Investigation of effect of retinal photoreceptor stimulations including melanopsin on brightness perception

Yuno Fujita, Aoi Takasu, Mizuki Takikawa, Tomoe Ito and Sei-ichi Tsujimura*

Graduate School of Design and Architecture, Nagoya City University, Nagoya, Japan
**Email: tsujimura@sda.nagoya-cu.ac.jp*

Brightness is perceived after photoreceptors are stimulated and signals from them are transmitted to the brain. Brightness perception differs depending on the wavelength. For example, yellow, a middle-wavelength light, is perceived brighter than blue light when the radiation intensity is the same. The direct heterochromatic brightness matching and the flicker photometry are widely known to measure brightness sensitivity. Although it is still unclear why there is a difference in spectral sensitivity between direct heterochromatic brightness matching and flicker photometry, the difference in brightness perception seems to be attributed to the temporal characteristics of physiological processes. The purpose of this study was to investigate the brightness perception caused by varying the amount of photoreceptor stimulations. In this study, we varied the amount of photoreceptor stimulation to clarify how each photoreceptor contributes to the brightness mechanism. It was found that observers perceived brighter as melanopsin stimulation increased according to psychometric function. The result was consistent with previous studies. In addition, we have found that there was a large difference in brightness when L- and M-cone stimulations varied whereas S-cone stimulation induced little change in brightness.

Extended version published online: 06 July 2024
Original source: Proceedings of the 15th Congress of the International Colour Association (AIC 2023)

Introduction

There are cone, rod and melanopsin photoreceptors on the human retina. Brightness is perceived after photoreceptors are stimulated and signals from them are transmitted to the brain. In general, brightness perception is proportional to radiance. We perceive brighter when the radiance is higher. Brightness perception differs depending on the wavelength. For example, yellow, a middle-wavelength light, is perceived brighter than blue light when the radiation intensity is the same. Brightness sensitivity has been measured as a function of wavelength. It is known that brightness sensitivity to short and long wavelength light is low, while brightness sensitivity to middle wavelength light is high [1].

The direct heterochromatic brightness matching and the flicker photometry are widely known to measure brightness sensitivity. Both measure the brightness sensitivity as a function of wavelength. Figure 1 shows the luminous efficiency functions measured by these two methods. Although both methods have the peak sensitivity around the middle wavelength the shapes are different [2-3]. The flicker photometry uses stimuli with a high temporal frequency of ~15 Hz. The L and M cones can respond to the stimuli, whereas S-cones and melanopsin photoreceptors do not respond to high temporal frequency stimuli [4].

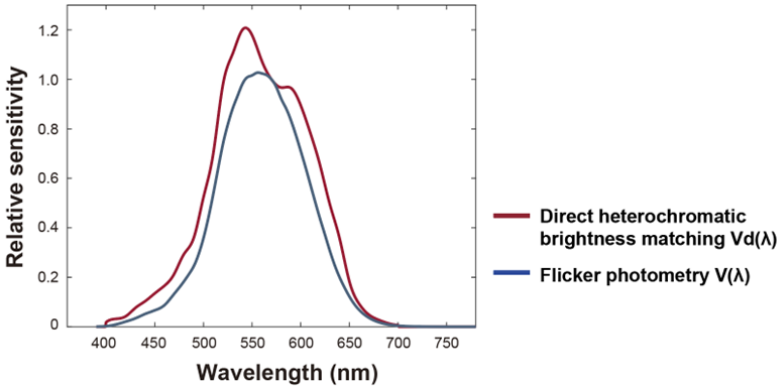

Figure 1: Shapes of luminous efficiency functions obtained by different method.

Although it is still unclear why there is a difference in spectral sensitivity between direct heterochromatic brightness matching and flicker photometry, the difference in brightness perception seems to be attributed to the temporal characteristics of physiological processes (Figure 2). For example, the temporal characteristics of photoreceptors, post-receptoral mechanisms and subsequent neural circuits appear to be related. In order to clarify the physiological processes associated with the brightness perception, it seems important to first consider the level of photoreceptor stimulation by the stimulus.

