



Rapid communication

The Purkinje rod-cone shift as a function of luminance and retinal eccentricity

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Abstract

In the Purkinje shift, the dark adapted eye becomes more sensitive to blue than to red as the retinal rods take over from the cones. A striking demonstration of the Purkinje shift, suitable for classroom use, is described in which a small change in viewing distance can reverse the perceived direction of a rotating annulus. We measured this shift with a minimum-motion stimulus (Anstis & Cavanagh, *Color Vision: Physiology & Psychophysics*, Academic Press, London, 1983) that converts apparent lightness of blue versus red into apparent motion. We filled an iso-eccentric annulus with radial red/blue sectors, and arranged that if the blue sectors looked darker (lighter) than the red sectors, the annulus would appear to rotate to the left (right). At equiluminance the motion appeared to vanish. Our observers established these motion null points while viewing the pattern at various retinal eccentricities through various neutral density filters. Results: The luminous efficiency of blue (relative to red) increased linearly with eccentricity at all adaptation levels, and the more the dark-adaptation, the steeper the slope of the eccentricity function. Thus blue sensitivity was a linear function of eccentricity and an exponential function of filter factor. Blue sensitivity increased linearly with eccentricity, and each additional \log_{10} unit of dark adaptation changed the slope threefold.

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1. Introduction

In 1825, the Bohemian physiologist Johannes Evangelista von Purkinje (Purkinje, 1825) passed white light through a prism and looked at the resulting spectrum during the early and late stages of dark adaptation, and noticed that the brightest region shifted toward the shorter wavelength end of the spectrum after about 10 min in the dark (Cornsweet, 1970; Wald, 1945). This is the Purkinje shift, and it reflects that fact that the retinal cones are maximally sensitive to a wavelength of 555 nm whilst the rods are maximally sensitive to 505 nm (Dowling, 1967). Thus as cone vision gradually switches over to rod vision during dark-adaptation the peak of visual sensitivity shifts towards shorter wavelengths and blues look relatively lighter than reds.

1.1. Human spectral sensitivity in the periphery

It is well established that the retinal cone density is maximum in the fovea and falls off with eccentricity, whereas rods are absent from the foveola and are most dense at an eccentricity of 20° (Curcio, Sloan, Kalina, & Henderson, 1990; Osterberg, 1935). This anatomical layout is reflected in psychophysical measurements of hue sensitivity at different eccentricities (Wald, 1945). In sum, these studies generally concur that the *light*-adapted retina has fairly constant color vision from the fovea out to the far periphery, provided that targets are scaled with eccentricity to compensate for the cortical magnification factor. However, the *dark*-adapted retina is more sensitive to short wavelengths at greater eccentricities, that is, it shows a clear Purkinje shift.

Thus, van Esch, Koldenhof, van Doorn, and Koendrink (1984) used heterochromatic flicker photometry to measure spectral sensitivity across the light-adapted retina. If a 20 Hz flicker was used, and target size was increased with eccentricity to compensate for

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cortical magnification, then sensitivity was approximately constant from 0° to 80° eccentricity. Wooten, Fuld, and Spillmann (1975) measured thresholds in the light-adapted periphery for colored spots on a white surround. Spectral sensitivity peaked at 440 nm. They then turned the surround off and estimated photopic thresholds during the cone plateau of the ensuing dark-adaptation curves. Spectral sensitivity now peaked at 550 nm all the way from the parafovea to the far periphery. Stabell and Stabell (1980) found that spectral sensitivity was fairly constant across the retina from the fovea out to 45° temporal during the cone plateau period. On the other hand, in the dark-adapted state the relative spectral sensitivity was purely scotopic in form, suggesting that it is dominated almost completely by rod activity even at intensity levels commonly labeled “photopic”. Similarly, Abramov and Gordon (1977), using heterochromatic flicker photometry, found a much higher sensitivity to short wavelengths at an eccentricity of 45° than in the fovea. A contribution from the rods could not be ruled out. Stabell and Stabell (1984) measured wavelength discrimination at different eccentricities. They concluded that color-vision characteristics outside the fovea were unlike those of congenital color blindness, but resembled acquired color-vision defects due to diseases of the optic nerve, suggesting that the loss of color discrimination with eccentricity and during progression of these diseases has a common underlying basis.

