Color Research & Application

WILEY

COLOR RESEARCH AND APPLICATION

RESEARCH ARTICLE OPEN ACCESS

Melanopsin Stimulation Modulates Blackness Induction

Masahiko Yamakawa[1] | Katsunori Okajima[1] | John S. Werner[2,3]

[1]Faculty of Environment and Information Sciences, Yokohama National University, Yokohama, Japan | [2]Department of Experimental Psychology and Department of Engineering Science, University of Oxford, Oxford, UK | [3]Department of Ophthalmology and Vision Science and Department of Neurobiology, Physiology & Behavior, University of California Davis, Davis, USA

Correspondence: Masahiko Yamakawa (yamakawa-masahiko-km@ynu.ac.jp)

Received: 25 August 2025 | **Revised:** 18 December 2025 | **Accepted:** 7 January 2026

Keywords: blackness induction | brightness | melanopsin cells | pairwise comparison | silent substitution

ABSTRACT

A central field will become darker with increasing intensity of a surrounding annulus until it appears uniformly black. We investigated the relation between blackness induction of a central field and the stimulation of melanopsin cells in a surrounding field. Silent substitution was used to selectively modulate melanopsin cells while the tristimulus values were kept constant (melanopic/photopic ratio = 0.51–1.21). Eight participants judged the perceived blackness of the center field using a pairwise comparison method for all visual stimulus combinations. Stimuli were presented monocularly for 0.5 or 5 s with 2-s inter-stimulus intervals. Statistical analysis was performed using Scheffé's pairwise comparison method (Nakaya variation). The results showed that perceived blackness of the center decreased significantly under the 5-s presentation condition with increasing stimulation of melanopsin cells in the surround, although perceived blackness of the center increased with increasing luminance in the surround. In contrast, under the 0.5-s presentation condition, no significant difference in perceived blackness of the center with stimulus intensity to melanopsin cells was found. These results demonstrate that the stimulation of melanopsin cells of the surround modulates blackness induction of the center at longer stimulus durations.

1 | Introduction

Black is an achromatic color that results from spatial (simultaneous) and/or temporal (successive) contrast. A central field surrounded by an annulus will become darker as the intensity of the annulus is increased until reaching complete blackness. Whatever the hue of the central field, it is darkened by the surrounding stimulus. This phenomenon is called blackness induction and has been reviewed by Volbrecht and Kliegl [1].

Werner et al. [2, 3] investigated blackness induction of a center-surround stimulus with a central stimulus 45′ in diameter surrounded by an annulus having a 120′ outer diameter separated by a 7.5′ dark gap with presentation time of 0.5 s in Maxwellian-view. It was demonstrated that spatial blackness induction depended on the luminance of the center and surrounding stimuli. In addition, the wavelength dependence of the irradiance intensity of the monochromatic surround was fitted to the inverse of the spectral luminous efficiency function ($V(\lambda)$). Shinomori et al. [4] reported similar results when the center stimulus was broadband (white); however, when the center stimulus was monochromatic, the central chromatic signal affected blackness induction. Fuld et al. [5] conducted their experiments in which the luminance of the white surrounding stimulus was adjusted to equate whiteness and blackness of the monochromatic center stimulus. They found that blackness induction of the center was related to the brightness of the center and the luminance of the surround. In addition, there are several studies to predict blackness of the center by evaluating the appearance of color patches with different hues under constant surrounding conditions. Westland et al. [6] showed that blackness of the center could be expressed as a nonlinear combination of L^*, a^*, and b^* by evaluating various hue patches placed on a Munsell N5 gray

card using a ranking method. Cho et al. [7, 8] also showed that blackness of the center surrounded by a gray colored board can be expressed as a nonlinear function of L^*, a^*, and b^*.

Kingdom [9] summarized the progress of studies to date regarding the explanation of the theory for the effects of context on brightness and lightness. The following are the theories identified for understanding brightness and lightness: (1) edge-integration models [10]; (2) Gestalt-anchoring models [11]; (3) spatial-filtering feature models [12]; (4) oriented difference-of-Gaussian (ODOG) models [13]; (5) intrinsic-image models [14]; and (6) empirical models [15]. Sinha et al. [16] showed that there were three mechanisms of brightness contrast: "low-level mechanisms" due to filters that result in lateral suppression in the early stages of the visual system [13], "medium-level mechanisms" due to grouping based on Gestalt principles [17], and "high-level mechanisms" due to advanced understanding of scenes and lighting layouts in images [18]. Blakeslee et al. [19] showed that brightness induction was affected by the characteristics of the surrounding ring. The following were mentioned: optical blur [20], Gaussian difference (DOG) model [21], multi-scale DOG model [13], influence of the output of the receptive field of retinal ganglion cells and lateral geniculate nucleus (LGN) [22], and edge integration model [23]. Taken together, although there was no explicit description of the research thus far from the perspective of blackness perception, it can be suggested that the evaluation of the influence of visual stimuli on cone stimulation and the spatial arrangement of the images are the basis of the research design.

Intrinsically photosensitive retinal ganglion cells (ipRGCs) were discovered about 23 years ago [24]. These cells contain melanopsin in their soma and dendrites but may also receive inputs from rods and cones [25]. They have the characteristics of intrinsic photosensitivity and extrinsic photoreception which are transmitted from cones, and project the visual information from photon absorption to various parts of the brain [25, 26]. From the discovery of ipRGCs to the present, the main research subjects have been related to the so-called non-image forming pathways, such as projection to the suprachiasmatic nucleus, which controls circadian rhythms, and the preoptic region, which is involved in the pupil light reflex [27, 28]. Their involvement in image forming pathways was elucidated using physiological methods [26, 29], while psychophysical methods have revealed that intrinsic melanopsin cells were involved in brightness perception [30], color perception [31] and contrast detection [32, 33]. In particular, studies on contrast detection by melanopsin cells have shown that when cone stimulation was identical but the melanopsin stimulation was different, the detection of sinusoidal gratings could be detected in the low spatial and temporal frequency domains [32], and that increasing stimulation intensity to melanopsin cells in the background light improved spatial contrast sensitivity [33]. While these studies demonstrate the involvement of melanopsin cells in visual information processing, there has been scant progress on understanding the relation between melanopsin cell stimulation and blackness induction; that is, the effects of melanopsin signals on spatial contrast processing.

