STUDIES ON ADAPTATION TO DEFLECTION OF THE VISUAL FIELD IN SPLIT-BRAIN MONKEYS AND MAN

Thesis by

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ABSTRACT

Experiments were performed with split-brain monkeys and human subjects to investigate several questions concerning the ability of higher mammals to compensate for errors in reaching produced by optical rearrangements of the visual field. The aim of these experiments was to determine 1) if the adaptive process or effect could be localized to or associated with particular structures or regions of the brain, 2) if the adaptive changes are made in visual, motor, or proprioceptive elements of coordination, and 3) how the process and effect of adaptation compare with other types of learning and memory.

Subjects were required to practice localizing movements with specified combinations of eyes and limbs while looking through prisms that deflected their visual field. They then were tested for transfer of the acquired adaptation to unpracticed members of the body. Normal monkeys and monkeys with differing degrees of midline section of the cerebral and midbrain commissures and of other structures showed normal adaptive ability with all eye-hand combinations and possessed no deficits when tested for interocular transfer. Normal reaching also appeared to be unaffected by split-brain surgery. Monkeys and human subjects did not transfer the acquired compensations from the practiced to the unpracticed arm in several experiments, although partial transfer to unpracticed members was found with human subjects in certain situations. The adaptive effects did not require vision for a return toward normal coordination.

It was concluded that the adaptive process is not organized completely at cortical levels and that subcortical centers are involved in reaching with both normal and adapted coordination. The effect of adaptation seems best described as recalibrations in position sense of particular limbs of the body. Under some conditions these alterations seem to be restricted to the level of the particular joints that were practiced during adaptation, while under other conditions generalization to unpracticed members was observed. The critical factor for the occurrence of generalization appears to be the kind or amount of movement rather than differences in visual stimulation. Adaptation differs from other forms of sensory and motor learning by the presence of interocular transfer in split-brain monkeys and by the complete absence of intermanual transfer in monkeys and man under some conditions.

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INTRODUCTION

When the visual field of human subjects is inverted, reversed, or otherwise rearranged, the subjects show definite compensation for the resulting errors in localization through changes in sensory-motor coordination. The initially disruptive effects on coordination of visually guided movement are overcome by extensive practice, as shown clearly by several experiments in which the extent of visuomotor adaptation was measured (1-9). In the most striking examples of readjustment subjects could "engage in fencing, skiing, or riding a bicycle in heavy traffic" (10) while wearing mirrors that produced up-down inversion of the visual field (6, 7). Despite such claims of remarkable recovery of coordination, it remains questionable that complete behavioral adaptation to inverted or reversed vision has ever been achieved (9, 11).

The subjects of all but one (3) of these experiments reportedly experienced significant reduction of the initial discrepancies between the position of the body as determined from vision and from proprioception. Thus, for many situations, some perceptual reorientation accompanied the behavioral adjustment to inverted and reversed vision. In some reports the perceptual changes were claimed to have occurred within the visual sphere (1, 4-7), while in others the changes were ascribed to alterations in the perception of body position (2, 11). In the one experiment in which perceptual alterations were not observed, the behavioral changes were interpreted as a form of motor learning (3). Typical learning curves were obtained in this and other experiments that determined the rate of acquisition of skilled performance of several motor tasks (3-5, 9).

Similar studies with infrahuman mammals also indicate the presence of some degree of adaptability to inverted vision. One monkey improved her ability to walk toward visually localized objects after wearing inverting and reversing lenses for seven days, although recovery was apparently not complete (12). Newborn kittens raised for many weeks with inverting prisms learned to perform several visuomotor tasks satisfactorily, but were not as competent as normally reared controls (13). On subsequent reversal of the optical conditions for the two groups of kittens, the originally "inverted" group showed an advantage in the ability to adapt to the new situation.

The adjustments to chronic inversion or reversal of the visual field require weeks of practice through the optical devices, and hence are rather cumbersome for use in more extensive analyses of the process of adaptation. On the other hand, deflections of the visual field such as produced by a wedge prism are easily compensated, often with only a few minutes' practice, and consequently have been more frequently employed in investigating the conditions necessary for establishing adaptation (8, 14-17). With this technique it has been found that while practice movements are required for adaptation, specific knowledge of errors is not (15, 16). Further investigations have shown that self-produced movement and the resultant visual feedback, called reafferent stimulation after von Holst's usage (18), are necessary for adaptation to occur (8, 17). Passive movement of the subject that produces similar visual and, presumably, similar proprioceptive feedback does not result in adaptation. These findings indicate that some component of the response mechanism, usually identified with corollary discharges from the motor system, is crucial for adaptation, and have led to a useful model for this process (19).

These short term experiments with deflecting prisms, and others employing displacements of vision by closed circuit television (9), have been concerned primarily with studying the adaptive process rather than the end effects that are produced. They have usually been interpreted as favoring the linkages between sensory and motor systems as the locus of the neural readjustment (9, 15, 19).

Adaptation experiments also have been taken to support the theory that vision and visuomotor coordination are acquired by experience rather than by genetically determined mechanisms of development (1, 2, 4-8, 12-14, 19). However, postulation of empirically organized mechanisms apparently does not explain coordination in submammalian vertebrates and insects. Rearrangement experiments in birds (20, 21), amphibians (22-24), fishes (25, 26), and insects (27) present strong evidence that visuomotor coordination in these classes is subject to little or no readjustment. For birds (20) and amphibians (23, 24), the results show directly that visuomotor coordination is innate. Thus it would appear from the evidence available to date that the ability to adapt to rearrangements is exclusively a property of the mammalian brain. It is as yet not certain if this ability reflects the employment by higher animals of a novel, empirical approach to the development of normal sensory-motor coordination.

A wide variety of questions concerning adaptation remain unanswered or unasked. This research was begun in an effort to learn something of the basis of adaptation in terms of the neural structures involved. For this purpose monkeys with surgical intervention in pathways thought likely to be involved in adaptation of reaching accuracy were extensively tested for adaptive ability. Some results from these experiments led to a corollary series of tests, performed with human subjects, that were directed toward establishing whether changes caused by adaptation were located in visual, proprioceptive, or motor components of the coordinational mechanism. During these experiments questions concerning the conditions that determine which members of the body are affected by adaptation arose and were investigated further. Finally, attention was paid to those aspects of the experiments that seemed likely to indicate the relation of adaptation to other forms of learning.

SECTION I

EXPERIMENTS ON THE FUNCTIONAL ANATOMY OF ADAPTATION

The usefulness of split-brain techniques for studying problems relating to learning, memory, and cerebral organization has been discussed in recent reviews (28, 29). These techniques were employed in the following experiments to determine if midline section of various commissures in the brain would have effects on adaptation similar to those found for other types of learning (30-39).

It is presumed that adaptation of reaching aim with deflected vision requires some kind of readjustment between the visually determined position of an object and the mechanisms that produce the aiming response, and therefore a functional association between the visual and proprioceptive-motor systems is implied. It would be expected that the retinal projection to the cerebral cortex (geniculo-striate system), along with the systems responsible for recording the position of the eyes and the head, would be employed in visual localization, and it would seem a plausible assumption that the cortical somatosensory and motor areas are used in directing the aiming response. If the adaptive process is cortically organized, some deficit would be predicted in adapting the hand ipsilateral to the exposed eye in split-brain monkeys due to the disruption of the direct connections between the visual and somatic sensory-motor centers. Similarly, it might be expected that when the sensory input is unilateral the adaptive effect would be restricted to the exposed hemisphere, as is the memory for other types of learning.

In the present work these possibilities were tested by allowing split-brain monkeys to adapt with one of the four possible combinations of eyes and hands and then testing for transfer of the adaptation effect to the other eye-hand combinations. Ipsilateral and contralateral combinations were adapted in successive experiments and the results were compared to determine their relative adaptability. Three variations on this basic procedure were used to test adaptation with free or forced choice of hands, and with short or long term exposure to deflected vision.

Subjects. Descriptions of the monkeys used in these experiments and of the structures in the brain that were sectioned in the midline, or ablated, in each are given in Table 1 and Fig. 1. Most of these animals were chosen from the Caltech split-brain colony and were not specifically operated on for these experiments. The surgery was performed on Tm, Hr, and Bn by H. L. Arora and on Rb, Bb, Dp, Hm, and Ll by R. W. Sperry. The extent of the surgery was checked histologically in all cases except that of Dp, who showed no evidence of transfer of pattern or brightness discriminations. The results of the post mortems are as follows.

Complete section of the structures indicated in Table 1 was confirmed for subjects Rb, Hr, and Hm.

Tm (see Fig. 1) had two strands of fibers, approximately 0.2-0.4 mm. in diameter, intact in the posteroventral portion of the optic chiasm. A very thin, band-like thread of fibers (about 1 x 0.1 mm.) remained in the most anterior portion of the callosum. The anterior

TABLE 1

DESCRIPTION OF SUBJECTS AND SURGERY

Subject			Surgery		
Name	Species	Sex	Forebrain	Midbrain	Other
Tm	R	m	oc, ac, cc, hpc, hbc, pc, mi	sc, ic	cb
Rb	R	f	oc, ac, cc, hpc, hbc, pc, mi	sc, ic	
Bb	R	m	oc, ac, cc, hpc, hbc, pc		
Hr	R	m	oc, ac, cc, hpc		
Bn	R	m	oc, ac, cc, hpc		
Dp	P	m	oc, ac, cc, hpc		
Hm_1	P	f	oc		
Hm_2	P	f	oc, ac, cc, hpc		
Ll	R	f	oc, ac, cc, hpc		right somatic arm area
Ln	P	m			
Sd	R	f			

Abbreviations: oc, optic chiasm; cc, corpus callosum; ac, anterior commissure; hpc, hippocampal commissure; hbc, habenular commissure; mi, massa intermedia; pc, posterior commissure; sc, commissure of the superior colliculus; ic, commissure of the inferior colliculus; cb, cerebellum; R, rhesus (*Macaca mulatta*); P, pigtail (*M. nemestrina*).

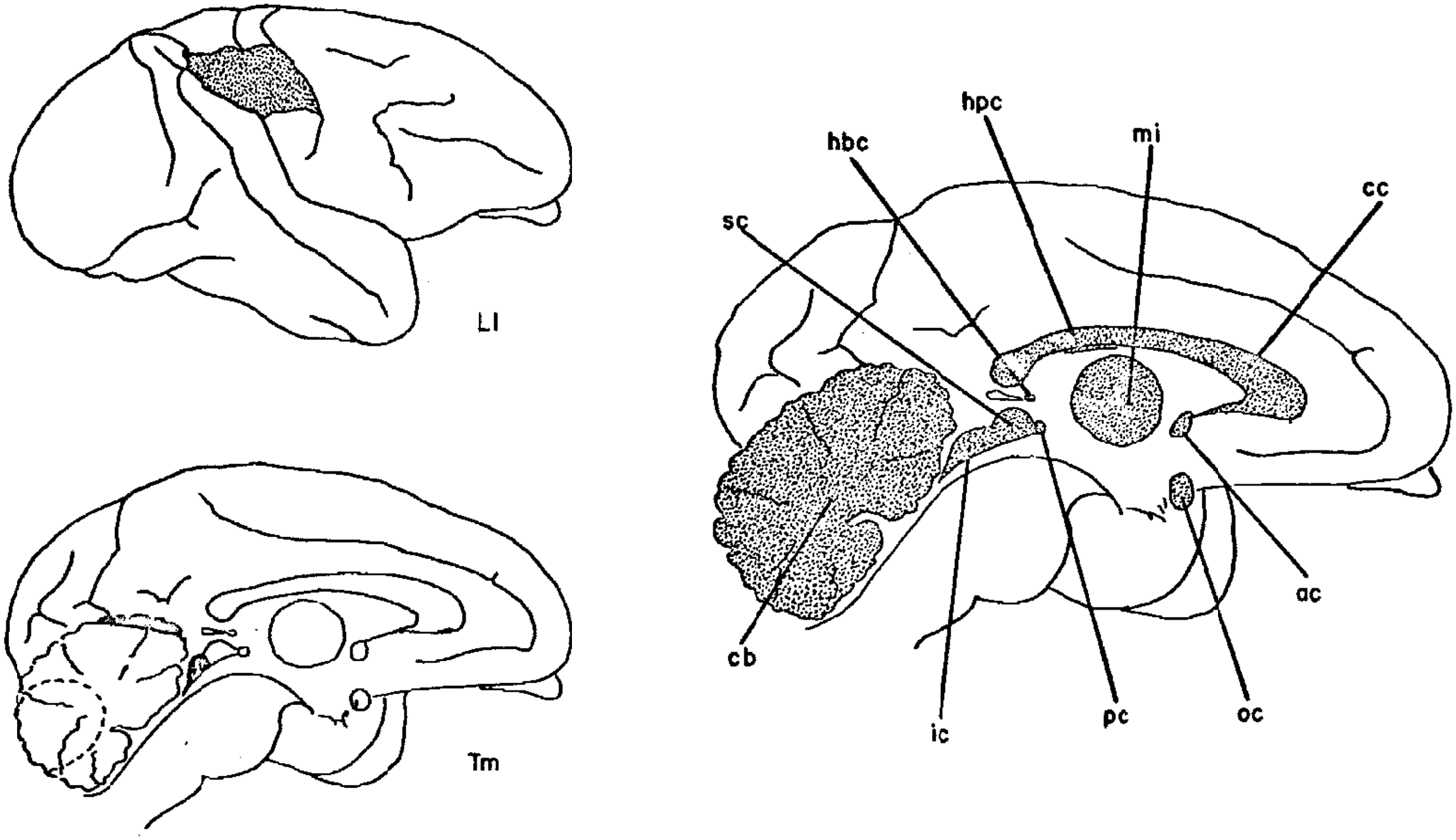

Fig. 1. Extent of surgery. Right: Stippling indicates the structures sectioned in various animals. Upper left: The stippled area shows the extent of the cortical lesion in Ll. Lower left: The black area indicates structures unintentionally left intact in Tm. The dotted line approximates the outline of the accessory cerebellar lesion in Tm. Abbreviations are the same as in Table 1.

and posterior portions of the commissure of the inferior colliculus were not completely sectioned. A midline remnant of the cerebellar cortex was unsectioned in the extreme dorsal portion of the anterior lobe (about 1-2 mm. from the surface) and a large spherical lesion (about 7-10 mm. diameter) had developed around the midline of much of the posterior lobe (Fig. 1). Only the fibers remaining in the chiasm are considered particularly critical to the validity of the present results, and they appeared to belong to the more peripheral parts of the retina. In view of the results concerning interocular transfer of adaptation in Tm and other monkeys it seems unlikely that this small "window" would be used in preference to the apparently accessable contralateral hemiretina. However, no proof that these fibers were not used during adaptation can be given.

