

VISUAL AND PROPRIOCEPTIVE ADAPTATION TO OPTICAL DISPLACEMENT OF THE VISUAL STIMULUS¹

JOHN C. HAY
Smith College

AND

HERBERT L. PICK, JR.
University of Minnesota

The effects of long-term optical displacement of the visual stimulus were measured in a wide variety of sensory coordinations. The pattern of changes observed indicated that a transient adaptation in the proprioceptive system is succeeded by a stable adaptation in the visual system. It was found that viewing the whole body during optical displacement, rather than just a part of it, serves to induce the visual adaptation.

When the environment's optical direction from the eye is displaced to one side of its objective direction, as by a wedge prism in front of the eye, the normal coordination of vision with the other spatial senses is correspondingly altered. There have been several studies of adaptation to optical displacement, and of the kind of experience needed to induce it (Held & Hein, 1958; Helmholtz, 1925). These studies have usually employed eye-hand coordination as the dependent variable. If *S* points to a visible target, while looking through a prism, his error is initially comparable to the optical displacement imposed by the prism, so long as he does not see his hand. If, however, he is allowed to look at his moving hand through the prism for a few minutes, his eye-hand coordination shows a compensatory change even when the hand is again concealed. This phenomenon shows that the visual and proprioceptive systems have been reordinated: A new hand position gives *S* the feel of coinciding with the visual direction of the target.

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But eye-hand recoordination does not, by itself, tell us whether the adaptive change occurred in the seen location of the target, in the felt location of the hand, or in some central system that relates the two (Walls, 1951).

Recent studies have indicated that the adaptation induced by looking at one's hand through a prism is proprioceptive in nature (Harris, 1963; Pick, Hay, & Pabst, 1963). The evidence comes from testing other hand coordinations along with eye-hand coordination. At the same time that *S* is found to reduce his error in pointing at visible targets, he starts to show errors in pointing at sounds or "straight ahead." The changes in pointing at visual and nonvisual targets are similar in size and direction. This uniform change in hand positioning, irrespective of the sense modality of the target, seems most reasonably explained by supposing that the proprioceptive system of the hand, during the prismatic view, was "re-calibrated" to match the externally imposed visual error.

The present study concerns the question of whether the optically displaced visual system always draws other systems into alignment with itself, or whether some kinds of prism exposure can induce an adaptation within the visual system itself. Our method involves studying the pattern

of changes in several different sensory coordinations, and then inferring the locus of the adaptation.

In Exp. I, Ss engaged in their normal activities during 6 wk. of continuous exposure to spectacle prisms. This exposure condition would seem to give the best opportunity for all possible adaptive mechanisms to operate. Changes in eye-hand and ear-hand coordination were measured throughout. In Exp. II, the battery of coordination tests was enlarged to isolate possible changes in the visual or auditory systems. Finally, Exp. III sought to identify the factors which determine the kind of adaptation that takes place.

EXPERIMENT I

Eye-hand and ear-hand coordination were measured in a group of eight Ss who wore prism spectacles continuously for 6 wk. (The general results for this group, including adaptation to various prismatic distortions, are summarized in Pick & Hay, 1964.) So long as a shift in the proprioceptive "feel" of the hand is the only adaptation, these two coordinations should show identical changes during exposure.

Method

Prism-exposure conditions.—Six women and two men, between the ages of 18 and 36, carried out their normal activities as college students while wearing 20 diopter prisms, mounted base left or base right in 40-mm. round spectacle frames. The optical displacement was approximately 11° , to the left for half the group, to the right for the others. The combined prismatic fields of the two eyes spanned about 60° vertically and 90° horizontally; side shields prevented any non-prismatic view. One S dropped out of the experiment after 33 days.

Coordination tests.—Eye-hand coordination was measured with an apparatus based on Held and Gottlieb's (1958) design. The S saw a set of six targets reflected in an oblique mirror, and he reached under the mirror to

mark their apparent locations on a concealed surface at the same distance as the targets. Ear-hand coordination was measured with a form of the apparatus used by Pick et al. (1963): While blindfolded, S heard a clicker sound from each of five positions, and he marked its apparent direction on a pad of newsprint mounted below the clicker. These two coordination tests were given before, during, and after the prism-exposure period.

Results

Figure 1 shows the group's mean errors on both eye-hand and ear-hand coordination over the course of the experiment. The error is expressed in terms of its angular extent relative to the right eye. Positive errors are in the direction of the optical displacement; thus adaptation is indicated by a declining error. Ninety-five percent confidence limits given in parentheses beside each test's record are based on the mean daily standard error of the test.