In this study, we investigated the relationship between blackness induction of a center stimulus and the stimulation of melanopsin cells of the surround. Visual stimuli were prepared using a silent substitution method. The stimulus intensity to melanopsin cells was modulated while keeping the stimulus intensity to cones constant. We hypothesized that the stimulation to melanopsin cells of the surrounding stimulus affects perceived blackness of the center stimulus. We evaluated blackness perception of the center stimulus surrounded by visual stimuli that varied stimulus intensities of melanopsin cell stimulation. To consider the relationship with brightness induction, we also evaluated brightness perception of the surrounding stimulus.

2 | Methods

2.1 | Visual Stimuli

Stimuli were generated using a combination of three commercially available projectors (PT-LW376J; Panasonic Corporation, Osaka, Japan, XJ-S400U and XJ-A257; Casio Computer, Tokyo, Japan) with different spectral power distributions of RGB primaries as light sources, and different optical filters attached to each projector. To maximize the stimulation contrast of melanopsin cells, we combined a custom-made optical filter (Itoh Optical Industrial, Aichi, Japan) and commercially available spectral filters (SV0530 and LV0550; Asahi Spectra, Tokyo, Japan). The lights were projected onto a white screen, and the participants observed the reflected light from the screen as a visual stimulus. Figure S1 shows the RGB spectral power distributions from the three projectors, the spectral transmission spectra of the optical filters used, and the RGB spectral power distributions from the projectors through the optical filters. To obtain the proper RGB spectral power distributions, the nine primary colors were reduced to six. The normalized six monochromatic spectral power distributions of the reflected light used in this experiment are shown in Figure 1A, and the experimental setup is shown in Figure 1B. The distance from the screen to the participants' cornea was 1.3 m. The visual stimulus consisted of a rectangular 7.5° × 7.5° surround and a rectangular 2° × 2° center (Figure 1C). The entire stimulus configuration was flashed for 0.5 or 5 s, with a 2-s interstimulus interval (Figure 1D).

Ten spectral power distributions of the surrounding stimuli (Figure 2A) that realize different stimulus intensities to melanopsin cells and cones for visual stimuli were designed using a silent substitution method. The colorimetric values (CIE2006: 10°) were constant ($(x, y) = (0.330, 0.330)$), the luminance value of stimuli #1 to #6 was 700 cd/m^2, and that of stimuli #7 to #10 was 375 cd/m^2. We confirmed that cone excitations remained constant. Table S1 shows the calculated % deviation of L-, M-, S- cone stimulation from the mean. The spectral power distributions of visual stimulation were measured using a spectroradiometer (SR-5A; Topcon Technohouse Corporation, Tokyo, Japan). Luminance and chromaticity values were calculated using CIE color matching functions (CIE2006). The stimulus intensity to melanopsin cells was modulated from 0.51 to 1.21 (#1; 0.51, #2; 0.65, #3; 0.78, #4; 0.93, #5; 1.09, #6; 1.21, #7; 0.51, #8; 0.67, #9; 0.95, #10; 1.21) in the melanopic/photopic ratio (M/P ratio) under both the 700 cd/m^2 and 375 cd/m^2 conditions. Here, the spectral data of CIE S026:2018 [34] were used for the melanopsin cell response curve $\underline{i}(\lambda)$, and the fundamental chromaticity diagram with physiological axes-Part

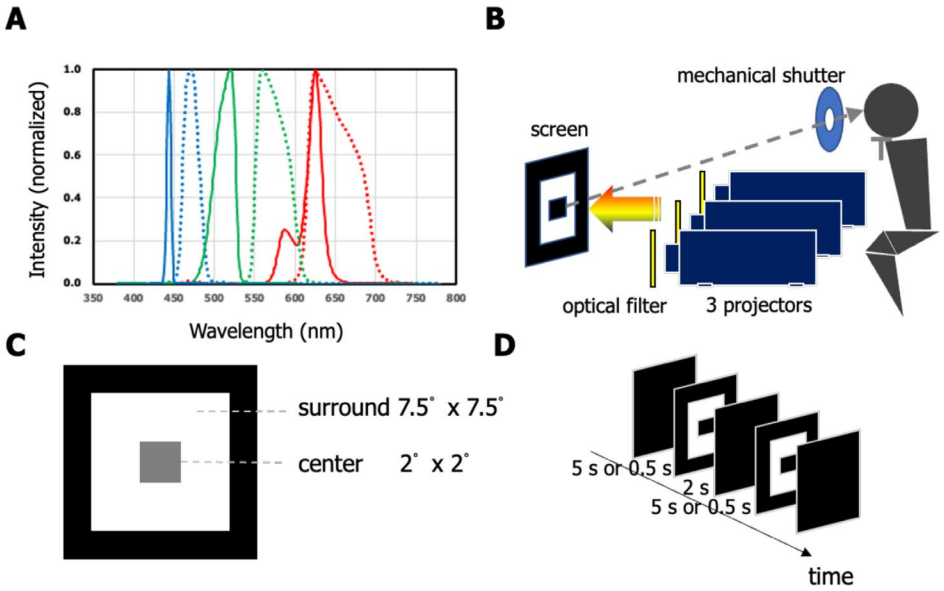

FIGURE 1 | Experimental setup. (A) Normalized spectral power distribution of the emission from the three projectors used in this experiment. (B) Timing of visual stimuli was controlled by a mechanical shutter placed in front of the right eye. (C) Center-surround configuration. The luminance outside the surround was confirmed to be less than 1 cd/m^2. (D) Time series of one trial.

