# The gap effect is exaggerated in parafovea

# MARINA DANILOVA<sup>1</sup> AND JOHN MOLLON<sup>2</sup>

<sup>1</sup>I.P. Pavlov Institute of Physiology, Laboratory of Visual Physiology, St. Petersburg, Russia <sup>2</sup>Department of Experimental Psychology, Cambridge University, Cambridge, United Kingdom

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## Abstract

In central vision, the discrimination of colors lying on a tritan line is improved if a small gap is introduced between the two stimulus fields. Boynton et al. (1977) called this a "positive gap effect." They found that the effect was weak or absent for discriminations based on the ratio of the signals of long-wave and middle-wave cones; and even for tritan stimuli, the gap effect was weakened when forced choice or brief durations were used. We here describe measurements of the gap effect in the parafovea. The stimuli were 1 deg of visual angle in width and were centered on an imaginary circle of radius 5 deg. They were brief (100 ms), and thresholds were measured with a spatial two-alternative forced choice. Under these conditions we find a clear gap effect, which is of similar magnitude for both the cardinal chromatic axes. It may be a chromatic analog of the crowding effect observed for parafoveal perception of form.

Keywords: Color vision, Chromatic discrimination, Gap effect, Proximity factor, Periphery, Crowding

## Introduction

## The foveal gap effect

When an observer is asked to discriminate the luminances of abutting foveal fields, as in classical photometry, his precision deteriorates as soon as a small separation is introduced between the two fields (Le Grand, 1933; Walsh, 1958; Traub & Balinkin, 1961; Sharpe & Wyszecki, 1976). In the case of color, however, the introduction of a thin line between two foveal fields may not impair discrimination (Traub & Balinkin, 1961; Sharpe & Wyszecki, 1976) and indeed may actually improve it (Malkin & Dinsdale, 1972). Boynton et al. (1977) introduced the term *gap effect* for the "phenomenon of altered discriminability due to a separation between fields." They spoke of a positive gap effect when discriminability was improved and a negative effect when discriminability was impaired.

Using semicircular foveal fields and a gap of 2.7 min of visual angle, Boynton and his colleagues found for luminance discrimination the negative gap effect reported by traditional photometrists. They found a positive gap effect for color discrimination along a tritan line, that is, for discrimination when only the signal of the short-wavelength (S) cones is varying. For discrimination along a deutan line, where only the ratio of the signals of the long-wavelength (L) and middle-wavelength (M) cones is varying, they found a small negative gap effect. Even for the tritan axis, the gap effect was not found when a forced-choice procedure was

found that the gap effect was reduced at short exposures. To explain the negative gap effect found for the discrimination of luminance or lightness, it is plausible to suppose that the

used to measure the thresholds. Montag (1997) did find a (reduced) gap effect when forced choice was used. Eskew (1989)

of luminance or lightness, it is plausible to suppose that the observer achieves the finest performance by using an edge signal deriving from the boundary between the two fields that are being compared. Such a signal would be provided by ganglion cells with antagonistic center-surround receptive fields. To explain the positive gap effect found for some color discriminations, it is traditional to suppose that chromatic signals are integrated spatially over a significant area and that the introduction of a gap between the stimulus fields serves to delimit this integration, thus preventing pollution of one chromatic signal by the other (e.g. Boynton et al., 1977; Montag, 1997). It is possible that the gap effect shares this explanation with the improvement of chromatic discrimination that is produced by coincident luminance contrast (Hilz et al., 1974; Eskew et al., 1991). However, there exists no detailed physiological model of how the chromatic integration is delimited by signals from contours or edges.

# The gap effect in the parafovea

In a recent study, concerned primarily with how observers compare stimuli that are distantly separated in the visual field, we found a robust gap effect for color discrimination in the parafovea (Danilova & Mollon, 2006). The stimulus patches were sectors of an imaginary annulus centered on the fixation point. The sectors were 2-deg wide at their center, and their centers fell at a constant eccentricity of 5 deg from the fixation point. We found that discrimination thresholds were highest when the edges of the sectors were touching.

