Journal of Experimental Psychology
1971, Vol. 89, No. 2, 250–257

VISUAL-MOTOR CONTROL LOOP: A LINEAR SYSTEM?[1]

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A model of prism adaptation is proposed suggesting that the visual-motor control loop is a linear system comprising a number of independent subsystems. Errors in the subsystems sum algebraically to produce the error of the total loop. This hypothesis was tested in two experiments. Exposure to visual-motor discordance produced by wedge prisms caused a change in the judged visual direction (V) of targets. Such exposure also produced a change in setting the hand to the median plane of the head (H). The prism-induced change in target-aiming performance (T) was equal to (H + V). Viewing a visual display through the prisms produced changes in V and H, but the data did not fit the linear model (H + V = T). Changes in pointing at visual targets with the untrained arm are fully accounted for by changes in V.

The paradigm of prism-adaptation studies has been to expose *S* to the effects of the optical transformation of the visual field on visually directed movements (closed loop condition) between tests in which he does not see the effects of his movements (open loop condition). The difference between preexposure and postexposure performance in tasks involving the whole sensory-motor control loop is taken as a measure of the extent to which *S* has adapted. Investigators such as Efstathiou, Bauer, Greene, & Held (1967), Harris (1965), and Helmholtz (1962) used tasks which they assumed involved part of the control loop and studied the change in these tasks in the hope of revealing the nature of the adaptive change.

The simplest model of prism adaptation is that in which one component of the visual-motor control loop undergoes change. Recent experiments by Hay and Pick (1966) and McLaughlin and Webster (1967) suggest that the adaptive change cannot be described as a single change in one component, but could be described as several changes in the components of a linear system. This means that if the control loop is cut into two parts, then the sum of the changes in the two parts should equal the change of the whole loop. Therefore, within an experiment, the sum of the component task changes for each *S* should predict his total adaptive change. If the sum of component changes for each of a number of *S*s is plotted against the total adaptive change, the points resulting should fall on a straight line with a slope of 1 and intercept at the origin.

The task of setting a visual target to the apparent median plane of the head and that of positioning the hand in the same plane might be a complete set of additive subtasks, on the assumption that the former would indicate changes in the egocentric visual direction of targets and the latter would indicate changes in reaching behavior. Changes in the performance of these two tasks should account for the total change in pointing at a visual target. Changes in the performance of the subtasks could be described as altered estimates of visual direction and hand position with respect to the head. The model predicts that the sum of the change in hand positioning (H) and change in estimated visual direction of targets (V) should equal the change in target aiming (T). An experiment involving measurements of these changes should indicate the part of the

[1] The research reported was conducted at the Institute of Experimental Psychology, Oxford University, while the author was in receipt of a Medical Research Council Scholarship for Training in Research Methods. It was included in a thesis submitted to the University of Oxford for the PhD. degree. The manuscript was prepared at York University.

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control loop involved in the total adaptive process. If *S* changed all his hand-positioning responses in the direction opposite to the displacement produced by the prism, this would be adaptive for pointing towards a target with the unseen hand (cf. Harris, 1965). However, adaptive changes in estimates of visual direction should be in the same direction as the displacement so that, for example, the point that during pretest appeared straight ahead of *S* appears to be straight ahead again despite the effects of the prism.

Experiments have shown that a change in hand positioning, in the absence of vision, can be produced after looking at the hand or a marker attached to it in a laterally displaced visual field (Craske, 1966, 1967; Harris, 1963; McLaughlin & Bower, 1965a, 1965b; McLaughlin & Rifkin, 1965). Photographic evidence has demonstrated that the position of the eyes in the head when *S* believes he is looking straight ahead can be altered by exposure to optical displacement of the visual field (Craske, 1967; Kalil & Freedman, 1966b; McLaughlin & Webster, 1967). Cohen (1967), Helmholtz (1962), and Kalil and Freedman (1966a) have found intermanual transfer of the aftereffect of pointing to a visual target. From this they have inferred that *S*'s estimates of visual direction have undergone change. This inference implies that the presence of transfer to the unexposed hand will not merely indicate that estimates of visual direction have changed, but that the amount of transfer is a precise measure of the extent of the visual change. It is assumed that the intermanual transfer exactly reflects a change at a common element in two control loops, rather than a transfer of motor learning to the unexposed hand.

