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# ADAPTATION TO DISPLACED VISION: A CHANGE IN THE CENTRAL CONTROL OF SENSORIMOTOR COORDINATION[1]

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In characterizing the changes that occur in sensorimotor coordination after viewing the prism-displaced image of the hand, four types of explanation can be advanced: visual, proprioceptive, motor, and sensorimotor. Each one predicts different consequences on different tests of coordination: reaching for visual targets, orienting head to hand, orienting eye to hand, and repositioning the hand in a learned posture. The results of four experiments using these tests are consistent only with the sensorimotor explanation. They imply a change in the control and assessment of coincidence between the direction indicated by the exposed arm and that of either a sensed external object or other body part.

After viewing the displaced image of his moving hand through a wedge prism, *S*'s direction of reach for a visible target with this hand is altered. The direction of reach shifts toward the prism base as if to compensate for the error induced by the optical displacement. Scholl (1926) reported that this shift generalized to reaching for the contralateral unexposed hand while *S* was blindfolded. Efstathiou, Bauer, Greene, and Held (1967) confirmed Scholl's results, and several investigators, cited by them, have found generalization of the shift to pointing at other nonvisual targets, including sound sources. More recently, publications by Craske (1966) and Webster (1969) have reported similar results. However, Efstathiou et al. (1967) did not find evidence of an adaptive shift on all of their tests following exposure to prisms. When a blindfolded *S* was trained to reposture his exposed arm in a position defined independently of either external targets or other body members, no compensatory shift was manifest.

Harris (1965) has reviewed six alternative explanations of prism adaptation. Some of these are relevant to experiments permitting direct knowledge of the prism-induced error; i.e., *S* is informed—either visually or verbally—that he is misreaching for a visual target during exposure (Coren, 1966; Day & Singer, 1967; Foley & Maynes, 1969; Howard & Templeton, 1966; Webster, 1969; Welch & Abel, 1970; Welch & Rhoades, 1969). This report deals with adaptation obtained under conditions in which such error information is precluded. We have analyzed the explanations pertaining to these conditions in terms of imputed changes in their input and/or output characteristics. Four types of explanation can be considered to account for the shift and its generalization.

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1. Visual: A change has occurred in the processing of visual input necessary for determining the direction of a visible target (information derived from retinal stimulation and eye position in orbit). Shifts are predicted only when visual targets are localized, and in such cases the changes should be in evidence irrespective of the response tested.

2. Response: A change has occurred in the processing of motor output responsible for directed movements of the arm. An altered direction of response should occur on any and all tasks that require responses similar to those employed during the exposure to prisms.

3. Proprioceptive: A change has occurred in processing sensory input from the exposed arm required for assessing the position of the arm. The direction of response should shift in any task involving this changed position sense of the exposed arm.

4. Sensorimotor: A change has occurred in the system that controls and assesses coincidence of the directions indicated by the exposed arm with those of objects, including other members of the body. Consequently, a shift in direction of response will occur whenever the exposed arm is deliberately oriented either to an external target or to an unexposed part of the body. A reciprocal shift will occur whenever the exposed arm is itself the target of an orienting or localizing task. Coincidence of directions includes what we formerly referred to as "matching orientations," but is not restricted to arm and head alignment as in Efstathiou et al. (1967).

Of these four explanations, only the last has seemed to us consistent with known results, including those of Efstathiou et al. (1967). We should have remained convinced of its validity but for some evidence of Bauer and Degner (1967), Harris, Harris, and Karsch (1966), and McLaughlin, Rifkin, and Webster (1966). They have reported that viewing the nonlinear distortions produced by the prisms can cause antiadaptive shifts in pointing straight ahead with eyes closed. The prisms optically rotate frontoparallel surfaces about their vertical axes. Therefore, when looking through prisms, *S* will shift his localization of the straight ahead toward the prism apex. If *S* does not open his eyes either before or during the posttest, this negative (antiadaptive) shift in pointing straight ahead persists. The *S* acts as if he felt turned with respect to the apparatus. A similar negative shift would occur on the relocated position test if *S* were treating the learned postures as orientations towards the apparatus and were not relying solely on the sensed position of the limb. Consequently, the inability to demonstrate a shift in the relocated position test, as reported by Efstathiou et al. (1967), could have resulted from a masking of adaptive shifts by antiadaptive changes.

The following experiments reexamine the generalization of the adaptive shift while controlling for antiadaptive aftereffects.

## Experiment I

Three tests were used to determine the generality of the adaptive shift.

1. Visual target (VT): The *S* pointed at visible targets without seeing his hand.

2. Head to arm orientation (HA): While blindfolded, *S* oriented his head to the index finger of his outstretched hand.

3. Relocated position (RP): While blindfolded, *S* was trained to reposition his arm in several different postures defined in terms of the sensed position of the responding limb.