Address correspondence and reprint requests to: Marina Danilova, Pavlov Institute of Physiology Nab. Makarova 6, St. Petersburg 199034, Russia. E-mail: dan@pavlov.infran.ru

We report separate measurements for discriminations along the two cardinal axes of color space (MacLeod & Boynton, 1979; Krauskopf et al., 1982). One axis corresponds to the phylogenetically ancient subsystem of color vision, and, at equiluminance, discrimination on this axis depends only on the signal of the short-wave cones. The other axis corresponds to the phylogenetically recent subsystem, and color discrimination on this axis depends on the ratio of the signals of the long-wave and middlewave cones (Gouras, 1984; Mollon et al., 1990).

In the case of the short-wave system, it is of interest to compare increments and decrements in stimulation of the short-wave cones, since it is thought that the two types of stimulus are signaled by morphologically distinct ganglion cells, which have dendritic fields of different size: the short-wave ON signal is carried by the small bistratified ganglion cell, whereas the corresponding OFF signal is carried by a monostratified ganglion cell (Dacey & Lee, 1994; Dacey et al., 2002). The latter has a larger but sparser dendritic field than the former. Psychophysically, Vassilev et al. (2003) have found that Riccó's area is greater for decrements than for increments, although only at eccentricities greater than used here. We therefore made different series of measurements for cases where the referent stimulus corresponded to an increment in S relative to an adapting field and cases where it corresponded to a decrement in S. There are similarly believed to be separate channels for signaling opposite changes in chromaticity along the L/M axis (Sankeralli & Mullen, 2001), although they are not known to differ in their spatial properties. So we have also made separate measurements for cases where the equiluminant referent stimulus corresponds to an increase in L (and decrease in M) relative to an adapting field and cases where it corresponds to a decrease in L (and increase in M).

### Materials and methods

#### Apparatus and stimuli

Stimuli were presented on a Sony Triniton 21-inch monitor (GDM-F500) and were generated by a VSG 2/5 graphics board (Cambridge Research Systems, Rochester, UK), allowing a precision of 15 bits per gun. The refresh rate of the screen was 80 Hz.

The cathode ray tube (CRT) screen was viewed binocularly from a distance of 57 cm. A steady background field was always present. The discriminanda were sectors of an annulus, and their centers lay on an imaginary circle that had a radius of 5 deg of visual angle (see Fig. 1). The imaginary circle was centered on a continuously present fixation point. The width of each target sector at its midpoint was 1 deg, and its radial length was 2 deg. On any trial, the midpoint of the two patches lay on a radius that had a random angle chosen in steps of 5° starting from 12 o'clock. Throughout this paper, the separation of the stimuli is expressed as the distance between the midpoints, and so the sectors are juxtaposed when the separation is 1 deg. The duration of the stimulus patches was 100 ms, a duration chosen to be too short to allow eye movements between them.

We represent our stimuli in a chromaticity diagram (Fig. 2) designed to be analogous to the diagram of MacLeod and Boynton



**Fig. 1.** A black-and-white example of the stimuli used in the experiments. The centers of the two stimulus patches lie on an imaginary circle indicated by the broken line. One stimulus, chosen at random, is the referent stimulus, and the other is the test or variable stimulus. The separation of the two stimuli is expressed as the distance between their centers in degrees of visual angle. The radial length of each stimulus sector is 2 deg, and its width at its midpoint is 1 deg. A central fixation point is continuously present. A thin bar marker, concurrent with the test and referent stimuli, points to the more clockwise of the two.

(1979) but constructed from the Stockman-Sharpe 10-deg fundamentals (Stockman & Sharpe, 2000), which are appropriate for our extrafoveal targets. To retain as far as possible the familiar structure of the MacLeod-Boynton diagram, we have scaled the Stockman-Sharpe 10-deg L and M fundamentals to have the same relative heights as the 2-deg fundamentals of Smith and Pokorny (1975), which were used to construct the classical MacLeod-Boynton diagram, and we have scaled S to give a value of 1.0 at the maximum value of S/(L+M), as in the classical diagram. As an analogue of Judd(1951) luminance, we took the sum of the scaled long-wave and middle-wave signals (L+M). One of our background fields (Field E in Fig. 2) had a chromaticity equivalent to that of equal-energy white and had a CIE luminance of approximately 10 cd.m<sup>-2</sup>. Our remaining backgrounds and our test and referent stimuli were adjusted to have the same value of (L+M) as the equal-energy white background. Calibrations were performed with a Spectrascan 650 spectroradiometer.

