PLASTICITY IN SENSORY-MOTOR SYSTEMS

An animal's own movements change what it sees and hears. Laboratory experiments that tamper with this feedback loop show that it is a key to developing and maintaining spatial orientation in advanced mammals

by Richard Held

Anyone who has worn eyeglasses is likely to have experienced distorted vision the first time he put them on. The distortion may have been severe enough to cause him trouble in motor coordination, as in reaching out to touch something or in being sure of where he stepped. Such a person will also recall, however, that in a day or two the distortion disappeared. Evidently his central nervous system had made some adjustment so that the things he saw through the glasses looked normal again and he could have renewed confidence in his touch and step.

This process of adjustment, particularly as it operates in recovery from radical transformations of vision (as when the world is made to appear upside down or greatly shifted to one side by special goggles), has attracted the attention of scientists at least since the time of the great 19th-century investigator Hermann von Helmholtz. What has intrigued us all is the finding that correct perception of space and accurate visually guided action in space are in the long run not dependent on unique and permanently fixed optical properties of the paths taken by light rays traveling from object to eye. This finding, however, must be squared with the normally high order of precision in spatial vision and its stability over a period of time. How can the visual control of spatially coordinated action be stable under normal circumstances and yet sufficiently modifiable to allow recovery from transformation? Recovery takes time and renewed contact with the environment. Adaptation must result from information drawn from this contact with the environment. If the end product of adaptation is recovery of the former stability of perception, then the information on which that recovery is

based must be as reliable and unvarying as its end product. The investigations my colleagues and I have undertaken (first at Brandeis University and more recently at the Massachusetts Institute of Technology) have been directed toward discovering this source of information and elucidating the mechanism of its use by the perceiving organism. A useful tool in our work has been deliberate distortion of visual and auditory signals, a technique we call rearrangement.

Visual rearrangement can be produced experimentally with prisms [see "Experiments with Goggles," by Ivo Kohler; SCIENTIFIC AMERICAN, May, 1962]. Similarly, the apparent direction of sounds can be distorted in the laboratory by suitable apparatus. We have used such devices to show that in many cases the viewer or the listener subjected to these distortions soon adapts to them, provided that during the experiment he has been allowed to make voluntary use of his muscles in a more or less normal way.

The proviso suggests that there is more to the mechanism of perceptual adaptation than a change in the way the sensory parts of the central nervous system process data from the eyes and ears. The muscles and motor parts of the nervous system are evidently involved in the adaptation too—a revelation that has been very important in our efforts to discover the responsible source of information. The concept of a relation between sensory and motor activities in the adaptive process is reinforced by what happens when humans and certain other mammals undergo sensory deprivation through prolonged isolation in monotonous environments, or motor deprivation through prolonged immobilization. Their performance on perceptual

and motor tasks declines. By the same token, the young of higher mammals fail to develop normal behavior if they undergo sensory or motor deprivation.

Taken together, these findings by various experimenters suggested to us that a single mechanism is involved in three processes: (1) the development of normal sensory-motor control in the young (2) the maintenance of that control once it has developed and (3) the adaptation to changes or apparent changes in the data reported by the senses of sight and hearing. A demonstration that such a mechanism exists would be of value in understanding these processes. Moreover, it would help to explain a phenomenon that otherwise could be accounted for only by the existence of enormous amounts of genetically coded information. That phenomenon is the adjustment of the central nervous system to the growth of the body—on the sensory side to the fact that the afferent, or input, signals must change with the increasing separation between the eyes and between the ears, and on the motor side to the fact that the growth of bone and muscle must call for a gradual modification of the efferent, or output, signals required to accomplish a particular movement. This problem is especially critical for animals that grow slowly and have many jointed bones. The possibility that the need for genetically coded information has been reduced by some such mechanism is of course contingent on the assumption that the animal's environment is fairly stable. For these reasons it is not surprising that clear evidence for adaptation to rearrangement and for dependence of the young on environmental contact in developing coordination has been found only in primates and in cats.

Such, in brief, is the background of

our effort to discover the operating conditions of the suspected mechanism. Our conclusion has been that a key to its operation is the availability of "reafference." This word was coined by the German physiologists Erich von Holst and Horst Mittelstädt to describe neural excitation following sensory stimulation that is systematically dependent on movements initiated by the sensing animal; von Holst and Mittelstädt also used the word "exafference" to describe the result of stimulation that is independent of self-produced movement. "Afference" alone refers to any excitation of afferent nerves. These concepts should become clearer to the reader from the remainder of this article.