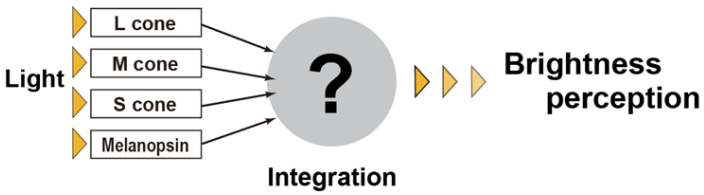

Figure 2: Physiological processes leading to brightness perception.

The purpose of this study was to investigate the brightness perception caused by varying the amount of photoreceptor stimulations. In this study, we varied the amount of photoreceptor stimulation to clarify how each photoreceptor contributes to the brightness mechanism. To this end, we selectively modulated the amount of photoreceptor stimulation using a four-primary illumination system. For example, we used the light stimuli that selectively modulate the amount of stimulation to melanopsin photoreceptors (Figure 3). These stimuli are called metameric pairs that have the same tristimulus values and the same amount of stimulation to the L, M and S cones. Thus, only the amount of melanopsin stimulation was different among these stimuli. Such a technique is called the silent-substitution paradigm that varies only the amount of stimulation to the target photoreceptor while keeping the other photoreceptor stimulations unchanged. Using this technique, we selectively increased or decreased the amount of stimulation to each photoreceptor and measured the brightness perception.

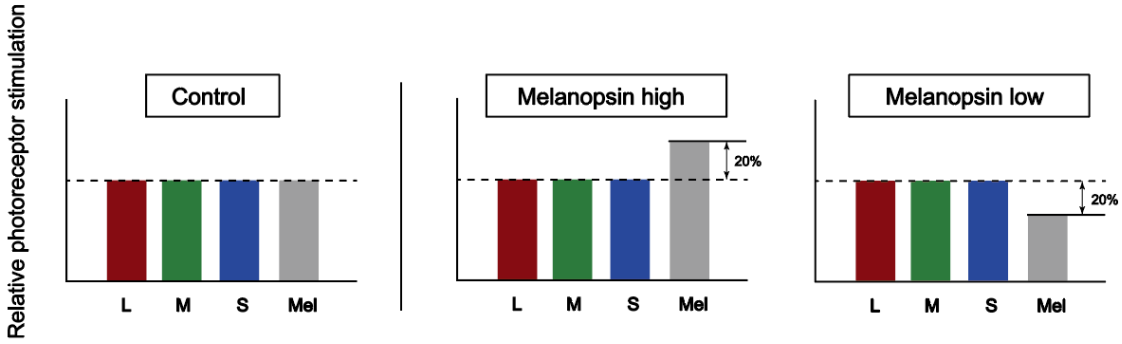

Figure 3: Relative photoreceptor stimulation.

Methods

In this study, we varied the amount of photoreceptor stimulations to clarify how each photoreceptor contributes to the brightness mechanism. To this end, we selectively modulated the amount of photoreceptor stimulations to L-, M-, S-cone and melanopsin photoreceptors. We used silent-substitution paradigm for the independent stimulations [5-7].

In the experiment, test stimuli were presented using a multi-primary illumination system [8]. The system consists of four different colours of LEDs with the peak wavelength of 633 nm, 531 nm, 462 nm and 569 nm, respectively (Figure 4). The output of the light flux from each LED was controlled by a stimulus control unit using pulse width modulation (PWM).

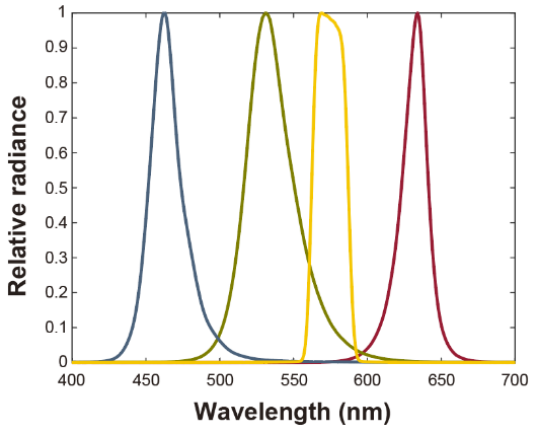

Figure 4: Spectra of four primaries.

