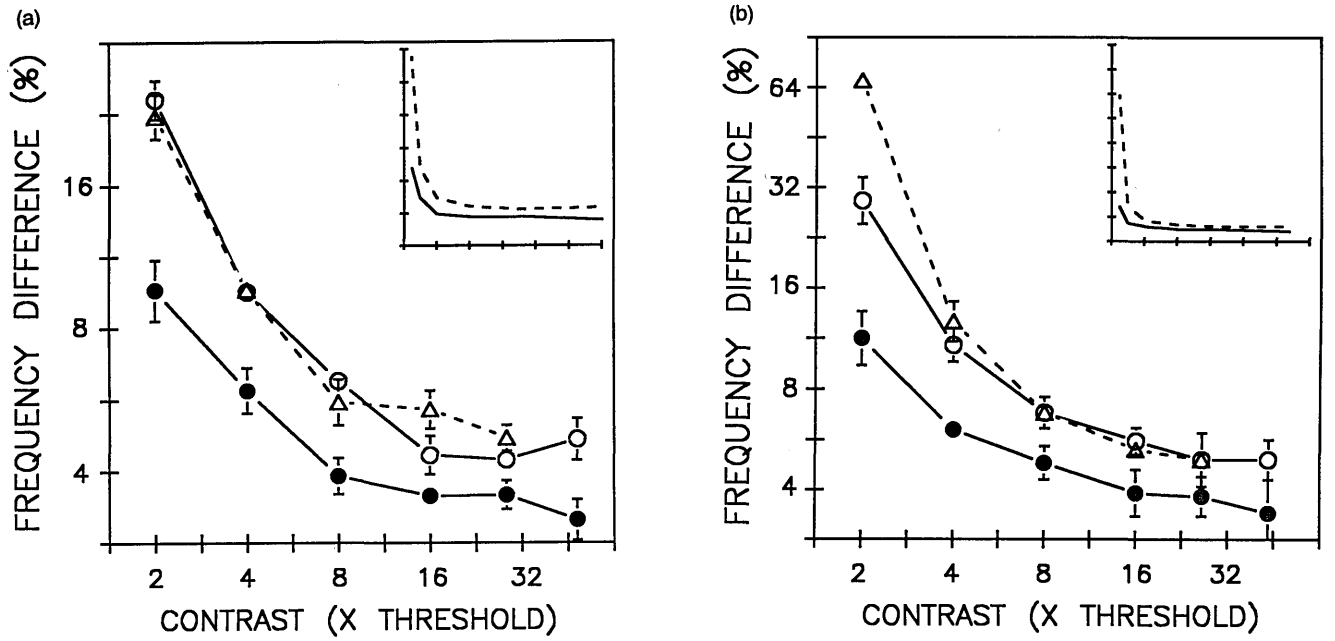

Fig. 5. Frequency discrimination thresholds as a function of the multiple of threshold contrast for luminance (filled circles), L–M (open circles), or S (open triangles) gratings: (a) results for observer MW, (b) results for observer SW. The insets show the thresholds replotted on linear axes.

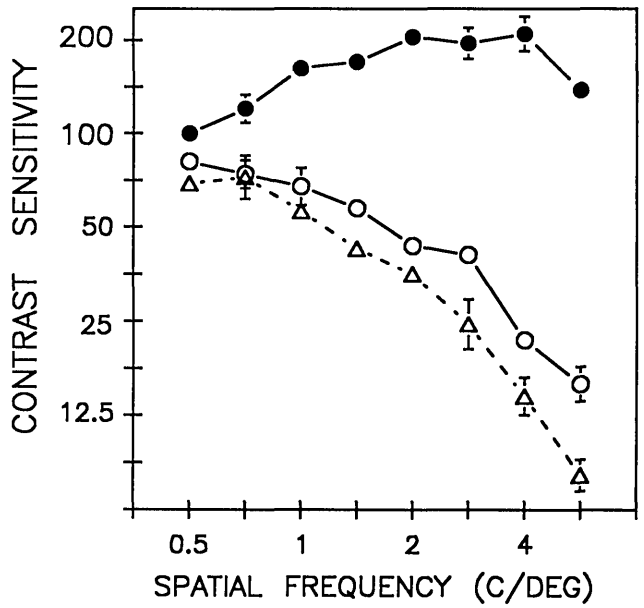

Fig. 6. Contrast sensitivity (reciprocal of nominal contrast detection thresholds) for luminance (filled circles), L–M (open circles), or S (open triangles) gratings as a function of spatial frequency. The observer was MW.

cal reasons, these thresholds were based on horizontal gratings with a field size of 5 deg. Consistent with a number of previous studies, sensitivity to luminance contrast was reduced at both the lower and higher spatial frequencies (though this change was small over the moderate frequency range of these measures), while the sensitivity to color contrast continued to improve as the spatial frequency decreased.[1] The loss of sensitivity at higher frequencies was slightly greater for the color gratings defined by the S variation than for the L–M color gratings.

In Fig. 7 the frequency discrimination thresholds have been plotted as a function of the base frequency for two observers. The absolute thresholds for these two subjects were different, perhaps because subject AL was less practiced. However, the pattern of results for both was similar: For both subjects the frequency thresholds for the two chromatic gratings were again similar and only slightly higher than the frequency thresholds for the luminance gratings (with some of the differences between the color and luminance thresholds not statistically significant). Thus these results suggest that the small differences in the frequency thresholds for luminance and color measured at 2 c/deg were probably not unique to that frequency.

Orientation Discrimination at Near-Threshold Contrasts

As we noted above, the discrimination thresholds for all the patterns rise sharply at low contrasts. We were interested in extending these measures to still lower contrasts in order to examine whether spatial differences could still be discriminated at the limit of the detection threshold. If the detection threshold depends on activity only in one visual mechanism, then the ability to discriminate between two orientations or frequencies at threshold would imply the existence of multiple mechanisms that are orientation or frequency selective and would imply that this property is somehow labeled by the visual system (so that which channels respond at threshold provide information about which orientation or frequency was presented).[25,26] On the other hand, if the detection thresholds for the patterns depended on mechanisms that were not spatially tuned, then the ability to discriminate anything about the orientation or frequency of the gratings might require a contrast higher than the detection threshold (for example, because the spatial properties of the grating could be judged only on the basis of retinotopic information from multiple mechanisms).

