

Additivity of components of prismatic adaptation*

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Ss pointed with each hand at a light or at the unseen toe and looked in the direction of the unseen toe before, during, and after training one arm to point to a visual target which was progressively displaced to one side by a prism. Results show that a proprioceptive change in the trained arm is a universal component of the adaptation. When a change in the eye-head system occurs, it and the proprioceptive change in the arm sum to the total adaptation and it is accompanied by a predictable degree of intermanual transfer of the adaptation, as a felt-position theory of adaptation would predict. However, when there is no change in the eye-head system, the proprioceptive shift is not always sufficient to account for the total adaptive shift.

Human beings readily learn to point to visual targets seen through prisms which displace the visual scene laterally. One of the main concerns of those who have studied this learning process has been to diagnose the site of the adaptive changes in the system which spatially codes the articulations linking the arm to the visual target, viz, arm joints, neck, eye socket, and the position of the retinal image. The most obvious feature of these articulations is that they form an in-series closed-loop system (Howard, 1971a, b).

It is generally agreed that adaptation to prisms does not involve any shift in retinal space values (at least for foveal targets), and it is also agreed that the change is not in specific motor commands. It seems that there is no alternative but to agree with Harris (1965) that the total adaptive shift in pointing with unseen hand at a visual target is the algebraic sum of changes in the felt position of each of the joints in the system (arm joints, neck, or eye socket). A similar additivity hypothesis has been discussed by Hamilton, and has been investigated by Hay and Pick (1966) and Wilkinson (1971). Wilkinson found that the sum of changes in two subtasks—setting a light in, and pointing to, the median plane of the head—equalled the change in the task of pointing to visual targets. This is what the felt-position hypothesis would predict, because the two subtasks together test for all felt-position changes.

On the other hand, Held has maintained that there is no simple additivity of this kind. For instance, Hardt, Held, and Steinbach (1971) found that viewing the moving arm through prisms led to a shift in a target-pointing task and head-to-arm orientation task, but produced no shift in the task of relocating the arm in a position that was remembered from before training. They interpreted their results in terms of what Held has called "matching orientations" (Efstathiou, Bauer,

Greene, & Held, 1967) or what he has more recently called "sensorimotor" changes (Hardt, Held, & Steinbach, 1971). These terms apparently imply that there can be changes in the internal spatial mapping of one element onto another (say, arm positions in relation to head positions) without any change in tasks involving each element separately (the relocation-of-the-arm task for instance). It is claimed that the simple additivity hypothesis does not hold and that Harris's felt-position hypothesis is therefore untenable. However, the subtasks which Hardt et al used did not test for felt-position changes at all the joints; for instance, they did not test for a possible change in the felt position of the neck, and until this is done, they cannot conclude that something other than felt-position changes is involved.

It was not at first clear to us just how Held's theory of sensorimotor changes differed from Harris's felt-position theory. One of us, Howard (1971b) eventually drew up a flow chart of the system which clarifies what we think may correspond to that which Held was suggesting. This is shown in Fig. 1. The basic structural sensory and muscular elements are depicted by solid lines, and the hierarchy of neural coding processes by dotted lines. Harris's felt-position theory posits a change at any of the coding elements marked "a." We interpret sites of Held's sensorimotor change to be at elements marked "b." The important point is that changes in lower coding elements necessarily affect tasks involving elements higher in the system, but changes in higher elements do not affect tasks involving only lower elements.

The present experiment is designed to show whether the total adaptive shift in pointing to a visual target is the sum of felt-position changes in the arm and in the head-eye system, that is, in sites marked "a" in the chart, or whether that total adaptive shift exceeds the sum of changes in composite tasks, forcing the assumption that there are changes in higher-order coordinators, that is, at sites marked "b." The experiment is an extension of that done by Wilkinson, but we have incorporated a direct measure of eye position, thus avoiding the possible contaminating effects of visual targets in the task of directing the eyes