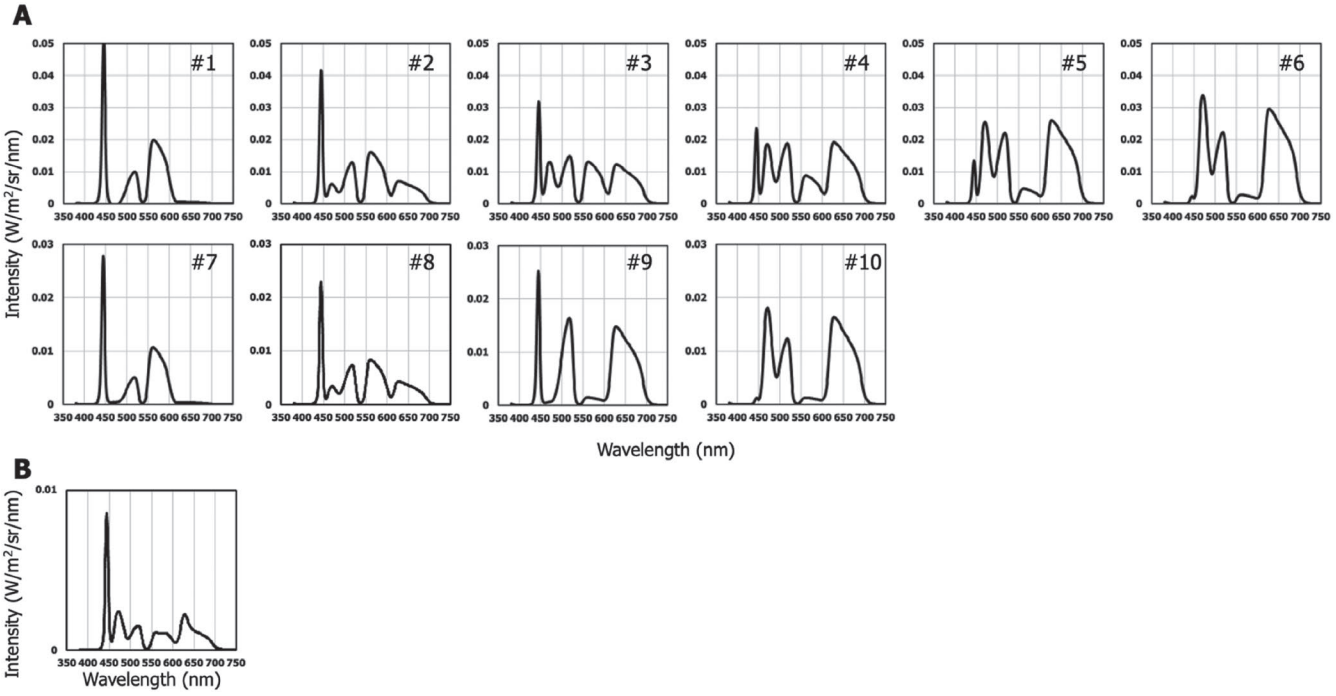

FIGURE 2 | Spectral power distributions of (A) the surround and (B) the center stimuli. $\Delta\lambda = 1$ nm.

1. CIE 170–1:2006 was used for the spectral visual efficiency curve $\underline{V}(\lambda)$. In combination with the spectral power distribution $\underline{P}(\lambda)$ of the visual stimulus, the M/P ratio was calculated using the following formula:

$$\text{M / P ratio} = \int \underline{P}(\lambda)\,\underline{i}(\lambda)d\lambda \Big/ \int \underline{P}(\lambda)\,\underline{V}(\lambda)d\lambda.$$

This is a linear ratio and based on the integrated radiance. The relative stimulus intensities to the L-, M-, and S-cones of the surrounding stimuli in each group of #1 to #6 and #7 to #10 were constant. The scotopic/photopic ratio (S/P ratio), which expresses the stimulus intensity to rods, was not controlled because rods are likely saturated at the luminance levels of this experiment. Table 1 shows the stimulus intensities to photoreceptors by surrounding stimuli #1 to #10. The center stimulus was not changed for all 10 types of visual stimuli, and the photometric colorimetric values were $(x, y) = (0.288, 0.238)$, luminance = 74 cd/m^2 (CIE2006: 2°). The spectral power distribution of the reflected light is shown in Figure 2B.

TABLE 1 | Characteristics of the visual stimulation to photoreceptors.

	Stimulus intensity to melanopsin cells	Luminance	Stimulus intensity to L-, M-, S-cones	Ratio of stimulus intensity to L-, M-, S-cones
#1~#6	Different	Same	Same	Same
#7~#10	Different	Same	Same	Same
#1 & #9, #2 & #10	Same	Different	Different	Same

2.2 | Participants

Six male and two female students (23.0 ± 1.7 years) of Yokohama National University participated in the experiments. They were normal trichromats based upon testing using Ishihara color plates, a Farnsworth-Munsell 100-hue test, and an anomaloscope (OT-II, NEITZ, Tokyo, Japan). Three participants required vision correction using non-tinted lenses. This study was conducted in accordance with guidelines of the Yokohama National University Committee on Life Science Research.

2.3 | Procedure

We evaluated the blackness of the center stimulus and the brightness of the surrounding stimuli. The experiments were conducted in a dark room. For all experiments, the procedure was explained and written informed consent was obtained, followed by a 5-min rest period. During the experiment, the head was stabilized with a chin rest, and visual stimuli were presented to the right eye. The fixation point was the center of the visual stimuli. Temporal presentation was controlled by a mechanical shutter placed in front of the eye. The time series of the visual stimulation of one trial is shown in Figure 1D. The evaluations of blackness and brightness were conducted on different days.

2.4 | Blackness of the Center Stimulus

Each trial consisted of two stimulus presentations, and participants responded whether the first or second stimulus of the pair was more black. A first visual stimulus (former) was presented by opening the shutter, and a blank of 2 s was provided after the shutter was closed; then, a second stimulus (latter) was presented by opening and closing the shutter. The experiment was conducted with two presentation times: 5-s and 0.5-s conditions, respectively. After the two presentations in a trial, participants answered either "former (or latter) was blacker," "former (or latter) was slightly blacker," or "former and latter had same blackness," and values of 2, 1, 0, −1, −2 were assigned to each answer. All combinations of 10 kinds of visual stimuli, totaling 90 pairs per participant, were evaluated. The order of the presentations was random.

