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MOVEMENT-PRODUCED STIMULATION IN THE DEVELOPMENT OF VISUALLY GUIDED BEHAVIOR[1]

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Full and exact adaptation to sensory rearrangement in adult human Ss requires movement-produced sensory feedback. Riesen's work suggested that this factor also operates in the development of higher mammals but he proposed that sensory-sensory associations are the prerequisite. To test these alternatives, visual stimulation of the active member (A) of each of 10 pairs of neonatal kittens was allowed to vary with its locomotor movements while equivalent stimulation of the second member (P) resulted from passive motion. Subsequent tests of visually guided paw placement, discrimination on a visual cliff, and the blink response were normal for A but failing in P. When other alternative explanations are excluded, this result extends the conclusions of studies of adult rearrangement to neonatal development.

Hebb's writing (1949) has stirred interest in the effects of exposure to the environment on the development of spatial perception and coordination. The main experimental attack on the problem has used the technique of rearing animals in restricted environments (deprivation) from the time of birth or shortly thereafter. An alternative approach consists in experimentally analyzing the conditions for modifying certain sensorimotor coordinations in adults on the assumption that they are similarly plastic during the entire exposure-history of the organism (Hein & Held, 1962; Held, 1955, 1961). If this supposition is true, the analysis carried out on adults must also define the kind of contact with the environment required for development. Use of the rearrangement technique for studying plasticity in adult human *S*s has yielded results which suggest its complementarity to the procedures of neonatal deprivation (Held & Bossom, 1961). This experiment demonstrates the convergence of the two approaches.

In the human adult, change in stimulation dependent upon the natural movements of *S* has been shown essential to the achievement of full and exact compensation for sensory rearrangements (Hein & Held, 1958; Held, 1955; Held & Bossom, 1961; Mikaelian & Held, in press). A suggestive parallel between these findings and those of deprivation studies comes from two experiments on kittens reared under different conditions of deprivation. In one experiment *S*s were allowed visual experience in an illuminated and patterned environment only while they were restrained in holders which prevented them from freely moving about (Reisen & Aarons, 1959). When subsequently tested they showed deficiencies in visually guided behavior compared with their normally reared litter mates. Related deficits followed rearing in a second experiment in which *S*s were allowed to move about freely in light but with diffusing hoods over their eyes (Reisen, 1961c). The exposure factor lacking under both conditions was the variation in visual stimulation produced by the full range of *S*'s movement in normal circumstances; a result consistent with our findings.

Riesen has suggested that his deprived *S*s showed deficits because they lacked sufficient opportunity for developing sensory-sensory associations in the manner proposed by Hebb (Riesen, 1961c)—even the patterned surroundings viewed by the holder-restrained *S*s may not have provided sufficient variation in visual stimulation for forming the necessary associations. This interpretation agrees with ours in asserting that the variation in visual stimulation accompanying movement is essential for the development of certain coordinations but it omits our qualification that this variation can be effective only when it is concurrent

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with and systematically dependent upon self-produced movements (Hein & Held, 1962; Held, 1961). The alternative to our interpretation asserts that changes in stimulation irrespective of their relation to self-produced movements are sufficient. To decide between these two alternatives, we reared different sets of kittens from birth under the two implied conditions of exposure and subsequently compared their development. Under one condition stimulation varied as a result of *S*s own locomotion whereas under the other it was equivalently varied by transporting *S*s through an equivalent range of motion while they were restrained from locomoting.

METHOD

Subjects

Ten pairs of kittens were used; each pair from a different litter.

Exposure Apparatus and Procedure

The exposure apparatus diagramed in Figure 1 was designed to equate the visual stimulation received by each member of a pair of *S*s. Stimulation varied with the locomotor movements of the active *S* (A in Figure 1) but varied with equivalent motion of the passive *S* (P). To attain this equivalence, the gross motions of A were mechanically transferred to P. These movements were restricted to rotations around three axes. The radial symmetry of the visible environment made variations in visual stimulation, contingent upon these movements, equal over time for the two *S*s.