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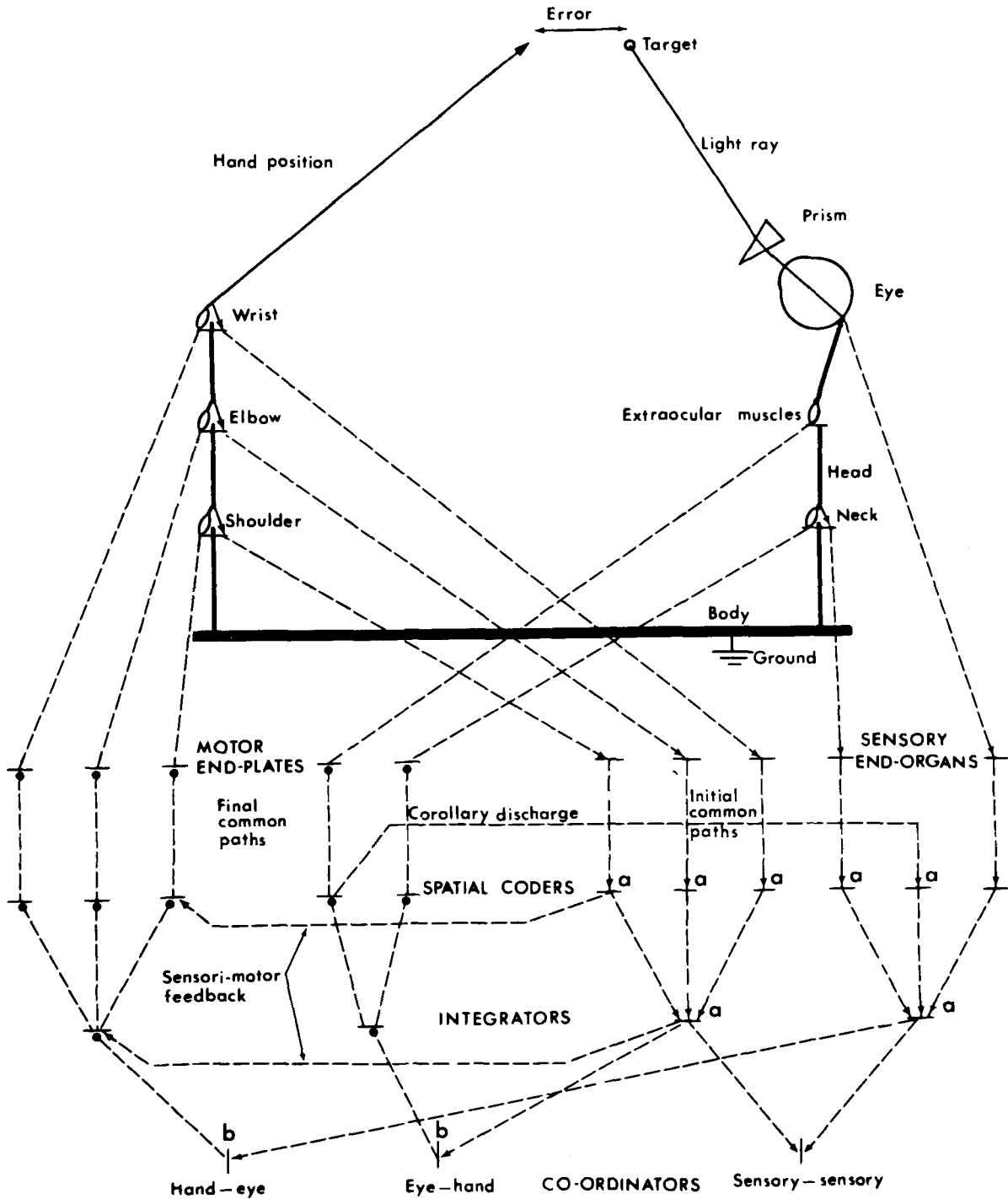


Fig. 1. Flow chart for the visual-motor system. In the upper half of the diagram, basic structural components of the eye-hand coordination system are drawn in lines of medium thickness (the instantaneous position of the hand and the light ray from target to eye and retina are also considered to be structural components—lighter lines). Components are linked by articulations; the following symbols are used: \blacktriangle position-sensitive receptors; \blacklozenge muscular elements. In the central and lower parts of the figure, neural elements are drawn in interrupted lines; junctions represent neural coding processes: arrows depict inputs to sensory elements; and filled circles depict inputs to motor elements. Sites marked "a" represent those which Harris postulates as the site of adaptive changes. Sites marked "b" represent those corresponding to what Held has called "matching orientations." (Adapted from *British Medical Bulletin*, 1971, 27, 249.)

to the median plane. Furthermore, for reasons which we shall explain shortly, we have compared additivity during the time error that feedback was given with additivity after error feedback was terminated.

Our subtasks are pointing the hand and directing the gaze to the hidden toe of one foot. We measured the direction of gaze by an objective method using nonvisible infrared light. We assume that these two subtasks are exhaustive, nonoverlapping components of the total task of pointing to visual targets at the levels below that of coordinators. Hence, if training-induced shifts in the subtasks fail to add to the total adaptive shift, this will be taken as demonstrating some change in a higher-order coordinating process which is not fully reflected in changes lower in the coding system. We shall refer to any such excess as an excess in the total adaptive shift.

When our early work revealed such an excess in the total adaptive shift, specific hypotheses about the conditions under which it occurs were proposed and tested. The hypotheses were derived by analogy from other types of skill learning: first, that the initial response to changes in error feedback will be that of the coordinators, resulting in a change in excess adaptation which is rapid relative to the changes in automatic functions; secondly, that as practice proceeds with constant error feedback, the site of the adaptive changes will come to occupy lower, more fundamental, components in the system, as reflected in a decrease in the relative degree of excess in the total adaptive shift; finally, that when error feedback is terminated after a period of training, the system will "forget" the more transient "coordinator" changes first and hence become more additive as it comes to rely wholly on the residual changes lower in the system.

The training procedure is one in which prismatic displacement is introduced gradually in small steps, a procedure referred to previously as "prismatic shaping" (Howard, 1968). This reduces or eliminates S's conscious awareness of the visual displacement and for that reason should minimize the opportunity for S to adapt by conscious correction.

