Color perception in the intermediate periphery of the visual field

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Color perception changes across the visual field. It is best in the fovea and declines in the periphery. Sensitivity to red–green color variations declines more steeply toward the periphery than sensitivity to luminance or blue–yellow colors. It is thought that this decline is due to the increasing size of receptive fields of parvocellular retinal ganglion cells and the unselective or random contribution of L- and M-cones to the receptive field surround. In earlier psychophysical studies it has been found that L − M cone opponency becomes absent above 30 deg. However, physiological experiments in macaque monkeys have shown that midget ganglion cells exist in the intermediate zone of the peripheral retina (20–50 deg) that are strongly cone opponent. Here we explore this contradiction between physiological and psychophysical research, using stimuli of variable size at eccentricities of up to 50 deg. We found that chromatic detection gets worse with increasing eccentricity but is still possible even at large eccentricities. Our results show that chromatic detection at these eccentricities is mediated by cone-opponent mechanisms.

Keywords: color vision, detection/discrimination, ganglion cells, peripheral vision, cone-opponent mechanisms

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Introduction

The variability of visual perception across the visual field is one of the most important characteristics of the primate visual system. While visual acuity and contrast sensitivity are exceedingly high in the fovea, they deteriorate rapidly with increasing eccentricity (Virsu & Rovamo, 1979). What is still debated is just how badly this deterioration is in the case of color vision. On the one hand it has been reported that color vision becomes dichromatic (more precisely, lacks L − M cone opponency) at eccentricities of about 25–30 deg and becomes absent at eccentricities larger than 40 deg (Ferree & Rand, 1919; Moreland, 1972; Moreland & Cruz, 1959), when tested with small stimuli. On the other hand, a number of studies have found that the size of the stimulus is the critical parameter and that fovea-like color vision exists out to at least 45 deg eccentricity (Abramov, Gordon, & Chan, 1991; Buck, Knight, Fowler, & Hunt, 1998; Gordon & Abramov, 1977; Johnson, 1986; Noorlander, Koenderink, den Ouden, & Edens, 1983; van Esch, Koldenhof, van Doorn, & Koenderink, 1984). Noorlander et al. (1983) even showed that under specific spatial and temporal conditions such as a large target size and a low temporal frequency (1 Hz) different hues can be perceived at eccentricities of up to at least 90 deg. However, results of a more recent study point in a different direction, claiming that L − M cone opponent vision is absent in peripheral vision (Mullen, Sakurai, & Chu, 2005). In this study, L − M cone contrast sensitivity declined steeply across the periphery and became behaviorally absent by 25–30 deg, suggesting that the L − M cone-opponent neurons in the primate peripheral retina are unlikely to contribute to color contrast detection measured behaviorally beyond this limit.

The decrease in color performance is likely a result of the spatial organization of the retina and not just a loss in sensitivity (Abramov et al., 1991; Martin, Lee, White, Solomon, & Rüttiger, 2001). The number of spectrally opponent ganglion cells decreases with eccentricity (Zrenner & Gouras, 1983), their receptive fields (RFs) get larger (Dacey, 1993; Goodchild, Ghosh, & Martin, 1996), and non-opponent cells become cone opponent if the stimulus size is increased (De Valois & De Valois, 1975; Krüger, 1977). Receptive field centers and the dendritic fields of parvo cells (PC) increase toward the periphery in humans and Old World monkeys and can encompass an area of about 20–40 M- and L-cones (Dacey, 1993; Goodchild et al., 1996). The larger dendritic trees and larger distances between neurons correspond to the cortical representation of the visual

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field in the cortex: The fovea has a large representation in visual cortex while the peripheral retina projects to a relatively smaller area in primary visual cortex (Engel et al., 1994; Horton & Hoyt, 1991; Tootell, Switkes, Silverman, Hamilton, 1988; Wässle, Grünert, Röhrenbeck, Boycott, 1989).

There is a long-standing debate whether the center and the surround of a retinal ganglion cell receive exclusive input from L- or M-cones (the selective wiring hypothesis) or random input from both cone types (the random wiring hypothesis). L − M cone opponent processing can only be achieved if the center and surround of the receptive field differ in the relative strengths of their cone inputs. In the fovea, this difference is given because the receptive field center of a foveal ganglion cell is driven by a single cone. Even if the surround contains a random mixture of cone types, the cells would have a cone-opponent response (Lennie, Haake, & Williams, 1991). In the intermediate periphery, midget bipolar cells receive direct input from single cones, but multiple bipolar cells converge on a single midget ganglion cell (Dacey, 1993). In this part of the retina, human chromatic sensitivity has been found to be consistent with the random wiring hypothesis (Mullen & Kingdom, 1996). Mullen and Kingdom (1996) developed a model that calculated the loss of cone opponency across the visual field under the assumption of unselective cone projections. The model was based on receptive field size of parvocellular retinal ganglion cells in primates and cone densities in human retina. Using a model based on binomial probability of L- and M-cones, Mullen and Kingdom (1996) found that if only a few cones (1–5) drive the RF center, cone opponency could arise by chance when different proportions of L- and M-cones contribute to the center and to the surround. They compared their model with psychophysical data collected from three observers at eccentricities up to 20 deg. The results revealed that there was a selective loss of red–green color sensitivity across the human visual field until 20 deg. They found that a model of unselective cone contributions is sufficient to account for this loss in sensitivity.