It has been suggested that the Purkinje shift might involve S cones rather than rods. But Verdon and Adams (1987) ingeniously used the Stiles–Crawford effect to show that S cones play no part the Purkinje shift. Over a 5 log-unit range they made flicker matches by 2-Hz flicker photometry. Their two reference lights (441 and 481 nm) differed only in their stimulation of S cones. However, despite the tenfold difference in S cone stimulation by the two lights, the pairs of luminosity functions were indistinguishable at each light level tested. This showed that S cones made no contribution to either photopic nor mesopic luminosity. Thus, by exclusion of the S cones, the presence of a Purkinje shift is good evidence for the presence of, and must be mediated by, functional retinal rods. (More recently, Stockman, Sharpe, & Fach (1999) have estimated short-wave (S) cone spectral sensitivity, both centrally and peripherally.)

Thus there is a wealth of evidence that the dark-adapted retina shows large increases in short-wave sensitivity with increasing eccentricity, that is, a marked Purkinje shift. It is these changes that we examine in this paper. Note that we did not study changes in dark adaptation over time. Instead, we varied the stimulus radiance over a 3 log-unit range and ensured that the observer was adapted to each stimulus.

1.2. Minimum-motion photometry

We measured the changes in sensitivity to blue relative to red by always using a blue of constant luminance (5.73 Cd m^{-2}) and measuring the red luminance that matched it in different conditions. Several methods are available to determine these red–blue equiluminance points. Classical methods of heterochromatic photometry include minimum flicker and minimum border (Kaiser & Boynton, 1996; Lennie, Pokorny, & Smith, 1993; Wagner & Boynton, 1972). These all give similar results, but they are not particularly easy to use, especially in peripheral vision where acuity for borders is not high. Instead, we used a “minimum-motion” technique, devised by Anstis and Cavanagh (1983), which displays flickering red and blue stripes that appear to move to the left (right) if the blue stripes are darker (lighter) than the red, as shown in Fig. 1. Gregory (1974) has devised a similar technique. The minimum-motion method has several advantages. It can be used on any non-verbal species, including infants and animals that show a behavioural response to motion. More to the point here, it is particularly easy to use in peripheral vision, where border and flicker judgements may be difficult but it is easy to judge the direction of motion of a drifting stimulus. In the past this technique has measured luminous efficiency in the awake monkey (Logothetis & Charles, 1990) and in human infants (Anstis, Cavanagh, Maurer, & Lewis, 1987; Cavanagh, Anstis, & Mather, 1984; Lia, Dobkins, Palmer, & Teller, 1999; Maurer, Lewis, Cavanagh, & Anstis, 1989; Teller & Lindsey, 1989; Teller, Brooks, & Palmer, 1997), using tracking eye movements as a dependent variable. Individual color-defective babies could be identified. The role of spatial and temporal factors in equiluminance has been studied (Cavanagh,