An extremely fine strand of fibers was intact in the anteriormost part of Bb's chiasm, but it is considered too small to be significant. The cerebral cortex contained at least 15 cysts 2-4 mm. in diameter, apparently cysticerci.

Bn's optic chiasm was largely destroyed during removal of the brain from the skull. However, he showed no evidence of interocular transfer of pattern discriminations and there was noticeable degeneration in each lateral geniculate nucleus. Both of these observations indicate at least partial section of the chiasm.

Ll had two strands (less than 0.1 mm.) intact in the posterior portion of the optic chiasm. Again, the fibers were presumably in the peripheral parts of the visual field and were probably not significant. The extent of the parietal lesion intended to remove her right somatosensory arm area is indicated in Fig. 1. It is roughly coincidental with the arm and leg regions of the somatosensory cortex as determined by electrical recording (4C). Her left arm and leg showed characteristic symptoms of parietal lobe damage.

Experiment 1

Interocular Transfer of Adaptation*

It was of primary interest to know if the effect of adaptation could be restricted to the exposed eye of split-brain monkeys. For this purpose, lateral errors in reaching movements were produced by deflecting the visual field approximately 13 degrees with a wedge prism worn in front of one eye. Following compensation for these errors, reaching aim with the unexposed eye was tested to determine if interocular transfer of adaptation had occurred. Interocular transfer is used throughout only as a term describing experimental results and does not in itself imply any mechanism. The animals were allowed free choice over which arm to use in case they preferred certain eye-hand combinations.

Apparatus and procedure. To carry out this type of experiment a semi-permanent headpiece to hold prisms and occluders and to exclude normal vision in the periphery was required. Several helmet designs made of leather or reinforced cloth were unsatisfactory. Some successful tests were completed with helmets of liquid latex and cloth molded

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*This work was reported in part in Reference 41.

directly on the monkeys' heads*, but continued difficulty caused by irritation and slipping out of place limited their usefulness.

Metal masks screwed to the skull proved to be the most satisfactory means for attaching prisms (Fig. 2). Stainless steel #6 woodscrews were modified by removing the heads and partially threading the shanks. A nut twisted to the end of the threaded portion allowed the screw to be driven, and later served as a spacer to keep the mask away from the monkey's skin. Under sterile conditions the skin was incised, three small holes were drilled in the skull, and the screws were inserted. One screw was placed in the center of the brow ridge and the others were positioned below and slightly lateral to each eyesocket. The masks were tailored to the animals' facial contours during this operation, but were not attached until after the skin had begun to heal. These masks could be used for about one month, after which the screws tended to loosen due to bone deterioration.**

A handcrafted circular plexiglass prism (5/8 inch diameter, approximately 13 degree deflection) when placed in the masks produced a monocular visual field of about 30 degrees. An occluder prevented vision through the remaining eyehole.

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*The latex helmets were developed by J. Bossom.

**If dental cement and small anchoring screws were also employed, the lifetime was extended to at least two or three months. Use of special alloys, or additional anchoring nuts behind the zygomatic bone might also extend the useful life of the preparation.

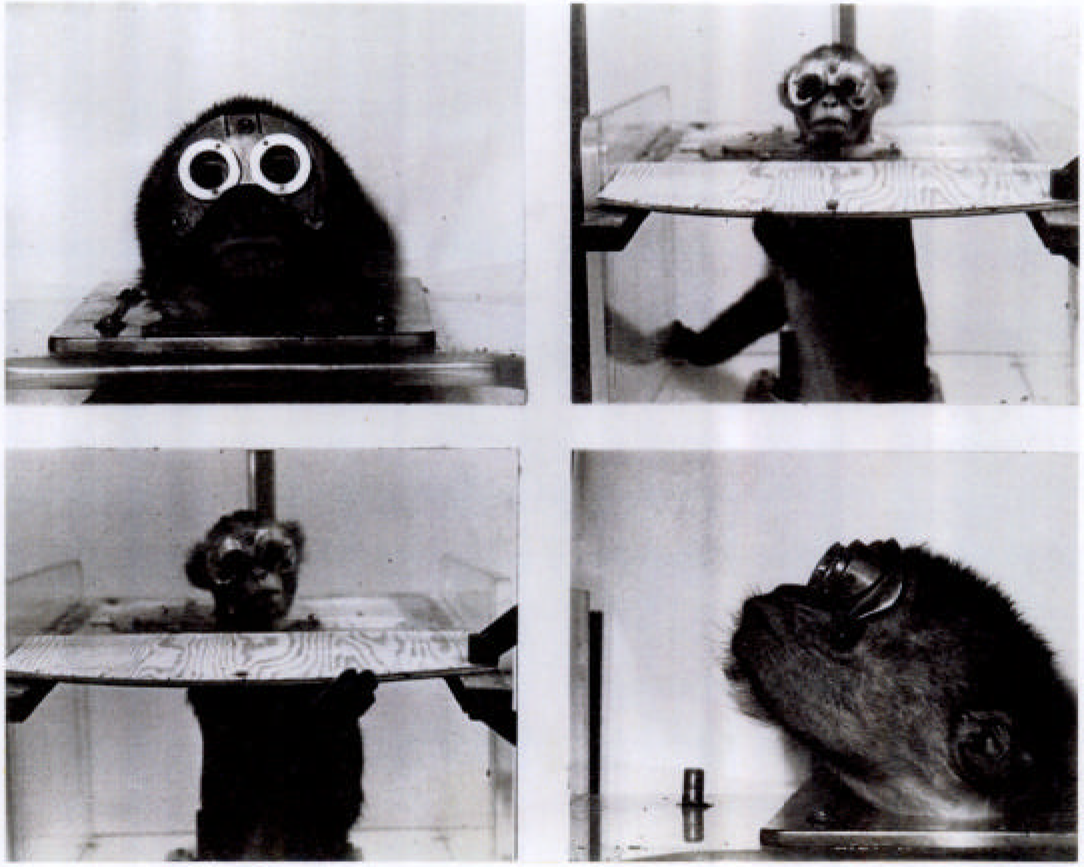

Fig. 2. Technique for chronic adaptation with monkeys. Upper right: Subject Rb, wearing prisms, reaches inappropriately in unexpected direction with ipsilateral eye-hand combination. Lower left: Rb overreaches in the expected direction with the contralateral combination. Upper left and lower right: Ll models the mask used in the chronic adaptation experiments.

The monkeys were kept in standard primate chairs for the duration of each adaptation session. An opaque board placed on the neck piece of the chair during the pre- and postexposure tests prevented visual feedback from the arm movements (see Fig. 2). The monkey could see his fingers at the end of each reach, but apparently this information was not used for immediate correction of the error. The targets for which he reached consisted of small pieces of food placed on the edge of the board, which was calibrated in centimeters. Accuracy of reaching was measured by recording the distance between the reward and the animal's index finger. The position of the reward was varied from trial to trial.

When prisms are removed after the exposure period, the effects of adaptation appear as errors in reaching in the direction opposite to the errors initially induced by the prisms. These errors are called aftereffects, and are useful measures of the amount of adaptation (8). Their magnitude was obtained in this experiment by taking the difference between pre- and postadaptation measures of reaching accuracy; their sign was taken as positive when the errors were in the expected direction. The differences between the means of the pre- and postexposure measures were tested for significance by t tests.

Three monkeys adapted monocularly to the deflected visual field and then were tested for interocular transfer of adaptation. Two animals had standard split-brain surgery (Hr, Bn), while the third had additional section of the midbrain commissures and the cerebellar hemispheres (Tm). These monkeys were allowed to use either or both hands while adapting and being tested. Base readings of reaching accuracy were taken for each eye to be tested. The prism was then mounted in one eyehole of the mask and the occluder was placed in the other, the opaque board was removed, and the monkey was allowed to adapt to these conditions for two to four days. The animals fed themselves and were otherwise encouraged to use their hands. Specific practice sessions of reaching for food were given, in which the experimenter held the reward before the monkey in different positions. Periodic tests of reaching accuracy, measured with the prism and opaque board in place, were made in order to follow the extent of adaptation. When the initial errors had been corrected or when four days had passed, the prism was removed and the amount of adaptation was measured, first for the unexposed eye and then for the exposed one. Each animal adapted four times; a different combination of eye exposed and lateral orientation of the prism was used each time.

In addition to these tests one subject (Tm) was returned to his home cage with the prism in place for four days and his general ability to compensate for the displacement of the visual field was observed.

Results. The results obtained in this experiment are indicated in Table 2. The data show that split-brain surgery did not restrict the effect of adaptation to the exposed eye. The mean aftereffect for the unexposed eye was 4.1 degrees and that for the exposed eye was 2.5 degrees. Both of these values are significantly greater than zero ($p < .001$). The greater aftereffect measured with the unexposed eye need not indicate that this eye was more adapted than the exposed one since the readings for the unexposed eye were always taken first, and some decay of the aftereffects was usually observed during the 25 test trials with each eye. The amount of transfer is investigated directly in subsequent experiments that were balanced to average any effects of aftereffect decay.

No difference in transfer was noted between the subject with the more extensive surgery (Tm) and the other two. The somewhat smaller aftereffects shown by Tm do not appear to be meaningful, since he often produced large ones in later tests.

There was no indication that the monkeys preferred their contralateral (i.e., intrahemispheric) eye-hand combinations in these tasks of reaching. All three subjects consistently chose to use their right hands during these tests regardless of which eye was being used or which eye had been first exposed. All animals were capable of using their left hands and did so in subsequent tests. Tm initially used both hands about equally, but before the base measurements were completed he settled on his right hand. Bn began with his right eye and therefore chose an ipsilateral combination from the very beginning. Hr initially chose a contralateral combination. Evidence for decreases in the precision of reaching with ipsilateral pairs was also sought; the pertinent data are presented in Table 5 and are discussed along with similar results from the other experiments.

While there is no indication that transfer is any less pronounced for any of the conditions of adaptation, there does seem to be a

TABLE 2

TRANSFER OF AFTEREFFECTS FOLLOWING CHRONIC ADAPTATION WITH FREE CHOICE OF HANDS

Adaptation Condition	Subject & Experiment	Aftereffect in Degrees			
		EE:EH	p <	UE:EH	p <
	Hm 2	6.6	.001	6.2	.001
LE, BR	Bn 2	2.0	.10	6.8	.001
	Tm 1	3.2	.025	3.8	.025
	Hm 1	4.2	.001	8.0	.001
LE, BL	Bn 4	2.4	.001	3.8	.001
	Tm 2	4.0	.001	4.6	.001
	Hm 3	3.4	.001	4.0	.001
RE, BR	Bn 1	2.0	.001	5.6	.001
	Tm 4	0.2	.45	3.4	.001
	Hm 4	0.6	.25	2.6	.001
RE, BL	Bn 3	-0.4	.65	0.8	.05
	Tm 3	1.8	.01	-0.6	.65

Abbreviations: LE, left eye; RE, right eye; BR, prism base to the animal's right; BL, prism base left; EE, exposed eye; EH, exposed hand; UE, unexposed eye.

tendency for a smaller aftereffect to be established with right eye, base left adaptation, for which the right hand was always used. This is plausibly explained by the geometry of the experimental situation. For ipsilateral adaptation the hand enters the visual field on the blind side and, if the animal is looking toward the target, the hand will not be seen until it reaches its goal. For example, base left prisms cause the animal to reach to the right of the reward and therefore the right hand will not be seen at all so long as reasonable fixation near the target is maintained. It follows that animals would receive much less visual feedback correlated with movement under these conditions. Even with base temporal prisms some deficit in adaptation would be expected with ipsilateral pairs due to decreased amount of stimulation.

Tm, when returned to his cage with the prism in place, quickly overcame the initial uncoordination and seemed at no greater disadvantage than when wearing the goggles without a prism. Accurate tests were not available, but he was able to reach accurately for food, climb around the animal room, and jump from one cage to another, a distance up to four feet. His performance, though not as good as that of normal monkeys, was roughly comparable to his coordination without the prism in the mask.

No definite effect attributable to section of the interhemispheric commissures on either the establishment of adaptation or its interocular transfer was evident in this experiment. Accordingly, it was decided to examine next the effect of split-brain surgery on intermanual transfer and to compare more carefully the adaptability of ipsi- and contralateral eye-hand pairs.

Experiment 2

Interocular and Intermanual Transfer of Adaptation: Chronic Exposure

In the previous experiment, in which no restrictions were placed on hand use, the monkeys chose to use the same hand with either eye, and no information on the extent of transfer of adaptation from the practiced to the unpracticed arm was obtained. The present experiment was designed to measure the amount of transfer from one to the other hand.

Apparatus and procedures. Five monkeys with varying degrees of surgical intervention (Bn, Bb, Rb, Tm, Ll) and one normal animal (Ln) practiced reaching while looking through a prism for several days as in the preceding experiment but with the following modifications in procedure. A hand restraint was used to restrict practice to one preselected eye-hand pair and to enable controlled testing of all four combinations for aftereffects following adaptation. During the post-exposure tests the practiced eye-hand pair was always tested or re-tested last to insure that significant aftereffects were still present. When some decay of the aftereffect was evident in the practiced pair, its influence on the data was roughly cancelled by averaging early and late measurements and comparing them to measurements of other combinations taken in between. No decay was observed that involved more than a 30-40% decrease in aftereffect. The intention was to have each animal adapt with every combination of eye and hand, but various difficulties with the monkeys and techniques prevented completion of this design. A standard sequence for presentation of the target was used and the significance (t test) of each aftereffect was calculated from the paired differences between pre- and postexposure measurements of reaching accuracy.

Results. The results from all of the cases in this experiment in which significant aftereffects were obtained are given in Table 3. Fig. 3 contains a graphic presentation of the data; the individual aftereffects are labeled if significant. Eleven cases failed to show significant aftereffects for the exposed eye-hand combinations; their distribution was RE,LH, 2; LE,RH, 3; RE,RH, 2; LE,LH, 4.

The data show that there was complete transfer from eye to eye, but no transfer from arm to arm when adaptation took place with contralateral eye-hand pairs. The one exceptional case of this group (Rb 1) in which there was a statistically significant aftereffect ($p < .05$, one tailed t test) in the unadapted hand showed also a significant negative aftereffect ($p < .005$) when the same hand was tested with the untrained eye. Neither result was obtained again on repetition of the experiment (Rb 2). This monkey required special consideration as is discussed below.

The results following adaptation of ipsilateral eye-hand pairs are not so clear. One case (Bb 3) showed good interocular transfer (as did most of the cases in the first experiment) and no intermanual transfer to the one combination with the unexposed hand that could be tested. Two cases (Tm 5, Bb 1) showed significant, although not large, intermanual transfer. No significant transfer to any unadapted combination was found in two cases (Bn 7, Tm 10) although good aftereffects were present in the adapted combination; in both of these cases the occluder was shifted back and forth between the eyes and the measurements were repeated several times to insure that there really was no interocular transfer. One similar, although less striking, case was found in Experiment 1 (Tm 3). No adequate explanation can be given for these observations. Perhaps the monkeys, upon not seeing their arms because of the hemianopia, sometimes learned to overcome the effects of the deflection by consciously overreaching. Such a learned motor response might not transfer.

