

Mesopic luminance assessed with minimally distinct border perception

Sabine Raphael

Department of Psychology,
University of California at San Diego, La Jolla, CA, USA
Institute of Neuroscience, Newcastle University,
Newcastle upon Tyne, UK



Donald I. A. MacLeod

Department of Psychology,
University of California at San Diego, La Jolla, CA, USA



In photopic vision, the border between two fields is minimally distinct when the two fields are isoluminant; that is, when the achromatic luminance of the two fields is equal. The distinctness of a border between extrafoveal reference and comparison fields was used here as an isoluminance criterion under a variety of adaptation conditions ranging from photopic to scotopic. The adjustment was done by trading off the amount of blue against the amount of red in the comparison field. Results show that isoluminant border settings are linear under all constant adaptation conditions, though varying with state of adaptation. The relative contribution of rods and cones to luminance was modeled such that the linear sum of the suitably weighted scotopic and photopic luminance is constant for the mesopic isoluminant conditions. The relative weights change with adapting intensity in a sigmoid fashion and also depend strongly on the position of the border in the visual field.

Introduction

Vision in the mesopic range is determined by the joint rod and cone responses. Here we examine how rods and cones combine their signals under a variety of adaptation conditions to form an achromatic luminance signal and how this signal is influenced by the state of adaptation. The motivation of our research is rooted in practical photometry especially in twilight conditions. Luminance is conventionally defined by CIE spectral sensitivity curves $V_{10}(\lambda)$ and $V'(\lambda)$ for large field photopic (cone) and scotopic (rod) vision, respectively. Since the photopic function is additively related to the cone sensitivities (see for instance Stockman, MacLeod, & Johnson, 1993) luminance in the photometric sense shows little influence of chro-

matic opponent signals. Determining luminance under dim light conditions involves challenges due to the different temporal behavior and spatial distribution of rods and cones (MacLeod, 1972; Stockman & Sharpe, 2006; Vienot & Chiron, 1992).

Here we examine the method of minimizing the distinctness of a border as a possible way to assess mesopic luminance under adaptation conditions ranging from photopic to scotopic. We ask how rod and cone contributions to this measure of achromatic luminance are influenced by rod and cone adaptation and the retinal position.

The criterion of border distinctness as a photometric method was described by Fraunhofer (1824) as early as 1824. Not until the late 1960s was the method extensively used by other scientists (e.g., Boynton & Kaiser, 1968). In this method, two adjacent fields are equated by minimizing the visibility of the border between them rather than by a comparative brightness judgment. For lights of the same chromaticity, the border between the two fields will completely disappear at equal luminance. When judging the border between two differently colored fields, the patches will not merge to one field but the border will at some point be minimally visible. At this minimum distinct border (MDB) the achromatic luminance of the two comparison fields will be equal. Here we investigate the feasibility of employing this simple method for the assessment of mesopic luminance, at light levels and retinal locations where the rod and cone systems are both influential.

Since the MDB method produces luminosity functions that resemble closely Judd's modified CIE photopic sensitivity function obtained by flicker photometry, it was concluded that border matches are accomplished with the same visual information as

Citation: Raphael, S., & MacLeod, D. I. A. (2015). Mesopic luminance assessed with minimally distinct border perception. *Journal of Vision*, 15(9):12, 1–14. doi:10.1167/15.9.12.

flicker matches, namely the achromatic luminance information only (Kaiser, 1971; Wagner & Boynton, 1972). Thus, in contrast to heterochromatic brightness matches, border settings do not incorporate information from the opponent color channels.

The predominant influence of achromatic contrast on border distinctness has found some support in neurophysiological considerations. Kaiser, Lee, Martin, and Valberg (1990) suggested that the parasol (phasic) ganglion cells that feed into the magnocellular pathway build the physiological basis for border perception. The parasol ganglion cells gave transient responses to borders depending on luminance contrast, whereas the response of the midget (tonic) ganglion cells that feed into the parvocellular channels were relatively insensitive to luminance changes at the border. They also showed that the response of parasol ganglion cells to borders is additive, proportional, and transitive.

Once the achromatic luminance between two fields with different chromaticity is equalized, the remaining distinctness of the border may be accounted for by chromatic signals, principally in the opponent red–green color channel (Frome, Buck, & Boynton, 1981; Tansley & Boynton, 1978; Tansley & Valberg, 1979; Valberg & Tansley, 1977; though see also Boynton, Eskew, & Olson, 1985). This residual border distinctness is generated by the difference signal of the L and the M cones and mediated by the midget ganglion cells. The poor response of the S-cone system to edges and borders may reflect the sparse distribution of the S cones on the retina (Ahnelt, Kolb, & Pflug, 1987; Curcio et al., 1991; Williams, MacLeod, & Hayhoe, 1981).

If border perception is accomplished by the sum of L- and M-cone signals only, the MDB photometric procedure agrees in this respect with luminance as assessed by flicker photometry (Eisner & MacLeod, 1980; Ripamonti, Woo, Crowther, & Stockman, 2009). MDB shares with flicker photometry several properties that seem to make it an applicable photometric criterion to assess luminance in the mesopic domain. It meets all the requirements of a photometric system; that is, additivity, transitivity, and proportionality (Boynton & Kaiser, 1968; Ingling et al., 1978; Kaiser, 1971; Kaiser et al., 1990; Wagner & Boynton, 1972).

But in contrast to flicker photometry, which was mainly used to determine the CIE spectral luminosity function $V(\lambda)$, border matches do not involve rapidly changing stimuli that can lead to inhibition and enhancements between rod and cone signals and between slow and fast rod signals. In mesopic photometry this is an advantage, since rod–cone phase lags prevent simple addition of flicker signal amplitudes and can lead to complete nulling by opposite-phase rod and cone stimuli (MacLeod, 1972). Moreover, because

the judgment depends on a well-localized stimulus feature (the border), the possible influence of retinal inhomogeneity is minimized. Also, in comparison to heterochromatic brightness matches, border matches seem to provide a more reliable and less variable measure (Boynton & Kaiser, 1968; Kaiser, 1971; Wagner & Boynton, 1972).

These characteristics of the MDB method make the criterion of border distinctness a potentially reliable and suitable measure of luminance under dim conditions and thus, a potential basis for mesopic photometry. However, the MDB method has not yet been investigated as a measure of peripheral luminance under dim conditions. Here, the criterion of border distinctness is used with the goal of determining the relative contribution of the cone and rod system to luminance under several states of adaptation ranging from scotopic to photopic and at several peripheral retinal locations.

Methods

If mesopic luminance depends on a weighted sum of scotopic and photopic luminances, then contours of constant mesopic luminance are approximately straight lines in scotopic and photopic luminance space (S – P space) and in scotopic and photopic contrast space (contrast here is defined as $(S_{cf} - S_{ref})/S_{ref}$ and $(P_{cf} - P_{ref})/P_{ref}$ where S_{cf} , P_{cf} , S_{ref} , and P_{ref} denote the scotopic and photopic luminances of the comparison field and of a constant reference). Along one such line passing through the origin, the mesopic luminance contrast (defined by replacing S and P values with some particular appropriately weighted combination of the two) will be zero, and the border therefore minimally distinct, to the extent that border visibility or distinctness depends on luminance alone. For a photopic adaptation level, the contour of constant border distinctness will form a line nearly parallel to the scotopic axis (vertical in Figure 2). This is because, under photopic conditions, border distinctness will depend mainly on the contrast as seen by the cones, and a stimulus contrast seen only by the rods will have to be relatively larger to produce a noticeable change in border perception. Similarly, the line of constant border distinctness for a scotopic adaptation level will be oriented nearly horizontally. In this case, since cones are not (or only to a small extent) involved, a large difference in photopic luminance is needed to create the same border distinctness. For mesopic adaptation levels, the contour's orientation will be intermediate. Thus, the orientation of the line of constant border perception represents the relative scotopic and photopic contribution to luminance. A vertical alignment of

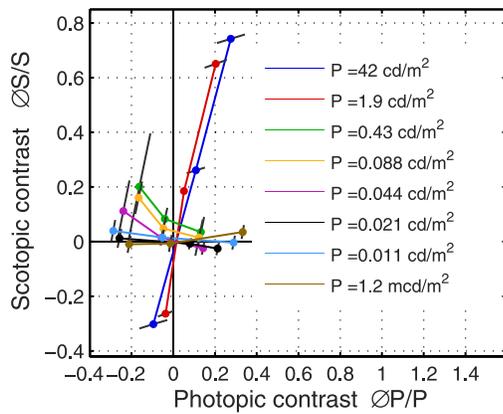


Figure 1. S–P contrast space showing the lines of minimum border perception for one observer and all tested adaptation levels. The data are means between the internal and external reference condition. The error bars represent ± 1 standard deviation of eight settings.

this isoluminance line reflects pure cone vision and a horizontal orientation pure rod vision.