Test stimuli

We used nine types of test stimuli which were modulated from a white control stimulus along L-, M-, S-cone and melanopsin photoreceptor axes. The amount of stimulation to each photoreceptor was calculated from the spectral sensitivities of the photoreceptors (Figure 5) and the spectral radiance of the test stimulus.

For example, Melanopsin-high and Melanopsin-low stimuli, which modulated the amount of stimulation to melanopsin photorecetors by ±20% from the control stimulus (Figure 6). Similarly, stimuli with ±5% modulation of the amount of stimulation to L, M, S cones were used as L-cone high, L-cone low, M-cone high, M-cone low, S-cone high and S-cone low stimuli (Table 1).

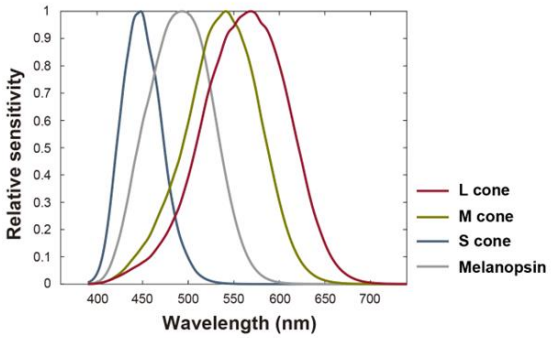

Figure 5: Normalised spectral sensitivities of L-, M-, S-cone and melanopsin photoreceptors.

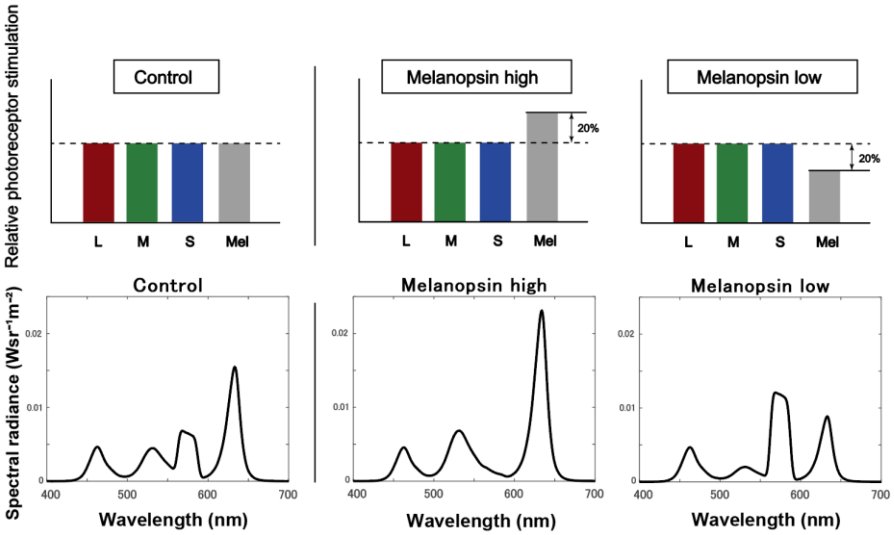

Figure 6: Relative photoreceptor stimulation of modulated stimuli and their spectra.

Table 1 shows the amount of stimulation to the L, M, and S cones and the chromaticity of these light stimuli. The spectral sensitivities of cones were designed so that the total amount of stimulation of L cones and M cones correspond to the photopic luminous efficiency function. The stimulation of each cone were calculated using the 10-deg cone fundamentals [9-10]. Since we assume that S-cone and melanopsin do not contribute to the photopic luminance we used the conversion factor for S cone [11]; the stimulation to S cone 1 cdm^{-2} was defined as the amount of stimulation to S cone produced by equal energy white with luminance of 1 cdm^{-2}. Similarly, we defined the conversion factor for melanopsin. The conversion factor, K_s for S cones is 1466 lmW^{-1} and the conversion factor for melanopsin, K_{mel}, was 872 lmW^{-1}.