The shift in direction of pointing to the visual targets with the exposed arm after exposure to prisms was chosen as the baseline measure of the adaptive aftereffect. Each of the four explanations summarized in the introduction predicts a similar change in response on the VT test. The question remains: Would this adaptation be manifested when *S*s performed the HA and RP tasks?

1. The visual change explanation would not predict an adaptive shift in response on these two tasks because they do not involve vision.

2. The response change explanation would not predict an adaptive change on the HA task because the head responds during the test, whereas the arm responds during exposure; it might predict an adaptive change on the RP test since the arm is used throughout test and exposure conditions.

3. The proprioceptive explanation predicts an adaptive shift in response on both of these tests since the position of the arm is crucial to both tasks.

4. The sensorimotor explanation predicts an adaptive change in the HA task because the exposed arm is the target of an alignment task; it predicts no adaptive shift on the RP test since the arm is neither localizing an external target nor orienting to another body part.

## *Method*

*Subjects.*—A different group of eight *S*s was used for each of the three tests. All *S*s were Massachusetts Institute of Technology (MIT) undergraduates and were naïve as to the purpose of the experiment.

*Apparatus and procedure.*—The *S* was seated at arm's length in front of a vertical marking surface with his head held fixed by a biteboard. The biteboard was rigidly attached to a head frame that could be locked into position or freed to rotate around a vertical axis (Fig. 1). Three tests were used:

1. Visual targets: Five nails were spaced at eye level, above, but in the same frontal plane, as the marking surface. A horizontal board extended out from the surface to prevent *S* from seeing his hand as he marked the targets. The *S* was asked to extend his arm and point his index finger directly under the visual target specified by *E*. When *S* touched the marking surface, the position of his finger was recorded electronically (Bauer, Woods, & Held, 1969). The targets were marked in a randomized order, predetermined by *E*. The *S* was instructed to start each response from a different position in order to prevent his learning a specific motor pattern.

2. Head orientation to arm: Five tacks were set into the vertical marking surface. When *E* specified the target, the blindfolded *S* extended his arm and felt around until he touched the correct tack. The *E* provided verbal feedback, and *S* then placed his forefinger upon the tack and rotated his head back and forth until it felt aligned with his fingertip. He was asked to align his head to his hand so that "his nose seemed to be pointing to the tip of his unseen finger." The position of *S*'s head was indicated by a meter reading.

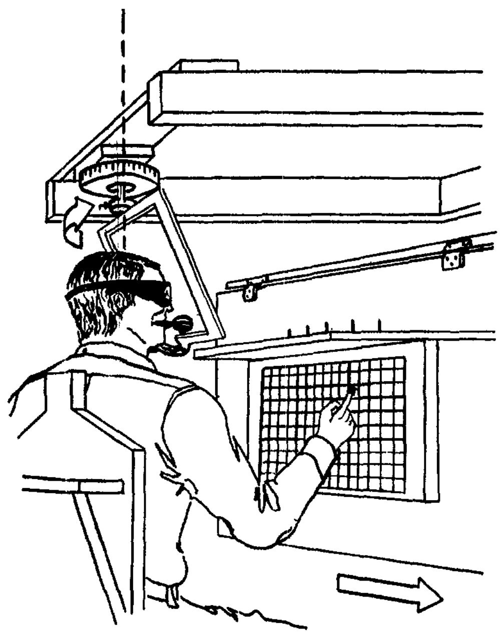

FIG. 1. Testing apparatus for localization of visual targets, orientation of head to arm, and relocation of learned postures.

3. Relocated position: The *S*s who performed the RP task were trained for nearly a week before being tested. The tacks used in the HA test were retained. During the training sessions, *S*, while blindfolded, learned five postures of his arm such that he could place his index finger upon each of the five tacks. In the beginning, *E* verbally helped to guide *S*'s finger to the tacks; then *S* held his arm in position and was told to concentrate on how his arm felt, i.e., its posture. Each training session lasted approximately 10 min., and it took an average of 1 wk. for *S* to reach the criterion of performance discussed below. Testing began the day *S* reached this criterion. During the test, the tacks were removed from the board and *S* was asked to reposition his arm in the previously learned postures. No feedback was given during the test. The *S* was instructed to start his arm movements from different positions so as to minimize the possibility of his learning a motor response instead of a postural set.

The *S*s used both their right and left hands during the three tests, although only one hand was used in a given experimental session. The RP *S*s were trained to relocate each hand on the five tacks before testing began.

During each of the three tests, *S* marked each of the five targets twice. The five RP and HA tacks were identical and were situated directly below the five visual targets. Therefore, the final positions of *S*s' arms were similar in all three tests, although each *S* was only acquainted with one target type.