Other data provide strong support for the notion that the surround gets its input from a specific cone type (Reid & Shapley, 1992, 2002; Martin et al., 2001). Reid & Shapley (1992) mapped receptive fields of parvocellular neurons with cone-isolating stimuli and found cone specificity in both center and surround. Martin et al. (2001) presented red and green lights at eccentricities from 20 to 50 degrees and recorded midget ganglion cell responses from macaque monkey's retinal periphery. Surprisingly, peripheral and foveal ganglion cells showed equivalent responses. Martin et al. (2001) proposed a model based on anisotropic, selective input to the RF center to account for the high selectivity in the periphery. In the simulations they found that an ellipsoidal RF center when properly oriented to optimize the sampling of one cone type results in a large change in the ratio of L- to M-cone input. However, human psychophysics using the same stimuli showed a sharp decrease in psychophysical performance with eccentricity. Derrington (2001) concluded from the findings of Martin et al. (2001) that either the information from cone-opponent cells is not used during further cortical processing or that the macaque monkeys are a poor model for human chromatic vision. Both explanations seem unlikely and would cause problems for the interpretation of psychophysical results in general.

Here we try to resolve these contradictory results by investigating chromatic sensitivity in the intermediate periphery. Unlike previous studies, we measured chromatic detection contours and discrimination ellipses, allowing us to make inferences about the properties of the mechanisms underlying chromatic sensitivity. Furthermore, we used a matte gray hollow sphere where stimuli of variable size could be presented at eccentricities up to 50 deg. Our data provide evidence that color vision persists in the periphery, at least up to an eccentricity of 50 deg.

Methods

Observers

Five naive male and female observers, aged between 21 and 31 years, participated in the study. All observers had normal or corrected-to-normal visual acuity and no color perception deficits as tested with the Ishihara pseudoisochromatic plates. Observers were paid for participating in the experiment; not all observers participated in all experiments.

Apparatus

Stimuli were presented in a VisionStation (Elumens, Crescent Green, North Carolina). The VisionStation consists of a large, curved surface (reminiscent of a large satellite dish), a high-resolution LCD projector, and a wide-angle lens. The VisionStation is 104 cm deep by 160 cm high by 165 cm wide. The display surface has a 150-cm projection area with an 84-cm spherical radius of curvature for the screen. The screen size is 163 × 145 cm with a depth of 53 cm. The stimuli are projected onto this sphere by a centrally mounted LCD projector (Epson 730c) with a resolution of 1024 × 768 pixels, equipped with a wide-angle projection "trutheta" lens. The trutheta lens compensates most of the distortions of the projection that occur due to the small distance and the curved surface of the projection area.

Observers were seated at a distance of 80 cm from the sphere with their heads supported by a forehead and chin

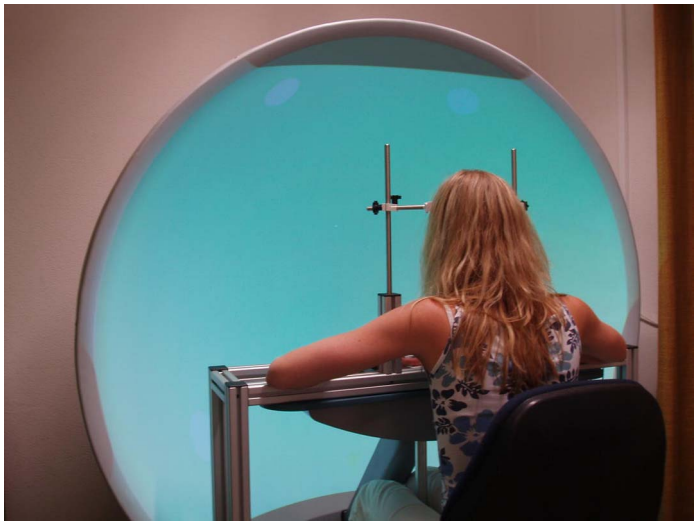

Figure 1. Experimental setup.

rest. For this setup, the VisionStation provides a field of view of 120 × 90 deg. The setup is depicted in Figure 1.

Calibration

We used a space-variant gamma correction and a spatial correction to ensure that the stimuli were of the same luminance and of equal size independent of their projected position.

Space-variant gamma correction

The VisionStation was gamma corrected and calibrated to ensure stimuli of the same luminance across the whole sphere. For gamma correction a standard procedure was applied: We measured for each of the three RGB primaries of the projector the luminance of the light reflected from the sphere with a Photo Research PR650 spectroradiometer for different pixel values between 0 and 255. A smooth function was used to interpolate between the measured points and was inverted to linearize the relationship between pixel values and intensity. We measured luminance values at different positions in the sphere to verify that the same shape of the gamma curve was present at different locations. While the shape was the same across the sphere, the overall intensity varied: the intensity was largest at the center and declined toward the periphery. To correct this decline, we measured the maximum intensity for each primary at different spatial locations and used a smooth function to interpolate between the measured values to obtain a map of intensity values for each pixel. The gamma-corrected intensity values were then normalized by this intensity map for each pixel of the stimulus image. Half-tone dithering was used to smooth the boundaries between the discrete intensity steps, resulting in a homogeneous visual impression of the homogeneous background. We verified that this procedure resulted in the same luminance across the whole sphere by measuring gamma-corrected luminance values at different spatial locations.

Spatial correction

We also used a spatial correction to compensate for geometrical distortions resulting from projection to the sphere that was present despite the trutheta lens of the projector. We first projected a calibration grid of horizontal and vertical lines spaced 64 pixels to the sphere and measured the (x, y, z) positions in space with an ultrasonic 3D tracking device (Zebris system, Zebris Medical, Isny, Germany). The surface of the measured points was interpolated to the full resolution of 1024 × 768 pixels, and an offset in x and y directions was computed for each pixel to ensure that the same solid angle results from a stimulus of fixed size shown at different positions in the sphere. The solid angle was computed for a reference point between the two eyes of the observer. We verified that this procedure resulted in stimuli of the same visual angle independent of the position in the sphere by measuring the visual angle for stimuli at all positions that were used in the experiment.

