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PRISMATIC ADAPTATION UNDER SCOTOPIC AND PHOTOPIC CONDITIONS [1]

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Prismatic rearrangement experiments were performed under scotopic and photopic conditions by suitably dark- or light-adapted *S*s. Adaptation to prismatic displacement was highly significant when exposure and test procedures were carried out under scotopic as well as photopic conditions. Transfer experiments suggest that scotopically induced adaptation can be demonstrated under both scotopic and photopic conditions of marking, whereas photopically induced adaptation is evidenced primarily under photopic test conditions and shows significantly reduced transfer to scotopic test conditions.

The experimental technique of rearrangement has been used extensively in recent years to study visually guided orientation in human *S*s. The method is based upon Helmholtz's (1867) account of the changes in eye–hand coordination that occur when one wears wedge prism spectacles causing a lateral displacement of the optical array. Initially, one misreaches in the direction of displacement for objects in the visual field. With continued reaching movements, one compensates for the displacement, and the prism-induced errors decrease and disappear. When the prisms are then removed, errors of similar magnitude but of opposite sign appear as aftereffects. Held and his collaborators (Held & Gottlieb, 1958; Held & Hein, 1958) have developed a method for the quantitative study of factors influencing adaptation which clearly separates exposure from test periods. In a test procedure, *S* marks, without sight of his hand, the locations of visual targets. During exposure, *S* observes through prismatic spectacles the movements of his own hand. The systematic discrepancy between the locations of marks made immediately before and after exposure serves as a measure of adaptation to the displaced images seen during exposure. On the basis of numerous studies emphasizing the importance of movement-produced visual feedback (reafference) for compensation, Held and Freedman (1963) have suggested that during exposure, the systematic transformation between movements of the arm and consequent visual feedback is registered and that an adaptive recorrelation occurs between the two.

In previous rearrangement studies, exposure as well as testing have been carried out at photopic light levels. As is well known, in the photopic state, human vision is exquisitely specialized for the resolution of fine detail and pattern. The central fovea may be used to fixate and track, and visual acuity is at or near its maximum value. Over a wide range of dim illumination, however, the visual system operates in the scotopic state. Rods replace cones as the predominant photoreceptors, the central fovea is blind, visual acuity is markedly reduced, and fine detail and color are no longer a part of visual experience. It is of interest to ask whether *S*s performing at scotopic light levels can adapt to prismatic displacements, or whether the specializations of photopic vision, necessary for efficient pattern vision, are also required for compensation of the errors of visually guided movement caused by prism exposure. The first experiment reported

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subsequently was designed to answer this question by comparing the magnitude of adaptation shown by dark-adapted *S*s performing at scotopic light levels with that of light-adapted *S*s performing at photopic light levels. The results indicated similar magnitudes of adaptation under the two conditions and posed the further question of whether adaptation transfers between the two states. A second experiment tested this possibility by exposing *S*s at one light level and testing them at the other.

Experiment I

Method

Apparatus.—During each experimental session, *S* sat with his head stabilized by a biteboard and his face pressed against a goggle frame fitted with variable wedge prisms that could be set at 0 diopters for test markings, 20 diopters base left (BL) or base right (BR) for exposure conditions. Filter mounts in front of the prisms held the color filters used: blue-green Wratten gelatin filters (No. 75) transmitting 18% at the predominant wavelength 490 nm. during scotopic sequences and red aviation filters transmitting wavelengths beyond 575 nm. during photopic sequences. The field of view was binocular and subtended approximately 50°. During exposure, *S* restricted his hand movements to tracing the borders of a white 10 × 15 cm. rectangle centered on an otherwise homogeneous black surface. The center of the rectangle was 38 cm. in front of his eyes and tilted down 36° from the plane defined by his lines of sight when fixating the center of the rectangle. Before and after exposure, *S* viewed a homogenous matte-white target surface tilted down 20°. Four targets consisting of black Xs, 2.5 cm. wide, were positioned about the center of this surface to form the corners of a 10-cm. square, 30 cm. in front of his eyes. The lines composing each Target X subtended approximately 35′ of visual angle. Ruled paper to receive marks made during testing was attached to the underside of the target surface. Illumination before, during, and after exposure was provided by a 60-w. frosted incandescent lamp mounted 80 cm. above the display and controlled by a Variac. Illumination was measured by means of a calibrated cadmium sulfide light meter (Science and Mechanics) and a Macbeth illuminometer.