Among the contributions von Helmholtz made to science were many that were later incorporated into psychology. His experiments included work on the displacement of visual images by prisms. He was the first to report that the misreaching caused by such a displacement is progressively reduced during repeated efforts and that on removal of the prism the subject who has succeeded in adapting to this displacement will at first misreach in the opposite direction.

Helmholtz' findings and those of similar experiments by many other workers have often been interpreted as resulting from recognition of error and consequent correction. We doubted this interpretation because of our conviction that a single mechanism underlies both
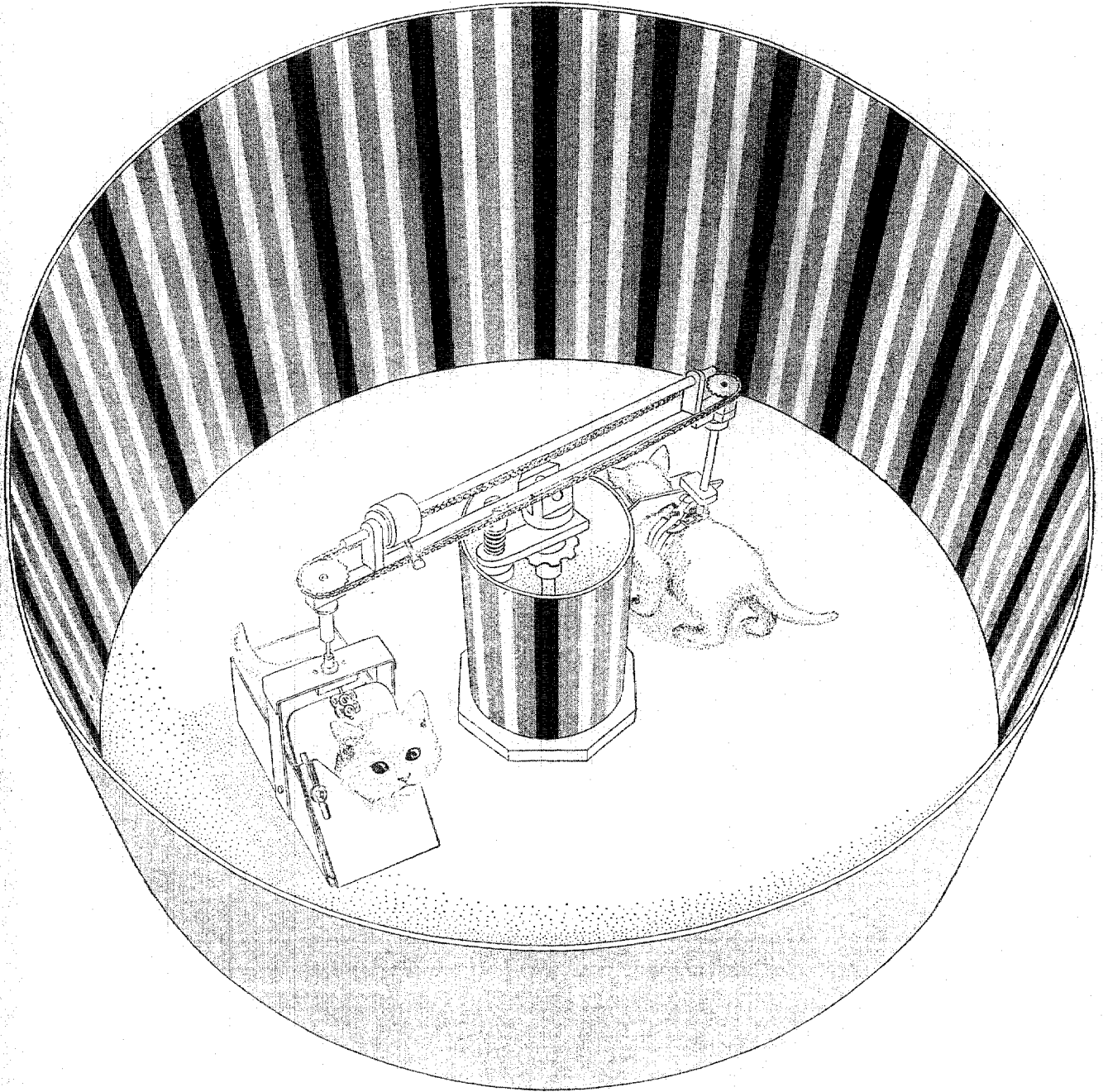