Color calibration

We measured the spectra of each primary at maximum intensity with a Photo Research PR650 spectroradiometer. The spectra were multiplied with the Judd-revised CIE 1931 color matching functions (Judd, 1951; Wyszecki & Stiles, 1982) to derive CIE 1931 xyY coordinates of the monitor phosphors (Irtel, 1992). In the following, luminance and photometric luminance refer to the $V(\lambda)$ curve as modified by Judd (1951). The xy coordinates of the monitor primaries are given by R = (0.5246, 0.3513), G = (0.2951, 0.5925), and B = (0.1787, 0.1186). The xyY coordinates were then used to convert between RGB and DKL color space. Cone contrasts were computed from the spectral distribution of the monitor primaries using the cone fundamentals of Smith and Pokorny (1975). We measured the xy chromaticity values at different locations in the sphere and found that the chromaticity values varied only approximately in the range of normal measurement fluctuations (on average only 0.0207).

Stimuli

Uniformly colored disks of two sizes (5 deg and 8 deg) were used as stimuli. All colors were defined in the DKL color space (Derrington, Krauskopf, & Lennie, 1984). A single disk was shown in any of the four quadrants (detection and identification task), or disks were shown in

all quadrants, with one disk of slightly different color (discrimination task).

Procedure

Detection

Colored disks were presented on a photometrically isoluminant gray background in a 2 × 2 arrangement. Observers had to detect the stimulus in the periphery while fixating a white point in the center. Stimuli were randomly presented at one of four possible positions (upper or lower, left or right quadrant), and the observers signaled the position of the stimulus by pressing a corresponding button. Stimuli were presented for 500 ms. The short presentation time was chosen to prevent subjects from making eye movements to more than one peripheral target; making an eye movement to just one peripheral target in a 4AFC paradigm would just worsen performance because the other positions would then become even more peripheral. Moreover, fixating stimuli at an eccentricity larger than 20 deg usually involves head movements that were prevented by the chin rest. Finally, we used trained observers that were instructed to maintain fixation.

All colors were defined in DKL color space (Derrington et al., 1984). Detection was measured for four chromatic directions along the cardinal axis of DKL space (0, 90, 180, 270 deg). Detection thresholds were determined by varying the chromatic contrast in a three-down-one-up staircase. The staircase terminated after six reversals or 100 trials. Thresholds were determined as the mean of the last five reversal points. Sessions, including breaks, were limited to 1 h.

Identification

The identification procedure was identical to the detection procedure with the only difference that observers had to press a button to identify the color of the stimulus (reddish, yellow-greenish, bluish-greenish, violet). In a training session observers learned the correspondence between the stimulus colors and the buttons.

Discrimination

The procedure to measure discrimination threshold was similar to the procedure we applied in previous discrimination studies (Hansen, Giesel, & Gegenfurtner, 2008; Krauskopf & Gegenfurtner, 1992). Colored disks were presented on a photometrically isoluminant gray background in a 2 × 2 arrangement. Three of the disks had the same color, the test color, and one disk at a randomly determined position differed in color (comparison color). The task of the observers was to signal the position of the differently colored disk by pressing a corresponding button on the keyboard. A standard staircase procedure was used to measure the discrimination thresholds between the test and comparison colors. Discrimination was measured parafoveally with disks of 5 deg diameter centered at 5 deg eccentricity, and peripherally at 50 deg eccentricity with disks of size 8 deg.

Results

Chromatic detection

In the first experiment we presented uniformly colored disks in all four quadrants of the visual field. Stimuli had a diameter of 5 deg and were presented at eccentricities of 10, 20, 30, 40, and 50 deg. Figure 2 shows the results averaged across seven observers. The main result is that thresholds could be reliably measured for all chromatic directions at all eccentricities: Color vision, in particular for colors varying along the L − M direction, exists at eccentricities up to at least 50 deg. For a fixed size of the stimulus, detection thresholds increase with increasing eccentricity. Thresholds along the S − (L + M) axis show an asymmetric behavior: S-cone increments are less affected by increasing the eccentricity compared to S-cone decrements. The +S − (L + M) or "blue-on" signals in primates are transferred by a separate opponent pathway that originates from a distinct type of bistratified ganglion

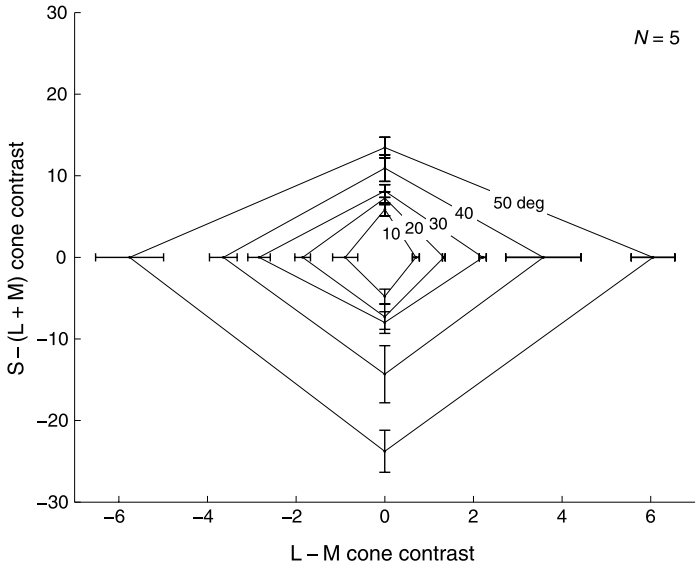

Figure 2. Detection thresholds for colored disks (size 5 deg) at five eccentricities (10, 20, 30, 40, and 50 deg) averaged across five observers. The fact that threshold could be measured at all eccentricities tested shows that color vision, in particular color vision mediated by the L – M cone-opponent channel, persists up to at least 50 deg.