Subjects.—Three female and 12 male *S*s, 17–26 yr. of age, were paid volunteers. All reported normal vision with or without contact lenses, as tested by recent clinical examination. Each *S* was tested with American Optical H-R-R pseudoisochromatic plates and found to have normal color vision. All were right-handed. Seven had prior experience with rearrangement experiments, but all were naïve with regard to the purpose of this experiment.

Procedure.—All *S*s participated on 2 consecutive days in sessions approximately 1½ hr. in duration. On each day, one complete testing and exposure sequence was performed under scotopic illumination, and another complete sequence under photopic illumination. The order of these sequences, each preceded by an appropriate period of dark or light adaptation, was balanced among *S*s. During scotopic sequences, the blue-green filters were used and the luminance level was maintained approximately midway between the rod and cone thresholds, which were measured separately for each *S* as described subsequently. During photopic sequences, a standard luminance of approximately 5 mL. incident upon the red filters was maintained for all *S*s. The experimental procedure for a scotopic-photopic session was as follows:

1. Dark adaptation and threshold determinations. After a 5-min. period of preadaptation to approximately 10-mL. ambient illumination, *S* was dark-adapted for 45 min. During this time, threshold measurements were taken at 2–5-min. intervals, using the method of ascending and descending limits (Guilford, 1954). Between observations, *S* sat in the darkened room with his eyes closed and occluded. For each threshold measurement, *S* viewed the target surface through the blue-green filters for successive 2–5 sec. intervals. The light intensity was raised until *S* indicated the presence of light, and then oscillated above and below this level for four successive judgments. Final rod thresholds were obtained at the end of the 45-min. period. To estimate *S*'s cone threshold, carefully selected colored papers were placed in the field of view and the light intensity raised. The method of limits was used again to determine the lowest light required for first color perception, which was taken as an approximate cone threshold. The luminance level for the scotopic session was set near the midpoint between these rod and cone thresholds, or approximately 2 log units above *S*'s absolute rod threshold. The *S* sat in darkness for a 5-min. period before the experiment was begun.
2. Pre-exposure marking. With his unseen right hand, *S* repeatedly marked on the underside of the target surface the position corresponding to each of the four target Xs. A total of 40 marks was made, *S* withdrawing his hand between marks.
3. Exposure BL and post-BL marking. Through 20-diopter BL prisms, *S* viewed his right hand as he traced with his index finger the borders of the exposure rectangle. These movements, paced by the 1-sec. beat of a metronome, continued for 3 min. The marking procedure was then repeated for a total of 40 marks, which served both as post-exposure marks for the first exposure period and preexposure marks for the second exposure period.
4. Exposure BR and post-BR marking. The exposure procedure was repeated using 20-diopter

BR prisms and was followed by the standard marking procedure.

After a complete scotopic sequence, *S* was light-adapted for 10 min. to approximately 10-mL. ambient illumination, then returned to the apparatus to repeat the entire sequence under photopic conditions. During the first day's session, the prisms were set at 0 diopters (NP) during exposure, and only one exposure period was given. The procedure was otherwise identical to that outlined earlier, and constituted a practice period for *S*s.

Results

The differences between mean horizontal locations of preexposure and postexposure markings were computed for each target location in all experimental sequences. These shifts, averaged across the four target locations, represented aftereffects and served as a measure of the magnitude of adaptation. Adaptive shifts were positive for BL, negative for BR exposure.