The goal of this experiment is to determine the orientation of the isoluminance line by minimally distinct border matches at photopic, mesopic, and scotopic adaptation levels. Thus, weights that describe the relative rod and cone contribution to border perception, which in this case corresponds to luminance, can be assigned to each adaptation level.

The border to assess was created by a centrally fixated round disc of (generally) 12° diameter on a uniform surround. The stimulus was presented on a calibrated CRT-monitor that was controlled by a Bits++ Graphics Card (Cambridge Research Systems, Rochester, UK). The monitor ran at a refresh rate of 75 Hz and with a resolution of 1280×1024 . The observers were seated 40 cm in front of the screen. At this distance, the screen subtended a field of $44^\circ \times 34^\circ$. The stimuli were viewed binocularly with the natural pupil. The border matches between the disc and the surround were done under two different conditions as shown in Figure 1. Under the “external reference condition,” the centrally fixated disc was the adjustable comparison field, whereas under the “internal reference condition,” the surround acted as comparison field. In each case, the reference field was fixed in intensity while the comparison field could be altered by the observer by pressing keys on a computer keyboard to meet the criterion of a minimally visible border between the two fields.

During each session the reference field was permanently set to a neutral equal energy white (EEW) according to the CIE 10° color matching functions with x, y chromaticity coordinates of 0.34 and 0.33. The luminance, according to $V_{10}(\lambda)$, of the reference was set between photopic (42 cd/m^2) and scotopic (1.2 mcd/m^2)

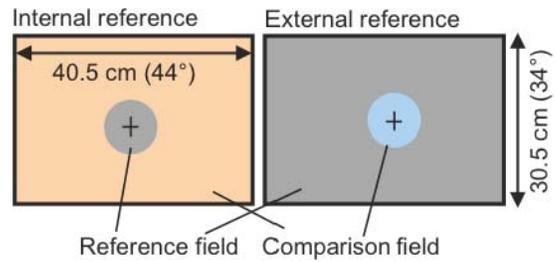


Figure 2. Sketch of the minimal distinct border stimulus. The visibility of the border between the inner 12° disc and the surround was minimized by adjusting either the surrounding field at a constant intensity of the disc (inner reference condition) or the disc at a constant surrounding field (external reference condition).

luminance levels (see Table 1 for a complete list). To provide mesopic and scotopic background luminance levels, calibrated neutral density filters (from LEE Filters, 4 stops, 3 stops, 2 stops, and their combinations) were set in front of the monitor screen. The calculation of all photometric quantities takes account of the spectra of each monitor phosphor and the spectral transmission of each filter.

The *comparison field* was defined by the intensities of the three monitor guns. The green phosphor in the comparison field was kept constant at the level of the reference green phosphor. In most conditions the blue phosphor intensity was also kept constant for each setting, while the red phosphor was adjusted by key presses by the observer. But at high adaptation levels (42 cd/m^2 and 1.9 cd/m^2) the red phosphor was kept constant and the blue phosphor served as the variable phosphor to keep the adjustment trajectory nearly orthogonal to the isoluminant line. These adjustment trajectories are straight lines with a constant slope in a plane where the horizontal axis is the photopic luminance and the vertical axis is the scotopic luminance. The constant phosphor (red or blue) was set to one of two to five intensities (e.g., to 0%, 30%, 70%,

P_{ref} [cd/m^2]	S_{ref}	$S_{ref} : P_{ref}$	t_{adapt} [min]
42.2	90.6	2.15	10
1.9	3.7	1.95	15
0.43	0.81	1.90	15
0.088	0.17	1.89	20
0.044	0.081	1.86	20
0.021	0.038	1.83	25
0.011	0.018	1.70	30
0.0012	0.002	1.64	45

Table 1. Photopic and scotopic luminance levels of the reference (P_{ref}, S_{ref}) fields. The $S : P$ ratios of the dim references are lower because of the higher transmittance for long wavelength of the used filters. The last column shows the dark adaptation times for each condition.

and 100% of the maximal luminance the gun can generate) to create a range of differently colored comparison fields for each adaptation condition. Each of these parameter combinations was presented four times in random order in one session for both the internal and external reference conditions. Due to the offset of the three phosphors on the monitor mask, color artifacts can be visible, especially under high adaptation levels. To minimize the artifacts, the border was slightly blurred by one pixel (≈ 2 arc min). Lindsey and Teller (1989) found that an edge blur of up to 8 arc min does not change the spectral characteristics and additivity of border settings.

Purple and green conditions

In two conditions, the white equal energy reference was replaced with a color reference as a test of generality of the results. For the purple condition, the green phosphor intensity was zero throughout, making both the reference and comparison fields purple with a chromaticity of 0.36 and 0.21. A green reference was also used, in which the green phosphor of the reference and the comparison fields was fixed at a level as high as practicably possible, leading to a greenish adaptation field with the chromaticity of 0.32 and 0.43. The purple and the green references were chosen to yield the same ratio between photopic and scotopic CIE luminance levels as the equal energy white (see Table 1).

A brief control experiment was also completed under an adaptation level of 42 cd/m² with and without an achromatizing lens to examine possible influences of chromatic aberrations. In this experiment, a smaller disc with a diameter of 3.5° was used.

Observers and procedure

Seven observers (aged between 18 and 35 years; mean 28 years) with normal vision (normal color vision, assessed using the Ishihara plate test, Visus of at least 0.8 corresponding to a Snellen-Index of 20/25) took part in the experiment. The observers were instructed to adjust the comparison field by pressing keys on a keyboard until the border between the disc and the surround disappeared or was minimally distinct. During the adjustment they were asked to fixate a black cross in the middle of the disc. The timing of the experiment was determined by the observer. The adaptation period prior to the experiment ranged from 10 min for the photopic adaptation level up to 45 min for the darkest adaptation level (see Table 1). During adaptation the observers received instructions and completed some practice trials to familiarize themselves with the setup. The experiments involving purple and

green backgrounds and the follow-up experiment with an achromatizing lens were completed by two subjects only.

Some effects were observed that made a precise adjustment difficult, especially under photopic and mesopic conditions. The border between reference and comparison fields tended to fade when fixation was maintained too long (Troxler effect; Clarke, 1960). To minimize fading due to stabilization of the retinal image, a uniform field of the reference intensities was shown for 3 s after each match was made. During the experimental sessions, we encouraged eye movements with fixation being carefully maintained only at the moment of making the final adjustment. In the following sections, the adaptation luminance is generally given as the photopic luminance based on $V_{10}(\lambda)$ of the reference field. However, it must be noted that the state of adaptation is influenced by the intensities of both the reference field and the comparison field. Since the comparison field varied in luminance as well as color, the state of adaptation could change slightly during adjustment. All luminance values are based on the 10° CIE standard observers.

Results

Representation and modeling of the data

The results are depicted in S – P contrast diagrams where the axes denote the scotopic and photopic luminance contrast formed between the reference and the comparison field. Recall that under the assumption that $V_{10}(\lambda)$ represents the cone sensitivity of the observer and that photopic MDB settings are based on luminance information only, a pure photopic response will result in a vertical straight line through the reference point in S – P contrast space (or S – P space). Correspondingly, a pure scotopic response leads to a horizontal straight line. If the signals of the rods and cones add up linearly in the mesopic range, mesopic MDB adjustments will lead to a straight line through the reference with a negative slope.