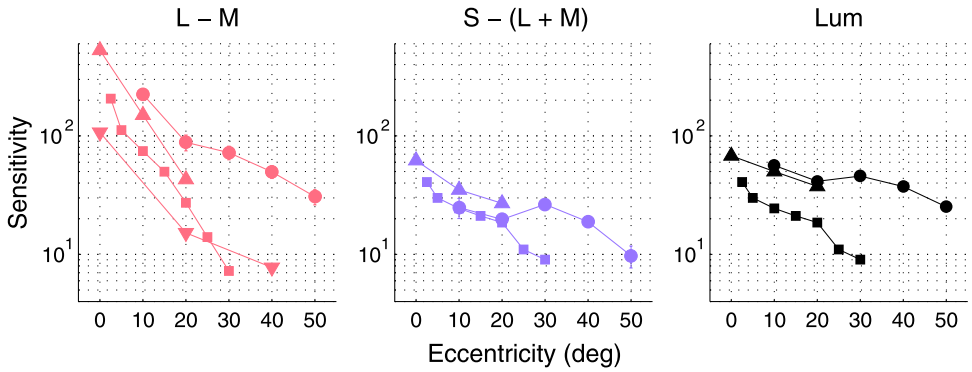

Figure 3. Cone contrast sensitivity at five different eccentricities (from 10 to 50 deg) for three cardinal stimuli (size 8 deg). Results are averaged across three observers for the chromatic stimuli (L – M and S – (L + M)) and across two observers for the achromatic stimuli. Data of the present study (circles) are compared to data from Mullen and Kingdom (2002; triangles), Mullen et al. (2005; squares), and Martin et al. (2001; downward pointing triangles, measured only for L – M).

cells in the retina (Dacey & Lee, 1994). The blue-off signals are not transmitted by a distinct pathway but are linked to the midget system of the parvocellular pathway (Dacey, 2000).

In the second experiment we measured chromatic detection with slightly larger disks (8 deg) at the same five eccentricities as in the first experiment (10, 20, 30, 40, and 50 deg) for three observers. We measured chromatic detection thresholds along the two chromatic cardinal axes (L − M, S − (L + M)) and also along the achromatic luminance axes (L + M) of the DKL color space. Data averaged across three subjects are shown in Figure 3, together with data from three previous studies (Martin et al., 2001; Mullen & Kingdom, 2002; Mullen et al., 2005). For the L − M cone-opponent channel there is a steep decline in sensitivity up to 20 deg, which becomes shallower above 20 deg. The conclusion that L − M chromatic vision becomes absent above 25 deg may result from a wrong extrapolation of data measured only below 30 deg. For S − (L + M) and achromatic stimuli we found a more shallow decline. Our results extend previous measured sensitivity curves farther into the periphery.

To clarify whether these sensitivities were truly owing to cone-opponent mechanisms we ran three further experiments. First we ran an identification experiment that allowed us to compare thresholds for detection and identification. Second we ran a detection experiment in cone contrast space to investigate whether the detection was based on cone-opponent channels instead of a luminance channel driven by residual luminance contrast between the photometrically isoluminant stimuli. Third we measured discrimination ellipses at different eccentricities.

Detection and identification

So far, we have just shown that observers could detect something but have not shown that they perceive any color. Therefore, we ran an identification experiment where the observers had to identify the color of the stimuli by pressing a corresponding button. This allows us to investigate whether there exist any differences between the detection thresholds at which observers could just sense something, and the thresholds at which they could reliably name the color of the stimulus. We presented disks of 5 deg at two eccentricities (10 and 50 deg) to seven subjects. We found no differences between detection and identification thresholds along the L − M axis, and only small, negligible differences along the S − (L + M) axes. Almost as soon as observers can detect the stimulus, they can identify the color. The data shows that the detection is mediated by chromatic processes and that color perception exists even at eccentricities as far as 50 deg (Figure 4).

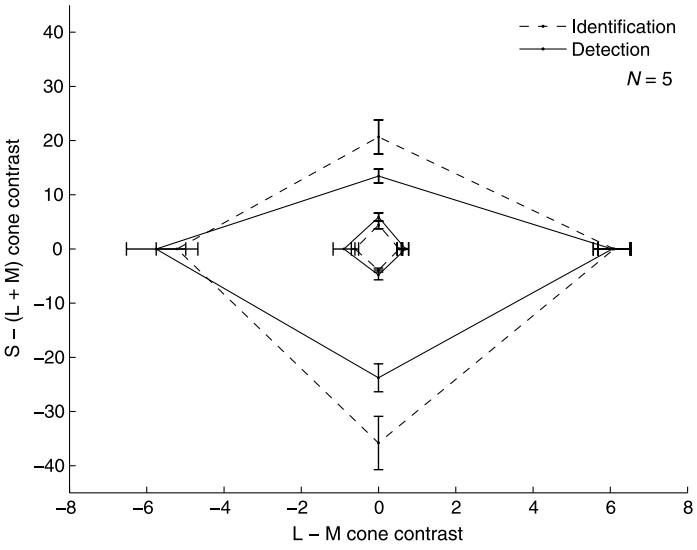

Figure 4. Comparison of detection thresholds (solid) to identification thresholds (dashed) for colored stimuli (5 deg) at two eccentricities (10 and 50 deg; from center to periphery). Data averaged across five subjects.

