Enhanced human contrast sensitivity with increased stimulation of melanopsin in intrinsically photosensitive retinal ganglion cells

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Abstract

The intrinsically photosensitive retinal ganglion cells (ipRGCs) are known to serve non-image-forming functions, such as photoentrainment of the circadian rhythm and pupillary light reflex. However, how they affect human spatial vision is largely unknown. The spatial contrast sensitivity function (CSF), which measures contrast sensitivity as a function of spatial frequency, was used in the current study to investigate the function of ipRGCs in pattern vision. To compare the effects of different background lights on the CSF, we utilized the silent subtraction technique. We manipulated the stimulation level of melanopsin (i.e., the visual pigment of ipRGCs) from the background light while keeping the cone stimulations constant, or vice versa. We conducted four experiments to measure the CSFs at various spatial frequencies, eccentricities, and levels of background luminance. Results showed that melanopsin stimulation from the background light enhances spatial contrast sensitivity across different eccentricities and luminance levels. Our finding that melanopsin contributes to CSF, combined with the receptive field analysis, suggests a role for the magnocellular pathway and challenges the conventional view that ipRGCs are primarily responsible for non-visual functions.

1. Introduction

The intrinsically photosensitive retinal ganglion cells (ipRGCs)—the third type of photoreceptors in addition to rods and cones (Hankins et al., 2008; Hattar et al., 2002; Lucas et al., 2001)—have attracted much attention mainly because of their effects on non-image-forming functions, such as circadian rhythm (Berson et al., 2002), sleep (Altimus et al., 2008), alertness (Vandewalle et al., 2009), and pupillary light reflex (Lucas et al., 2001, 2003; Tsujimura et al., 2010). ipRGCs are a small subset of retinal ganglion cells that express melanopsin, a photopigment with an absorption spectrum peaking around 480 nm (Lucas et al., 2001), which is within the same range that human perceives as the color blue. IpRGCs project to the suprachiasmatic nuclei (SCN) in the retinohypothalamic tract pathway (Hattar et al., 2006), and the SCN receives and decodes the irradiance of environmental light, which is important for circadian photoentrainment (Panda et al., 2002, 2003). As a result, the encoding of irradiance by melanopsin as a photon counter of environmental light has been considered the primary function of ipRGCs.

This study aimed to investigate how stimulation of melanopsin from an adapting background light affects the spatial Contrast Sensitivity Function (CSF) in humans. To achieve this objective, we measured the CSF by presenting Gabor patches with varying spatial frequencies against different background luminance and eccentricities—all while manipulating background lights to selectively stimulate melanopsin. First, because ipRGCs have a large dendritic field (Hattar et al., 2002; Zhao et al., 2014), any effect of melanopsin on pattern vision should be manifest with a large field (e.g., background) stimulation. Second, manipulating melanopsin stimulation in the background light could be analogous to changes in ambient light, which would be most suitable for
investigating melanopsin. Third, the CSF model is frequently used to study photopic pattern vision in the human visual system (Legge & Foley, 1980; Pandele & Sekuler, 1968; Watson & Solomon, 1997) because it graphs contrast sensitivity as a function of spatial frequency and offers information about the limits of pattern vision (Blakemore & Campbell, 1969; De Valois et al., 1982).

Several previous studies have highlighted the visual function of melanopsin. For instance, it has shown that ipRGCs, which contain melanopsin, project to the LGN in animals (Brown et al., 2010; Dacey et al., 2005; Eckert et al., 2010). Allen et al. (2017) found evidence for melanopsin’s contribution to early visual processing in mice. Mice lacking either non-M1 ipRGCs or melanopsin showed reduced contrast sensitivity at low spatial frequencies (Schmidt et al., 2014). In addition, Brown et al. (2012) demonstrated that melanopsin stimulation in involved brightness discrimination in both mice and humans while recent studies have suggested its role in color perception (Barriouneau et al., 2022; Gao et al., 2018; Spitschan et al., 2017; Zaidi et al., 2007; Zele, Adhikari, Cao, & Feigl, 2019). Zele, Feigl, Adhikari, Maynard, and Cao (2018) reported that melanopsin stimulation could enhance temporal contrast sensitivity, and Uprety, Adhikari, Feigl, and Zele (2022) found that melanopsin stimulation interacted with rod- and cone-mediated vision depending on the temporal frequency of the test stimulus. Finally, Allen et al. (2019) used silent-substitution to show that melanopsin contributed to human pattern vision at low spatial frequencies, below 1 cycles/degree.

However, Vincent et al. (2021) did not observe that melanopsin stimulation altered the sensitivity for the detection of luminance flicker. This result was consistent with the findings of Brown et al. (2012), who demonstrated that perceived luminance, as determined by flicker photometry, did not vary under metameric backgrounds with different melanopsin stimulation. These findings appear to disagree with those of Zele et al. (2018, 2019) and Uprety, Adhikari, Feigl, and Zele (2022), but it should be noted that there were differences in the methodologies of these studies. Vincent et al. (2021) and Brown et al. (2012) manipulated the melanopsin stimulation of the background and measured flicker sensitivity, while Zele, Feigl, Adhikari, Maynard, and Cao (2018) and Uprety, Adhikari, Feigl, and Zele (2022) utilized silent substitution to test stimuli but not to the background. Therefore, it is possible that the effects of melanopsin on the background light are different from those of the test stimulus.

To date, there have not been any systematic studies that have demonstrated the contribution of ipRGCs to the modulation of human spatial CSF by background lighting. Previous research has shown that CSF varies with eccentricity (Banks et al., 1991) and retinal illuminance (Kelly, 1972). Furthermore, combining cone and melanopsin stimulations elicits brightness perception (Brown et al., 2012). Thus, it is reasonable to hypothesize that melanopsin stimulation might influence CSF. Given that the CSF sets the limits of pattern vision and is considered the basis function of pattern vision, it is important to investigate whether ipRGCs, which were conventionally believed to carry mainly non-image-forming functions, also play a role in human CSF.

The current study aimed to investigate the effect of melanopsin stimulation under different background light conditions on the human spatial CSF across various spatial frequencies, eccentricities, and background luminance levels. In the present study, the background lights in different experimental conditions were metamers: background lights in different conditions had different spectral power distributions but were perceived as the same colors. In Experiment 1, we examined the CSF at low spatial frequencies with a 16 eccentricity, and in Experiment 2, we increased the background luminance. Experiments 3 and 4 measured the CSF as the eccentricity decreased to 4 while varying the spatial frequencies. Spatial contrast sensitivity is highest in the fovea and decreases with increasing eccentricity, and the peak of the CSF shifts towards higher spatial frequency with decreasing eccentricity (Rovamo, 1978). Therefore, we expect the shape of the CSF to vary with eccentricity.