# Procedure

We separately measured thresholds along the two cardinal axes of color space (Krauskopf et al., 1982), which correspond to the two axes of the modified MacLeod-Boynton diagram (Fig. 2). In Experiment 1, the ratio of the long-wave and middle-wave cone signals was held constant, and only the signal of the S cones was varied. In Experiment 2, the value of L/(L+M) was varied, and the signal of the S cones was held constant.

At the beginning of an experimental session, the subject adapted to the steady background for 1 min before measurements began. Thresholds were measured by a method of two-alternative spatial



**Fig. 2.** Chromaticity diagram representing the referent stimuli and the backgrounds. The diagram is an analog of the standard MacLeod-Boynton diagram but is constructed from the 10-deg Stockman-Sharpe (2000) fundamentals. The left-hand panel shows the locations of the referent and background values for Experiment 1 (discrimination on the S axis), while the right-hand panel shows the corresponding values for Experiment 2 (discrimination on the L/M axis). G and R denote the chromaticities of the green and red phosphors of the monitor, and the solid lines delimit the gamut of the possible colors that the monitor can produce.

forced choice. When the S axis was being tested, the subject's task was to indicate by pushbuttons whether the more clockwise of the two stimuli was the bluer or the less blue. When the L/M axis was tested, the subject indicated whether the more clockwise stimulus was redder or greener than the other stimulus. On any trial, one stimulus was conceptually the referent stimulus and the other was the test stimulus, but the subject could not predict which of the two would be in the more clockwise position. Tone signals indicated to the subject whether his or her response was correct or incorrect.

In Experiment 1, S-cone discrimination was measured under four conditions, which were tested in separate, counterbalanced, experimental sessions. In each condition, there was a referent stimulus (either Ref 1 or Ref 2) of fixed chromaticity (see Fig. 2, left-hand panel, and Table 1), and thresholds were measured as increments in S-signal from the referent value. In two of the four conditions, the targets were presented on a background with the chromaticity of equal-energy white (Field E in Fig. 2); Ref 1 corresponds to a decrement in S excitation relative to this field, while Ref 2 corresponds to an increment. In the remaining two conditions, Ref 1 was presented on a background (Field 1) of lower S value, and Ref 2 was presented on a background (Field 3) of higher S value. Since we wished to measure the discrimination of hue rather than the discrimination of saturation, the referent and test stimuli have an L/(L+M) value of 0.7 rather than the value of the background fields, which all have the same value as equalenergy white (0.656). Our purpose in using the same referent stimuli on more than one background was to examine whether the gap effect differed according to whether the referent represented an increment or a decrement relative to the S value of the background.

In Experiment 2 we examined the L/M axis of color space, using an analogous design. In two of four counterbalanced conditions, the referent stimuli Ref 1 and Ref 2 were presented on a background (Field E) with the chromaticity of equal-energy white (see Fig. 2 right-hand panel, and Table 1). In a third condition, Ref. 1 was presented on a background of lower L/(L+M) value (Field 1), and in a fourth condition Ref 2 was presented on a background of higher L/(L+M) value (Field 3).

In Experiment 3 the two cardinal axes were explicitly compared in alternating sessions. For each axis we used just one referent (Ref 2 in each case), and in both cases the background had the chromaticity of equal-energy white (Field E in Fig. 2).

Within a single block of trials, the separation of the stimulus patches was held constant. An experimental session, lasting 20–

	L/(L+M) coordinate	S/(L+M coordinate
Di	scrimination in S direction	on
Ref 1	0.70	0.021
Ref 2	0.70	0.033
Field 1	0.656	0.0168
Field 2 (E)	0.656	0.0262
Field 3	0.656	0.0410
Di	scrimination in L direction	on
Ref 1	0.640	0.0036
Ref 2	0.672	0.0036
Field 1	0.624	0.0262
Field 2 (E)	0.656	0.0262
Field 3	0.689	0.0262