Two experiments are described. The first is an attempt to show that the sum of the visual estimation and hand positioning changes is equal to the total adaptive change. This hypothesis was tested after *S* had been exposed to the asymmetry of the visual display produced by the prisms and again after he had been exposed to visual-motor discordance produced by viewing his performance in pointing to a visual target.

The second experiment was used to test the hypothesis that transfer of training to the unexposed hand was exclusively produced by changes in estimated visual direction of targets. This experiment also yielded a second test of the hypothesis tested by the first experiment.

Method

Experiment I

Apparatus.—Two visual displays were used. The first consisted of a vertical white screen across which ran a scale marked in tenths of an inch. Each inch was labeled with a randomly selected pair of digits. A different portion of the scale could be presented to *S* on each trial. The second display was a similar white screen on which was marked a vertical target line.

The *S* was seated in a chair of adjustable height, with his head pulled tightly into a headrest by straps round the forehead, and with his chin on a chinrest. The *S* wore variable prisms, mounted in welder's goggles. A plywood board ran from the level of *S*'s neck to within 2 cm. of the screen. The end of this board near the target could be lowered so that *S* could receive visual terminal feedback about his target aiming performance, or raised so that he could not. Visual terminal feedback means that *S* could see the relative positions of his finger and the target at the end of his response but could not visually guide his hand onto the target.

Subjects.—The *S*s were 12 undergraduate and graduate students, aged 20–25 years.

Procedure.—The *S*s were randomly assigned to one of two groups, with six *S*s in each group. One group adapted to prisms base left (BL), the others to prisms base right (BR). For both groups, the prisms displaced the visual field by 12°. The targets were so positioned that they were in the optically determined median plane of the head under prism exposure. The *S*s in the BR group used the right arm, while *S*s in the BL group used the left. The *S* was placed in the apparatus and completed the following set of 10 tasks: (*a*) pretests (no prism). (*i*) Identifying the visual straight ahead 20 times, (*ii*) Pointing the hand straight ahead 20 times, (*iii*) Pointing 20 times at the target; (*b*) Pretests (prism on). (*i*) Identifying the visual straight ahead 20 times, (*ii*) Pointing the hand straight ahead 20 times, (*iii*) Pointing 20 times at the target; (*c*) Exposure period. (*i*) Pointing 40 times at the target; (*d*) Posttests (no prism). (*i*) Identifying the visual straight ahead 20 times, (*ii*) Pointing the hand straight ahead 20 times, (*iii*) Pointing 20 times at the target.

The *S*s received knowledge of results during Task (*c*)(*i*) only, when they received terminal visual feedback. The visual field was displaced in Tasks (*b*) (*i*)(*ii*)(*iii*), and (*c*)(*i*). Before the experiment, *S* was shown that when a prism displaces the visual field the point that is physically straight ahead no longer appears to be. He was instructed that whenever he was asked to identify the visual straight ahead on the scale he was to indicate the apparent straight ahead (apparent median plane of the head). The points *S* indicated as being straight ahead were recorded by *E* on a scale out of *S*'s view. Similarly, in pointing straight ahead, he was asked to point to the median plane of the head. While he made this response, he closed his eyes and occluders were placed over the prisms.

The *S* held a marker pen that protruded just beyond the tip of his index finger and marked the screen each time he pointed. For each different pointing task, he held a different colored marker.

Experiment II

Apparatus.—The apparatus described in the previous experiment was also used for Exp. II.

Subjects.—Eight *S*s aged 20–25 yr. were used in the experiment.

Procedure.—The *S* was placed in the apparatus and given the same instructions as those given in the previous experiment, and he was also informed that in the course of the experiment, he would be required to point at the target sometimes with his left and sometimes with his right hand. All *S*s viewed the display with the right eye, and the right hand was used in the exposure condition. The *S* performed the following set of tasks: (*a*) Pretests. (*i*) Pointing at the target with the right hand 20 times, (*ii*) Pointing straight ahead 20 times with the right hand, (*iii*) Visually identifying straight ahead 20 times, (*iv*) Pointing at the target with the left hand 20 times; (*b*) Exposure. (*i*) Pointing 40 times at the target with the right hand, correcting errors between responses; (*c*) Posttests. (*i*) Pointing at the target with the left hand 20 times, (*ii*) Visually identifying straight ahead 20 times, (*iii*) Pointing straight ahead 20 times with the right hand, (*iv*) Pointing at the target 20 times with the right hand.