2. Experiment 1

2.1. Ethics

The present study was approved by the Research Ethics Committee at National Taiwan University (NTU REC: 201505SH071) and Kagoshima University (permit number: H24SE002). All experiments were performed following the guidelines of the Declaration of Helsinki.

2.2. Methods

2.2.1. Participants

We recruited seven participants (mean age = 24.6) from National Taiwan University. All participants had normal or corrected-to-normal visual acuity and gave written informed consent before participating.

2.2.2. Stimuli

All the test stimuli were generated via a four-primary system consisting of three projectors (NEC PA500) and interference filters. The projectors could provide 10-bit color processing. Each of the three projectors had three primaries. The minimum contrast was less than 0.003, depending on the test stimulus. This system was the same system used in Yang et al.’s study (2018). See Fig. 3B in Yang et al. (2018) for a schematic illustration. We used an independent graphic board (NVIDIA Quadro K5000) to output the stimuli to the three projectors simultaneously from the host PC. Therefore, each projector was synched with the others. The experimental program was written in C++ with Microsoft Visual Studio 2015 using OpenCV and OpenGL libraries.

In addition, a steady background in each measurement was used. Because the background did not change in time, the three projectors were time-synchronized. The three projectors were also spatially aligned: We aligned the pixels before uniform calibration, and observers saw the test Gabor patches and background on a diffuser which reduced the pixel-based misalignment. The diffuser was an Opal Diffusing Glass (Edmund Optics Inc., New Jersey, USA), with a resolution of 1024 × 768.

We performed uniform calibration across the display to reduce luminance unevenness in each color channel (see Supplementary Material 1). No participants reported a change in the color of the stimuli presented. With the silent substitution technique (Brown et al., 2012; Chien et al., 2020; Estévez & Spekreijse, 1982; Tsujimura et al., 2010; Yang et al., 2018), we could independently increase the stimulation of melanopsin without changing the stimulation of each cone type (L-, M-, and S-cones) under the same background color and luminance; i.e., the background lights in different experimental conditions were metamers.

Three background light conditions were used: melanopsin-high, lightflux-high, and control. The melanopsin-high condition and the control condition contained backgrounds as a metameric pair, meaning they had the same tri-stimulus values, i.e., the same color and luminance. The lightflux-high condition varied radiant flux from the control condition without changing the spectral composition, which increased the radiant flux uniformly at all wavelengths. As shown in Fig. 1, compared to the control condition, the melanopsin-high condition included an increased melanopsin stimulation, and the lightflux-high condition included increased melanopsin and cone stimulations. By comparing each pair of backgrounds, we were able to separate the contribution of melanopsin stimulation (by comparing the melanopsin-high condition and the control condition), cone stimulation (by comparing the lightflux-high condition and the melanopsin-high condition), and the combination of melanopsin and cones (by comparing the lightflux-high condition and the control condition).

Gabor patches consisting of sinusoidal gratings with a Gaussian envelope (sigma = 5.2) were used as the target, as they could drive early visual cortical activity in a controlled manner (Tadin et al., 2003). A Gabor patch was presented at either the left or right side of the fixation (10 in width and 10 in height, Fig. 2A) at the eccentricity of 16. The
targets and backgrounds were presented to the participant on a gray background via a diffuser. When the trial began, the temporal profile of the Gabor was presented as follows: In the first 250 ms, the contrast (i.e., Michelson contrast) between the background and the Gabor ascended with an initial contrast at 0.05 and gradually changed with a sinusoidal function to the designated contrast level, stayed at the designated contrast for 500 ms, and then descended to zero with a gradual change of a sinusoidal function in the last 250 ms (Fig. 2B). The test stimulus increased the radiant flux uniformly at all wavelengths with the same shape of spectral distribution, indicating that all photoreceptor classes including melanopsin respond to the spatial contrast modulation. The contrast in each trial varied in 0.1 log units according to a three-down, one-up staircase procedure to estimate the 79% correct accuracy.

The melanopsin stimulation in the melanopsin-high condition was 2.1 times higher than in the control condition (i.e., 2.1 times melanopsin contrast; Weber contrast: 1.08). The melanopsin and cone stimulations in the lightflux-high condition were 2.1 times higher than those in the control condition. The amount of cone stimulation was calculated based on cone fundamentals at the peripheral visual field in human (Stockman & Sharpe, 2000; Stockman, Sharpe, & Fach, 1999), and that of melanopsin stimulation was calculated based on the sensitivity curve of ipRGCs (Tsujimura & Okajima, 2015; Yang, Tsujimura, Matsumoto, Yamashita, & Yeh, 2018). The cone and melanopsin stimulations were identical to those in Experiment 2 of Yang et al. (2018). Summaries of

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**Fig. 1.** Three experimental conditions (melanopsin-high, lightflux-high, and control) in the present study. The four-primary stimulating system can independently stimulate the cones and melanopsin. L, M, and S represent long-wavelength, middle-wavelength, and short-wavelength cones, respectively. This figure was adapted from Yang et al. (2018).

**Fig. 2.** Experimental design and stimuli used in this study. (A) Illustration of the trial sequence. (B) Temporal profile of the Gabor contrast change. The viewing distance was 28 cm and the stimulus eccentricity was 16° in Experiments 1 and 2, while it was 120 cm and 4° in Experiments 3 and 4.
cone, rod, and melanopsin stimulations and their spectra for all conditions in the present study are included in Fig. 3 and Table 1, respectively.

To clarify, we want to note that in this study, we use the term "stimulation" to refer to a different concept than "excitation". Specifically, we assumed that the excitation of the photoreceptor is determined by the product of photoreceptor stimulation and its sensitivity, which varies with wavelength, temporal frequency, spatial frequency, and background light level (Schneeweis & Schnapf, 1999). In the current study, rod stimulation increased with increased melanopsin stimulation. Additionally, in Experiments 1 and 2, rod stimulation was higher in the lightflux-high condition than in the melanopsin-high condition. To minimize the effect of rods, we used a steady background, as rods have a low sensitivity to steady backgrounds. We also used high luminance levels to prevent rod contamination.

The individual variation in luminance was found to be more than 50% different from the standard observer (Uprety, Zele, Feigl, Cao, & Adhikari, 2021). However, we hypothesized that the variation in luminance is not a result of individual differences, but rather due to the deviation of the LM ratio in the luminance mechanism caused by the background color. To select the background color, we considered the LM ratio of the luminance mechanism, which is defined by the quadrature protocol exhibiting variation with both background color and temporal frequency. It should be noted that the LM ratio is constant for ~570 nm light (Stromeyer et al., 1997). Therefore, we chose the background color whose LM ratio matched that of the 570 nm light. For instance, in Experiment 1, the CIE coordinate of the background gray was (0.40, 0.38), and the LM ratio was 2.58, which corresponded to the LM ratio of the 570 nm light. For these reasons, we assumed that the deviation of luminance from the standard observer was minimal in our experiment.