To measure orientation discrimination at these low con-

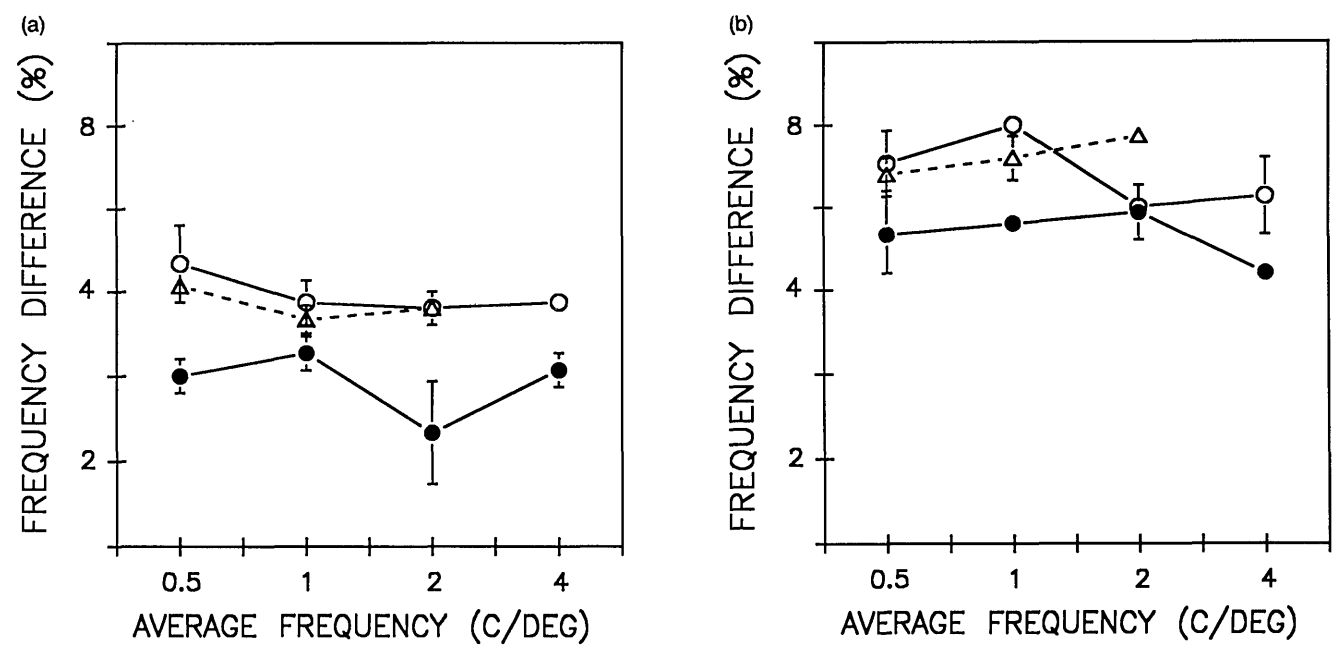

Fig. 7. Frequency discrimination thresholds at 20 times contrast as a function of the reference frequency for luminance gratings (filled circles), L–M gratings (open circles), or S gratings (open triangles). (a) Observer MW, (b) observer AL.

trasts, we used a procedure in which the contrast thresholds for both discrimination and detection were measured concurrently by following similar previous measures of near-threshold luminance gratings by Thomas and Gille.[27] As before, on each trial a single grating of one of two possible orientations was presented, but in this case the grating could occur in one of two possible time intervals. The subject therefore had to indicate both which orientation was presented (the discrimination task) and in which interval the pattern was presented (the detection task). Tones again marked the presentation intervals and provided feedback for both tasks. Within each run the contrasts of the gratings on any trial were randomly varied over a range of 4 to 6 levels (0.125 log unit apart) chosen to bracket both thresholds.

Figure 8 shows an example of the results obtained for two gratings that differed by 16 deg (±8 deg from vertical). The three different figures are for the luminance, L–M, and S stimuli. In each case, the percentage of correct detection (open symbols) or discrimination (filled symbols) judgments is plotted as a function of log contrast. (A log contrast of 0 corresponds to the mean of the range of log contrasts that were tested.) Each symbol is based on at least 300 trials from three or more different sessions. Note that at any given contrast the subject could more reliably detect in which interval the pattern was presented than discriminate between the two pattern orientations. Thus an orientation difference of 16 deg was not enough to permit the patterns to be discriminated reliably at the detection threshold contrast. This result is true for all three types of grating, though the difference between the discrimination and detection thresholds is clearly smaller for the luminance gratings.

We obtained similar measures for a wide range of orientation differences. In Fig. 9 the contrast necessary either to detect (open symbols) or to discriminate (filled symbols)