Highly significant shifts were found not only during the photopic, but also during scotopic, sequences. A *t* test performed on each mean shift demonstrated that each was significantly different from zero. These mean shifts, in centimeters, together with their significance levels, are shown in Table 1. In addition, a four-factor analysis of variance (Subjects × Light Levels × Targets × Shifts) showed that the light-condition effect failed to reach significance at the .05 level, F (1, 14) = 1.08, indicating that the level of illumination did not differentially affect the magnitude of the mean shift resulting from exposure. The Light Conditions × Shifts interaction was not significant. It is interesting to note, however, that in the photopic sequences the mean shift after the second exposure period was considerably larger than that following the first exposure, as has frequently been observed in pilot experiments. This tendency is not present in the scotopic sequences; first and second shifts are nearly identical.

TABLE 1

Prismatic Adaptation (in cm.): Exp. I

Light condition	1st shift (BL)	2nd shift (BR)	No prism (NP)	*M* -- 1st and 2nd shifts
Scotopic	2.11*	−2.41*	.051	2.26
Photopic	1.50*	−2.46*	.025	1.98

Note.- Abbreviated: BL = base left; BR = base right.
* $p < .001$, two-tailed t test for difference from zero.

The standard deviations in the horizontal direction of preexposure and postexposure markings were remarkably similar for scotopic and photopic sequences. The mean standard deviations for all marks during the second session were .84 cm. for the scotopic and .81 cm. for the photopic sequences. The effects of practice in reducing marking dispersion (Sekuler & Bauer, 1966) were small; the standard deviations for the first day's marks were .97 cm. for scotopic and .89 cm. for photopic sequences. A slightly greater practice effect was shown for the scotopic sequences.

Experiment II

In the preceding experiment, both exposure and testing were carried out under similar light conditions. While the results indicated that comparable magnitudes of adaptation can be obtained under photopic and scotopic conditions, they could not indicate whether adaptation built up under one light condition would be demonstrable under the other. In order to evaluate this question, transfer experiments were performed in which exposure periods were conducted at one light level, marking periods at the other. During these tests of transfer, the two eyes were kept at different levels of light adaptation, and one eye was used during exposure, the other during marking periods. This design takes advantage of the potential for maintaining independent levels of light adaptation for the two eyes (Mandelbaum, 1941) and the occurrence of a high level of interocular transfer of adaptation to prismatic displacement (Hajos & Ritter, 1965; Pick, Hay, & Willoughby, 1966). In addition to transfer sequences, controls were carried out in which either photopic or scotopic illumination was used throughout the testing and exposure sequences. Thus, four experimental conditions were available for study. With prism exposure carried out at photopic light levels, preexposure and postexposure marking periods could be photopic or scotopic. Similarly, with prism exposure performed under scotopic conditions, marking periods could be scotopic or photopic. Table 2 summarizes these conditions, each of which represents one daily session and introduces abbreviations used for reference. If the photopic (P) and scotopic (S) states are dissociable with regard to this orientation task, one might expect a decrement in adaptation under one or both of the conditions of transfer, comparing P-S-P with S-S-S, and S-P-S with P-P-P.

TABLE 2

EXPERIMENTAL CONDITIONS: EXP. II

Session or condition abbreviation	Preexposure marking—right eye	Exposure left eye	Postexposure marking—right eye
P-P-P	Photopic	Photopic	Photopic
S-P-S	Scotopic	Photopic	Scotopic
S-S-S	Scotopic	Scotopic	Scotopic
P-S-P	Photopic	Scotopic	Photopic

Note.—Abbreviated: P = photopic; S = scotopic.

Method

Subjects.—One female and 16 male *S*s, ranging in age from 19 to 24 yr., were paid volunteers. Criteria for accepting *S*s were the same as those for Exp. I.