Comparisons between ipsilateral and contralateral exposure show that the magnitudes of the aftereffects established in the two types of adapted combinations are not strikingly different, but these comparisons are not very meaningful in the present experiment because of the incomplete nature of the final experimental design.

The results in two cases require additional comment. Rb was the only subject in all the experiments that showed, even to casual observation, clear ipsilateral deficits in reaching ability. Each hand reached accurately when paired with its contralateral eye but became rather uncontrollable when used with its ipsilateral eye. On some reaches no deficits were noticed but on others the arm seemed to reach at random, and no meaningful attempt to correct the error was

TABLE 3

TRANSFER OF AFTEREFFECTS FOLLOWING CHRONIC ADAPTATION WITH FORCED EYE-HAND COMBINATIONS

Adaptation Condition	Subject & Experiment	Aftereffects in Degrees			
		EE:EH	EE:UH	UE:EH	UE:UH
RE, LH, BR	Bn 5	12.8	0.8	15.4	0.6
	Ln 3	8.0	-1.6	6.6	-0.2
	Rb 3	9.8	-0.2	10.0	-0.4
	Tm 6	2.2	1.0		
	Ll 2	6.8	-1.4	3.0	0.8
LE, RH, BL	Ln 2	6.0	0.0	6.4	0.8
	Rb 1	5.0	3.6	3.2	-3.8
	Rb 2	6.6	0.2	4.8	-2.0
	Tm 9	8.8	-0.2	8.8	-1.8
LE, LH, BR	Bn 7	8.0	1.2	1.0	-0.8
LE, LH, BL	Bb 1	3.2	1.8	2.8	2.4
	Tm 10	10.6	1.6	1.0	0.6
RE, RH, BR	Tm 5	7.4	2.0		
RE, RH, BL	Bb 3	4.0		4.0	0.0

Abbreviations: RE, right eye; LE, left eye; RH, right hand; LH, left hand; BR, prism base to the animal's right; BL, prism base left; EE, exposed eye; UE, unexposed eye; EH, exposed hand; UH, unexposed hand.

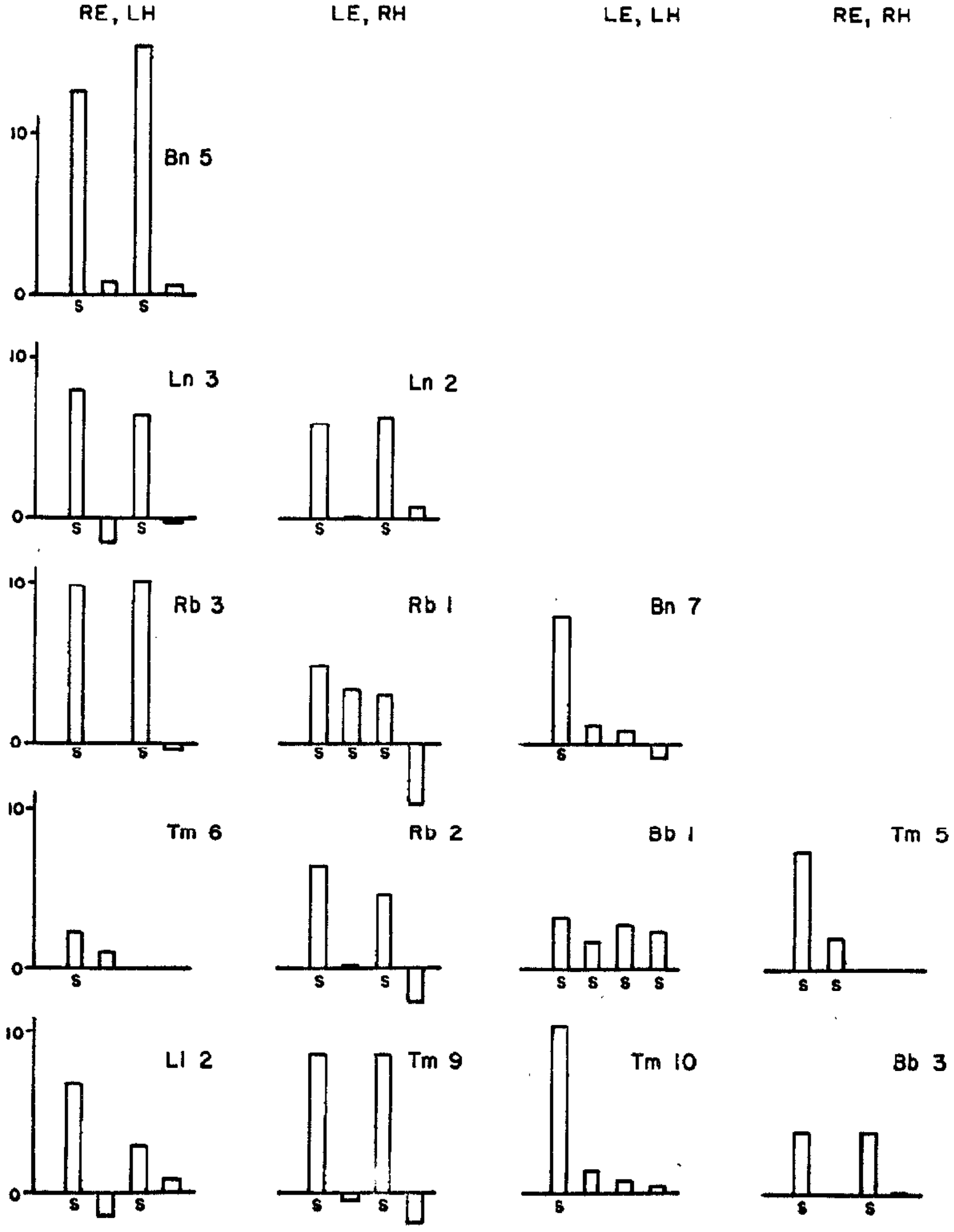

Fig. 3. Graph of data in Table 3. Ordinates represent the magnitude of the aftereffects in visual degrees. Significant aftereffects are marked by *s*. The bars are in the same order left to right as the data in Table 3: EE:EH, EE:UH, UE:EH, UE:UH.

made when the hand came into view at the end of a trial. This behavior could be observed even when visual feedback was permitted during the testing. All reaches that were more than 15 degrees off were arbitrarily disregarded in the calculation of the aftereffects. This selection may have altered the mean of the base or aftereffect measurements and thereby may have produced the peculiar aftereffects in the monkey's first adaptation (Rb 1). The scatter of normal reaching (bases) calculated from these selected measures was still significantly greater than that obtained with contralateral combinations (Table 5).

Special treatment was required for L1 when she was reaching with her left hand after she had sustained the right parietal lesion, because she was not able to use her fingers and hand well enough to grasp the small food rewards in the somewhat dexterous manner required. However, she quickly learned to make an appropriate aiming response of the arm and hand toward the reward, which was then fed to her by the experimenter. L1 showed no difficulty in adapting with her affected arm, but, as shown in Table 5, her precision with the affected hand was noticeably decreased.

The results up to this stage still present no clear indication of any effect of split-brain surgery on the acquisition or bilateral transfer of adaptation. The lack of success encountered in consistently demonstrating aftereffects suggested that some use of the visual knowledge gained at the end of each reach might have been made. It was decided to study further the relative adaptability and transferability with ipsi- and contralateral eye-hand pairs in a more controlled situation.

Experiment 3

Interocular and Intermanual Transfer of Adaptation: Acute Exposure

The previous technique did not give consistent enough results for satisfactory comparison between adaptation with the ipsilateral and the contralateral eye-hand pairs. The present experimental conditions avoided several earlier sources of difficulty by permitting more accurate control over the amount of practice received by the monkeys, by eliminating the visual and tactile knowledge of errors at the end of each reach, and by reducing other technical problems that led to a number of unsuccessful experiments.

Apparatus and procedures. An apparatus in which a monkey could be adapted and tested in a single half-hour session was constructed for this experiment. The general design of the apparatus is shown in Fig. 4.* It provided full control over visual feedback during testing procedures and allowed occluders, prisms, and hand restraints to be switched conveniently. The mirror was removed during the adaptation process so that the monkey could view his arm through a 20 diopter (about 11 degree) prism mounted in front of one of the eye holes in the box. The other eye hole was covered by an occluder. The mirror

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*R. W. Sperry and R. F. Mark designed the monkey compartment, which permits free lateral movements of the arm yet excludes vision through the arm holes.

was moved back into position for the tests, during which the monkey saw the virtual image of a "dummy" reward in the same plane in which the "real" reward was usually located. Thus, testing could be carried out in a situation in which no visual information regarding the movements or the final position of the arm was available to the animal. He was rewarded at any position to which he reached in order to deprive him of tactual clues to his inaccuracies. A sliding screen inserted in a slot above the position of the mirror (see Fig. 4) covered the mirror or opening between trials. The dummy or real reward tray was illuminated when in use, as was the space through which the monkey moved his arm.

A standardized procedure was adopted for all adaptation sessions using this apparatus. The mirror and occluder were inserted and baselines were recorded for each hand paired with the eye to be adapted. The baselines for the other eye could not be recorded during the same session because of limitations in the number of trials the animals were willing to perform at one session. However, the mean of the bases was known to be the same for a particular hand no matter which eye was used. Next the prism was placed before the open eye and the prism-induced shift was measured. The mirror was then removed and the monkey reached for 35 trials to the reward tray. The initial ten trials were recorded. If, after the 35 trials, reaching was still noticeably in error an additional 25 trials were given. The mirror was then replaced, the prism was removed, and aftereffects were measured for all four eye-hand pairs. The order of checking was

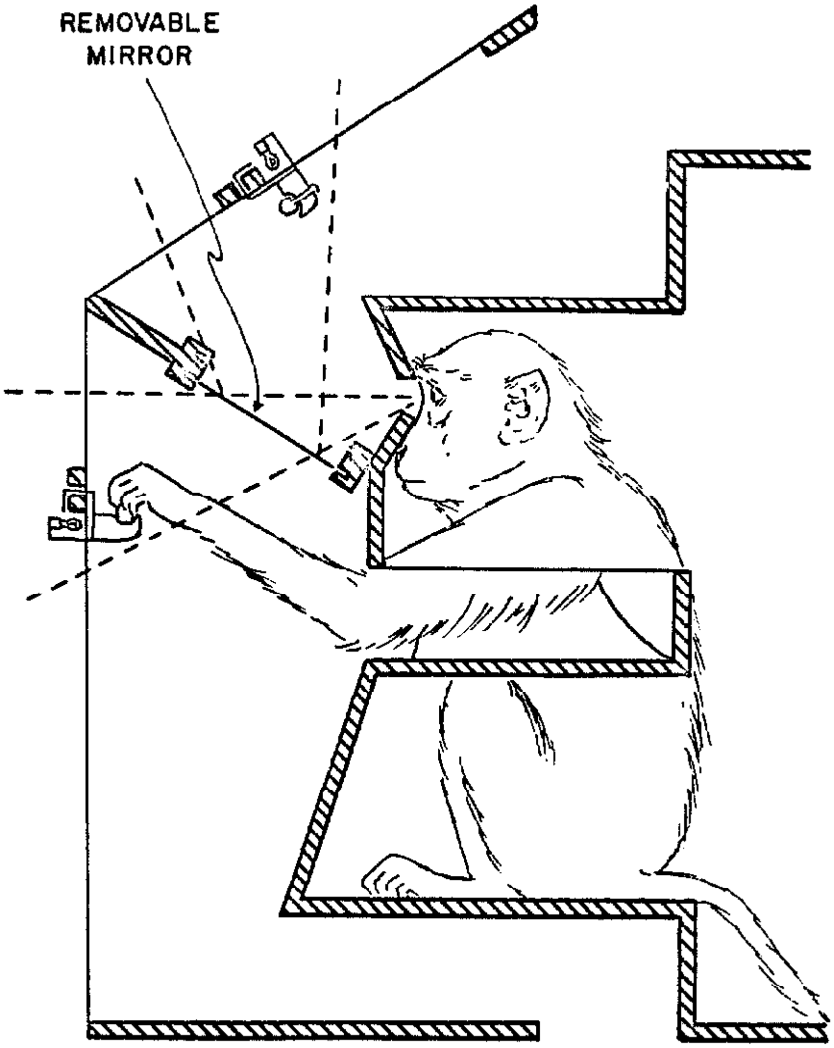

Fig. 4. Apparatus used for acute adaptation. A sliding opaque screen was positioned in the slots above the mirror between test trials. The illuminated reward tray could be moved to the monkey's left or right. The prisms and occluders were placed immediately in front of the eyeholes. For further explanation see text.

systematically varied, but the final tests were always made with an adapted combination to insure that significant aftereffects were still present. Each measurement consisted of ten trials.

Two monkeys (Hm, Dp) were tested for transfer of adaptation in this apparatus. One was tested after chiasm section only (Hm_1) as well as after additional section of the forebrain commissures (Hm_2) to provide a control for possible effects on adaptation of the temporal field hemianopia of each eye that results from chiasm section. The chiasm-control adapted with all eye-hand combinations, but with only the prism orientations (base nasal) that, because of the direction of shift of the visual field, might be expected to favor better contralateral and worse ipsilateral performance. The other split-brain monkey (Dp) adapted with all eight combinations of eye, hand, and prism relations. Any session that was not successfully completed (four) or that produced questionable aftereffects (one) was repeated on a subsequent day.