TABLE 1

SHIFT IN DEGREES

| | Test cond. | | | | | |
|---|---|---|---|---|---|---|
| | Visual targets | | Head orienting to arm | | Relocated position | |
| | 1st shift | 2nd shift | 1st shift | 2nd shift | 1st shift | 2nd shift |
| Exposed hand | +2.46°** | +3.67°**** | +2.44°* | +3.36°*** | −1.69° | −2.81° |
| Unexposed hand | +1.17° | + .40° | +1.13° | + .85° | −3.03° | −4.71° |

Note.—Symbols: + = adaptive; − = antiadaptive.
* $p < .025$.
** $p < .01$.
*** $p < .005$.
**** $p < .001$.

During exposure, *S* wore 20-diopter prisms over his eyes. The marking surface was replaced by a slanted exposure surface, which was white with the outline of a black rectangle, 10 cm. high × 20 cm. long, in its center. The *S* traced the rectangle with his right forefinger as he watched his hand through the prisms under room illumination. The exposure periods each lasted 2 min.

*Experimental session.*—In each experimental session the following procedure was employed: (*a*) Practice: At the beginning of each session, *S* was given 10 practice marks, 2 on each of the five targets, presented in a randomized order. (*b*) Pretest: *S*s marked the targets as in the practice. (*c*) Exposure 1: *S* watched his right hand through 0-diopter prisms as he traced out the perimeter of the rectangle drawn on the inclined exposure surface. (*d*) Posttest 1: *S* marked the targets as in the pretest. (*e*) Exposure 2: *S* repeated the procedure of Exposure 1 except that 20-diopter, base-right prisms were used. (*f*) Posttest 2: *S* marked the targets as in the pretest. (*g*) Exposure 3: *S* repeated the procedure used in the previous exposure periods except that 20-diopter, base-left prisms were used. (*h*) Posttest 3: *S* marked the targets as in the pretest.

A screening procedure was adopted in order to equate the three different test groups with respect to stability of performance. The VT and HA *S*s were accepted only if their Posttest 1 responses did not change more than 2° (1.4 cm. at the marking surface) from their pretest responses after the exposure period with 0-diopter prisms. This criterion was also used to judge when the RP *S*s were sufficiently proficient at the relocated position task.

*Experimental design.*—Each *S* was tested twice, once using his right hand for the test and exposure conditions, once using his left hand during the test and his right hand during the exposure. These two sessions were separated by at least 24 hr., and the order in which the hands were tested was counterbalanced across *S*s.

The logic for testing the unexposed (left) hand is as follows: we expected from pilot studies that there would be little intermanual transfer of adaptation to the linear displacement of the prisms under the exposure conditions employed in these experiments; i.e., no adaptive shift should occur on any test when the unexposed hand was used. Any antiadaptive aftereffects caused by viewing the nonlinear distortions of the prisms, however, should be in evidence on the RP task irrespective of the hand tested. These negative aftereffects can be generated merely by looking through the prisms without sight of either hand (see Bauer & Degner, 1967). Consequently, antiadaptive shifts obtained when the unexposed hand was used in the RP test would indicate the magnitude of the negative effects induced by our exposure condition. Given these assumptions, a significant difference between the behaviors of the two hands would provide a reliable measure of compensation for the lateral displacement produced by the prisms.

## *Results*

The difference between the mean positions of marking on Posttest 1 and Posttest 2 was the measure of adaptation to Exposure 2, and the difference between Posttest 2 and Posttest 3 means was the measure of compensation for the Exposure Period 3. These shifts are presented in Table 1.

*Visual targets.*—The shifts obtained when the exposed hand marked the visual targets after both the second and third exposure periods were significantly greater than zero by one-tailed tests, $t\ (7) = 4.3$, $p < .01$; $t\ (7) = 8.75$, $p < .001$. However, neither of the two shifts obtained with the unexposed hand was significant at the .05 confidence level, $t\ (7) = 1.7$; $t\ (7) = .64$. After the third exposure period, a significant difference was found between the two hands using a one-tailed test for correlated means, $t\ (7) = 4.05$, $p < .005$. These results support the notion that there is no significant intermanual transfer of adaptation under our exposure conditions and justify using the difference in mean shift of the two hands as the measure of adaptation.

*Head orientation to arm.*—The difference between the two hands after the second exposure period just missed being significant at the .05 level by a one-tailed test, $t$ (7) = 1.81. The difference between the mean shifts of the two hands after the third exposure period was statistically significant, $t$ (7) = 2.58, $p < .025$. Furthermore, when the head oriented to the exposed arm, the shifts obtained after each of the two exposure periods were significantly greater than zero, $t$ (7) = 2.65, $p < .025$; $t$ (7) = 4.95, $p < .005$.

*Relocated position.*—The behavior of *S*s on this task was radically different from the behavior of *S*s on the VT and HA tasks. Significant, but negative shifts were obtained when the unexposed hand performed the test. These shifts, after each of the two prism exposure periods, were negative, i.e., toward the prism apex, and were significantly less than zero by two-tailed tests, $t$ (7) = 2.83, $p < .05$; $t$ (7) = 6.81, $p < .001$. The differences in mean shifts for the two hands after each exposure period did not reach significance at the .05 confidence level, $t$ (7) = .84; $t$ (7) = 1.21.