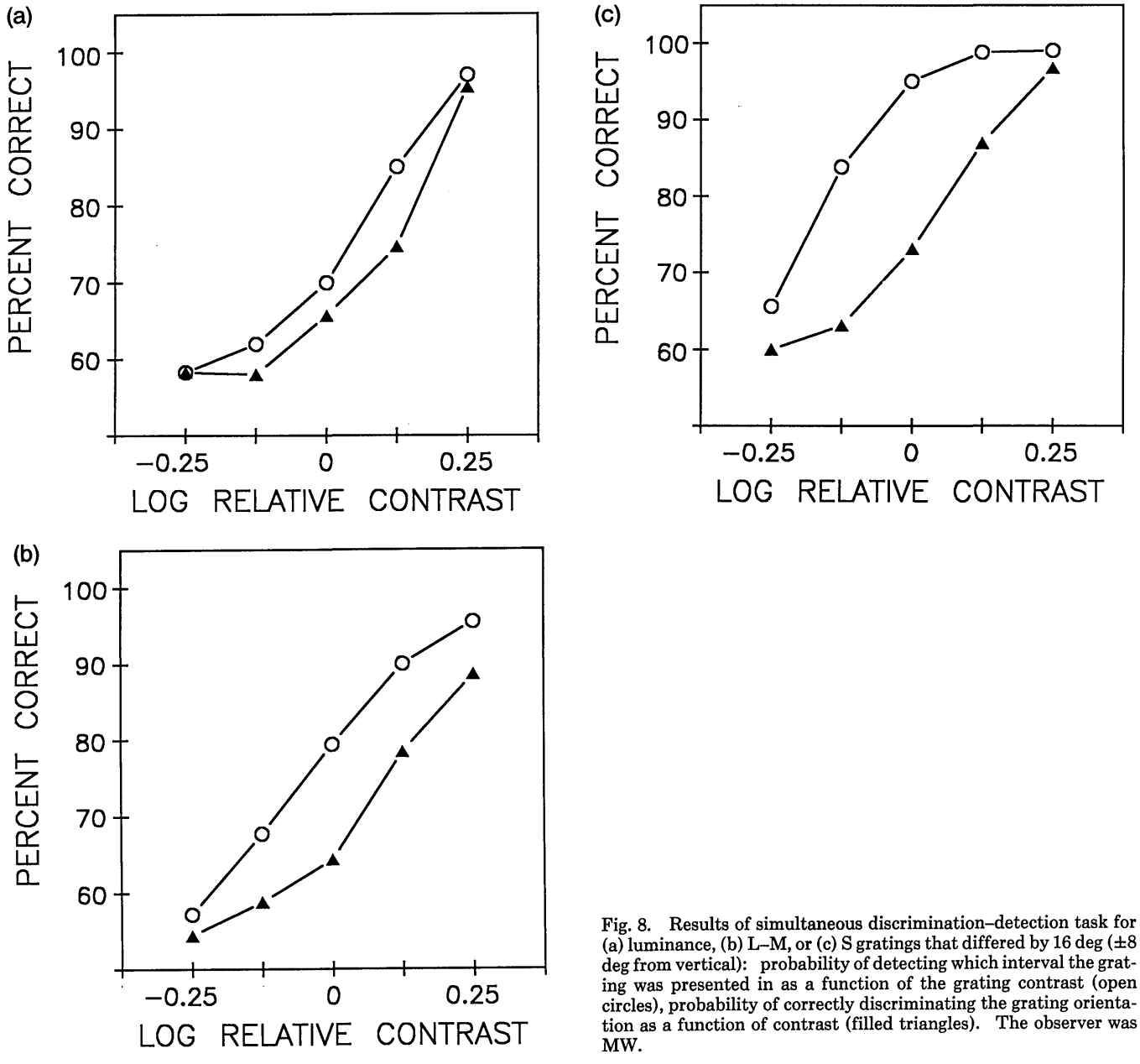

Fig. 8. Results of simultaneous discrimination–detection task for (a) luminance, (b) L–M, or (c) S gratings that differed by 16 deg (±8 deg from vertical): probability of detecting which interval the grating was presented in as a function of the grating contrast (open circles), probability of correctly discriminating the grating orientation as a function of contrast (filled triangles). The observer was MW.

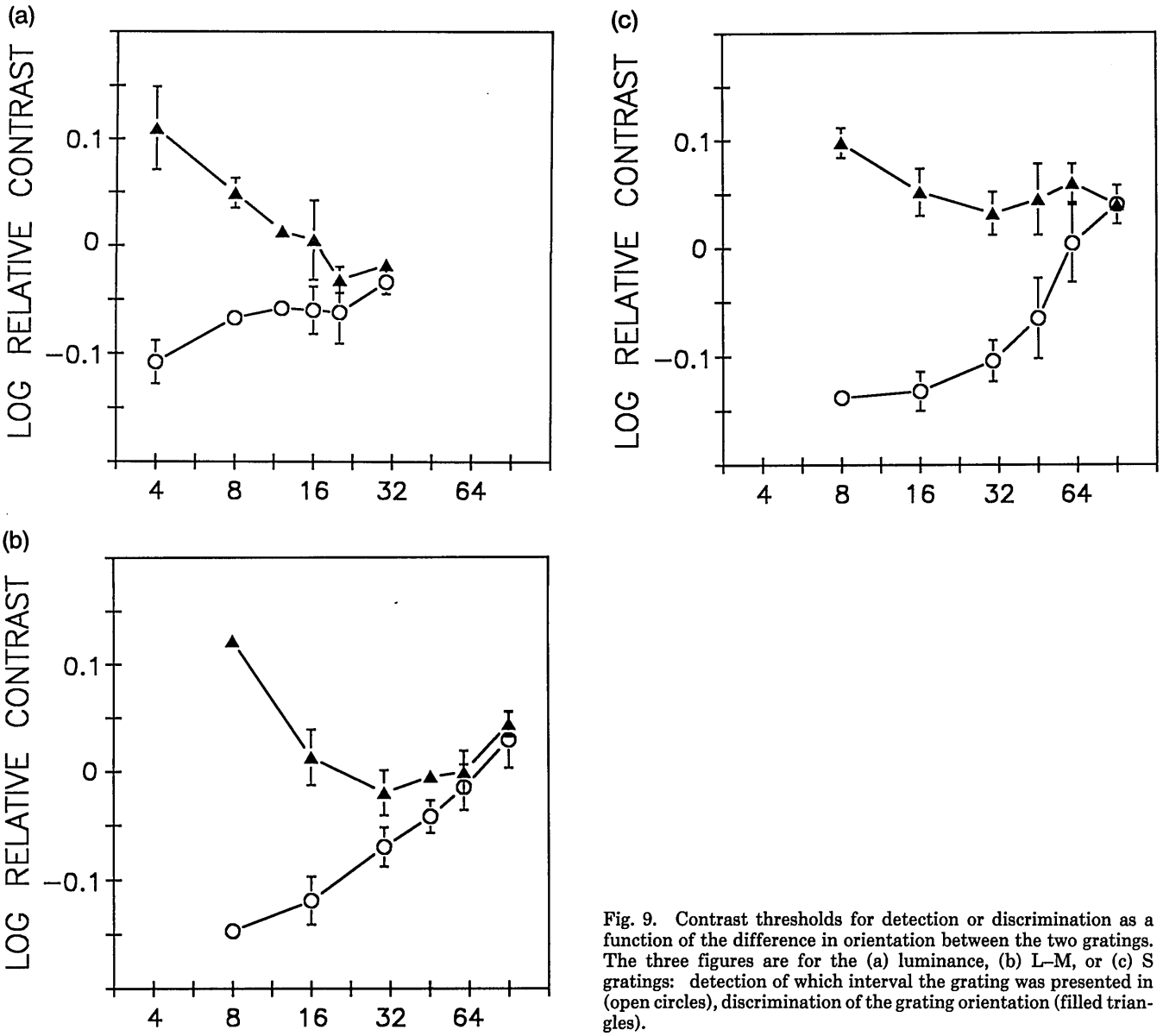

Fig. 9. Contrast thresholds for detection or discrimination as a function of the difference in orientation between the two gratings. The three figures are for the (a) luminance, (b) L–M, or (c) S gratings: detection of which interval the grating was presented in (open circles), discrimination of the grating orientation (filled triangles).

between the patterns 75% of the time is plotted as a function of the difference in orientation for each of the three types of grating. As the orientation difference increases, the contrast thresholds for the two types of judgment become more similar, and they eventually reach the same level, though this requires a substantially larger difference for the color gratings.