ACTIVE AND PASSIVE MOVEMENTS of kittens were compared in this apparatus. The active kitten walked about more or less freely; its gross movements were transmitted to the passive kitten by the chain and bar. The passive kitten, carried in a gondola, received essentially the same visual stimulation as the active kitten because of the unvarying pattern on the wall and on the center post. Active kittens developed normal sensory-motor coordination; passive kittens failed to do so until after being freed for several days.
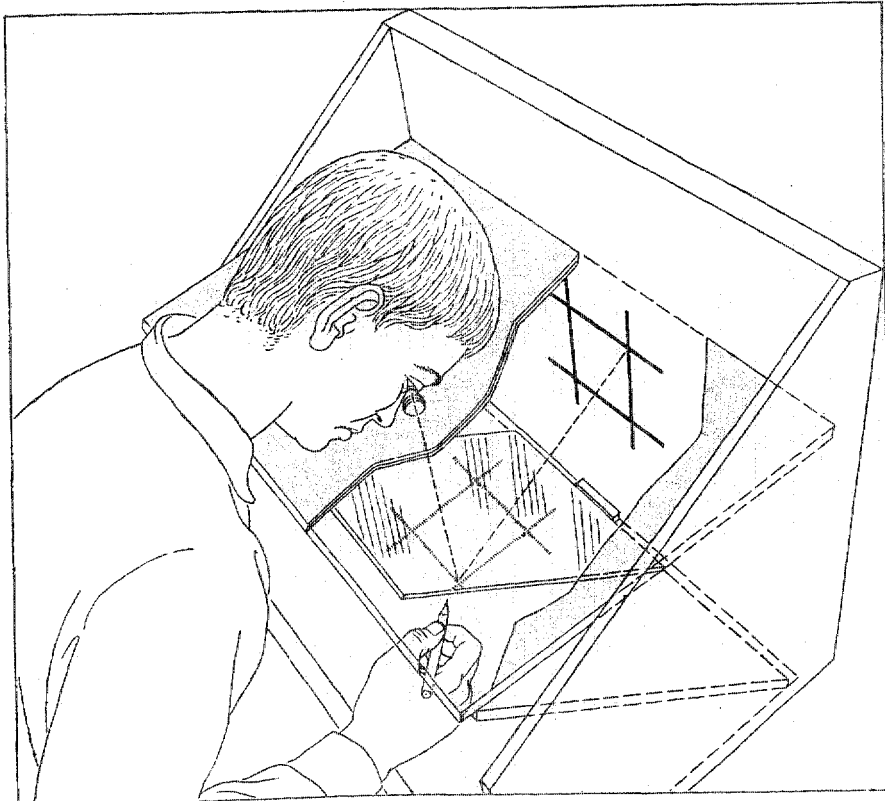
MIRROR APPARATUS tests subject's ability to guide his unseen hand to a visible target. Subject first marks under the mirror the apparent location of the corners of the square as he sees them in the mirror. He then looks through a prism, as depicted in the illustration below, after which he makes more marks. They show his adaptation to the prism effect.
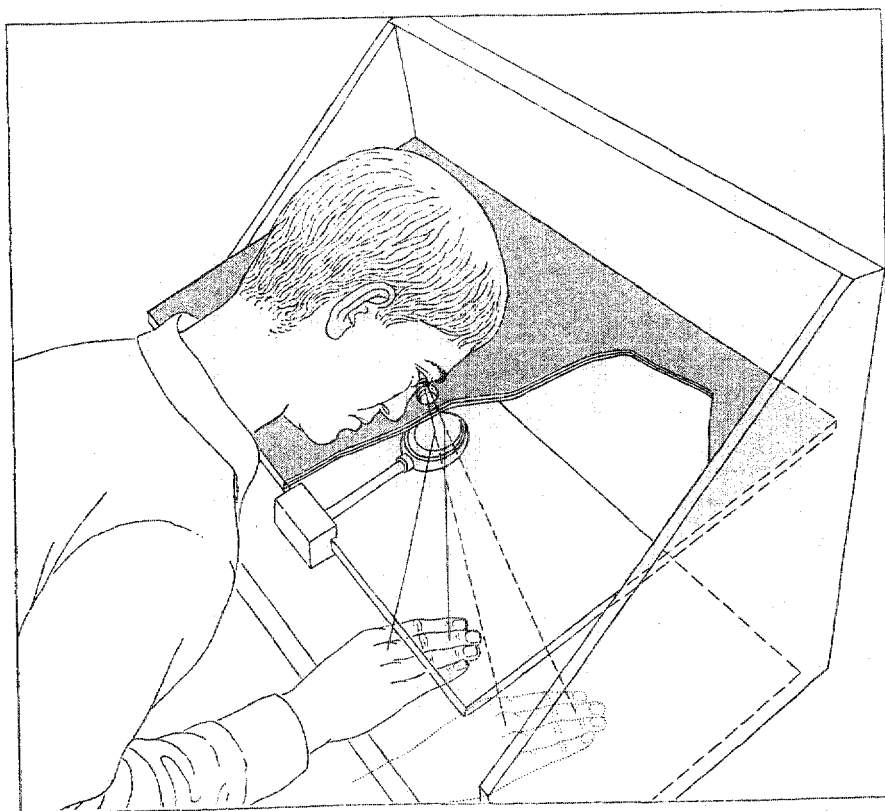
VIEW THROUGH PRISM displaces a visual image. Some subjects looked at their motionless hand, some moved the arm back and forth in a left-right arc, and some had the arm moved passively in a similar arc. They then made marks under the mirror as shown in the illustration at the top of the page. Typical results appear in illustrations on opposite page.