2.5 | Brightness of the Surround

Brightness of the surround was tested with the same participants using the same procedure as that for blackness evaluation of the center. Participants responded either "first interval (or latter) was definitely brighter," "former (or latter) was slightly brighter," or "former and latter had same brightness," and values of 2, 1, 0, −1, −2 were assigned to each answer. The experimental process and analyses were conducted according to the blackness evaluation described above. Seven participants of eight in blackness evaluation also participated in the brightness evaluation for the 0.5-s condition.

3 | Results

Figure 3A,B show the results of perceived blackness of the center stimulus. Each panel presents the mean numerical scale as defined above. Analyses from Scheffé's pairwise comparison method (Nakaya variation) showed that the p-value between the #1 to #6 group and the #7 to #10 group in ANOVA was less than 0.01, and the yardstick value (a benchmark value that is used as a fixed reference value when comparing paired items) was $Y = 0.45$ ($p = 0.05$) and 0.52 ($p = 0.01$) under the 5-s presentation condition. The p-value (ANOVA) was also less than 0.01, and the yardstick value was $Y = 0.49$ ($p = 0.05$) and 0.57 ($p = 0.01$) under the 0.5-s presentation condition. Table 2 shows the results of ANOVA, mean and SEM. There were significant differences in blackness perception between the #1 to #6 group (700 cd/m^2) and the #7 to #10 group (375 cd/m^2) under both the 5-s and 0.5-s conditions (Figure 3A left and 3B left, 10 samples analysis). This is a comparison between the different luminance stimuli, so it behaves differently. This is the typical result for blackness induction.

In the comparison among #1 to #6 stimuli (M/P ratio modulation) under the 700 cd/m^2 condition, perceived blackness decreased with increasing M/P ratio under the 5-s presentation condition (Figure 3A center, six samples analysis). Significant differences were observed between the several M/P ratio conditions (the yardstick value; $Y = 0.63$ ($p = 0.05$) and 0.75 ($p = 0.01$)). However, no significant difference was observed among the M/P ratio modulation under the 0.5-s presentation condition (Figure 3B center, six samples analysis, the yardstick value; $Y = 0.77$ ($p = 0.05$) and 0.93 ($p = 0.01$)). In the analyses of the 375 cd/m^2 condition (Figures 3A right and 3B right, four samples analysis), no significant difference among the M/P ratio modulation was observed under both the 5-s (Figure 3A right, four samples analysis, the yardstick value; $Y = 0.84$ ($p = 0.05$)) and 0.5-s presentation conditions (Figure 3B right, four samples analysis, the yardstick value; $Y = 0.65$ ($p = 0.05$)).

Figure 4 shows the pairwise comparisons of perceived brightness of the surround stimuli under the 700 cd/m^2 condition.

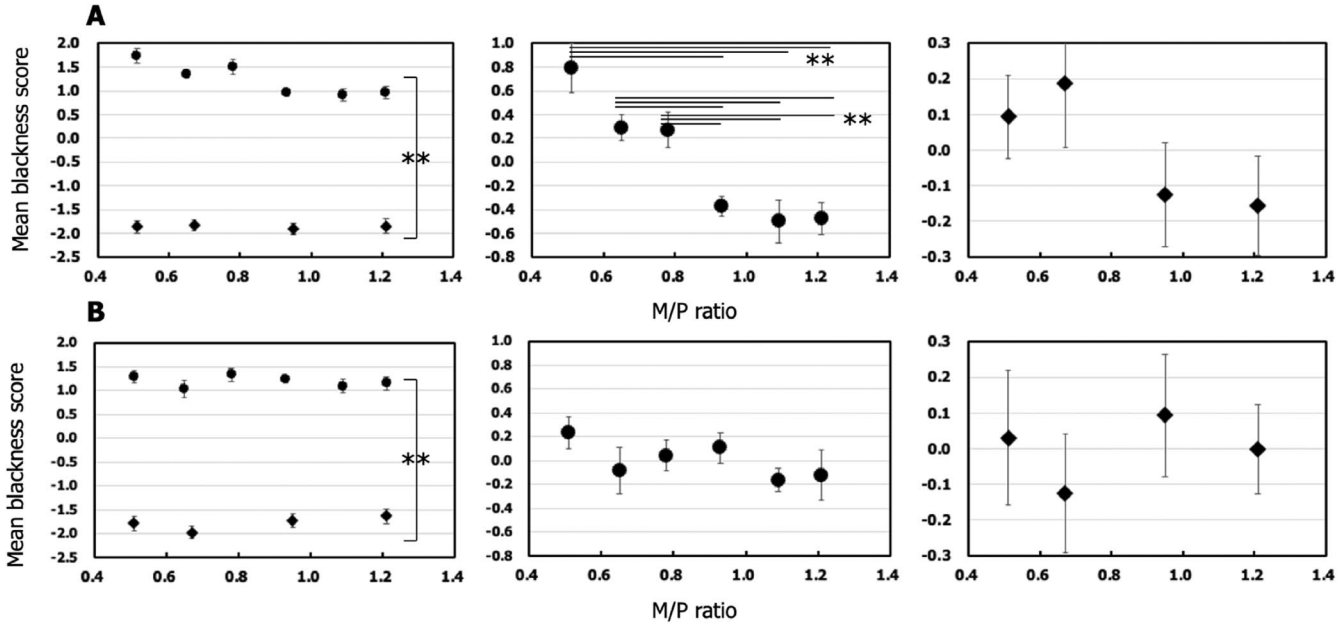

FIGURE 3 | Results of paired comparison evaluation of blackness of the center stimulus. (A) 5-s condition ($n=8$), (B) 0.5-s condition ($n=8$). Left; all stimuli (analysis of 10 samples), center; 700 cd/m^2 stimuli (analysis of six samples), right; 375 cd/m^2 stimuli (analysis of four samples). **; $p<0.01$. Error bars represent standard errors of the mean. ●; 700 cd/m^2 data, ◆; 375 cd/m^2 data.