### *Discussion*

The similarity in magnitude and direction of the VT and HA shifts indicates that adaptation is confined to neither the visual system nor to the response mechanism of the arm. The remaining question—whether adaptation represents a change in either sensorimotor coordination or the sensed position of the arm—can be answered by considering the results of the RP task.

The large negative shifts obtained with each hand on the RP task indicate that the nonlinear distortions produced by the prisms in our exposure condition generated antiadaptive aftereffects. To determine whether an adaptive shift was being concealed on the exposed hand, we looked at the difference between the shifts of the two hands. This difference, although substantial, was not significant, and thus we could not conclude that there was evidence for a change in the sensed position of the exposed arm. One problem still remained. When we looked at the variability of shifts across *S*s for each of the three test conditions, we found that for the exposed hand, *S*s' standard deviations were much greater on the RP task ($\sigma = 4.27$) than on either VT ($\sigma = 1.21$) or HA ($\sigma = 1.89$). This increased variability of shifts in the RP task renders it more difficult to detect a significant difference between the shifts of the two hands. Consequently, we performed a second experiment in which we tried to prevent the occurrence of negative shifts and to decrease the variability of shifts on the RP test.

## EXPERIMENT II

Having demonstrated that the relocated position test is influenced by the nonlinear distortions produced by the prisms, we tried to eliminate these effects so as to reveal any adaptive changes that may have been masked by the negative shifts. The new exposure condition was designed to reduce visual information about prismatic distortion other than lateral displacement. We also reduced the number of postures to be learned in the RP test. The *S*s in the first experiment had complained about the difficulty of the RP task; some reported referring the positions of the tacks to directions from the body. Thus, to locate the position of the tacks, *S* tried to place his hand in front of his shoulder, neck, etc., rather than relying on the sensed position of his arm. If, after exposure, *S* felt (as some reported) turned with respect to the apparatus, he would have to compensate by reaching past his shoulder, neck, etc., in the direction opposite to his perceived rotation in order to reach the positions on the marking surface located in the preexposure test. This strategy produces apex-ward or negative shifts since the nonlinear distortions make *S* feel turned toward the base of the prisms. Furthermore, if *S* were indeed using other body parts as implicit reference points for relocating his arm, the task becomes one of alignment. Under these conditions, the sensorimotor explanation would predict a difference between the two hands on the RP test, just as it does for the HA task.

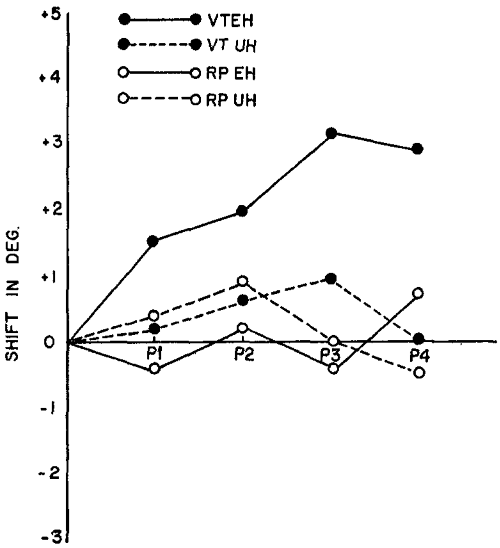


FIG. 2. Cumulative shift in degrees for both the exposed hand (EH) and the unexposed hand (UH) on both of the two tests: visual targets (VT) and relocated position (RP). (P1–P4 represent the four posttests; + = adaptive; − = antiadaptive).

We hoped that *S* could rely solely on the sensed position of his arm if he had to remember only two positions rather than five as in Exp. I. To prevent *S* from associating the learned postures with objects in remembered visual space, he was blindfolded before being led into the experimental room. Given these changes in the RP test, we expected to find reduced variability of shifts by forcing all *S*s to use the same strategy, i.e., relying on the sensed position of the limb. We also expected that under these conditions, the difference between the two hands on the RP test would disappear.

The VT and RP tests described in the first experiment were repeated with minor modifications to determine whether adaptation represented a change in the sensed position of the adapted arm.

## *Method*

*Subjects.*—Eight MIT undergraduates, naïve as to the purpose of the experiment, were used as *S*s.

*Apparatus and procedure.*—The marking apparatus was retained from Exp. I. Two luminous points of light in an otherwise dark room replaced the nails as the visual targets and two, rather than five, tacks were used to train *S*s on the relocated position task.

During exposure, *S* held a luminous plaque, 7.5 × 1.3 cm. in his hand, which rested on the slanted exposure surface of Exp. I. The room was completely dark, the only visible object being the luminous plaque. The *S* watched the movement of the light through 20-diopter prisms as he moved his hand back and forth to the beat of a metronome. He was instructed to maximize rotational movements about his wrist and thereby provide optimal information about the lateral displacement of the prisms.

