Peripheral detection and resolution with mid-/long-wavelength and short-wavelength sensitive cone systems

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This study compared neural resolution and detection limits of the human mid-/long-wavelength and short-wavelength cone systems with anatomical estimates of photoreceptor and retinal ganglion cell spacings and sizes. Detection and resolution limits were measured from central fixation out to 35° eccentricity across the horizontal visual field using a modified Lotmar interferometer. The mid-/long-wavelength cone system was studied using a green (550 nm) test stimulus to which S-cones have low sensitivity. To bias resolution and detection to the short-wavelength cone system, a blue (450 nm) test stimulus was presented against a bright yellow background that desensitized the M- and L-cones. Participants were three trichromatic males with normal visual functions. With green stimuli, resolution showed a steep central–peripheral gradient that was similar between participants, whereas the detection gradient was shallower and patterns were different between participants. Detection and resolution with blue stimuli were poorer than for green stimuli. The detection of blue stimuli was superior to resolution across the horizontal visual field and the patterns were different between participants. The mid-/long-wavelength cone system’s resolution is limited by midget ganglion cell spacing and its detection is limited by the size of the M- and L-cone photoreceptors, consistent with previous observations. We found that no such simple relationships occur for the short-wavelength cone system between resolution and the bistratified ganglion cell spacing, nor between detection and the S-cone photoreceptor sizes.

Introduction

Williams (1985) used a laser interferometric technique to effectively bypass the optics of the eye and determine grating foveal contrast threshold at long wavelengths (633 nm). With light scatter as the only source of optical aberrations, gratings could be detected at spatial frequencies of up to 150–200 c/°. A limit of 150 c/° corresponds to the first zero crossing of the modulation transfer function for a circular aperture of 2.3 μm, which is similar to anatomical measurements.


Thibos and colleagues investigated resolution and detection of green monochromatic and white grating targets in the peripheral visual field (Anderson, Wilkinson, & Thibos, 1992; Cheney, Thibos, & Bradley, 2015; Thibos, Bradley, & Still, 1991; Thibos, Cheney, & Walsh, 1987; Thibos, Still, & Bradley, 1996; Thibos, Walsh, & Cheney, 1987; Wilkinson, Anderson, Bradley, & Thibos, 2016). Resolution was sampling limited and corresponded well to midget ganglion cell density. Detection was contrast limited and as high as 30 c/° at 30° in the horizontal field. It corresponded well to the aperture of the cone inner segments. At 30° eccentricity, a simple approach of having the aperture covered by less than one cycle to register contrast gives 37 c/° as the upper limit to detection, while using the zero crossing of the modulation transfer function for a cone aperture indicates 45 c/°.

Several Thibos et al. studies (Anderson, Wilkinson, & Thibos, 1992; Cheney, Thibos, & Bradley, 2015; Thibos, Cheney, & Walsh, 1987; Wilkinson, Anderson, Bradley, & Thibos, 2016) used a Visometer (Lotmar, 1972, 1980; also Lotmar interferometer, Haag-Streit, Berne, Switzerland) in which two small spots of light are formed at or near the eye entrance pupil and interfere to produce high contrast gratings on the retina, effectively bypassing the eye's optics, and a simple methodology was used to measure spatial frequency limits to detection and resolution. Between these two limits was a range of spacing frequencies in which aliasing was experienced, which means that although gratings were detected, they did not appear like gratings, or appeared as gratings with incorrect orientations and/or frequencies lower than their actual frequencies.

Other studies have investigated neural limits to peripheral detection and resolution by the use of adaptive optics systems (Lundström et al. 2007; Rosén, Lundström, & Unso, 2010) or careful peripheral correction using ophthalmic lenses (Anderson, 1996; Artal, Derrington & Colombo, 1995; Atchison, Mathur, & Varnas, 2013; Lewis et al., 2014; Rosén, Lundström, & Unso, 2011, 2012; Wang, Thibos, & Bradley, 1997). In these cases the detection acuities were less than those obtained by Thibos and colleagues (Thibos, Cheney, & Walsh, 1987; Thibos, Walsh, & Cheney, 1987) with the interferometer. For example, at 20° in the nasal field, Thibos, Cheney, and Walsh (1987) obtained about 35 c/°, while Artal et al. (1995) obtained about 14 c/deg, Wang et al. (1997) obtained about 20 c/° and Rosén et al. (2011) obtained about 17 c/°. These differences may reflect the more rigorous forced-choice psychophysical methodology and incomplete correction of aberrations of the latter study, and possibly the influence of a sharp (high frequency) edge to the gratings in the Thibos et al. studies.

