Journal of Comparative and Physiological Psychology
1961, Vol. 54, No. 1, 33-37

NEONATAL DEPRIVATION AND ADULT REARRANGEMENT:

COMPLEMENTARY TECHNIQUES FOR ANALYZING PLASTIC SENSORY-MOTOR COORDINATIONS[1]

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Development of pattern vision in neonatal mammals requires prolonged exposure to certain contiguities of stimulation according to Riesen (1958) and Hebb (1949). Consistent with this viewpoint are many studies reviewed by these authors demonstrating that certain mammals deprived of patterned visual stimulation early in life show deficiencies in visual-spatial performance when compared with normally reared animals. However, Riesen (1958) and Riesen and Aarons (1959) have demonstrated similar deficits in a chimpanzee and in kittens reared with visual stimulation from nearby objects but deprived of the opportunity for gross bodily movement in their presence. Since contiguities of stimulation are not eliminated under this condition of contact with the environment, they are apparently not sufficient for the development of at least some forms of visual-spatial discrimination. The excluded factor, gross bodily movement in a stimulus-rich environment, appears to be essential for development.

This interpretation of Riesen's findings agrees with that of results obtained in another, but obviously related, area of research: studies of the effects of sensory rearrangement[2] in man, the type of experiment exemplified by Stratton's (1897) classic on inverted vision. Predictable errors in coordination are induced by such rearrangement, but prolonged exposure to the environment reduces them. The suggestion, often implicit in older rearrangement studies, that such results may tell us something about the original acquisition of coordination was explicitly made by Held (1955). Moreover, Kohler (1953) has reported similar findings. Recently, partial compensation for errors induced by certain rearrangements has been shown to depend upon prolonged exposure to that sensory stimulation which is produced by natural movements of the recipient (Held & Hein, 1958; Held & Schlank, 1959). These demonstrations of the importance of response-produced stimulation in compensation for rearrangement are consistent with Riesen's implication of bodily movement in development. They reinforce the view that an identical process underlies both the original development of coordination and its later adaptability to rearrangement. The present experiment attempted to demonstrate that the necessary conditions for full and exact compensation of one consequence of human rearrangement closely parallel those found critical for development by Riesen, namely, gross bodily movement under natural conditions of exposure.

Prisms of equal power placed over the eyes with bases either left or right cause a lateral displacement of the retinal image and a corresponding error in egocentric localization or visual direction-finding. Previous experiments have shown that errors in hand-eye coordination induced by this prism rearrangement (Held & Hein, 1958) were partially compensated only after *S* had moved his hand while viewing it under the rearranged condition. After *S* had viewed his motionless hand through the prism for a comparable period, no compensation resulted. A more interesting result, and one in contradiction to the theory of learning by contiguities of stimulation, was the finding that after *S*'s passive hand and arm had been moved in a comparable manner by *E*, no compensation occurred. The same results were found in a study of compensation for increased optical distance of the hand from the eye (Held &

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[1] This research was supported by a grant from the National Science Foundation.

[2] The term "disarrangement" has been used with the same meaning in previous reports (Held & Gottlieb, 1958; Held & Hein, 1958; Held & Schlank, 1959) and other communications. Rearrangement, however, is a better descriptive term for simple transforms, such as those produced by a prism, which preserve the uniqueness of discriminable points on the retina. The term "disarrangement" can then be reserved to describe transforms that do not preserve this uniqueness (Cohen & Held, 1960).

Schlank, 1959). The movements of the hand, produced in one case by *S*'s own responses and in the other by externally imposed motion of his passively held arm, caused identical stimulation of the retinae of *S*. Hence, these conditions were distinguished only by the presence or absence, respectively, of response-produced or *reafferent* (von Holst, 1954) stimulation accompanying movements of the hand. According to these results, not simply movement but *self-produced* movement with its contingent reafferent stimulation is the critical factor in compensation for rearrangement.

If compensation for the prism-induced errors of hand-eye coordination required reafferent stimulation produced by hand and arm movements, we may expect that compensation for the errors of egocentric localization requires reafferent stimulation produced by gross bodily movements or locomotion. A test of the necessity for reafferent stimulation in compensation for these prism-induced errors of localization must therefore compare the consequences of self-produced movement of the body as a whole with comparable movement of the body when kept passive. In particular, the movements of the body must include translational components of motion, a factor implicated in study of shifts following rearrangement of auditory direction finding: the analog of visual direction-finding (Held, 1955). Two experiments are reported. In Experiment 1 the compensation of egocentric localization following brief exposure with passive movement was compared with that following equivalent exposure with self-produced movement. Experiment 2 tested the consequences of long-term exposure.