The background luminance was 110 cd/m² in the control condition and the melanopsin-high condition, and 228 cd/m² in the lightflux-high condition. Participants placed their heads on a chin rest at a distance of 28 cm from the diffuser, making the size of the background 54° (width) and 46° (height) in visual angle. We did not measure accommodation. Since the near point of a young adult could be smaller than 25 cm (Duane, 1922) we assumed that the influence was small. For analysis, we measured the contrast sensitivity at six spatial frequencies: 0.09, 0.17, 0.34, 0.68, 0.85, and 1.28 cycles/degree.

2.2.3. Design and procedure

A 3 (Background) × 6 (Spatial frequency) within-subject design was used. The sequence of the background conditions was counterbalanced across every three participants and in a pseudorandom order for the seventh participant. Participants experimented with one background condition on each day, and they came in on three separate days. All experiments in the present study were conducted during daytime hours between 10:00 and 17:00. It is important to consider that pupil size can vary depending on the time of day. However, we found that the influence of retinal illuminance on pupil size was relatively minor in our study. For more information, please see the Limitations section in the General Discussion.

At the beginning of the experiment, all participants went through a five-minute light adaptation to the background light before the main task. During the task, each participant was instructed to look at the fixation and initiate the experiment when ready. Participants were asked to perform a two-alternative forced-choice location-judgment task regarding the location of the Gabor (left or right) by clicking on the left or right side of the mouse, respectively. Each participant completed six staircase procedures in each background condition. There were 12 reversals to end a staircase procedure. The threshold in each staircase procedure was estimated from the average of the last six reversals. Contrast sensitivity was calculated as the inverse of the reciprocal of the threshold (i.e., the minimum luminance contrast required for detecting a Gabor patch). Artificial pupils were not used in the present study.

2.3. Results

Fig. 4(A) shows the results of Experiment 1. The black, gray, and green points represent the average contrast sensitivity at tested spatial frequencies in the melanopsin-high, control, and lightflux-high conditions. The black, gray, and green points represent the average contrast sensitivity at tested spatial frequencies in the melanopsin-high, control, and lightflux-high conditions.
The effects of Background (Spatial frequency as within-subject factors) showed the significant main analysis of variance (ANOVA) on contrast sensitivity with Background and parameters of the DoG model are in Table A1 of Appendix A. Generally, Enroth-Cugell the Difference-of-Gaussians (DoG) model (Derrington & Robson, 1966; Rohaly & Buchsbaum, 1989). The parameters of the DoG model are in Table A1 of Appendix A. Generally, contrast sensitivity in the melanopsin-high condition was higher than in the control condition and the lightflux-high condition. The curve lines based on DoG model showed that the peak frequency was around 0.6 cycles/degree.

Average data were analyzed by calculating the contrast sensitivity in three background light conditions. A two-way repeated-measures analysis of variance (ANOVA) on contrast sensitivity with Background and Spatial frequency as within-subject factors showed the significant main effects of Background ($F(2,12) = 6.87, p = .010, \eta^2_p = 0.53$) and Spatial frequency ($F(5,30) = 45.80, p < .001, \eta^2_p = 0.88$) and their interaction ($F(10,60) = 3.66, p < .001, \eta^2_p = 0.38$). Simple main effects of Background was observed at 0.34 cycles/degree ($F(2,12) = 8.32, p = .005, \eta^2_p = 0.58$), 0.68 cycles/degree ($F(2,12) = 4.123, p = .043, \eta^2_p = 0.41$), and 0.85 cycles/degree ($F(2,12) = 10.78, p = .002, \eta^2_p = 0.64$). Post-hoc comparisons with Bonferroni Correction showed that at 0.85 cycles/degree contrast sensitivity in the melanopsin-high background was higher than both the control ($t(6) = 3.63, p = .011$, Cohen’s $d = 1.37$) and the lightflux-high condition ($t(6) = 3.86, p = .008$, Cohen’s $d = 1.46$). At 0.34 cycles/degree contrast sensitivity in the control background was higher than the lightflux-high condition ($t(6) = 3.48, p = .013$, Cohen’s $d = 1.31$).

### 2.4. Discussion

Experiment 1 showed that increased melanopsin stimulation enhanced contrast sensitivity at 0.85 cycles/degree when comparing the melanopsin-high and the control backgrounds, which merely differed in their melanopsin stimulation. There was a puzzle as well. The lightflux-high curve resembled the control condition’s curve in shape. Even though melanopsin and cone stimulation were nearly doubled in the lightflux-high condition compared to the control condition, contrast sensitivity in the former was lower than in the latter at 0.34 cycles/degree and identical at other spatial frequencies, according to a comparison of the results from the lightflux-high and control conditions. We investigated the consistency of this result with higher background luminance levels in Experiment 2.

### 3. Experiment 2

In this experiment, the background luminance, i.e., the combination of melanopsin and cone stimulation, was increased, while other experimental details were the same as in Experiment 1.

#### 3.1. Methods

#### 3.1.1. Participants

There were eight participants (mean age = 23.6) from Kagoshima University. All participants had normal or corrected-to-normal visual

### Table 1

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Condition</th>
<th>L-cone (cd/m²)</th>
<th>M-cone (cd/m²)</th>
<th>S-cone (cd/m²)</th>
<th>Melanopsin (cd/m²)</th>
<th>Rod (cd/m²)</th>
<th>Luminance (cd/m²)</th>
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<tr>
<td>Experiment 1</td>
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<td>187.5</td>
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<td></td>
<td>Lightflux-high</td>
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<td>216.9</td>
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<td>Experiment 2</td>
<td>Control</td>
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<td>147.0</td>
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<td>180.0</td>
<td>406.2</td>
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*Fig. 4.* Contrast sensitivity as a function of spatial frequency in the three background light conditions at an eccentricity of 16 in Experiment 1 (A) and 2 (B). The numbers in parentheses represent the background luminance values. Contrast sensitivity on the vertical axis was calculated as the inverse of the detection threshold. The peak frequency was around 0.6 cycles/degree.
acuity and gave written informed consent before participating. Participants reported that they could accommodate during the experiment.

