Visual adaptation to tilt and displacement: Same or different processes?*

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Visual adaptation to tilt and displacement were compared to test whether they were dependent on the same or different processes. Although interocular transfer was essentially complete for both transforms, marked differences occurred between the two kinds of optical transforms in terms of rate of adaptation as a function of exposure time and transform magnitude, level of compensation, and rate of decay. Tilt and displacement appear to be quantitatively different, consistent with the idea of a different locus for each adaptation effect. This conclusion was supported by the absence of a correlation between individual performance under the two transforms. The possibility is discussed that displacement and tilt adaptation involve independent visual systems for the perception of location and form.

Theories of perceptual adaptation have been tested against perceptual change following exposure to a variety of optical transformations of the visual field (e.g., Harris, 1965; Rock, 1966); however, there have been few attempts to compare different transforms experimentally (e.g., Pick & Hay, 1964; Hajos & Ritter, 1965), and little data are available relevant to the relationship between adaptation to tilt and displacement.

Comparative studies of the various distortions produced by wedge prisms reveal considerable differences in the level of adaptation achieved for a constant exposure period. Pick and Hay (1964) found essentially complete compensation for errors produced by displacement in pointing with the unseen hand at a visual target. The smallest amount of adaptation occurred to form distortions (stretching and shearing) with intermediate levels for curvature and color fringes. Hay and Pick (1966a) replicated these findings and provided a more detailed account of the time course of adaptation to the various distortions. Adaptation to form, curvature, and color transforms was a negatively accelerated function of exposure time (120 h). On the other hand, the function for compensation of errors in eye-hand coordination produced by displacement was nonmonotonic, decreasing after 12 h. Furthermore, adaptation to form distortions and displacement was affected by prism orientation (horizontal or vertical), while adaptation to curvature and color fringes was independent of prism orientation. Additional evidence for different mechanisms in adaptation to the various wedge prism distortions is given by Hajos and Ritter's (1965) investigation of interocular transfer. Over an

exposure period of 12 days, these authors report essentially complete transfer of displacement adaptation. Smaller amounts of transfer were found for curvature. Transfer of color-fringe adaptation was nonexistent. Such comparative studies suggest a multiplicity of compensatory mechanisms rather than a single unitary adaptive process.

Held and his collaborators have evaluated tilt and displacement adaptation in terms of sensory-motor recorelation theory (Held, 1961), and they conclude that the same principle of adaptation applies to both transforms. Held and Bossom (1961) reported that active movement during exposure to displacement was necessary for compensatory changes in apparent straight-ahead. Selected Ss showed complete adaptation to displacement. Mikaelian and Held (1964) found similar results for tilt adaptation: active movement was necessary and selected Ss showed complete adaptation. Mikaelian and Held measured adaptation in two ways: by having the S adjust a luminous line to appear vertical and by having the S rotate his body so that a luminous dot, presented either above or below eye level, appeared straight ahead. (Held and Bossom also used this latter procedure in measuring displacement adaptation, except that a single dot at eye level was used). Judgment of the dots above and below eye level was not significantly different from the judged vertical of the line. Mikaelian and Held concluded, on the basis of these data, that sensory-motor recorelation of the point localization system underlies both kinds of adaptation. The corollary of this conclusion is that visual orientation and visual direction are reducible to the same process of point localization (see also Held, 1968).

The conclusion that both tilt and displacement adaptation involve sensory-motor recorelation rests on three assumptions: (a) adaptation to tilt and to displacement is (or can be) complete; (b) active movement is necessary for both kinds of adaptation; and (c) equivalent changes occur whether tilt adaptation is measured by localization (dots) or orientation (line)

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judgments. Recent evidence challenges these assumptions. Tilt adaptation is clearly limited at less than complete adaptation for unselected Ss (e.g., Ebenholtz, 1966). The selected Ss of Mikaelian and Held, who showed complete adaptation, must be considered exceptions rather than the general rule. Considerable evidence exists that active movement is not a necessary condition for adaptation (e.g., Wallach, Kravitz, & Lindauer, 1963; Mack, 1967). It appears that it is the information derived from movement and not movement per se which is crucial (Rock, 1966). While such evidence weakens sensory-motor theory, it does not necessarily invalidate the conclusion that change in point localization underlies both adaptation to tilt and displacement. The supporting rationale behind the conclusion is, however, weakened. Without the supporting rationale from theory, the equivalence between changes in localization and orientation found by Mikaelian and Held becomes only a covariation with no assurance that point localization is responsible for both measures of adaptation. Thus, available data are inconclusive regarding the relationship between tilt and displacement adaptation.