Note that there is a clear tendency for the detection thresholds for the color gratings to increase with increasing differences in orientation. Kelly[28] reported that there is no oblique effect for the contrast detection of chromatic stimuli. We did not directly test for this effect for our conditions because the observers always had to detect one of *two possible* oblique gratings. It is therefore possible that the increases in threshold that we observed at oblique orientations are partly due to uncertainty about the stimulus orientation in the detection task.[29] We also found a tendency for the detection thresholds to increase when the subject had to detect one of two possible types of contrast variation (for example, color or luminance; see below). Such uncertainty effects are thought to occur because the observer must monitor multiple, independently noisy mechanisms encoding the variable stimulus dimension and would thus be consistent with detection of the chromatic patterns by orientation-selective channels. (On the other hand, because the phases of the gratings were randomized from trial to trial, any uncertainty for local spatial features of the grating—which might be important if detection involved nonoriented mechanisms—would not be expected to be orientation dependent.)

As we noted above, the fact that sufficiently different orientations can be reliably discriminated at the detection threshold also suggests that the mechanisms for detecting the luminance and chromatic patterns are orientation selective. To compare this for the three types of grating, the ratios of the discrimination to detection thresholds have been plotted in Fig. 10(a). Figure 10(b) shows corresponding results for the second subject. For luminance gratings, we found that the patterns had to differ by ~20 deg before they could be discriminated with the same accuracy with

which they could be detected. This difference is consistent with the measures of Thomas and Gille.[27] The orientation of the chromatic gratings could also be accurately discriminated at threshold, but the orientation difference required for this was substantially larger. (It is interesting that, perceptually, the errors in discrimination at threshold for both the luminance and chromatic stimuli did not seem simply to be due to a loss of the spatial structure of the pattern but also involved large errors in judging the correct orientation of what often seemed to be a well-defined grating. For example, on a given trial a physically oblique grating might appear to be clearly vertical. This appearance is again suggestive of the possibility that the patterns were detected by labeled, orientation-selective mechanisms and that the discrimination errors were due in part to trials in which the highest levels of activity occurred in mechanisms that were labeled for the wrong orientation; see Ref. 2.)

Surprisingly, while the two types of chromatic grating did not differ at higher contrasts, at near-threshold contrasts there was a clear tendency for the orientation discrimination with the S gratings to be poorer. This tendency is most apparent in the data of subject MW [Fig. 10(a)], who was substantially more practiced on this task, but is also suggested by subject SW's results [Fig. 10(b)]. Subject MW required a difference of 30 to 45 deg to discriminate reliably the orientation of the L–M gratings at threshold, while similar performance with the S stimuli was not possible until the gratings were 60 to 90 deg apart. (Note that 90 deg is the largest possible orientation of difference.) This difference in performance for the two types of color grating was necessarily small, since the contrasts were always restricted to near-threshold levels, but once it emerged it appeared to be consistent. For example, Fig. 11 shows the individual results from a repeated series of runs for either L–M or S gratings that differed by 30 deg. Except for the earliest sessions, in which the performance for the two was similar, the differences in the threshold ratios remained fairly constant. (Because of these initial practice effects, subject MW received extensive practice on all the conditions before his final data were collected.)

To ensure that the superior performance for the L–M gratings near threshold was not due to a luminance imbalance in the flicker settings for the L–M axis, the equiluminance ratio was reestimated with the following alternative procedure based on stimuli that were much more similar to those actually used in the measures of the discriminations. Switkes *et al.*[12] have shown that the presence of a threshold contrast chromatic grating has no effect on the detectability of a luminance grating. However, if our chromatic grating contained significant residual luminance contrast, then the presence of this artifact should sum with the luminance test grating to either raise or lower its detectability (depending on the relative phases of the color and luminance test gratings). For example, a bright-green–dark-red grating should facilitate the detection of a luminance grating (of the same average color) when the bright bars of the luminance test are superimposed upon the green, while reducing the detectability when the bright bars are added to the dimmer red. We therefore varied the relative luminances of the two component colors of the L–M color grating to find the balance that minimized any phase-specific interaction with the luminance test. (Since for our conditions the blue gun of the monitor contributed equally to both component colors, the titration only required that we vary the relative balance between the red and green guns.) The results of this procedure are shown in Fig. 12, in which we have plotted the contrast thresholds for the luminance test superimposed upon the color pedestal at either phase, as a function of the red–green balance. The revised equiluminance estimate (corresponding to the cross point of the two curves) differed only slightly from the initial flicker estimates (requiring a roughly 10% increase in the green–red gun ratio), and, not surprisingly, this small revision did not alter the discrimination–detection threshold ratios (as shown in Fig. 11 for the final two L–M grating runs). Thus it is unlikely that a luminance artifact in the chromatic gratings is responsible

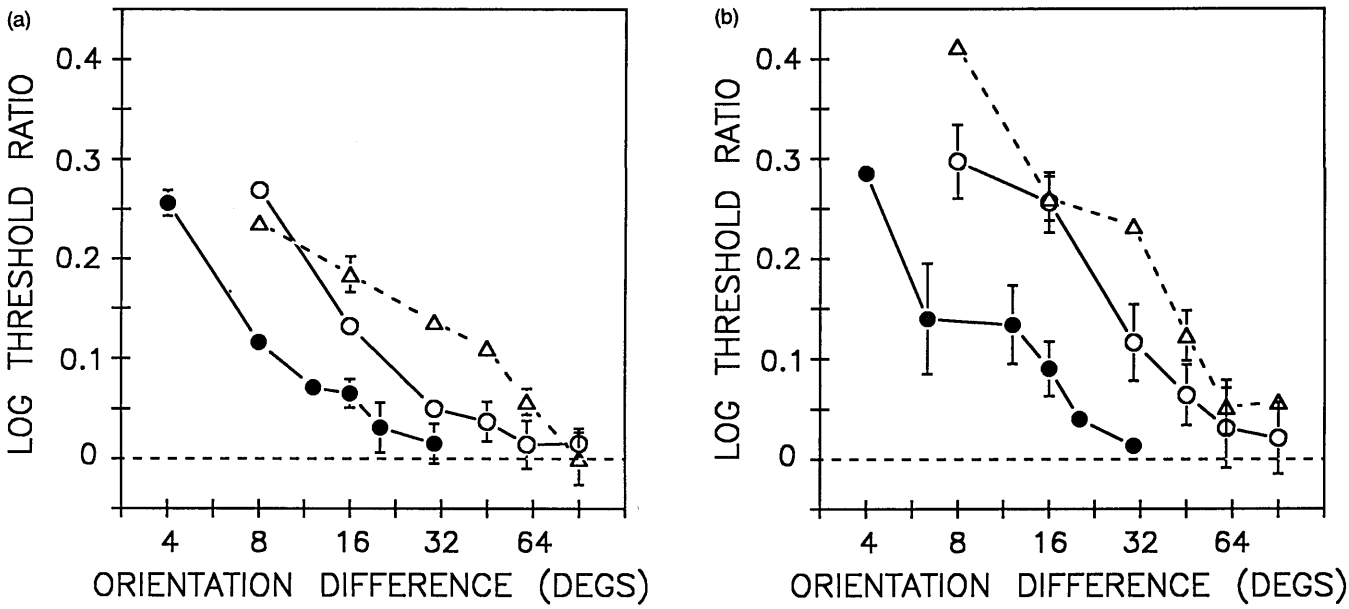

Fig. 10. Ratio of the discrimination to the detection contrast thresholds for the luminance (filled circles), L–M (open circles), or S gratings (open triangles): (a) results for subject MW, (b) results for subject SW.