3.1.2. Stimuli, design, and procedures

In Experiment 2, the melanopsin stimulation in the melanopsin-high background was 1.8 times higher than the control background (Weber contrast: 0.78), and the melanopsin and cone stimulations in the lightflux-high background were both 1.8 times higher than the control background. In the control and the melanopsin-high conditions, the background luminance was 248 cd/m², and in the lightflux-high condition, it was 442 cd/m², the highest luminance affordable in the current setup. The CIE coordinate of the background gray was the same as in Experiment 1 (0.40, 0.38). The experimental design and procedure were identical to those in Experiment 1, except that each participant completed 8–12 staircase procedures in each of the background conditions. The sequence of the background conditions was counterbalanced across every three participants, as in Experiment 1.

3.2. Results

Fig. 4B shows that although the size of the melanopsin effect was smaller in Experiment 2 compared to Experiment 1, contrast sensitivity in the melanopsin-high condition was generally higher than that in the control and lightflux-high conditions. The peak frequency was also observed to be around 0.6 cycles/degree, as same as that in Experiment 1, which suggests that the same mechanism was involved in the CSFs in Experiments 1 and 2.

A two-way repeated-measures ANOVA on the data of average contrast sensitivity showed the significant main effects of Background (F(2,14) = 10.32, p = .002, n² = 0.60) and Spatial frequency (F(5,35) = 34.37, p < .001, n² = 0.83) and their interaction (F(10,70) = 3.73, p < .001, n² = 0.35). Post-hoc comparisons using Bonferroni Correction on contrast sensitivity in different background light conditions showed that the contrast sensitivity in the melanopsin-high condition (M = 65.19, SD = 38.84) was significantly higher than that in control (M = 56.87, SD = 35.95; t(7) = 3.30, p = .013, Cohen’s d = 0.65) and lightflux-high conditions (M = 57.57, SD = 36.38, t(7) = 3.59, p = .009, Cohen’s d = 0.70) across spatial frequencies.

Moreover, the simple main effects of Background at 0.09 cycles/degree (F(2,14) = 13.89, p < .001, n² = 0.66), 0.17 cycles/degree (F(2,14) = 4.069, p = .041, n² = 0.368), 0.34 cycles/degree (F(2,14) = 15.20, p < .001, n² = 0.68), and 1.28 cycles/degree (F(2,14) = 7.54, p = .006, n² = 0.52) were significant. Post-hoc comparisons using Bonferroni Correction showed that, at 0.34 cycles/degree, contrast sensitivity in the melanopsin-high condition (M = 71.22, SD = 28.27) was higher than that in both the control (M = 54.34, SD = 20.22; t(7) = 4.34, p = .003, Cohen’s d = 1.53) and lightflux-high conditions (M = 54.78, SD = 18.48; t(7) = 4.01, p = .005, Cohen’s d = 1.42). At 0.09 cycles/degree, the contrast sensitivity in the lightflux-high condition (M = 18.75, SD = 9.33) was lower than the melanopsin-high condition (M = 21.89, SD = 10.07, t(7) = 6.39, p < .001, Cohen’s d = 2.26).

3.3. Discussion

In both Experiments 1 and 2, we found that the peak of contrast sensitivity was around 0.6 cycles/degree. The contrast sensitivity in the melanopsin-high condition was significantly higher than that in the control condition at 0.85 cycles/degree in Experiment 1 and 0.34 cycles/degree in Experiment 2 when the background luminance was almost doubled in Experiment 2 compared to that in Experiment 1. These results suggest that increased melanopsin stimulation could enhance contrast sensitivity at low spatial frequencies (below 0.85 cycles/degree, peaks of the spatial CSF curves: around 0.6 cycles/degree) with different background luminance levels. The magnitude of the melanopsin effect was larger in Experiment 1 than in Experiment 2, implying that the lower the background luminance, the stronger the melanopsin effect.

Some might wonder why contrast sensitivity was not enhanced in the lightflux-high condition compared to the control condition. According to the principle of light adaptation known as Weber’s Law, contrast sensitivity at low spatial frequencies rises with background luminance up to a certain point and stays constant with further increased luminance (Shannon et al., 1996; Van Nes & Bouman, 1967; Wandell, 1995). The background luminance used in Experiments 1 and 2 ranged from 110 cd/m² to 442 cd/m², corresponding to approximately 780 trolands and 3,120 trolands at a pupil diameter of 3.0 mm, respectively. At this light level, the Weber region, contrast sensitivity is constant at low spatial frequencies (below ~4 cycles/deg). Hence, our results (similar contrast sensitivity in the control and the lightflux-high condition) are consistent with the literature (Shannon et al., 1996; Van Nes & Bouman, 1967; Wandell, 1995).

Our results of Experiments 1 and 2 indicated that increased melanopsin stimulation enhanced contrast sensitivity at low spatial frequencies. However, the gain control mechanism, such as Weber’s adaption, was not affected by increased melanopsin stimulation. According to the receptive field analysis shown later, melanopsin stimulation influences contrast sensitivity by varying receptive field structure.

4. Experiment 3

The CSF also varies with eccentricity. To establish that the melanopsin effect observed in Experiments 1 and 2 varies with eccentricity, in Experiment 3, we decreased the eccentricity by increasing the viewing distance to 120 cm as opposed to 28 cm in Experiments 1 and 2. It is known that melanopsin contributes to encoding ambient irradiance and conveying the information of the ambient light to the brain (Brown et al., 2010). If melanopsin only encodes ambient irradiance and not luminance (as in this experiment, where the luminance was 245 cd/m²), we would anticipate a reduction in the melanopsin effect as the viewing distance increases. However, our findings indicate that the effects of melanopsin on CSF remained consistent at different viewing distances. These results suggest that, at least in terms of enhancing CSF, melanopsin may encode luminance but not irradiance.

Consequently, the range of spatial frequencies examined in Experiment 3 was expanded. Experiment 3 examined only the melanopsin-high and control conditions since the contrast sensitivity in the lightflux-high condition did not differ significantly from the control condition in the previous two experiments.

4.1. Methods

4.1.1. Participants

Three participants (mean age = 21.7) from Kagoshima University took part in Experiment 3. All participants had normal or corrected-to-normal visual acuity and gave written informed consent before their participation.