The experiment also has another purpose. Helmholtz (1924, pp. 246-247) argued that adaptation of visual-motor coordination to prismatic displacement involves a change in the judgment of the direction of gaze, because the effects fully transfer from a trained hand to an untrained hand, as they would not if there had been a change in the judged direction of the trained hand. The argument is not quite valid, because a change in the judged direction of the head in relation to the body would also lead to intermanual transfer. In any case, it is now known that intermanual transfer does not always occur, and when it does, it is not complete (Hamilton, 1964; Kalil & Freedman, 1966a; Cohen, 1967; Goldberg & Taub, 1968). It is known, however, that exposure to prismatic displacement may lead to some change in the position of the eyes when S is asked

to look straight ahead (Kalil & Freedman, 1966b; Craske, 1967; Craske & Templeton, 1968; McLaughlin & Webster, 1967). This study is, in part, an attempt to relate these two functions; intermanual transfer and the change in judged direction of gaze as reflected in an objective measure of eye position. It is hypothesized that whatever intermanual transfer occurs in a particular set of circumstances will equal the objectively measured change of eye position in response to the task of directing the gaze to some hidden body landmark (large toe of one foot) under similar circumstances. Because the head is held in a bite bar, any change in this latter task is assumed to reflect a change in the judged position of the head on the body or of the eye in the eye socket, that is, a change related to those joints involved in pointing to a visual target which are common to both arms, and which should therefore underlie any intermanual transfer. The possibility of shifts in retinal local sign may be ignored because the visual target is imaged on the very salient retinal landmark, the fovea. As far as we know, this is the first attempt to relate directly the amount of intermanual transfer of prismatic adaptation to a measure of the shift in judged direction of the neck-eyeball system and, although the confirmation of the hypothesized equality between the two functions will not explain why intermanual transfer (changes in neck-eyeball system) occurs more under some circumstances than under others, it will reveal the coherence of the visual-motor system.

One study by McLaughlin and Bower (1965) is most relevant to the purpose of this experiment. They found that intermanual transfer of target-pointing behavior after prismatic adaptation equaled the difference between the shift in ipsilateral target pointing and the shift in ipsilateral pointing to straight ahead. The ipsilateral straight-ahead task was taken as a measure of any change in the judged direction of the arm on the body, and hence, reasonably, as a measure of that component of the shift in ipsilateral target pointing which would not transfer to the other hand. Their finding provides indirect evidence that a shift in the judged direction of the head-eye system was responsible for whatever transfer did occur. Our experiment is in part a more direct approach to this question.

It is hoped that our use of the tasks defined by the instructions "point towards" and "look towards the hidden toe" will overcome the ambiguities involved in the more commonly used tasks of pointing and looking "straight ahead."

The hypotheses investigated may be summarized thus: (1) change in visual-target pointing with trained hand equals the sum of changes in looking at toe and pointing at toe with trained hand; (2) change in pointing at toe with untrained hand equals zero; (3) consequently, change in visual-target pointing with untrained hand should equal the change in looking at the toe; and (4) the degree to which Eqs. 1 and 3 do not hold, i.e., the nonadditivity or excess of the total adaptive shift,

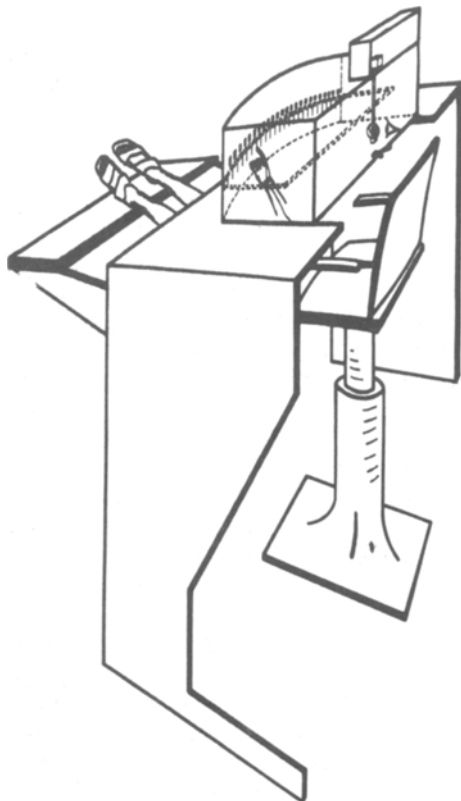


Fig. 2. Apparatus used in the experiments.

should (a) be most prominent under conditions of changing prismatic displacement, (b) diminish progressively with constant prismatic displacement, and (c) disappear rapidly when error feedback is terminated.

EXPERIMENT I

Method

Apparatus

The basic unit consisted of a semicylindrical metal screen curved from left to right with a radius of 50 cm and centered on a point midway between S's eyes (Fig. 2). The S reclined in a dental chair with his head held in a bite opposite the middle of the screen and his feet supported on a shelf so that his toes were in the median plane slightly below eye level. S looked with his right eye through a prism which could be adjusted to displace visual targets from 0 up to 16 deg to the S's right.

The target lights were miniature incandescent lamps mounted at eye level in a horizontal array on the inside of the screen. One of the lamps, "light zero" was in S's median plane, with the others spaced at 1-deg intervals, 8 to the right and 16 to the left of it.