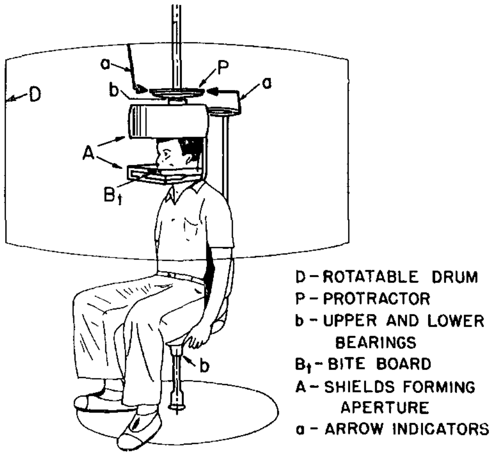

FIG. 1. Apparatus used to measure egocentric localization.

METHOD

General Procedure

Apparatus and measurement. The most precise and stable measurements of egocentric localization were obtained when *S* was instructed to orient himself so as to find a stationary target straight ahead of him. This method of measurement was facilitated by use of the apparatus shown in Figure 1. The *S* was seated on a chair that he could rotate by leg movements around a vertical axis defined by upper and lower bearings (*b*). The position of *S*'s head was fixed by a biteboard (B_t) that rotated around the same vertical axis and was attached by a rigid extension to the chair. A drum (*D*) 5 ft. in diameter was mounted on a bearing that allowed it to rotate around the same vertical axis (*b-b*). One of two targets could be mounted on the inside surface of the drum at *S*'s eye level. (1) a dimly luminous vertical slit 2 in. long, viewed in total darkness and (2) a vertical line 2 in. long, viewed in room illumination. When Target 2 was used, the horizontal aperture formed by shields (*A*) restricted *S*'s view to the inside of the drum and precluded any cues to direction based on the position of the drum relative to other objects in the field of vision. This aperture extended more than 90° to right and left of *S*'s median plane of vision. The direction in which *S* faced and the direction of the target were indicated on a protractor (*P*) by arrows (*a*) that were fixed to biteboard and drum, respectively. In taking each measurement *E* repositioned the drum and instructed *S* to rotate himself until the target appeared straight ahead of him. Fifteen measurements were taken at each sitting of *S*, who always viewed the target with unaided eyes (without prisms). When localizing with unaided eyes following exposure, compensation for the prism-induced error is usually evidenced as an increased error of localization (sometimes called an aftereffect of exposure). Under properly controlled conditions, the measurements taken with prisms differ from those taken without prisms by exactly the amount of lateral deviation introduced by the prisms. Measuring with unaided eyes is convenient for a number of reasons of which the most important is that of a control against the presence of unwanted cues to the objective direction of the target. The *S* who shows *increasing* errors of localization cannot be utilizing such cues. The measuring procedure was performed before and after exposure of *S* under the conditions described below.

Exposure. During exposure *S* wore goggles that eliminated from view all but the central 60° of the field of each eye. Each eye viewed this central field through a 20-diopter trial-case prism, fitted into the goggles, that caused a lateral deviation of 11°. Both prisms had the same base orientation, either right or left, and consequently displaced images equally for each eye. Two conditions of exposure were used. Self-produced movement entailing reafferent stimulation was obtained

TABLE 1

SHIFTS OF LOCALIZATION IN DEGREES AFTER ONE HOUR OF EXPOSURE

Exposure Condition	Subject															Mean
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Self-produced movement																
Base right	2.4	1.9	1.5	3.0	2.0	2.0	−0.2	−0.6	2.0	2.6	1.8	2.5	0.8	0.9	−1.5	1.42
Base left	2.3	2.0	0.1	4.2	0.9	2.6	0.2	−0.4	0.6	0.9	0.4	1.8	−0.7	0.8	0.7	1.16
Passive movement																
Base right	−0.8	0.2	−0.3	−0.3	1.1	−3.0	−1.2	−0.2	−0.6	1.0	−0.3	0.4	0.4	0.3	−1.3	−0.31
Base left	−1.3	−0.2	1.0	1.3	2.0	−3.8	1.0	−0.1	−1.5	−0.7	−1.2	0.8	0.5	1.0	−0.8	−0.13

by having *S* walk leisurely along a path bordered by trees and an occasional building. The equivalent passive movement was obtained by having *S* sit in a wheel chair that was pushed along the same path at the same speed.