	Luminance (cdm^{-2})	L (cdm^{-2})	M (cdm^{-2})	S (cdm^{-2})	Melanopsin (cdm^{-2})	x	y
Melanopsin high	282	206	76	132	209	0.429	0.389
Melanopsin low	282	206	76	132	140	0.429	0.389
L-cone high	293	217	76	132	174	0.445	0.383
L-cone low	272	196	76	132	174	0.411	0.396
M-cone high	286	206	80	132	174	0.415	0.400
M-cone low	278	206	72	132	174	0.442	0.378
S-cone high	282	206	76	139	174	0.426	0.385
S-cone low	282	206	76	126	174	0.432	0.393
Control	282	206	76	132	174	0.429	0.389

Table 1: The luminance and chromaticity of the light stimuli.

Previous studies in the similar condition have shown that rods have little or no effect at high illuminance [12]. Since we used the luminance more than 200 cdm^{-2} the effect of the rods was not considered in the present experiment. The modulation of melanopsin photoreceptor does not change any colour whereas the modulations in the other photoreceptors produce the colour change. Such a colour difference makes observers difficult to judge the amount of brightness between two stimuli [2]. Hence, we used light stimuli with a small modulation of 5% in order to reduce the colour difference.

The control stimulus was a white stimulus (Figure 7). The Correlation Colour Temperature (CCT) was 3000 K. The control stimuli were chosen to ensure that the eight modulating stimuli could be generated in the multi-primary stimulation system (Figure 8).

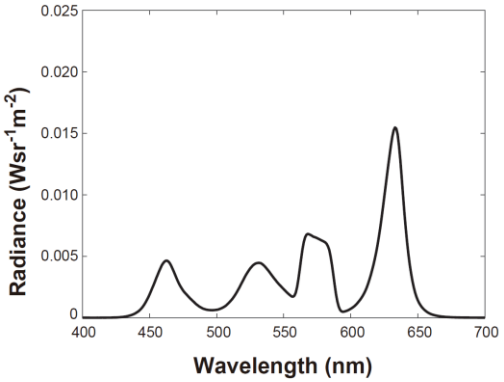

Figure 7: The spectrum of the control stimulus.

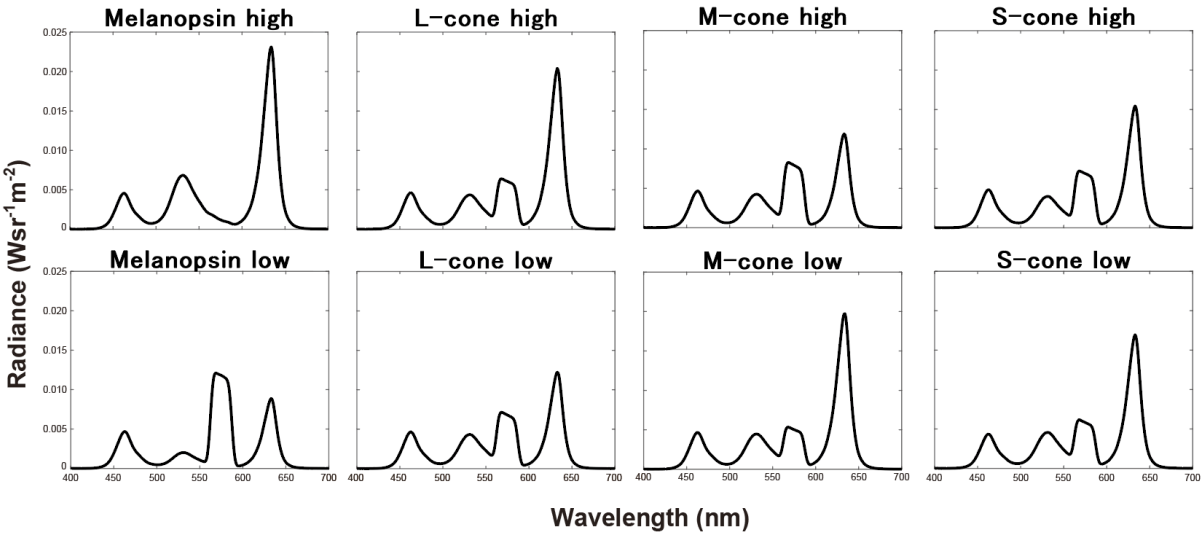

Figure 8: Spectra of the modulated stimuli from white control stimuli.