Brightness increased with increasing M/P ratio under the 5-s presentation condition and significant differences were observed between the several M/P ratio conditions (Figure 4A, 10 samples analysis, the yardstick value; Y = 0.54 ($p=0.05$) and 0.63 ($p=0.01$)). In contrast, there was no significant difference under the 0.5-s presentation condition among the M/P ratio modulation (Figure 4B, 10 samples analysis, the yardstick value; Y = 0.49 ($p=0.05$) and 0.57 (p = 0.01)).

4 | Discussion

In this study, we investigated blackness induction when the melanopsin stimulation of a surrounding stimulus was modulated while the stimulus intensity to cones remained constant at 700 cd/m^2. We hypothesize that the stimulation of melanopsin cells in the surround affects perceived blackness of the center. It is possible that the mechanism by which melanopsin facilitates blackness induction of the center is due to the influence of the large receptive fields of melanopsin cells in the surround. It was found that blackness induction was influenced by melanopsin stimulation of the surround under the 5-s presentation condition. Blackness induction at 700 cd/m^2 (conditions #1~6) was significantly greater than that at 375 cd/m^2 group (#7~#10) under both the presentation times. We speculate that the effect of presentation time on blackness induction is related to the latency to the first spike of ipRGCs after the stimulation which is longer than that of cones [26]. However, we cannot exclude the possibility that the differences in response to presentation time may be due to other factors, such as adaptation, temporal summation, or attentional differences. In the case of 375 cd/m^2 stimulation, no significant difference on blackness perception was observed under both the 5-s and 0.5-s presentation condition among the M/P ratio modulation. The reason is that, although blackness induction does occur under the 375 cd/m^2 condition, the stimulation of melanopsin cells is not sufficient to make a difference. We have previously shown that melanopsin cells were involved in brightness perception [30], and the presentation time dependence of brightness perception characteristics among the M/P ratio modulation of the surrounding stimulus also supports the speculation involving melanopsin cells.

Shinomori et al. [4] assumed that blackness induction of the center resulted from an antagonistic interaction between achromatic non-opponent signals arising from the surround, and achromatic and chromatic signals arising from the center originating from the stimulation of cone photoreceptors. They concluded that when the center was broadband white of fixed illuminance, spatial blackness induction was determined only by the center-to-surround illuminance ratio, not by the chromatic properties of the surround under 0.5 s presentation condition because the action spectrum of blackness induction agreed with each observer's heterochromatic flicker photometry function. Bimler et al. [35] proposed a stage model for blackness induction, originating from the stimulation of photoreceptors, in which the spatial contrast influenced each stage, and showed that blackness induction involved brightness considering the Helmholtz-Kohlrausch effect of the center and luminance of the surround. In both models, blackness induction of the center was related to illuminance or luminance of the surrounding stimulus. It must be noted that although these models were derived from the results of the experiments in which the presentation time of visual stimuli was shorter (0.5 s and 1 s) compared with our experiment, their results cannot explain the results of our experiment, in which blackness induction of the center was modulated even when luminance of the surround was constant. We are not aware of any previous psychophysical studies related to blackness perception involving melanopsin cells, and this is the first study to demonstrate blackness induction modulated by melanopsin stimulation.

TABLE 2 | (A) Results of ANOVA (top; 5-s condition and bottom; 0.5-s condition) of Scheffé's pairwise comparison method (Nakaya variation) and (B) mean and standard errors of the mean (SEM) per condition.

A					
Source	**SS**	**df**	**Variance**	***F*-value**	***p***
Main effect (stimulation)	1891	9	210.2	254.3	5×10^{-121}
Main effect × personal	104.8	63	1.663	2.013	8×10^{-5}
Combined effect	55.6	36	1.544	1.868	0.003
Error	208.2	252	0.826		
Total	2260	360			

A					
Source	**SS**	**df**	**Variance**	***F*-value**	***p***
Main effect (stimulation)	1702	9	189.1	192.8	1×10^{-107}
Main effect × personal	128.9	63	2.046	2.085	3×10^{-5}
Combined effect	34.6	36	0.96	0.978	0.51
Error	247.3	252	0.981		
Total	2113	360			

B										
	#1	**#2**	**#3**	**#4**	**#5**	**#6**	**#7**	**#8**	**#9**	**#10**
Luminance (cd/m^2)	700	700	700	700	700	700	375	375	375	375
M/P ratio	0.51	0.65	0.78	0.93	1.09	1.21	0.51	0.67	0.95	1.21
5-s condition										
Mean	1.74	1.36	1.50	0.96	0.91	0.96	−1.86	−1.83	−1.90	−1.85
SEM	0.15	0.09	0.15	0.09	0.13	0.14	0.13	0.12	0.11	0.16
0.5-s condition										
Mean	1.29	1.04	1.33	1.24	1.09	1.15	−1.79	−1.98	−1.73	−1.64
SEM	0.14	0.18	0.13	0.08	0.14	0.14	0.16	0.13	0.14	0.16

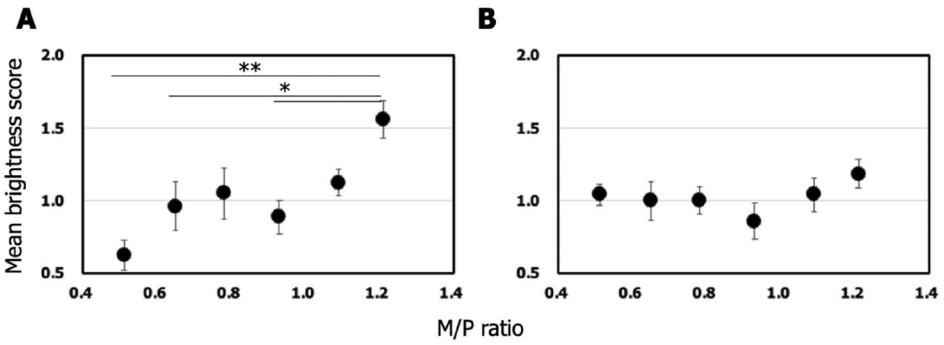

FIGURE 4 | Analysis results of paired comparisons of brightness of the surround stimuli. (A) 5-s condition ($n=8$), (B) 0.5-s condition ($n=7$), showing the results of the 700 cd/m^2 stimuli condition (analysis of 10 samples). Error bars represent standard errors of the mean. $^{**}p<0.01$, $^{*}p<0.05$.