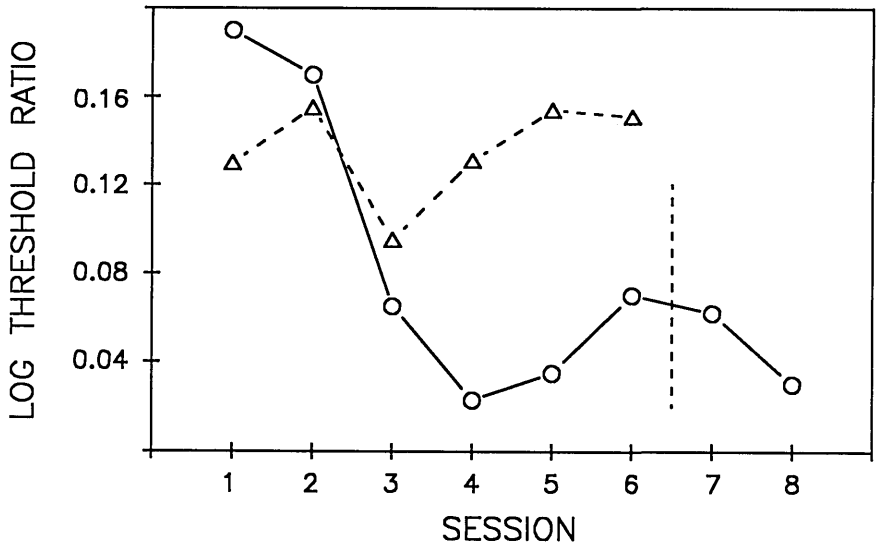

Fig. 11. Ratio of discrimination to detection contrast thresholds for a 30-deg orientation difference estimated from successive sessions: L–M gratings (open circles), S gratings (open triangles). The final two estimates for the L–M gratings were made with slightly revised estimates of the equiluminant balance of the colors. The observer was MW.

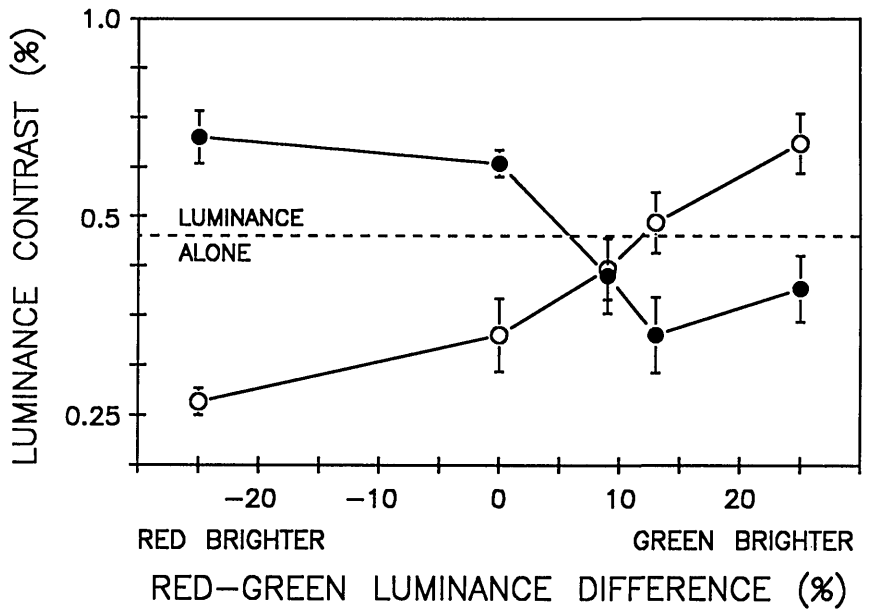

Fig. 12. Contrast thresholds for detecting a luminance grating superimposed upon a near-threshold contrast, L–M chromatic grating, as a function of the luminance balance between the red and green components of the color grating: bright bars of the luminance grating superimposed upon green bars of the color grating (open circles), bright bars superimposed on red bars of color grating (filled circles). The cross point of the two curves represents an estimate of the luminance balance for the red and green colors.

for the small differences that we found in orientation discrimination for the two types of color grating at near-threshold contrasts.

Spatial-Frequency Discrimination at Near-Threshold Contrasts

Figure 13 shows the results of similar measures for spatial-frequency discrimination for the two subjects. In this case the ratio of the discrimination to detection contrast thresholds has been plotted as a function of the difference in the frequency of the two gratings. For the luminance gratings a difference of from 0.75 to 1 octave was required in order for the two gratings to be discriminated reliably at the contrast detection threshold for subject MW, while the second observer (subject SW) required between 1 and 1.5 octaves. These values are comparable with previous measures of frequency discrimination for luminance gratings at near-threshold contrasts.[25,29] For the chromatic gratings, a somewhat larger frequency separation was required for reliable discrimination at detection threshold contrasts, but discrimination was nevertheless possible for a frequency difference of 1.5–2 octaves for both observers.

For these discriminations there were no obvious differences in the thresholds for the two different color gratings. These results therefore differ from the measures of orientation discrimination near threshold, which again were consis-

tently poorer for the gratings defined by the *S* color variation. As we noted, this difference was apparent for orientation only after subjects had received considerable practice on the task. Accordingly, for observer MW we made additional measures of the discrimination and detection thresholds for both color gratings for a 1-octave frequency difference. However, even after five separate sessions there was little change in the threshold ratios for either of the two patterns and therefore no consistent difference between them. Thus, whatever the basis of the differences that we found for orientation, they apparently do not reflect a general characteristic of spatial processing by the mechanisms responding to the L–M and S gratings.

Discrimination between the Luminance and Chromatic Gratings at Near-Threshold Contrast

The preceding results showed that observers could reliably discriminate the orientation and frequency of chromatic gratings even at the limit of the detection threshold, though this clearly required larger stimulus differences for color than for luminance gratings. As a final question, we also asked whether subjects could discriminate which type of grating had been presented at threshold contrast, for example, whether it varied in luminance or color or along which color axis. To test this, we again measured the contrast thresholds for both discriminating and detecting pairs of patterns. However, in this case the two possible gratings had the same orientation (vertical) and spatial frequency (2 c/deg) and thus differed only according to whether a luminance or color variation defined the pattern.