The research reported here was undertaken to provide a direct comparison of adaptation to optical tilt and optical displacement. The experiments provide comparisons of the two kinds of adaptation in terms of rate of change as a function of exposure time and transform magnitude, level of compensation, and rate of decay. Similarity on these parameters may be presumed to reflect similarity in adaptive process. The correlation between individual performance under the two transforms was also assessed. The degree of intertransform correlation may be taken to indicate the amount of commonality of systems involved in the two kinds of adaptation. Finally, transfer of adaptation effects from exposed to unexposed eyes was measured. Failure to find complete interocular transfer could be interpreted as meaning that the kind of adaptation under consideration does not involve the oculomotor system, but may, for example, involve local retinal cortical areas (Ebenholtz, 1970).

EXPERIMENT I

In Experiment I, adaptation to tilt and displacement were compared as a function of exposure time and transform magnitude. Adaptation in the unexposed as well as the exposed eye was measured to assess interocular transfer. All Ss received both transforms on different occasions so that S reliability could be assessed. It was expected that if adaptation to tilt and displacement are to be subsumed under a single theoretical system, not only should exposure and transform magnitude functions be comparable, but the relative level of adaptation attained under one transform for a given S should be comparable to the level under the other transform. Whatever individual factors determine

whether a S will show high or low adaptation to displacement, relative to other Ss, should be effective in adaptation to tilt as well.

Method

Procedure

Ss walked through a hallway while viewing an optically transformed visual field with the right eye, the left eye being occluded. Tilt was produced by a pair of Dove prisms mounted in tandem and affixed by a headset over the right eye. Displacement was produced by variable Risley prisms set in a goggle frame over the right eye. The visual field given by the Dove and Risley prisms was approximately 10 and 20 deg in diam, respectively. Each set of prisms could be rotated to produce any desired amount of distortion up to 180 deg of tilt and 30 D of displacement. All Ss were exposed to tilt and displacement separately during two 1½-h periods with 47 h intervening between exposures to the two transforms.

Prior to the start of the adaptation period for tilt, each S was tested on visual orientation by setting a luminous line (30.48 cm long, .32 cm wide) to look lined up with his chin-forehead axis. Measurements were made to the nearest degree of rotation from objective vertical. All testing was conducted without prisms. The Ss viewed the line monocularly in a dark room at a distance of 121.92 cm. The bottom of the line was the pivot point and was at eye level, on line with the right eye. Both eyes were tested separately, and the head was held stationary in a forehead-and-chinrest. Subsequent postadaptation tests were made at 15-min intervals thereafter. In the preadaptation tests, Ss made eight judgments with the starting position of the line alternately at 25 deg clockwise (CW) and 25 deg counterclockwise (CCW) of objective vertical. Right and left eyes were alternated every two judgments. Subsequent postadaptation tests involved only four judgments, alternating starting position of the line every judgment and eye tested every two judgments. Level of adaptation (LA) was defined separately for exposed (right) and unexposed (left) eyes as the difference between the mean of the last two preadaptation judgments (the first two judgments were considered practice and were dropped) and the mean obtained for each eye on subsequent tests.

Prior to the start of the adaptation period for displacement, each S was tested on visual direction by setting a vertical row (.79 cm long, .16 cm wide) of three illuminated dots to appear straight ahead of his nose in the horizontal plane. Measurement was to the nearest ½-arc-deg deviation from objective straight-ahead. The Ss viewed the dots monocularly in a dark room. The dots were at eye level and moved along an arc so that a constant distance of 121.92 cm from the S was maintained. Three dots were used to reduce autokinetic movement found to occur with a single dot. The dots were very close together, the total visual angle subtended by the row being approximately 20 min, and Ss experienced no difficulty in judging the location of the entire row. To further minimize autokinetic movement, Ss were instructed not to fixate or track the dots, but rather to look straight ahead of their noses and say when the dots reached that position. In all other respects, test for visual direction was identical with test for visual orientation, except that starting positions were 8 arc deg right (R) and left (L) of the objective straight-ahead, corresponding to CW and CCW tilt of the line in visual orientation tests. During tests for both direction and orientation, taped white noise was played to mask any auditory cues from the operation of the measurement apparatus.