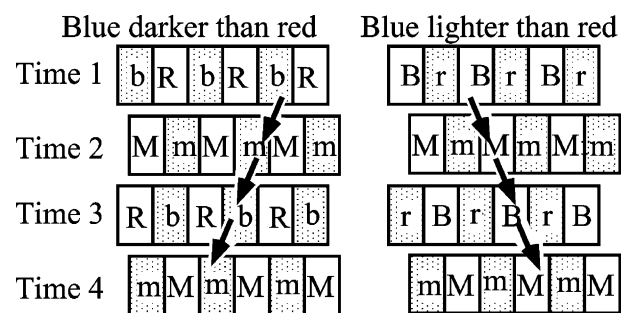


Fig. 1. Motion-nulling at equiluminance of two colors. (a) In this four-frame movie the blue stripes are darker than the red. Hence each (dark) blue stripe in frame 1 jumps to the left, to the nearest dark stripe in frame 2, and each (light) red stripe also jumps to the left, to the nearest light stripe in frame 2. The four cycling frames give continuous apparent motion to the left. (b) Conversely, when the blue stripes are lighter than the red, each (light) blue stripe in frame 1 jumps to the right, to the nearest light stripe in frame 2, and each (dark) red stripe also jumps to the right, to the nearest dark stripe in frame 2. The four cycling frames give continuous apparent motion to the right.

MacLeod, & Anstis, 1987) and also the contribution of color to motion in normal and color-defective observers (Cavanagh & Anstis, 1991). Anstis, Hutahajan, and Cavanagh (1998) have also used the technique to measure the equiluminance point in adult guppy fish, using the optomotor response. Chien, Teller, and Palmer (2000) have used a similar motion technique to measure the gradual change from photopic (cone) through mesopic to scotopic (rod) vision in human infants and adults. They found that for both adults and infants, motion null values varied with light level, agreeing with $V_{10}(\lambda)$ at high light levels and $V'(\lambda)$ at low light levels, and the transition curve relating motion null values to light levels was highly similar or identical in infants and adults. This suggests that the combination rules for combining rod and cone signals were the same at each light level for the two age groups. $V(\lambda)$ curves have been tabulated by Wyszecki and Stiles (1967).

In short, this display efficiently and rapidly measures the mean equiluminance point of two colors in humans and in many non-verbal species.

2. Method

2.1. Motion nulling at equiluminance of two colors

We measured the Purkinje shift—that is, the increase in blue sensitivity—at various retinal eccentricities and levels of dark adaptation, by recording relative sensitivity to the red and blue phosphorus of a computer-controlled monitor screen. The CIE coordinates for the red and blue phosphorus, as measured with a Minolta Chromameter II photometer, were $x = 0.601$, $y = 0.341$ for red and $x = 0.147$, $y = 0.076$ for blue. Our “minimum-motion” display was a rotating annulus of radial sectors, which was designed to convert lightness into motion. Fig. 1 demonstrates the principle using horizontal strips of vertical bars, but in practice our actual stimulus was an iso-eccentric annulus filled with radial sectors (Fig. 2). The movie consisted of only four frames that cycled repetitively to generate strong apparent motion. A disk was divided into 36 blue sectors interleaved with 36 red sectors, alternating over time with 36 light magenta sectors interleaved with 36 dark magenta sectors, as diagrammed in Fig. 2. Each movie frame was displaced by one-quarter of a spatial cycle (half a sector width) from the previous frame, so that each sector jumped tangentially through a rotation angle of 2.5° between frames. The direction of the jump could not depend upon the hue of the magenta sectors, since all magenta sectors had the same hue. Instead it had to depend upon luminance. Thus if the blue sectors were, or looked, darker than the red, they appeared to jump to the left, to the nearest dark magenta sectors. If the blue sectors were, or looked, brighter than the red, they ap-