The above studies involved white light or long wavelength monochromatic (or quasimonochromatic) light and were dominated by mid- and long-wavelength sensitive cones (M-/L-cones). To study detection and resolution mediated via the S-cone system, Williams and colleagues (Williams & Collier, 1983; Williams, Collier, & Thompson, 1983) used centrally fixated 10° diameter blue gratings (420 nm or 440 nm) set against a yellow background that desensitized the L- and M-cones, and obtained resolution and detection limits of 10–14 and 23–35 c/°. Careful attention was given to correct refraction for wavelength. Metha and Lennie (2001) used a laser interferometric technique out to 20° from fixation and found that the inferred S-cone mediated resolution was 6–14 c/° at the fovea and showed a steep reduction into the periphery, being 1–3 c/° at 20° from fixation in both temporal and nasal field directions. Detection acuity was on average 1.6 times higher than for resolution acuity, but showed considerable variation between and within three participants. The much poorer detection limits of the S-cone system, than for the longer wavelength sensitive system, indicates that this is limited not only by cone size.

Other investigations of resolution and detection for the S-cone system out to 35° from central fixation used conventional imaging rather than interferometry, and involved careful refraction in the periphery (Anderson, Coulter, Zlatkova, & Demirel, 2003; Anderson, Zlatkova, & Beirne, 2002a; Anderson, Zlatkova, & Demirel, 2002; Beirne, Zlotkova, & Anderson, 2005). Anderson, Zlatkova, and Demirel (2002b) found that resolution reduced from 4.6 c/° at the fovea to 1.1 c/° at 20° in the nasal field, with corresponding detection limits being 6.0 c/° and 1.6 c/°, somewhat lower than those reported by Metha and Lennie (2001). They noted that the ratio of detection to resolution limits in the periphery was much smaller than reported by Thibos and colleagues for achromatic gratings and monochromatic gratings of longer wavelengths (Thibos, Cheney, & Walsh, 1987; Thibos, Walsh, & Cheney, 1987). As for the longer wavelengths (Anderson, 1996; Atchison et al., 2013; Wang et al., 1997), detection, but not resolution, for the S-cone system was highly dependent on focus (Anderson et al., 2003).

With the exception of one of the Anderson et al. studies (Anderson et al., 2002b), there have been no direct comparisons of detection and resolution between the S-cone and L-/M-cone systems. Anderson et al. (2002b) concluded that S-cone resolution is sampling limited according to bistratified ganglion cell spacing. Despite careful refractive correction in that study, it is likely that S-cone resolution was affected by aberrations because of dilated pupils and did not give an accurate estimate of the neural limits to vision.
conducted an interferometric study out to 35° eccentricity across the horizontal visual field to directly compare the performance of the S-cone and L-/M-cone cone systems with anatomical estimates of photoreceptor and retinal ganglion cell spacings and sizes. Our intention is to evaluate the proposal that bistratified ganglion cell spacing limits the resolution of the S-cone system.

**Methods**

The study was conducted in accordance with the tenets of the Declaration of Helsinki. Approval was obtained from the Queensland University of Technology Human Research Ethics Committee and participants gave written consent.

**Participants**

Three male participants were in good ocular and general health, and had normal color vision. The right eyes were tested. The FM100 hue scores for right eyes were in the range 4–12, placing the participants in the superior discrimination range (Farnsworth, 1957). Macular pigment optical densities estimated with a Macular Pigment Densitometer (Macular Metrics II, LLC, Providence, RI) were 0.41 to 0.49, close to average for a young adult group of 0.49 ± 0.16 (Kyle-Little, Zele, Morris, & Feigl, 2014). DB was a 30-year-old South Asian with refraction +0.50 DS/–0.25 DC×134 and 23.60-mm axial length. H-FZ was a 39-year-old East Asian with refraction –4.50 DS/–0.25 DC×26 and 25.77-mm axial length. DAA was a 61-year-old Caucasian with refraction –2.50 DS and 25.14-mm axial length. To estimate the effect of attenuation of the short wavelength (450 nm) stimulus by the optical media of the human eye, we applied the model of van de Kraats and van Norren (2007) for stimuli <1° diameter. The estimated difference in optical density between the oldest and youngest observers in the sample was ~0.25 log units; there was no obvious effect of these differences in optical media density on resolution or the detection data reported in the Results section. The sample of three participants is consistent with the sample size of the studies reported in the introduction (~100 hr per participant). Given the subtleties of the psychophysical judgments, participants undertook considerable training before experiments commenced.