The procedure during each of the experimental sessions was nearly identical. The *S* was blindfolded and led into the experimental room. At no time did he see the apparatus or the surrounding environment. He was seated in a chair positioned according to guide marks on the floor. This insured that the position of his body in relation to the apparatus remained constant across all test and training conditions.

1. Visual targets: *S*s were first tested on the visual targets. The selection criterion of Exp. I was adopted. After biting on the biteboard, *S* was asked to mark each of the two luminous targets five times. The *S* was instructed to start his movements from different rest positions in order to minimize the possibility of his learning a specific motor response. He then marked each target five more times. Following this pretest, *S* watched the luminous plaque through 0-diopter prisms as he moved his hand in time to the metronome for 1 min. Posttest 1 was then administered. Four subsequent exposure periods were given, each 1 min. in length, and each was followed by a posttest identical to the pretest. Half of the *S*s used 20-diopter, base-right prisms in these four exposure periods, and half used base-left prisms.

2. Relocated position: After two sessions on the visual targets, *S*s were trained to criterion on the RP task (about 1 wk.). They were then tested on RP in two sessions. Only two postures of the arm were learned; otherwise, the training and testing procedures were similar to those employed in the previous experiment.

*Experimental design.*—Each *S* was run on each type of target, visual and relocated position. And, as in the first experiment, *S* was tested with both exposed and unexposed hands. Only one hand and one target type were tested in a given session.

## *Results*

The differences between the mean positions of markings on Posttest 1 and each of the subsequent posttests were calculated to yield the cumulative shift after each of the four prism exposure periods. The mean cumulated shifts for the eight *S*s in each of the four test sessions are presented in Fig. 2. Of the four conditions, only the total shift in marking the visual targets with the exposed hand differed significantly from zero by a one-tailed test, $t\ (7) = 5.90$,

$p < .0005$. There was a significant difference, $t$ (7) = 5.19, $p < .005$, between the magnitudes of the total shifts obtained with the exposed and unexposed hands on the visual target test but not on the relocated position test.

### *Discussion*

The data from Exp. II indicate that the new exposure condition—watching a moving luminous line in the dark—eliminated negative shifts on the RP task. Two other procedural changes—using only two targets and preventing *S* from seeing the apparatus—eliminated the difference found in Exp. I between the shifts of the two hands on the RP test. As can be seen from Fig. 2, there is no suggestion of either an adaptive shift with the exposed hand or a differential shift been the two hands on the RP test. The variability of shifts on RP was $\sigma = 3.15$, a reduction from the value obtained in Exp. I, but still greater than the variability measure on VT ($\sigma = 1.31$).

The results of this experiment are in accord with the predictions of the sensorimotor explanation of prism adaptation. No evidence was found for either a change in the sensed position of the arm or for significant intermanual transfer of adaptation.

Although we believed these results sufficient to negate the claims of the proprioceptive explanation, we thought that further positive evidence was necessary to make a convincing case for the sensorimotor explanation. The third experiment was designed to show adaptive shifts occurring on an alignment task (HA) but not on a postural task (RP) performed during the same experimental session.

## Experiment III

The decision to contrast head orientation with relocated position was based on the following considerations. Experiment I indicated that the HA and VT tasks yield comparable measures of eye–hand adaptation. The magnitude and direction of shift were roughly equivalent for the two tests. However, the head orientation task has one advantage over pointing at a visual target: it is a nonvisual task, and thus more similar to the relocated position test. Furthermore, the use of this HA test obviates any criticism which might have been raised by the experiments of Craske (1967) and Kalil and Freedman (1966). They found that there may be a change in perceived eye position after exposure to prisms. Craske (1967) maintains that this change could be responsible for a portion of the adaptation evidenced in pointing at visual targets. If there were such a change in the felt position of eye in head, produced by our exposure conditions, it would be expected to affect only visually guided behavior. Neither the relocated position test nor the head orientation task should be influenced by such a change.

### *Method*

*Subjects.*—Ten MIT undergraduates served as *Ss*. Each was naïve as to the purpose of the experiment.

*Apparatus and procedure.*—The apparatus from the first two experiments was modified for Exp. III. Instead of the vertical marking surface, a horizontal shelf extended out from the wall just under the level of *S*'s chin. The relocated positions were defined by two thumbtacks placed at arm's reach on the underside of the horizontal shelf. One position was to the right of *S*'s midline, the other to the left. When *S* put his finger on the tack, he could then orient his head to his outstretched hand.

Each *S* was blindfolded before being led into the experimental room. He was not permitted to view any part of the apparatus until the experiment was terminated. The *S* was seated with his head held by a biteboard rigidly attached to the head frame. During the RP test and all exposure conditions, this frame was locked into the straight-ahead position. During the HA test, it was free to rotate about a vertical axis through *S*'s head.