The P was placed in the gondola and held there by a neckyoke and body clamp. The lever from which the gondola was suspended was then balanced by appropriate placement of a counterweight. When attached to the opposite end of the lever by a second neckyoke and body-clamp assembly, A was free to move itself in both directions around the three axes of rotation a-a, b-b, and c-c while pulling P through the equivalent movements around a-a, b-b, and d-d by means of the mechanical linkages to the gondola. The distance between c-c and d-d was 36 in. The range of motions normally performed by *S*s was somewhat reduced by the experimental apparatus. Use of ball bearings and aluminum in the construction of the apparatus reduced friction and inertia insofar as possible. The importance of these restraints is mitigated, we believe, by previous findings in rearrangement studies which indicate that similar restraints, and constant changes in the inertia over-

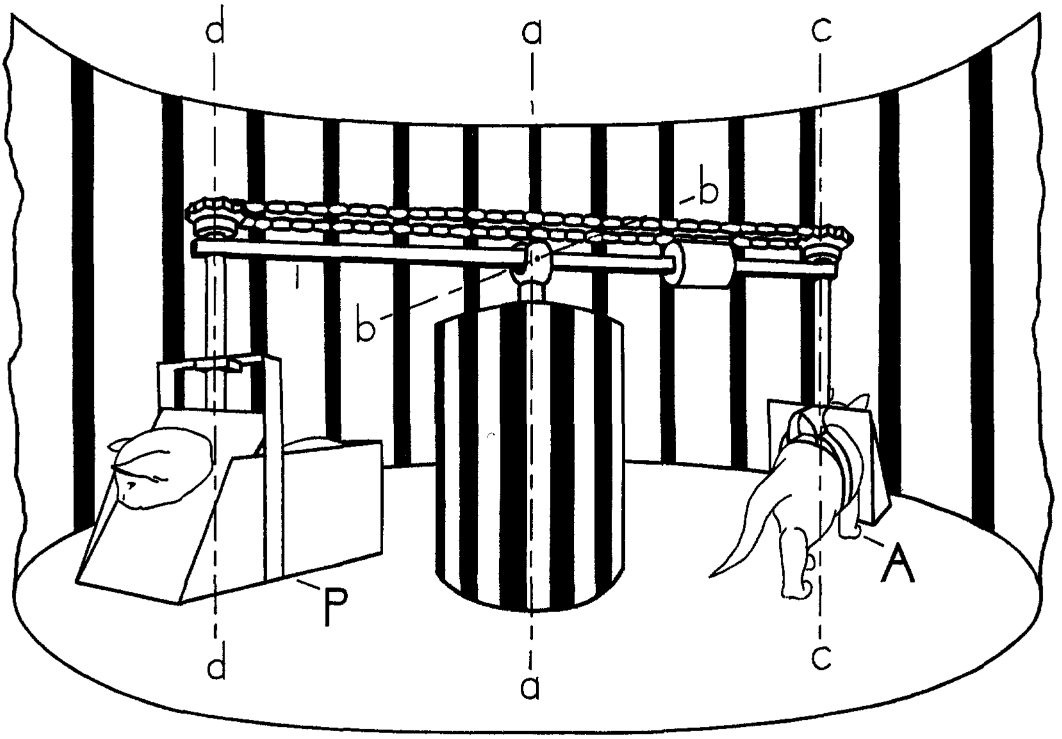

FIG. 1. Apparatus for equating motion and consequent visual feedback for an actively moving (A) and a passively moved (P) *S*.

come by muscular movement, do not affect the adaptation process (Held & Hein, 1958; Held & Schlank, 1959). Head motion was not restricted for either A or P. This restriction seemed unnecessary since Riesen and Aarons (1959) have shown that kittens reared from birth with variation in visual stimulation consequent upon free head motions, but otherwise restricted, failed to learn a simple spatial discrimination. Because of its constraints, P could not locomote. However, its limbs were free to move and to slide along the smooth floor of the gondola. According to our observations these movements frequently occurred.

The apparatus was surrounded by a galvanized iron cylinder that was 24 in. high with a diameter of 48 in. The lever support mechanism was enclosed within a second cylinder that was 11 in. high with a diameter of 12 in. The smaller cylinder served to obscure each *S*'s view of its mate. Patterning was provided by vertically oriented 1 in. wide stripes of black and white masking tape separated by 1 in. of bare metal. Additional texture was provided by the rough side of a piece of masonite which served as the floor. The floor was uniform throughout thus providing equivalent visual stimulation for the two *S*s. Sight of the paws and other body parts was excluded by appropriate extensions of the neck stocks.