The 12° displacement, prism base right, was introduced during the exposure period only, and this was the only period in which *S* obtained knowledge of results. When *S* pointed straight ahead, his eyes were closed and occluders were placed over the prism. The test of transfer and judgements of visual direction immediately followed the exposure trials because the chief aim of the experiment was to compare these two measures. This would minimize the risk of spontaneous decay of the aftereffect obscuring the effects of exposure. The pointing tasks took about 1 min., and the visual judgements less than 3 min.

TABLE 1

Adaptive Change in Hand Positioning (H), Visual Estimation (V), and Target Aiming (T) Responses for Each Subject after Exposure to the Optical Transformation of the Visual Field

Prisms	*S*s	H	V	T
Base Right	S_1	−3.8	7.1	4.4
	S_2	.0	1.0	.5
	S_3	.0	−.3	1.3
	S_4	−3.4	3.0	2.4
	S_5	.0	1.8	1.9
	S_6	1.4	3.0	4.6
Base Left	S_7	−6.9	7.9	2.0
	S_8	1.7	1.5	−2.5
	S_9	−2.3	5.8	3.8
	S_{10}	−4.3	5.7	2.9
	S_{11}	2.8	1.5	−2.3
	S_{12}	.0	.3	2.0
	$\bar{X}$	−1.70	3.21	1.44
	SD	2.61	2.76	2.52

Note.—Adaptive change measured in centimeters.

TABLE 2

Estimated Slopes and Intercepts of Regression Lines for Three Combinations of the Data Presented in Table 1 and Their Correlation Coefficients

Ordinate *x*	Ordinate *y*	Estimated slope	Estimate of intercept	*r*	*p*
T and	H + V	.551	.52	.40	>.10
V and	T − H	1.335	−.39	.83	<.01
H and	T − V	1.214	.20	.55	<.10

Results

Experiment I.—Before exposure to visual-motor discordance, measures of hand positioning (H), estimated visual direction (V), and target aiming (T) were taken with the prisms in place. Performances on these pretests were compared with performance of the same tasks before the prisms were introduced. According to the null hypothesis that there would be no adaptive effects produced by just looking through the prisms, there should be no adaptive change in H, V, or T. This implies that the mean H responses should be unchanged from the first pretest performance, and the V and H responses should be shifted by the amount that the prisms displaced the visual field. In fact, the mean H responses did change and the mean V and T shifts were not as great as the geometric optics predict. The departures from expected values were significant for the V and H scores, t_V (11) = 4.032, $p < .01$, and t_H (11) = 2.261, $p < .05$. The mean change in T scores was not statistically different from the expected value, t_T (11) = 1.973, $.05 < p < .10$. The individual scores are presented in Table 1, with changes in the adaptive direction scored positive. The changes in V and T scores were in the adaptive direction, but the change in H scores was nonadaptive for pointing at targets. Since *S* had not seen his hand at this point, the effects must be produced by the asymmetry of the visual array. These results are very similar to those of McLaughlin, Rifkin, & Webster (1966).

The model to be tested predicts that H + V = T and therefore that plotting the T score for each *S* against the sum of his H and V scores should yield a straight line with a slope of 1 and intercept at the origin. McLaughlin et al. (1966) assumed that this linear relationship held and calculated V from measures of H and T. The same function should be produced by plotting H against T − V and V against T − H. The model also predicts that H + V and T, H and T − V, and V and T − H should all be significantly correlated.

The slopes and intercepts of the best-fitting lines were calculated by using an orthogonal regression technique because

TABLE 3

Adaptive Change in H, V, and T Responses for Each Subject after Exposure to Intersensory Discordance

Prisms	*Ss*	H	V	T
Base Right	S_1	3.3	2.5	9.5
	S_2	8.3	.5	7.5
	S_3	4.2	1.0	5.8
	S_4	1.8	2.8	5.5
	S_5	.4	1.9	2.0
	S_6	1.3	2.7	4.9
Base Left	S_7	2.5	.9	3.8
	S_8	2.5	2.0	1.3
	S_9	7.1	1.1	4.4
	S_{10}	4.4	.0	4.2
	S_{11}	2.5	6.7	7.2
	S_{12}	4.8	.0	5.9
	$\bar{X}$	3.60	1.51	5.19
	SD	2.32	2.14	2.28

Note.—Adaptive change measured in centimeters.