Directly below the lamps was a horizontal row of 50 copper strips (each 8 mm wide x 70 mm high) placed at 1-deg intervals from straight ahead of S out to 30 deg right and 18 deg left. The strips were connected together by a series of resistors, and the whole connected to a 24-V supply.

The S wore a metal thimble on each index finger, which completed the circuit through whichever copper strip he

touched, which in turn produced an appropriate record of his aiming movements on a polygraph (sensitivity: 1 mm/deg).

The horizontal light array was separated from the copper strips by a horizontal panel, which was normally flush with the top of the copper strips. On feedback trials, when S was allowed to view his finger, the panel was retracted and S could slide his finger up through a 1-cm gap until its tip came into view at the level of the target lights. The finger carried a miniature lamp which E could switch on when he heard the click of S's finger on the copper strips on feedback trials. Screens above and to the sides of S prevented him from seeing anything but the target and finger lights. Two photodetectors mounted before each eye were aimed at the nasal and temporal boundaries of each iris, with the eyes converged on the center target light. An infrared emitting diode was directed to the center of each eye (modulated at 10 kHz to avoid excessive heating). The nasal photodetector on one eye was connected in series with the temporal detector on the other eye, and the two resulting signals subtracted to cancel the effects of vergence movements. The final measure of the horizontal position of the eyes was recorded on the polygraph with a sensitivity of 1 mm/deg. Readings on a dummy eye showed no spurious variation due to vertical or vergence movements or other causes, and revealed that the system was linear for ± 20 deg.

Each session started with the straight-ahead or zero light being in circuit and the prism at zero displacement. The S was allowed 5 sec to make each response or trial (pointing at target, looking at toes, etc.), and after each sixth trial the prism was rotated to give one additional degree of displacement to the right, up to a maximum of 16 deg. At the same time, the next target light, 1 deg to the left, was engaged, so that when illuminated the target was always optically straight ahead. No light was visible during the actual change in prism power.

Procedure

The S was first fitted with the eye-monitoring device and his chair and bite adjusted so that the zero light appeared centered with prism strength zero. The S's feet were supported on a stool so that one of his big toes was straight ahead of him and slightly below eye level.

The eye-position recorder was calibrated by asking S to fixate lights at known eccentricities. The eye-monitoring device was adjusted to give a repetition accuracy of at least 0.5 deg. Several Ss who could not maintain fixation with sufficient constancy were rejected.

The S was then informed that during the experiment he would be given a verbal command every 5 sec. There would be six different commands: (1) "Look at toe"; he was to look in the direction of his large toe. (2) "Look at target"; one of the target lights would be lit, and he should look steadily at it. (3) "Left at toe"; he should point with his left index finger in the direction of his large toe so that the electrical contact on his fingertip was pressed against the copper resistance strip. (4) "Right at toe." (5) "Left at target"; one of the target lights would be illuminated, and he should point at it with his left index finger so that he made contact with the copper strip. (6) "Right at target." In each case, he was asked to hold his response position until the next command.

With respect to Commands 5 and 6, S was told that one of his hands, right or left, was his "training hand," and that on some occasions when he pointed at the target with it he would find that a gap had opened above the copper strip so that he could slide his finger vertically up the strip that he was contacting, thus enabling him to see his finger by means of the small light fixed to its tip. He could thus see his fingertip and the target light simultaneously, and he was asked to use this information about his pointing error to make a more accurate aiming on the next

occasion. On other "training-hand-at-target" trials and on all pointing trials of any other category, the gap was closed.

The S was then given a dummy run of 36 trials, in which he could rehearse all the required responses. During the dummy run, S's feet were placed so that when he looked at one of the big toes his eyes were straight ahead, as indicated by the eye monitor. Several Ss were discarded because of wide variation in eye position when they were asked to look at their toes.

Each experimental session consisted of repetitions of a basic sequence of 12 trials, each trial lasting 5 sec. Each S was given two sessions. Half the Ss used the left hand as training hand in the first session, the right hand in the second session; the other half used their hands in the reverse order. Half of each of these groups had Sequence A in the first session, Sequence B in the second; the other half of each group had the two sequences in reverse order.

The basic pattern for both sequences was that trials on which S pointed at the light with his trained hand (and got visual feedback when appropriate) occurred in pairs, interspersed by one of the other types of trial—untrained hand pointing at the light, untrained hand pointing at toe, trained hand pointing at toe, and eyes looking at toe. The second of each pair of trained-hand target-pointing trials was used to indicate the total adaptive shift in pointing at visual targets. The second one was used rather than the first because the other test trials also followed a trained-hand target-pointing trial. (In fact, the other test trials followed a pair of such trials, but since the total adaptive shift with trained hand was complete after one feedback trial, the imbalance in the design was not considered important.) The distinguishing feature of the two sequences was the ordering of the interspersed test trials which are shown in Table 1. One exception to the regular sequence was that the trial immediately following a gaze-at-toe trial was one in which the eye position was recorded as S fixated a light optically straight ahead. This provided the baseline for the measure of eccentricity of gaze during the gaze-at-toe trials.