Testing Apparatus and Procedure

We used tests of visually guided behavior that minimized *S*'s gross movements in the visible environment in order not to confound the conditions of testing with those of exposure, a confusion which past investigators have generally disregarded. For this purpose responses to stimuli were used that require no conditioning with repetition of movements but which are nonetheless contingent upon a capacity to make visual-spatial discriminations. Following the leads of earlier work, we have used three such tests:

1. Visually-guided paw placement (Riesen, 1961c). *S*'s body was held in *E*'s hands so that its head and forelegs were free. It was slowly carried forward and downward towards the edge of a table or some other horizontal surface. A normally-reared *S* shows visually-mediated anticipation of contact by extending its paws as it approaches the edge.

2. Avoidance of a visual cliff (Walk & Gibson, 1961). The visual cliff consists essentially of a narrow platform supported by vertical sides that drop a few inches to a large plate of glass. The *S* placed on the platform can descend to the glass on either one of two sides. Its view on the "deep" side is through the glass to a patterned surface 30 in. below. On the other side it views a similarly patterned surface attached to the underside of the glass. In our apparatus, both surfaces were illuminated from below and hence the clean glass surface was practically invisible. For the vertical sides of the platform, we substituted planes inclined 35° from the vertical.

3. Blink to an approaching object (Riesen, 1958). The *S* was held in a standing position in a neckyoke and body clamp with a large sheet of Plexiglas positioned directly in front of its face. The *E* moved his hand quickly toward *S*, stopping just short of contact with the Plexiglas.

Several additional tests were performed to check the status of peripheral receptor and response mechanisms. These included observations of pupillary reflex to light, the tactual placing response, and visual pursuit of a moving object. The *S*, held in a standing position in a neckyoke and body clamp, was light-adapted in the normally illuminated laboratory prior to observation of the pupillary reflex. Change in pupillary size was then noted when a light beam from a penlight was moved across the eye from outer to inner canthus. To determine the presence of the tactual paw-placing response *S* was supported as in the visual paw-placing test. It was then carried to the edge of a table where the dorsa of its front paws were brought into contact with the vertical edge of the table. Observations of experimental *S*s were compared with those of normals which, in response to this stimulus, place the paws on the horizontal surface of the table. Visual pursuit was elicited by *E*'s hand moving slowly across *S*'s visual field.

General Procedure

The 10 pairs of *S*s were divided into two Groups, X and Y, whose members were reared with minor differences. Each of the eight pairs of Group X was reared in darkness from birth until member A attained the minimal size and coordinational capacity to move itself and its mate in the apparatus. This age varied between 8 and 12 weeks. They then began exposure in the apparatus for 3 hr. daily. The two pairs of Group Y received 3 hr. daily exposure, beginning at 2 and ending at 10 weeks of age, to the patterned interior of the laboratory while restrained in holders that allowed some head movement but prevented locomotion. They then began exposure in the apparatus for 3 hr. daily. When not exposed, all *S*s were kept in lightless cages together with their mothers and litter mates. We had found in pilot studies that *S*s reared in this fashion did not show the freezing, agitation, or fear responses reported to follow social isolation by Melzack (1962) and Riesen (1961a).

Six repetitions of the paw-placement test were performed after each daily exposure period for all *S*s. On the first day that one *S* of each pair in Group X displayed visual paw placing, both were tested on the visual cliff. They were retested on the following day. For each test and retest *S* was required to descend from the central platform six times. Immediately following trials on the visual cliff on the second day, member P of each pair was put in a continuously illuminated room for 48 hr. Retesting of visual placing and renewed trials on the visual cliff followed this unrestricted exposure. The testing procedure differed slightly for pairs of Group Y. On the first day that A displayed visual paw placing, it was tested on the visual cliff and retested on the following day. However, its mate (P) was not placed on the cliff at this time;

instead, the passive exposure procedure was continued for 3 hr. daily for a total of 126 hr. The paw placing and visual cliff tests were then administered to P.