adaptation to rearrangement in the adult and the development of the young. An error-correcting process could hardly explain the original acquisition of coordination. If an infant initially has no sense of the spatial relation between his efforts to move his hand and their visual consequences, he cannot recognize a visible error in reaching. Yet infants do acquire eye-hand coordination in their earliest months. Hence we suspected that error recognition was no more necessary for adaptation in the adult than it was in the development of the infant's coordination. To test this assumption we designed an experiment that prevented the subject from recognizing his error. If he still managed to correct his reach to allow for a displaced image, it would be evident that there was more to the matter of adaptation than the simple fact that the subject could see his error directly.

With this objective in mind we designed the apparatus shown in the top illustration at the left. In this apparatus the subject saw the image of a square target reflected by a mirror and was asked to mark on a piece of paper under the mirror the apparent position of the corners of the square. Because of the mirror, he could see neither the marks nor his hand. After he had marked each point 10 times, withdrawing his hand between markings so that he would have to position it anew each time, the mirror and marking sheet were removed and a prism was substituted. Looking through the prism, the subject then spent several minutes moving his hand in various ways, none of which involved deliberate reaching for a target. Thereafter the original situation was restored and the subject made more marks under the mirror. These marks revealed that each of the subjects was making some correction for the displacement of image that had been caused by the prism.

Having thus established that at least partial adaptation can occur in the absence of direct recognition of error, we used the apparatus to test the role of motor-sensory feedback in adaptation. Our main purpose was to see what degree of adaptation would occur under the respective conditions of active and passive movement—in other words, under conditions of reafference and exafference in which the afference was equivalent. In these experiments the subject's writing arm was strapped to a board pivoted at his elbow to allow left and right movement. He then looked at his hand through a prism under three

conditions: (1) no movement, (2) active movement, in which he moved the arm back and forth himself, and (3) passive movement, in which he kept his arm limp and it was moved back and forth by the experimenter. In each case he marked the apparent location of points under the mirror before and after looking through the prism.

Comparison of these marks showed that a few minutes of active movement produced substantial compensatory shifts [see illustrations at right]. Indeed, many of the subjects showed full adaptation, meaning exact compensation for the displacement caused by the prism, within half an hour. In contrast, the subjects in the condition of passive movement showed no adaptation. Even though the eye received the same information from both active and passive conditions, the evidently crucial connection between motor output and sensory input was lacking in the passive condition. These experiments showed that movement alone, in the absence of the opportunity for recognition of error, does not suffice to produce adaptation; it must be self-produced movement. From the point of view of our approach this kind of movement, with its contingent reafferent stimulation, is the critical factor in compensating for displaced visual images.