Specific Procedure

Experiment 1. Fifteen *S*s with normal visual acuity and with no visual-motor anomalies were used. Each *S* was given two 1-hr. exposure trials under self-produced movement and two 1-hr. trials under passive movement. On one of each of the paired trials *S* wore base-right prisms; on the other, base-left prisms. The order of the four trials per *S* was varied among *S*s. At least one day intervened between trials. Measurements were taken before and after each trial using Target 2 in room illumination.

Experiment 2. Fifteen *S*s wearing prisms walked for periods ranging from 11 hr. distributed over two days to 21 hr. distributed over four days. Two of these *S*s were then exposed passively for equivalent periods. Measurements were distributed over the intervals as shown in the results. Target 1, a luminous slit viewed in darkness, was used. The daily exposure periods did not exceed 7 hr. of continuous exposure. No attempt was made to control visual exposure when *S* was not wearing the prisms.

RESULTS

Experiment 1

Table 1 shows the mean shift of localization in degrees for each trial of each *S*. Positive shifts compensated for the induced error; negative shifts were anticorrective. The two mean shifts for the 15 *S*s exposed with self-produced motion were positive and statistically significant: both exceeded the .01 level according to *t* tests of the significances of the differences of the means from zero. These shifts represented slightly more than 10% of full compensation for the prism-induced error. On the other hand, the corresponding mean shifts after exposure with passive motion were negative and nonsignificant.

Experiment 2

Eight out of the 15 *S*s reached full compensation, a shift in egocentric localization of 11°, within four days of exposure with self-produced movement. The remaining *S*s all compensated more slowly and had not reached full compensation after four days of exposure. The results for the eight *S*s are graphed in Figure 2 with solid lines. Two of these *S*s were then given equivalent exposure periods with passive movement. These results are graphed in Figure 2 with dashed lines. Many *S*s who reached 100% compensation (labeled "adaptation" in Fig. 2) before completing their periods of exposure subsequently dropped below this level only to return again to full compensation. No *S* exceeded full compensation by a significant amount. Of all the fluctuations in amount of compensation, the most striking were those that ranged from almost full compensation to zero (Fig. 2, Subject D). These fluctuations may have been related to occasional reports from *S*s, showing large compensations, of the presence of a secondary image of the target during the measuring period. These reports, which suggest the presence of diplopia, were similar to reports obtained in the analogous experiment with auditory rearrangement (Held, 1955). The two *S*s run with passive motion showed no significant compensation despite the duration of exposure.

DISCUSSION

Full and exact compensation for the prism-induced errors of visual localization required gross bodily movement—and, more specifically, self-produced movement—of *S* during exposure to a natural environment. These