Procedure

Constant method was used to measure the brightness perception of each light stimulus. Two-intervals alternative-forced-choice procedure (2IAFC) was used in the experiment. The test stimulus and nine reference stimuli were compared 20 times each, i.e. a total of 180 comparisons were conducted to measure the amount of brightness perception for the test stimulus. The order of the stimulus presentation was counterbalanced. Observers had the initial adaption for 5 minutes in a dark booth before the session. A reference stimulus and a test stimulus were presented as shown in Figure 9. The test and reference stimuli were presented for 3 seconds with the adaptation stimulus in between. The test and reference stimuli were gradually varied to avoid artifacts caused by abrupt change (See Figure

9). The luminance of the nine reference stimuli varied ranging from -80% to +80% from the white control stimulus.

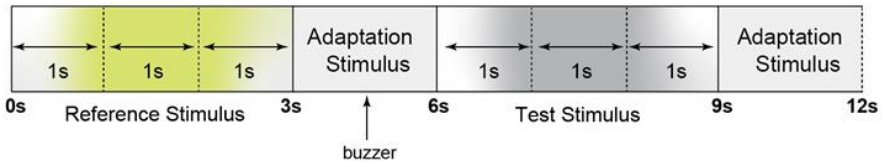

Figure 9: Presentation sequence.

Results and discussion

Three observers participated in the experiment. They are females aged from 22 to 25 years old. The average age was 23 years old. Figures 10 and 11 showed the relative brightness to the white control stimulus for each observer. Please note than the modulation contrast was 20% for melanopsin and 5% for cones.

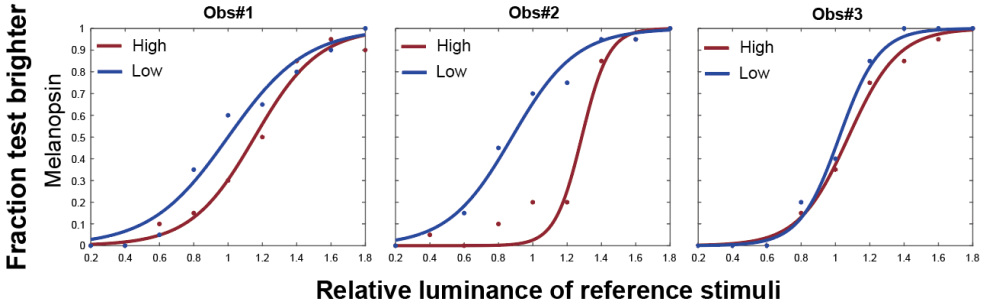

Figure 10: Psychometric functions for melanopsin-high and -low stimuli.