Each *S* performed all experimental conditions by participating in four approximately 1½-hr. sessions separated by no less than 24 hr. These were preceded by a practice session, during which *S* was familiarized with the apparatus and procedures. The *S*s were assigned in order of their appearance to one of the seven daily session orders used.

Apparatus and procedure.—Experiment II was conducted in a light-tight dark room with a modified Held-Gottlieb apparatus (Held & Gottlieb, 1958). The goggle frame was fitted with variable wedge prisms, which could be set at 0 diopters for test marking and 20 diopters BR for exposure. Filter holders for Wratten gelatin filters were mounted in front of the prisms. The color filters used were red Wratten No. 25 transmitting wavelengths beyond 580 nm. and blue-green Wratten No. 75 described in Exp. I. An adjustable light occluder mounted between prisms and filter holders insured monocular viewing at all times. The elliptical field of view of each eye subtended approximately 40° horizontally and 52° vertically.

During both marking and exposure procedures, ambient (background) light was provided by 16 6-w. bulbs mounted behind white Plexiglas diffusers positioned on either side of the prism bracket. These lights, operated at a voltage controlled by a Variac, provided diffuse illumination of the exposure and target surfaces. Luminance levels were calibrated as in Exp. I.

During exposure, *S* used his left eye to view a black surface perpendicular to his line of sight and 40 cm. in front of his eyes. A white, .63 cm. (1°) wide, zig-zag line, painted on this surface and extending throughout the visible field, provided a path for *S* to trace while watching his hand through prisms. These tracing movements by the index finger of *S*'s right hand were paced to the beat of a metronome, one segment per beat.

The *S* used his right eye during marking periods before and after exposure. He viewed, by means of a first-surface mirror, the reflection of a flat black, cloth-covered target surface. Five miniature 6.3-v., .2-amp. incandescent lamps, mounted behind diffusing paper and the cloth, were distributed throughout the field. These lamps, activated sequentially, provided individual targets 1° in diameter. The image of each target appeared to lie on a surface approximately coplanar to the exposure surface. This marking surface was fitted with ruled paper to receive pen marks during test periods. During each test period, *S* repeatedly marked the apparent locations of the target lights with a pen held in his right hand, withdrawing his hand between markings. Each target was presented four times in semirandom sequence for a total of 20 marks.

At the midpoint of the experiment, a modified apparatus became available and was used for the remainder of the experiment. The target surface of this apparatus held 10 target lights, each of which was marked five times for a total of 50 marks during each test period. The marking board was fitted with conducting Teledeltos paper to receive electrode pen contacts. Pen contact generated a voltage, which was converted to a measure of distance along the horizontal dimension. This device is fully described in Bauer, Woods, and Held (1969). The apparatus and procedure remained otherwise unchanged.

In all sessions, the sequence of events was similar. The *S* was dark-adapted for 45 min., then positioned at the apparatus for threshold measurements described subsequently. After experimental light conditions were determined, *S* was adapted to them for 3 min. and then made a series of practice marks. Another 3-min. period of appropriate adaptation preceded the preexposure period in which *S* again made practiced marks. Prism exposure followed for 3 min., after which the marking procedure was repeated. Transition periods between marking and exposure were approximately 10 sec. in duration. While not in use, the exposure or test eye was occluded.

The ambient luminance level during photopic exposure was approximately 6 mL. incident upon the red filter. During photopic marking periods, the ambient luminance incident upon the red filter was approximately 4 mL., and the target light luminance was approximately 1.3 log units above this level, or about 70 mL.

The ambient luminance level during scotopic procedures was determined separately for each *S*. For exposure periods, absolute thresholds were taken with *S*'s left eye looking at the exposure surface through the blue-green filter by using the method of ascending and descending limits. Subsequent thresholds were taken in similar fashion with Wratten neutral density filters .8, 1.0, and 2.0 log units inserted in the filter mounts. With the ambient light approximately 1 log unit above absolute threshold, all *S*s were able to trace the zig-zag line, and this value was used for scotopic exposure conditions. For marking periods, individual thresholds for the target lights were taken with the blue-green filter in front of the right eye and the ambient luminance approximately .5 log units above absolute threshold. The target luminance values used were set no more than 1.0–1.3 log units above absolute threshold, providing targets which vanished upon fixation yet could be marked without difficulty by *S*. Thresholds were checked at the beginning of each session, and proved consistent from day to day.