Several steps were taken to minimize the possibility that a proprioceptive change outside the eye-head system might be involved in the experiment. During exposure, Ss were encouraged to move about freely in the hall, but were instructed not to look at any part of their bodies (particularly hands and

feet) and not to touch walls. No Ss were observed to violate these prohibitions. As a double precaution, S wore a black cloak which covered the entire body from neck to knee. Thus, it seems unlikely that any proprioceptive change, such as in felt position of the hand (Harris, 1963), or specific visual-motor compensation, such as eye-hand coordination (Mikaelian, 1967), occurred. The test procedure was designed to minimize the possibility that a change in head-body proprioception might be confounded in the adaptation measure. By the use of egocentric (relative to the head) test instructions, it was hoped that since the head was always normally oriented in test, any abnormal proprioception would not influence the adaptation measure. Head position was monitored at intervals throughout testing to prevent atypical head posture, and five Ss were replaced when postexperimental questioning revealed that their judgments had clearly implicated the felt position of the head relative to the trunk. These Ss felt their heads to be either turned or tilted during test, and compensated by adjusting the dots or the line to appear aligned with their trunks. Of the Ss retained, seven reported their heads turned in test for displacement; however, they continued to adjust the test targets relative to their heads, and no consistent tendency appeared. Four Ss said that their heads felt turned right during test and three Ss reported their heads turned left. Two Ss said their heads felt tilted in test for tilt adaptation. One of the two felt his head tilted left and the other reported his head tilted right. The net effect of these specifications is to restrict consideration to the eye-head system, where adaptive changes alter the phenomenal appearance of the visual world. To the extent that precautions were adequate, the adaptation measures may be assumed to reflect only changes in the visual system.

Design

Twenty-four undergraduates (18 female and 6 male) were run in three groups of 8 Ss each. The Ss were assigned alternatively to one of three groups as they arrived for experimentation. In addition to the previously mentioned 5 Ss who failed to follow instructions, 10 other Ss did not complete the experiment and had to be replaced. Nine Ss failed to show at least 1 deg of adaptation in either eye after 45 min exposure to tilt or displacement. One S was unable to perform the visual direction test. Rejected Ss were replaced by the next available S such that alternate assignment to groups was maintained.

The groups differed only in the magnitude of the transform used. Tilt and displacement were arbitrarily paired for application to groups such that a given group received the same number of degrees of tilt as diopters of displacement. For example, Ss receiving 20-D displacement received 20 deg of tilt. Only CW tilt and rightward displacement were used. Counterbalancing within groups was complete for order of transforms (tilt first or displacement first), order in which eyes were tested (exposed eye first or unexposed eye first), and order of starting positions in test (CW and R first or CCW and L first).

Results and Discussion

Separate analyses of variance were performed for tilt and displacement, and the data were examined to provide comparisons of adaptation to the two transforms.

Exposure Time

No significant effect of exposure time appeared for tilt, $F(2,42) = 1.57$, indicating that all measurable tilt adaptation occurred in the first 15 min. Exposure time did not interact with any other variable in tilt

Fig. 1. Mean level of adaptation in the exposed eye as a function of exposure time for three levels of optical tilt and displacement. (Smooth curves represent the best fit by the method of least squares; Experiment I.)

adaptation. On the other hand, displacement adaptation continued to increase beyond 15 min of exposure, $F(2,36) = 17.96$, $p < .001$, and a significant interaction, $F(2,36) = 3.96$, $p < .05$, of Day by Time was found. Subsequent multiple comparisons revealed a significant difference, $F(1,36) = 5.05$, $p < .01$, in displacement adaptation at 15 min between Day 1 ($\bar{X} = 4.69$) and Day 2 ($\bar{X} = 2.81$). Adaptation to displacement is somewhat slower to develop when preceded (47 h) by exposure to tilt, but reaches the same level at 30 and 45 min as when displacement precedes tilt.

Figure 1 represents LA in the exposed eye as a function of exposure time for three levels of tilt and displacement. The smoothed curves represent negatively accelerated exponential growth functions fitted to the data by the method of least squares. The fitted functions have the form $LA = a(1 - e^{-bt})$, where a is the estimated asymptote of adaptation and b estimates the rate at which adaptation approaches the asymptote as a function of exposure time, t . Since the interaction of exposure time and transform magnitude was not significant for either displacement, $F(4,36) = 1.02$, or tilt, $F(3,42) = .58$, rate of adaptation was assumed to be independent of transform magnitude and a single rate parameter, b , was estimated for the nine data points under tilt and displacement, respectively. The functions employing four parameters for nine data points fit the data reasonably well, yielding standard errors of estimate¹ of .77 for displacement and .35 for tilt. The asymptotes estimated for 10-, 20-, and 30-D displacement were 5.50, 7.14, and 9.56 deg, respectively, and the rate at which displacement adaptation approaches asymptote was .06. For 10, 20, and 30 deg of tilt, the asymptotes were 3.00, 4.13, and

Fig. 2. Mean level of adaptation as a function of transform magnitude for three lengths of exposure time in the exposed eye. (From bottom to top for displacement adaptation, the lines represent 15-, 30-, and 45-min exposures, respectively. For tilt adaptation, the lines represent 15-, 45-, and 30-min exposures. The lines represent the best linear fit by the method of least squares; Experiment I.)