Eye-hand coordination changes.—For 12 days prior to prism exposure, the eye-hand record shows close to zero constant error. When the spectacles are first put on, on Day 0, the discontinuity in the record shows that an error of about 8° is produced. (The discrepancy from the optical displacement of 11° may be due to some rapid adaptation before this test was administered.) An adaptive change is found by Day 1, compensating for 70% of the initial error. Further exposure leads to essentially complete compensation, although the last 12 tests continue to show a slight but significant ($p \leq .05$) difference from the preexposure tests. When the prisms are removed, on Day 42, the adaptation state is manifested by an aftereffect error opposite to the initial prism effect. This negative aftereffect shows a readaptation which approximately mirrors the prism adaptation curve.

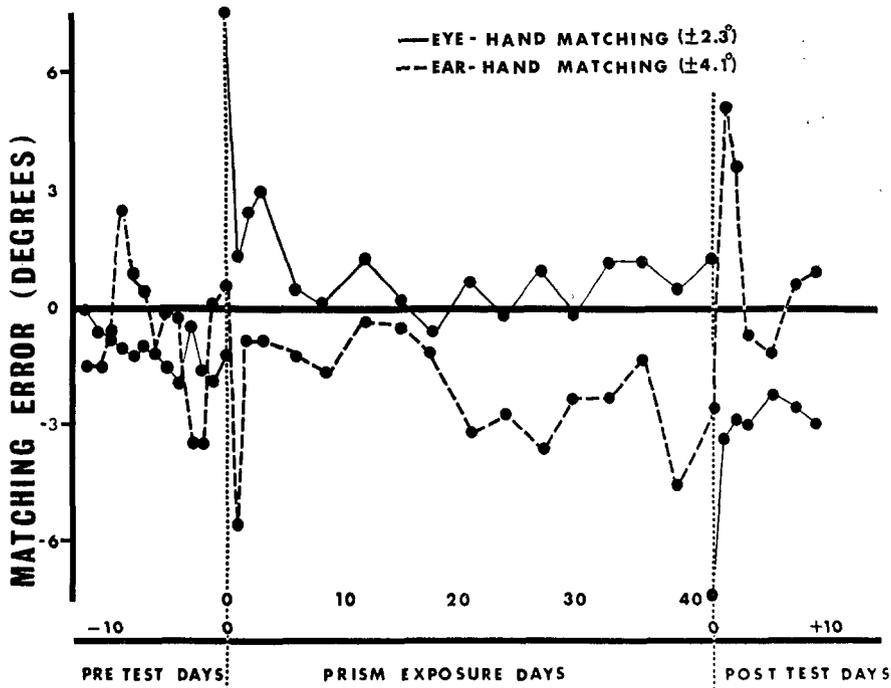


FIG. 1. Errors in eye-hand and ear-hand coordination during 42-days exposure to optical displacement. (Ninety-five percent confidence limits given in parentheses.)

Ear-hand coordination changes.— The ear-hand record before exposure shows no consistent bias, but manifests less precision than the eye-hand record. No change is registered, of course, when the prisms are first put on. Concurrent with the compensatory eye-hand change on Day 1, the ear-hand record shows a parallel change, as if both were due to a shift in felt hand position, in accord with the short-term exposure findings of Harris (1963) and Pick et al. (1963). The ear-hand error is transitory, however, being succeeded by a reverse shift on Day 2. During the following 15 days of exposure, no evidence of a chronic ear-hand error is found, as would be expected if there were a purely proprioceptive adaptation to the prisms. On Day 20 and thereafter, a negative drift develops which

is not readily explained by any theory.

During the first day without the spectacles, a transitory ear-hand error again appears, opposite to the first, as if the beginning of readaptation induced an opposite constant error of hand localization.

Discussion

The first stages of adaptation during the "naturalistic" prism-exposure conditions of the present experiment appear to induce the same pattern of coordination changes that Harris (1963) and Pick et al. (1963) found in short-term exposure to the hand alone. The ear-hand error disappears quickly, however, while the eye-hand compensation remains. A second process of adaptation is therefore indicated, one which develops at a slower rate.

Assuming that a proprioceptive alteration occurs in the first stages of prism

exposure, slower acting changes in either vision or audition could explain the subsequent coordination pattern. A visual system change might take place, stabilizing the eye-hand compensation, while allowing the quick acting proprioceptive adaptation to dissipate. Alternatively, the binaural localization system could be drawn along with proprioception into alignment with vision, cancelling the ear-hand error. The same interpretations apply to the events during readaptation.