<u>Results</u>. The data from this experiment are reported in Table 4 and graphed in Fig. 5. It is evident that the monkeys can adapt equally as well in these short term experiments as they do with chronic exposure. Furthermore, the same pattern of complete interocular and no intermanual transfer of prism-adaptation is present. The following comparisons may be made from the data on the split-brain cases. The mean aftereffects with the exposed eye (6.1 degrees) are not significantly different ($p \gg .05$) from those for the unexposed eye (6.3 degrees). Neither the individual aftereffects for the unadapted hand nor their average is significantly greater than zero. The mean value

TABLE 4

TRANSFER OF AFTEREFFECTS FOLLOWING ACUTE ADAPTATION

Subject & Experiment		Adaptation Condition	Aftereffects in Degrees			
			EE:EH	EE:UH	UE:EH	UE:UH
Hm, Chiasm	4	RE, LH, BL	10.3	-0.3	5.7	2.3
	1	LE, RH, BR	6.3	1.5	6.9	1.7
	3	RE, RH, BL	9.2	-0.6	7.4	-0.6
	2	LE, LH, BR	3.4	-1.7	3.1	-1.7
Hm, Split	4	RE, LH, BL	9.4	0.6	9.7	0.6
	1	LE, RH, BR	8.0	1.4		
	6	LE, RH, BR	9.2	-1.7	8.6	-2.9
	3	RE, RH, BL	2.9	2.0	5.1	0.6
	5	RE, RH, BL	6.9	1.1	6.3	1.7
	2	LE, LH, BR	6.3	-0.6	6.3	0.9

(continued on next page)

TABLE 4
(Continued)

Subject & Experiment		Adaptation Condition	Aftereffects in Degrees			
			EE:EH	EE:UH	UE:EH	UE:UH
Dp, Split	3	RE, LH, BR	4.0	-0.6	4.9	-0.9
	1	RE, LH, BL	8.9		8.9	
	6	RE, LH, BL	6.9	-0.3	7.4	-0.9
	5	LE, RH, BR	5.1	-2.9	4.6	-1.7
	7	LE, RH, BL	3.7	0.0	5.7	-0.9
	8	RE, RH, BR	4.6	0.0	4.0	-1.1
	9	RE, RH, BL	6.3	0.6	4.6	0.0
	2	LE, LH, BR	3.4			
	10	LE, LH, BR	6.9	0.3	6.6	-0.6
	4	LE, LH, BL	0.6	2.0		
	11	LE, LH, BL	4.9	-0.6	5.7	1.4

Abbreviations: RE, right eye; LE, left eye; RH, right hand; LH, left hand; BR, prism base to the animal's right; BL, prism base left; EE, exposed eye; UE, unexposed eye; EH, exposed hand; UH, unexposed hand.

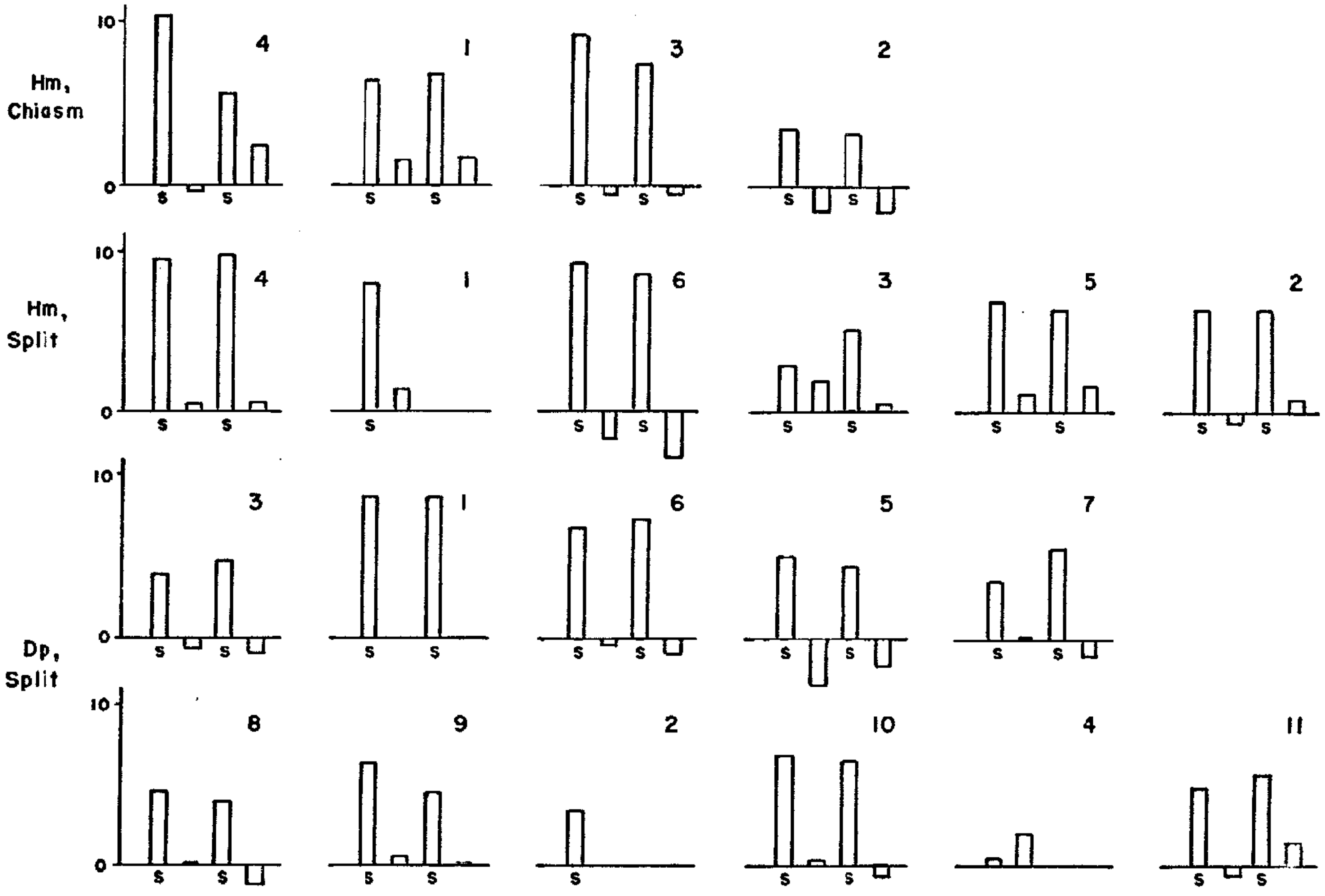

Fig. 5. Graph of data in Table 4. For explanation see legend, Fig. 3.

of the aftereffect for the exposed eye-hand combination when contralateral pairs were adapted is 6.9 degrees, which is significantly larger ($p < .05$) than the mean of 4.8 degrees found for the ipsilateral cases. There are not enough data from the chiasm case to test statistically but the same tendency is seen (contralateral mean, 8.3; ipsilateral, 6.3). The data on precision of reaching are given in Table 5 and are discussed below.

In addition to these numerical results, it was noticed that while the animals were adapting to the prisms with visual feedback available, frequent errors were made with the ipsilateral combinations, and often repeated, incorrectly aimed attempts to retrieve the reward were observed. This behavior, which was never noticed with contralateral combinations, was observed in the chiasm-sectioned control as well. It appears that the animals did not see their ipsilateral hands when reaching. All the data and observations on ipsilateral reaching support the interpretation (p. 17) that the smaller aftereffects with these combinations are a result of the visual field defects produced by cutting the chiasm, and not of commissure section.

Precision of Reaching

The standard deviations calculated from the base readings of the three experiments are given in Table 5. The number of readings ranged from 20 to 150, usually about 50. The mean errors are not given because they are biased by the use of the index finger as the reference point of the measurements. However, the monkeys showed no tendency

TABLE 5

STANDARD DEVIATIONS FOR NORMAL REACHING MEASURED WITHOUT VISUAL FEEDBACK[a]

Subject	Combinations Tested RE,RH	RE,LH	LE,RH	LE,LH	Conclusions from F Tests
Sd			0.82	0.69	no differences
Hm_1	0.62	0.89	0.48	0.85	LH > RH
Hm_2	1.35	1.23	1.38	1.26	no differences
Dp	1.37	1.30	1.24	1.32	no differences
Bn	1.02	1.04	0.66	0.76	RE > LE[b]
Bh	1.45	1.37	0.90	1.17	RE > LE[c]
Rb	1.34	0.96	1.15	1.76	I > C[d]
Tm	1.55	0.70	1.38	1.49	I > C[e]
Ll	0.91	1.41	1.06	1.31	LE > RH

Abbreviations: RE, right eye; LE, left eye; RH, right hand; LH, left hand; I, ipsilateral eye-hand pairs; C, contralateral eye-hand pairs.

[a] The values in this table are in cm.; one cm. = 2.9 degrees.

[b] Of the four pertinent ratios, one did not reach significance at $p < .05$; for LE,LH/RE,RH, $.1 > p > .05$.

[c] For LE,LH/RE,LH, $.25 > p > .1$; other ratios, $p < .05$.

[d] For LE,LH/RE,RH, $.1 > p > .05$; other ratios, $p < .05$.

[e] For RE,RH/LE,RH, $p = .1$; for LE,LH/LE,RH, $p = .75$; other ratios, $p < .05$.

toward a constant overreach in any of the tests; all of the movements appeared to be accurately centered around the position of the target image. Table 5 also presents a summary of conclusions drawn from F tests performed on the variances for precision of reaching with the different eye-hand combinations. For the normal, chiasm, and forebrain-sectioned animals there is no evidence that normal reaching with ipsilateral combinations is any less precise than that with contralateral pairs. It appears that the two animals (Tm, Rb) with the additional section of the massa intermedia and the quadrigeminal plate showed some increased scatter with the ipsilateral combinations. Rb gave significantly greater scatter with her ipsilateral combinations in all the comparisons except one, and that one closely approached significance. Strongly significant differences appear for Tm only when the ipsi/contra comparisons are done between LE,LH/RE,LH and RE,RH/RE,LH; the LE,RH/RE,LH comparison is also highly significant. Apparently Tm had a less precise right hand than left and a less precise left eye than right. The interaction of these deficits with the poorer ipsilateral performance prevents significance from being reached with every ipsilateral pair compared to every contralateral pair in these cases, and precludes reliable interpretation.

Ll showed significantly greater scatter with her left hand in all comparisons, as would be expected from her right parietal lesion. Bn and Bb showed poorer performance with their right eyes and Hm, as a chiasm-sectioned animal, gave greater scatter with his left hand. No specific asymmetries in surgery were noted in the post mortem examination for any cases. In general the overall scatter for any combination was greater in the split-brain than in the chiasm-sectioned and normal animals.

Summary of Results

The principal results from the experiments performed with monkeys are summarized in the following list.

1. The monkeys adapted to deflection of the visual field as readily as do human subjects under similar conditions.

2. No preferences for using contralateral eye-hand combinations were observed.

3. Adaptation was established with equal success regardless of whether the practiced eye and arm were predominantly represented in the same or in surgically separated hemispheres. The slightly smaller aftereffects measured after adaptation with ipsilateral eye-hand combinations seem attributable to the effects of chiasm section on the visual field of each eye.

4. Adaptation established through one eye was immediately and completely available to testing through the unexposed eye in monkeys with extensive bisection of the brain as well as in normal monkeys, although in three cases interocular transfer was not found after adaptation with ipsilateral eye-hand pairs.

5. In split-brain and normal monkeys, adaptation was restricted to the arm that was practiced in reaching with deflected vision.

6. A lesion in the somatic area for one arm did not noticeably affect adaptive ability with that arm.

7. No deficit in performance, as determined by precision of reaching without the prism in place, was measurable for ipsilateral eye-hand pairs in animals with section of the forebrain commissures. Two monkeys with additional section of midbrain commissures and the massa intermedia showed a greater tendency toward less precise reaching with ipsilateral combinations, although adaptation and bilateral transfer were not affected.

Discussion

The experiments on monkeys reported in this thesis were concerned primarily with investigating the effect of split-brain surgery on adaptation of reaching ability to deflected vision, as a first step toward determining which parts of the brain are most directly responsible for this process. Since the cerebral cortex is usually regarded as the locus of learning and practice effects (42-44), it seemed plausible to attempt restriction of adaptation to one half of the brain as an aid to further surgical intervention. The effect of the split-brain surgery on normal reaching ability was also investigated.

Adaptive ability. Monkeys easily compensated for directional errors in localization after a few minutes of practice in reaching. Subsequent testing showed aftereffect errors of approximately the same magnitude as were found with human subjects under similar conditions. In the experiments in which monkeys adapted to prisms for two to four days, larger aftereffects were usually present; three cases showed apparently complete adaptation with the exposed hand. The monkey that was released to his cage with prisms in place showed good generalized compensation for deflected vision. Finally the monkeys, who adapted under relatively restricted conditions of movement, showed little tendency toward intermanual transfer of adapted reaching. There seems to be no reason to think the adaptation to deflected vision by monkeys differs essentially from that by man.

The results from all the adaptation experiments indicate little or no detectable effect of the split-brain surgery on the monkeys' ability to adapt with either ipsi- or contralateral eye-hand combinations. The somewhat smaller aftereffects usually obtained with ipsilateral pairs can be attributed to chiasm section, which results in the ipsilateral hand being used predominantly in the blind half of the visual field and therefore leads to less visual feedback of arm movements.

The effect of adaptation, while specific to the adapted hand as in normal animals, was immediately and completely available to the unexposed eye in the split-brain monkeys in 38 out of 41 cases. The exceptions were discussed on p. 20. The interocular transfer, with the three exceptions, was as complete following adaptation with ipsilateral eye-hand pairs as with contralateral ones. The lack of intermanual transfer is discussed in Section II.

It is concluded that the sectioned structures are not required for either the establishment or subsequent use of adaptation to deflected vision, regardless of whether the particular eye and hand being tested are predominantly connected to the same or to the separated hemispheres. Furthermore, in addition to being unnecessary, it seems probable that the sectioned structures are not normally used by animals in adapting to displaced vision. Deficits in performance generally accompany vicarious function, yet no deficit was detectable in the present experiments. This implies that new pathways or centers were not suddenly forced into use. The structures ruled out as necessary for the establishment or transfer of adaptation include, in addition to the optic chiasm, the corpus callosum; the anterior, posterior, hippocampal, and habenular commissures; the commissures of the superior and inferior colliculus; and the massa intermedia. Midline section of the cerebellar hemispheres also did not in itself affect the establishment or transfer of adaptation with any combinations, but as a split-brain experiment this is not conclusive because of the few fibers remaining in the optic chiasm of the animal with cerebellar section.

Some mechanism not requiring use of these sectioned structures must be sought to explain the ability to adapt with ipsilateral eye-hand combinations and, subsequently, to reach in an adapted manner for targets presented to either eye. Eye and head position may be bilaterally represented in the brain; therefore the basic problem centers on explaining how retinal information arriving in one hemisphere can be correlated with positional information regarding the arm primarily represented in the opposite hemisphere, and how the adaptive changes, once formed, are equally available to testing through either eye.

The presence of connections between an arm and the cortex on the same side could explain adaptation of ipsilateral eye-hand combinations solely in terms of cortical mechanisms. However, while there is some evidence for ipsilateral motor control of the limbs (45), there is none for ipsilateral proprioceptive inputs to the cortex, and in fact there is considerable evidence to the contrary (46). Even if the required ipsilateral paths and centers do exist, it would be surprising to find no deficit in adaptive performance when they are called into use. Furthermore, ipsilateral inputs and outputs to and from the cortex are not in themselves sufficient to explain interocular transfer of adaptation. A subcortical interhemispheric pathway capable of laying down a bilateral engram or of allowing the untrained eye to direct responses mediated by the trained hemisphere would still be necessary.