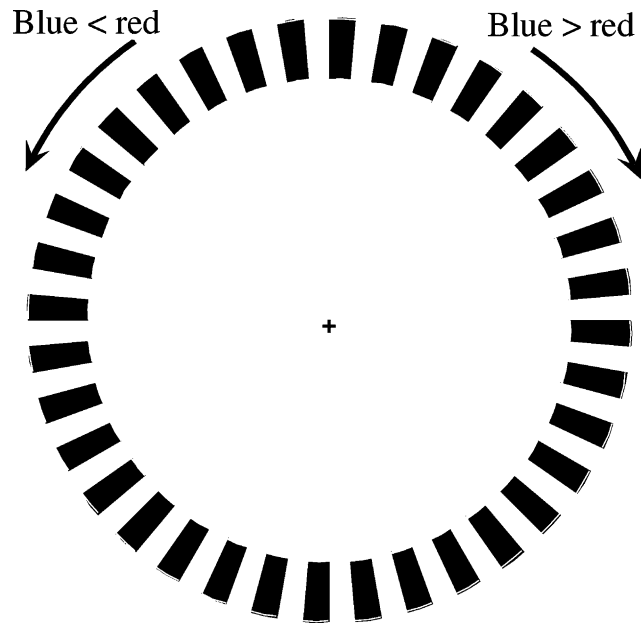


Fig. 2. Iso-eccentric annular stimulus, based upon Fig. 1, was filled with 36 radial red and blue sectors, alternating over time with 36 light and dark magenta sectors. Observers fixated the centre of the annulus and judged the direction of rotation of the annulus. It appeared to rotate counterclockwise (clockwise) when blue looked darker (lighter) than red. Mean radius of the annulus was 11.25 cm on the screen; the retinal eccentricity in degrees varied inversely with viewing distance.

peared to jump to the right, to the nearest bright magenta sectors. At equiluminance the motion seemed to vanish and was perceptually replaced by non-directional flicker. This equiluminance point was recorded. As a precaution to reduce flicker and unwanted changes in adaptation across frames, the space-average of the magenta movie frames was always made equal in both hue and luminance to the space-average of the frames that contained red + blue.

We used an annulus in order to sample only iso-eccentric regions of the retina. In pilot work we used a complete sectorized disk and found that over a certain mesopic range the motion of the stimulus looked non-uniform, with the central region rotating counterclockwise and the remainder of the disk clockwise. In other words the cone-rich central region appeared to turn in the light-adapted direction and the rod-rich peripheral regions in the dark-adapted direction owing to the pronounced non-uniformity of the retina, in which cone density peaks in the fovea but rod density peaks at an eccentricity of 20° (Anstis, 1998; Curcio et al., 1990; Osterberg, 1935). To ensure that we sampled iso-eccentric, presumably uniform retinal regions, the disk was masked down to form an annulus filled with radial sectors. The outer and inner diameters of the annulus were 12.5 and 10 cm on the monitor screen, so the thickness of the annulus measured radially was 2.5 cm. The effective rate of rotation was 11 rev/min

(5.5 s/rotation = 26 frames/s). (This frame rate avoids the loss of flicker visibility that Sharpe & Stockman (1999) reported at frequencies near 15 Hz, resulting from destructive interference between sensitive ‘slow’ and insensitive ‘fast’ rod signals in the visual pathways.) The annular stimulus was programmed using Macro-media Director for the Macintosh.

2.2. Procedure

We examined the direction in which this pattern appeared to move when it was covered with various neutral density filters. Artificial pupils were not used because we found that they blocked the observers’ view of the largest, most eccentric stimuli. The observers dark adapted for an initial period of 10 min. They then viewed the drifting patterns on the monitor screen. The level of dark adaptation was set by covering the eyes with a neutral filter, of density (0), 0.67, 1.33, 2, 2.67 or 3.33 log-units. (This corresponds to factors of approximately (1), 4.64, 21.38, 100, 464 and 2138). Since dark adaptation tends to be slower than light adaptation, the darkest filter (3.33 log-units) was used first, and then the next darkest and so on.

On each trial the experimenter pre-set the adaptation level, by selecting one of the seven filter factors, and set the red luminance to one of eight luminance values, namely 3.77, 4.8, 9.14, 9.98, 12.6, 15.35, 19 and 21.2 Cd m^{-2} . The observer then found the retinal eccentricity for which the blue (fixed at 5.73 Cd m^{-2}) was equiluminant to that red luminance. He or she sat in a wheeled chair, fixating the centre of the annulus, and moved bodily back and forth by rolling the chair toward and away from the screen, adjusting his viewing distance and hence the retinal eccentricity of the annulus. When conditions were right, at short viewing distances the annulus lay far out in the periphery, blue looked brighter than red, and the annulus appeared to rotate clockwise. Viewed from farther away, the annulus lay