Detection contours in cone contrast space

Next we investigated the underlying chromatic mechanism by presenting stimuli in cone contrast space and measuring the detection contours at different eccentricities. Thresholds were measured at three eccentricities (5, 30, and 50 deg). The size of the stimuli was 8 deg for 50 deg eccentricity and 5 deg for the other eccentricities. We used purely achromatic stimuli and isoluminant stimuli, as well as colored stimuli with slight changes in luminance (elevation ±1, 2, 3, 4, and 5 deg in DKL space).

Figure 5 shows the results in L/M cone contrast space. (In the L/M cone contrast space, achromatic stimuli excite both the L- and M-cones and fall on the main diagonal; isoluminant stimuli differentially excite L- and M-cones and fall on a chromatic direction of about 120 deg.) Low thresholds occur along the isoluminant axis where all thresholds for all three eccentricities are projected on lines parallel to the luminance axis, showing that the underlying detection mechanism was cone opponent.

Chromatic discrimination ellipses

In the final experiment we measured chromatic discrimination contours (Hansen et al., 2008; Krauskopf & Gegenfurtner, 1992). Subjects had to select the odd one out of four colored disks presented in the periphery at 50 deg. Stimuli had a diameter of 8 deg. Chromatic discrimination thresholds were measured at eight different test locations with chromatic directions of 0, 45, 90, 135, 180, 225, 270, and 315 deg and with an amplitude of 0.5. Figure 6 shows thresholds measured at the parafovea (5 deg) and at 50 deg eccentricity. The discrimination ellipses at the parafovea were similar to previous results (Hansen et al., 2008; Krauskopf & Gegenfurtner, 1992), showing that discrimination can be reliably measured with the present setup. Next we measured chromatic discrimination ellipses at 50 deg eccentricity. Chromatic discrimination thresholds could be measured at all test locations for all comparison colors, providing clear evidence that chromatic vision is present at large eccentricities. However, discrimination is poorer as shown by the larger overall thresholds, which are about 4.5 times larger compared to parafoveal presentation. Further, the shape of the discrimination ellipses along the L − M axis are similar to those measured in the parafovea, but the shapes of the other ellipses are different and more rounded. Behaviorally, this means that hue discrimination is poorer in the periphery, in particular for orange and bluish colors that have elongated discrimination ellipses in the fovea and in the parafovea. In terms of chromatic mechanisms, round ellipses occur if discrimination is mediated solely by the cardinal mechanisms. Unlike in the fovea, where evidence for multiple cortical mechanisms has been found (Hansen & Gegenfurtner, 2006), the chromatic detection in the periphery seems to be mediated by fewer mechanisms. In this experiment we did not use stimuli larger than 8 deg for peripheral presentation, thus we cannot rule out that larger stimuli may ultimately compensate for the observed changes. However, the 8 deg large stimuli represent a 16-fold increase in area compared to the 2 deg disks used by Hansen et al. (2008), and this is presumably large enough to compensate the coarser peripheral resolution. Note that the disk stimuli used in our experiment cannot be made arbitrarily large without compromising localization: A disk of, e.g., 20 deg presented at 50 deg eccentricity would allow us to measure peripheral performance only up to 40 deg. Overall, our findings suggest that we can see colors in the periphery, but that we can distinguish them worse than in the fovea, even if the stimuli are large.

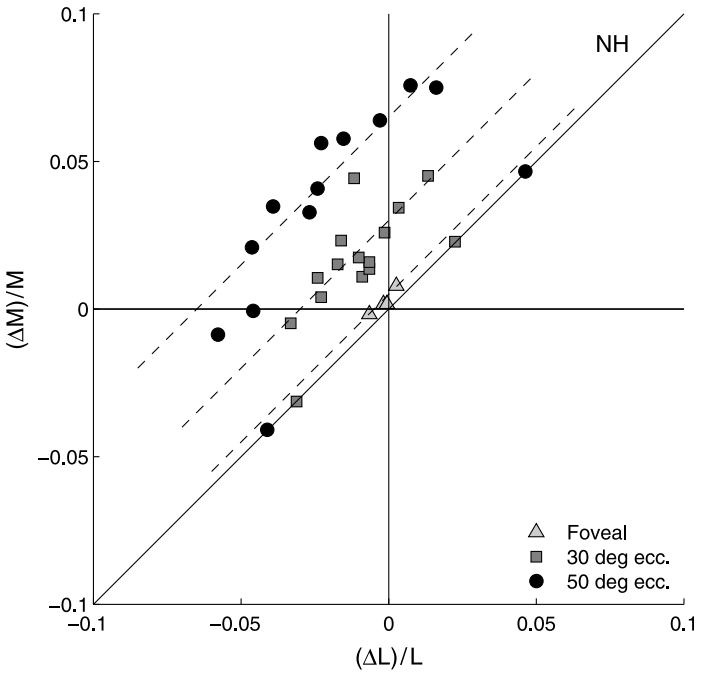

Figure 5. Detection contours measured in cone contrast space (subject NH). The stimuli were presented at three eccentricities (5, 30, and 50 deg). Thresholds are indicated by the distance from the origin and are much smaller for isoluminant stimuli than for luminance stimuli (main diagonal).