Other interpretations require the participation of some type of brainstem mechanism. For example, centrencephalic pathways and centers of the type proposed by Penfield (47), capable of interrelating cortical sensory and motor areas, could underly the present results. Under this view, much of the adaptive activity might remain cortical but interconnection, and perhaps some measure of control, of cortical areas would be carried out by brainstem centers. A minimal amount of interhemispheric communication could suffice to explain interocular transfer, assuming eye and head position are bilaterally represented in the cortex. The adapted hemisphere, regardless of which eye is tested, would have positional information from the eyes, neck, and arm, and would only need to be informed via brainstem pathways that a desirable object was present and that the gaze was centered on the object. Transfer of the adaptation-effect, therefore, would result from the ability of appropriate retinal stimulation of either eye to mobilize the adapted localizing mechanisms of the hemisphere governing the practiced arm.

Alternatively, a larger part of the process and/or effect of adaptation may be organized subcortically, a view more in line with Lashley's interpretation of visuomotor coordination (48). The retinal input signaling the presence of the target and perhaps its position on the retina would presumably arrive via the visual cortex, but then be relayed to subcortical centers where the required adjustments in the localizing mechanisms could occur. Visual control of reaching or other localizing activity would be viewed as a more primitive mechanism, less dependent on cortical control, than the acquisition of skilled acts, perhaps more like the complex sensory-motor coordination of the postural reflexes. The lack of effect on adaptation of the parietal lesion in L1, which presumably removed most if not all of the cortical representation for arm position, indicates that the adaptive mechanism is independent of this cortical area and may be taken as support for subcortical involvement. Again, interocular transfer is viewed not as a result of memory transfer from one side of the brain to the other but of the establishment of changes in an area of the brain equally accessible to testing through either eye.

Normal reaching ability. The effect of adaptation presumably is a change in some part of the normal coordinational mechanism. Conclusions derived from studies of transfer of adaptation concerning the parts of the brain used in adapted reaching therefore should be equally valid for normally coordinated reaching. Consequently the previous suggestion that subcortical mechanisms are involved in adapted reaching also applies to normal coordination.

The effect of split-brain surgery on normal coordination was also directly examined. The precision of reaching under conditions of no visual feedback or other knowledge of errors was measured for ipsilateral and contralateral eye-hand combinations. The data (Table 5) indicate that ipsilateral combinations were as precise in reaching as contralateral pairs for subjects with section of the forebrain commissures. The two cases with additional section of the midbrain commissures and massa intermedia suggest a possible ipsilateral deficit, but this cannot be regarded as definite. It is concluded, for forebrain section at least, that there is little or no effect of separating the hemispheres on reaching for visually localized targets under conditions of no visual feedback. It is again suggested that direct control of reaching with the arm ipsilateral to a given eye is more likely to occur through the participation of brainstem centers than via ipsilateral motor fibers in these basic visuomotor coordinations. If the monkeys were forced to depend upon a few percent of the normal motor control, considerable deficit in reaching ability would be expected.

No preferences for the use of contralateral rather than ipsilateral eye-hand combinations were noticed in the monkeys allowed free choice of the hand to be paired with the unoccluded eye. Since the animals often voluntarily chose to use ipsilateral combinations, sometimes for several days, it would seem that split-brain surgery also had little effect on this aspect of coordination.

The present results and interpretations regarding normal reaching ability confirm and extend a recent report by Myers et al., in which section of the forebrain commissures after removal of the visual area of one hemisphere and the motor areas of the other hemisphere in cats and monkeys did not further affect the ability of the relatively intact eye-hand pair to pick up pieces of food and to work together in other coordinational and reflex tasks (49). It seems probable that the present technique of measuring coordinational ability in the absence of knowledge of errors is more sensitive than previous techniques in testing for disruption of function. It eliminates any advantage of contralateral over ipsilateral eye-hand pairs caused by greater visual feedback from a contralateral pair during reaching. Furthermore, comparisons between ipsilateral and contralateral combinations can be made on the same animals under similar conditions, which is impossible after lesions in the visual and motor cortices.

There is apparent disagreement between the present results and those that indicate moderate to severe impairment of ipsilateral performance after section of the forebrain commissures. Downer reported an almost complete inability in split-brain monkeys to control the arm ipsilateral to an unoccluded eye when performing simple visual discrimination of objects (50). He observed that this difficulty is partially overcome with extensive practice and suggested that control may occur via an ipsilateral effector system. A strong preference for the hand contralateral to the exposed eye was also noted. None of these effects were noted with chiasm-sectioned monkeys, and therefore they cannot be attributed to monocular visual field deficits. Trevarthen has noted moderate preferences for contralateral combinations and some coordinational difficulties with ipsilateral pairs in learning involving visual discriminations (51). Similarly, Gazzaniga has recently reported very poor motor control with ipsilateral combinations, especially with the least retentive eye, when testing for retention of preoperatively trained visual discriminations (52).

The result that control of reaching ability does not depend upon cortico-cortical connections and the interpretation in terms of subcortically organized mechanisms therefore does not seem to explain these situations in which discrimination learning is involved. This may represent an example of hierarchical organization of function in the nervous system (53). Reaching ability can be thought of as a more basic, or at least more practiced, task for which control has been delegated to lower centers, while the learning of discriminations, and probably skilled acts, requires greater cortical participation which might increase the amount of motor control assumed by the cerebral cortex.

In summary, the results of this series of experiments on monkeys demonstrate that there is little or no effect of extensive split-brain surgery on normal reaching, on the ability to adapt to deflected vision, or on the interocular transfer of adapted reaching. These results are most easily interpreted in terms of at least partial participation of brainstem centers in establishing adaptation to displaced vision and in carrying out normal or adapted reaching in a coordinated manner. The adaptive mechanisms could operate largely at cortical levels, provided that appropriate sub-cortical pathways are available for transferring whatever retinally derived information is necessary for adaptation, or the mechanisms could be organized predominantly at subcortical levels. The latter alternative appears to account for the results more economically.

SECTION II

EXPERIMENTS ON THE EFFECT AND PROCESS OF ADAPTATION

Experiments in which subjects have described their impressions of the perceptual changes that accompany adaptation to rearranged vision have not led to agreement concerning the nature of these alterations. It apparently has been difficult for subjects to decide whether their visual, motor, or proprioceptive perceptions have been modified (1-7, 9). Other experiments, primarily investigating the conditions required for the occurrence of adaptation, have led to the suggestion that the adaptive process produces changes in the links between visual input and motor output (9, 15, 19). The experiments in this section investigate the nature of the adaptive effect by determining how adaptation affects the use of the various members of the bodies of human subjects.

The lack of intermanual transfer of adapted reaching found with monkeys indicates that the adaptive effects are not necessarily generalized to members of the body other than those actually practiced. Differential effects such as these can be used in determining which components of the body have had their performance directly altered by adaptation to displaced vision. In so doing, it is convenient to think of adaptation as resulting from some type of "recalibration" of sensory input from, or motor output to, particular members of the body relative to messages from or to other members, or as resulting from changes in the relationship between sensory and motor components of the coordinational system. Other descriptions of adaptation, presented in psychological terms such as alterations of visual or kinesthetic perception, are presumably reducible to similar changes.

The possible alterations resulting from adaptation of reaching ability then can be of the following basic types. Recalibrations could occur in the interpretation of the position of the target image relative to the position of the eye, of the position of the eye relative to that of the head, or of head position relative to body position. These types of alteration, because of their effect on visual localization of the target in space, could account for adaptation. A similar reinterpretation of arm position relative to body position, or alteration in the motor programming governing the response of the arm, could be the result of adaptation. In this case the physical localization of the target would be affected. Adjustments in the linkage or correlation between visual and motor components can be considered as a case intermediate between recalibrations of the input and output stages. All of these possibilities, in principle, may be differentiated by appropriate tests for transfer to different members of the body or to different types of sensory stimulation. For example, recalibration of neck position would affect reaching to visual and auditory targets while recalibration of eye position would affect only visual localization.

Three of the experiments reported in this section test the extent to which adaptation effects established through practice with some members of the body generalize to unpracticed members under various conditions of exposure to prism-deflected vision. Additional experiments testing transfer to auditory or tactile-proprioceptive localization had meanwhile been completed by others (54-57). From all of these experiments the nature of the adaptive changes was inferred and suggestions were made concerning the levels of organization at which such changes occur under different conditions.

A fourth experiment was run to determine if active movement and the visual feedback contingent upon it, a necessary condition for adaptation (19), are required for the return of normal coordination following adaptation.

The subjects for all of the experiments on man were students and research fellows from Caltech. No selection criteria other than willingness to cooperate and reasonably good overall vision were employed.

Experiment 1

Intermanual Transfer with Restricted Movement*

The lack of intermanual transfer of adaptation found with monkeys contrasts with a report by Helmholtz of complete hand to hand transfer for human subjects (14). In view of the importance of these results in deciding which parts of the coordinational mechanism are affected by adaptation, it was decided to recheck the extent of intermanual transfer in man.

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*This work was reported in part in Reference 58.

Apparatus and procedure. The experimental technique is similar to that described by Held and Gottlieb (16). The subject looked into an illuminated box (see Fig. 6) through a binocular eyepiece which held laterally oriented 20 diopter (about 11 degree) wedge prisms. The eyepiece also served to hold the head in a relatively fixed position during the exposure and test periods. The subject adapted one arm by moving it back and forth for 15 minutes at a rate of about 25 times per minute. He was observed by the experimenter, and if necessary corrective suggestions were made to insure that he obtained adequate exposure. Before and after exposure the subject was tested for reaching accuracy without the prisms in place. The use of a mirror arrangement permitted him to mark the apparent positions of three dots, arranged in the form of a triangle four inches on a side, while preventing him from seeing his arm. The subject marked each dot five times with the hand being tested; he removed his arm from the box after each trial. The positions of the 15 marks were averaged to give a measure of reaching accuracy, and the magnitude of the aftereffect was computed by taking the difference between the average pre- and postadaptation measurements for that hand. The results were measured in units of 0.1 inch and were converted to visual degrees; one inch equalled approximately three degrees in these experiments.

Sixteen subjects adapted with one hand to prisms fixed in the eyepiece of the apparatus and were tested for intermanual transfer of the aftereffects. Each subject adapted twice under these conditions, which restricted head and trunk movement. Half of the subjects adapted with

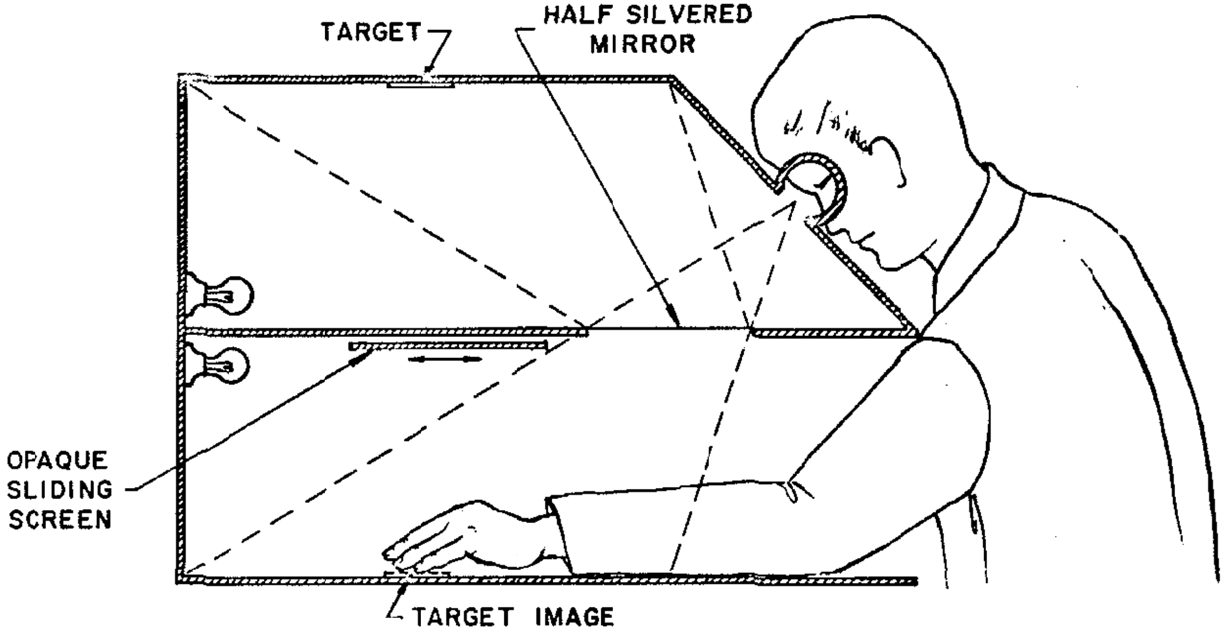

Fig. 6. Apparatus used for eye-hand adaptation of human subjects. The prisms were inserted in the eyeholes. For additional explanation see text.

their right hands first and half with their left. Half of each of these groups used base right prisms and half base left. The conditions for the second exposure of the subjects were permuted so that any sequential effects on adaptive ability would be equalized. Subjects were otherwise arbitrarily assigned to the different exposure conditions. The two results from each subject were averaged and the means of the 16 subjects were tested for significance by t tests.

The time course of adaptation was sequentially determined in a separate experiment for the two hands of eight subjects. The subjects first adapted with one hand for ten minutes and immediately afterward adapted with the other hand. Measurements were taken for both hands before and after each one was practiced. In addition, the adaptation process for each hand was interrupted after 1/4, 1/2, 1, and 5 minutes of practice and the aftereffects for that hand were determined.