Results for one subject are shown in Fig. 14, in which the probability of detecting or discriminating the patterns is plotted as a function of contrast for each of the three possible combinations of gratings. Clearly, for each pair of gratings the contrast thresholds for discrimination and detection are similar. Reliable discrimination among these three stimulus dimensions at the detection threshold was previously reported by Krauskopf *et al.* for circular uniform fields.[30] The fact that they can also be accurately discriminated in the same patterns that permit discriminations of orientation and spatial frequency at threshold suggests that the mechanisms involved in the detection of these stimuli are selective for both spatial and chromatic information. Further, the ability to discriminate whether the patterns are defined by color or luminance at threshold provides a final control against the possibility that the spatial discriminations for the color gratings (at least near threshold) arise from an unintended luminance contrast in the chromatic gratings.

DISCUSSION

To summarize, we have found that observers can accurately judge the orientation or spatial frequency of patterns on the basis of the chromatic information in the stimulus. Spatial differences as low as 1 deg (orientation) or 4% (spatial frequency) could be reliably discriminated in the chromatic gratings; these differences were close to the thresholds for comparable luminance-varying stimuli. Further, except for orientation discrimination at contrasts near the detection threshold, the discrimination thresholds did not depend on the particular form of the color variation defining the pattern. Thus even equiluminant patterns that could be detected only by the S cones yielded equally low discrimination thresholds under most of the conditions that we tested.[31] Once differences in absolute sensitivity were compensated for by scaling the luminance and chromatic contrasts according to their respective threshold values, the spatial discriminations for luminance and color showed a similar dependence on stimulus contrast. These results therefore suggest that the visual processes subserving these discriminations are functionally similar for luminance and chromatic stimuli.

As we have noted, our nominally equiluminant chromatic stimuli undoubtedly included some residual luminance con-

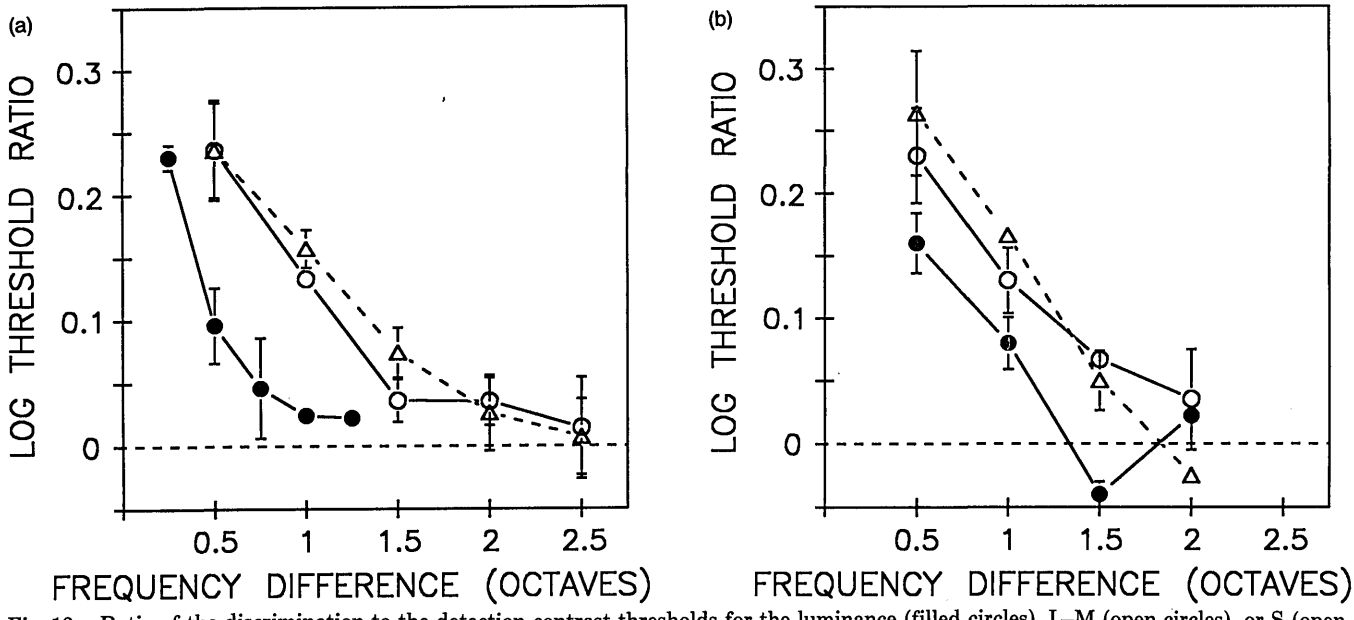

Fig. 13. Ratio of the discrimination to the detection contrast thresholds for the luminance (filled circles), L–M (open circles), or S (open triangles) gratings as a function of the difference in spatial frequency between the two gratings: (a) results for MW, (b) results for SW.