nearer to the fovea, blue looked darker than red and the annulus appeared to rotate counterclockwise. The observer’s task was to find a viewing distance at which the motion was ambiguous in direction because it lay just at the boundary between appearing to rotate clockwise and counterclockwise. This defined the motion null at which red and blue were equiluminous. This indirect method had several advantages over pre-setting the filter factor and eccentricity, and then asking the observer to adjust the red luminance to a null point. First, it was easier and more accurate to adjust the viewing distance than to adjust the red level. Observers reported quite sharp and dramatic reversals in the perceived direction of rotation for quite small changes in viewing distance. Second, we avoided building up motion adaptation and motion after effects, which we found could be troublesome if the stimulus was always fixed on a constant retinal region. Third, this display makes a striking classroom demonstration, in which students can see for themselves that slight changes in viewing distance can reverse the perceived motion with no change whatever in the stimulus on the screen. Fourth, shortening the viewing distance increased not only the eccentricity of the annulus, but also its thickness ($r_{\max} - r_{\min}$), measured in degrees of visual angle, in a way that automatically compensated for the cortical magnification factor. Kuyk (1982) and van Esch et al. (1984) have demonstrated the desirability of such compensation. Anstis (1998) has briefly reviewed psychophysical aspects of cortical magnification.

The observers were three practised college students (2M, 1F), aged 19–22, who were compensated for their time.

3. Results and discussion

Fig. 3 shows the data from three observers. The abscissa shows the red luminance, in Cd m^{-2} , at which the motion nulled, and the ordinate shows retinal eccen-

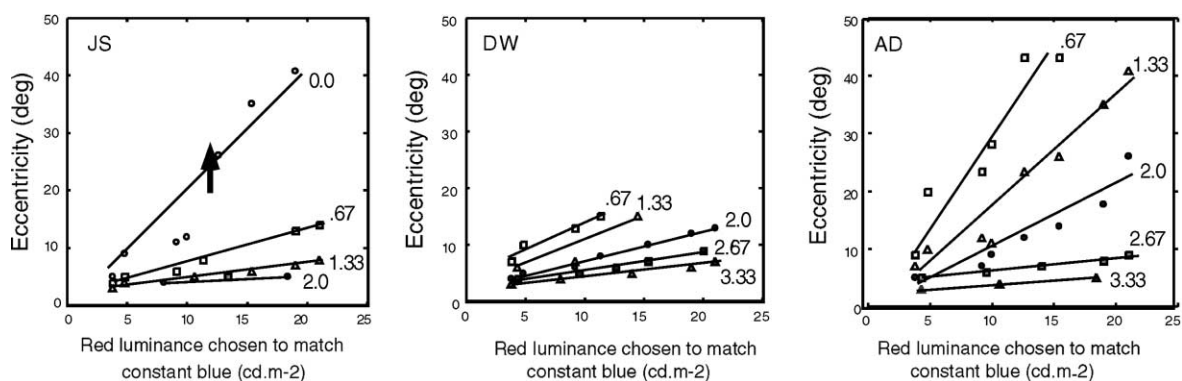


Fig. 3. Results from three observers. The matching red luminance, which is a measure of blue sensitivity, increases with eccentricity. Data for all observers are fitted by straight lines of the form $\text{Eccentricity} = s\text{BS} + c$. Thus blue sensitivity (relative to red) is a linear function of eccentricity (see text).

tricity. The red equiluminance point on the abscissa is, of course, our measure of the apparent brightness of the blue. The blue luminance on the screen was always held constant at 5.73 Cd m^{-2} (before filtering), so if the eye did not vary in sensitivity then all the data for all filter conditions would lie along a single vertical line. In fact, however, sensitivity to blue (relative to red) did vary considerably as a function of eccentricity and filter factor, such that the data appeared to lie along lines that fanned out from a point near the origin. Results were broadly similar for all three observers, differing only in the values for various parameters. Four straight-line fits are shown for observer JS and five for observers DW and AD, since observers were unable to make judgments in some filter conditions. These straight line fits were determined by linear regression to the data obtained at a given filter factor. No corrections were made for macular pigment.