EXPERIMENT II

Four new coordination tests were added to the eye-hand and ear-hand tests in a replication of the first stages of Exp. I. These tests were designed to confirm the occurrence of a non-proprioceptive adaptation; to show more clearly whether this adaptation is in one of the other sensory systems; and, if so, whether the new adaptation occurs in vision or in audition.

An *ear-eye coordination* test required *S* to identify the visual direction of a concealed sound source. Changes in this test should confirm the existence of adaptation elsewhere than in body proprioception.

An *eye-head coordination* test required *S* to turn his head until he was directly facing a visible target. The *S*'s setting of his head identifies what combination of ocular posture and retinal image position evokes in him the visual impression of straight ahead. Changes in this test therefore suggest an alteration within the visual system.

An *ear-head coordination* test required *S* to turn his head so that he was directly facing a concealed sound source. His head setting identifies what binaural stimulation evokes in him the auditory impression of straight ahead. Changes here would therefore suggest an alteration in the auditory system.

Finally, a *head-hand coordination* test required *S* to point straight ahead of his nose, with his eyes shut. Changes in this test should identify alterations in the felt position of the hand relative to the head.

Method

Prism-exposure conditions.—The prism exposure of the first 6 days of Exp. I was repeated on seven new *Ss*, four women and three men, from the same population. Four wore base-left, three base-right prisms.

Coordination tests.—A new apparatus was used in order to administer all coordination tests, except the head-hand coordination, on the same measurement scale, and to improve the precision of auditory localization. A horizontal scale of numerals, 2 cm. apart at 50 cm. from the eye, provided visible targets, and identifying markers for reporting the visual directions of sounds. Three loudspeakers, 5 cm. in diameter, were mounted just below the visual scale, one straight ahead and the others 5 cm. to the right and left. They were concealed from view by a cloth screen running the length of the visual scale. Half-second pulses of white noise could be delivered to them from a tape recorder to provide audible targets. The surrounding walls were lined with sound-absorbent tile. Beneath the speakers and the visual scale, there was a row of 30 push buttons, 2 cm. apart on centers, which registered *S*'s manual judgments of target position. The buttons, along with *S*'s hands and body, were concealed from view by a shelf that projected from below the speakers to *S*'s chin. The *S*'s head rested on a chin piece, and was rigidly located by a bite board molded in dental impression compound. The bite piece and chin rest were mounted on a Bausch and Lomb head support which permitted rotation. The *S* could thus turn his head, aiding himself with his left hand on the support post, and his head position could be measured by means of a pointer at the base of the support post.

Three test procedures were administered with this apparatus, and they provided measures of eye-hand, ear-hand, ear-eye, eye-head, and ear-head coordination. In one procedure, *S* was told a number on the visual scale, turned his head so that he was facing it (eye-head coordination), and then pushed the button which he felt to be directly under the number (eye-hand coordination). In the second procedure, *S* was presented with a train of white noise pulses from one of the

speakers, turned his head so that he was facing it (ear-head coordination), and then pushed the button directly under the sound (ear-hand coordination). In the third procedure, *S* was again given the audible target, again turned his head towards it (ear-head coordination again), and then reported the visual scale number closest to the direction of the sound (ear-eye coordination). These tests were given in a mixed order, 10 measures on each (doubled for the ear-head test), and they took about 20 min. in all. They were given before, during, and after prism exposure. In this experiment, *S* did not wear the prisms during testing, but he did wear a pair of empty spectacle frames to match the visual framework of exposure.

The head-hand test was given in another apparatus which held *S*'s head in a fixed position, giving a stable direction for hand pointing. His head fixed by a bite board, and his eyes blindfolded, *S* reached out and put his right index finger on a glass pane 57 cm. from his head, locating it so that it felt to be directly in front of his nose. Ten measures were taken on this test on each testing occasion.

Results

Figure 2 shows the changes in coordination on the six tests over the course of the experiment, using the preexposure measures as the base line. Positive changes are compensatory for the optical displacement (or error producing for nonvisual tests in the direction opposite the optical displacement). An analysis of variance shows a significant variation between coordination tests, $F(4, 24) = 5.84$, $p \leq .01$; but does not show a reliable interaction among their records over time, $F(16, 96) = 1.21$, $p \leq .20$.