**Table 1.** Chromaticities of referent and background

 stimuli used in the experiments<sup>a</sup>

<sup>a</sup>The coordinates are constructed from the Stockman-Sharpe (Stockman & Sharpe, 2000) 10-deg fundamentals and are designed to be analogs of MacLeod-Boynton (MacLeod and Boynton, 1979) coordinates (see text). 30 min, consisted of nine blocks, in which different spatial separations were tested in random order. At the minimum separation of 1 deg between the midpoints of the test and referent sectors, there was no gap between their edges. The maximum separation was 5.63 deg between the midpoints. In Experiments 1 and 2, we included a tenth condition, which could occur anywhere but first in the random sequence of blocks: the computer program was exactly the same except that the less clockwise stimulus was suppressed on every trial and the subject was asked to base a decision on the single stimulus presented as if the second had been present. This "absolute judgment" condition allowed us to check that subjects were truly comparing the two stimuli in the primary conditions and not simply basing their judgment on one of them (Danilova & Mollon, 2003, 2006). Thresholds in this condition were invariably higher than those obtained when two, maximally separated, stimuli were present, suggesting that subjects were actively comparing the two patches in the primary conditions.

In each block of trials, the difference between the test and referent stimuli was adjusted according to an adaptive staircase rule: after three correct responses, the difference was reduced, and after an incorrect response, it was increased. This three-to-one rule converges to 79.4% correct responses (Wetherill & Levitt, 1965). The step size was 10% of the difference between test and referent. Data from the first 5 reversals of the staircase were not used, and

the subsequent 10 reversals were averaged to give an estimate of the threshold. Each data point in the figures is based on at least six independent threshold estimates from different experimental sessions.

#### Subjects

All subjects had normal color vision as tested by the Cambridge Colour Test (Regan et al., 1994). All except J.M. were female, and all except M.D. and J.M. were unaware of the purpose of the experiment and were paid for their participation.

## Results

#### Experiment 1: Discrimination on the S axis

In Fig. 3 we show thresholds for the S axis as a function of the log center-to-center distance of the stimulus patches. In each panel, data are shown separately for the four combinations of referent and background chromaticities. Note that the ordinate scales vary in order to accommodate individual differences in absolute sensitivity.

With only one exception in 16 data sets, a positive gap effect is observed, in that the threshold is highest when the two stimulus patches are abutting, that is, when the center-to-center separation is



Fig. 3. Individual results for Experiment 1 (discrimination on the S axis). The four panels show results for individual observers. The abscissa in each case shows the spatial separation between the centers of referent and test stimuli, expressed on a logarithmic scale. When the separation of the midpoints is 1 deg, the edges of the stimuli are abutting. The ordinate shows the threshold as a percentage change in the S-cone signal. The error bars represent  $\pm 1$  SEM and are based on between-session variance. The four data sets in each panel correspond to the four combinations of referent and background chromaticity (see legend and Fig. 2). The fitted smooth curves are inverse third-order polynomials and are not intended to have theoretical significance.

1 deg of visual angle. One of our naive observers (I.K.) spontaneously reported that the colors of the two patches spread into one another when they were abutting and gave some average color. This was certainly the impression of the two authors (M.D., J.M.), for both chromatic axes.

One-way analyses of variance (ANOVAs) were applied to the individual data sets, and in all but one case there was a significant effect of stimulus separation (2.1 < F(8) < 21.7, 0.0001 < P < 0.05). *Post hoc* Tukey tests showed that in all but two cases, the threshold for minimum separation (leftmost data point) differed significantly from at least one point in the middle of the range, where the midpoints of the stimuli were separated by 2–3 deg. Most of the gain in sensitivity occurs rapidly, as the separation increases from its minimum value of 1 deg (edges touching) to a value of 1.3 deg: by Tukey tests, the second data point never differs significantly from the remaining points.

In Fig. 4 the data have been averaged across subjects and across conditions to show separately the mean thresholds for those cases where the referent corresponded to an increment in the S value of the field and those cases where it corresponded to a decrement. The two functions have similar forms: in both cases there is a clear gap effect and a minimum threshold when the stimulus patches are separated by 2.74 deg. In the region of the minimum, the average thresholds have a value approximately half the values obtained with no gap. A repeated-measures two-way ANOVA showed a significant effect of separation (with Greenhouse-Geisser correction, F = 11.3, d.f. = 1.239, P < 0.05) and a significant difference between increments and decrements (F(1) = 12.1, P < 0.05).