The uppermost line shows the most light-adapted condition, with a filter factor of 0 log-units (that is, with no filter) for JS (−0.67 log-units for DW and AD), while the bottom line shows the most dark-adapted condition with a filter factor of −3.33 log-units (−2.0 log-units for JS). Each line slopes up to the right, showing that relative sensitivity to blue increased linearly with eccentricity. The very gradual slope of the bottom line (dense filter over the eyes) shows that at low luminance levels, sensitivity to blue was high even at small eccentricities, and increased rapidly even with small increases in eccentricity. The uppermost line represents the highest luminance levels. Here blue sensitivity was low and increased only gradually with eccentricity. The intermediate lines, for filter factors ranging between −1.33 and −2.67 log-units, show intermediate results.

Each line on the graph specifies a filter factor (0, 0.67, 1.33, 2, 2.67, 3.33 log-units), and the points along each line define conditions for which red and blue looked equiluminous and no motion was seen, neither clockwise nor counterclockwise. Each line divides the graph into two regions. In the region below and to the right of the line, if the observer moved away from the screen, the display became slightly smaller on the retina and fell on more foveal regions in which cones were relatively more active than rods, so red looked brighter than blue, and the annulus appeared to rotate counterclockwise. On the other hand, in the region above and to the left of the line, if the observer moved toward the screen the display became slightly larger and fell on more peripheral retinal regions in which rods were relatively more active than cones, so blue looked brighter than red, and the annulus appeared to rotate clockwise. For points along the line the annulus appeared to flicker but without rotating. The upward pointing arrow superimposed on the data of JS (Fig. 3(a)) gives an example. At the tail of the arrow, JS viewed a stimulus with red sectors of 12 Cd m^{-2} , with no neutral density filters, at a retinal ec-

centricity of approximately 20° . At this eccentricity the cones dominated and red looked lighter than blue. Now JS slid his chair slightly toward the screen, which made the stimulus a little larger and more eccentric. This effectively moved the operating point upwards to the tip of the vertical arrow and crossed over the line fitted to JS' data, so that now the rods dominated over the cones and blue looked lighter than red, reversing the perceived direction of rotation.

We fitted straight regression lines to the data for each filter factor, in the form

$$E = sBS + c \quad (\text{Fig. 3}) \quad (1)$$

where E is the eccentricity and BS is the blue sensitivity relative to red. Thus blue sensitivity increased linearly with eccentricity. A glance at Fig. 3 shows that the slope s of the line decreased markedly for a dark adapted eye (denser filter), so we plotted the slopes of the data lines of Fig. 3 as a function of filter factor F (in log units). These are shown as a log–log plot in Fig. 4:

$$\text{Log}(dE/dBS) \sim \text{log filter factor} \quad (\text{Fig. 4}) \quad (2)$$

The slope in Eq. (2) is steepest at high luminances.

Re-writing Eq. (2) as a power function of luminance:

$$dE/dBS \simeq \text{Luminance}^k \quad (\text{Fig. 4}) \quad (3)$$

where the exponent $k = 0.555, 0.625$ and 0.274 for observers AD, JS and DW respectively (geometric mean $\bar{k} = 0.456$). Specifically, adaptation level had a multiplicative effect upon retinal eccentricity, with each additional \log_{10} unit of light adaptation increasing the slope of the eccentricity function by a factor of $10^k = 3.6, 4.2$ and 1.9 for observers AD, JS and DW respectively (geometric mean $= 10^{\bar{k}} = 2.86$). This shows that adding a filter of 2.67 log-units, which reduced the overall luminance by a factor of 464, decreased the mean slope of the blue-sensitivity versus eccentricity curves for by approximately 16-fold ($= 10^{2.67\bar{k}}$).