Werner et al. [2, 3] showed that the inverse of the profile of blackness induction in the wavelength dependence of the radiance of the surrounding stimulus was fitted to the spectral luminous efficiency ($V(\lambda)$). In these experiments, brightness perception of the surround increased with increasing melanopsin stimulus intensity of the surround. The results of our study cannot be explained by conventional models of color vision. To interpret this phenomenon, it is necessary to consider the involvement of melanopsin cells in visual information processing pathways. Dacey et al. [26] found that there was a pathway from cones to ipRGCs. Brown et al. [29] conducted electrophysiological experiments using cone knock-out mice

and revealed that stimulation of melanopsin ganglion cells projected to the lateral geniculate nucleus (LGN) and then to the primary visual cortex. These results demonstrate that melanopsin cells are involved in the image formation pathway. In addition, Prigge et al. [36] clarified that there was a projection to amacrine cells from melanopsin cells as a feedback mechanism. This indicates that visual stimulation of melanopsin cells affects the pathway from photon reception at cones to the visual cortex. Milosavljevic et al. [37] found that the projection from melanopsin cells to retinal ganglion cells had a function of regulating the rate of optic nerve activity. DeLawyer et al. [38] investigated the effect on the color perception of the center when modulating the stimulus intensity to melanopsin cells of the surround. These authors suggested that this was evidence of the role of melanopsin cells in brightness perception, but the detailed mechanism was not shown. To sum up, these findings do not fully explain the results of our study.

Do [25], in a review article of melanopsin cells (mice M1 cells), described the spatial information integration of visual information from the size of the dendrites and the structure of the receptive field of melanopsin cells. In addition, studies of the receptive field originating from melanopsin cells have shown the existence of a large pericentral antagonistic receptive field in animal experiments. Zhao et al. [39] investigated the polymorphic receptive field of melanopsin cells involved in visual information processing in mice and showed that it peaked when the spot diameter reached between 200 and 500 μm, and that it had an antagonistic surround. Procyk et al. [40] showed that the receptive field diameter was between 15° and 25° in visual angle and between 450 and 750 μm in diameter on the retina of cone and rod knock-out mice. In contrast, the surrounding radius of the receptive fields in the LGN originating from cones was reported to be ~1° in the primate retina [41]. Thus, the size of the receptive field originating from melanopsin cells is very large compared to that of ganglion cells driven by cones. In brightness contrast studies with monkeys and humans, Yund et al. examined the long-range effects of brightness contrast that could not be predicted from the LGN response and explained that the contrast effects occurred over at least 10° of distance [42, 43]. Taken together, we believe that blackness induction of the center stimulus by the surround might occur due to their large receptive fields.

There are several prior related studies that merit further attention. Pinna et al. [44] found that the insertion of a light blue ring between the tip of a black radial line and the white area of the center of an Ehrenstein figure resulted in anomalous brightness induction. One notable result of their experiments was related to the color of the ring. It was shown that when the color of the ring was blue, brightness induction increased compared to when it was gray. The authors mentioned the diffusion of brightness as one of the neurophysiological mechanisms. It was reported that the stimulation to rods affected brightness assimilation [45]. Although the involvement of melanopsin cells could not be ruled out due to the similarity of spectral sensitivity between rods and melanopsin cells, the authors noted that the contribution of melanopsin cells was negligible due to their experimental conditions. Studies on the effects of spatiotemporal frequency on brightness induction [46, 47] may also be useful in understanding our results. Rossi et al. [46] found that brightness induction is maximized in low spatial frequencies, and that the process responsible for brightness induction is much slower than the process responsible for brightness change due to direct luminance modulation. The authors stated that this phenomenon might involve a filling-in mechanism. De Valois et al. [47] also found that the brightness change of the center induced by the time modulation of the surround occurred only at low temporal frequencies that were less than approximately 2.5 Hz. They concluded that this phenomenon reflects cortical processes rather than retinal factors. Since these studies, except for the study by Barrionuevo et al. [45], were conducted before the discovery of melanopsin cells, the involvement of melanopsin cells could not be considered. However, when combined with our experimental results, it cannot be ruled out that melanopsin cells were involved.

In this experiment, pupil diameter was not controlled or measured. We know that pupil diameter depends on the stimulus intensity to melanopsin cells and cones [28]. In addition, brightness perception is affected by pupil diameter. However, it can be assumed that pupil constriction was almost complete [48, 49] for the luminance levels of our experiment. Pupil diameter estimates were 2.6 mm for all stimuli in the 700 cd/m^2 condition using the relationship we previously formulated [30], and no differences were observed between the visual stimuli. This study has some limitations. The stimulus intensity to cones was calculated with the L-, M-, and S-cone sensitivities of standard observers. Specifically, individual differences in wavelength dependence of the cone sensitivity were not considered. In addition, when the stimulus intensity to melanopsin cells was modulated, the stimulus intensity to rods was also changed. Luminance of the experimental conditions was 700 or 375 cd/m^2, which is generally considered to saturate the rods, so they did not likely influence the results in this experiment.

In summary, in previous blackness studies, the effect of the luminance was mainly measured, as the large effect of the luminance and the small effect of melanopsin cells stimulus were combined because the melanopsin stimulus intensity increases at the same rate with increasing luminance. This is evident from the results in this experiment that when comparing blackness of stimuli #1 & #5 (same luminance (Table 1), 1.9 times melanopsin cell stimulation ratio) with stimuli #1 & #9 (same melanopsin stimulation (Table 1), 1.9 times luminance ratio), the difference of blackness for stimuli #1 & #9 was much greater (Figures 3A,B left). In this study, we were able to separate the effect of luminance and the effect of melanopsin stimulation in blackness induction. There is no contradiction with the results of previous blackness studies but does demonstrate a role for melanopsin stimulation not previously considered.