6.10 deg, respectively, and the rate parameter was estimated at .19.

Assuming that the functions accurately represent the time course of adaptation, some striking differences between the two kinds of adaptation are suggested. Adaptation to tilt reaches asymptote in a remarkably short time, the greater portion occurring before the first test at 15 min. On the other hand, displacement adaptation develops much more slowly and continues to increase at least up to 30 min of exposure. While negatively accelerated time functions have generally been common in adaptation research (e.g., Hay & Pick, 1966a; Ebenholtz, 1966), the present results indicate that it would be erroneous to conclude similarity of process from such gross characteristics of growth functions, since the two kinds of adaptation differ quantitatively in terms of the parameters specifying the exposure time function.

Level of Compensation

To provide comparable measures of compensation for tilt and displacement, individual scores were transformed to percent compensation by the ratio LA/TM , where TM is the transform magnitude used. For tilt, the transform magnitudes were 10, 20, and 30 deg. For displacement, 10, 20, and 30 D were expressed in arc-deg equivalents of 5.7, 11.4, and 17.1, respectively. The percent scores

were averaged over tests to provide a single mean for each S under tilt and under displacement. A Wilcoxon matched-pairs signed-ranks test showed the difference of .34 between mean percent compensation for the exposed eye under tilt (.23) and displacement (.57) to be significant, $p < .01$.

These results confirm the general impression gleaned from the literature that compensation is considerably greater for displacement (e.g., Hay & Pick, 1966b) than for tilt (e.g., Ebenholtz, 1966). Under comparable exposure and test conditions, compensation for displacement is at least twice as great as it is for tilt. Examination of the fitted curves in Fig. 1 suggests that even complete compensation for displacement may be possible, given enough exposure. Complete compensation for tilt seems extremely unlikely, no matter how long the exposure.

Transform Magnitude

Transform magnitude was a significant source of variance for both tilt, $F(2,21) = 5.85$, $p < .01$, and displacement, $F(2,18) = 3.94$, $p < .05$, and trend analysis revealed only a significant linear component for both tilt, $F(1,21) = 11.35$, $p < .001$, and displacement, $F(1,18) = 8.36$, $p < .01$. Transform magnitude did not interact with any other variable for either transform. Figure 2 represents LA as a function of transform magnitude for three exposure times in the exposed eye. The straight lines represent linear functions fitted to the data by the method of least squares. The standard error of estimate for functions employing four parameters for nine data points was .52 for displacement and .34 for tilt. The estimated slope coefficient was slightly greater for displacement (.17) than for tilt (.15). The fact that the intercepts are greater than zero suggests a curvilinear function for small magnitudes of distortion. However, a linear rule best describes adaptation over the range of magnitudes studied for both transforms.

Similar linear functions have been reported for tilt (Ebenholtz, 1966; Morant & Beller, 1964) and displacement (Lazar & van Laer, 1968). Two studies (Efsthathiou, 1969; Dewar, 1970) reported nonmonotonic magnitude functions for displacement, adaptation showing a sharp drop beyond about 20 D. The difference between these studies and the present results may, in part, be due to a limitation in the motor response system. Unlike the present study, both Efsthathiou and Dewar employed a change in pointing behavior as an index of adaptation as well as restricted exposure conditions (eye-hand coordination). However, motor limitation cannot be the complete explanation, since Lazar and van Laer also used a motor response measure and restricted exposure. The nature of the magnitude function for displacement under different conditions of exposure and test remains problematical.

Interocular Transfer

The mean LA to tilt for the exposed eye (4.33) was not significantly greater, $F(1,21) = 1.29$, than for the unexposed eye (3.78). Similarly, displacement adaptation was not significantly greater, $F(1,18) = .48$, in the exposed eye (5.95) than in the unexposed eye (5.59). To obtain a quantitative measure for purposes of comparison, a ratio of unexposed to exposed eye was computed for each S's LA under each combination of conditions. A Wilcoxon test on S means averaged over time found the difference between mean percent transfer for displacement (.93) and tilt (.95) to be nonsignificant. Consistent with previous findings of complete interocular transfer of adaptation to displacement (Hajos and Ritter, 1965) and tilt (Quinlan, 1970; Mack & Chitayat, 1970), present results may be interpreted as showing complete transfer.