Each *S* was given several days of training on each of the two tests, RP and HA, before he participated in the two experimental sessions. The procedure was as follows:

The blindfolded *S* was seated in front of the apparatus and the biteboard adjusted. His right hand was guided to each of the two tacks by *E*. He was told that the object of the task was to learn the two postures of his arm such that he could accurately reposture his index finger upon the head of each of the tacks. He was told to concentrate on the feel of the different joint angles and to keep his eyes closed, even though blindfolded. When *S* missed the tack during training, he was given verbal commands that guided his finger along the surface until he made contact with the target. After he had placed his finger upon one of the tacks, the head frame could be unlocked to allow *S* to move his head back and forth until he was satisfied that his head was pointing directly at the tip of his unseen finger.

An average of three training sessions was given, each lasting approximately 10 min. Many more training trials were given in the RP task than in the HA test.

Each experimental session consisted of six parts:

1. Training: The *S* was given a 5-min. training

TABLE 2

Shift in Degrees

| | Test cond. | | | |
|---|---|---|---|---|
| | Head orienting to arm | | Relocated position | |
| | 1st shift | 2nd shift | 1st shift | 2nd shift |
| Exposed hand | +.67° | +2.66°* | −.79° | +.36° |
| Unexposed hand | −.84° | −.28° | +.44° | −.64° |

Note.—Symbols: + = adaptive; − = antiadaptive.
* $p < .001$.

session on both tests; the procedure was identical to the training sessions of the preceding days.

2. Pretest: The thumbtacks were removed from the underside of the marking surface and *S* was instructed to relocate his arm in each of the two learned positions without receiving any error information. Once contact with the surface was made, the head frame was unlocked and *S* oriented his head to the forefinger of his outstretched arm. After completing the task, *S* returned his hand to his lap and his head to the straight-ahead position. The head frame was then locked and *S* was instructed to relocate his arm in the other learned posture. The arm movements were initiated from different starting points, and *S* was reminded to concentrate on where his arm felt. No rapid reaching movements were allowed. The arm was repostured five times in each of the two positions, and there were thus 10 orientations of head to finger.

3. Exposure: After the pretest was completed, the exposure surface was placed in front of *S*. A pair of 20-diopter wedge prisms oriented base right or base left, was placed over *S*'s eyes and the head frame was tilted forward through an angle of 24° so that *S*'s line of sight was more nearly perpendicular to the plane of the slanted exposure surface. The exposure condition was the same used in Exp. II; *S* tracked the luminous plaque which he held in his moving hand. This luminous line was the only visible object in the darkened room. The exposure period lasted 3 min., and upon its termination the prisms were removed, the blindfold replaced, and *S* returned to an upright position.

4. Posttest 1: Following the exposure period, *S* performed the RP and HA tasks as described in the pretest.

5. Exposure 2: This second exposure period was identical to the first, except that *S* now wore prisms of opposite orientation to those worn in the first exposure period.

6. Posttest 2: A second posttest, identical in nature to the two previous tests, was administered after the second exposure period.

*Experimental design.*—Each *S* was run in two experimental sessions, on separate days. On 1 day, he used the right hand for both test and exposure conditions. On the other day, he used the right hand for the tests, and the left during exposure. This latter condition allows us to look once more for intermanual transfer, and also served as a control for any negative shifts produced during the exposure period. The *S* was also exposed to both orientations of prisms within a given session. The order of the prisms as well as the order of hands used was counterbalanced across *S*s.

## *Results*

The differences between the mean positions of markings on the pretest and Posttest 1 were calculated to determine the adaptation to Exposure 1, and the difference between Posttest 1 and Posttest 2 served as an indication of compensation for Exposure 2. The second shift (Posttest 2–Posttest 1) was entered into a three-factorial analysis of variance. The factors were *S*, hand, and test. The *F* ratios for the main effects and higher order terms were computed using the appropriate interaction with *S*s as error term. A significant Hand × Test interaction was found, $F\ (1, 9) = 5.48$, $p < .05$, indicating that the differences between the shifts of the exposed and unexposed hand differed significantly for the two tests. The mean shifts for the Hand × Test interaction are presented in Table 2.

After Exposure 2 a shift, significantly different from zero by a one-tailed test, $t\ (9) = 4.60$, $p < .001$, was obtained with the exposed hand on the HA task but not on the RP test, $t\ (9) = .62$. There was also a significant difference between the shifts of the two hands on the HA test, $t\ (9) = 3.40$, $p < .005$, but not on the RP test, $t\ (9) = 1.13$, after the second exposure period.