Figure 2 shows the results of one subject in S – P contrast space. The data points are the means from the internal and external reference condition. The standard deviations are shown in black. Each colored line corresponds to one adaptation level, represented here by the photopic luminance of the reference P_{ref} . The different points on such a line represent the settings made using a range of color differences between the reference and comparison fields.

The transition from a rod response to a cone response is depicted in the change of the slope of the lines from horizontal to vertical. The graph shows, at

luminance levels of 0.021 cd/m² and below, an almost purely scotopic response.

From the slope of the MDB curves in S – P space the relative weights for the photopic and scotopic responses can be retrieved. Any one setting defines a relative rod and cone weight such that the weighted linear sum of photopic and scotopic luminance is the same for test and reference; this weighted sum is the linearly modeled measure of mesopic luminance consistent with the setting. Thus, if S_{cf} , P_{cf} , S_{ref} , and P_{ref} are the scotopic and photopic luminance levels of the comparison and reference fields at a minimum border setting, then W_P' and W_S' , the weights for the photopic and scotopic luminance appropriate for defining mesopic luminance under that condition of adaptation, satisfy

$$S_{cf} \cdot W_S' + P_{cf} \cdot W_P' = S_{ref} \cdot W_S' + P_{ref} \cdot W_P'. \quad (1)$$

For each of the comparison field colors used in a particular adapting condition, the linear model predicts a setting that satisfies Equation 1 when the weights are chosen for a best fit to the whole collection of settings made by that subject for the different reference colors. That setting corresponds to zero contrast in mesopic luminance, modeled as a linear combination of photopic and scotopic luminance values for that subject and adapting condition. The settings of a subject for a particular test color condition may, however, deviate from the predictions of the linear model. The linearity assumption was tested by calculating the difference between the linearly modeled mesopic luminances of the reference field and the comparison field at the MDB setting, expressed as a percentage of the reference mesopic luminance (percent contrast). This was averaged over all test colors (between two and five for each adapting condition) and then over all subjects ($N = 7$). Figure 3 shows the resulting percent root mean squared error ($RMSE_{\%}$) introduced by the assumption that the MDB data are linear. The average linearity error is small; it never exceeds 2.5% for all adaptation levels. The high degree of linearity allows us to regard the results as straight lines and validates the linear model described above. Hence, the mesopic response on which border distinctness depends can well be described as a linear addition of weighted cone and rod signals.

Since the absolute values of W_P' and W_S' are not constrained by Equation 1, we can normalize the sum to 1 to retrieve the relative weights $W_P = W_P' / (W_P' + W_S')$ and $W_S = W_S' / (W_P' + W_S')$ such that $1 = W_P + W_S$. Hence, a relative cone weight W_P of 1 ($W_S = 0$) represents pure cone vision as defined by $V_{10}(\lambda)$ and vice versa, a relative rod weight W_S of 1 ($W_P = 0$) corresponds to pure rod vision as defined by $V'(\lambda)$.

The relative cone contribution is expected to increase from 0 to 1 as adapting intensity increases, owing primarily to the desensitization of the rod system with increasing intensity. We attempted to model this

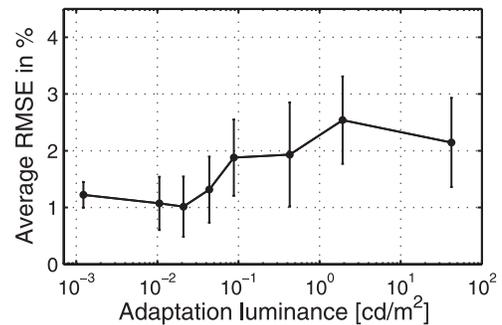


Figure 3. Linearity failure with \pm standard deviation of the MDB data expressed as the percent $RMSE_{\%}$ for all luminance levels.

increase with an equation that has a simple rationale described below:

$$W_P = 1 / \left(1 + (M/S')^k \right). \quad (2)$$

The adaptation level is expressed here in terms of the scotopic sensation luminance S' , which is based on the individual observer's scotopic sensitivity (Kaiser, 1988; Raphael & MacLeod, 2011; and see Appendix). On the simple model described in Raphael and MacLeod (2011; appendix B), from which Equation 2 is derived, the absolute weight for rods is proportional to rod sensitivity. The transition from scotopic to photopic vision is driven by the decrease of rod system sensitivity as the adapting intensity seen by rods increases across the mesopic intensity range. The parameter k is equal to the log-log slope of the rod threshold versus intensity curve (TVI-curve), according to which rod sensitivity varies inversely as the k^{th} power of luminance. In particular, a value of $k = 1$ is expected where rod sensitivity conforms to Weber's law. The parameter M is the *mesomesopic* luminance in scotopic cd/m², which is the luminance at which rods and cones contribute equally to luminance so that $W_P = 0.5$. The best fitting M and k values for the averaged cone weights are 0.33 sc cd/m² and 0.81 sc cd/m², respectively (black curve, Figure 4), with an average root mean squared error of the fit of 0.1. The individual values for each subject are shown in Table 2 along with the fitted individual M and k values of the dark adaptation curves measured with minimum motion (Raphael & MacLeod, 2011) for nearly the same observers (six out of eight observers from the minimum motion experiment took part in the MDB experiment).

A complication: Tangent bias

In all of these experiments, the adjustment of either the red or the blue phosphor while the other two phosphors were kept constant led to a constant slope of the adjustment trajectory in S – P contrast space. This

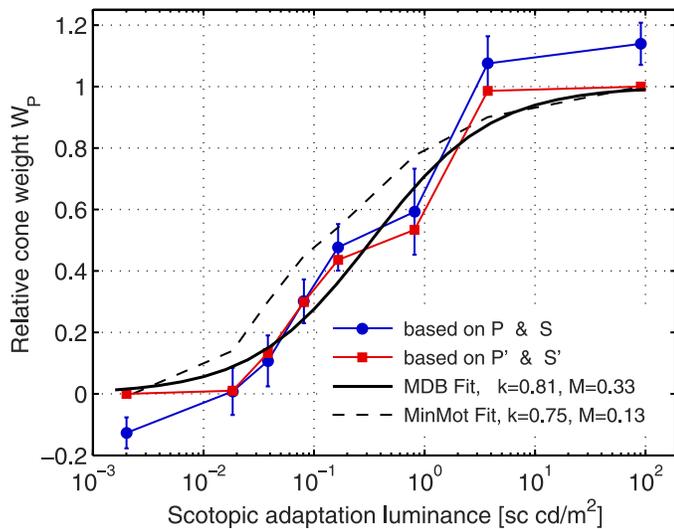


Figure 4. Relative average cone weights with ± 1 standard deviations (between observers) for increasing adaptation luminance based on CIE photopic and scotopic luminance P and S (blue curve), individual photopic and scotopic sensation luminance P' and S' (red curve). The black solid curve shows the model fit (Equation 2) of the MDB results and the black dashed curve shows the model fit of the average cone weights of eight observers for minimum motion settings.

constraint might introduce a potential bias in the measured orientation of the MDB contour. Figure 5 schematizes a hypothetical contour of constant border distinctness, along with the two adjustment trajectories corresponding to variation of the red and blue phosphor intensities. The contour is modeled as a closed curve centered on the reference point. This roughly elliptical contour is an idealization of the behavior to be expected if rod and cone signals do *not* add up linearly in a perfectly additive manner to

Observer	MDB		Minimum motion	
	M [sc cd/m ²]	k	M [sc cd/m ²]	k
1	0.37	0.91	0.14	0.90
2	0.21	0.96	0.22	1.00
3	0.30	0.86	–	–
4	0.38	0.85	0.11	0.74
5	0.19	1.10	0.15	0.70
6	0.44	0.91	0.16	0.86
7	0.36	0.86	0.06	0.73
Average	0.32	0.92	0.14	0.82

Table 2. Best fitting mesomesopic luminance M and exponent k for minimum border matches and minimum motion settings for a stimulus radius of 5° (Raphael & MacLeod, 2011) for those subjects that took part in both experiments. Fits for the minimum motion data for observer 3 could not be obtained because this subject could not do the setting at the three dimmest adaptation levels.