In all conditions, the first 36 trials (three 12-trial blocks) of each session were preadaptation control trials to establish a baseline against which later changes in the various functions could be assessed. The gap opened to allow feedback after all trained-hand target-pointing trials, but the prism and target light remained at zero. The next 96 trials (eight 12-trial blocks) formed a training sequence during which the target light stepped 1 deg and the prism increased its power by 1 deg after the third and ninth trial of each block. Thus, by the end of the 11th block of the experiment (Trial 132), the operative light was 16 deg to the left though still optically straight ahead. Of the 6 trials which occurred at each step of the prism's progress, 4 were target-pointing trials with feedback (except when one was an eye-calibration trial).

The procedures in the three conditions diverged after Trial 132. In Condition 1, feedback ended at this point, and the light and prism remained fixed at 16 deg so that the decay of the various effects could be studied. In Condition 2, the light and prism remained fixed at 16 deg, but feedback continued so that changes in the relative contribution of the component functions could be studied with constant prism displacement. This asymptotic condition was maintained for nine blocks (up to Trial 240). In Condition 3, the light and prism returned to zero in the same progressive manner as their outward excursion. Each session in Condition 1 lasted 18 min, and in Conditions 2 and 3, 20 min.

Subjects

Eight paid Ss completed Condition 1, with three Ss in Condition 2 and four in Condition 3. All were undergraduates, naive about the purpose of the experiment and capable of seeing the target lights clearly with unaided vision.

Table 1
Within-Block Order of Trials for Four Groups of Ss in Experiment I

	Trial					
	1	2	3	4	5	6
Sequence A	Tl	Tl	Et	El	Tl	Tt
Sequence B	El	Tl	Ul	Tl	Tl	Ut
	7	8	9	10	11	12
Sequence A	Tl	Tl	Ut	Tl	Tl	Ul
Sequence B	Tl	Tl	Tt	Tl	Tl	Et

Group	Session 1		Session 2	
	Trained Hand	Sequence	Trained Hand	Sequence
A	R	A	L	B
B	R	B	L	A
C	L	A	R	B
D	L	B	R	A

Note—Trials used to compute total adaptive shift are in italics. T = trained hand, U = untrained hand, E = eye, l = light, t = toe.

Treatment of Data

The data from each S in each session consisted of a polygraph record of eye position, and a polygraph record of finger position for each pointing response. The data were treated as follows: (1) All trials of a particular type in the three control blocks of trials were averaged to give preadaptation control means for each of the various functions. (2) Each subsequent block of trials provided four scores for the trained hand pointing at target, which were averaged, and a single score for each of the other four functions. The corresponding control means were subtracted from each of these to give progressive measures of training-induced shifts in the five functions, namely: the total adaptive shift for each hand, the arm-pointing-at-toe shift for each hand, and the gaze shift. (3) Since the target was actually progressively shifted to the left, changes in all hand-pointing functions, either to the light or the toe, were expected to be to the left. The change in the direction of gaze in response to the request to look at the toe, on the other hand, was expected to be to the right, since this would be implied by the leftward shift in felt direction of gaze required to explain a leftward shift in pointing to visual targets. The sign of the gaze shift was therefore changed so that all expected shifts would be in the same direction on the graph, thereby making comparison simpler. This completes the processing of the data within a single session. (4) Corresponding points in the two sessions of a single S were averaged. This, of course, involved averaging right-hand functions in one session with left-hand functions in the other. (5) For each block, the gaze shift was added to the arm-pointing-at-toe shift for both trained and untrained hand to give the respective hand-to-light scores which would be predicted on a simple additive model. These predicted values were then subtracted from the actual value. The resulting difference functions are thus a measure of the amount by which the shift in pointing at visual targets exceeds the sum of the changes in the eye-head system and in the arm system, i.e., the degree to which pointing at a visual target is not merely a matter of bringing into coincidence the felt position of the arm and the seen position of the target. These will be termed "excess" functions for trained and untrained hands. (6) The resulting seven functions for each S were finally smoothed by taking moving point averages on a base of three.

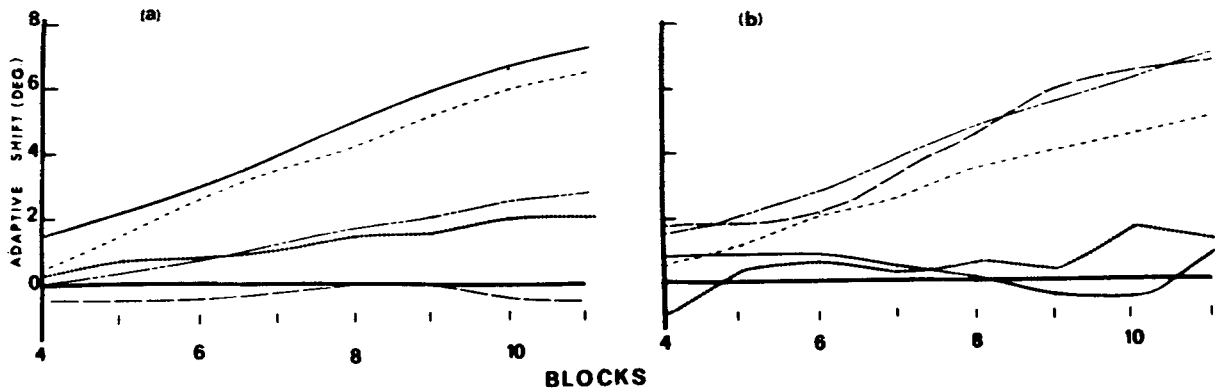


Fig. 3. Experiment I up to Block 11. (a) Twelve Ss without gaze shift; (b) three Ss with gaze shift. — — — — — Arm-to-toe shift—trained arm. — — — — — Excess of the total adaptive shift—trained arm. — — — — — Gaze shift. - - - - - Excess of the total adaptive shift—untrained arm. - - - - - Total adaptive shift—untrained arm.