The relative acuity of *S*s during scotopic and photopic exposure was estimated by placing a photographically reduced eye chart of black Es upon the exposure surface and requiring *S* to state the orientation of the letters for each line of decreasing size. Under the scotopic conditions of this experiment, the acuity of *S*s was reduced on the average by a factor of more than 30 relative to the photopic level: the estimated photopic acuity was approximately 1.16, scotopic acuity, approximately .036 reciprocal minutes.

Results

The means and standard deviations of preexposure and postexposure marking positions were computed for each target in every experimental sequence. The differences between these means, averaged across target locations, represented aftereffects and served to measure the magnitude of adaptation in each exposure period. Two-tailed t tests for correlated means were performed to compare individual pairs of conditions.

The mean shifts in centimeters for the four conditions were: P-P-P, 1.96, $t\ (16) = 7.33$, $p < .001$; S-P-S, .79, $t\ (16) = 2.31$, $p < .05$; S-S-S, 1.27, $t\ (16) = 5.08$, $p < .001$; P-S-P, 1.04, $t\ (16) = 3.93$, $p < .01$. These results strengthen the conclusion of the previous experiment that adaptation can be produced (exposure period) and demonstrated (marking periods) during scotopic as well as photopic sessions. By comparing transfer conditions with their respective controls, however, a contrast in the degree of adaptation is apparent.

In order to discover (*a*) whether the magnitude of the transfer shift was significantly less than that of the control and (*b*) whether the amount of transfer obtained under photopic and scotopic exposures differed, a three-factor analysis of variance was performed on the four mean shifts obtained for each of the 17 *S*s. For the transfer-control main effect, $F\ (1, 16) = 5.99$, $p < .05$, indicating that the transfer shifts were indeed significantly smaller than the control shifts. However, individual t tests revealed that although the transfer shift following photopic exposure was less than its control shift, $t\ (16) = 3.74$, $p < .01$, the difference between transfer and control shifts for scotopic exposure did not approach the .05 level of significance, $t\ (16) = .51$. This difference in amount of transfer was borne out by the significance of Transfer-Control × Exposure Condition interaction, $F\ (1, 16) = 10.65$, $p < .01$. Thus a significant asymmetry in the degree of transfer of photopically and scotopically induced adaptation is revealed. Transfer between the two states is reduced under photopic, but not under scotopic, exposure conditions.

The individual differences shown by *S*s in their scores for the P-P-P and S-P-S conditions were similar to those of other experiments using the rearrangement paradigm. Only two *S*s showed a clear reversal with S-P-S shifts .3 cm. and .8 cm. greater than the P-P-P shifts. Ten *S*s showed P-P-P shifts greatly exceeding the S-P-S shifts; the average difference was 2.3 cm. Five *S*s showed similar scores on the two conditions. As in Exp. I, no influence of daily session order was apparent.

The standard deviations of markings in the four conditions demonstrate the greater scatter under conditions of scotopic marking: P-P-P, .81; P-S-P, .86; S-P-S, 1.12; and S-S-S, 1.09.