Results. The results from the transfer part of this experiment are presented in Table 6. The mean of the aftereffects is greater than zero for the exposed hand ($p < .005$) but not for the unexposed hand ($p > .4$); the mean of the exposed hand is significantly larger than the mean of the unexposed hand ($p < .005$). Similar results have recently been independently obtained in four other laboratories (55-57, 59). Fig. 7 graphs the data from eight subjects, averaged point by point, for the time course of adaptation for each hand. There does not appear to be any savings in the adaptation curve for the second hand. Both parts of this experiment show that the compensation for errors in

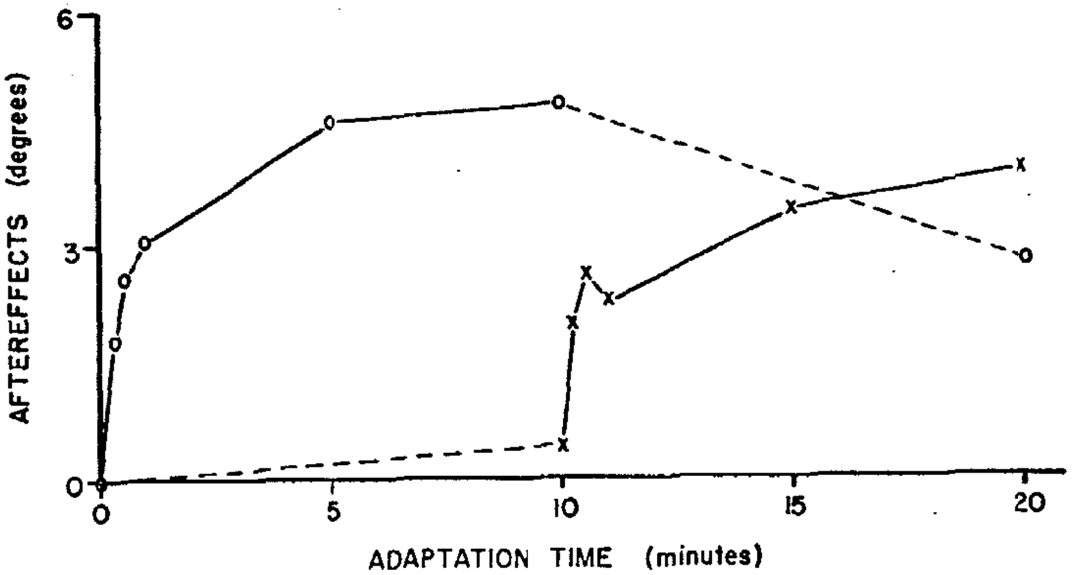

Fig. 7. Plot of aftereffect magnitude *vs.* time of adaptation for successive adaptation of the two arms. Circles correspond to hand adapted first, x's to hand adapted second. Dotted lines represent time during which the hand not being adapted rested in the subject's lap.

TABLE 6

AFTEREFFECTS WITH RESTRICTED MOVEMENT

		Aftereffect in Degrees	
	N	Mean	S.D.
Exposed Arm	32	2.94	2.31
Unexposed Arm	32	0.13	1.71

visually guided hand localizations produced by looking through wedge prisms affected only the hand that was actually practiced.

Enough data was collected in this and in preliminary experiments to enable some statistical investigation of the effects of the various conditions, which were balanced in the designs, on the magnitude of the aftereffects in the adapted hand. Three analyses of variance were performed on the data. No effects due to prism orientation ($F = 1.88$; $df = 1, 28$), to hand adapted ($F = 1.62$; $df = 1, 28$), or to their interaction ($F = 1.84$; $df = 1, 28$) were significant. Sequential effects arising from adapting subjects twice were also examined. The magnitudes of the aftereffects of the second adaptation were checked for possible differences caused by previous adaptation with the same hand and/or the same prism orientation. No significant differences were found ($F = .23$; $df = 3, 12$). Significant variation in "adaptability", as measured by the magnitudes of the aftereffects produced during the same time of practice, was observed between subjects ($F = 2.03$, $df = 15, 29$; $p < .05$). This type of variation makes the previous tests rather insensitive. As a control, the reaching abilities of the unexposed hands were also investigated; there were no significant differences between subjects for these checks on normal reaching accuracy (F = .7; df = 15, 29). A plot of the magnitude of the aftereffect measured for the exposed hand _vs._ that for the unexposed hand showed no evidence that they were correlated.

Experiment 2

Transfer with Non-restricted Movement*

Two tests were performed to see if intermanual transfer would occur when the conditions of adaptation more nearly coincided with those used by Helmholtz (14).

Apparatus and procedure. The method used in this experiment was the same as that employed in the previous one, except that no restrictions were placed on head and trunk movements during the adaptation and test periods. This was accomplished by removing the front panel of the box, which contained the prisms and eyepiece, and by either placing the same prisms in goggles worn by the subject or substituting a large (3 inch by 9 inch surface) 20 diopter water prism in place of the small fixed prisms. Goggles without prisms restricted the size of the visual field when the large prism was used.

Twelve subjects adapted one hand while looking through prisms placed in goggles. They were told that head and torso movements were

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*This work was reported in Reference 58.

permissible; most of them were observed to move while watching their hands through the prisms. Equal numbers of subjects adapted under the four conditions of prism orientation and hand adapted. After adaptation, aftereffects were determined for each hand. In addition, the changes in accuracy of reaching with the prisms in place were recorded for each hand. The latter type of measurement was used by Helmholtz (14), although in the present case the measurements were made without visual feedback. The readings were taken immediately after putting the prisms on and just before removing them.

An additional eight subjects adapted once with prisms mounted in goggles and once with the large water prism affixed to the eye-hand box, and aftereffects were determined for each hand. Four subjects adapted under one condition first and four under the other. The design was balanced as before except for the use of base left prisms only.

Results. The results for the 12 subjects are presented in Table 7. There were significant aftereffects in the unexposed as well as the exposed hands (both, $p < .005$). The mean aftereffect of the exposed hand, however, was significantly greater than that of the unexposed hand ($p < .05$). Adaptation in both hands was again significant ($p < .005$) when determined by the measurements of reaching accuracy with the prisms in place, and the exposed hand was again significantly more adapted than the unexposed hand ($p < .005$). The magnitude of adaptation of the exposed hand, when determined as an aftereffect, did not differ significantly from the amount of adaptation determined with the prisms in place ($p > .1$).

TABLE 7

INTERMANUAL TRANSFER WITH NON-RESTRICTED MOVEMENT

		Aftereffect in Degrees			
Effect Measured	N	Exposed Arm		Unexposed Arm	
		Mean	S.D.	Mean	S.D.
Aftereffect	12	2.79	2.07	1.26	1.11
Adapted reaching	12	4.14	2.58	1.23	1.62

The results from the eight subjects are presented in Table 8. Significant aftereffects were found for all cases ($p < .05$), and the differences between the two conditions were not significant (exposed hands, $p > .2$; unexposed hands, $p > .1$). There was no indication that transfer was increased when the prisms were mounted on the subjects.

TABLE 8

INFLUENCE OF PRISM ON AFTEREFFECTS

		Aftereffect in Degrees			
Type of Prism	N	Exposed Arm		Unexposed Arm	
		Mean	S.D.	Mean	S.D.
Goggle-mounted	8	3.09	1.59	1.14	1.38
Box-mounted	8	3.90	1.77	2.25	1.38

It is apparent that significant intermanual transfer occurs if the subject is not rigidly constrained during adaptation, and that it does not depend on measuring the extent of adaptation with the prisms in place. The possibility that the cues inducing this partial transfer arise from optical distortions that appear when the prisms move with the head is ruled out by the result of the second part of the experiment.

Experiment 3

Other Transfer and Generalization Experiments

The previous results on intermanual transfer, and all other reports of transfer or generalization (14, 61, 62), can be explained by assuming that the effects of adaptation remain restricted to the joints of the body that are actively engaged in the movements necessary for adaptation (see discussion). An additional series of experiments was run to see if the adaptation-effect would remain specific to the practiced joints in other cases as well.

Apparatus and procedure. Fig. 8 shows a diagram of the apparatus used in these experiments. The mirror served to screen leg or arm movements when it was in position. The grid for measuring the placement of the foot at the end of a reach was adjustable for subjects of different height.

The targets to be localized by the hand were three dots spaced four inches apart in a straight line and located 24 inches from the subject's eyes; similar targets for the foot were spaced five inches

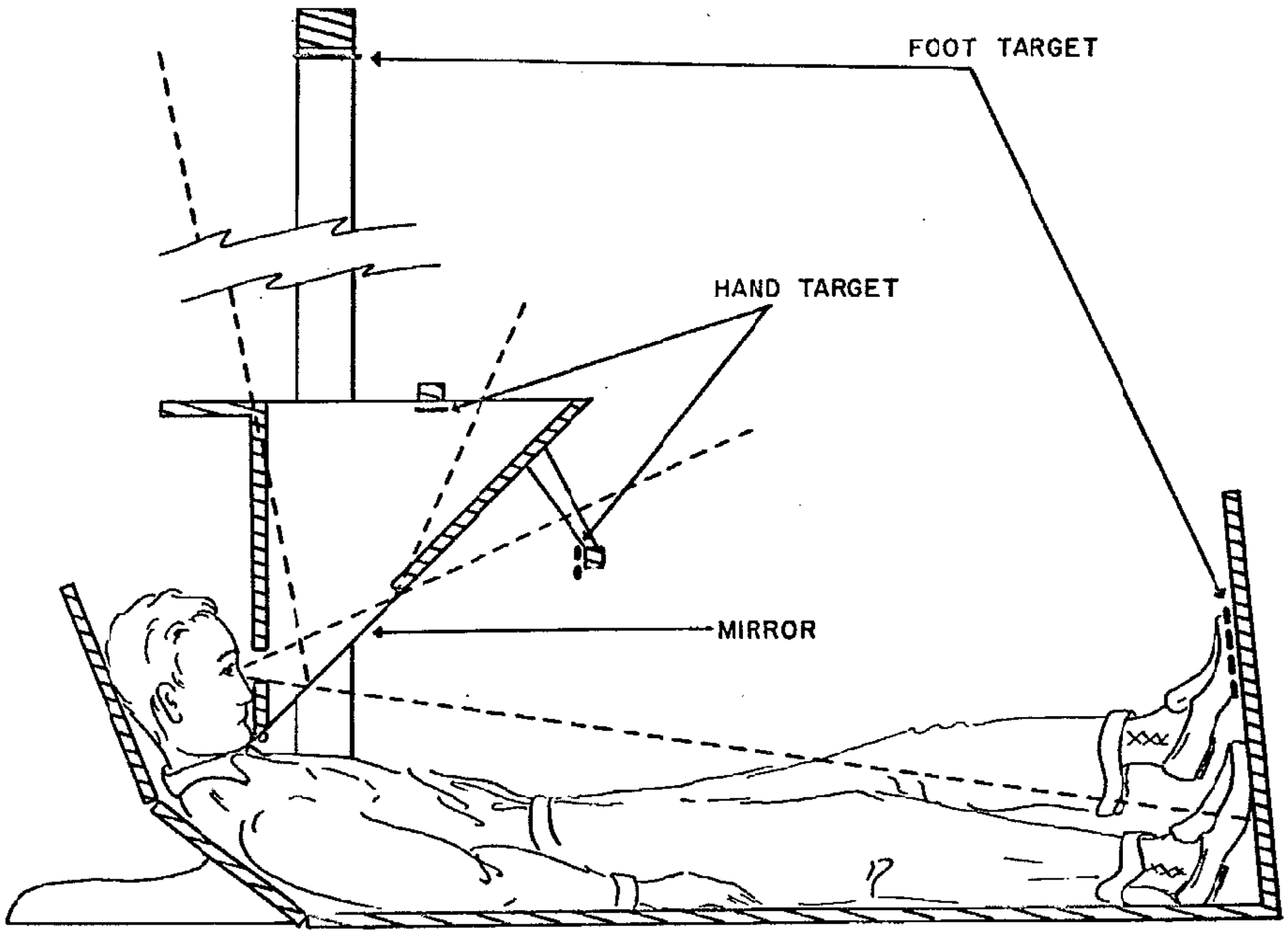


Fig. 8. Apparatus for adapting either arms or legs. The mirror was hinged and could be lowered to a horizontal position. The prisms were inserted in the eyeholes. For additional explanation see text.

apart and placed about 55 inches from the eyes. The targets were drawn on graph paper to facilitate the estimation of the distance between the subject's index finger or the center of his shoe and the targets. Readings were subsequently converted to degrees for comparison. The average of six reaches, two per dot, constituted a base or aftereffect determination.

All subjects adapted by pointing to one of the dots 50 times with the specified limb. Aftereffects were then determined for pointing accuracy with both hands and feet. In addition to these tests, the accuracy of eye-body localization was checked before and after adaptation of the hands or feet. This was determined by the subject's ability to localize a target by vision and then to walk to the target with his eyes covered. In this case the targets were three dots, spaced five degrees apart and located nine feet away on the floor. Radial lines drawn on the floor enabled estimation of the lateral distance between the target and an imaginary line centered between the subject's heels.

Eight subjects were checked for interpedal transfer of adaptation and for generalization from pointing with the feet to pointing with the hands and to walking toward a visually localized target. Bases were taken for walking accuracy and for pointing accuracy with each foot and hand. The subject adapted one foot by pointing to a target 50 times. Aftereffects were then determined for each hand and foot in a predetermined sequence. This was followed by adaptation of the second foot. Aftereffects were again measured for the hands and feet in the same order. Then the ability to walk to a visually localized target was rechecked.

Half of the subjects adapted their right foot first, half the left. From each of these groups half were tested for aftereffects with their hands first, half with their feet. Finally, half of each of the last subgroups were tested first with the side of the body that was adapted first and half with the side that was adapted second. Thus there was no favoring of any particular limb in case of interaction between limbs or of possible decrement of the aftereffect magnitude. The body localization tests were always run before and after the tests with the feet and hands because of the impracticability and undesirability of the subject moving from and returning to the adaptation and test apparatus any more often than necessary.

Two control tests were also run, each identical to the previously described experiment in all aspects but one. The first control involved adapting hands rather than feet. The second was a repeat of the foot adaptation procedure, but no visual feedback of the movements was allowed at any time; a screen covered the area in the visual field in which the feet were moved during "adaptation" as well as during testing. Both of these controls were intended to separate out possible adaptation due to uncontrolled movement or to other undefined factors.

Results. The results of these three tests are presented in Table 9. The average aftereffects of the eight subjects are graphed in Fig. 9 along with their significance as determined by t tests. One singularly atypical result which was obtained for body localization in the

TABLE 9

GENERALIZATION OF ADAPTATION FOLLOWING EXPOSURE OF ARMS OR LEGS

		Aftereffects in Degrees[a]									
Experiment	Tested After Adapting:	Limb 1		Limb 2		Limb 1-i		Limb 2-i		Body	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Foot Adaptation	Foot 1	2.6	1.4	1.0	1.2	1.2	1.6	0.9	1.3		
	Foot 2	3.4	1.3	2.3	1.4	2.4	1.7	2.3	1.6	2.2[b]	0.9[b]
Foot Blank	Foot 1	0.2	0.9	0.7	1.2	0.4	1.1	-0.1	1.3		
	Foot 2	0.2	1.9	0.7	2.9	0.0	2.0	0.3	1.8	0.2	0.6
Hand Adaptation	Hand 1	5.1	2.1	0.7	1.7	0.9	1.1	0.4	1.7		
	Hand 2	4.9	1.2	5.0	2.2	1.0	0.8	1.1	1.6	-0.3	0.7

[a] Limb 1 denotes limb exposed first; Limb 2, limb exposed second; Limb 1-i, limb ipsilateral to Limb 1; Limb 2-i, limb ipsilateral to Limb 2.

[b] This value is computed using data from seven subjects only -- see text.