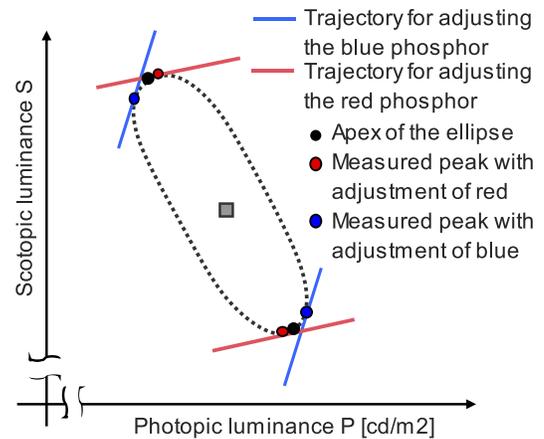


Figure 5. Schematic illustration of the tangent bias. The gray square depicts the reference field. The apex points of the ellipse (black circles) can only be found with a trajectory that is perpendicular to the orientation of the ellipse. The trajectories produced by the red and blue phosphors lead to points offset from the apex.

determine mesopic luminance, or if border distinctness does not depend on a single mesopic luminance signal alone; for instance, if it can also be increased by chromatic contrast (Chaparro, Stromeyer, Kronauer, & Eskew, 1994; Helmholtz, 1896). In the limiting case where border distinctness is determined strictly by a single additive luminance signal, the line of constant luminance (a straight line through the origin in $S-P$ contrast space) is a locus of zero border distinctness; lines of constant nonzero border distinctness are arranged in pairs that flank the zero border distinctness line, but the settings of minimum border distinctness should, in principle, lie exactly on that line. Next, consider the more realistic case where zero border distinctness is not attainable. The theoretically expected minimum distinctness settings are the points shown as blue and red circles where the adjustment trajectory is tangent to the constant distinctness contour, and these necessarily differ slightly from the two apex points shown in black. The true apex point of the ellipse in $S-P$ space can only be found if the adjustment trajectory is a tangent at the apex point, and every adjustment trajectory not perpendicular to the orientation of the MDB contour will introduce some bias into the results.

To mitigate and assess this bias, the experiment was redesigned so that the adjustment was made by moving in a circle in $S-P$ contrast space. This was realized by changing both the red and the blue phosphor intensities at a constant green phosphor intensity. With such a circular adjustment trajectory, the tangent bias is reduced or eliminated.

The extent of the tangent bias was examined at adaptation levels of 0.044 cd/m^2 , 0.12 cd/m^2 , and 0.43 cd/m^2 under both reference conditions. Two subjects of the main experiment took part in this control

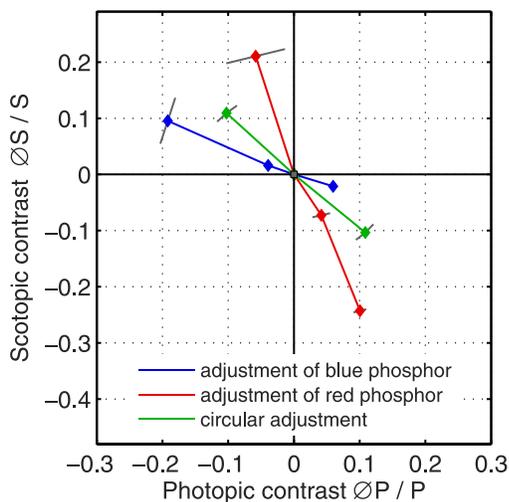


Figure 6. Comparison of MDB results in S–P contrast space for three adjustment trajectories for one observer with the external reference conditions at 0.12 cd/m². Blue lines = adjustment of the blue phosphor, red lines = adjustment of the red phosphor, green lines = circular adjustment in S–P contrast space. The calculated relative cone weights are $W_p = 0.48$ for the adjustment of the blue phosphor, $W_p = 0.84$ for the adjustment of the red phosphor, and $W_p = 0.66$ for the circular adjustment trajectory.

experiment. The bias is evident at the three tested adaptation levels. Figure 6 shows the MDB settings in S–P contrast space for one of the two observers for an adaptation luminance of 0.12 cd/m². The blue, red, and green curves correspond to the three different adjustment trajectories: adjustment of the blue phosphor, red phosphor, and circular adjustment trajectory, respectively. If we assume that the circular adjustment trajectory leads to an unbiased setting, the green line in Figure 6 will define the major axis of the ellipse of constant border distinctness.

The tangent biases illustrated in Figure 5 for variation of the red and blue phosphor result in an

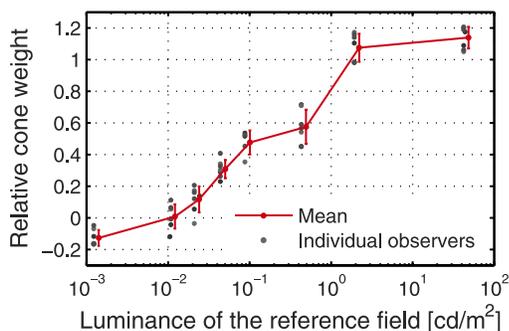


Figure 7. Relative cone weights as a function of adapting luminance for all observers (gray dots). The red curve shows the mean relative cone weights with error bars resembling the \pm standard deviation (slightly shifted for better visibility).

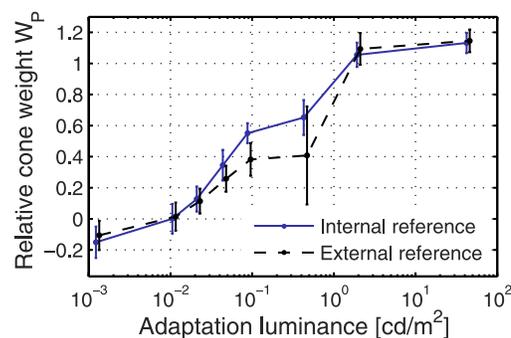


Figure 8. The relative cone weights \pm standard deviation for the internal (blue solid line) and external (dashed black line) reference condition versus the adaptation luminance. The relative cone weight is averaged among all observers.

increased or decreased cone weight, seen respectively in the clockwise and anticlockwise skewing of the red and blue null points in Figure 6 from the ellipse major axis. The generated biases in the relative cone weights, based on the control experiment of Figure 6 are ± 0.18 at 0.12 cd/m². The effect would be to exaggerate the rapidity of the transition depicted in Figure 2 and Figure 4, due to an underestimation of cone weight at intensities up to 0.43 cd/m², where we adjusted the blue phosphor, and an overestimation at and above 1.9 cd/m², where we adjusted the red phosphor. This might have resulted in the rather shallow gradient between 0.088 cd/m² and 0.43 cd/m², and a subsequent steepening of the sigmoid function at high mesopic intensity levels (beyond 0.43 cd/m²; Figure 4).

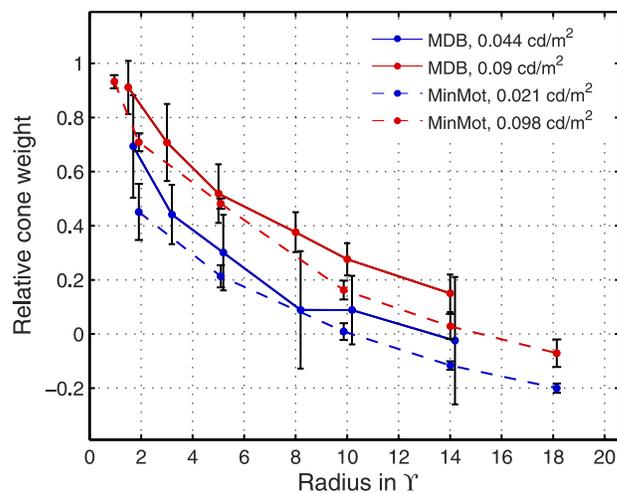


Figure 9. Relative cone weights for minimum border and minimum motion (MinMot) settings versus the eccentricity (radius of the stimuli). Results of observer 1 are shown for two adaptation levels of each method. The data points are the average of five settings (MinMot) and 10 measurements (MDB, averages of internal and external reference condition).