5 | Conclusion

We demonstrated that blackness induction of the center in a center-surround stimulus depends not only on the luminance of the surround but also on the stimulation of melanopsin cells by the surround. This effect depends on the exposure duration and light level. Contributions of melanopsin cells may provide a

new perspective when interpreting previous and future studies of lightness and darkness spatial contrast.

Author Contributions

Conceptualization: M.Y., K.O., and J.S.W. Methodology: M.Y., K.O., and J.S.W. Measurement and analysis: M.Y. and K.O. Writing – original draft preparation: M.Y. Writing – review and editing: M.Y., K.O., and J.S.W. All authors have read and agreed to the published version of the manuscript.

Acknowledgments

This work was supported by JSPS KAKENHI Grant Number 22H00531. Author J.S.W. was a visiting professor in Experimental Psychology and Engineering Science of the University of Oxford, funded by the Leverhulme Trust.

Funding

This work was supported by Japan Society for the Promotion of Science (22H00531) and the Leverhulme Trust.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

References

1. V. J. Volbrecht and R. Kliegl, "The Perception of Blackness: An Historical and Contemporary Review," in *Color Vision*, ed. W. G. K. Backhaus, R. Kliegl, and J. S. Werner (Walter de Gruyter, 1998), 187–206.

2. J. S. Werner, C. M. Cicerone, R. Kliegl, and D. DellaRosa, "Spectral Efficiency of Blackness Induction," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 1, no. 9 (1984): 981–986.

3. C. M. Cicerone, V. J. Volbrecht, S. K. Donnelly, and J. S. Werner, "Perception of Blackness," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 3, no. 4 (1986): 432–436.

4. K. Shinomori, B. E. Schefrin, and J. S. Werner, "Spectral Mechanisms of Spatially Induced Blackness: Data and Quantitative Model," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 14, no. 2 (1997): 372–387.

5. K. Fuld, T. A. Otto, and C. W. Slade, "Spectral Responsivity of the White-Black Channel," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 3, no. 8 (1986): 1182–1188.

6. S. Westland, T. L. V. Cheung, and O. R. Lozman, "A Metric for Predicting Perceptual Blackness," in *IS&T/SID's Fourteenth Color Imaging Conference* (Society for Imaging Science and Technology, 2006), 14–17.

7. Y. J. Cho, L. C. Ou, and R. Luo, "A Cross-Cultural Comparison of Saturation, Vividness, Blackness and Whiteness Scales," *Color Research and Application* 42 (2017): 203–215.

8. Y. J. Cho, L. C. Ou, G. Cui, and R. Luo, "New Colour Appearance Scales for Describing Saturation, Vividness, Blackness, and Whiteness," *Color Research and Application* 42 (2017): 552–563.

9. F. A. A. Kingdom, "Lightness, Brightness and Transparency: A Quarter Century of New Ideas, Captivating Demonstrations and Unrelenting Controversy," *Vision Research* 51, no. 7 (2011): 652–673.

10. E. H. Land and J. J. McCann, "Lightness and Retinex Theory," *Journal of the Optical Society of America* 61, no. 1 (1971): 1–11.

11. A. Gilchrist, C. Kossyfidis, F. Bonato, et al., "An Anchoring Theory of Lightness Perception," *Psychological Review* 106, no. 4 (1999): 795–834.

12. M. C. Morrone and D. C. Burr, "Feature Detection in Human Vision: A Phase Dependent Energy Model," *Proceedings of the Royal Society of London, Series B: Biological Sciences* 235, no. 1280 (1988): 221–245.

13. B. Blakeslee and M. E. McCourt, "A Multiscale Spatial Filtering Account of the White Effect, Simultaneous Brightness Contrast and Grating Induction," *Vision Research* 39, no. 26 (1999): 4361–4377.

14. B. L. Anderson, "A Theory of Illusory Lightness and Transparency in Monocular and Binocular Images: The Role of Contour Junctions," *Perception* 26, no. 4 (1997): 419–453.

15. S. M. Williams, A. N. McCoy, and D. Purves, "An Empirical Explanation of Brightness," *Proceedings of the National Academy of Science USA* 95, no. 22 (1998): 13301–13306.

16. P. Sinha, S. Crucilla, T. Gandhi, et al., "Mechanisms Underlying Simultaneous Brightness Contrast: Early and Innate," *Vision Research* 173 (2020): 41–49.

17. H. Boyaci, F. Fang, S. O. Murray, and D. Kersten, "Perceptual Grouping-Dependent Lightness Processing in Human Early Visual Cortex," *Journal of Vision* 10, no. 9 (2010): 4.

18. E. H. Adelson, "Perceptual Organization and the Judgment of Brightness," *Science* 262, no. 5142 (1993): 2042–2044.

19. B. Blakeslee and M. E. McCourt, "Isolation of Brightness Induction Effects on Target Patches From Adjacent Surrounds and Remote Backgrounds," *Frontiers in Human Neuroscience* 16 (2023): 1082059.

20. V. C. Smith, P. Q. Jin, and J. Pokorny, "The Role of Spatial Frequency in Color Induction," *Vision Research* 41, no. 8 (2001): 1007–1021.

21. B. Blakeslee and M. E. McCourt, "Similar Mechanisms Underlie Simultaneous Brightness Contrast and Grating Induction," *Vision Research* 37, no. 20 (1997): 2849–2869.

22. Q. Zaidi, B. Yoshimi, N. Flanigan, and A. Canova, "Lateral Interactions Within Color Mechanisms in Simultaneous Induced Contrast," *Vision Research* 32, no. 9 (1992): 1695–1707.

23. M. E. Rudd and I. K. Zemach, "Contrast Polarity and Edge Integration in Achromatic Color Perception," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 24, no. 8 (2007): 2134–2156.