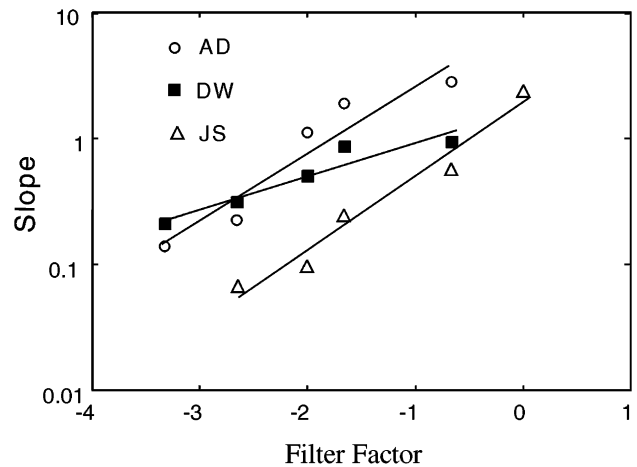


Fig. 4. The log of the slope of the fitted straight lines in Fig. 3 increases with luminance (see text).

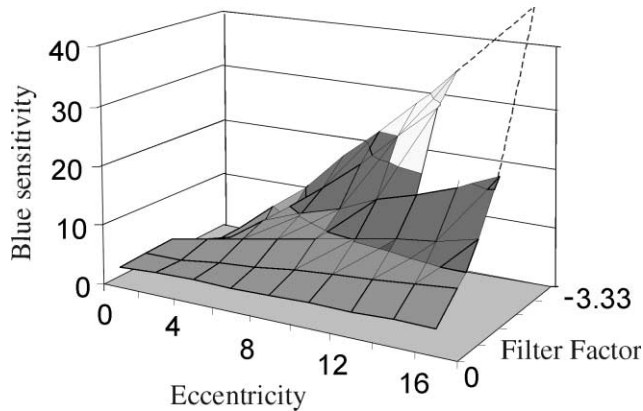


Fig. 5. 3-D plot shows the relationship between eccentricity, luminance and blue sensitivity.

Fig. 5 replots the data of Fig. 3(b) (observer DW) as a 3-D surface. This shows that blue sensitivity increases linearly with eccentricity, and increases exponentially as the log filter factor increases (becomes darker).

In conclusion, the data plotted in Figs. 3 and 5 show that blue sensitivity increases as a joint function of increasing eccentricity and of decreasing luminance. Relative blue sensitivity increases linearly with eccentricity, which projects the stimulus on to a larger population of rods, and this effect is multiplied by dark adaptation, which increases the activity of this enlarged population of rods relative to cones. This increasing activity in larger numbers of rods leads to a progressive increase in blue sensitivity.

