The Activation of Cones in Scotopic and Rods in Photopic Vision

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SUGITA, Y. and TASAKI, K. *The Activation of Cones in Scotopic and Rods in Photopic Vision.* Tohoku J. exp. Med., 1988, **156** (4), 311-317 — Over the whole course of dark adaptation, light- and color detection thresholds were measured. At 6° in the nasal visual field, the effect of wavelength was examined. After the rod-cone break (Kohlrausch kink), the color threshold began to rise while the light threshold was progressively decreasing. The rise of the color threshold was more remarkable as the test wavelength was more close to the peak wavelength for rod sensitivity. With green test light, the sensitivity difference of retinal position was investigated. The rise of the color threshold was more prominent at the retinal position where rods were more densely packed. Finally, the Stiles-Crawford effect was examined with a green test light at 12° in the nasal visual field. This effect appeared for the color threshold over the whole course of dark adaptation but not for the light threshold even before the rod-cone break. It was concluded that the rod activation interferes with cone sensitivity and the interference effect becomes stronger as rods become progressively more dark adapted, and that the rod system is also acting even before the rod-cone break. ——— rods; cones; rod-cone interaction; dark adaptation; color vision

Dark adaptation can be expressed psychophysically in terms of the decrement in the intensity of light required to evoke a just noticeable visual sensation. As dark adaptation commences, cone sensitivity increases rapidly for the first several min and then slowly until the rod-cone break (Kohlrausch kink), after which the cone sensitivity had been believed to remain at the same level while rod sensitivity increases (see, for example, Grüsser and Grüsser-Cornehls 1978). However, decrease in cone sensitivity after the rod-cone break was found by Sugita and Tasaki (1988), who suggested the presence of an inhibitory influence from dark adapted rods upon the cone pathway. In their study, only a limited retinal area was examined with a green light (555 nm) alone. In the present experiments, much wider areas in the retina were investigated with several different colored lights.

As to the rod sensitivity during the early stage of dark adaptation, it is

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generally supposed that its sensitivity begins to increase immediately with commencement of adaptation but is lower than cone sensitivity before the rod-cone break is reached. Thus, in this early phase, the color of test flashes should be perceived even at the threshold intensity of light. This was indeed confirmed in this study so far as the test flashes were presented around the foveal region. However, the opposite results were also obtained, showing higher thresholds for color even before the rod-cone break. Such dissociation of thresholds for color and light detection before the break has already been noted in the early study of Sugita and Tasaki (1988).

METHODS

Subjects. All figures represent data from Y.S., a relatively experienced psychophysical observer with normal vision. At least three other observers were tested and similar results were obtained from all of them. The observer's head was stabilized with a bite bar, and all tests were made on the right eye.

Apparatus. All stimuli were produced by a simple optical system. The light sources were light emitting diodes (LEDs; Stanley Electric, Tokyo) run from regulated power supplies. The LED is a proven source of light, the intensity and duration of which can be accurately controlled (Tasaki et al. 1988). Four different LEDs were used as test targets: blue (provided sample; wavelength $\lambda = 490$ nm, halfband width $\Delta\lambda = 80$ nm), green (type BG5534S; wavelength $\lambda = 555$ nm, $\Delta\lambda = 30$ nm), yellow (type EAY5534S; $\lambda = 580$ nm, $\Delta\lambda = 30$ nm) and red (type BR5534S; $\lambda = 660$ nm, $\Delta\lambda = 30$ nm). The fixation spot was another red LED. LEDs for the test target and the fixation were placed 57.6 cm from the observer's cornea. The maximum intensity (indicated as "0" log-units in the text and figures) at the surface of the LED was $33 \mu\text{W}$. A 250 W tungsten lamp was placed 30 cm from the cornea to ensure uniform light adaptation before dark adaptation.

Procedure. Thresholds both for light flash detection and for color detection, during the progressive process of dark adaptation, were measured after 5 min of light adaptation. The inter-stimulus interval was 2 sec for light flash detection. But, it was 10 sec for color detection so that stimulus itself did not alter the threshold value of light flash detection. The duration of the light flash was 100 msec. All tests were made in the nasal visual field.

RESULTS

Effect of wavelength

During the course of dark adaptation, thresholds both for light- and color detections were measured at 6° from fixation in the nasal visual field with four different colored lights. As can be seen in Fig. 1, the decrease in the threshold for light detection is parallel to that for color detection within the first 10 min for all wavelengths. After that, the light threshold becomes lower than the color detection threshold. The rod-cone break is found about 15 min of dark adaptation. The color detection threshold then begins to rise again while the light threshold continues to decrease. The dissociation of the light- and the color detection thresholds is more marked for shorter wavelength. However, it is not found for 660 nm.