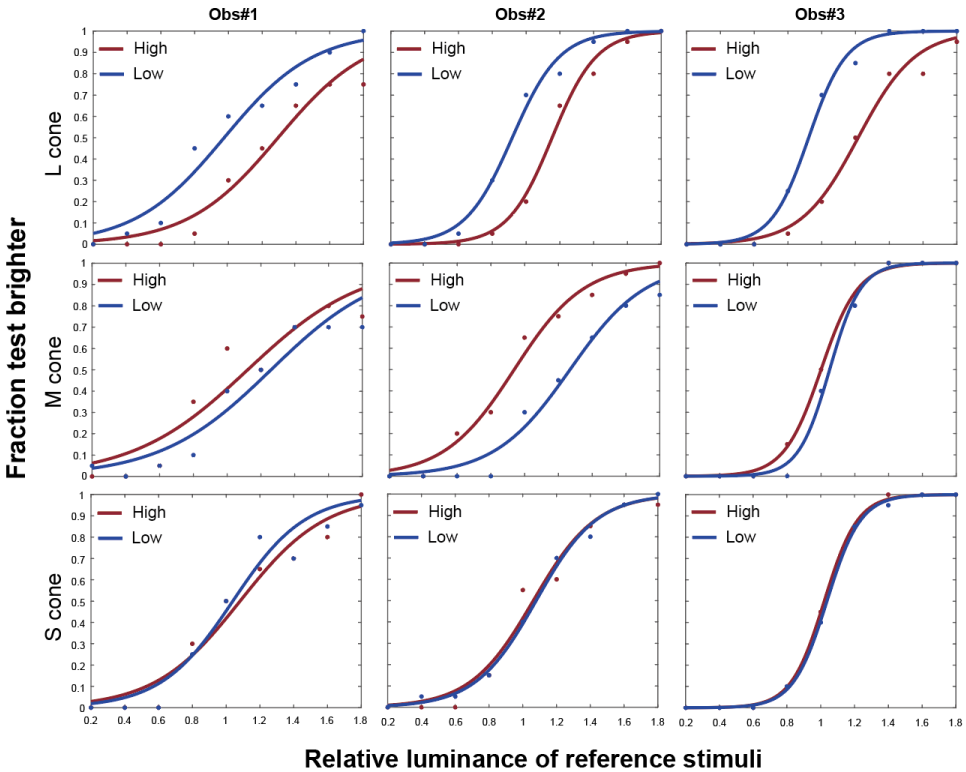

Figure 11: Psychometric functions for modulated stimuli to each cone.

A large difference in brightness was found in the L, M-cone and melanopsin modulations, whereas little difference was found in S-cone modulation, consistently for all three observers (Figure 12). The melanopsin-high stimulus, MelH, was perceived brighter than the melanopsin-low stimulus, MelL, although MelH and MelL were metamers, i.e. had the same luminance and colour. Similarly, L-cone high stimulus, LH was perceived brighter than the L-cone low stimulus, LL. On the other hand, M-cone low stimulus, ML, was perceived brighter than the M-cone high stimulus, MH although the luminance of the MH was higher than ML. All three observers had a similar tendency for all test stimuli. In the future, we are going to increase a number of observers for further verification of the results.

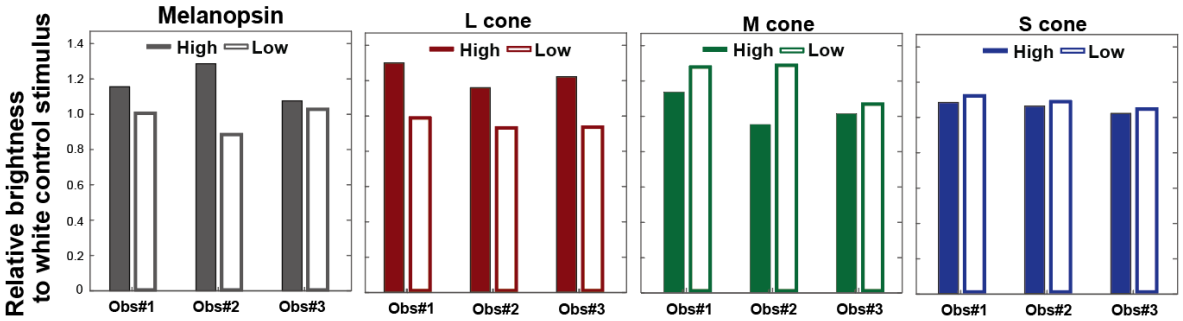

Figure 12: Relative brightness to white control stimulus.

The results showed that observers perceived brighter as melanopsin stimulation increased although there was no difference in luminance and colour. The results were consistent with previous studies [8,13-17]. Brown *et al.* showed that observers perceived brighter in the entire field stimulation [8]. DeLawyer *et al.* showed the similar facilitation of brightness when only melanopsin stimulation increases [17]. They also noted that the induced brightness was small when colour and melanopsin stimulation varied simultaneously.

We investigated the brightness perception caused by varying the amount of stimulation to photoreceptors and varied the amount of stimulation to photoreceptors to clarify how each photoreceptor contributes to the brightness mechanism. It was found that observers perceived brighter as melanopsin stimulation increased. The result was consistent with previous studies [1-3]. In addition, we have found that there was a large difference in brightness when L- and M-cone stimulations varied, whereas S-cone stimulation induced little change in brightness.