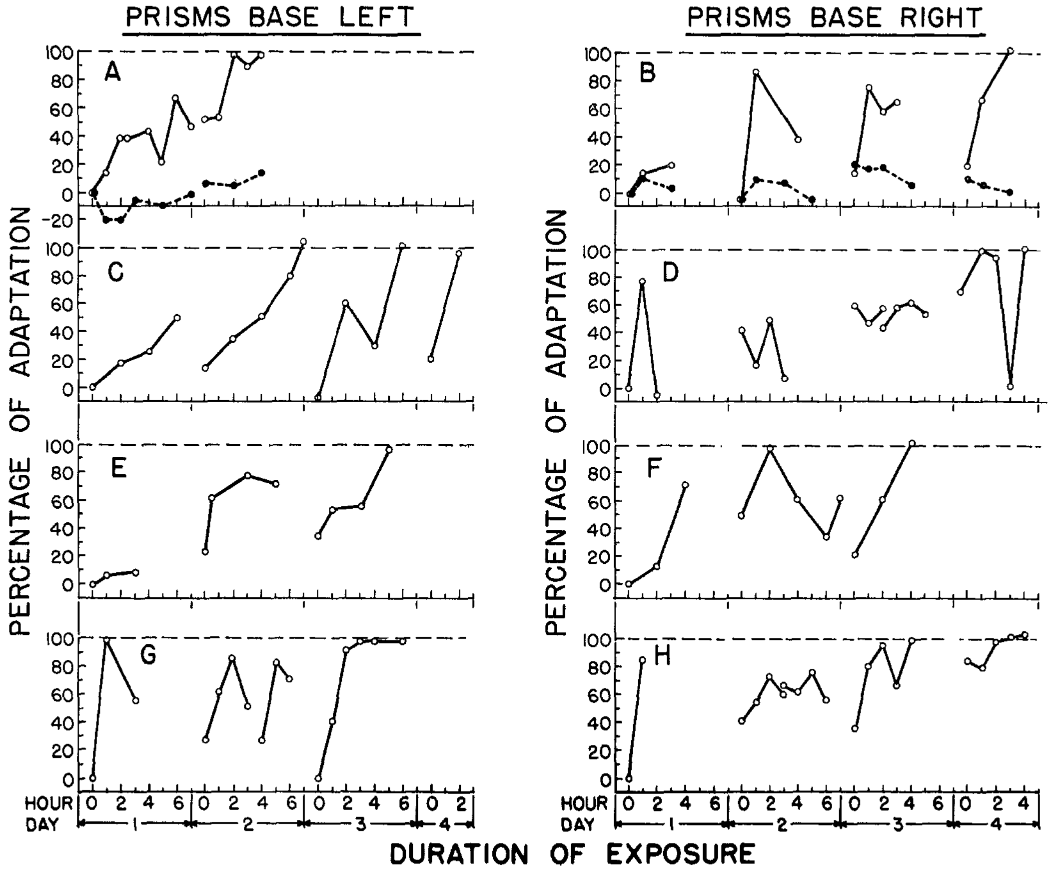

FIG. 2. Compensation for prism-induced errors of localization during prolonged exposure.

exposure conditions closely paralleled those shown by Riesen to be critical for the visual development of a chimpanzee and of kittens. The achievement of 100% compensation and its maintenance with further exposure is consistent with the view that the same process operates in developing and maintaining localization in neonatal mammals. Further evidence for this view comes from comparisons of the extent of deficit following deprivation with the extent of compensation for rearrangement when both studies have been performed on the same or related species of mammal. Relevant deprivation studies have been performed on the rat by Lashley and Russell (1934) and Hebb (1937); on the cat by Riesen, Kurke, and Mellinger (1953) and Riesen and Aarons (1959); on the chimpanzee by Riesen (1958); and the results of similar deprivation in man have been summarized by von Senden (1932). Corresponding rearrangement studies have been performed on the rat by Sperry (1942); on the cat by Bishop (1959); on the monkey by Foley (1940) and Sperry (1947); and for man, Kohler (1951) discusses the most striking findings among those in a literature too extensive to review here. A rough agreement appears in comparisons of the extent of the two effects found in the same or in closely related species. Both signs of plasticity in coordination are most evident in man, least in rats, and intermediate in other species. This evidence also adds further justification for the cross-species comparison attempted here.

If development and compensation for rearrangement reflect the same process, then findings concerning the essential properties of movement—e.g., the need for self-produced movement and contingent reafferent stimulation in compensation—are equally applicable to development. We may then predict that the gross bodily movement required for visual-motor development must be self-produced movement. The importance of movement in Riesen's studies cannot then be interpreted as merely a matter of increasing the amount of contiguous visual stimulation. Instead, we can apply the theory that reafferent stimulation is the source of ordered contact with the environment which is responsible for both the stability, under typical conditions, and the adaptability, to certain atypical conditions, of visual-spatial performance. The procedures of deprivation are essential for deciding the importance of behavioral factors in development. However, they are time-consuming, expensive, and consequently not as well suited as the rearrangement technique to the factorially designed studies required to isolate these factors. The rearrangement technique may complement deprivation procedures by making feasible the extensive experimentation required to isolate the critical variables common to both early development and adaptability to rearrangement in the adult.

SUMMARY

Adult human *S*s viewed their environments through prisms that optically rearrange the retinal images and induce errors in visual direction-finding. Experimental procedures showed that full and exact compensation for these errors requires gross bodily movement and, more specifically, self-produced movement for prolonged periods of exposure under otherwise natural conditions. Visual stimulation accompanying the gross bodily movements of a neonatal chimpanzee (Riesen, 1958) and of kittens (Riesen & Aarons, 1959) has been shown necessary for development of their visual-spatial performance. The similarity of exposure conditions essential in the one case for adaptation and maintenance and in the other for development is consistent with the view that an identical process underlies both achievements. If the findings of both deprivation and of rearrangement reflect the operation of the same process, then these procedures may complement each other in the analysis of mammalian coordination.

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(Received January 4, 1960)