Results

The three conditions were identical as far as Block 11, i.e., during the outward excursion of light and prism. The combined results of this phase of the experiment will now be considered. All 15 Ss demonstrated an arm-pointing-at-toe shift in the trained arm, with peak (Block 11) values ranging from 4 to 9 deg, with an average around 6 deg—less than half the total adaptive shift of 15-16 deg but highly significant [$t(14) = 11$, $p < .001$]. No S showed a corresponding shift in pointing-at-toe with the untrained arm.

Three Ss in Condition 1 showed a large and consistent gaze shift; for the remaining 12, changes were small and apparently random. All functions are shown separately for these two groups in Fig. 3. It should be recalled that the mean actual target location, to which total adaptive shift in the trained arm closely approximates, changes linearly from 1 deg on Block 4 to 15 deg on Block 11. In the group with a gaze shift, it ranges between 6 and 7 deg—comparable with the overall average pointing-at-toe shift in the trained arm. For this group, the pointing-at-toe is sufficient when combined with the gaze shift to account for the total adaptation in pointing at the visual target. Consequently, the excess adaptation is negligible. For the other group, the gaze shift is replaced by an equal amount of excess adaptation to supplement their pointing-at-toe shift. Group differences in the behavior of the untrained arm are equally marked. The gaze-shift group shows an intermanual transfer in pointing at the visual target of almost 60%. This total adaptive shift in the untrained arm corresponds very closely with the gaze shift, and again the excess adaptation is negligible. The no-gaze-shift group, on the other hand, shows an intermanual transfer of less than 35%, and this is largely accounted for by excess adaptation, the latter being about 30% of the value of the excess in the trained arm. The group difference in intermanual transfer gave $t(13) = 3.7$, $p < .01$.

Turning to the final phase of the experiment,

following Block 11, where the three conditions diverged, the theoretically significant functions are shown in Fig. 4. In Condition 1, feedback was terminated at this point. The pointing-at-toe shift in the trained arm declines rather slowly to an apparent plateau of about 5 deg, and, in Ss without gaze shift, the total adaptive shift in the trained arm declines rapidly to about the same level; consequently, the excess adaptation in the trained arm quickly falls to an insignificant level upon termination of feedback (Fig. 4a). For those Ss with a gaze shift, this decline in total adaptive shift in the trained arm is much less marked, matching the slow decay of the pointing-at-toe change and the tendency of the gaze shift to increase somewhat. Similarly, the total adaptive shift in the untrained arm continues to match closely the gaze shift, and declines but little (Fig. 4b).

In Condition 2, where feedback was maintained with prism and light at 16 deg, there was no sign of the expected tendency for excess adaptation to be progressively replaced by a change in automatic functions under asymptotic conditions—in fact, both excess adaptation and pointing-at-toe shift remain quite stable throughout this phase (Fig. 4c). Similarly, the intermanual transfer of about 35% of total adaptive shift remains stable throughout the phase, maintained mainly by a stable degree of excess adaptation in the untrained arm (not shown).

Finally, in Condition 3, feedback continued, but prism and light stepped progressively from 16 deg on Block 12 back to 0 deg on Block 20. It can be seen that even under these conditions of changing error feedback the rates of decline of excess adaptation and pointing-at-toe shift (both trained arms) are very similar (Fig. 4d), just as their rates of rise were in the first phase of the experiment (Fig. 3). There is, thus, none of the expected tendency for a change in stimulus demand to be met first by a change in excess adaptation.

A fourth S in Condition 2, though he met the criteria for inclusion in terms of gaze and pointing stability, was quite atypical in his response pattern. He had a gaze shift