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References

- Abramov, I., & Gordon, J. (1977). Color vision in the peripheral retina. I. Spectral sensitivity. *Journal of the Optical Society of America*, 67, 195–202.
- Anstis, S. (1998). Picturing peripheral acuity. *Perception*, 27, 817–825.
- Anstis, S. M., & Cavanagh, P. (1983). In J. Mollon & L. T. Sharpe (Eds.), *Color Vision: Physiology and Psychophysics*. London: Academic Press.
- Anstis, S. M., Cavanagh, P., Maurer, D., & Lewis, T. (1987). Optokinetic technique for measuring infants' responses to color. *Applied Optics*, 26, 1510–1516.
- Anstis, S. M., Hutahajan, P., & Cavanagh, P. (1998). Optomotor test for wavelength sensitivity in guppyfish (*Poecilia reticulata*). *Vision Research*, 38, 45–53.
- Cavanagh, P., & Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research*, 31, 2109–2148.
- Cavanagh, P., Anstis, S., & Mather, G. (1984). Screening for color blindness using optokinetic nystagmus. *Investigative Ophthalmology and Visual Science*, 25, 463–466.
- Cavanagh, P., MacLeod, D. I., & Anstis, S. M. (1987). Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America*, 4, 1428–1438.
- Chien, S. H., Teller, D. Y., & Palmer, J. (2000). The transition from scotopic to photopic vision in 3-month-old infants and adults: an evaluation of the rod dominance hypothesis. *Vision Research*, 40, 3853–3871.
- Cornsweet, T. N. (1970). *Visual perception*. London, New York: Academic Press.
- Curcio, C., Sloan, K. R., Kalina, R. E., & Henderson, A. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, 292, 497–523.
- Dowling, J. (1967). The site of visual adaptation. *Science*, 155, 273–279.
- Gregory, R. L. (1974). *Concepts and mechanisms of perception*. London: Duckworth.
- Kaiser, P. K., & Boynton, R. M. (1996). *Human color vision* (second ed.). Washington, DC: Optical Society of America.
- Lennie, P., Pokorny, J., & Smith, V. C. (1993). Luminance. *Journal of the Optical Society of America A*, 10, 1283–1295.
- Lia, B., Dobkins, K. R., Palmer, J., & Teller, D. Y. (1999). Infants code the direction of chromatic quadrature motion. *Vision Research*, 39, 1783–1794.
- Logothetis, N. K., & Charles, E. R. (1990). The minimum motion technique applied to determine isoluminance in psychophysical experiments with monkeys. *Vision Research*, 30, 829–838.
- Maurer, D., Lewis, T. L., Cavanagh, P., & Anstis, S. (1989). A new test of luminous efficiency for babies. *Investigative Ophthalmology & Visual Science*, 30, 297–303.
- Osterberg, G. (1935). Topography of the layer of rods and cones in the human retina. *Acta Ophthalmologica*, 6(Suppl.).
- Purkinje, J. (1825). *Beobachtungen und Versuche zur Physiologie der Sinne*. Zweites Bändchen (p. 192). G. Reimer, Berlin.
- Sharpe, L. T., & Stockman, A. (1999). Rod pathways: the importance of seeing nothing. *Trends in Neurosciences*, 22, 497–504.
- Stabell, B., & Stabell, U. (1980). Spectral sensitivity in the far peripheral retina. *Journal of the Optical Society of America*, 70, 959–963.
- Stabell, B., & Stabell, U. (1984). Color-vision mechanisms of the extrafoveal retina. *Vision Research*, 24, 1969–1975.
- Stockman, A., Sharpe, L. T., & Fach, C. (1999). The spectral sensitivity of the human short-wavelength sensitive cones derived from thresholds and color matches. *Vision Research*, 39, 2901–2927.
- Teller, D. Y., Brooks, T. E., & Palmer, J. (1997). Infant color vision: moving tritan stimuli do not elicit directionally appropriate eye movements in 2- and 4-month-olds. *Vision Research*, 37, 899–911.
- Teller, D. Y., & Lindsey, D. T. (1989). Motion nulls for white versus isochromatic gratings in infants and adults. *Journal of the Optical Society of America A*, 6, 1945–1954.
- van Esch, J. A., Koldenhof, E. E., van Doorn, A. J., & Koenderink, J. J. (1984). Spectral sensitivity and wavelength discrimination of the human peripheral visual field. *Journal of the Optical Society of America*, 1, 443–450.
- Verdon, W., & Adams, A. J. (1987). Short-wavelength-sensitive cones do not contribute to mesopic luminosity. *Journal of the Optical Society of America A*, 4, 91–95.

Wagner, B., & Boynton, R. M. (1972). Comparison of four methods of heterochromatic photometry. *Journal of the Optical Society of America*, *62*, 1508–1515.

Wald, G. (1945). Human vision and the spectrum. *Science*, *101*, 653–658.

Wooten, B. R., Fuld, K., & Spillmann, L. (1975). Photopic spectral sensitivity of the peripheral retina. *Journal of the Optical Society of America*, *65*, 334–342.

Wyszecki, G., & Stiles, W. S. (1967). *Color science: concepts and methods, quantitative data and formulae*. New York: John Wiley.