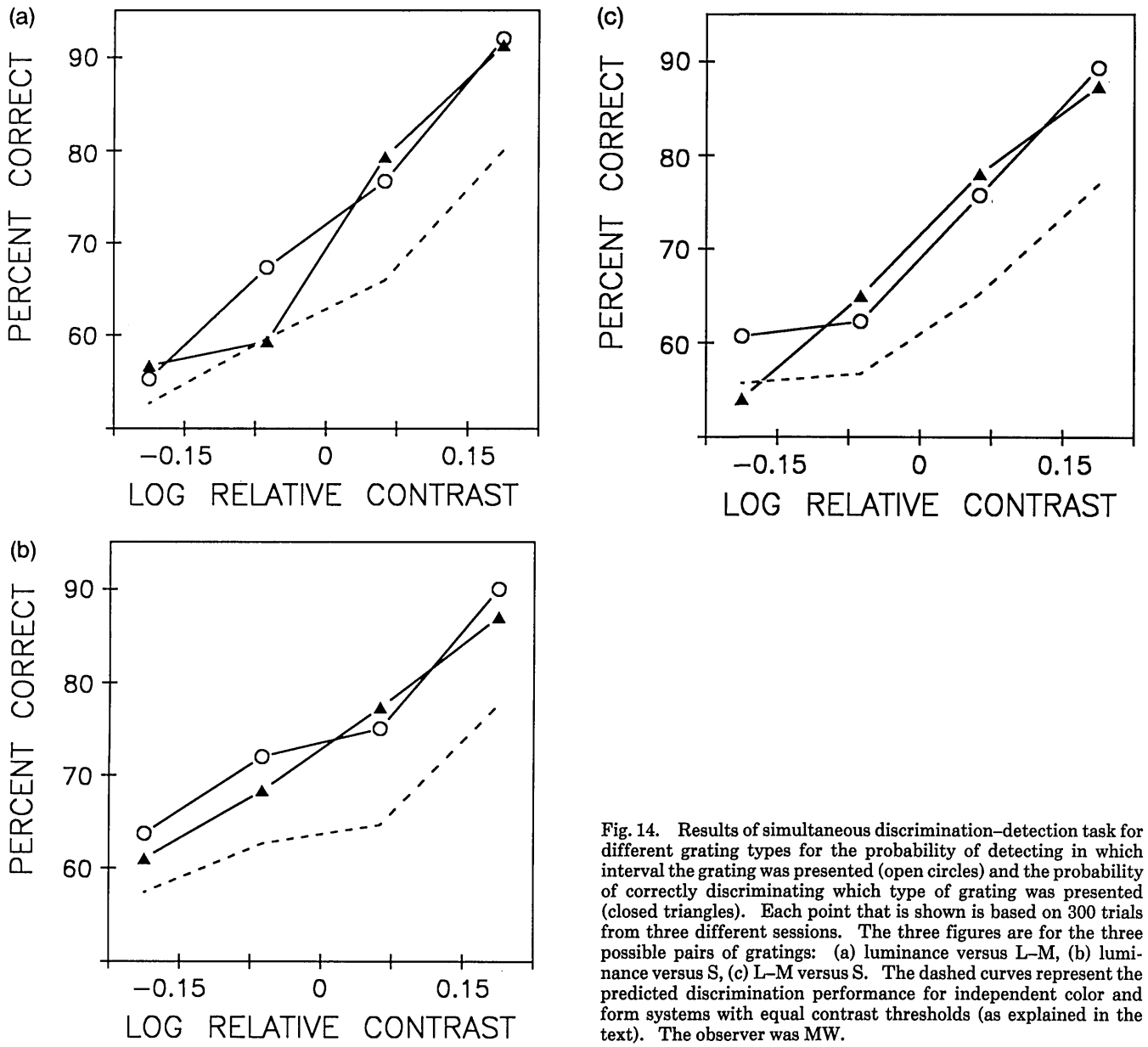

Fig. 14. Results of simultaneous discrimination–detection task for different grating types for the probability of detecting in which interval the grating was presented (open circles) and the probability of correctly discriminating which type of grating was presented (closed triangles). Each point that is shown is based on 300 trials from three different sessions. The three figures are for the three possible pairs of gratings: (a) luminance versus L–M, (b) luminance versus S, (c) L–M versus S. The dashed curves represent the predicted discrimination performance for independent color and form systems with equal contrast thresholds (as explained in the text). The observer was MW.

trast owing to factors such as lateral chromatic aberration and retinal inhomogeneities, neither of which we tried to correct. However, a number of our results argue against the possibility that this residual luminance contrast was responsible for the detection or discrimination thresholds for the chromatic gratings. At near-threshold contrasts, these results include the findings that (a) the detection thresholds for the luminance and chromatic gratings followed characteristically different functions of spatial frequency (Fig. 6); (b) the two different chromatic gratings were reliably discriminable both from the luminance grating and from each other at the detection threshold (Fig. 14); and (c) orientation discrimination for the L–M grating at threshold contrasts was not affected by the slight revisions in the equiluminance estimates required to minimize threshold summation between the L–M and luminance gratings (Figs. 11 and 12). At suprathreshold contrasts, our conclusion that the spatial discriminations for the chromatic gratings were based on chromatic contrast is supported by the findings that (a) the discrimination thresholds for the luminance and chromatic gratings reached different asymptotic levels (Figs. 4 and 5); (b) orientation discrimination for the *S* grating was unaffected by the addition of a long-wavelength adapting background, even though this greatly reduced luminance-contrast sensitivity [Fig. 4(a)]; (c) the differences between the discrimination thresholds for the luminance and chromatic gratings were largely independent of the type of color variation defining the pattern, though the potential sources of equiluminance errors make it likely that any residual luminance contrast was different for the two chromatic gratings (Figs. 4, 5, and 7); and (d) the differences in spatial-frequency discrimination thresholds between the luminance and chromatic gratings were similar for gratings ranging in frequency from 0.5 to 4 c/deg, even though the ratio of luminance to chromatic contrast sensitivity (and thus the potential salience of any luminance artifact) changed by a factor of

10 over this range (Figs. 6 and 7). Thus, taken together, these various results strongly suggest that subjects were in fact basing their spatial judgments on the chromatic content of the stimuli.

Some capacity to discriminate the orientation and spatial frequency of the chromatic gratings remained even when the contrasts of the gratings were at the level of the detection threshold. These threshold discriminations indicate that the mechanisms involved in signaling the presence of the chromatic stimuli can also convey spatial information. In turn, this result suggests that these chromatic detection mechanisms have some degree of orientation and spatial-frequency selectivity and that this selectivity is a labeled property of the channels. Orientation and frequency selective channels for color have also been indicated by both adaptation[32,33] and masking[12,34] procedures. Further, both orientation[35] and spatial-frequency[36] selective contrast adaptation effects have been demonstrated for the S-cone system isolated by chromatic adaptation.

It has been suggested that any tasks that can be performed well with isoluminant stimuli must involve the parvocellular visual pathways, for these pathways are much more sensitive to color variations than the magnocellular pathways.[37,38] On the other hand, under some conditions, cells in the magnocellular pathways appear to be more sensitive to luminance contrast, and this finding has led to suggestions that any visual task that can be performed well at low luminance contrasts must involve the magnocellular system. However, the present results show that the ability to discriminate the orientation and spatial frequency of gratings can be done well under both of these conditions. As a number of previous studies have shown, both orientation and frequency discriminations reach nearly asymptotic performance at low luminance contrasts.[16–18,20,21] For example, a contrast of 16 times threshold in Figs. 4 and 5 corresponded to a luminance contrast of only 6–8% for these subjects, yet there was little tendency for their accuracy to improve at higher levels. Again, however, the discrimination thresholds for the chromatic gratings were to a first approximation similar (averaging only 1.5 times higher than the luminance thresholds) and showed a similar dependence on stimulus contrast. This result suggests either that the parvocellular and magnocellular systems behave similarly with regard to these spatial discriminations or that the two stimulus conditions of low luminance contrast or equiluminant chromatic contrast, at least as we have used them, do not effectively isolate these two different systems.[39] Consistent with the second alternative, there are arguments to suggest that the parvocellular pathways do play some role in luminance vision at low contrasts[40] and may therefore be reflected under all the conditions that we have examined.