Intertransform Correlation

Rank-order correlation coefficients were computed on the geometric mean LA in the exposed eye over the three tests at each level of transform magnitude. The coefficients, in order of increasing transform magnitude were .14, -.24, and .24. None of the correlation coefficients were significantly different from zero. This essentially zero correlation between adaptation to tilt and to displacement might be due either to instability of individual adaptability over days or to differences in individual adaptability for the two transforms. The question of stability of individual performance was examined in Experiment II.

EXPERIMENT II

The low intertransform correlation obtained in the first experiment may have been due to a general instability over successive days of adaptability, rather than a basic difference in the process for tilt and displacement adaptation. Since no comparison over time of adaptation to the same transform was available, this possibility could not be evaluated. Experiment II provided for the assessment of within-transform correlation. It was expected that should intratransform correlation prove better than intertransform correlation, the conclusion of a basic difference in process would be supported.

A common view (e.g., Held, 1961; Rock, 1966) is that adaptation to prisms reflects the same processes involved in establishing and maintaining normal perceptual behavior, i.e., that the "normal" preadaptation state is itself a state of adaptation. The fact that adaptation decays in the absence of visual stimulation (Ebenholtz, 1969; Hamilton & Bossom, 1964) makes it difficult to identify adaptive processes with developmental processes, since normal perceptual discriminations are not known to show a loss during a period of no visual stimulation (e.g., during sleep). Attempts to deal with

this apparent inconsistency between adaptation and normal states have taken the form of comparing decay of adaptation during a period of no visual stimulation (occlusion of the eyes or a period of darkness following exposure) with readaptation upon exposure to normal, untransformed visual stimulation. A difference in favor of readaptation for recovery of normal discriminative performance may be taken as support for the view of perceptual adaptation as a model for perceptual development. Hamilton and Bossom (1964) failed to find a significant difference between decay and readaptation after exposure to displacement. Ebenholtz (1968), however, found that readaptation proceeds at a faster rate than does decay after exposure to optical tilt. It is possible that displacement adaptation is more susceptible to decay than is tilt adaptation. Ebenholtz (1969) found decay of tilt adaptation to asymptote at a nonzero value. Similar data on decay of displacement adaptation is not available. A primary concern of Experiment II was the evaluation of decay of tilt and displacement adaptation.

Method

Procedure

Several modifications were made of the procedure followed in Experiment I. In testing for tilt adaptation, the test line was shifted so that the bottom of the line was at eye level and on line with the nose of the S. Each S received either tilt or displacement twice on separate days, 47 h intervening between the two exposures. Following the last adaptation test on the second day, Ss continued to sit in the dark, and four decay tests were made at 8-min intervals. Otherwise, procedure was essentially the same as in the first experiment.

Design

Sixteen undergraduates (11 female and 5 male) were run in two groups of 8 Ss each, with alternate assignment to groups as Ss arrived for experimentation. Eight Ss failed to complete the experiment and were replaced. Two of the 8 failed to follow test instructions (1 in each group), 1 S failed to show at least 1 deg of tilt adaptation after 45 min, 3 Ss (2 in the tilt group) did not return on the second day, 1 S receiving tilt became nauseated, and 1 S could not perform the visual direction test. In general, rejected Ss were replaced with the next available S; however, this was not always possible when a S failed to return the second day. Alternate assignment was, therefore not perfect. The groups differed only in the transform received. One group received 30-D displacement and the other 30-deg tilt. Only CW tilt and rightward displacement were used. Order in which the two eyes were tested and order of starting position in test were counterbalanced.

Results and Discussion

Separate analyses were performed for tilt and displacement adaptation, and for decay of tilt and displacement adaptation. The data were examined to provide comparisons of the two transforms.