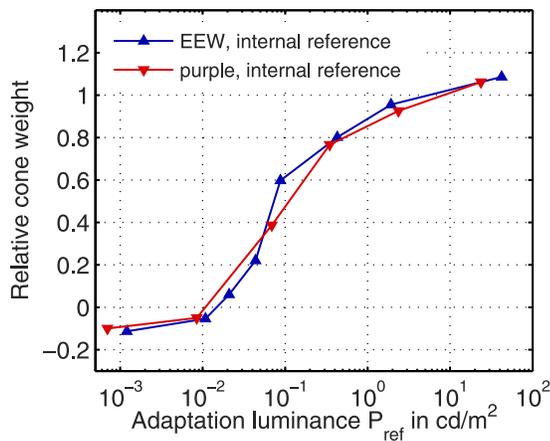


Figure 10. Relative cone weights as a function of adaptation luminance for purple and EEW (equal energy white) reference fields with straight lines as adjustment trajectories; internal reference condition for observer 1.

The results suggest that the loci of constant border distinctness may be rather plump ellipses, for instance, because chromatic signals are involved in border matches. This is unexpected in view of the good linear additivity found in these data and also in earlier results by Boynton and Kaiser (1968), Ingling and Drum (1973), Kaiser (1971), and Wagner and Boynton (1972). The apparent simplicity and linearity of MDB settings may conceal an underlying complexity; for example, on the analysis given here, it is possible that our linearity check is satisfied only if the same phosphor adjustment is used in all conditions. However, the effect of the tangent bias on fitted values k and M of is small.

Change of relative receptor weights with state of adaptation

Figure 7 shows the relative cone weights for all observers as a function of the photopic adaptation luminance (gray dots). The data of the internal and external reference condition were averaged for each observer. The red bold curve is the mean over all subjects. As expected, for increasing adaptation levels the importance of photopic contrast for the MDB settings raises. For the photopic level of 42.2 cd/m² the relative cone weights unexpectedly exceed unity for all observers, which simply implies a higher sensitivity for red than $V_{10}(\lambda)$ suggests. For some observers this is also apparent at luminance levels as low as 1.9 cd/m². Similarly, at scotopic adaptation levels, the relative cone weights reach values below 0, which means that bluish stimuli at the MDB isoluminance point have lower intensity than expected under the assumption that $V'(\lambda)$ resembles the scotopic spectral sensitivity of the eye. The curve in Figure 7 shows a flat part between

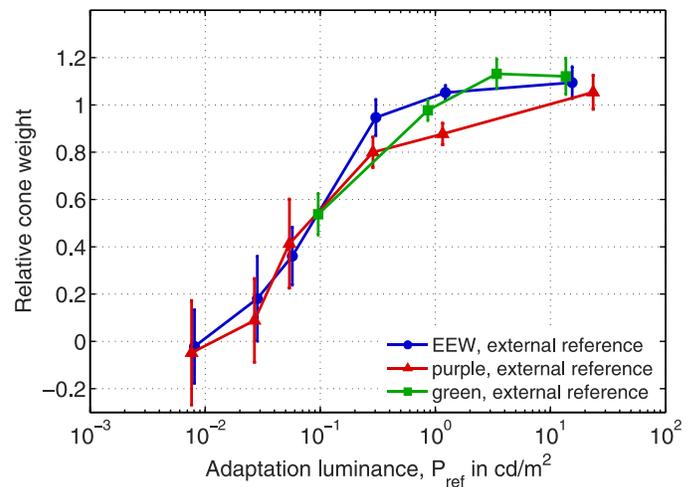


Figure 11. Relative cone weights as a function of adaptation luminance for EEW, purple, and green reference fields. All data are from observer 1 and were measured with circular adjustment trajectories; external reference condition only.

0.1 cd/m² and 0.43 cd/m² and a steepening between the adaptation luminances of 0.43 cd/m² and 1.9 cd/m². This double inflection is also present in most individual observers data. A possible explanation for this was discussed in the previous section about tangent bias.

Comparing the internal and external reference condition

In Figures 2 and 7, the MDB settings from the internal and external reference conditions were averaged. Considering the two conditions separately, (Figure 8) shows good agreement at photopic and scotopic adaptation levels. However, at high mesopic levels (0.43 cd/m² and 0.088 cd/m²) a discrepancy between the two conditions was evident in the average data. We have no plausible explanation for this difference.

Change of rod and cone contribution with eccentricity

We investigated the effect of retinal eccentricity on receptor weights for a range of centrally fixated disc sizes at 0.044 cd/m² and 0.09 cd/m² with one subject. The eccentricity was manipulated by changing the radius of the disc between 2° and 14°.

Figure 9 shows the distinct decrease in cone weight for border matches from 2° to 14° off-axis. At the lower luminance level of 0.044 cd/m² sensitivity is rod-dominated at or beyond 8° in the periphery (blue solid line in Figure 7), in contrast to an intensity of 0.09 cd/

m^2 at which a pure scotopic response is not reached at 14° (red solid line in Figure 7). Comparison of the two curves suggest that the influence of rods is roughly unaffected if both the adapting luminance and the eccentricity are doubled. Thus, a doubling of eccentricity (e.g., from 5° to 10°) is equivalent to a doubling of adaptation luminance (e.g., from 0.044 cd/m^2 to 0.09 cd/m^2) in maintaining the same rod–cone input to border discrimination.

In a similar experiment using minimum motion photometry, Raphael and MacLeod (2011) found a quantitatively similar eccentricity dependence (dashed lines in Figure 9), and showed that this observer is typical of a larger group of subjects.

The effect of the chromaticity of the adapting field

As noted under Methods, the border settings were defined with reference fields of three chromaticities. In addition to the gray equal energy reference, a purple and a green reference that was set to the same scotopic–photopic luminance ratio ($S : P$ ratio) as the EEW reference was used. In the purple reference condition, the comparison and reference fields were both composed of the blue and the red monitor gun only, whereas for the greenish field the green monitor phosphor was set to the maximal possible value. This setting allows a comparison of, in terms of luminance, photometrically identical but chromatically different conditions.

Figures 10 and 11 show the relative cone weights for all reference fields. The results of Figure 10 were collected with the usual straight adjustment trajectories, by adjusting only the blue or the red phosphor. To avoid a potential bias (the tangent error discussed previously), the experiment was repeated with circular trajectories in the (S, P) plane (Figure 11). The results for the circular and the straight adjustment trajectories agree well, as do the results for differently colored adapting fields. Some significant differences are apparent at high mesopic levels in Figure 11. However, given the high uncertainty that seems to accompany border matches in the periphery the deviations around 1.0 cd/m^2 can be regarded as minor.

A sigmoid function (Equation 2) was fit to the data of Figures 10 and 11. For the purple and white adaptation conditions, the parameter values were well constrained and similar: $k_{\text{EEW}} = 0.83$ and $k_{\text{purple}} = 0.78$, $M_{\text{EEW}} = 0.19 \text{ sc cd/m}^2$ and $M_{\text{purple}} = 0.17 \text{ sc cd/m}^2$ for the internal reference condition (Figure 10) and $k_{\text{EEW}} = 1.50$ and $k_{\text{purple}} = 1.14$, $M_{\text{EEW}} = 0.18 \text{ sc cd/m}^2$, $M_{\text{purple}} = 0.21 \text{ sc cd/m}^2$ for the external reference condition (Figure 11). Under greenish adaptation at the lowest intensities below 0.1 cd/m^2 , the border was

invisible across the whole range of settings so the model parameters could not be estimated with useful precision, but clearly the available data are in general agreement with those for the other adapting colors.