The absolute difference seen in Fig. 4 between contrast thresholds for incremental and decremental cases could be attributed to the different adaptive states of the eye when Field 1 or 3 is in use, although it is still apparent in the case of the equal-energy white field (E) where the referent stimulus represents a decrement or an increment in the S signal from the same background (compare filled circles and open squares in Fig. 3). But is the spatial extent



separation between the centers, degrees of visual angle

**Fig. 4.** Average results for incremental and decremental targets in Experiment 1 (discrimination on the S axis). Data have been averaged across the four observers. The abscissa shows the spatial separation between the centers of referent and test stimuli, expressed on a logarithmic scale, and the ordinate shows the log S-cone contrast at threshold. The error bars represent  $\pm 1$  SEM and are based on intersubject variance; their size reflects the absolute differences between subjects' thresholds. The curves fitted to the data points are inverse third-order polynomials and are not intended to have theoretical significance.

of the gap effect different in the two cases? From Fig. 4 it appears that the initial drop in threshold at small separations is more rapid for increments than for decrements, a difference that might reflect the different dendritic fields of the ganglion cells that carry the incremental and decremental S signals (see introduction). However, the interaction between the factors separation and increment *vs.* decrement—which would correspond to a difference in shape of the function—is not significant after a correction is made for nonsphericity (with Greenhouse-Geisser correction, F = 5.6, d.f. = 1.50, P = 0.085).

#### Experiment 2: Discrimination on the L/M axis

The data of Fig. 5 are analogous to those of Fig. 3 but are for discrimination along the horizontal axis of the chromaticity diagram. Two subjects completed all four conditions. Different combinations of referent and background give small differences in absolute sensitivity, but the functions all have a similar form. In all data sets, a clear positive gap effect is seen, in that the threshold is highest when the sectors abut one another. One-way ANOVAs were applied to the individual data sets, and in all cases there was a significant effect of stimulus separation (3.9 < F(8) < 9.3, P <0.0001). Post hoc Tukey tests showed that in all but one case the threshold for minimum separation (leftmost data point) differed significantly from at least one of the data points in the middle of the range, when the midpoints of the stimuli were separated by 2-3 deg. As on the S axis, most of the gain in sensitivity occurs rapidly, as the separation increases from its minimum value of 1 deg (edges touching) to a value of 1.3 deg: by Tukey tests, the second data point never differs significantly from the remaining points.

As is classically found (Wyszecki & Stiles, 1982), the absolute values of the thresholds on this axis are much lower than those obtained when only the short-wave signal is varied: the minimal values are here well under 1%, even though the stimuli are parafoveal and only 100 ms in duration.

In Fig. 6 the data have been averaged across subjects and across conditions to show separately the mean thresholds for those cases where the referent corresponded to an increment in the L value of the field and those cases where it corresponded to a decrement. Error bars are omitted, since the data are drawn from only two subjects, whose thresholds have different absolute values.

The size of the improvement seen for the L/M axis is similar to that found for the short-wave axis: near the minima of the functions, the average thresholds have values approximately half those obtained when the edges are adjacent (compare Figs. 4 & 6). The functions for incremental and decremental stimuli are similar to one another. Two-way ANOVAs, performed separately for each subject, showed highly significant effects of separation (M.D.: F(8) = 15.1, P < 0.001; N.T.: F(8) = 25, P < 0.001) and of increment *vs.* decrement (M.D.: F(1) = 27.4, P < 0.001; N.T.: F(1) = 40.3, P < 0.001). The interaction was nonsignificant in both cases; that is, we cannot reject the hypothesis that the spatial functions have the same form for incremental and decremental stimuli.