Fig. 1. The color detection threshold (open circles) and the light threshold (closed circles) measured during the course of dark adaptation. The wavelength of the test light was 494 nm (blue), 555 nm (green), 580 nm (yellow) or 660 nm (red). Measurements were made at 6° in the nasal visual field. Closed circles in the first 10 min, if they coincide with open circles, were omitted.

Regional difference in the retina

Using the green test light (555 nm), the light threshold and the color detection threshold was measured in five different retinal positions, fovea, 3°, 6°, 9° and 12°

Fig. 2.

in the nasal visual field. Results are represented in Fig. 2. In the fovea, neither the rod-cone break nor the dissociation of the light and the color detection thresholds can be found. In other retinal positions, however, the break can be clearly observed around 15 min of dark adaptation. The color threshold begins to rise again after the break while the light threshold progressively falls. The rise of the color threshold and the fall of the light threshold are more marked in the more peripheral retina. Of special interest is that the dissociation of the light and the color thresholds begins prior to the appearance of the break.

Stiles-Crawford effect

To present a light to the retinal surface either perpendicularly or obliquely, an artificial aperture (1 mm in diameter) was placed 5 mm from the cornea. In the retinal periphery (12° in the nasal visual field), both the light and the color thresholds to the green test flash were measured not only when the artificial aperture was placed so that the test light entered the eye through the center of the pupil, but also when the artificial aperture was displaced 0.5 mm upper to the

Fig. 3. The color detection threshold (squares) and the light threshold (circles) to the green test light (555 nm) measured during the course of dark adaptation. Both close squares and circles represent threshold measured when the aperture was placed so that quanta entered the eye near the center of the pupil. Both open squares and circles represent thresholds measured when the aperture was displaced so that quanta entered the eye near the edge of the pupil. Measurements were made at 12° in the nasal visual field.

Fig. 2. The color detection threshold (open circles) and the light threshold (closed circles) to the green test light (555 nm) measured during the course of dark adaptation. Measurements were made at five different retinal positions in the nasal visual field. Data at 6° are identical with those in Fig. 1. Closed circles in the first 10 min, if they are coincide with open circles, were omitted.

original position. As can be seen in Fig. 3, the light threshold over the course of dark adaptation was not affected by the position of the artificial aperture. However, the color threshold rises more than 0.1 log units when the aperture is displaced upper to the original position. The Stiles-Crawford effect is, therefore, observed in the color threshold but not in the light threshold even when the threshold is measured before the rod-cone break.

DISCUSSION

Sugita and Tasaki (1988) showed that the cone-mediated sensitivity to a green light flash decreases as rods become progressively more dark adapted. This finding was further confirmed by the first two experiments in the present study. However, the color threshold did not increase, when the red test flash (660 nm) was employed or tests were made in the fovea. The color threshold increased much more as the shorter wavelength of the test flash was employed. The color threshold was also increased as the test area contained rods more densely. Therefore, the decrement of cone sensitivity might be observed only when rods were activated.

Rodieck and Rushton (1976), studying the cat retina, showed that most ganglion cells receive signals from rods as well as cones, and that the cone signals can be cancelled by those of rods at the ganglion cell level. After the rod-cone break in the course of dark adaptation, rod sensitivity progressively increases. The effect of rod activation upon the cone system, the cancellation of cone signals by rods, would increase as well. This effect should be represented as the increase of the color detection thresholds. The present study indeed demonstrated that the color detection threshold increases gradually as rod sensitivity progressively increases.

Stiles and Crawford (1933) found that the visual system is most sensitive to the light entering the eye near the center of the pupil and progressively less sensitive as the light enters further from the center of the pupil. The Stiles-Crawford effect appears only when the stimulus light is acting upon the cone system (see, for example, Cornsweet 1970). In the present study, the color threshold was found to elevate when the artificial pupil was displaced so that the light entered the eye near the edge of the pupil, suggesting that the color threshold was determined by the cone system. In the dark adapted state, the light threshold was not changed by displacing the artificial aperture, suggesting that the light threshold was mediated by the rod system. Of special interest is that, even before the rod-cone break in the course of dark adaptation, the light threshold was not affected by displacing the artificial aperture. It has been believed that, before the break, the light threshold is mediated only by the cone system (see, for example, Grüsser and Grüsser-Cornehls 1978). The present study demonstrated that the rod sensitivity is much higher than previously estimated and that the rod system is also acting even before the break. Accordingly the so-called rod-cone

break would represent the abrupt increase of the rod sensitivity. The break can not be found in the retina containing only rods (see, for example, Grüsser and Grüsser-Cornehls 1978). Therefore, some influence upon rod pathway might be exerted by cones. Sugita et al. (1988) indeed found that the cone activation results in inhibitory influence upon the recovery process of the rod sensitivity.

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