Exposure Time

Figure 3 represents LA as a function of exposure time

Fig. 3. Mean level of adaptation to optical displacement (unfilled points) and to optical tilt (filled points) as a function of exposure time on successive days and of decay time on the second day for both exposed and unexposed eyes. (Smooth curves represent the best fit by the method of least squares; Experiment II.)

on successive days for the two transforms. The best-fit negatively accelerated growth functions are represented by smoothed curves. Unlike Experiment I, exposure time was not a significant source of variance, $F(2,14) = 3.18$, in displacement adaptation; however, this appears to be due to the presence of an Eye by Time interaction, $F(2,14) = 7.92$, $p < .005$. Subsequent comparisons showed the difference between eyes to be significant at 15 min, $F(1,14) = 7.66$, $p < .025$, and 45 min, $F(1,14) = 7.88$, $p < .025$, but not at 30 min, $F(1,14) = .43$. Greater adaptation in the unexposed eye occurred early in exposure and adaptation remained relatively constant thereafter, but adaptation in the exposed eye continued to increase throughout the exposure and surpassed the unexposed eye. Since the interaction of Eye by Time was significant in displacement, a separate rate parameter was estimated for exposed (.04) and unexposed (.10) eyes. The estimated asymptotes were 10.33 for the exposed eye and 8.07 for the unexposed eye on the first day, and 11.38 and 7.70 on the second day. The standard error of estimate for functions employing six parameters for 12 data points was .56 for displacement adaptation.

As in Experiment I, exposure time was not a significant variable in tilt adaptation, $F(2,14) = 1.16$, but a Day by Time interaction did appear, $F(2,14) = 5.84$, $p < .025$. Examination of Fig. 3 shows an increase in adaptation after the first test on the first day, but no corresponding increase on the second day. Analysis by linear contrasts revealed a significant difference between days for the contrast of LA at 15 min, with the mean LA at 30 and 45 min, $F(1,14) = 8.04$, $p < .025$. Successive exposure to tilt appears to lower the amount of adaptation attained for a constant exposure time. Interpretation of the Day by Time interaction in tilt adaptation as a change in asymptote allowed a single rate parameter (.15) to be estimated. The estimated asymptotes were 5.20 for the exposed eye and 4.20 for

the unexposed eye on the first day, and 4.42 and 3.29 on the second day. The standard error of estimate for functions employing five parameters for 12 data points was .34 for tilt adaptation.

The growth functions constitute a replication of the results of the first experiment. The rate of adaptation seems relatively constant over experiments. The estimated rate parameter for the exposed eye for displacement in Experiment I was .06 compared with .04 in Experiment II. For tilt adaptation, the parameters estimated for the exposed eye were .19 and .15 for Experiments I and II, respectively. Variations in asymptote between experiments are probably due to sampling differences. Clearly, adaptation to tilt approaches asymptote at a faster rate than does adaptation to displacement. The percent compensation in tilt adaptation was .15 for the exposed eye compared to .44 for displacement. As in the first experiment, compensation for displacement is greater than for tilt.

Decay Time

Also represented in Fig. 3 is the LA for the exposed and unexposed eyes at five decay tests for displacement and tilt. The last test at 45 min on the second day was taken as the starting LA, zero time, from which to measure decay. The smoothed curves represent negatively decelerated exponential functions fit to the data by the method of least squares. For tilt decay, significant sources of variance were eye, $F(1,7) = 8.00$, $p < .05$, and time, $F(4,28) = 6.18$, $p < .005$. Trend analysis revealed significant linear, $F(1,7) = 6.53$, $p < .05$, and quadratic, $F(1,7) = 21.50$, $p < .005$, components in tilt decay. A fit for tilt decay required the estimation of an added constant since decay is asymptotic at greater than zero, i.e., $LA = ae^{-bt} + c$, where $a + c$ is the LA at the beginning of the decay period, different for the two eyes, b indicates the rate of

decay per unit of time, t , in either eye, and c is the asymptote for decay, different for the two eyes. The standard error of estimate for functions employing four parameters for 10 data points was .10 for tilt decay.

The difference between exposed and unexposed eyes in displacement decay was not significant, $F(1,7) = 2.61$. Time was a significant factor, $F(4,28) = 6.40$, $p < .005$, with only a linear component, $F(1,7) = 9.71$, $p < .05$. However, since simple linear decay seems unlikely and to facilitate comparison with tilt decay, a negatively decelerated exponential function was fit to the displacement decay data. For decay of displacement adaptation, the standard error of estimate for functions of the form, $LA = ae^{-bt}$, employing three parameters for 10 data points was .35.

As in acquisition, decay of tilt adaptation occurs at a faster rate than does decay of displacement adaptation. Tilt decay reaches asymptote perhaps within the first 8 min, while displacement decay occurs more slowly and did not reach asymptote after 32 min. The fact that tilt decay appears to asymptote at less than complete decay suggests a further difference between the two kinds of adaptation. Displacement adaptation seems entirely subject to decay, while tilt adaptation involves an additional, more persistent component. However, this conclusion must be qualified by the fact that the decay period was not long enough for displacement to reach a stable level.