#### Experiment 3: Comparison of axes

Long tradition holds that integration areas are greater for the signals deriving from the short-wave cones than for signals deriving from the long- and middle-wave cones (Stiles, 1949; Brindley, 1954; Regan & Mollon, 1997). And in the fovea, the positive gap



**Fig. 5.** Individual results for Experiment 2 (discrimination on the L/M axis). The two panels show results for individual observers. The abscissa in each case shows the spatial separation between the centers of referent and test stimuli, expressed on a logarithmic scale. The ordinate shows the threshold as a percentage change in the L-cone signal. The error bars represent  $\pm 1$  SEM and are based on between-session variance. The four data sets in each panel correspond to the four combinations of referent and background chromaticity (see legend and Fig. 2). The fitted smooth curves are inverse third-order polynomials and are not intended to have theoretical significance.

effect is more prominent for the S axis (Boynton et al., 1977), while the Liebmann effect—the melting of one color into another (Liebmann, 1927; West et al., 1996)—is also a characteristic of foveal color pairs that lie along a tritan line (Tansley & Boynton, 1976). Moreover, the effects of chromatic aberration are likely to be greater for our S-cone stimuli, since in this case it is largely the blue phosphor of the monitor that is modulated. We were therefore interested in asking whether a larger gap is required for optimum performance on the S axis of color space than for discrimination on the L/M axis. The results of Experiments 1 and 2 suggest that any difference is small, but these data were obtained in different



Fig. 6. Average results for incremental and decremental targets in Experiment 2 (discrimination on the L/M axis). The plots show data averaged across observers. The abscissa shows the spatial separation between the centers of referent and test stimuli, expressed on a logarithmic scale, and the ordinate shows the log L-cone contrast at threshold. The smooth curves fitted to the data points are inverse third-order polynomials and are not intended to have theoretical significance.

experimental series and for different subjects. In a third experiment, therefore, we compared the gap effects for incremental stimuli on the two axes. For both conditions, the background had the chromaticity of equal-energy white (i.e. Field E in Fig. 2), and the referent stimuli corresponded either to an increment in the S value of the field or to an increment in its L/(L+M) value (i.e. Ref 2 in each panel of Fig. 2). For six subjects (M.D., J.M., ED, N.T., I.K., I.B.), these two conditions were tested in alternating runs. Each subject completed at least nine repetitions of each condition.

Average data for six subjects are shown in Fig. 7. The upper panel shows the thresholds for the two chromatic axes, plotted on the same logarithmic scale. Although there is the expected difference in absolute sensitivity for the two axes, the forms of the two functions are very similar. In order to compare directly the two functions, the thresholds are reexpressed in the lower panel as ratios of the threshold at minimum separation. From the lower panel, it can be seen that the two chromatic axes show no systematic difference at small separations: the gap effect is similar in magnitude and in spatial extent. At larger separations, there is a tendency for L/M thresholds to rise more quickly than do thresholds on a tritan line.

In order to give similar standard deviations for the two axes, the subjects' mean scores for each conditions were log transformed, and a repeated-measures two-way ANOVA was then performed on the transformed data. There were highly significant effects of separation (F(8) = 33.6, P < 0.001) and of chromatic axis (F(1) = 496.4, P < 0.001), but the interaction of these factors was not significant after correction for nonsphericity (with Greenhouse-Geisser correction F = 2.79, d.f. = 2.525, P = 0.09).

The short-wave pathway has sometimes been held to respond more slowly than the pathway that carries the L/M chromatic signal (Cottaris & De Valois, 1998; McKeefry et al., 2003; but cf. Smithson & Mollon, 2004). Although our subjects were not asked to respond as quickly as possible, our program automatically records the actual response time for every trial, and it is of interest to compare the response times for the two chromatic axes and for different spatial separations.



**Fig. 7.** Results for Experiment 3 (counterbalanced comparison of discriminations on the two cardinal axes). The upper panel shows the thresholds for S and for L/M axes, expressed on a logarithmic scale in order to accommodate the differences in absolute sensitivity. In the lower panel, to allow a direct comparison of the relative shapes of the functions for the two axes, thresholds are reexpressed as a ratio of the threshold when the edges of the sectors are abutting. The error bars represent  $\pm 1$  SEM and are based on intersubject variance. The smooth curves fitted to the data points are inverse third-order polynomials and are not intended to have theoretical significance.



Fig. 8. Mean response times in Experiment 3. The error bars represent  $\pm 1$  SEM and are based on intersubject variance. The smooth curves fitted to the data points are inverse third-order polynomials and are not intended to have theoretical significance.