Livingstone and Hubel[38] have proposed that there may be two major subdivisions of the color-sensitive parvocellular system. According to their model one of these subdivisions, which is associated with the cytochrome oxidase blobs of striate cortex, mediates information about both color and brightness but not about form; the second subdivision, which is associated with the interblob regions, encodes spatial information based on both luminance and chromatic contrasts but is insensitive to the particular type of color or brightness variation that defines the pattern. Some dissociation of color and form is suggested by the results of a variety of psychophysical studies.[41] If the color and spatial properties of the patterns that we used were encoded by different systems, then one might expect only one of these attributes to be discriminable at the level of the detection threshold. However, we found that subjects were able to discriminate not only the orientation and spatial frequency of the patterns at threshold but also whether the patterns were luminance or color varying or whether the color variations were along an S or L–M chromatic axis. Even if these attributes were detected by two independent systems with identical contrast thresholds, the effects of probability summation would be expected to favor the detection task and should therefore lead to different contrast thresholds for discrimination and detection. This difference is indicated by the dashed curves in Fig. 14, which plot the predicted discrimination performance [P'(discriminate color)] under the assumption that the observed detection rate [P(detect), corrected for guessing] reflects probability summation between two independent and equally sensitive systems. In that case either the color or the form system (or both) might detect the grating on any given trial, but the color could be discriminated only when the stimulus is detected by the color system (or guessed when the stimulus is detected by the form system). Thus for those assumptions

$$P'(\text{discriminate color}) = 1 - [1 - P(\text{detect})]^{0.5}.$$

Clearly, these predictions fall consistently below the observed discrimination performance. Improving them by increasing the probability that the stimulus is detected by the color system results in correspondingly poorer predictions for the similar psychometric functions that we obtained for the discrimination of large orientation or frequency differences. Thus, instead, our results suggest that, at the level (presumably cortical) at which this task is determined, the mechanisms involved in detecting the patterns are both spatially and color selective and that they are labeled for both of these attributes.

Despite the fact that the orientation and spatial frequency of the color gratings could be precisely discriminated, these discriminations were consistently worse than for luminance gratings at comparable contrasts. Orientation discrimination and vernier acuity are often considered to be closely related judgments. Morgan and Aiba[42] obtained a difference of a factor of 3 between the vernier thresholds for luminance and chromatic bar stimuli. However, Mulligan and Krauskopf[43] found no difference in color and luminance vernier thresholds for conditions that were similar to those that we used.

The small differences that we found between the orientation and spatial-frequency thresholds for color and luminance could potentially be due to a number of different factors. To examine whether preneural factors might play a role in these differences, we used a program developed by Geisler[44] to calculate the discrimination thresholds for an ideal observer whose performance is limited only by quantal fluctuations and the known preneural properties of the visual system (including optics, lens and macular absorption, and receptor sensitivities and distributions). Predicted orientation and frequency discrimination thresholds were calculated for 2-c/deg luminance and chromatic gratings (truncated by a Gaussian envelope to avoid any effects of the stimulus edges on the thresholds). However, no differences were predicted in the discrimination thresholds for the luminance and L–M color gratings once their contrasts were

equated for equal multiples of their respective detection thresholds, and, for both types of grating, the discrimination thresholds decreased approximately linearly with increasing contrast. Thus the observed differences between the luminance and chromatic discrimination thresholds (and their tendency to level off by moderately low contrasts) presumably arise from postreceptoral factors. (For the theoretical stimuli that we examined, the predicted thresholds for the *S* grating were similar to those for the luminance and L–M gratings at low and intermediate contrasts but declined more slowly at higher contrasts. This difference apparently resulted from the substantially coarser sampling of the pattern by the S cones, which for these predictions were assumed to be regularly arrayed and constituted only 1/49 of the total cone population. Our failure to observe a comparable effect may be due to differences in the actual S-cone distributions or due to the dominant influence of other factors on the observed discrimination thresholds, such as those underlying the saturation of the thresholds at moderate contrasts.)

Many current models of orientation and spatial-frequency discrimination assume that the discriminations depend on or are limited by the properties of an array of orientation- and frequency-selective mechanisms.[29,45] Within a single mechanism, the accuracy with which information about orientation or frequency is represented is limited by the mechanism's tuning function and the signal-to-noise ratio of its response.[46] However, the fact that we scaled the contrasts of the luminance and chromatic patterns relative to their respective detection thresholds (and the fact that this scaling leads to similar contrast discrimination functions[12]) makes it unlikely that increased noise in the chromatic channels underlies the observed differences in the color and luminance discrimination thresholds (unless this noise difference is independent of the stages limiting detection[47]). On the other hand, our results are consistent with the possibility that the chromatic channels are less selective for orientation and spatial frequency and thus change their response less for a given difference in these dimensions. Both physiological[6,48] and psychophysical[33] studies have suggested that the mechanisms detecting chromatic patterns tend on average to have broader spatial tuning than luminance mechanisms. A scaled broadening of the tuning function of a single channel would be expected to result in a proportional increase in the channel's discrimination thresholds independently of contrast, which is a prediction that is close to the results that we obtained. The average ratio of ~1.5 for the color to luminance thresholds might therefore be consistent with spatial-tuning functions in the chromatic channels that were ~1.5 times as broad. However, a wide variety of factors may influence the actual relationship between the discrimination thresholds and the individual channel selectivities, and the differences that we have found between the color and luminance thresholds could also be due to other properties of the color and luminance systems. For example, the chromatic pathways might be less efficient at integrating the spatial information from different retinotopic regions.

The differences between the orientation discrimination thresholds for the S and L–M axes at near-threshold contrasts but not at higher levels suggest that these differences cannot be due to a single scaling difference in the orientation-tuning profiles of the mechanisms encoding the two types of pattern. Instead, one possibility is that the actual shapes of the profiles differ. For example, near the detection threshold the ability to discriminate different orientations may depend on the range of orientations that are likely to activate a mechanism at threshold contrasts, while at suprathreshold levels the more critical feature of the channels may be how steeply tuned the profiles are (regardless of the full bandwidths). Thus the observed results might be expected if the S-cone channels had broader overall bandwidths but similarly steep flanks in their tuning functions. Again, however, the differences that we found were limited only to orientation discriminations at a narrow range of near-threshold contrasts and were not found in comparable measures of spatial frequency discrimination. Thus for most conditions that we examined there are no measurable differences in the accuracy of spatial discriminations for stimuli defined by the different chromatic axes.

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