The shifts produced by the first exposure period were not significantly different from zero at the .05 confidence level. We have found in previous experiments that the reverse base paradigm used during the exposure periods of Exp. I and III results in larger and more consistent shifts after the second exposure to prisms, i.e., exposure to the opposite prism base (Graybiel & Held, 1970). The fact that the first HA shift with the exposed hand was not significant is probably a result of the short exposure period (3 min.) coupled with the reduced visual input, i.e., viewing the luminous line in the dark. The variability measures for the HA and RP tests were comparable: RP, $\sigma = 1.80$; HA, $\sigma = 1.81$.

We therefore felt justified in using the difference in the shifts of the two hands as an indicator of adaptation for both RP and HA.

### *Discussion*

The results of this experiment confirm the findings of the first two experiments. We have been able to show significant adaptation occurring when the head orients to the unseen but adapted arm, at the same time that the reposturing of the exposed arm does not change. Since both tasks were nonvisual, it is doubtful that any postulated change in the registration of eye position (Craske, 1967; Kalil & Freedman, 1966) could be responsible. The predictions of the sensorimotor explanation are verified by these data.

## Conclusion
## (Experiments I, II, and III)

Some fairly subtle differences in the procedures of these three experiments led to quite different results. We believe that the difficulty *S* experienced in learning five relocated positions (Exp. I) resulted in his making either an implicit alignment of arm to torso or a directed reach to a point in remembered visual space during the RP test. These strategies led to a substantial difference in the behaviors of the two hands on RP in the first experiment. Using fewer targets and preventing sight of the experimental room seemed to eliminate such tactics and therefore the difference between the two hands. The pattern of results obtained also depended upon the procedure used during exposure. Minimizing information about the nonlinear effects of the prisms by using the luminous line in the dark reduced or eliminated antiadaptive shifts.

Much of the confusion in the literature generated by contradictory results might be explained if we considered the variations in procedures used by different *E*s (Kennedy, 1969; Hamilton, Sullivan, & Hillyard, in press). These variations are most crucial when dealing with a task such as relocated position where it is very difficult for *E* either to determine or to control the cues used by *S* to perform the task.

Although we have no independent measure of how *S* learned the relocated position test, i.e., whether he relied solely on proprioception or not, we can certainly conclude from these three experiments that *S*'s behavior on the RP test did not resemble his behavior on either the task of localizing visual targets or of orienting his head to his unseen arm. In each experiment, a significant adaptive shift was found in the latter two tasks when the exposed arm was tested, and in each experiment a significant difference was found after exposure between the behaviors of the two hands on these VT and HA tasks. No such systematic changes were found for the relocated position test. Consequently, it is difficult to conceive of adaptation as a change in the position sense of the adapted limb, i.e., a change in the initial common pathway of proprioceptive input from that limb. Such a change, if it had occurred, should have been in evidence on all three tasks alike.

The results of the above experiments were consistent only with the sensorimotor explanation of prism adaptation. Therefore, we decided to test for further generalization to other orienting tasks. Operationally, the task of pointing to a visual target involves aligning the hand or fingertip to a given visual direction (retinal) of the target. The related task, that of orienting the eye to a given position of the hand, had not yet been directly tested. Hillyard and Hamilton (in press) used the alignment of a visual target over the adapted arm to indicate the alignment of eye to arm, but no measurements of eye orientation were actually made. On the basis of the sensorimotor explanation, one could expect that such changes would be complementary. In order to test for this reciprocity, the following experiment was performed in which measures of the orientations of the eye to the unseen fingertip were used as the indicant of adaptation.

## Experiment IV

### *Method*

*Apparatus.*—The orientations of eye and hand were simultaneously registered by means of a device described in detail elsewhere (Steinbach, 1969; 1970). It consisted, in essence, of a photoelectric monitor of eye position (Stark, Vossius, & Young, 1962) together with an electrical recorder of the position of *S*'s forearm, which was strapped to a lever as rigidly as was feasible. The lever was pivoted near *S*'s elbow and moved horizontally between stops set so as to allow the tip of the middle finger to move over a range of 20° of visual angle. When desired, the signal registering position of the fingertip was fed into an oscilloscope so as to drive a spot trace. This spot was imaged by a lens on a ground-glass screen viewed by *S* in a fully reflecting mirror that covered the arm and made the image of the spot appear in the plane through which the fingertip moved.

Measurements of the static alignment of eye and hand were calibrated by having *S* fixate the oscilloscope spot superimposed spatially on the tip of his middle finger when held in a stationary position. The screen, viewed at an illumination low in the photopic range, had a narrow black line extending across it, approximating the trajectory through which the fingertip moved when the arm moved the lever between its stops. With the spot trace turned off, *S* was instructed to "look at" his fingertip, as if it were visible, holding his gaze on the black line. By this means, vertical misalignments were eliminated without constraining horizontal alignment. The arm and hand were, of course, completely occluded from view. The *S*'s head was fixed by a biteboard mounted to the front of the apparatus, which also held the eye monitor.