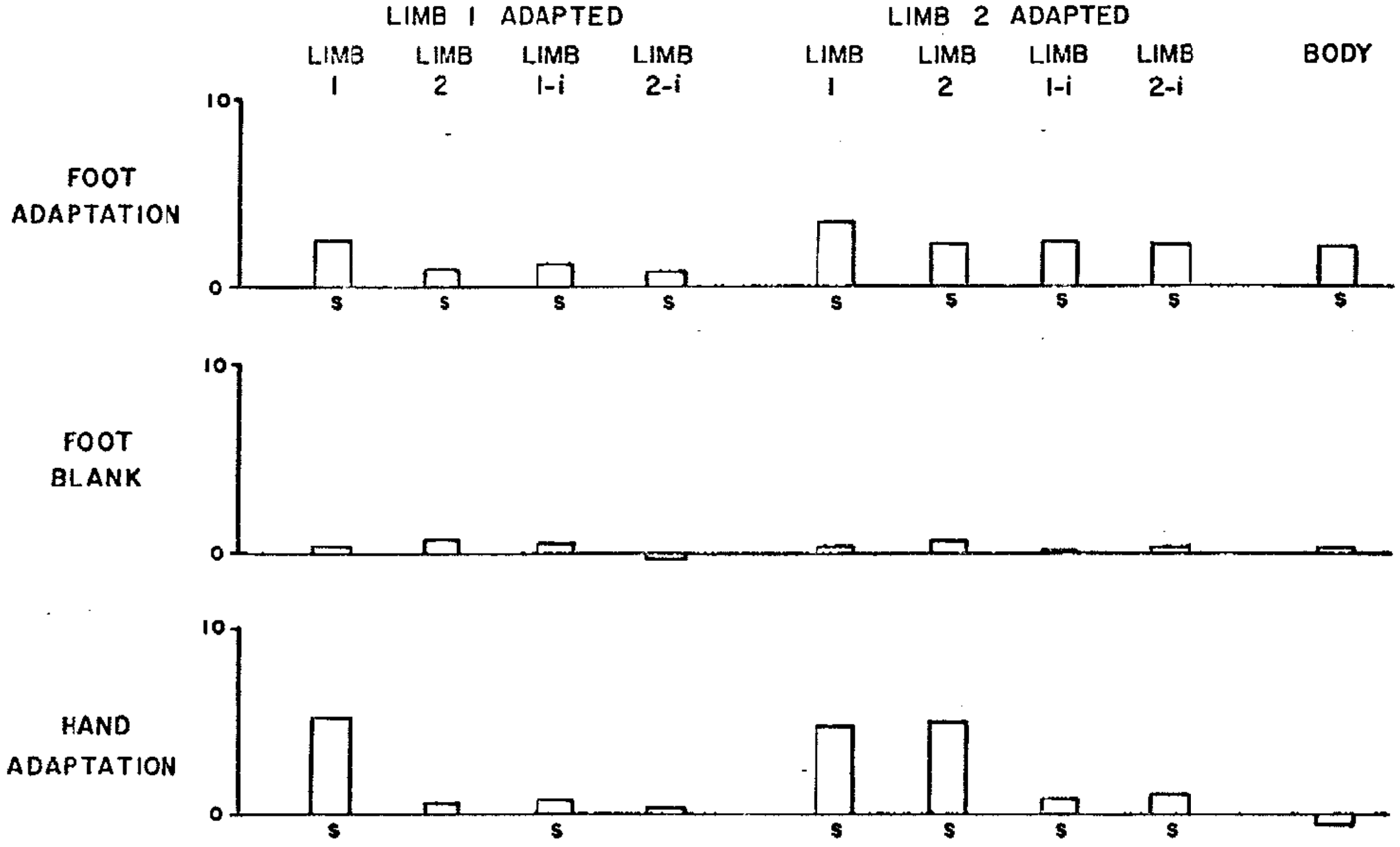


Fig. 9. Graph of data in Table 9. Ordinates represent the magnitude of the aftereffect in visual degrees. Significant aftereffects are marked by *s*. The order of the aftereffects and the abbreviations are the same as in Table 9.

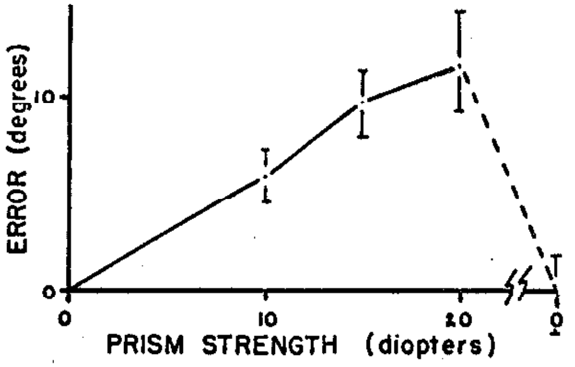
first experiment with one subject was not included in the average. This value, -3.8, was significantly different from the other seven, 1.0, 1.2, 1.9, 2.0, 2.9, 3.1, 3.1.

Significant aftereffects were found for all limbs after adapting one (all, $p < .05$) or both (all, $p < .005$) legs. No significant aftereffects were found for any case in the "blank" adaptation of the legs. Small, but in some cases significant (see Fig. 9), aftereffects were found after adaptation of the hands. It should be noted that there was no evidence of intermanual transfer under these conditions, in accordance with the earlier experiments with restricted movement. Comparisons between the magnitudes of the aftereffects in the arms and legs cannot profitably be made until the relative efficiency of adaptation of these limbs is determined.

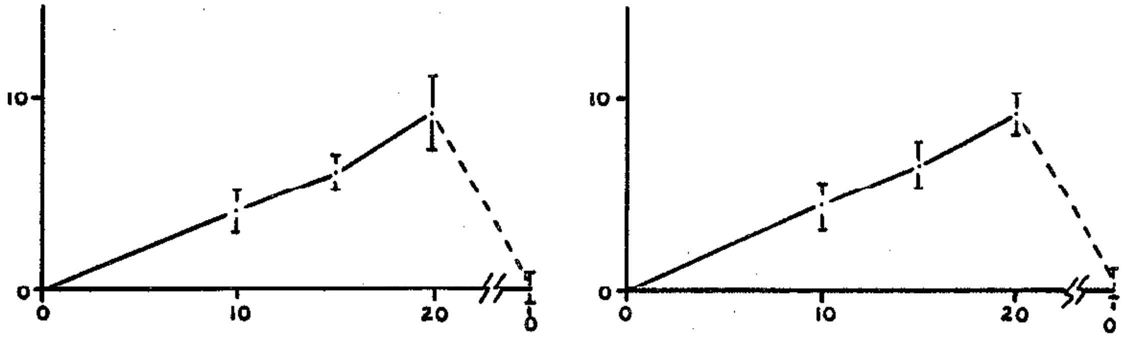
Effects of visual displacement on localizing responses. Since the aftereffect magnitudes following 50 practice movements were larger for hand than for foot adaptation, it was decided to determine whether physiological limits had been surpassed for reaching with the foot, whether the foot was actually less adaptable than the hand, or whether the subjective estimates of distance by the foot were in fact smaller than those made by the hand.

Four subjects were tested twice each for the amount of deflection produced in their foot, hand, and body localizations while they were looking through the prisms (without adapting) with the mirror in place. This procedure was carried out, always under conditions of no visual feedback, with 10, 15, and 20 diopter prisms. Half of the subjects were initially tested using an increasing sequence of prism power and half with a decreasing sequence. Measurements of reaching accuracy in the absence of prisms were taken before and after these tests. The same measurements were then made on each group in the opposite sequence. These results are graphed in Fig. 10. Each point for each hand was significantly greater than the corresponding point for either foot.

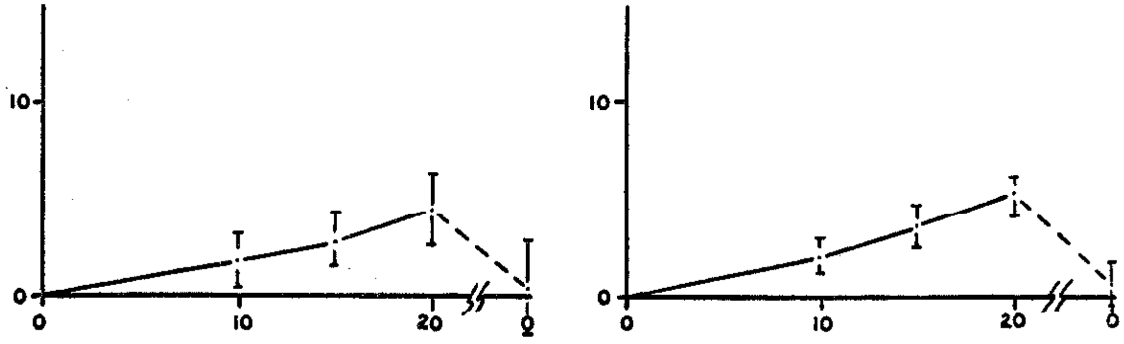
All of the curves are approximately linear, indicating that physiological limits in reaching had not been passed for the 20 diopter deflection. Furthermore, the ratio (0.51) of prism-induced shifts in localization by the feet to those by the hands computed from the data used for Fig. 10 is the same as the ratio (0.51) of aftereffect magnitude of first adapted feet to first adapted hands computed from data in Table 9, indicating that the relative efficiency of adaptation is the same for feet and hands but that the relative efficiency in reproducing visually determined distances by proprioceptively determined displacements is only one half. The absolute efficiencies in reproducing the visually estimated distances were 43.4% for feet, 85% for hands, and 109% for body localization. The manner in which these results affect interlimb comparisons of aftereffects will be mentioned in the discussion.



BODY



RIGHT HAND LEFT HAND



RIGHT FOOT LEFT FOOT

Fig. 10. Plot of the deflection in direction of walking or reaching with a specified limb *vs.* the deflection of the visual field produced by wedge prisms of different strengths. The error is zero if the response is directed toward the real position of the object. The initial direction of walking or reaching was taken as zero. For additional explanation see text.

Experiment 4

Decay of Adaptation*

This experiment determines the necessity of visual feedback from self-produced movement in producing decay of adaptation.

Apparatus and procedure. Aftereffects in reaching accuracy were established with the apparatus used in Experiment 1 of this section (Fig. 6). The survival of the aftereffect errors was then checked under two contrasting conditions. In the "reafferent condition" visual feedback of self-produced movement was intentionally used to help restore normal coordination; the subject moved his hand back and forth for 15 minutes while watching the movement without the prisms in the apparatus. In the "non-reafferent condition" visual reafference was completely absent; the subject sat quietly in the dark for 15 minutes. At the end of these periods the aftereffects were again measured.

The eight subjects that were used were assigned in the following way for testing. Four subjects viewed the preferred and four the unpreferred hand during adaptation. Half of each group was run on the non-reafferent condition first while the other half began with the reafferent condition. All subjects had a right hand preference and all were adapted with the bases of the prisms to their left.

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*This work was reported in Reference 60.

TABLE 10

DECREASE IN AFTEREFFECTS WITH AND WITHOUT VISUAL REAFFERENCE

		Difference in Degrees	
Condition	N	Mean	S.D.
Reafferent	8	2.58	2.04
Non-reafferent	8	1.62	1.11

Results. The reductions in aftereffect errors found after 15 minutes of normal reafferent exposure and after 15 minutes in the dark are presented in Table 10. Paired differences between the aftereffects before and after each of the two conditions were used because a correlation exists between the initial magnitude of the aftereffect and its final value after decay. Both of these means are greater than zero (one tailed t test, $p < .005$), indicating that the aftereffects diminished under each condition. The decrement for the reafferent condition is greater than that for the dark one, but this difference is not significant ($p > .2$) in this experiment. The initial aftereffect was 3.21 degrees for each condition. It is concluded that visual reafference is not necessary for a return toward normal coordination.

Summary of Results

The results from the experiments in Section II are summarized here.

1. There was no transfer of aftereffects from the practiced to the unpracticed arm when adaptation took place under restricted conditions of movement.

2. Partial intermanual transfer of adaptation (about 40%) was found if the subjects moved their heads and torsos during the adaptive process. This was true regardless of whether adaptation was measured as aftereffect errors or as correctness of reaching with the prisms in place. Furthermore, transfer was present both when the prisms were mounted in goggles and hence moved with the subject's head and when the subject moved behind a large, fixed prism.

3. Significant (about 40%) transfer to unpracticed limbs occurred following adaptation of one leg even though head and body movement were minimized. After adaptation of the second leg, additional transfer to the other limbs and to localization by walking to a target was observed. No adaptation or transfer occurred in the absence of visual feedback, and little or no transfer took place following adaptation of one arm under similar conditions.

4. Under the effect of a displaced visual field, walking ability was deflected by an amount approximately equal to the prism deflection (109% of the optical displacement), reaching with the arms slightly underestimated the deflection (85%), and reaching with the legs

greatly underestimated the deflection of the visual field (43.4%). The magnitude of the response was a linear function of the optical deflection.

5. The mean magnitude of the aftereffects established with the first adapted leg was half that of the first adapted arm. This ratio is numerically the same as that found in comparing the response of a leg to a deflected visual field with the response of an arm to the same displacement.

6. Aftereffects present in one arm decayed about 80% after 15 minutes of viewing normal reaching of the arm and 52% after 15 minutes of sitting quietly in the dark.

Discussion

Effect of adaptation. There was no indication of any transfer of adaptation from the practiced to the unpracticed arm so long as movement during exposure was restricted to the eyes and exposed arm. This seems sufficient evidence to exclude, for these conditions, interpretations of adaptation that consider changes in visual localization of the target as the end effect, for changes of this type would affect equally reaching with either arm. Thus reinterpretations of the position of the retinal image, the eye, or the head are not involved in adaptation under conditions of restricted movement. It is concluded, therefore, that the changes must involve recalibration of either the sense of position or the control of movement of the practiced arm.

Harris has recently shown that it is the sense of position of the arm that has been recalibrated in this type of experiment (54). He required his subjects to adapt their reaching accuracy to deflected vision with one arm and then with their eyes closed to position their unadapted arm at specified distances from the adapted one. The errors in positioning of the unadapted hand were in the direction that would be predicted if, after adaptation, the subjects felt that the position of their adapted hand was different from its actual placement by the amount of adaptation. Apparently they localized an illusory image of their adapted limb. Harris concluded that the effect of adaptation was an alteration in the proprioceptively determined position of the arm (54). Harris (56) and Pick _et al._ (57) have also shown that the effect of adaptation to deflected vision generalizes to pointing to auditory targets and to "straight ahead", and therefore cannot be thought of as a purely visuomotor recorrelation.

Experiment 2 reconciles the recent findings of no intermanual transfer of adapted reaching with Helmholtz' report to the contrary (14). When subjects were permitted to move their necks and torsos during exposure through the prisms, there was about 40% transfer from the adapted to the unadapted arm. Helmholtz presumably permitted movements of at least this magnitude, which would lead to similar or perhaps greater transfer. His technique of looking at the target and then closing his eyes and reaching to it was probably less accurate a measure of reaching ability, and might aid the impression of complete transfer.