**Apparatus**

The experiment was conducted using a modified Visometer, based on the Thibos et al. studies (Anderson et al., 1992; Cheney et al., 2015; Thibos, Cheney, & Walsh, 1987; Thibos, Walsh, & Cheney, 1987; Wilkinson et al., 2016). This produced high-contrast sinusoidal gratings on the retina. The horizontal visual field was examined out to 35° from fixation. Except for the central field testing, the fixation eccentricity was set using a 1-mm diameter (0.15°) white fixation spot viewed through the center of the instrument mount. Stimulus diameter subtended 1.5° for foveal testing and 2.5° for peripheral positions, except that foveal detection was also determined for a 2.5° grating.

Illumination of the stimulus field was provided by the instrument’s tungsten light source, altered in luminance by a variable power supply. The color appearance of the stimulus was generated by attenuating the spectral power distribution of the tungsten light with a green (550 nm, 10 nm full width at half maximum) or a blue (450 nm, 10 nm) interference filter (65098/65079, Edmund Scientific, Barrington, NJ) positioned near the usual locations of other filters in the interferometer path. The stimulus field luminance was determined by a brightness match to an adjacent field with the same adaptation level. We determined that a yellow background (740 cd/m²) was in approximate equality of the blue test stimulus (7.1 cd/m²) and the green stimulus was 365 cd/m² (2580 Troland with a 3-mm pupil) and the blue stimulus was 7.1 cd/m² (50 Troland with a 3-mm pupil). We inferred that, because the wavelength of the green test stimulus is beyond the spectral response of the S-cones, the M-/L-cone system mediates it. To infer which postreceptoral process limits the resolution data, we compared the results with anatomical estimates of the midget and parasol ganglion cells.

In order to bias the measurements to the S-cone system, the blue test stimulus was combined with a 7.5°-diameter yellow background that desensitized the L- and M-cones. The yellow field was generated using a high irradiance white LED (SP-03-W3VKL1, Luxeon Star) combined with a yellow filter (27-905 Edmund Scientific, transmittance at 480 nm 1.3%, transmittance at 490 nm 6%, half maximum transmittance at 514 nm), and joined the interferometer beam at a cube beam-splitter placed in front of the interferometer. Therefore, the entire area of the blue test stimulus was exposed to the same adaptation level. We determined that a minimum luminance of 740 cd/m² of the yellow background was sufficient as resolution and detection did not decrease at higher levels. The ratio of the luminance of the blue test stimulus (7.1 cd/m²) and yellow background (740 cd/m²) was in approximate proportion with the experimental conditions used by Vassilev et al. (2003) to bias their measurement to the S-cone system with undilated pupils; increasing the
background luminance did not affect results for a selection of positions for either detection or resolution. For both green and blue stimulus gratings, 4000 K room fluorescent lighting was turned on and reflective white panels (spectrally flat across the visible spectrum) were placed behind the Visometer to give a surround luminance of approximately 100 cd/m².

Under the experiment conditions, pupils were 3.5–4.5-mm diameter, which was sufficient for the entire range of spatial frequencies (for example, 30 c/° stimulus corresponded to 0.75 mm separation between the coherent light spots at the pupil). Accordingly, there was no need to dilate pupils.

Procedure

Participants were stabilized by a bitebar and aligned with a xyz translation stage so that the entrance pupil coincided with the coherent point sources 53 mm in front of the instrument. The x and y alignments were achieved by finding the eye position midway between the horizontal and vertical locations at which gratings started to disappear. This was checked for the larger angles during the experiment.