4.1.2. Stimuli, design, and procedure

In Experiment 3, the melanopsin stimulation in the melanopsin-high background was 2.2 times higher than the control background (Weber contrast: 1.18). The background luminance was 245 cd/m² (Table 2). The CIE coordinates of the background color were all the same (0.39, 0.33). The LM ratio was 2.71, which corresponds to the LM ratio of a 573 nm light. The viewing distance was 120 cm from the diffuser, making the background 14 in width and 11 in height (6.18% of the stimulus field used in Experiments 1 and 2). Therefore, the six spatial frequencies tested in Experiment 3 were 0.55, 1.10, 3.31, 8.27, 9.93, and 11.03 cycles/degree. The center of the Gabor patch was 4 away from the fixation (sigma = 1.3). Although the sample size (n = 3) in Experiment 3 was relatively small compared to Experiments 1 and 2, there were five repetitions of the staircase procedure to estimate the contrast sensitivity at each spatial frequency in each background condition for each
contrast sensitivity was conducted in Experiment 3. Results showed that contrast sensitivity in the melanopsin-high condition was higher than in the control condition at 0.55 (Experiment 4B), 1.10 (Experiments 3 and 4B) and 3.31 (Experiments 3, 4A, and 4B) cycles/degree.

4.2. Results

Fig. 5A shows the results of Experiment 3. The CSF curves suggested that contrast sensitivity in the melanopsin-high condition was higher than in the control condition when the spatial frequency was lower than 8.27 cycles/degree. The peak frequency was around 2 cycles/degree.

A two-way repeated-measures ANOVA with the within-subject factors of Background (melanopsin-high, control) and Spatial frequency (0.55, 1.10, 3.31, 8.27, 9.93, and 11.03 cycles/degree) on average contrast sensitivity was conducted in Experiment 3. Results showed main effects of Background ($F(1,2) = 84.19, p < .012, \eta^2 = 0.98$), Spatial frequency ($F(5,10) = 52.62, p < .001, \eta^2 = 0.96$), and their interaction ($F(5,10) = 34.31, p < .001, \eta^2 = 0.94$). The significant simple main effects of Background indicated higher contrast sensitivity at 1.10 ($F(1,2) = 229.26, p < .004, \eta^2 = 0.99$) and 3.31 cycles/degree ($F(1,2) = 42.18, p < .023, \eta^2 = 0.96$) in the melanopsin-high condition (1.10 cycles/degree: $M = 146.22, SD = 25.66$; 3.31 cycles/degree: $M = 207.45, SD = 46.76$) than in the control condition (1.10 cycles/degree: $M = 90.54, SD = 20.87$; 3.31 cycles/degree: $M = 89.48, SD = 19.21$; Fig. 5A).

4.3. Discussion

Experiment 3 showed enhanced contrast sensitivity in the melanopsin-high condition than in the control condition at 1.10 and 3.31 cycles/degree with a 4˚ eccentricity. Although a longer viewing distance was used than in Experiments 1 and 2, an increase in contrast sensitivity was also observed. If melanopsin encodes ambient irradiance but not luminance, the melanopsin effect would decrease as the viewing distance increases. Therefore, the results suggest that melanopsin encodes luminance rather than irradiance. To further confirm whether the melanopsin effect was consistent with this small eccentricity, we investigated the influence of background luminance with a 4˚ eccentricity.

5. Experiment 4

The purpose of Experiment 4 was to test the robustness of the melanopsin effect on the CSF. Two sub-experiments were conducted in Experiment 4. The background luminance was 245 cd/m² in Experiment 4A and 195 cd/m² in Experiment 4B. Although we did not intend to manipulate the melanopsin contrast, the melanopsin contrast was slightly reduced because of the limitation of the apparatus (1.9 times, Weber contrast: 0.94, see Table 2 for a summary of experimental conditions). Other experimental conditions were the same as in Experiment 3.

5.1. Methods

5.1.1. Participants

For Experiments 4A and 4B, different groups of five participants from Kagoshima University participated, with a mean age of 22.4 years old for Experiment 4A and 22.8 years old for Experiment 4B.

5.1.2. Stimuli, design, and procedure

The experimental design and procedure were the same as Experiment 3 except for the manipulation of the background luminance. Participants completed five staircase procedures in each background condition in Experiment 4A. Four participants performed three staircase procedures, and one participant performed two staircase procedures in each background condition in Experiment 4B. The presentation order of background conditions was counterbalanced across every two participants.

Table 2

<table>
<thead>
<tr>
<th></th>
<th>Melanopsin contrast (melanopsin-high/ control)</th>
<th>Weber contrast</th>
<th>Background luminance (cd/ m²)</th>
<th>Eccentricity (degree)</th>
<th>Range of spatial frequency (cycles/ degree)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment1</td>
<td>2.1</td>
<td>1.08</td>
<td>110</td>
<td>16</td>
<td>0.99-1.28</td>
</tr>
<tr>
<td>Experiment 2</td>
<td>1.8</td>
<td>0.78</td>
<td>248</td>
<td>16</td>
<td>0.99-1.28</td>
</tr>
<tr>
<td>Experiment 3</td>
<td>2.2</td>
<td>1.18</td>
<td>245</td>
<td>4</td>
<td>0.55-11.03</td>
</tr>
<tr>
<td>Experiment 4A</td>
<td>1.9</td>
<td>0.94</td>
<td>245</td>
<td>4</td>
<td>0.55-11.03</td>
</tr>
<tr>
<td>Experiment 4B</td>
<td>1.9</td>
<td>0.94</td>
<td>197</td>
<td>4</td>
<td>0.55-11.03</td>
</tr>
</tbody>
</table>

Fig. 5. Contrast sensitivity as a function of spatial frequency in the three background light conditions in Experiments 3 and 4. Contrast sensitivity on the vertical axis was calculated as the inverse of the detection threshold. The curve lines represent values predicted by DoG models. Error bars represent SE. * indicates significant (p < .05 with Bonferroni correction) differences between the melanopsin-high and the control conditions. The contrast sensitivity in the melanopsin-high condition was higher than in the control condition at 0.55 (Experiment 4B), 1.10 (Experiments 3 and 4B) and 3.31 (Experiments 3, 4A, and 4B) cycles/degree.
5.2. Results

5.2.1. Experiment 4A

The general patterns of CSF curves were similar to those found in Experiment 3 (Fig. 5B, compared to Fig. 5A). That is, higher contrast sensitivity in the melanopin-high condition than in the control condition, and the peak frequency was around 2 cycles/degree.

The ANOVA results on the average contrast sensitivity showed that there were main effects of Background ($F(1,4) = 9.86, p = 0.035, \eta^2_p = 0.711$), Spatial frequency ($F(5,20) = 64.87, p < 0.001, \eta^2_p = 0.94$), and their interaction ($F(5,20) = 5.02, p = 0.004, \eta^2_p = 0.56$). The simple main effect of Background at 3.31 cycles/degree ($F(1,4) = 9.47, p = 0.037, \eta^2_p = 0.70$) indicated a higher contrast sensitivity in the melanopin-high condition than that in the control condition at this frequency.