Intratransform Correlation

Rank-order coefficients on the geometric means over tests in the exposed eye revealed significant correlation ($p < .05$) between days for both tilt adaptation (.76) and displacement adaptation (.74). The possibility that the obtained positive correlations might be due to some specific transfer of adaptation from the first to second days was evaluated by a comparison of baseline measures from the 2 days. The mean error from objective straight-ahead was .22 deg in the leftward direction on the first day and .09 deg in a rightward direction on the second day. The difference between days was not significant, $t(7) = .45$. The mean error from objective vertical was .00 deg on the first day and .59 deg in a clockwise direction on the second day. The difference between days was not significant, $t(7) = 1.16$. Specific adaptation effects do not transfer over a 47-h interval, although all differences were in the direction expected if transfer were to occur.

In contrast to the lack of correlation between transforms found in the first experiment, S performance is positively related within the same transform over successive days. The low intertransform correlation obtained in Experiment I must, therefore, be taken to indicate a basic difference in process between adaptation to tilt and to displacement. Whatever the factors are that produce individual differences in adaptation, they differ for the two transforms.

Interocular Transfer

As in Experiment I, the difference between exposed and unexposed eyes was not significant in either tilt, $F(1,7) = 3.61$, or displacement, $F(1,7) = .02$, adaptation; however, the interocular difference for both transforms was in the direction of incomplete transfer. Mean percent interocular transfer was .98 for displacement and .82 for tilt. Furthermore, an Eye by Time interaction appeared in displacement adaptation and in tilt decay the interocular difference was significant. The fact that the Eye by Time interaction did not appear in Experiment I minimizes the importance of such a finding. Similarly, tilt decay was the only instance of a significant difference between eyes in either experiment. In light of the nonreplicability of these interocular differences, it is reasonable to conclude that interocular transfer is complete for both tilt and displacement adaptation.

CONCLUSION

The parametric comparisons suggest qualitative differences between adaptation to tilt and to displacement. Tilt adaptation is clearly limited. Ebenholtz (1966) also found tilt adaptation to be limited. Adaptation did not increase after 4 h beyond the level obtained after 1 h of exposure. Complete adaptation seems unlikely, regardless of exposure duration. Such a limitation is less readily apparent for displacement adaptation. Adaptation continued to increase throughout exposure, and complete compensation seems possible. Since the decay period was not long enough for decay of displacement adaptation to reach a stable level, conclusions must be made cautiously; however, the best-fit models for the present data suggest a marked difference in decay of adaptation to the two transforms. Adaptation to displacement seems more subject to decay without restimulation by untransformed input than does tilt adaptation. The two kinds of adaptation appear to be basically different, consistent with the idea of a different locus for each adaptation effect. The zero intertransform correlation supports this conclusion and suggests that tilt and displacement adaptation are independent processes.

These conclusions are consistent with an analysis, similar to that made by Rock (1966), of the information processing from the pattern of retinal stimulation necessary for the perception of direction and orientation. Locus-specific information is necessary for visual direction. Eye position and the position on the retina of an image must be known to determine the direction of the stimulating object. For visual orientation, relational information is necessary. For example, the ratio of the distance separating retinal points along the retinal vertical to the distance along the retinal horizontal may be necessary to determine the orientation of the stimulating object. Since retinal slope

is relatively invariant as the eye moves or as different areas of the retina are stimulated, eye position and locus-specific information may not be necessary in the perception of orientation. This difference in processing is further supported by the phenomenal independence of direction and orientation. A short vertical line, viewed in the frontal plane, continues to appear vertical, whether displaced right, left, up, or down. Conversely, a rightward displaced line continues to appear to the right, regardless of how it is tilted. Therefore, if the perception of direction and orientation depend upon different and independent kinds of retinal information, it is reasonable to expect modification of these perceptual functions (i.e., displacement and tilt adaptation) to show parametric differences. Moreover, it should be possible to demonstrate independence of the two kinds of adaptation.

Furthermore, a separation of systems is compatible with an increasing body of data that indicates a dissociation between neural mechanisms mediating perceptual constancy and form perception (Bishop & Henry, 1971). Visual direction requires that successive eye positions be taken into account so that a constant location for a stimulus object is maintained, and adaptation to displacement clearly involves such a compensatory process. On the other hand, since orientation is necessarily a characteristic only of extended objects, the perception of orientation and adaptation to tilt involves the mechanisms of form perception, the identification of ordered relationships between features of single objects and between various objects in the visual field. Both the phenomenal distinctiveness of visual direction and visual orientation and the obtained differences between displacement and tilt adaptation may, therefore, have their origin in a basic difference in process and mediating neural mechanisms.