Discussion

Summary of findings

We have measured chromatic detection and discrimination in the near periphery and found that chromatic discrimination, in particular along the L − M axis, is possible even at high eccentricities up to 50 deg for stimuli of 8 deg. We confirmed in three control experiments

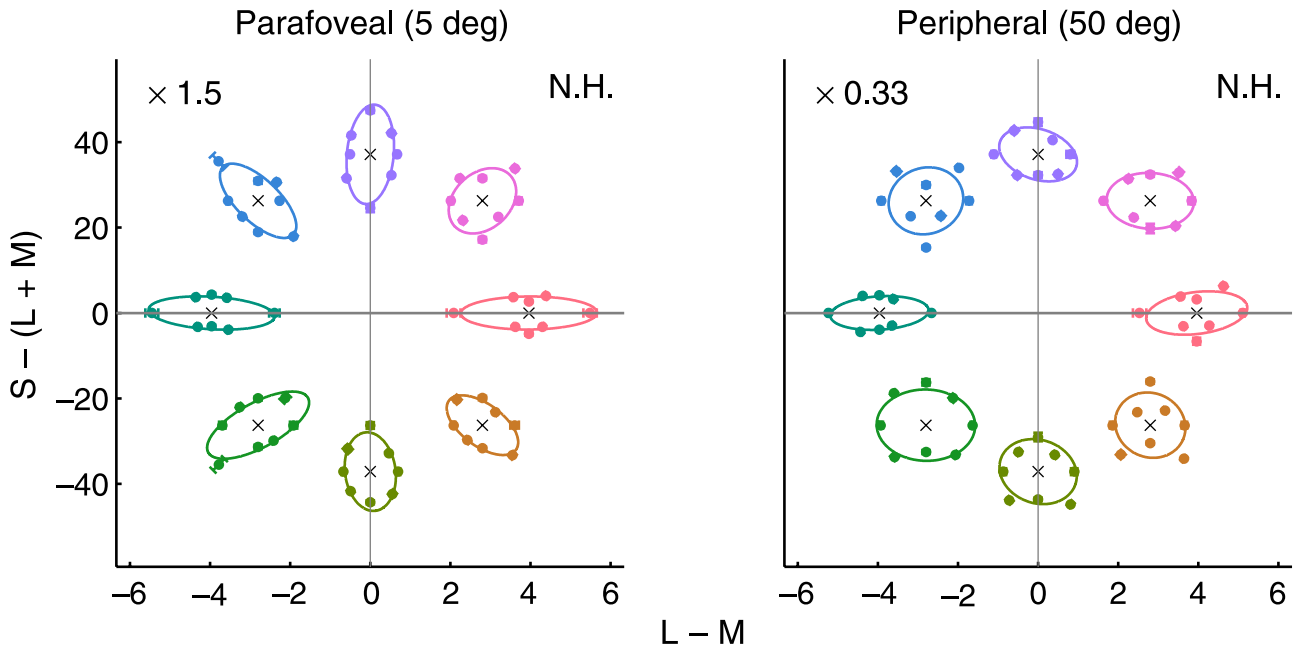

Figure 6. Chromatic discrimination at the fovea and peripherally at 50 deg. Discrimination is measured at eight test locations equally spaced around the medium gray adaptation point. The resulting discrimination ellipses have been scaled by 1.5 (parafoveal) and by 0.33 (50 deg) for better comparison of their shapes.

(identification, detection in cone contrast space, and chromatic discrimination) that chromatic mechanisms operate at these eccentricities.

Chromatic mechanisms in the periphery

The detection contours reveal that detection in the far periphery is supported by cone-opponent processing with increasing threshold from the fovea to 50 deg. Our data point to another, more cortical change from foveal to peripheral color processing. Discrimination contours for peripheral targets became more circular, indicating that the multitude of chromatic detection mechanisms that has been reported psychophysically (Hansen et al., 2008; Krauskopf & Gegenfurtner, 1992) and physiologically in visual cortex in V1, V2, V3, and IT (Gegenfurtner, Kiper, & Levitt, 1997; Kiper, Fenstemaker, & Gegenfurtner, 1997; Komatsu, 1998, Komatsu, Ideura, Kaji, & Yamane, 1992; Lennie, Krauskopf, & Sclar, 1990; Wachtler, Sejnowski, & Albright, 2003) is a specialization of the fovea and the parafovea. Overall, chromatic discrimination is possible for suitable large stimuli at eccentricities up to at least 50 deg, but sensitivity is lower and hue discrimination is not as good as in the fovea.

Comparison to other psychophysical studies

Our results confirm a number of psychophysical studies that have investigated peripheral color sensitivity (Abramov et al., 1991; Murray, Parry, & McKeefry, 2006; Noorlander et al., 1983, Vakrou, Whitaker, McGraw, & McKeefry, 2005). These studies agree that a decrease in chromatic sensitivity with peripheral presentation can be compensated by increasing the size of the stimuli.

Noorlander et al. (1983) determined contrast detection thresholds for red–green and blue–yellow spatiotemporal color modulations at several eccentricities. They found that color vision becomes worse if a stimulus of constant size was moved away from the fovea; however, when the stimulus was enlarged with increasing eccentricity, the decreased sensitivity could be compensated, such that color discrimination in the periphery was comparable to that in the fovea. Noorlander et al. (1983) found that chromatic bars were detectable up to at least 30 deg, and temporal chromatic modulations were detectable up to at least 90 deg. They concluded that spatiotemporal chromatic discrimination is approximately constant across different eccentricities if the number of stimulated ganglion cells is constant.

Abramov et al. (1991) measured color appearance based on hue and saturation scalings at different eccentricities. Abramov et al. (1991) found that increasing the size of the stimulus in the periphery produced a fovea-like performance, up to eccentricities of 20 deg. They presented stimuli from 0.25 to 6 deg of diameter at the fovea and from 5 to 40 deg of eccentricity in a perimeter-like setup with movable rear projection. Due to limited technical equipment, they could not find an adequate equivalent for presentations at 40 deg eccentricity. They concluded that it was not possible to find a stimulus that elicits fovea-like perception in this peripheral part of the retina.