The experiment was conducted in the following order: green resolution, green detection, blue resolution, and blue detection. The resolution experiment used a four-alternative choice procedure (possible grating orientations 45°, 90°, 135°, and 180°). Participants used a descending method of adjustment starting from a randomly chosen frequency above the resolution limit and lowered the spatial frequency slowly until the grating orientation was identified. Unlimited viewing time was allowed. The detection experiment used the same protocol as the resolution experiment, except that the participant lowered the spatial frequency until the presence of spatial contrast could be perceived. For both resolution and detection, gratings were presented in a pseudorandom order with five measurements for each orientation. Means and standard deviations were based on measurements across all orientations.
Results

Figure 1 shows detection and resolution grating acuities for the green and blue test stimuli measured along the horizontal meridian for each participant. The resolution data for the green stimulus show a central–peripheral gradient with a ~15-fold difference. Participant DB shows steady, close to symmetrical, reductions in acuity from the center into the periphery for both detection and resolution and for both colors (Figure 1a). For green gratings, resolution and detection are the same at the center of the field at 37 c/°, but resolution reduces more steeply than detection away from the center so at ±30°–35° the former is 2–4 c/° and the latter is 18–20 c/°. Unlike for green gratings, for blue gratings the detection is higher at the center of the field than is resolution (12 vs. 9 c/°, respectively) with an approximate plateau to ±10°. Detection and resolution reduce to 5–7.5 c/° and 1–2 c/°, respectively, at ±25° eccentricities. Foveal detection improves to 16 c/° for a 2.5° field.

Participant H-FZ shows a similar pattern for green resolution as does participant DB (Figure 1b). However, now green detection changes little across the peripheral field at 19–24 c/°. Central blue detection (8 c/°) is poorer than for participant DB (12 c/°), but it is still higher than the corresponding resolution (4 c/°). Detection and resolution reduce to 6 c/° and 2 c/°, respectively, at ±20° eccentricity. Foveal detection is not improved for a 2.5° field over that for a 1.5° field.

Participant DAA shows asymmetries between temporal and nasal visual field sides (Figure 1c). Most noticeably for green grating detection is the presence of a temporal–nasal asymmetry, with a steep change in gradient from the fovea to 22 c/° at (~)10° temporal, but then improvement to 34 c/° at (~)25° before reducing again, while on the nasal side acuity reduces more regularly. As for the other participants, central blue detection (10 c/°) is higher than central blue resolution (7 c/°). The patterns for blue detection and blue resolution across the field are similar to their green counterparts. Foveal detection improves to 12 c/° with a 2.5° field.

Figure 2 includes the same data as for Figure 1, but shows separate results for green and blue gratings to emphasize the similarities and differences between participants. Green resolutions are similar across the field for the all participants, but the green detection patterns are very different (Figure 2a). Participants H-FZ and DAA have their poorest detection at (~)10° temporal. All participants have higher blue detection than blue resolution at the center of the field, but blue resolution and detection patterns are different between participants (Figure 2b).

Discussion

Resolution for the green grating shows a central–peripheral gradient out to 30° eccentricity in the nasal and temporal visual fields with an 15-fold change and is similar for our three participants across the horizontal visual field. At the field center, detection acuity for the green stimulus cannot be distinguished from resolution, but decreases slowly into the periphery and patterns are different between participants (Figure 2a). Detection and resolution with the blue stimulus are poorer than their green counterparts. All participants have higher
blue detection than blue resolution at the center of the field (1.4–2.5 times), which continues into the periphery, and both blue detection and resolution patterns are different between participants (Figure 2b).

To compare our mean results with previous psychophysical and anatomical studies, Figure 3 shows that our green detection (Figure 3a) results are lower than those of Thibos, Cheney, and Walsh (1987) by...
about 40%; given that the same type of instrument was used to bypass the eye optics, it is not clear to us why this is the case. Our results in turn are much higher than those of Anderson et al. (2002b), whose detection data showed a steeper decline into the periphery. Our data are lower than detection derived from G-/R-cone sizes (Curcio & Sloan, 1992), but close enough to support Thibos et al.’s contention that detection is limited by cone size.