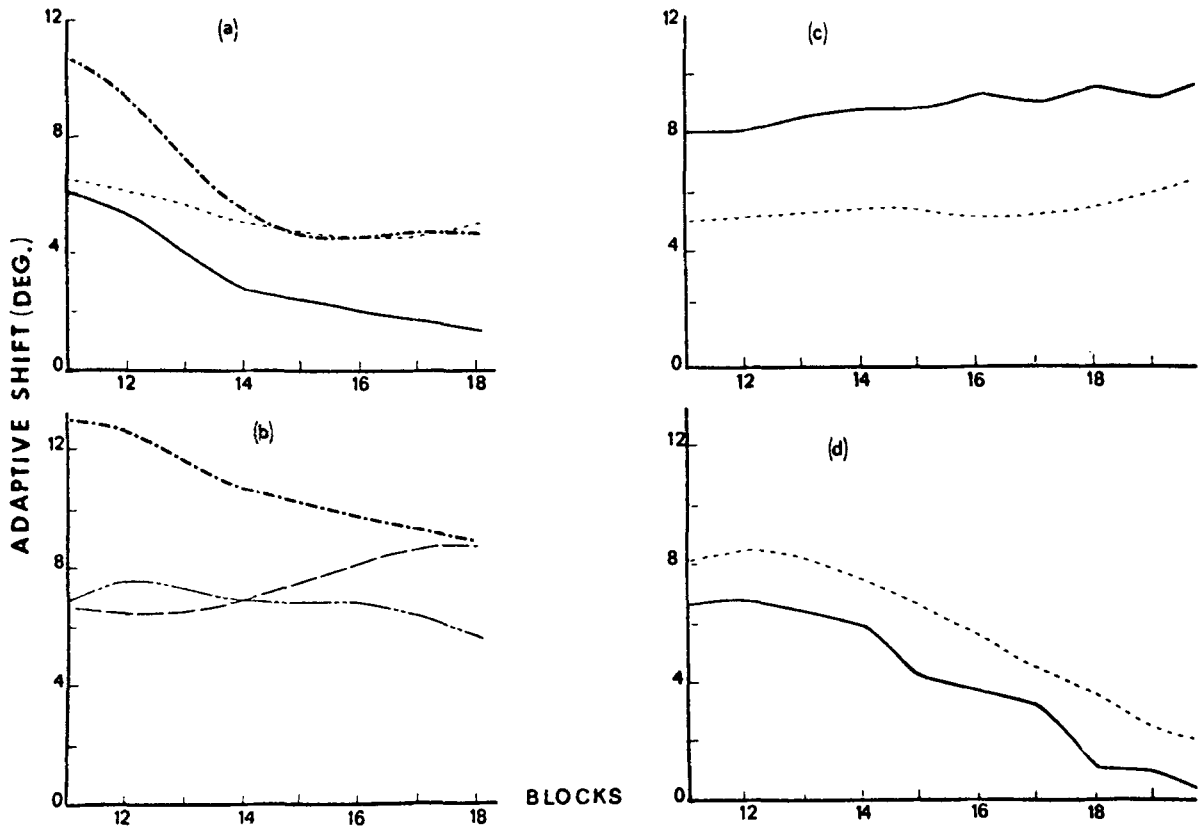


Fig. 4. Experiment I from Block 11 to end. (a) Ss without gaze shift in Condition 1. (b) Ss with gaze shift in Condition 1. (c) Condition 2. (d) Condition 3. ■ — ■ — ■ — ■ Total adaptive shift—trained arm (other curves as in Fig. 3).

comparable to the gaze-shift Ss of Condition 1, together with large pointing-at-toe shifts for *both* arms; for each arm, the gaze shift and pointing-at-toe shift together were greater than the respective total adaptive shifts, i.e., the excess functions were negative. His results are excluded from this discussion.

EXPERIMENT II

Method

Procedure

The apparatus and basic procedure in pretraining were the same as in the previous experiment, except that a block of trials consisted of 8 rather than 12 trials, since successive test trials were separated by only a single arm-to-target trial, and that control measures of eye position were taken during target-pointing trials rather than in special trials as in Experiment I.

The first 24 pretest trials of the session (three blocks) followed the basic sequence in which there was no visual feedback of finger position. The pretest was immediately followed by the training phase, which consisted of only 72 target-pointing trials, on each of which the S was provided with visual feedback. For the first 48 of these trials, the target light stepped 1 deg to the left on every fourth trial, and the prism displacement increased by 1 deg to the right until the light was finally 12 deg to the left though still optically straight ahead. This condition was maintained for the final 24 training trials.

The S was instructed to point as accurately as possible on each trial by making use of the feedback obtained on the previous trial. This phase of the experiment lasted approximately 6 min. The final 48 trials of the session comprised the six blocks of the posttest which were, from S's point of view, identical with the pretest blocks, the only difference being that the target light remained at 12 deg left, though of course optically straight ahead. This phase lasted about 4 min.

Subjects

There were six paid Ss, between the ages of 18 and 25, naive about the purpose of the experiment, and capable of seeing the target lights clearly with unaided vision.

Results

The stages of processing of the data were: (1) All trials of a particular type in the pretest were averaged to give control means for the various functions. (2) The posttest scores for the trained hand pointing at target were averaged, as were the scores for each of the other four functions. The corresponding pretest means were subtracted from these values to give measures of the training-induced shifts in the five functions. (3) As in the previous experiments, the sign of the gaze shift was reversed, the two sessions were averaged for each S, and excess functions were derived for the trained and

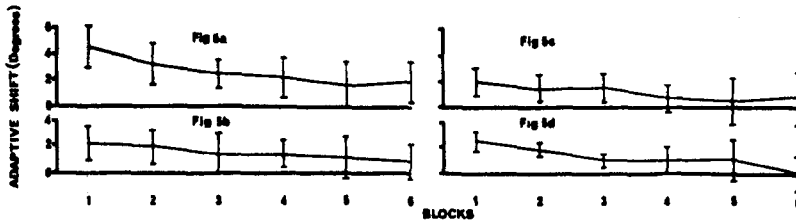


Fig. 5. Results of Experiment II: means and 95% confidence intervals. (a) Total adaptive shift—trained arm. (b) Arm-to-toe shift—trained arm. (c) Gaze shift. (d) Total adaptive shift—untrained arm.

untrained hands by subtracting the appropriate sums of gaze and pointing-at-toe shifts from the total adaptive shifts. Figure 5 displays the mean values of each of four functions for each of the six posttest blocks, together with the 95% confidence interval for each point.