TABLE 4

Estimated Slopes and Intercepts of Regression Lines for Three Combinations of the Data Presented in Table 3, and Their Correlation Coefficients

Ordinate *x*	Ordinate *y*	Estimated slope	Estimate of intercept	*r*	*p*<
T and	H + V	.933	.27	.64	.05
V and	T − H	1.197	.04	.69	.02
H and	T − V	1.036	.12	.71	.01

both variables were liable to error. The slope of the regression line, the intercept of line, and the correlation coefficient for the three combinations of the data are shown in Table 2.

In contrast to the changes produced by the purely visual effects of the prisms, the effects of exposure to sensorimotor discordance produced strong support for the linear model. The V, H, and T scores, measured as aftereffects of exposure to sensorimotor discordance, are presented in Table 3. Significant changes from pretest performance were found in all three measures. The values of *t* for correlated scores were, t_H (11) = 5.732, t_V (11) = 2.447, and, t_T (11) = 7.887. The mean of the algebraic sum of H and V did not differ significantly from the mean value of T, *t* (11) = .05. The estimated slopes of the orthogonal regression lines for three pairs of ordinates and the three relevant correlation coefficients are presented in Table 4. The correlations are all statistically significant, and the estimates of slope and intercept accord well with those predicted by the model. The values of H + V are plotted against the T values obtained in Exp. I and Exp. II and are shown in Fig. 1. The best straight-line fit to the data and the predicted line are also shown. These results strongly support the hypothesis that the sum of subtask scores should equal the change in target aiming performance.

Experiment II.—Aftereffect measures were obtained for the responses H (trained-hand positioning), V (estimated visual direction), T (target aiming with trained hand), and Tr (transfer, target aiming with untrained hand). The mean changes for

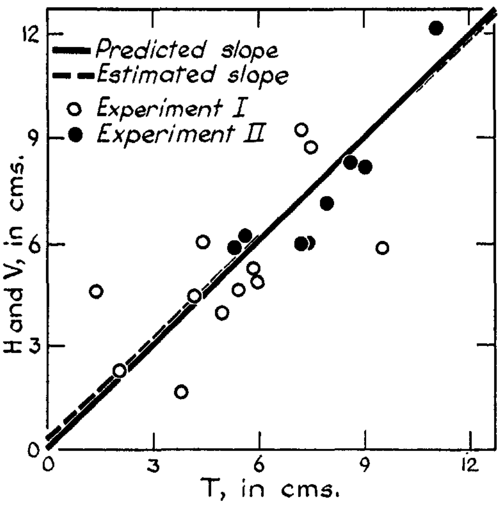

FIG. 1. Change between pretest (no prism) and posttest performance in pointing at a visual target plotted against the sum of visual straight ahead and hand straight ahead changes for *S*s in Exp. I and Exp. II.

each *S* are shown in Table 5. The mean change in performance of the tasks was significant in all cases. The t test for correlated scores yielded the following values, t_V $(7) = 2.606$, t_H $(7) = 4.356$, t_T $(7) = 11.822$, t_{Tr} $(7) = 2.215$, the last having a chance occurrence probability of .05 for a one-tailed test. As predicted by the model, the mean Tr score did not differ significantly from the mean V score, t $(7) = .31$; and the V and Tr scores for the eight *S*s were found to be significantly correlated, $r = .932$, $p < .001$. The values

TABLE 5

ADAPTIVE CHANGE IN H, V, T, AND TR (TRANSFER) RESPONSES SUBSEQUENT TO EXPOSURE TO INTERSENSORY DISCORDANCE

*S*s	H	V	Tr	T
S_1	13.7	−1.5	−2.8	11.0
S_2	4.7	1.3	1.8	7.2
S_3	4.6	3.6	2.8	9.0
S_4	4.1	1.9	2.3	7.3
S_5	.9	5.3	4.2	5.6
S_6	5.6	1.5	1.3	8.0
S_7	6.1	2.2	1.8	8.6
S_8	5.2	.6	1.3	5.3
$\bar{X}$	5.60	1.86	1.57	7.78
SD	3.63	2.01	2.01	1.86

Note.—Adaptive change measured in centimeters.

are plotted in Fig. 2. The best-fitting straight line can be seen to correspond closely to the predicted function. It can be seen that S_1 showed a nonadaptive V score that was reflected in a negative Tr score and produced a value of H + V consistent with his target-aiming performance.