Eye-hand coordination changes.—A stable compensation is again found, almost reaching its maximum in the first 12 hr. of exposure.

Ear-hand coordination changes.—A transient change is found here as in

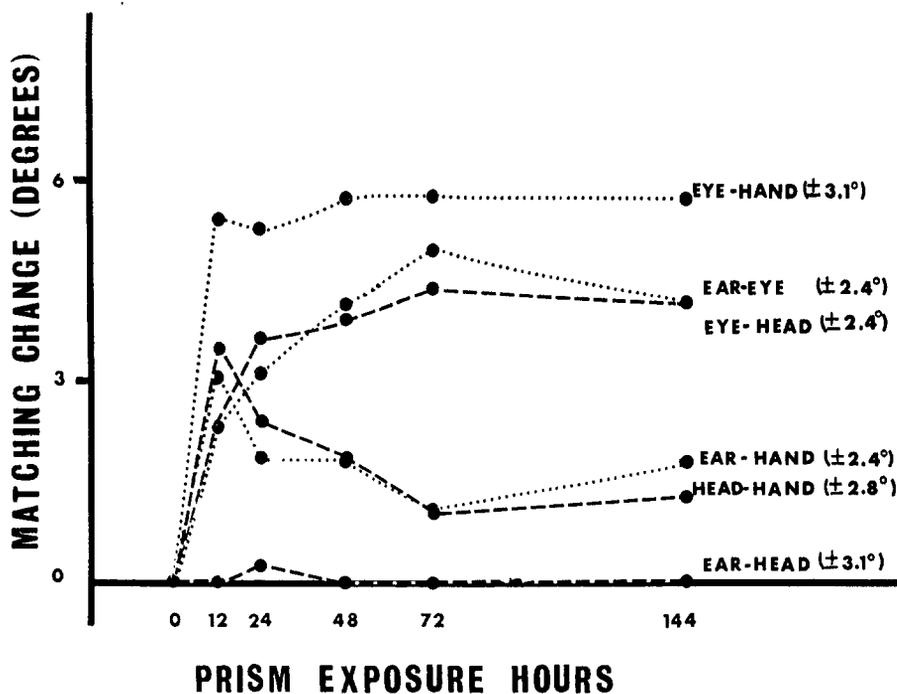


FIG. 2. Changes in six coordination tests during 6 days exposure to optical displacement. (Ninety-five percent confidence limits given in parentheses.)

Exp. I, showing a gradual decline after a rapid initial rise. The error does not return to zero as in Fig. 1; the improved precision of the present apparatus may be a factor in this difference.

Ear-eye coordination changes.—A compensatory change is found in this new test, showing a gradual rise, and thus confirming the hypothesis of a nonproprioceptive adaptation developing more slowly than the proprioceptive adaptation.

Eye-head coordination changes.—The compensatory change in this test matches that of the preceding test throughout, suggesting that the two coordinations reflect in common an adjustment in the visual system.

Ear-head coordination changes.—No reliable change is found in this coordination, indicating that no alteration occurred in the binaural localization system.

Head-hand coordination changes.—This test shows the same transient change as the ear-hand test, confirming a brief adjustment to the proprioceptive system.

Relationships between the coordination changes.—The ear-eye and ear-hand changes taken together seem to equal the eye-hand change over the course of the prism exposure. This suggests that processes acting in the first two coordinations are having a combined influence on eye-hand coordination. It is reasonable to suppose that these processes are adaptations in the visual and proprioceptive systems.

Discussion

The pattern of coordination changes shown in Fig. 2 is exactly that to be expected if a gradual adaptation in the visual system accompanies a rapid, largely transitory one in the proprioceptive system. The visual adaptation by

itself accounts for the ear-eye and eye-head records; the transient proprioceptive adaptation by itself accounts for the ear-hand and head-hand records; and the two together account for the eye-hand record.

Supplementary study.—A similar experiment, using 3 days of prism exposure, was summarized in Pick and Hay (1964). This study measured ear-eye coordination along with eye-hand and ear-hand coordination, in nine Ss not used in any of the present experiments. The records for this group are congruent with Fig. 2, showing a large eye-hand adaptation, a somewhat smaller ear-eye change, and a transient ear-hand error.