Discussion

The results of these experiments demonstrate for the first time that compensation for prismatic displacement can occur and be measured under scotopic as well as photopic conditions. That the magnitude of adaptation was not significantly different under the two conditions is of considerable interest in view of the striking differences between vision at photopic and scotopic light levels. It is clear that close to the photopic threshold, a number of visual phenomena show marked discontinuities in accord with the classic duplicity theory (Hecht, 1937); thus the curves for brightness discrimination, visual acuity, critical flicker fusion, as well as the dark-adaptation curve itself, show branches representing function in the photopic and scotopic states. The results of the present experiments suggest that the specialized functions of photopic vision are neither necessary aspects of the visual feedback allowing recorrelation, nor necessary for the marking procedures which reflect adaptation. It would appear that the limits of precision necessary for detection of the transformation produced by rearrangement are not exceeded during scotopic exposure in spite of the greatly reduced acuity (Mandelbaum & Sloane, 1947), absence of foveal fixation, and increased latency of visual response (Arden & Weale, 1954) in the scotopic state.

A comparison of the means for Exp. I and II shows that the values for scotopic (S-S-S) sequences were somewhat lower than those for the photopic (P-P-P) sequences in Exp. II, whereas they were nearly identical to the photopic means in Exp. I. The scotopic light levels in Exp. II were about 1 log unit lower than those of the first experiment, and it is worth considering whether this factor might account for the smaller shifts in the scotopic sequences of Exp. II. It is possible that sequences carried out at very high photopic levels would reveal significantly larger shifts than sequences performed at low scotopic levels.

It would be of interest in this regard to vary systematically the scotopic light levels and to compare the shifts obtained under these conditions with those at mesopic and high photopic levels. Under the scotopic conditions of these experiments, vision is mediated by the rods of the parafoveal and peripheral retina. At the photopic levels used, cones dominate visual processes by virtue of their great concentration at the central retina, although evidence suggests that rods are sensitive at light levels far above the photopic threshold and may have responded under the photopic conditions of these experiments (Aguilar & Stiles, 1954; Stiles, 1954; Wald, 1960; Weale, 1953). By comparing the shifts obtained under carefully selected scotopic, mesopic, and photopic conditions, one should be able to determine the influence of varying the ratio of rod to cone receptors active during exposure. In addition to the differential involvement of the two photoreceptor populations, the complex neural interactions at the retinal level and beyond, known to play a significant role in dark and light adaptation and in response to converging rod and cone inputs (Barlow, Fitzhugh, & Kuffler, 1957; Dowling, 1963; Gouras & Link, 1966; Hubel & Wiesel, 1966; Rushton, 1961), could be considered in an experiment involving systematic comparisons at these light levels.

The results of the transfer experiments suggest that the sensorimotor change of state associated with photopic exposure may be to some degree distinct from that induced by scotopic exposure. The means of Exp. II indicate that photopically induced adaptation is evidenced primarily under photopic test conditions and shows significantly reduced transfer to scotopic test conditions, whereas scotopically induced compensation is demonstrable under both conditions. If the changes in eye–hand coordination were equivalent for photopic and scotopic exposure, one would expect similar shifts in the transfer and nontransfer sequences. However, this is evidently not the case. The possibility deserves consideration, therefore, that the mechanisms underlying compensation in the two states are to some degree dissociable. It is noteworthy, in this regard, that several authors have argued for the dissociability of mechanisms involved in visually guided behavior from those concerned with analysis of pattern (Held, 1968; Ingle, 1967; Schneider, 1967; Trevarthen, 1968; Wald & Burian, 1944). If one assumes that adaptation to rearrangement reflects primarily a change in state of orienting mechanisms, then these experiments provide a suggestion that photopic and scotopic visual pathways may be differentially organized with regard to these orienting mechanisms.

Cohen (1966) has reported experiments, apparently conducted under photopic conditions, indicating that a differential effect upon the magnitude of prismatic adaptation may be exerted by selective stimulation of central and peripheral retina. Such experiments, while not directly comparable to the results of the present experiments, also indicate that the precise nature of visual stimulation during exposure and testing may play a significant role in rearrangement experiments.

It is naturally of interest to determine whether the differential effects of the photopic and scotopic exposure used in the present experiments would be influenced by restricting the area of retina stimulated. Experiments designed to investigate this question should help to elucidate the mechanisms involved in asymmetric transfer.

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