*Subjects.*—Four male and two female employees and students at M.I.T. served as volunteer *S*s. The visual acuity of all *S*s was sufficient to perform the task without corrective lenses and none had any reported or noticeable visual defects.

*Procedure.*—A session consisted of the following, in sequence:

1. Initial calibration measurements.
2. Pretest: *S* moved his arm to a self-adopted position, held it there, and attempted to "look" at his nonvisible fingertip. The spot trace was off. When satisfied that he was accurately oriented to his fingertip, *S* operated a switch that simultaneously recorded the position of the eye and hand. He then moved his hand to a new position, being instructed not to move it in any systematic or orderly sequence, repeating the measurement sufficient times to insure a distribution of positions throughout the 20° range of movement of the arm. The number of measurements averaged 15. Typical data are plotted in the figure reproduced in Steinbach (1970).
3. Exposure 1: Following the pretest, the spot trace was turned on by *E* and laterally displaced from the true position of *S*'s middle finger by an amount equal to 9° 20′ in visual angle. This displacement is equivalent to that produced by a prism of about 16.5-diopter power. When *S* moved his arm back and forth between the stops, the scope trace moved in perfect synchrony but was displaced to one side of *S*'s fingertip by 5 cm. The *S* was instructed to track the spot while moving it irregularly, i.e., varying amplitude and frequency of movements, for a period of 3 min.
4. Posttest 1: Following Exposure 1, the scope trace was extinguished and *S* was instructed to align his eye to his statically positioned fingertip, as in the pretest. Again, approximately 15 alignments of eye to hand were taken, with *S* instructed to vary unsystematically the position of his hand.
5. Exposure 2: The trace was again turned on, but this time the spot was horizontally displaced 9° 20′ from *S*'s fingertip in the direction opposite to that of Exposure 1. The *S* again tracked the spot for 3 min., as in Exposure 1.
6. Posttest 2: The scope trace was extinguished and eye–hand alignments tested as before.
7. Final calibration: A final calibration of eye position was taken with the spot trace on and with zero displacement of the spot with respect to *S*'s fingertip.

Each *S* was exposed to both sequences of spot displacement (i.e., Right–Left and Left–Right) in two different sessions separated by at least 24 hr. The Postexposure 2–Postexposure 1 difference in eye–hand alignments was used as the measure of adaptation.

*Supplementary experiment.*—In order to be sure that the changed alignment of the eye to the hand was not merely a consequence of maintaining an asymmetrical posture of the eye, four of the *S*s were run in an additional condition. A small fixation light was projected onto the ground-glass screen in *S*'s midline and the experiment repeated exactly as described above except that *S*'s eyes remained stationary during the two exposure periods. During the tests the fixation light was turned off.

## *Results*

*Calibration of eye position.*—In 9 of the 12 recording sessions of the main experiment (6 *S*s × 2 Displacement Sequences), the initial and final calibrations of eye position agreed within 1°. During two sessions, there was a shift in a direction opposite that which would favor an adaptive shift; for the shifts obtained in these two sessions, *no* compensation for calibration shift was made. In one session, the calibration change favored the adaptive shift and was *subtracted* from the total shift obtained.

The sets of points representing eye–hand alignments for the Postexposure 2 and Postexposure 1 measurements were plotted and straight lines were fitted by eye through each set. The lateral displacement of the straight line fitted to the Posttest 2 measurements from that fitted to Posttest 1 measurements represents the shift produced by exposure. All of the 12 shifts were in the adaptive direction and averaged 8.0°. For the four *S*s in the supplementary experiment, run while fixating during exposure, the shifts obtained were in all cases in the adaptive direction and of about the same magnitude as those found when *S* actually tracked the displaced spot.

## *Discussion*

The results of this experiment are in accord with the notion that changes in hand–eye coordination, generated by exposures of the type used in this experiment, should be accompanied by reciprocal changes in eye–hand coordination. The supplemental result that fixation of gaze does not reduce amount of adaptation eliminates the possibility that a prolonged asymmetry in gaze produced the shifts.

## General Conclusion

When *S* views his hand through a wedge prism, depending upon conditions of exposure, he may receive several kinds of abnormal information. We have been primarily concerned with that derived from the displacement between the image of the hand and its actual location. When this is either the primary or the sole source of information, as in the above exposure procedures, the results bear out our contention that the changes are of the sensorimotor type. They are specific to responses involving the exposed arm in spatially directed behavior. The changed response generalizes over targets in several sense modalities. Furthermore, the change is evident when the exposed arm serves as either target or target indicator. Taken together, these characteristics implicate recalibration of a central control system.

Appealing as they are for their simplicity, explanations in terms of change in either input processing (analogous to an initial common path) or output processing (a final common path) simply do not account for the data. To these difficulties must be added recent results of Graybiel and Held (1970) and others, which are not amenable to explanation in peripheralistic terms. These newer results must also be taken into account in modeling the control mechanism for spatially directed acts.

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