5.2.2. Experiment 4B

The pattern of CSF curves (Fig. 5C) was similar to that in both Experiment 3 and Experiment 4A. The ANOVA analysis showed that there were main effects of Background ($F(1,4) = 45.47, p = 0.003, \eta^2_p = 0.92$), Spatial frequency ($F(5,20) = 19.09, p < 0.001, \eta^2_p = 0.83$), and their interaction ($F(5,20) = 7.93, p < 0.01, \eta^2_p = 0.66$). The simple main effects of background at 0.55 ($F(1,4) = 8.49, p = 0.044, \eta^2_p = 0.68$), 1.10 ($F(1,4) = 19.89, p = 0.011, \eta^2_p = 0.83$) and 3.31 cycles/degree ($F(1,4) = 13.62, p = 0.021, \eta^2_p = 0.77$) indicated higher contrast sensitivities in the melanopin-high condition than that in the control condition at these three frequencies.

5.3. Discussion

Despite lowering the melanopin contrast and background luminance, the results of Experiments 4A and 4B were in line with those of Experiment 3 with similar patterns of curves. Specifically, in Experiments 3 and 4, the effect of melanopin stimulation was observed at 3.31 cycles/degree, indicating the consistency of results at this spatial frequency.

6. General discussion

The present study examined the effect of melanopin stimulation on the basis function of human pattern vision: the spatial CSF. Experiment 1 showed that increased melanopin stimulation in the background light enhanced spatial contrast sensitivity (Fig. 4A). When both cone and melanopin stimulations were increased in Experiment 2, we still observed enhanced contrast sensitivity in the melanopin-high condition than the control condition (Fig. 4B). In Experiment 3 (Fig. 5A) and 4 (Fig. 5B and C), we decreased the eccentricity of the stimuli by increasing the viewing distance. The results showed that the melanopin effect on contrast sensitivity was still observed with different background luminance levels. Taken together, when spatial CSFs were measured at different spatial frequencies, eccentricities, and background luminance levels under different background light conditions from Experiment 1 to 4, results showed enhanced contrast sensitivity with increased melanopin stimulation at different eccentricities and luminance levels.

6.1. Effect of background light isoluminance variations on ipRGC-mediated responses

The present study did not include individual calibration for each participant to ensure isoluminance of the background lights. However, we do not expect the small variation in participants’ perception of the color and luminance of the backgrounds in the experiments to significantly affect the results for the following reasons. First, the cone-mediated signals responsible for color and luminance detection are less sensitive to very low temporal frequency stimuli such as the steady background used in the present study (Kelly, 1971; Umino et al., 2008). Since the dendritic field size of ipRGC is approximately 7–10 times larger than that of parasol ganglion cells at the eccentricities we used (Dacey et al., 2005), it is expected that ipRGCs favor the larger background stimulus or stimulus at a low-spatial frequency than the parasol ganglion cells (i.e., cone-mediated signals). Although individual calibration may be required when applying the silent substitution method to test stimuli with a higher spatial frequency preferred by cones (Nungert et al., 2023; Pokorny et al., 2004), this is not relevant to the current study. Second, there was a very small difference in cone stimulation between the control condition and melanopin-high condition but a large stimulation change for melanopin (see Table 1). Even if there were a slight difference in luminance and color, it would not exceed the large difference in the ipRGC signals we manipulated.

6.2. The melanopin effect not affected by background luminance

It is possible that some readers might question whether the difference in background luminance (110 cd/m² in Experiment 1 and 248 cd/m² in Experiment 2) could have influenced the magnitude of the melanopin effect on contrast sensitivity, given that the effect appears to be larger in Experiment 1 compared to Experiment 2 (as shown in Fig. 4). It has been shown that the peak of a CSF shifts according to the background luminance (van Ness & Bouman, 1967). As the luminance of the background increases, the peak of the spatial frequency response shifts towards higher frequencies. Conversely, under low luminance backgrounds, the peak is located at lower spatial frequencies. The peaks of CSFs in Experiment 1 and 2 were similar to each other (around 0.5–0.6 cd喜欢吃, Fig. 4A & B) although the background luminance was different, suggesting that the same mechanism was involved in the CSFs in both experiments. Similarly, there was a 20% difference in background luminance between Experiment 4A and 4B (background luminance: 245 and 197 cd/m², respectively), and the peaks of the CSFs in Experiment 4A and 4B were also similar to each other (around 2–3 cycles/degree, Fig. 5B and C). Together, these results implied that the melanopin effect was not affected by the background luminance in the present study.

6.3. The estimated receptive field of parasol retinal ganglion cells from the DoG model

Since the present study measured contrast sensitivity of detecting the luminance-modulated stimuli (i.e., the achromatic Gabor patches) and varied melanopin stimulation in the background, the increased melanopin stimulation is most likely to enhance the contrast sensitivity in the magnocellular pathway. To test this hypothesis, we examined the possible receptive field structures by fitting the average data in all experimental conditions to the DoG model. We estimated the size of the receptive field center at zero-crossing (Fig. A1 in Appendix A) using the model in Enroth-Cugell and Robson’s study (Enroth-Cugell & Robson, 1966), which roughly corresponds to the dendritic field diameter in physiology (Peichl & Wässle, 1979, 1983). Results indicated that the zero-crossing diameters of the receptive field center were 25–46 min in Experiments 1 and 2 and 12–13 min in Experiments 3 and 4 (See Table A1 in Appendix A for the parameters of these models).

Dacey and Petersen (1992) showed that at eccentricity around 16 and 4 used in our Experiments 1–2 and 3–4, respectively) and 10–20 min for parasol ganglion cells, whereas they are approximately 4–8 and 1–3 min for midget ganglion cells. Since we used achromatic test stimuli, we expected to stimulate the ganglion cells in the magnocellular pathway. Furthermore, the current modeling showed that the zero-crossing diameters of the receptive field center correspond to the dendritic field diameters in the morphology of parasol ganglion cells. These results suggested that we have adequately isolated parasol ganglion cells in the magnocellular pathway. Hence, the results here not only demonstrate that increased melanopin stimulation enhances contrast sensitivity but
also suggest that melanopsin stimulation modulates contrast detection in the magnocellular pathway.

6.4. Effect of melanopsin stimulation on different eccentricities

Some might be interested in whether the melanopsin effect on different eccentricities (i.e., 16 in Experiments 1 and 2, and 4 in Experiments 3 and 4) was consistent. Previous studies suggested that although CSF varies with eccentricity, the shape of the contrast sensitivity curve is invariant when the cortical magnification factor is considered to compensate for the reduced cortical area for increased eccentricity (Rovamo & Virsu, 1979; Rovamo, 1978). We therefore checked whether the shapes of CSF curves in the melanopsin-high conditions in all experiments were invariant.