Vakrou et al. (2005) studied chromatic sensitivity up to 20 deg of the nasal field with Gabor stimuli that were modulated along the cardinal axes of the DKL color space. They found that performance could be equated across the visual field by changing the size of the stimuli. They found no qualitative loss of chromatic sensitivity across the visual field.

Murray et al. (2006) studied changes of color perception in the peripheral field up to 30 deg using an asymmetric simultaneous matching paradigm. They found that saturation changes could be neutralized if the test stimulus was increased in size. Hue changes, however, could not be compensated: some hues remained unchanged whereas others exhibit substantial changes. Hues signaled by the S − (L + M) channel were more robust compared to hues mediated by the L − M channel.

In contrast to these studies, there are a number of recent experiments where diverging results were obtained. Those studies found that L − M cone opponency was highly sensitive in the fovea but fell steeply across the periphery (Mullen, 1991; Mullen & Kingdom, 1996, 2002; Stromeyer, Lee, & Eskew, 1992) resulting in a complete loss of L − M cone opponency at the behavioral level by 25–30 deg (Mullen et al., 2005). Mullen et al. (2005) tested cone contrast sensitivity at different eccentricities. They used a 138 cm by 104 cm flat CRT monitor and showed stimuli at eccentricities between 2 and 30 deg. Contrast detection thresholds were measured using a staircase procedure. Their results showed that L − M cone opponency steeply declined across the visual periphery and became behaviorally absent by 25–30 deg in the nasal field. Mullen et al. (2005) used a sine-wave ring pattern as stimulus. The sine-wave ring pattern was chosen because large spatial wavelengths (up to 16 deg) could be displayed without compromising localization. In the present study, we used disks of up to 8 deg centered at the particular eccentricity; thus, we measured chromatic detection and discrimination in a range of −4 deg and +4 deg around the particular eccentricity. However even if one takes this into account, our data show that chromatic detection is behaviorally present at eccentricities up to 46 deg, a value far above the cut-off eccentricity of about 25–30 deg reported by Mullen et al. (2005).

What could be the cause for this discrepancy? One potential reason may be that the sine-wave ring pattern used by Mullen et al. (2005) was not an optimal stimulus for chromatic detection because of its small radial size. The sine-wave ring was an angular sinusoidal modulation with a large angular size of 5 deg but shown in a small annulus of 1.5 deg radial size (at 30 deg eccentricity). The spatial frequency of the angular sinusoidal modulation was chosen to optimize cone contrast sensitivity. Since the chromatic contrast sensitivity is low pass (Mullen, 1985), a low angular spatial frequency of 0.0625 cycles/deg (i.e., a wavelength of 16 deg) was used at eccentricities of 25 deg and above. However, the fixed radial size (1.5 deg) was non-optimal for chromatic detection. We suspect that the reported breakdown of chromatic detection of L − M stimuli above 25–30 deg may be due to the small radial size of the stimuli.

Comparison to physiological findings

Chromatic signals originate from the absorption of light by three different types of cones with peak sensitivities at short (S-cones), medium (M-cones), and long (L-cones) wavelengths. The signals of the three types of cones are combined already in the retina in two chromatic channels, S − (L + M) and L − M, that have different spatial characteristics and are transmitted in distinct pathways to the cortex: S − (L + M) is signaled by the koniocellular pathway, while L − M is signaled by the parvocellular pathway; L − M cells have an antagonistic center–surround organization of their receptive fields (type I), while S − (L + M) cells have coextensive receptive fields (type II). Only few (<10%) of all cones are S-cones, resulting in fewer cells of the koniocellular pathway compared to the parvocellular pathway. The blue-off −S + (L + M) signals are not transmitted by a distinct pathway but are linked to the midget system of the parvocellular pathway (Dacey, 2000).

The parvocellular L − M cells can signal a cone-opponent response if the center and surround differ in their input from L- and M-cones. The strongest cone-opponent response would occur if the center and surround were driven exclusively by a single type of cone, such that the RF center receives input only from L-cones and the surround is driven only from M-cones, or vice versa. It has been shown that it is sufficient for a robust cone-opponent signal that only the center of the receptive fields gets input from a single type of cones, while the surround can be indiscriminately fed by both L- and M-cones (Lennie et al., 1991; Mullen & Kingdom, 1996). The layout of the wiring of cones to the receptive field centers of midget ganglion cells changes with eccentricity (for a review, see Dacey, 2000 or Derrington, 2001). In the fovea, a cone-specific input to the RF center is guaranteed because the receptive field center of a midget ganglion cell is exclusively driven by a single bipolar cell, which is in turn driven by a single cone: there is a private pathway from a cone to a midget ganglion cell center. In the far periphery, a cone-opponent signal is almost impossible if the wiring is random because several cones converge directly on bipolar cells (Wässle, Grünert, Martin, & Boycott, 1994). In the intermediate retina, bipolar cells receive input from single cones, but several bipolar cells converge on a single ganglion cell (Dacey, 1993).