The four variables measured in this experiment produced six combinations of three, which when plotted on a graph should yield lines with a slope of 1 and intercept at the origin. The estimated slopes and intercepts together with the six values of r obtained are presented in Table 6.

All the values of r obtained are significant and the estimated slopes lend support to the linear model.

DISCUSSION

The results obtained after *S*s had been exposed to visual-motor discordance all strongly support the proposed linear model. The changes in H and V can be summed to predict the change in T. This result has been found for group scores by McLaughlin and Webster (1967), Held and Bauer[3], and Hay and Pick (1966), all of whom used different but comparable behavioral tests. The present experiments replicate the results for individual scores.

The results of Exp. II showed that transfer of training to the unexposed hand could be fully accounted for in terms of the V responses and showed that this phenomenon can be regarded as reflecting a change in an element common to the control loops governing visually guided responses in both arms, rather than a change in a cognitive component or a generalization effect.

The results produced by exposing *S* to the transformed optical array, but giving him no feedback about his pointing responses, are much less comprehensible. This part of the experiment is very similar to the conditions used by McLaughlin et al. (1966), and the results are similar also. McLaughlin et al. assumed that the linear model was appropriate and estimated changes in V from measures of H and T. When *S* did not receive feedback about his pointing responses, McLaughlin et al. found a change in hand positioning counteradaptive to accurate pointing responses. This finding was confirmed in the present experi-

[3] Held, R., & Bauer, J. Personal communication, 1969.

ment. However, in the present experiment, direct measurement was made of V changes so that the linear model could be tested. The results could not be fitted to the linear model. The most significant result of this part of the experiment was that V and H were significantly correlated. Somehow transforming the optical array affected setting the hand straight ahead and judging a point to be straight ahead. Since *S* positioned his hand while his eyes were closed, it is implausible to ascribe the change to visual capture; however, no more plausible explanation seems available. The change in V responses was probably produced by the apparent rotation of the target screen, caused by the prisms, as suggested by McLaughlin et al. (1966).

The model predicts that H + V = T. Experimental conditions that produce an adaptive change in V and a counteradaptive change of similar size in H should therefore produce small changes in T. In the present experiment, the mean V change was significantly larger than the mean H change so that a small adaptive T change is predicted. The magnitude of the mean T change was very similar to the mean algebraic sum of H and V changes. It is possible that the linear model is applicable in this condition, but that the opposed effects of the H and V changes served to reduce the range of observed scores while the variance was unaffected, and hence the probability of the data fitting the model was reduced.

The change of state in the visual-motor control loop has recently been described in two ways. The first description has been most explicitly stated by Harris (1965). He states that all adaptive changes can be described in terms of a modification of the "felt position" of a part or parts of the body. Harris (1965) states that it is possible that the felt position of more than one body part can undergo change and that if two of these parts are in a visual-motor control loop, the changes will be additive, so that their sum predicts the change in performance when the whole loop is used.

The felt position of a body part can depend upon a variety of afferent inputs or upon efference. According to Harris (1965), therefore, the adaptive change can be produced by a change in the coordinates of a point about a mechanical point of articulation in the system (e.g., the arm in the shoulder socket or the eye in the skull) or by a change in the perceived shape of the rigid components of the system (e.g., the forearm). Harris (1965) excludes the possibility of a change in retinal space

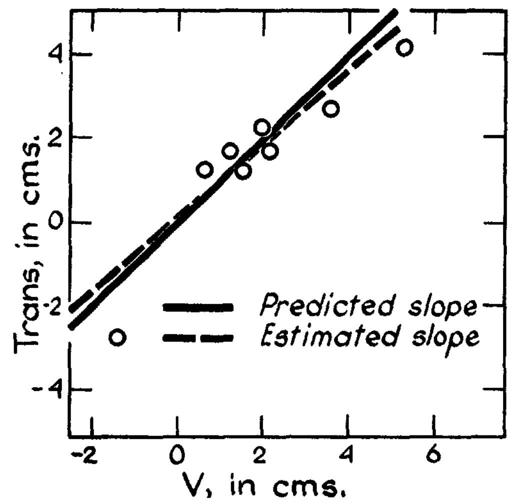

FIG. 2. Change in visual estimates of straight ahead resulting from exposure to intersensory discordance plotted against intermanual transfer of training for *S*s in Exp. II.

values as the adaptive process, presumably because stimulation of points on the retina leads to estimation of visual direction of the stimulus rather than a felt position of stimulation on the body surface.

