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Invited

The Role of Intrinsically Photosensitive Retinal Ganglion Cells in Brightness Perception

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ABSTRACT

We applied psychophysical techniques to investigate the role of intrinsically photosensitive retinal ganglion cells (ipRGCs) in brightness perception in comparison with cones. The results suggest that ipRGCs play a role in acquiring the absolute value of the visual environmental information and in offsetting the cone response. Furthermore, it was found that the contribution of ipRGCs exceeded 50% as the visual stimulus intensity increased.

1 INTRODUCTION

The origin of neural activity in the processing of visual information from the retina to the cerebrum is the reception of light by L-, M-, and S-cones and rods, photoreceptors in the retina (the Image-Forming Pathway). Brightness perception or color perception results from the coding of light absorption signals at the visual cortex. In recent years, novel photoreceptors besides cones and rods have been discovered in the retina [1-4]. These photoreceptors, intrinsically photosensitive retinal ganglion cells (ipRGCs) or melanopsin-expressing retinal ganglion cells (mRGCs), function primarily to transmit external light environment signals to the central clock controlling biological rhythms [5] and the pupillary light reflex [6]. Since this pathway has nothing to do with image information, it is called the non-Image-Forming Pathway. On the other hand, subsequent physiological studies have found ipRGCs to be involved in the Image-Forming Pathway. That is, it has become necessary to add the ipRGCs to the visual information processing mechanism that starts from the light reception in the cones. Here, we focused on brightness perception, which current photometry understands to be a function of the stimulus intensity at the cones, and investigated the role of ipRGCs by quantitatively analyzing their involvement in brightness perception [7].

2 EXPERIMENT

Figure 1 shows the response sensitivity curves of the five types of photoreceptors. The ipRGC response sensitivity curve is different from that of cones and rods. The objective of this study was to clarify the functions of ipRGCs, whose responses must be separated from the responses of the cones and rods. As is clear from Fig. 1, the response curves of the photoreceptors overlap at all wavelengths, and the response from a plurality of photoreceptors is detected regardless of the wavelength of light irradiation. Therefore, we prepared visual stimuli using the silent substitution method to extract the signals of the ipRGCs. The principle of this method is as follows: While keeping the stimulus intensity at the cones or rods constant, we prepared several kinds of visual stimuli in which the ipRGC stimulus intensity was modulated by adjusting the spectral power distribution of the visual stimuli. The ipRGC response can be detected by analyzing the differences in response under several types of visual stimuli. We used six primary color projectors to prepare luminance-modulated (20–110 cd/m^2) visual stimuli for presentation to the participants. The appearance of the stimuli was white, with (x, y) = (0.328, 0.367). The stimulation size was circular 5°, and the stimulation position was at 7° on the peripheral nasal side of the right eye. The evaluation was conducted by the subjective measurement of brightness perception and pupil diameter measurement under visual stimuli. Brightness perception was evaluated by magnitude estimation relative to the reference stimulus. The pupil diameter was measured using an infrared camera, as it has been shown that the pupil diameter is a function of the ipRGC stimulus intensity, and the stimulus intensity at the retina depends on the pupil diameter.

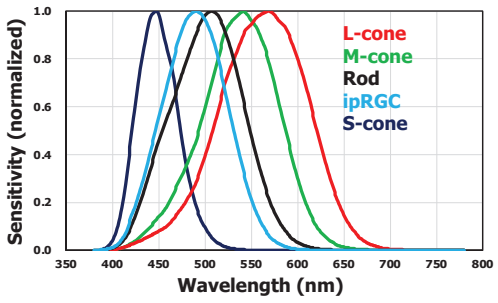

Fig. 1 Response sensitivity curves of five types of photoreceptors

3 RESULTS

Figure 2 shows the relationship between the perceived brightness and the retinal illuminance, which is the stimulus intensity at the cones. For all types of stimuli, the perceived brightness had a non-linear relationship with retinal illuminance, which is within the scope of current photometric understanding when viewed individually. However, when the ipRGC stimulus intensity differed under the same retinal illuminance, the perceived brightness was different. We took this difference as the difference in ipRGC visual stimulation and expressed the brightness perception as a function of the cone stimulus intensity and the ipRGC stimulus intensity:

$$R = 4.84 \cdot 10^{-3} \cdot G^{1.1} + 2.31 \cdot E^{0.48}$$
$$= 4.84 \cdot 10^{-3} \cdot (kE)^{1.1} + 2.31 \cdot E^{0.48}$$

where G is the ipRGC stimulus intensity, E is the retinal illuminance (the cone stimulus intensity), and k is the ipRGC stimulus intensity per 1 Td.

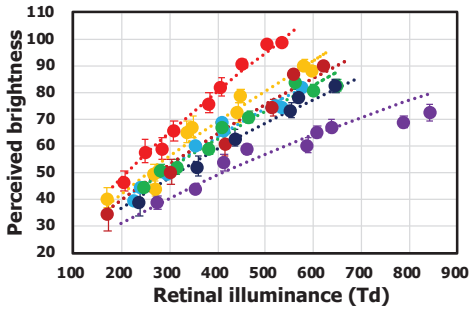

Fig. 2 Perceived brightness as a function of retinal illuminance

Difference in stimulus intensity to ipRGCs (per 1 Td) was identified by colors. The points indicate the measured values, the broken lines indicate the fitting by the power function, and the error bars indicate the SEM.

4 DISCUSSION

We note first that the exponent of the cone term is 0.48, which reflects Weber-Fechner's law, while that of the ipRGCs term is approximately 1.0, indicating a nearly linear relationship with stimulus intensity. This suggests that the pathway from the cones to the visual cortex transmits contrast information of the visual environment, whereas the pathway from the ipRGCs transmits absolute visual information. Second, as the expression is the sum of cone and ipRGC terms, the ipRGC response is offset by the cone response. This relationship is shown in Fig. 3. The contribution of the ipRGC term depends on the spectral power distribution of the visual stimulus. Third, this expression quantifies the contribution of the ipRGCs to brightness perception. Under experimental conditions, there was a region where the ratio exceeded 50%.

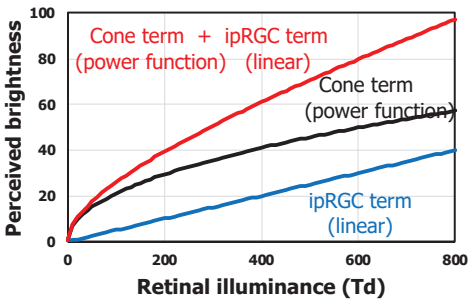

Fig. 3 Contribution of ipRGC and cone in brightness perception

5 CONCLUSIONS

Studies of brightness perception must consider the ipRGC stimulus intensity, not only the cone stimulus intensity currently considered in photometry. In the future, the role of the ipRGCs will become even more important in the design of light-emitting devices such as lighting and displays [8].

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