Martin et al. (2001) measured chromatic sensitivity with red and green isoluminant LED stimuli of 4.7 deg foveally and at eccentricities between 20 and 50 deg in macaque monkey. They reported that most parvocellular (PC) ganglion cells in the periphery had an L − M sensitivity close to that of foveal PC cells. This finding is hard to

reconcile with psychophysical results showing a steep decrease in L − M sensitivity with eccentricity, and possible ways out are "not very palatable" (Derrington, 2001). Is the monkey retina different from that in humans? Or do postretinal mechanisms determine the deterioration of chromatic discrimination in the periphery, as suggested by Martin et al. (2001)? An inspection of the number of cells studied by Martin et al. (2001) suggests another possible way to reconcile these findings: only some midget cells exhibit a high selectivity, but the average selectivity declines with eccentricity. Martin et al. (2001) recorded from 131 cells at eccentricities above 20 deg, 54 cells (41%) were PC cells, of which 34 displayed overt red–green opponent responses. A quantitative analysis of 35 peripheral cells revealed that 28 cells were unambiguously cone opponent (showing a larger response to isoluminant modulation compared to luminance modulation produced by in-phase modulation of the red and green LEDs), while 7 cells (20%) responded weakly to isoluminant modulation. From the pool of these 28 cone-opponent cells a sample of 11 cells recorded above 30 deg was chosen for further analysis. Average red–green modulation sensitivity of these 11 cells was 0.8 and not significantly different from a sample of 18 foveal cells with a selectivity of 1.2 that was recorded in another study. There are several problems with this analysis. First, only a sample of 11 cells (20%) from a total of 54 PC cells was used in the analysis. Second, the average sensitivity tended to be higher in the fovea than in the periphery. This higher foveal sensitivity might become significant for a larger sample of cells. Third, foveal recordings were taken from another study with different animal subjects, stimuli, and apparatus (Lee, Pokorny, Smith, Martin, & Valberg, 1990) and may thus not be fully comparable to the peripheral recordings. We argue here that based on these data the strong claim that most peripheral cells have the same sensitivity as foveal cells is not fully supported. Instead, the study shows that only a subset of all peripheral PC cells has a selectivity that is comparable to the fovea, but that this sensitivity still tends to be smaller, and that this high selectivity is definitely not present in all peripheral cells. Overall, the findings of Martin et al. (2001) seem to be in agreement with most psychophysical findings.

Solomon, Lee, White, Rüttiger, and Martin (2005) recorded parvo, magno, and konio cells in vivo in the fovea and periphery of macaque retinae. They found evidence for chromatic responses of M- and K-cells being equivalent in foveal and peripheral parts of the retina. Most peripheral P-cells showed color-opponent behavior for low temporal frequency stimuli below 10 Hz. Some P-cells showed no color opponent behavior. Except for these cases chromatic properties of the inner 50 deg of visual angle were preserved. Solomon et al. (2005) conclude that the main change between foveal and peripheral ganglion cells was a higher responsiveness to high temporal frequency in the periphery.

Evidence for at least a high degree of cone specificity to both center and surround comes from the work of Reid and Shapley (1992, 2002). Reid and Shapley used cone-isolating stimuli made up of arrays of squares whose colors were randomly modulated to map RFs. Spike trains were correlated with the patterns that preceded them. Using this reverse-correlation technique, Reid and Shapley (1992, 2002) found spatially antagonistic receptive fields that predominantly receive input from a single cone type both in the center and in the surround. However, their method does not exclude that RF center and surround may be modulated simultaneously. The random grid stimuli can activate both the center and the surround, and optical blur could cause signals from the center to mask mixed input in the surround (Reid & Shapley, 2002, p. 6173). However, the findings clearly indicate that cone inputs are not entirely random but at least biased.

Not all physiology is in favor of a highly selective input to midget retinal ganglion cells. Contrary to Martin et al.'s (2001) report of color opponent mechanisms in the periphery, Diller et al. (2004) found that nearly all peripheral midget cells (except a single one) were non-opponent at eccentricities of 30–60 deg. One potential reason for this result, which seems to be in contradiction to most other studies, could be the high temporal frequency (about 10 Hz) used to stimulate the cells.

Buzás, Blessing, Szmajda, & Martin (2006) measured L- and M- cone inputs to PC receptive field in marmosets between the fovea and 30 deg eccentricity. They found that response strength depended on the overall segregation of L- and M-cone inputs to center and surround, consistent with the random wiring hypothesis. The majority of PC cells in both foveal and peripheral retina showed cone-opponent responses; the cone purity in the RF surround was at least as high as in the center. Buzás et al. (2006) found that the inhibitory input to a PC cell was not constituted by the local ratio of L- and M-cones but are biased by some unknown additional factors. They propose a random wiring model with a functional bias.

Momiji, Hankins, Barath, and Kennard (2007) developed a dynamic model of the peripheral retina that incorporated the random arrangement of L- and M-cones in the retinal cone mosaic and anatomically reasonable degrees of convergence between cones, bipolar cells, and ganglion cells. Numerical simulations of ganglion cell responses in the periphery were compared to model responses of the primate fovea (Momiji, Bharath, Hankins, & Kennard, 2006). Both models were based on random wiring and found that peripheral ganglion cells were less color sensitive than foveal cells but remained color sensitive.

Overall, a complete random wiring model does not seem to be able to account for most of the data. Such models at least need to be augmented by additional factors (such as the elongated RF surrounds as suggested by Martin et al., 2001), which bias the functional segregation of cone inputs.

Summary

The range of eccentricities over which red–green color vision is still possible is larger than previously thought. Color stimuli can be reliably detected and identified by chromatically opponent mechanisms even at 50 deg eccentricity. Earlier studies most probably underestimated this range. Differences could be caused by technical limitations and the use of stimuli of non-optimal size. In agreement with previous studies we found that the decline in reddish-greenish L − M color sensitivity was greater than for luminance and bluish-yellowish S − (L + M) signals. We interpret our findings as being consistent with a functional bias in the wiring of cone inputs to ganglion cells (Buzás et al., 2006) that predicts a decrease but not a lack of cone-opponent responses in the retinal periphery.

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