EXPERIMENT III

What conditions of prism exposure induce an adaptation of the visual system? In the two foregoing experiments, where a visual adaptation was found, an indefinite variety of prismatic views was experienced by S as he carried out his normal life activities, and a long period was allowed for those experiences to have an effect. These exposure conditions contrast with those of the studies by Harris (1963) and Pick et al. (1963), in which prism exposure was limited to a view of one hand, and lasted 5 min. or less. The latter studies appear to have produced a purely proprioceptive adaptation. Does the difference in things viewed through the prism, or the difference in exposure time, account for the difference in adaptations? The present experiment varied the kind of visual experience during prism exposure, to see if this factor could account for differences in the nature of adaptation.

An *expansion pattern-exposure* condition (Cond. A) was tested, during which S walked towards a visible target and experienced the optical displacement of the center of expansion in the visual field (cf. Held &

Freedman, 1963). It was hypothesized that the purely visual discrepancy between the normal and the prismatic expansion pattern might induce adaptive adjustments within the visual system. To keep the effects of this visual discrepancy distinct from those of intersensory conflict (see below), all parts of *S*'s body were concealed from his view during this exposure condition.

The *hand-exposure condition* (Cond. B) used by Harris (1963) and by Pick et al. (1963) was repeated, using an ear-eye coordination test to check the absence of a visual adaptation in this condition.

A *body-exposure condition* (Cond. C) was tested, during which *S* viewed the greater part of his own body, and saw and heard his own movements and their consequences. In this condition, a great many nonvisual stimuli were placed in conflict with vision, and might reasonably be expected to induce a change in it.

Method

Prism-exposure conditions.—Fifteen minutes of prism exposure was given to 54 undergraduate girls divided into three treatment groups of 18 each. The exposure conditions, ordered in terms of the amount of his body which *S* was allowed to see through the prism, were as follows:

Condition A: expansion pattern exposure.—The *S* walked back and forth between two eye-level targets, which he was instructed to fixate during approach. The targets were at opposite ends of a 20-ft. track; the pace was uncontrolled, and varied between 30 and 120 sec. for each 40-ft. circuit. A cardboard box was fitted over *S*'s shoulders to conceal his body from view.

Condition B: hand exposure.—The *S*'s head was on a chin rest, his body concealed by a curtain suspended from the chin rest. He reached under the curtain with his right hand to sort playing cards.

Condition C: body exposure.—The *S* walked the same track as in Cond. A, but this time he controlled his course by watching two guidelines on the floor 1 ft. apart. Each foot-

step was required to just touch the edge of a floorboard, and to be preceded by dropping and catching a small ball on an elastic cord. These requirements effectively forced *S* continually to watch his moving body.

In order to maximize the adaptation effects to be compared, the prism strength used was 26 diopters, giving a displacement of approximately 15°. A Risley variable prism, mounted in a modified skin diver's mask, was used: The right eye had a 60° round field, the left eye was covered. The mask was worn throughout the experiment, providing a uniform visual framework during exposure and testing. The rotary prism was set to zero power for pre- and posttests; during exposure, it was set to produce left displacement for half the *S*s in each condition, right displacement for the others.

Coordination tests.—The three coordinations between eye, ear, and hand were tested, using the same apparatus as in Exp. II. The *S*'s head was not free to turn in this experiment. Twenty measures on each coordination were taken in mixed order, before and after prism exposure; this took about 5 min. each time.

Results

The coordination changes produced by the three exposure conditions are shown in Fig. 3. An analysis of variance shows significant variation between exposure conditions, $F(2, 51) = 26.3, p \leq .001$; between coordination tests, $F(2, 102) = 32.5, p \leq .001$; and an interaction between them, $F(4, 102) = 3.90, p \leq .01$.

As the amount of the body seen through the prism increases, the eye-hand and ear-hand changes show a common pattern, with a maximum change produced by hand exposure. This is consistent with the theory that a proprioceptive adaptation underlies them both, during short-term exposure. It also suggests that the change imposed on proprioception by optical displacement is reduced when the "feel" of the whole body is put into conflict with vision.