To infer the postreceptoral pathway limiting the resolution data for the green gratings, Figure 3b plots the midget and parasol ganglion cell receptive fields size along with our resolution data and previous reports. There is good agreement between our studies and those of Wilkinson et al. (2016) and Anderson et al. (2002b) with the resolution derived from midget ganglion cell spacing (Dacey, 1993b), but not from the parasol ganglion cell spacing. This supports Thibos’ contention that resolution is sampling limited according to midget ganglion cell spacing.

Detection is poorer with the blue stimulus than with the green stimulus across the field (compare Figure 3c with Figure 3a). Our blue detection results are higher in the periphery than those of Metha and Lennie (2001), who used a laser interferometer technique and both results are higher than those of Anderson et al. (2002b), which we attribute to the influence of aberrations in the latter study. Converting the limited histological S-cone size data provided by Curcio et al. (1991) gives detection limits of 86 c/° and 55 c/° at 1° and 2.4° eccentricities, respectively, so all the results are much lower than the predicted detection limit set by S-cone diameter, suggesting that detection by the short wavelength system is not limited solely by S-cone size. There may be a sufficient number of ganglion cells to support the cones in green detection, but this does not appear to be the case for S-cones.

The resolution and detection of blue stimuli have a similar relationship as is observed between the resolution and detection of green stimuli, except that for blue stimuli the resolution is poorer than detection at the fovea (compare Figure 3d and 3c for our data, those of Metha and Lennie, 2001, and those of Anderson et al., 2002b). As for the green gratings, the ratio of detection to resolution is much higher in our study than that of Anderson et al. Figure 3d includes resolutions based on densities of S-cones and of small bistratified ganglion cells. Anderson et al.’s (2002b) results are in good agreement with the latter, and, as mentioned earlier, they concluded that the resolution is sampling limited according to bistratified ganglion cell spacing. Our results and those of Metha and Lennie (2001) are more similar to those derived from S-cone density than to the ganglion cell density. We would not claim that the former limits S-cone resolution alone, but ganglion cell spacing does not appear to be the limiting factor as claimed by Anderson et al. (2002b) The model observer for the S-cone pathway developed by Metha and Lennie (2001) used noise in cone pathways and postreceptoral pooling of cone signals, but took no account of the size of S-cones; the model results were in reasonable agreement with their experimental detection and resolution results.

We found no evidence of foveal aliasing in green light with the Lotmar interferometer, whereas Williams (1985) reported a large range using a 623.8-nm HeNe laser. Peripheral cone contrast is high for frequencies just beyond the resolution limit and the perceived contrast of aliasing is very high, whereas cone contrast is low foveally because of summation over cone apertures. Combining this with the contrast lowering effect of chromatic aberration provided by the bandwidth of interference fringes and a conservative influence of a descending method-of-adjustment psychophysics makes gathering evidence of foveal aliasing difficult.

The study had other shortcomings. The descending method of adjustment is a criterion dependent psychophysical task. We used this because of the design of the equipment and for the need to get measurements efficiently. We compensated by extensive training and by taking multiple measurements at each position using a different starting point to minimize errors of habituation or expectation. As mentioned earlier for the Thibos’ interferometer studies, there is a possible influence of a sharp (high frequency) edge to the gratings.

Conclusions

We used an interferometer to estimate neural resolution and detection limits of mid-/long-wavelength and short-wavelength cone systems. Resolution for the green stimuli shows a steep central–peripheral gradient and is similar between participants, but the change in detection of the green stimuli is shallower and patterns are different between participants. The patterns support previous investigations indicating the mid-/long-wavelength system’s resolution and detection are limited by cone size and ganglion cell spacing, respectively. Blue detection and resolution are much poorer than their green counterparts. Blue detection is superior to resolution across the field and patterns are different between participants, with no simple relationship of either with cell type or size.

Keywords: acuity, detection, mid- and long-wavelength sensitivity cones, neural, short-wavelength sensitive cones, resolution
Acknowledgments

Haifeng Zhu was sponsored by a scholarship from the Shandong Provincial Education Association for International Exchanges. This work was supported by the Australian Research Council Discovery Projects DP140101480 and DP140100333. The authors thank Larry Thibos for advice on modifying the Lotmar interferometer. The authors thank Dipesh Bhattarai for being a participant.

Commercial relationships: None.

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