Sharpe, Fach, Nordby, & Stockman (1989) found that the rod sensitivity decreases due to interference by cone signals when red backgrounds are present, leading to an increase of the TVI-slope from 0.78 to 0.92 (see also Makous & Boothe, 1974). No such decreased rod sensitivity for red backgrounds was evident here, perhaps because the monochromatic lights used by Sharpe et al. (1989) is more chromatic in comparison to the purple background used here that shows a rather wide spectrum. However, the results suggest that to a useful approximation, color has no influence on mesopic sensitivity independent of S and P , and that the width of the mesopic range is consistent with a model in which rod sensitivity roughly obeys Weber's law.

This formulation provides a much simpler characterization of mesopic luminance than, for example, that of Kokoschka (1980) who proposed a four-parameter model based on the CIE 10° tristimulus values and the scotopic luminance to account for chromatic contributions.

Change of rod and cone contribution with the $S : P$ ratio of the reference: Separate manipulation of rod and cone adaptation level

In the previous experiment, the scotopic and photopic adapting luminances were varied together, so the results do not reveal whether it is the scotopic or the photopic adapting intensity that mainly determines the relative rod and cone contributions. Here we address this by manipulating the adaptation level independently for rods and cones by changing the $S : P$ ratio of the reference under a constant photopic luminance level.

If rod sensitivity is a decreasing function of scotopic background intensity S (as in Equation 2), with negligible influence of cone stimulation by the background, then a bluish reference with a high $S : P$ ratio will result in a decreased relative rod weight, and a reddish reference field with a low $S : P$ ratio in an increased relative rod weight, at a given photopic luminance.

These hypotheses were tested by making minimum border settings with reference field $S : P$ ratios ranging from 0.7 to 3.4 for four adaptation levels. Figure 12 shows the course of the relative cone weights over a range of $S : P$ ratios. A substantial increase of relative cone weights (corresponding to a decrease of the relative rod weights) for increasing $S : P$ ratios is evident for the two mesopic adaptation levels tested

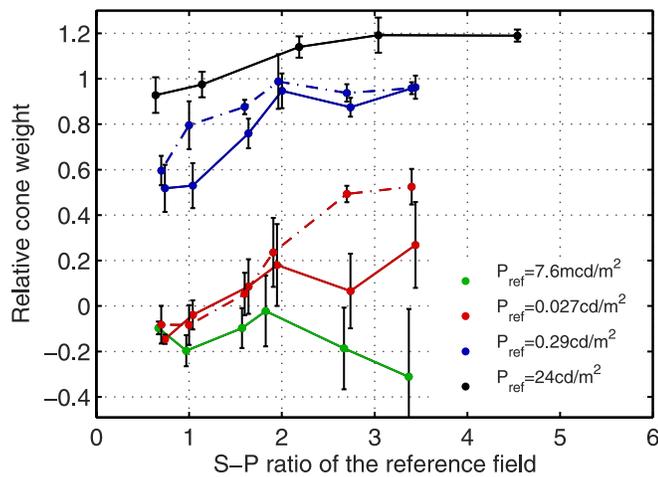


Figure 12. Relation between S : P ratio of the adaptation field (reference) and the relative cone weights for two subjects (solid curve and dashed curves). All data were collected with the external reference condition and a circular adjustment trajectory.

(0.027 cd/m² and 0.29 cd/m²), in agreement with the expectations explained above.

The steepness of the mesopic transition in the curves of Figure 12 is theoretically influenced by the value of the exponent k in Equation 2. The derived estimates for k are imprecise since the relevant data points are few and span only a limited range. The average k values obtained were around 1.35 for 0.027 cd/m² and 1.4 for 0.29 cd/m², somewhat greater than Weber's law would suggest; however, it is not clear whether this difference is statistically significant.

Discussion

We examined the effect of various adaptation conditions on minimum border settings with the intention first to evaluate the method of MDB as a tool to assess luminance, and second, to examine how signals from rods and cones add up to form luminance signals in the mesopic domain. MDB matches between a surround and a centrally fixated disc were made under adaptation conditions ranging from photopic to scotopic.

The minimally distinct border method has promise as a suitable way to assess luminance under dim light conditions when rods and cones are active: Border perception does not rely on fast-changing stimuli that might cause phase-dependent interaction between rod and cone signals. Further, foveal border matches under photopic conditions have been shown to obey additivity and linearity laws (Boynton & Kaiser, 1968; Kaiser et al., 1990). Also, cone sensitivity functions measured

with border matches resemble closely the CIE $V(\lambda)$ functions (Kaiser, 1971; Wagner & Boynton, 1972). This encourages the assumption there is no contribution or only a negligible contribution of chromatic information of the opponent visual channels to border matches. Accordingly, we found that a linear weighted sum of scotopic and photopic luminance is sufficient to describe the mesopic response under all adaptation conditions.

The decrease of relative cone weights with dark adaptation was described mathematically by optimizing two parameters that describe the horizontal shift of the W_P versus $\log(S)$ curve which is set by the mesomesopic luminance M , and its steepness which is set by the exponent k in Equation 2; k is theoretically linked to the log-log slope of the rod threshold-versus-intensity curve, as explained by Raphael & MacLeod (2011, appendix B). With individual values for k of around 0.92, our results are consistent with earlier results regarding the TVI slope, (see, for example, Wyszecki & Stiles, 1982).

Unexpected asymptotic sensitivities

For most of the participating observers, the MDB spectral sensitivity under photopic and scotopic adaptation levels swung beyond a pure photopic and scotopic response as defined by $V_{10}(\lambda)$ and $V'(\lambda)$, respectively (Figures 2 and 7). This reflects an increased sensitivity for red for the photopic case and for blue in the scotopic case, compared to the CIE standard observers. The increased sensitivity for long wavelength could be due to a reduced effectiveness of blue light relative to red in MDB settings, as compared with flicker photometry, at light levels where rod contribution is negligible. It may mean that MDB spectral sensitivity is simply more red-sensitive than the flicker sensitivity on the basis of which $V_{10}(\lambda)$ was defined. This is surprising, given that earlier evidence suggests that the minimum border criterion and flicker photometry lead to very similar luminosity curves as was found by Kaiser (1971) and Wagner and Boynton (1972).

The negative relative cone weights (unexpectedly high blue sensitivity) apparent in five out of seven subjects at scotopic adaptation levels quantitatively replicates results obtained with nearly the same group of subjects using the minimum motion criterion for equiluminance (Raphael & MacLeod, 2011). Thus, both the minimum motion and the MDB results under scotopic conditions for these observers indicate a scotopic spectral sensitivity slightly greater at short wavelengths than $V'(\lambda)$; this can speculatively be attributed either to individual differences in rod photoreceptor sensitivity (Bowmaker, Loew, & Lieb-

	No lens	Achromatizing lens	<i>p</i> -value
Normal color vision	$W_P = 1.1 \pm 0.07$	$W_P = 1.14 \pm 0.07$	$p = 0.24$
Deuteranomalous trichromat	$W_P = 1.04 \pm 0.02$	$W_P = 1.08 \pm 0.04$	$p < 0.01$

Table 3. Relative cone weights for border settings with and without an achromatizing lens.

man, 1975) or to a lower macular pigment density than is characteristic of the standard observer, as discussed in Raphael and MacLeod (2011). Other sources of individual variations like lens density and pigment density have a much decreased influence on changes in sensation luminance of the red and blue CRT phosphors as shown by Golz and MacLeod (2003).