Efstathiou et al. (1967) have produced experimental evidence that does not fit the description of the adaptive change given by Harris (1965). They showed that after exposure to visual-motor discordance, *S*s can

TABLE 6

ESTIMATED SLOPES AND INTERCEPTS OF THE REGRESSION LINES OF SIX COMBINATIONS OF THE DATA PRESENTED IN TABLE 5 AND THEIR CORRELATION COEFFICIENTS

Ordinate x | y	Estimated slope	Estimate of intercept	r	$p <$
V and Tr	.876	.15	.93	.001
T and H + V	.940	.23	.90	.01
V and T − H	1.122	.19	.93	.001
H and T − V	.968	.36	.97	.001
T and H + Tr	.887	.28	.89	.01
T and T − H	1.219	.28	.95	.001
H and T − Tr	1.015	.36	.97	.001
T and H + V (Exp. I & Exp. II)	.971	.332	.97	.001

Note.—Also presented are the same values for V and Tr and the combined H + V scores from Table 3 and Table 5.

relocate the position of targets they have never seen without systematic reaching errors. However, S's ability to reach for the unseen finger of the unexposed arm was affected by prism exposure. Harris (1965) has stated that the extent to which S misreaches for his unexposed hand after exposure is a measure of the change in felt position of the exposed arm. Harris (1965) would therefore predict the same error in reaching for the remembered location of a tactile target as was produced when S reached for the unexposed hand. Harris (1965) cannot therefore account for the results of Efstathiou et al. However, Efstathiou et al.'s results cannot be reconciled with those of Kennedy (1969), who found a change in a relocation task when the exposed hand was tested after exposure to visual-motor discordance.

Efstathiou et al. (1967) describe the change of state in the visual-motor control loop as a change in the "matched orientations" of eye on hand. Further work by the same group (see Footnote 3) has produced two changes in matched orientation. These are head to hand and head to target. The sum of these two changes indicates the extent of the adaptive change. Here again is evidence for a linear system. Recent work from the same laboratory (Hardt, Held, and Steinbach 1971) has produced different results using different tasks. In these experiments the tasks were pointing to a visual target without feedback about accuracy, orienting the head to the arm while blindfolded, and relocating the remembered position of a tactile target. Exposure to the effects of the prisms produced changes of similar size in the first two tasks, but no significant changes in the last task. From these results, the authors concluded that the nature of the adaptive change must be what they term "the sensorimotor type." This type of change includes what Efstathiou et al. referred to as "matching orientations." However, as Howard (1971) has pointed out, Hardt et al. did not exclude the possibility that the adaptive change in their experiment was the result of a change in the felt position of the eyes or the neck. Their results do not, therefore, warrant the rejection of the hypothesis that changes can occur in several components of the visual-motor control loop. The results of the present experiments represent strong evidence for the hypothesis that separate changes in the subcomponents of the control loop can change and that these changes can be summed algebraically to predict the total adaptive change. The results of Hay and Pick (1966) and McLaughlin and Webster (1967) also support the hypothesis.

An interesting feature of a linear system with independent additive components is that the variance of the whole loop should equal the sum of the variances of the subloops. In the pretest condition of Exp. I, the sum of the subtask variances in all Ss exceeded the variance of target aiming. This result is not consistent with the model, but does not invalidate it. The subtasks selected were assumed to form a subset of the processes of the total visual-motor control loop. Some of the processes in these subtasks (e.g., response processes) were undoubtedly not part of the control loop. The parts not involved in the visual-motor loop could therefore have contributed the extra variance, while the parts of the subtasks that underwent change were those parts which were in the control loop. An attempt should be made to control the variance of subtask performance before exposure to the optical transformation and then test for the sum of the variances against the variance of the total loop. The subtasks used in experiments are often unfamiliar, so some of the variance with which they are performed may be eliminated by practice. The nearer the sum of the subtask variances is to the total loop variance, the more appropriate is the use of those subtasks in studying sensorimotor rearrangement.

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(Received December 8, 1970)