Average response times for the six subjects are shown in Fig. 8. Although the figure suggests that responses are slower for the short-wave axis, this difference is present for only five of the six subjects, and a repeated-measures two-way ANOVA shows no significant effect of axis (F(1) = 2.9, ns). Spatial separation, however, has a significant effect on response time (with Greenhouse-Geisser correction F = 4.97, d.f. = 2.1, P < 0.05). Inspection of Fig. 8 suggests that subjects have longest response times at the short separations, where their thresholds are highest.

#### Discussion

#### The parafoveal gap effect

Our results reveal a reliable gap effect for chromatic discrimination in the parafovea. By "gap effect," we refer to the fall in threshold over small separations (the subsequent rise in threshold at greater separations is discussed separately below). Whereas the foveal gap effect is obtained easily only for the S axis and is attenuated or abolished when brief flashes or forced-choice methods are used, we here find a clear effect for both axes, using brief (100-ms) flashes and a spatial forced-choice procedure. It is interesting that Eskew et al. (1991) found that the enhancement of color discrimination by a luminance pedestal—a phenomenon perhaps related to the gap effect—was similarly more marked in the parafovea.

Despite the extensive evidence that integration areas are greater for the short-wave cone system, the parafoveal gap effect has a similar spatial extent for increments along the two axes (Fig. 7). It remains to be seen whether this is also true for decrements. For discriminations based on the signal of the short-wave cones, there is a suggestion in the data of Fig. 4 that decremental thresholds change more slowly at small separations than do incremental thresholds—a result that might be related to the different dendritic field sizes of the neurons thought to carry the two signals.

It is interesting to draw an analogy between our parafoveal gap effect and the crowding effect that is observed for discrimination of form at a similar eccentricity (Hess & Jacobs, 1979; Wolford & Chambers, 1984). There may be an obligatory spatial integration of chromatic information that is analogous to the second-stage integration of features thought to underlie the crowding effect (Levi et al., 2002; Pelli et al., 2004). A similar phenomenon is the compulsory pooling of signals for orientation when a group of gabor patches is presented at an eccentricity of 2.5 deg (Parkes et al., 2001).

In its spatial extent, the present gap effect does resemble the crowding effects seen for parafoveal spatial vision. By Bouma's rule, the crowding of letters occurs for separations up to half the eccentricity (Bouma, 1970), and the present results would be roughly consistent with such a rule, in that thresholds are elevated when the total array subtends less than 2.5 deg at an eccentricity of 5 deg. However, a simple averaging account would not explain why most of the gain in sensitivity is introduced by a thin gap that is small relative to the total extent of the two stimulus patches. Our smallest gap subtends only 0.3 deg. Thus, as in the foveal case, the gap seems to have its effect by differentiating the two chromatic samples and inhibiting an averaging process.

## The rise in threshold at large separations

Most of the functions in Figs. 3 to 7 show a shallow minimum with a further rise in sensitivity at large separations. Fig. 7 suggests that this rise may be steeper for the L/M axis than for the tritan axis, a result that is also apparent in our earlier measurements with larger stimulus patches (Danilova & Mollon, 2006, Fig. 4).

A recurrent idea in visual science is that spatial integration occurs at very small separations and lateral inhibition at somewhat greater separations (e.g. Rentschler & Fiorentini, 1974). In the present case, an averaging process may elevate thresholds at short separations, but at intermediate separations there may be lateral inhibitory interactions that enhance stimulus differences. These longer range interactions may be the same as those that underlie spatial color contrast and color constancy. The slow loss of sensitivity at large separations may then reflect an increasing attenuation of such long-range interactions.

The threshold elevation at large separations could alternatively be explained in terms of the rate of translation of attention. It has been held that selective attention takes time to travel across the internal representation of the visual field and that the time required is a positive function of the distance in the corresponding external stimulus (Kosslyn et al., 1978). Our stimuli are brief (100 ms), and thus the subject's judgment is likely to be based on a decaying iconic representation that outlives the stimulus. If the comparison process requires that attention is successively directed to one target and then to the other, and if the rate of displacement of attention is relatively slow, then the mild impairment of discrimination at large separations could be attributed to the increased decay of the internal representation that would take place before the comparison process was complete. The results of Fig. 8 argue against this hypothesis: there is no indication that response times increase at large separations, as might be expected if the total response time included a variable component that was due to translation of attention across the visual field.

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