Conclusions

In this study, we varied the amount of photoreceptor stimulation to clarify how each photoreceptor contributes to the brightness mechanism. To this end, we selectively modulated the amount of photoreceptor stimulation using a four-primary illumination system. It was found that observers perceived brighter as melanopsin stimulation increased according to psychometric function. In addition, although we have found that there was a difference in brightness when L- and M-cone stimulations varied there was a little difference when S-cone stimulation varied. The use of test stimuli defined in photoreceptor stimulation is expected to advance future research.

Acknowledgement

This research was supported by the Ministry of Education, Science, Sports and Culture of Japan, Grants-in-Aid for Scientific Research (A) 21H04426 (Prof. Kitaoka) and 20H00614 to ST, the Grant in Aid for Challenging Research (Exploratory) 22K19333 to ST.

References

1. Commission Internationale de l'Éclairage. Principales Decisions (6e Session, 1924), CIE Sixième Session, Genève, Juillet, ise
2. Commission Internationale de l'Éclairage (1978), Light as a true visual quantity: Principles of measurement, CIE-041-1978.
3. Wagner G and Boynton RM (1972), Comparison of four methods of heterochromatic photometry, *Journal of the Optical Society of America*, **62** (12), 1508-1515.
4. de Lange Dzn H (1954), Relationship between critical flicker-frequency and a set of low-frequency characteristics of the eye, *Journal of the Optical Society of America*, **44** (5), 380-389.
5. Shapiro AG, Pokorny J and Smith VC (1996), Cone-rod receptor spaces with illustrations that use CRT phosphor and light-emitting-diode spectra, *Journal of the Optical Society of America A*, **13** (12), 2319-2328.
6. Pokorny J, Smithson H and Quinlan J (2004), Photostimulator allowing independent control of rods and the three cone types, *Visual Neuroscience*, **21** (3), 263–267.
7. Tsujimura S, Ukai K, Ohama D, Nuruki A and Yunokuchi K (2010), Contribution of human melanopsin retinal ganglion cells to steady-state pupil responses, *Proceedings of the Royal Society B: Biological Sciences*, **277** (1693), 2485-2492.
8. Brown TM, Tsujimura S, Allen AE, Wynne J, Bedford R, Vickery G, Vugler A and Lucas RJ (2012), Melanopsin-based brightness discrimination in mice and humans, *Current Biology*, **22** (12), 1134-1141.
9. Stockman A, Sharpe LT and Fach C (1999), The spectral sensitivity of the human short-wavelength sensitive cones derived from thresholds and color matches, *Vision Research*, **39** (17), 2901-2927.
10. Stockman A and Sharpe LT (2000), The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype, *Vision Research*, **40** (13), 1711-1737.
11. Boynton RM and Kambe N (1980), Chromatic difference steps of moderate size measured along theoretically critical axes, *Color Research and Application*, **5** (1), 13-23.
12. Chien S-E, Yeh S-L, Yamashita W and Tsujimura S (2023), Enhanced human contrast sensitivity with increased stimulation of melanopsin in intrinsically photosensitive retinal ganglion cells, *Vision Research*, **209**, 108271, 1-13.
13. Zele AJ, Feigl B, Adhikari P, Maynard ML and Cao D (2018), Melanopsin photoreception contributes to human visual detection, temporal and colour processing, *Science Reports*, **8** (1), 3842, 1-10.
14. Cao D, Chang A and Gai S (2018), Evidence for an impact of melanopsin activation on unique white perception, *Journal of the Optical Society of America A*, **35** (4), B287-B291.
15. Allen AE, Storchi R, Martial FP, Bedford RA and Lucas RJ (2017), Melanopsin contributions to the representation of images in the early visual system, *Current Biology*, **27** (11), 1623-1632.e4.
16. Yamakawa M, Tsujimura S and Okajima K (2019), A quantitative analysis of the contribution of melanopsin to brightness perception, *Scientific Reports*, **9** (1), 1-8.
17. DeLawyer T, Tsujimura S and Shinomori K (2020), Relative contributions of melanopsin to brightness discrimination when hue and luminance also vary, *Journal of the Optical Society of America A*, **37** (4), A81-A88.