To find the best fit for aligning the CSF curves, the spatial frequencies of the CSF curves in Experiments 3 and 4 were divided by 4, which is close to the cortical magnitude factor (2.8 on the nasal retina and 3.0 on the temporal retina) between 4 and 16 eccentricities (Rovamo, Virsu, & Näsänen, 1978). With the CSF curve found in Experiment 3 as the anchor, sensitivities of the CSF curves in Experiment 1, 2, 4A, and 4B were multiplied by 1.4, 2.5, 1.4, and 1.7 respectively, to be aligned with the sensitivities of the CSF curves in Experiment 3.

Fig. 6 shows the results of shifted CSF curves. As can be seen, the shapes of the shifted CSF curves were invariant even with different eccentricities. More importantly, the spatial frequencies at which significant differences in the sensitivity were found were similar among the curves, even at different eccentricities. That is, the melanopsin effects observed with 16 and 4 eccentricity were consistent.

6.5. Effect of melanopsin stimulation on receptive field organization

Fig. 7 shows the sensitivity of the receptive field in the space domain using parameters of the DoG models from all experiments. The horizontal axis represents the space in minutes, and the vertical axis represents contrast sensitivity. Black, gray, and green curves represent the sensitivity in the melanopsin-high, the control, and the lightflux-high conditions, respectively. Fig. 7A and B correspond to Fig. 4A and B in the frequency domain; Fig. 7C, D, and E correspond to Fig. 5A, B, and C.

The shape of the receptive field varied with melanopsin stimulation in different experiments. In Experiment 1, compared to the control condition, the negative increase in sensitivity of the surround was observed in the melanopsin-high condition (Fig. 7A). On the other hand, in Experiment 2, the peak sensitivity of the center was more enhanced in the melanopsin-high condition than in the control condition (Fig. 7B). In Experiments 3 and 4, both the positive peak at the center and the antagonistic surround in the melanopsin-high condition were more enhanced than in the control condition, which is essential for edge detection in contrast processing. The results of Experiments 3 and 4 (Fig. 7C, D, E) were consistent with both the increase of the peak at the center and the negative increase of the surround, while the results of Experiments 2 and 1 only met one of these two criteria, respectively. This difference in results could be attributed to the limited range of spatial frequencies tested in Experiments 1 and 2, which ranged from 0.09 to 1.25 cycles/degree, compared to the range of 0.55 to 11.03 cycles/degree tested in Experiments 3 and 4. A limited range of spatial frequencies can make it difficult to estimate a receptive field accurately.

6.6. Relation to physiology

In Experiments 1 and 2, we observed that contrast sensitivity in the lightflux-high condition did not differ from that in the control condition (Fig. 4A and B). The general pattern of no difference between lightflux-high and control conditions can be explained by Weber’s law. Contrast sensitivity remains the same with increased luminance at low spatial frequencies, as the luminance levels we used here fell into the Weber region. Our result that no enhanced CSF in the lightflux-high condition is consistent with the results found for CSF at low spatial frequencies and high luminance levels in the literature (Shannon et al., 1996; Van Nes & Bouman, 1967; Wandell, 1995). In addition, since the luminance detection mechanism is most likely achromatic, and an achromatic test stimulus was adopted in the present study, we assumed that the test stimulus was detected by the luminance mechanism. The test stimulus used in the current study uniformly increased the radiant flux at all wavelengths with the same spectral distribution. This is consistent with our analysis, which suggests that the estimated receptive field diameter from our results falls within the same range as the dendritic field of parasol retinal ganglion cells.

How do ipRGCs affect visual function, as we have demonstrated here? ipRGCs may influence the shape of the receptive field of parasol ganglion cells, which is reflected in CSF in our measurements but not the adaptation effect following Weber’s law. ipRGCs may influence visual processing through the displaced amacrine cells in the inner plexiform layer (IPL), a type of interneuron in the retina that receives inputs from ipRGCs (Reifler et al., 2015). A previous study has reported that M1 ipRGCs stratify in the OFF sublamina in the IPL; M2, M4, and M5, stratify in the ON sublamina; and M3 and M6 stratify in the ON and OFF sublamina (Quattrochi et al., 2019; Schmidt et al., 2011). Other studies have also found that melanopsin-expressing ipRGCs could provide ambient light signals to adjust cone-based vision (Allen et al., 2014; Sonoda et al., 2018; Storchi et al., 2015, 2017). Hence, signals from ipRGCs might be sent to the magnocellular pathway via the displaced amacrine cells.

Future research should investigate whether all these interactions of cone and melanopsin signals exist in the magnocellular pathway or they can exist in the parvocellular pathway as well. Also, whether there are
further melanopsin visual functions that remain unidentified, in addition to pupillary responses (Tsujimura et al., 2010), brightness discrimination (Brown et al., 2012), and cone-directed CSF with varying melanopsin stimulation from the background light in the present study and hinted elsewhere (Allen et al., 2019; Spitschan et al., 2017), which may also lead to a better understanding and provide a more comprehensive picture of the functions and mechanisms of ipRGCs.

Consistent evidence from animal studies further supports our current finding of enhanced human contrast sensitivity by melanopsin stimulation as mentioned that ipRGCs project to the LGN in mice and primates (Brown et al., 2010; Dacey et al., 2005; Ecker et al., 2010), and the LGN that connects the retina to the visual cortex is thought of as a relay station of retinal information to the visual cortex (Grubb & Thompson, 2003; Hubel & Wiesel, 1961; Tavazoie & Reid, 2000). Hence, ipRGCs have access to the primary visual pathway, which could explain melanopsin’s contribution to the representation of images in the early visual system (Allen et al., 2017, 2019). Indeed, melanopsin could adjust activity in the LGN according to the intensity of background light (Storchi et al., 2015, 2017). Patterns visible only to melanopsin could evoke responses in the mouse LGN (Allen et al., 2017). With human psychophysics adopting the silent substitution method, our results provide evidence of melanopsin’s contribution to human spatial CSF. The receptive field analysis also further suggests that such modulation occurs in the magnocellular pathway.

The results of the receptive field analysis suggest that the zero-crossing diameters of the receptive field center are consistent with the dendritic field diameters in morphology. This finding indicates that the parasol ganglion cells in the magnocellular pathway were effectively isolated in our study. It is worth noting that magnocellular ganglion cells receive both achromatic and chromatic signals. For example, Smith et al. (1992) proposed a model of the receptive field of the magnocellular ganglion cells, which receive a + L-M chromatic signal at the receptive field surround (see also Lee, 1996). Stromeyer et al. (1997) proposed a comparable model of the magnocellular ganglion cells, where the surround of the receptive field receives + L-M chromatic signals on the orange background, +M–L chromatic signals on the green background, and null on the yellow background, with an LM ratio corresponding to 570 nm light.