It can be seen that the trained hand shows an average residual effect of 4.6 deg in pointing at the light during the first posttest block (Fig. 5a). There is a sharp drop from the approximately 12 deg common at the end of training. In subsequent blocks, the total adaptive shift drops off, though by the sixth block it is still about 2 deg, still significantly different from zero. As expected, there is no pointing-at-toe shift in the untrained hand. But there is a mean gaze shift and a mean pointing-at-toe shift in the trained hand, both of which drop to insignificance by the fourth or fifth block (Figs. 5b and 5c). The most marked difference from the previous experiments, however, is the absence of any excess of the total adaptive shift for either hand. The gaze and pointing-at-toe effects together account for the total adaptive shift in the trained hand. Because of the absence of a pointing-at-toe shift in the untrained arm, the total adaptive shift of the untrained arm closely follows the gaze-shift curve (Fig. 5d).

DISCUSSION

Since Experiment II was very similar to the extinction phase of Condition 1 in Experiment I and all Ss in the former showed a gaze shift, it is useful to compare their behavior with that of the Ss with a gaze shift in Experiment I. The two groups show marked similarities though the significant effects in Experiment II are much smaller, even taking into account the fact that the final prism displacement was 12 deg instead of 16 deg. Experiment II reveals the usual arm shift in the trained arm—declining slowly, as in Experiment I—and absence of an arm shift in the untrained arm. Both groups show a close correspondence between the gaze shift and the target-pointing of the untrained arm—though both functions are declining in Experiment II but remain around their peak value in Experiment I—and there is therefore no excess adaptation in the untrained arm. Nor does either group have an excess adaptation in the trained arm.

A major puzzle which remains is that a gaze shift occurred in only 3 out of 15 Ss in Experiment I but in all 6 Ss in Experiment II. If this is more than random sampling error, one possibility is that all Ss would

eventually develop a gaze shift during extinction and that in Experiment II we are somehow looking at a later stage in the process than we are in Experiment I. The first of these assumptions is lent some support by the tendency of the gaze shift to increase during extinction in Experiment I (Fig. 4), and the second by the smallness of the total adaptive shift in Experiment II. A second possibility is that massed training is especially conducive to the development of a gaze shift.¹

In general, it seems that prism displacement under conditions studied here leads to a pointing-at-toe change in the trained arm, which is slow to revert to normal in the absence of feedback, and which does not transfer to the untrained arm. This is accompanied by gaze shift, that is, a change in the eye-head or head-body linkage in a few Ss at least and perhaps in all under certain conditions. When there is a gaze shift, it accounts for any intermanual transfer of the adaptive change in visual-target pointing and, together with the arm change, it accounts for the change in visual-target pointing with the trained arm. When a gaze shift does not occur, the arm change is not sufficient to account for the change in visual-target pointing and is supplemented by an excess of total adaptive shift which disappears rapidly when feedback is terminated. This excess of total adaptive shift transfers in some measure to the untrained hand.

These conclusions may be listed in relation to the hypotheses set out in the introduction: (1) In Ss who showed a gaze shift, it summed with their arm shift to give the change in pointing at the target with the trained arm; in other Ss, there was a trend towards additivity as soon as feedback was terminated, i.e., the total adaptive shift came to equal the pointing-at-toe shift in the trained arm. (2) There was no change in pointing at the toe with the untrained hand, confirming the hypothesis. (3) The change in visual-target pointing with untrained hand equaled the change in looking at the toe in those Ss with such a change, confirming the hypothesis. (4) Nonadditivity changed at the same rate as the pointing-at-toe change with changing prismatic displacement, contrary to Hypothesis 4c. Nor was there any diminution of nonadditivity with constant prismatic displacement and continuing feedback, contrary to Hypothesis 4b. However, nonadditivity disappeared after error feedback was terminated, confirming Hypothesis 4c.

We may conclude, therefore, that for those Ss who showed a gaze shift there was no evidence of the operation of what we have called coordinators (or Held's

matching orientation) either before or after feedback was terminated. However, there was a clear indication of the operation of coordinators in those Ss who did not show a gaze shift. But, as we predicted, after feedback was terminated, the contribution of coordinators ceased and the residual level of adaptation is accounted for by the pointing-at-toe shift.

All this makes sense if the coordinators are thought of as involved in processing current error feedback. They constitute a sort of override system which modifies behavior beyond the level of the more deep-seated changes. The more long-lasting effects of prismatic adaptation, however, are clearly centered below the level of the coordinators, for soon after feedback is terminated, the total adaptive shift is accounted for in terms of gaze shift (where present) and pointing-at-toe changes. Why the pointing-at-toe shift should be supplemented by a gaze shift in some Ss or conditions and by the operation of the coordinators in others remains as a question for future research.

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NOTE

1. This possibility is unlikely, according to evidence cited by Taub and Goldberg (*Science*, 1973, 180, 755-757).

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