In contrast, ear-eye coordination shows a different dependence on exposure conditions: The only reliable

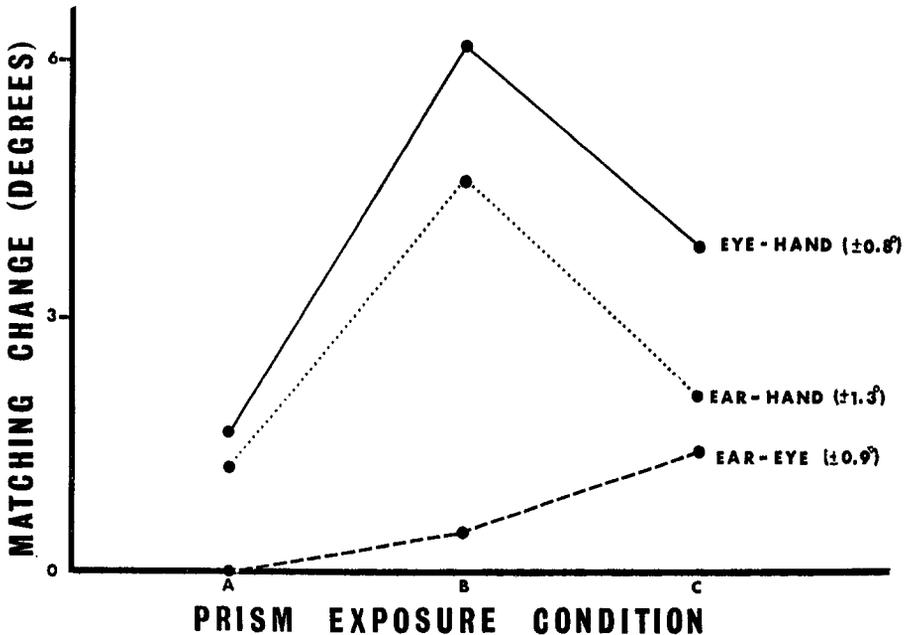


FIG. 3. Changes in coordinations between eye, ear, and hand as a result of different visual exposures during optical displacement. (Exposure conditions ordered in terms of increasing S's exposure to his own body. Ninety-five percent confidence limits given in parentheses.)

change was produced by body exposure, $p \leq .001$. A visual adaptation is thus indicated, and this interpretation is supported by the fact that the eye-hand change reliably exceeds the ear-hand change only in this condition, $p \leq .05$.

Discussion

Prism exposure to the moving body appeared to induce a visual adaptation. At the same time, body exposure reduced the proprioceptive adaptation from that produced by hand-only exposure. Exposure to the prismatic displacement of the optical expansion pattern induced no visual adaptation.

The body-exposure condition involves a high degree of discrepancy between vision and the other sensory systems. The S saw and felt his body moving, and he saw, heard, and felt contacts of his body with the floor and the ball. The expansion pattern-exposure condition,

instead of an intersensory conflict, provided a discrepancy from the usual optical results of walking. We may infer that visual adaptation to optical displacement is induced by a sufficiently strong conflict with other sensory systems. The hand-exposure condition, inducing no visual adaptation, may be supposed to provide insufficient intersensory conflict.

Supplementary study.—The body-exposure condition was repeated on 12 new Ss, and eye-hand coordination was tested with both hands. The results were in agreement with those of Fig. 3: $4.2 \pm 0.9^\circ$ change in the coordination of the right hand with the eye, $4.2 \pm 1.3^\circ$ for the same with the left hand; $3.1 \pm 1.8^\circ$ change in ear-hand coordination; and $1.5 \pm 1.1^\circ$ change in ear-eye coordination (95% confidence limits).

GENERAL DISCUSSION

Adaptations appear to occur in both the visual and the proprioceptive systems to optical displacement. The visual

adaptation occurs less readily than the proprioceptive one, but is more enduring when prism exposure is long extended. Proprioceptive adaptation can be induced, as has been previously reported (Harris, 1963; Pick et al., 1963), by viewing one's hand through a prism for a few minutes. Visual adaptation requires putting a greater variety of nonvisual stimuli into conflict with the optical displacement, by viewing most of one's body through a prism. The visual adaptation appears to replace an initial, quick acting proprioceptive adaptation during long-term prism exposure.

To what part of the visual system might this adaptation be due? Helmholtz (1925) originally suggested that optical displacement is compensated for by a change in "sensed" eye position: An oblique position of the eyes comes to evoke the impression of straight ahead. Such an eye-position adaptation may seem attractively consistent with the proprioceptive adaptation in "felt" hand position, but this parallel may be misleading: Neurological theory does not attribute the registration of eye posture to a proprioceptive system (Whitteridge, 1960). Some neurological evidence does make it reasonable to attribute changes in eye-hand coordination to modifications in eye posture, whatever the basis for its registration: Patients with a newly paralyzed eye muscle tend to point to one side of visual targets (Alpern, 1962). As a further argument for assigning any visual adaptation to eye posture or its sensing, the anatomical structure of the rest of the visual system

appears unsuited for adaptive changes in visual direction (Walls, 1951).

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