RESULTS

The principal results of this experiment are summarized in Table 1. The amount of time required for the development of a visually-guided paw-placement in the members of each pair of litter mates is indicated in the column under the heading Exposure in Apparatus. After those periods of exposure required by A, every P mate failed to display the response. Observations suggest a tendency for the placing response to develop in the livelier of the active *S*s with fewer hours of exposure than required by the quieter ones. The blink response to an approaching hand developed concurrently with the placing response. Pupillary reflex to light, tactual placing response, and visual pursuit were each noted on first elicitation, just prior to the initial exposure in the apparatus.

On the day that the visually-guided placing response was shown by A, he was tested on the modified visual cliff. All As behaved like normally reared *S*s which had been observed previously in a pilot experiment. As shown by the totals of Table 1, each A descended to the shallow side of the cliff on every trial of the first day and repeated this performance on the trials of the following day. The P members of Group X were tested on the cliff on the same days as their actively exposed litter mates. They showed no evidence of discriminating the shallow from the deep side. Observations of the P members of Group Y on the cliff, after their prolonged passive exposure, gave similar results and they also failed to perform visual paw placement. Following the 48 hr. period of freedom in an illuminated room, the P members of Group X were retested. They then displayed normal visually-guided paw-placement and performed all descents to the shallow side of the visual cliff.

TABLE 1

RATIO OF DESCENTS TO SHALLOW AND DEEP SIDES OF VISUAL CLIFF

Pair number	Age in weeks[a]	Exposure in apparatus (in hr.)		Ratio of descents shallow/deep	
		A	P	A	P
1X	8	33	33	12/0	6/6
2X	8	33	33	12/0	4/8
3X	8	30	30	12/0	7/5
4X	9	63	63	12/0	6/6
5X	10	33	33	12/0	7/5
6X	10	21	21	12/0	7/5
7X	12	9	9	12/0	5/7
8X	12	15	15	12/0	8/4
1Y	10	30	126	12/0	6/6
2Y	10	33	126	12/0	8/4

[a] At the beginning of exposure in the experimental apparatus.

DISCUSSION

The results are consistent with our thesis that self-produced movement with its concurrent visual feedback is necessary for the development of visually-guided behavior. Equivalent, and even greatly increased, variation in visual stimulation produced by other means is not sufficient. However, before concluding that our thesis is valid we must consider other alternative explanations of the deficits in the behavioral development of neonates following deprivation. These alternatives assert that loss of function does not reflect deficiencies in a process of the central nervous system that depends upon exposure for its development. Instead, the capacity to perform is allegedly present but prevented from operating by either peripheral blockage or other suppressive effects of the special rearing conditions. Such negative effects fall into two categories: (*a*) anatomical or physiological deterioration and (*b*) behavioral inhibition.

Included under anatomical or physiological deterioration said to result from deprivation, are the findings of atrophy in peripheral parts of the visual nervous system, a literature reviewed by Riesen (1961b); the assumption that maturation of the retina is prevented (Walk & Gibson, 1961); and the suggestion that general debility results from lack of use of various organs (Hess, 1962). In the present experiment, the relevance of peripheral atrophy is contraindicated by the presence of pupillary and pursuit reflexes and the rapid recovery of function of the passive *S*s once given their freedom. Debility specific to the motor systems of these *S*s can be ruled out on the grounds that their tactual placing responses and other motor activities were indistinguishable from those of normals. In addition, differential losses in the periphery or differential debility could hardly be expected to result from those differences between active and passive exposures which occurred in the experimental apparatus.

Inhibition of performance attributable to the effects of shock, fright, or overactivation upon exposure to the novel and increased stimulation that follows release from the deprived state has been suggested by Sutherland (1959) and Melzack (1962). Sutherland has also suggested that habits developed during deprivation may compete with and inhibit the normal response. However, both our active and passive *S*s were raised under very similar conditions insofar as restriction was concerned and under the rather mild conditions of deprivation of this experiment we did not observe any signs of shock, excitement, or fright. Moreover, the passive *S*s were not observed performing responses that might have competed with the expected response.

These findings provide convincing evidence for a developmental process, in at least one higher mammal, which requires for its operation stimulus variation concurrent with and systematically dependent upon self-produced movement. This conclusion neither denies nor affirms that other processes, such as maturation, occur concomitantly. The results demonstrate the complementarity of studies of adult rearrangement and neonatal deprivation.

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