However, the hypothesis of prereceptoral filtering is less successful in accounting for the photopic deviation. The same observers with increased blue sensitivity under scotopic conditions also exhibit an increased red sensitivity under photopic conditions. Further, the subjects of this experiment also did minimum motion settings with a counterphasing stimulus under the same adaptation conditions (Raphael & MacLeod, 2011). As noted, those motion nulls do show the same unexpectedly high blue sensitivity at scotopic light levels as found in the border settings here, consistent with the proposal that the effective macular pigment density for these subjects and conditions may be slightly lower than for the standard scotopic observer. However, the unexpectedly high photopic sensitivity for red was not evident in minimum-motion results. Hence, it is unlikely that the asymptotic effects are due either to prereceptoral filtering or to the use of broadband CRT stimuli in comparison to monochromatic lights used to determine $V(\lambda)$. It is possible that this photopic effect is specific to the border setting method.

One possible cause of such a discrepancy is loss of contrast in the blue-phosphor image as a result of chromatic aberration in the eye. Aberrations caused by the optical system of the eye are wavelength dependent. If the eye is in focus for the middle part of the visible spectrum (yellow) the blue phosphor will generate a blurred retinal image and this could limit its contribution to border perception. This hypothesis was tested in a follow-up experiment with two observers (the authors, one with normal color vision and the other a deuteranomalous trichromat) by correcting for chromatic aberrations with an achromatizing lens in front of one of the eyes. The other eye was covered with an eye patch. Since the achromatizing lens corrects for aberrations only in the 14° central visual field, the border settings were done with a smaller disc with a 3.5° radius. Using an adaptation level of 42 cd/m² and a circular adjustment trajectory (see the discussion of tangent bias above) the relative cone weights were hardly affected by use of the achromatizing lens. Although the data of one of the observers are significantly different with and without the achroma-

tizing lens, the direction and the minuscule size of the effect can not explain the cone weights greater than 1. The resulting average relative cone weights from 10 settings and the *p*-values for both observers are given in Table 3. Rejection of the factors considered above leaves us with no explanation for the slight photopic MDB overshoot of Figures 4 and 7.

Variation with retinal eccentricity

Since the fovea and near parafovea are dominated by cones, a photopic or nearly photopic response would be expected even at low light levels where rods influence vision for far peripheral stimuli. Psychophysical evidence for such a change of sensitivity with retinal position has been found in many studies (e.g., Drum, 1980; Jamar, Kwakman, & Koenderink, 1984; Kishto 1970; Raphael & MacLeod, 2011; Weale, 1951).

Here we compared border matches for a variety of disc sizes at two mesopic adaptation luminances. The strong influence of retinal position that was evident in minimum motion settings under dim light conditions (Raphael & MacLeod, 2011) is also evident in border matches. The spectral sensitivity at a mesopic light level can range from purely cone based to almost purely rod based depending on the position on the retina (Figure 9).

Comparison with minimum motion

The intensity-dependence of rod and cone weighting for mesopic luminance demonstrated here with the MDB procedure agrees well with that obtained in a previous paper using the more complex minimum motion procedure (Raphael & MacLeod, 2011), but the experimental results suggest unanticipated complexities in the MDB procedure itself.

For example, the generally obvious color difference present in the MDB display makes the nulls uncertain. Perhaps for this reason, the way the chromaticity and luminance of the comparison field are changed plays an important role: adjustment trajectories of different slopes in *S-P* diagram yield measurably different results (tangent bias, see Figure 5) at mesopic luminance levels. Such a bias is expected in principle in any situation where a heterochromatic null (whether based on minimum motion, MDB, or flicker) requires a compromise between signals that are not identical in

spectral sensitivity, so that the null point is not subjectively identifiable with high precision. In the minimum motion and flicker methods, however, the reduced salience of color makes the luminance nulls well defined and reduces the scope for tangent bias. When the tangent bias was avoided by using an adjustment trajectory approximately orthogonal to the line of minimum border distinctness in S – P space (Figure 5), the MDB matches show close agreement with the minimum motion results (with mesopic luminances of 0.18 sc cd/m² and 0.14 sc cd/m² at 2cpd, respectively, for observer 1).

Precise and general agreement is not possible, since the minimum motion nulls may vary with temporal and spatial frequency (Raphael & MacLeod, 2011, figures 13 and 15), whereas the MDB nulls at a single sharp edge involve an unknown integration over spatial and temporal frequency. At the relatively low temporal frequency (generally 2 Hz) adopted in the minimum motion experiments, the minimum motion null is in fact almost independent of temporal frequency (Raphael & MacLeod, 2011, figure 13), but the influence of spatial frequency is more pronounced: the cone weight implied by the minimum motion null is greater at 4 cpd than at 0.5 cpd by as much as a factor of 2, presumably because of the larger receptive fields of the rod system (Barlow, Fitzhugh, & Kuffler, 1957; Hallett, 1969; Troy, Bohnsack, & Diller, 1999).

Rod adaptation state determines the mesopic transition

The alteration of scotopic luminance at a constant level of photopic luminance revealed the decreased effectiveness of rods relative to cones with an increase in $S : P$ ratio expected on the assumption that rods work nearly in accordance with Weber's law in the Weber range of the TVI-curve.

In the purple and green reference conditions we investigated how receptor contribution is influenced by adaptation fields of the same $S : P$ ratio as the gray equal energy field but different chromaticity. We find a good agreement between the equal energy white, the green, and the purple adaptation conditions, which are identical in terms of luminance but chromatically different. This conformity and the high linearity of the results suggest that border matches are accomplished with the achromatic information in the luminance pathway only. Thus, we suggest that a mesopic luminance can be specified as a weighted sum of scotopic and photopic luminance, in which the weights are set by the adaptation level of the rod system with the appropriate scotopic spectral weighting. A contribution of chromatic opponent mechanisms seems unlikely.

Based on these results, a description of mesopic achromatic vision can be accomplished by a linear two-parameter model (Equation 2), where the relative rod and cone contribution varies with scotopic adaptation luminance and retinal position.

In summary, it was shown that the MDB method is also viable under dim lighting conditions and in the periphery. However, one has to consider some aspects in the experimental design to avoid unwanted side effects:

- To prevent afterimages and fading due to the Troxler effect, it is necessary to alternate the comparison field frequently with an intermittent adaptation screen as done by Kaiser (1971).
- The tangent bias noted above (Figure 5) requires some care in the design of the experiment if precision is important.
- The recognized artifact of chromatic aberration, on the other hand, seems to have only a minor effect on border settings with a CRT monitor.
- When conducting border settings with an internal and an external field, as was done here, results may not be precisely consistent (Figure 8).

With these caveats, it can be concluded that MDB is a viable method for assessing luminance in the mesopic adaptation range with some limitations that can be minimized by a suitable experimental design.

Keywords: border perception, minimally distinct border, luminance, mesopic

Acknowledgments

This research was supported by NIH Grant EY-01711 to DIAM, and by the Deutscher Akademischer Austauschdienst with the grant DAAD D/07/50125 to SR.

Commercial relationships: None.

Corresponding author: Sabine Raphael.

Email: SabineRaphael@gmail.com.

Address: Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, United Kingdom.

References

- Ahnelt, P., Kolb, H., & Pflug, R. (1987). Identification of a subtype of cone photoreceptor, likely to be blue sensitive, in the human retina. *Journal of Comparative Neurology*, 255(1), 18–34.
- Barlow, H. B., Fitzhugh, R., & Kuffler, S. W. (1957).