We used a background color with an LM ratio close to 570 nm light, indicating that the influence of the chromatic mechanism on the magnocellular pathway was minimal. Although both midget and parasol ganglion cells exhibit sensitivity to changes in achromatic contrast (Kaplan & Shapley, 1986), Leonova et al. (2003) found that when the test stimulus was presented on a steady luminance pedestal, spatial CSF showed a low-passed shape with decreased sensitivity at high spatial frequencies. The low-pass CSF reflected the mediation of the magnocellular pathway, suggesting that the spatiotemporal characteristics of the achromatic stimulus could bias the contrast detection towards the magnocellular pathway. Therefore, the results of the receptive field analysis are consistent with previous findings in the literature.

7. Limitations

We did not use an artificial pupil in the present study. Tsujimura et al. (2010) found that pupil size varied with melanopsin stimulation of the background. Steady-state pupil diameter was reduced by about 10% when amount of melanopsin stimulation was doubled (see also Watson & Yellott, 2012). There might be an effect of retinal illuminance on pupil size. However, we observed consistent results with background illuminance ranging from luminance 110 to 248 cd/m², suggesting that changes in retinal illuminance due to changes in pupil diameter had little/no significant effect on the results.

As previously mentioned, the peak of the CSF curve under low luminance level is at low frequency (van Ness & Bouman, 1967), which reflects the receptive field of rods to integrate light from a large field. We can assume that the peak of the CSF curve would shift toward low spatial frequency if rod contribution is significant. However, the peaks of the CSF curves in Experiment 1 and 2, as well as in Experiment 4A and 4B,
were similar to each other, implying that the rod contribution was much smaller than cones at the background light level used in the present study. To avoid potential rod intrusion effects, we did not test background luminance below 100 cd/m² in the present study.

Uprety, Adhikari, Feigl, and Zele (2022) found the melanopsin-rod interaction for a test stimulus using temporal summation. The incremental threshold for rod-based detection increased sharply at a light level above 1000 scotopic trolands (Fuortes et al., 1961). However, the scotopic luminance (rod stimulation) in the present study ranged from 104 cd/m² to 406 cd/m², corresponding to 700 scotopic troland and 2800 scotopic troland (Table 1), suggesting rod saturation in our experiments.

Zele, Adhikari, Cao, and Feigl (2019) and Uprety, Adhikari, Feigl, and Zele (2022) used a five-primary system to control all five photoreceptor (i.e., L-, M-, S-cones, rod, and melanopsin) stimulations. On the other hand, Vincent et al. (2021) and Brown et al. (2012) attempted to suppress the rod excitation with a high-luminance background. The present study adopted a four-primary system to control the stimulations of L-, M-, S-cones and melanopsin. We carefully minimized the effect of rods by using a steady background and used high background luminance levels (i.e., above 100 cd/m²) to avoid rod contamination. A five-primary system typically demands a narrower primary band and consequently results in greater individual differences in photoreceptor stimulation than a four-primary system. It is due to photoreceptor stimulation is determined by the sum of products of the power of the primary and the corresponding sensitivity at each wavelength. When the wavelength range is narrow (i.e., the narrowband primary), the stimulation differs depending on individual difference in photoreceptor sensitivity. Conversely, when the wavelength range is broad (i.e., the broadband primary), the individual differences in photoreceptor stimulation integrated within the wavelength range are small. Since using a broadband five-primary system is technically difficult in the silent substitution paradigm, we used the four-primary system and minimized individual differences in the present study. The Full Width Half Maximum (FWHM) of our four primaries was 65 nm for red, 27 nm for green, 25 nm for yellow, 10 nm for blue, respectively.

Although the results of Uprety et al.’s study (2022) implied the possibility that rods were not saturated in the range of luminance levels used in the present study. However, they used a Maxwellian view, whereas the present study adopted a Newtonian view. The spatial configurations of the stimulus were also different. Furthermore, to the best of our knowledge, the rod contribution at high irradiance is still in the controversial stage. Hence, it may be overly simplistic to compare the presence or absence of rod effects between the current study and the Uprety, Adhikari, Feigl, and Zele (2022) study based solely on the luminance levels of the background light.

8. Future directions

The current study manipulated melanopsin stimulation of the steady background, while Uprety, Adhikari, Feigl, and Zele (2022) manipulated melanopsin stimulation of the test stimulus. Zele, Adhikari, Cao, and Feigl (2019) investigated sensitivity when detecting a cone stimulus with or without a melanopsin pedestal, and the latter is more similar to our experimental conditions. Their results showed a ~50% increase in sensitivity with a melanopsin pedestal of ~20% contrast, compared to detecting a cone stimulus without a melanopsin pedestal. In our experiment, we observed a small effect despite using a melanopsin background of ~100% in Weber contrast. However, it is possible that the melanopsin effect of the background light may differ from that of the test stimulus with a pedestal, which warrants further investigation.

Based on the current findings, future research can further examine how melanopsin affects contrast detection and whether it interacts with ipRGCs’ non-visual functions. For example, one of melanopsin’s major functions is to regulate circadian rhythm. Thus, melanopsin’s contribution to contrast detection may vary in different time windows within a day. Similar to the melanopsin-high condition in the present study, the degree of enhanced contrast sensitivity caused by melanopsin stimulation may be larger at night than in the daytime. Furthermore, melanopsin’s effect of top-down modulation on conscious object vision warrants further investigation as LGN neurons in the magnocellular pathway also contributes to conscious object vision in the ventral object-recognition stream via top-down modifications (Tapia & Breitmeyer, 2011).

9. Conclusion

We reported five experiments that investigated the effect of melanopsin stimulation on human spatial CSF. The results from Experiment 1 revealed enhanced contrast sensitivity with increased melanopsin stimulation at low spatial frequencies. Experiment 2 demonstrated that the melanopsin effect observed in Experiment 1 was not affected by the strength of the combination of cones and melanopsin stimulations when the background luminance was increased. Experiments 3 and 4 further confirmed the melanopsin effect with decreasing eccentricity and still observed it. Overall, the findings suggest that increased melanopsin stimulation leads to enhanced CSF at low spatial frequencies, regardless of different melanopsin contrasts, background luminance levels, spatial frequencies, and eccentricities.

Data accessibility

Data and the code of the Experiment are available on OSF (http://osf.io/nz4w/).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

We have shared a link to the data.

Acknowledgments

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Appendix A. Supplementary material

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References