24. S. Hattar, H. W. Liao, M. Takao, D. M. Berson, and K. W. Yau, "Melanopsin-Containing Retinal Ganglion Cells: Architecture, Projections, and Intrinsic Photosensitivity," *Science* 295, no. 5557 (2002): 1065–1070.

25. M. T. H. Do, "Melanopsin and the Intrinsically Photosensitive Retinal Ganglion Cells: Biophysics to Behavior," *Neuron* 104, no. 2 (2019): 205–226.

26. D. M. Dacey, H. W. Liao, B. B. Peterson, et al., "Melanopsin-Expressing Ganglion Cells in Primate Retina Signal Colour and Irradiance and Project to the LGN," *Nature* 433, no. 7027 (2005): 749–754.

27. S. Panda, T. K. Sato, A. M. Castrucci, et al., "Melanopsin (Opn4) Requirement for Normal Light-Induced Circadian Phase Shifting," *Science* 298, no. 5601 (2002): 2213–2216.

28. R. J. Lucas, R. H. Douglas, and R. G. Foster, "Characterization of an Ocular Photopigment Capable of Driving Pupillary Constriction in Mice," *Nature Neuroscience* 4, no. 6 (2001): 621–626.

29. T. M. Brown, C. Gias, M. Hatori, et al., "Melanopsin Contributions to Irradiance Coding in the Thalamo-Cortical Visual System," *PLoS Biology* 8, no. 12 (2010): e1000558.

30. M. Yamakawa, S. I. Tsujimura, and K. Okajima, "A Quantitative Analysis of the Contribution of Melanopsin to Brightness Perception," *Scientific Reports* 9, no. 1 (2019): 7568.

31. D. Cao, A. Chang, and S. Gai, "Evidence for an Impact of Melanopsin Activation on Unique White Perception," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 35, no. 4 (2018): B287–B291.

32. A. E. Allen, F. P. Martial, and R. J. Lucas, "Form Vision From Melanopsin in Humans," *Nature Communications* 10, no. 1 (2019): 2274.

33. S. E. Chien, S. L. Yeh, W. Yamashita, and S. I. Tsujimura, "Enhanced Human Contrast Sensitivity With Increased Stimulation of Melanopsin in Intrinsically Photosensitive Retinal Ganglion Cells," *Vision Research* 209 (2023): 108271.

34. CIE, *System for Metrology of Optical Radiation for ipRGC-Influenced Responses to Light. CIE S 026/E:2018* (International Commission on Illumination, 2018).

35. D. L. Bimler, G. V. Paramei, and C. A. Izmailov, "Hue and Saturation Shifts From Spatially Induced Blackness," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 26, no. 1 (2009): 163–172.

36. C. L. Prigge, P. T. Yeh, N. F. Liou, et al., "M1 ipRGCs Influence Visual Function Through Retrograde Signaling in the Retina," *Journal of Neuroscience* 36, no. 27 (2016): 7184–7197.

37. N. Milosavljevic, R. Storchi, C. G. Eleftheriou, A. Colins, R. S. Petersen, and R. J. Lucas, "Photoreceptive Retinal Ganglion Cells Control the Information Rate of the Optic Nerve," *Proceedings of the National Academy of Science USA* 115, no. 50 (2018): E11817–E11826.

38. T. DeLawyer and K. Shinomori, "Melanopsin-Driven Surround Induction on the Red/Green Balance of Yellow," *Journal of the Optical Society of America. A, Optics, Image Science, and Vision* 40, no. 3 (2023): A40–A47.

39. X. Zhao, B. K. Stafford, A. L. Godin, W. M. King, and K. Y. Wong, "Photoresponse Diversity Among the Five Types of Intrinsically Photosensitive Retinal Ganglion Cells," *Journal of Physiology* 592, no. 7 (2014): 1619–1636.

40. C. A. Procyk, C. G. Eleftheriou, R. Storchi, et al., "Spatial Receptive Fields in the Retina and Dorsal Lateral Geniculate Nucleus of Mice Lacking Rods and Cones," *Journal of Neurophysiology* 114, no. 2 (2015): 1321–1330.

41. L. J. Croner and E. Kaplan, "Receptive Fields of P and M Ganglion Cells Across the Primate Retina," *Vision Research* 35, no. 1 (1995): 7–24.

42. E. W. Yund and J. C. Armington, "Color and Brightness Contrast Effects as a Function of Spatial Variables," *Vision Research* 15 (1975): 917–929.

43. E. W. Yund, J. D. M. Snodderly, N. K. Hepler, and R. L. De Valois, "Brightness Contrast Effects in Monkey Lateral Geniculate Nucleus," *Sensory Processes* 1, no. 3 (1977): 260–271.

44. B. Pinna, L. Spillmann, and J. S. Werner, "Anomalous Induction of Brightness and Surface Qualities: A New Illusion due to Radial Lines and Chromatic Rings," *Perception* 32, no. 11 (2003): 1289–1305.

45. P. A. Barrionuevo, A. C. Schütz, and K. R. Gegenfurtner, "Increased Brightness Assimilation in Rod Vision," *iScience* 28, no. 2 (2025): 111609.

46. A. F. Rossi and M. A. Paradiso, "Temporal Limits of Brightness Induction and Mechanisms of Brightness Perception," *Vision Research* 36, no. 10 (1996): 1391–1398.

47. R. L. De Valois, M. A. Webster, K. K. De Valois, and B. Lingelbach, "Temporal Properties of Brightness and Color Induction," *Vision Research* 26, no. 6 (1986): 887–897.

48. B. H. Crawford, "The Dependence of Pupil Size Upon External Light Stimulus Under Static and Variable Conditions," *Proceedings of the Royal Society of London. Series B* 121 (1936): 376–395.

49. M. Guillon, K. Dumbleton, P. Theodoratos, M. Gobbe, C. B. Wooley, and K. Moody, "The Effects of Age, Refractive Status, and Luminance on Pupil Size," *Optometry and Vision Science* 93, no. 9 (2016): 1093–1100.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Spectral power distributions of the projectors and transmission spectra of the optical filters. **Table S1:** Calculated % deviation of L-, M-, S- cone stimulation from the mean for all 10 stimuli.