- Change of organization in the receptive fields of the cat's retina during dark adaptation. *Journal of Physiology*, *137*, 338–354.
- Bowmaker, J. K., Loew, E. R., & Liebman, P. A. (1975). Variation in the lambdamax of rhodopsin from individual frogs. *Vision Research*, *15*, 997–1003.
- Boynton, R. M., Eskew, R. T., & Olson, C.X. (1985). Blue cones contribute to border distinctness. *Vision Research*, *25*, 1349–1352.
- Boynton, R. M., & Kaiser, P. K. (1968). Vision: The additivity law made to work for heterochromatic photometry with bipartite fields. *Science*, *161*(839), 366–368.
- Chaparro, A., Stromeyer, C. F., III, Kronauer, R. E., & Eskew, R. T., Jr., (1994). Separable red-green and luminance detectors for small flashes. *Vision Research*, *34*, 751–762.
- Clarke, F. J. J. (1960). A study of Troxler's effect. *Optica Acta*, *7*, 219–236.
- Curcio, C. A., Allen, K. A., Sloan, K. R., Lerea, C. L., Hurley, J. B., Klock, I. B., & Milam, A. H. (1991). Distribution and morphology of human cone photoreceptors stained with anti-blue opsin. *Journal of Comparative Neurology*, *312*(4), 610–624.
- Drum, B. (1980). Relation of brightness to threshold for light-adapted and dark-adapted rods and cones: effects of retinal eccentricity and target size. *Perception*, *9*, 633–650.
- Eisner, A., & MacLeod, D. I. A. (1980). Blue-sensitive cones do not contribute to luminance. *Journal of the Optical Society of America*, *70*, 121–123.
- Fraunhofer, J. (1824). On the refractive and dispersive power of different species of glass, in reference to the improvement of achromatic telescopes, with an account of the lines or streaks which cross the spectrum. *Edinburgh Philosophical Journal*, *10*, 26–40.
- Frome, F. S., Buck, S. L., & Boynton, R. M. (1981). Visibility of borders: Separate and combined effects of color differences, luminance contrast, and luminance level. *Journal of the Optical Society of America*, *71*, 145–50.
- Golz, J., & MacLeod, D. I. A. (2003). Colorimetry for CRT displays. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, *20*, 769–781.
- Hallett, P. E. (1969). Rod increment thresholds on steady and flashed backgrounds. *Journal of Physiology*, *202*, 355–377.
- Helmholtz, H. (1896). *Handbuch der physiologischen Optik* (2nd ed.). Hamburg, Germany: Verlag von Leopold Voss.
- Ingling, C. R., Jr., & Drum, B. A. (1973). Retinal receptive fields: Correlations between psychophysics and electrophysiology. *Vision Research*, *13*, 1151–1163.
- Ingling, C. R., Jr., Huong-Peng Tsou, B., Gast, T. J., Burns, S. A., Emerick, J. O., & Riesenbergl, L. (1978). The achromatic channel. I. The nonlinearity of minimum-border and flicker matches. *Vision Research*, *18*, 379–390.
- Jamar, J. H., Kwakman, L. F., & Koenderink, J. J. (1984). The sensitivity of the peripheral visual system to amplitude-modulation and frequency-modulation of sine-wave patterns. *Vision Research*, *24*, 243–249.
- Kaiser, P. K. (1971). Minimally distinct border as a preferred psychophysical criterion in visual heterochromatic photometry. *Journal of the Optical Society of America*, *61*, 966–971.
- Kaiser, P. K. (1988). Sensation luminance: A new name to distinguish CIE luminance from luminance dependent on an individual's spectral sensitivity. *Vision Research*, *28*, 455–456.
- Kaiser, P. K., Lee, B. B., Martin, P. R., & Valberg, A. (1990). The physiological basis of the minimally distinct border demonstrated in the ganglion cells of the macaque retina. *Journal of Physiology*, *422*, 153–183.
- Kishto, B. N. (1970). Variation of the visual threshold with retinal location. Part I. The central 20° of the visual field. *Vision Research*, *10*, 745–767.
- Kokoschka, S. (1980). Photometrie niedriger Leuchtdichten durch äquivalente Leuchtdichte des 10°-Feldes. *Licht- Forschung*, *2*(1), 1–13.
- Lindsey, D. T., & Teller, D. Y. (1989). Influence of variations in edge blur on minimally distinct border judgments: a theoretical and empirical investigation. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, *6*, 446–458.
- MacLeod, D. I. A. (1972). Rods cancel cones in flicker. *Nature*, *235*(5334), 173–174.
- Makous, W., & Boothe, R. (1974). Cones block signals from rods. *Vision Research*, *14*, 285–294.
- Raphael, S., & MacLeod, D. I. (2011). Mesopic luminance assessed with minimum motion photometry. *Journal of Vision*, *11*(9):14, 1–21, doi:10.1167/11.9.14. [PubMed] [Article]
- Ripamonti, C., Woo, W. L., Crowther, E., & Stockman, A. (2009). The S-cone contribution to luminance depends on the M- and L-cone adapta-

- tion levels: silent surrounds? *Journal of Vision*, 9(3): 10, 1–16, doi:10.1167/9.3.10. [PubMed] [Article]
- Sharpe, L. T., Fach, C., Nordby, K., & Stockman, A. (1989). The incremental threshold of the rod visual system and Weber's law. *Science*, 244(4902), 354–356.
- Stockman, A., MacLeod, D. I., & Johnson, N. E. (1993). Spectral sensitivities of the human cones. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, 10, 2491–2521.
- Stockman, A., & Sharpe, L. T. (2006). Into the twilight zone: The complexities of mesopic vision and luminous efficiency. *Ophthalmic & Physiological Optics*, 26, 225–239.
- Tansley, B. W., & Boynton, R. M. (1978). Chromatic border perception: The role of red- and green-sensitive cones. *Vision Research*, 18, 683–697.
- Tansley, B. W., & Valberg, A. (1979). Chromatic border distinctness: not an index of hue or saturation differences. *Journal of the Optical Society of America*, 69, 113–118.
- Troy, J. B., Bohnsack, D. L., & Diller, L. C. (1999). Spatial properties of the cat X-cell receptive field as a function of mean light level. *Visual Neuroscience*, 16(6), 1089–1104.
- Valberg, A., & Tansley, B. W. (1977). Tritanopic purity-difference function to describe the properties of minimally distinct borders. *Journal of the Optical Society of America*, 67, 1330–1336.
- Vienot, F., & Chiron, A. (1992). Brightness matching and flicker photometric data obtained over the full mesopic range. *Vision Research*, 32, 533–540.
- Wagner, G., & Boynton, R.M. (1972). Comparison of four methods of heterochromatic photometry. *Journal of the Optical Society of America*, 62, 1508–1515.
- Weale, R. A. (1951). The foveal and para-central spectral sensitivities in man. *Journal of Physiology*, 114, 435–446.
- Williams, D. R., MacLeod, D. I., & Hayhoe, M. M. (1981). Punctate sensitivity of the blue-sensitive mechanism. *Vision Research*, 21, 1357–1375.
- Wyszecki, G., & Stiles, W. S. (1982). *Color science: Concepts and methods, quantitative data and formulae* (2nd ed.). New York: Wiley.

Appendix: Defining sensation luminance

To allow for differences in sensitivity between the CIE standard observers and the psychophysically measured sensitivities that are evident in Figure 7, as relative cone weights above 1 and below 0, the scotopic and photopic luminance definitions were redefined as sensation luminance to match the scotopic and photopic results of the tested observers. The photopic sensation luminance P' was redefined by weighting the luminance contribution of the blue and red phosphor to account for isoluminance between the reference and the matched comparison field at 42 cd/m².

$$P' = r\omega_{R,phot}P_R + gP_G + b\omega_{B,phot}P_B \quad (3)$$

Equation 3 shows the sensation luminance P' as the sum of the luminance contribution of all three phosphors. Here, P_R , P_G , and P_B are the maximal photopic luminances the three phosphors can produce; r , g , and b denote the phosphor intensities that are the linearized output voltages of the CRT monitor normalized between 0 and 1. The phosphor weights for the red and blue phosphor are $\omega_{R,phot}$ and $\omega_{B,phot}$, respectively. The green phosphor g is the same for both fields, hence does not influence luminance in this case. The phosphor weights were found to be $\omega_{R,phot} = 1.32$ and $\omega_{B,phot} = 0.22$. Scotopic sensation S' luminance was defined accordingly with the scotopic isoluminance match at 0.001 cd/m² ($\omega_{R,scot} = 0.66$, $\omega_{B,scot} = 1.06$).

The descent of the relative cone weight with dark adaptation was fit with a sigmoid function of S' (Equation 2) by minimizing the root mean squared error.