The partial transfer of adapted reaching to the unadapted hand, *a priori*, could result from recalibration of any of the body members involved in the visual localization of the target or in the motor response. If Harris' conclusion that proprioceptive changes result from adaptation is valid for situations other than adaptation under conditions of restricted movement,* then recalibration of either the retinal image or the eye position is excluded, since proprioception is not involved in these cases.** This leaves the position sense of the neck and unadapted arm as possible candidates for recalibration. As long as there is no evidence to the contrary, it will be assumed that the position sense of one of these members has been affected by adaptation in cases where transfer is found, for then no new types of adaptive effects need to be postulated.

The results from Experiments 1 and 2 may be interpreted most simply by assuming that the effects of adaptation remain restricted to the position sense of the joints of the body actually moved during practice in reaching with the prisms rather than by postulating an indirect effect on unpracticed members (58). In Experiment 1 only the position sense of the arm was affected; in Experiment 2 the position

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*Harris has discussed at length how proprioceptive changes can interpret adaptation to other types of visual rearrangement (54).

**A direct test for the occurrence of recalibration of the retinal image or eye position might be made by comparing the amount of adaptation present in auditory localization with that for visual localization after adaptation under non-restrictive conditions.

sense of the neck may have been altered as well.* This interpretation offers a simple explanation for all the previous reports of generalization to unpracticed members of the body (14, 61, 62).

The results from Experiment 3, however, show that in the case of adaptation of the feet, the adaptive effects cannot be interpreted as remaining restricted to the joints specifically moved during exposure to prisms. In this experiment there was about 40% transfer of adaptation from the adapted foot to the unadapted foot and to the arms, even though head movements were controlled. Similarly, after adaptation of the second foot there was additional generalization to the first foot and to the arms as well as generalization to body localization. The lack of aftereffects in the control with blank adaptation ruled out fatigue effects or adaptation due to possible uncontrolled head movements as sources of generalization. The lack of intermanual transfer in the control in which hand adaptation occurred also indicated that the technique itself was satisfactory. The latter control also suggests that a critical difference may exist between adaptation with arms and with legs (<u>vide infra</u>), and therefore the suggestion, made above, that adaptive effects remain specific to the practiced joints may still be valid for the case of arm adaptation.

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*It may be noted that reinterpretation of the position of the
ad would affect certain aspects of body sensibility as well as visu-
ocalization and may have contributed to the varied reports of the
t of adaptation on the perceptions of subjects who have adapted
to rearranged vision.

It may still be asked what members of the body are affected by the component of adaptation that generalizes. Does adapting one or both legs cause changes to be made in the sense of position of the unpracticed limbs or in the mechanisms involved in visual localization of the target? The results from the part of Experiment 3 in which various optical displacements of the visual field were estimated by pointing with the different limbs taken together with the results of adaptation with the legs suggest that the adaptive changes are not made in mechanisms of visual localization. Recalibrations involving the retinal image or the position of the eyes or neck, by their effect on visual localization, would be expected to produce the same effect on pointing with the limbs or walking to a target as would optical displacements of the visual field. However, the estimates of target position following adaptation of one or both legs appear to be equally displaced for pointing with arms or legs and for walking to a target (Fig. 9), while a differential effect on localization is found with optical displacement (Fig. 10). The sense of position of the unexposed limbs remains as a possible site for the changes that result in generalization following adaptation of the feet.*

Requirements for generalization. It was of interest to know what differences in experimental conditions were responsible for the transfer

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*If, as proposed earlier, intermanual transfer results from specific adaptation of the neck, then generalization to the legs should be only one half the amount of transfer to the unadapted arm.

and generalization reported in Experiments 2 and 3. Previous work (14, 61, 62) has only indicated that transfer can occur when fewer restrictions are placed on the subject's actions during exposure through the prisms. In these cases transfer might result from differences in the type of visual stimulation or from differences in the amount or type of movement.

Two types of visual stimulation peculiar to movements of the head in space while wearing prisms were available as cues in the earlier experiments. The first type consists of the expansions and contractions of the visual field that accompany head movements. These distortions were removed by using the large fixed prism in Experiment 2, and were not present in Experiment 3, yet in both cases transfer of aftereffects to unpracticed limbs was found. It is therefore concluded that this sort of information is not necessary for generalization.

The second type of visual stimulation characteristic of head movement associated with deflected vision results from a shift on the retina of the point on the image corresponding to the "center of flow" of movement in the visual field (63). Normally this point represents the projection on the retina of the point in space to which the eye is advancing or from which it is receding. When prisms intervene, this point is correspondingly displaced. Held has proposed that information concerning this displacement, resulting from translational movements of the head in space, is necessary for complete adaptation to displaced vision (63). It is conceivable that this kind of stimulation led to transfer in previous experiments (14, 62) and possibly in the present studies on eye-hand coordination. However, it cannot underlie the generalization following adaptation of the feet since head movements were not present.

An increase in amount of movement involved in compensating for prism-displaced vision might induce a more widespread effect of adaptation in the body. Under this view, increased muscular effort and/or its proprioceptive feedback could either cause specific adaptation in the joints which were moved or provide a signal for adaptation to occur at a higher organizational level of nervous control, with consequent generalization of the effect. The additional movement of head and torso in Experiment 2 could presumably provide the required information for such specific or non-specific generalization. It is less certain how this would happen in the experiments on adaptation of the feet, in which attempts were made to restrict extraneous movement of nonexposed parts of the body. However, a greater amount of effort is required for pointing with the feet than for pointing with the hands when lying down, which would cause more widely spread tension in much of the body. Such a non-specific increase in muscular effort might call into use a more generalized mechanism of adaptation. Some evidence against this interpretation is indicated by the results of a preliminary experiment in which subjects adapted their feet while standing instead of while lying on their backs. These subjects showed approximately the same degree of generalization as observed in Experiment 3 even though there was much less generalized tension in the rest of the body.

An alternative explanation would differentiate the kind rather than the amount of movement. According to this view, movement of the feet would by its own nature activate compensation at a more general level of organization than would similar movement of the hands. The use of the legs is most often associated with movements of the body as a coordinated unit. On the other hand, use of the hands has been progressively divorced during evolution from locomotive movements and other forms of activity requiring the participation of the body as a functional unit. Generalization following foot adaptation therefore might reflect changes in a more primitive, bodily-organized system of coordination.

The simplest interpretation consistent with all the generalization experiments would view the kind and/or amount of movement rather than differences in the nature of the resultant visual feedback as the critical factor in promoting generalization of adaptation.

Requirements for decay of adaptation. The suggestion that normal and prism-altered coordinations are two states of the same system (8), and that adaptation is the replacement of old correlations between motor corollary discharges and visual feedback from movement by new ones (19) implies that adaptation to prisms and "adaptation" back to normal should have similar requirements. The partial return of normal coordination observed in adapted subjects who sat for 15 minutes in the dark shows that visual reafferent stimulation is not necessary for a return toward normal coordination after adaptation to deflected vision. This contrasts with its requirement for the establishment of adaptation to deflected vision (8, 17, 19), and suggests either that the mechanisms establishing adaptation are different from those responsible for normal coordination or that the effect produced by adaptation is independent of the type of sensory stimulation that can utilize and modify it.

The partial reinstatement of normal coordination could be due to the action of an innate mechanism favoring normal coordination, to incomplete replacement of the old correlations associated with a mechanism that can reestablish the more practiced ones, or to uncontrolled tactile-proprioceptive reafference which might substitute for visual reafference in "adapting" back to normal. Cohen has recently carried out extensive experiments on adaptation to deflected vision that suggest which of these alternatives is correct (55). His subjects showed slight loss of adaptation when they sat motionless in the dark, moderate loss when either vision or movement was permitted, and greatest decay when both movement and the resultant visual feedback was allowed. Harris has also found little or no decay of adaptation with his subjects, who placed their hands on a fixed rest after each trial (54). These results suggest that the critical factor producing decay in the present experiment was tactile-proprioceptive feedback from uncontrolled movements and contact between parts of the body. Therefore the decay results may be taken as evidence against the suggestion that visuomotor recorrelations are the end effect of adaptation since it would seem unlikely that visuomotor correlations would be changed by other types of sensory stimulation.

Nature of the adaptive process. The learning of motor skills generally shows evidence of considerable bilateral transfer from the practiced to the unpracticed limbs (42, 43, 64). For example, intermanual transfer has been reported for such tasks as ball tossing (65, 66), mirror drawing (67, 68), mirror aiming (69), and maze solving (70). This contrasts with the lack of savings* shown by human subjects when adapting one hand after another (Experiment 1), and appears to differentiate the process of adaptation from these types of motor learning.

The interocular transfer of adaptation to deflected vision in split-brain monkeys (Section I) also indicates a difference between prism-adaptation and other types of learning situations. The memories for all types of visual (30-35) and of somatosensory and motor (36-39) learning previously tested in split-brain animals can be restricted to the trained hemisphere by section of the forebrain commissures. The effect of adaptation, on the other hand, was found to be equally available to testing with either eye. Furthermore, the adaptation process can take place equally well for cases in which the primary cortical areas for the eye and hand are in the same or separated hemispheres. This contrasts with the deficits reported for all other learning

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*It is important to compare savings in adaptation curves, rather than measures of initial transfer (as has been done (59)), with the results for motor learning to insure similarity in the measuring conditions. If transfer measures for adaptation allowed visual feedback, as do most tests for motor learning, rapid learning might occur and produce a large practice effect.

situations in split-brain monkeys in which comparisons between information directed into the separated hemispheres has been required (51, 71-73). The results on intermanual and interocular transfer suggest that the adaptation process is functionally and anatomically distinguished from other forms of learning.

Reafference model and motor corollary discharges. Many types of perceptual or behavioral phenomena require that sensory stimulation caused by self-produced movement be differentiated from similar stimulation caused by changes in the environment. For example, even though identical retinal stimulation can result from an object moving in space and from eye movements made while viewing an object, the perceptual effects are strikingly different. In such cases, it is generally considered that additional information relating to the body movement is used to discount the changes in sensory stimulation caused by the self-produced motion. Such correction could be accomplished by comparing exteroceptive input with either a proprioceptive measure of the amount of movement that occurs or with a centrally generated estimate of the expected amount of movement.

For perceptual or behavioral constancy phenomena associated with eye movements, such as movement constancy of the visual field and size constancy, explanations based on proprioceptively induced corrections have been inadequate. Many reports have indicated that proprioceptive information is insufficient to induce such corrections (11, 14, 18, 74, 75) and in fact is unnecessary for the application (or misapplication) of these corrections (14, 74-76). Recently it has been shown directly that the eye has no position sense, either conscious or reflex (75).

This and related evidence has led to the postulation that eye position is determined from central commands initiating eye movements, and it has been inferred that these commands are monitored by sensory or perceptual centers for maintaining perceptual constancy. Helmholtz referred to these "expectancy" messages as "effort of will" (14). Later investigators, in attempting more physiological explanations, have thought of them as corollary discharges from motor paths or centers to areas of sensory interpretation. Sperry (74) referred to "corollary discharges" to visual centers, Walls (11) to "innervation patterns" to area 19, and von Holst (18) to "efferent patterns" to unspecified "lower centers". Von Holst, in particular, has extended his "reafference principle" to account for many types of constancy phenomena associated with self-produced movement.

Held observed the resemblance between the requirements for maintaining perceptual constancy and the necessity for self-produced movement in adapting to deflected vision, and suggested that a similar mechanism might be involved in adaptation (19). In order to remove the dependency of von Holst's reafferent model on the simultaneous presence of corollary discharges and sensory feedback, he proposed the addition of a correlation and memory element to allow the storage of frequently associated visual and motor corollary patterns. These patterns were assumed to be used in subsequent behavior as the basis on which to select appropriate response patterns to particular visual stimulation. This mechanism, therefore, could adjust to novel sensory-motor relations by replacing old, unreinforced correlations with new ones, and could select from its memory the proper "mate" for a motor or sensory input, thereby producing an appropriate perception or response. Many aspects of adaptation and related phenomena have been interpreted with this model (19).*

Explanations of perceptual constancies or of "constancies" in coordination, based on the concept of motor corollary discharges, have in common the requirement for accurate, anticipatory information concerning the magnitude and direction of the intended movement. In the case of eye movements this should present no particular problem, "for there is no reason why we should not be able to judge the size of motor volleys leaving the brain as accurately as we can judge the size of sensory volleys arriving" (77). In fact, the position of the eyes can be judged as accurately as that of the hand (77). For movements of the limbs, however, motor volleys would not seem an accurate measure of movement because of the differential loading caused by variations in external conditions that often affect such movements. Motor corollary information would seemingly need to come from centers organized in terms of the goal to be reached rather than from the actual output stage.**

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*While several results discussed previously suggested that this model did not in itself explain the effect of adaptation, they do not bear on the model's validity in accounting for the process.

**Even in the case of corollary discharges from the eye it is unlikely that the discharges arise after the oculomotor nuclei, since perceptual constancies of the visual field are not maintained during vestibular nystagmus.

For some cases of constancy often associated with changes in eye muscles the source of corrective information seems to originate from levels completely divorced from motor connotations. Size constancy has been interpreted in terms of corrections based on corollary discharges from convergent or accommodative movements (10, 18). However, constancy corrections are also introduced when motion pictures of rotating Necker cubes and some of the rotating Ames demonstrations are viewed; in this situation no changes in convergence or accommodation seem likely. Similarly, corrections are introduced in the viewing of the rotation of the actual object where, during apparent movement in the illusory direction, the changes in convergence and accommodation postulated by reafferent interpretations should be out of phase with those required for clear, single vision. Yet no blurring or double vision is noticed, indicating that eye changes follow the actual rotation of the object. Teuber (10) mentions a similar effect in which some subjects report size changes when projecting an afterimage "into" a drawing of a tunnel. It would seem that the corrective information for these situations stems from an expected change in the object rather than from the eye changes that occur in response to the real variations in the object. This suggests that corollary discharges arise at some premotor stage, and that their usual association with motor volleys producing eye changes has led to their motor identification. Clearly, measurements of the actual eye changes accompanying illusory movement in these situations are required before this suggestion can be seriously considered.

In the case of adaptation to deflected vision, alternatives to the employment of corollary discharges as the source of positional information that is correlated with visual feedback should be mentioned. The corollary discharges might serve only as a trigger or switch that in some manner enables correlations to be made between visual and proprioceptive estimates of the position of the members of the body. On the other hand, proprioception during active movement might differ from that during passive movement in some way that allows visual-proprioceptive correlations to be made. Such possibilities should not be neglected as long as proprioception and visual feedback have only been shown to be insufficient for adaptation and have not been shown to be unnecessary. These suggestions avoid the problem of attributing specific positional information to corollary discharges from limb movements.

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