REFERENCES

- Bishop, P. O., & Henry, G. H. Spatial vision. In P. H. Mussen and M. R. Rosenzweig (Eds.), *Annual Review of Psychology*. Palo Alto: Annual Reviews, 1971.
- Dewar, R. Adaptation to displaced vision: Amount of optical displacement and practice. *Perception & Psychophysics*, 1970, 8, 313-316.
- Ebenholtz, S. M. Adaptation to a rotated visual field as a function of degree of optical tilt and exposure time. *Journal of Experimental Psychology*, 1966, 72, 629-634.
- Ebenholtz, S. M. Readaptation and decay after exposure to optical tilt. *Journal of Experimental Psychology*, 1968, 78, 350-351.
- Ebenholtz, S. M. Transfer and decay functions in adaptation to optical tilt. *Journal of Experimental Psychology*, 1969, 81, 170-173.
- Ebenholtz, S. M. On the relation between interocular transfer of adaptation and Hering's law of equal innervation. *Psychological Review*, 1970, 77, 343-347.
- Efstathiou, E. Effects of exposure time and magnitude of prism transform on eye-hand coordination. *Journal of Experimental Psychology*, 1969, 81, 235-240.
- Hamilton, C. R., & Bossom, J. Decay of prism aftereffects. *Journal of Experimental Psychology*, 1964, 67, 148-150.
- Hajos, A., & Ritter, M. Experiments to problems of interocular transfer. *Acta Psychologica*, 1965, 24, 81-90.
- Harris, C. S. Adaptation to displaced vision: Visual, motor, or proprioceptive change? *Science*, 1963, 140, 812-813.
- Harris, C. S. Perceptual adaptation to inverted, reversed, and displaced vision. *Psychological Review*, 1965, 72, 419-444.
- Hay, J. C., & Pick, H. L. Gaze-contingent prism adaptation: Optical and motor factors. *Journal of Experimental Psychology*, 1966a, 72, 640-648.
- Hay, J. C., & Pick, H. L. Visual and proprioceptive adaptation to optical displacement of the visual stimulus. *Journal of Experimental Psychology*, 1966b, 71, 150-158.
- Held, R. Exposure-history as a factor in maintaining stability of perception and coordination. *Journal of Nervous & Mental Disease*, 1961, 132, 27-32.
- Held, R. Dissociation of visual functions by deprivation and rearrangement. *Psychologische Forschung*, 1968, 31, 338-348.
- Held, R., & Bossom, J. Neonatal deprivation and adult rearrangement: Complementary techniques for analyzing plastic sensory-motor coordinations. *Journal of Comparative & Physiological Psychology*, 1961, 54, 33-37.
- Lazar, G., & van Laer, J. Adaptation to displaced vision after experience with lesser displacements. *Perceptual & Motor Skills*, 1968, 26, 579-582.
- Mack, A. The role of movement in perceptual adaptation to a tilted retinal image. *Perception & Psychophysics*, 1967, 2, 65-68.
- Mack, A., & Chitayat, D. Eye-dependent and disparity adaptation to opposite visual-field rotations. *American Journal of Psychology*, 1970, 83, 352-371.
- Mikaelian, H. H. Relation between adaptation to rearrangement and the source of motor-sensory feedback. *Psychonomic Science*, 1967, 9, 485-486.
- Mikaelian, H. H., & Held, R. Two types of adaptation to an optically rotated visual field. *American Journal of Psychology*, 1964, 77, 257-263.
- Morant, R. B., & Beller, H. K. Adaptation to prismatically rotated visual fields. *Science*, 1965, 148, 530-531.
- Pick, H. L., & Hay, J. C. Adaptation to prismatic distortion. *Psychonomic Science*, 1964, 1, 199-200.
- Quinlan, D. Effects of sight of the body and active locomotion in perceptual adaptation. *Journal of Experimental Psychology*, 1970, 86, 91-96.
- Rock, I. *The nature of perceptual adaptation*. New York: Basic Books, 1966.
- Wallach, H., Kravitz, J. H., & Lindauer, J. A passive condition for rapid adaptation to displaced visual direction. *American Journal of Psychology*, 1963, 76, 568-578.

NOTE

1. The standard error of estimate is defined as the square root of the averaged squared deviation of obtained from predicted L.A.

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