What about an adaptive situation involving movements of the entire body rather than just the arm and hand? We explored this situation in two ways, using an apparatus in which the subject judged the direction of a target only in reference to himself and not to other visible objects [see top illustration on next page]. This kind of direction-finding is sometimes called egocentric localization.

The apparatus consisted initially of a drum that could be rotated by the experimenter, after which the subject, sitting in a chair that he could rotate, was asked to position himself so that a target appeared directly in front of him. Later we dispensed with the drum and merely put the subject in a rotatable chair in a small room. After the experimenter had randomly positioned the target, which was a dimly illuminated slit, the subject rotated himself to find the target.

The first of the two ways in which we tested the role of reafferent stimulation involving movement of the whole body was an experiment in adaptation to short-term exposure to prisms. After several trials at locating the target, the subject put on prism goggles. He then,
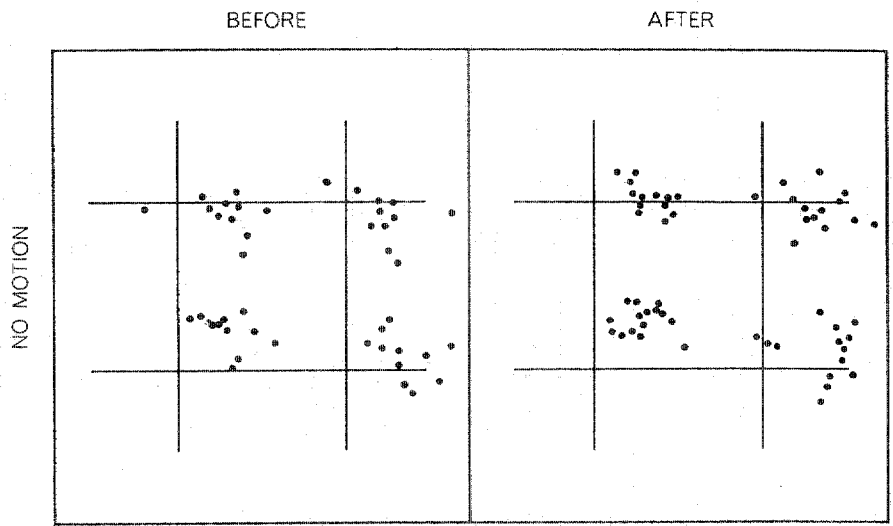

MARKINGS made by a subject before and after looking through a prism as described in illustrations on opposite page are shown. He kept hand still while viewing it through prism.
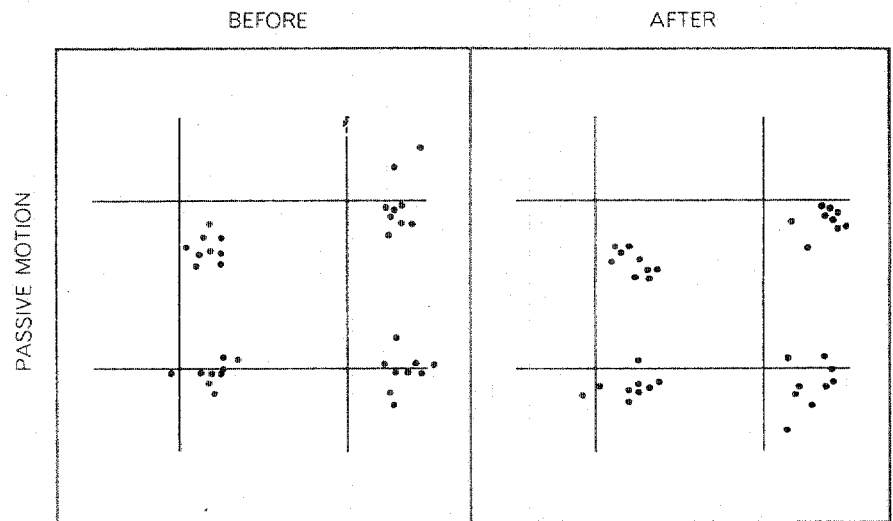

PASSIVE MOVEMENT of subject's hand as he viewed it through prism produced these marks. They show no adaptation to horizontal displacement of images caused by the prism.
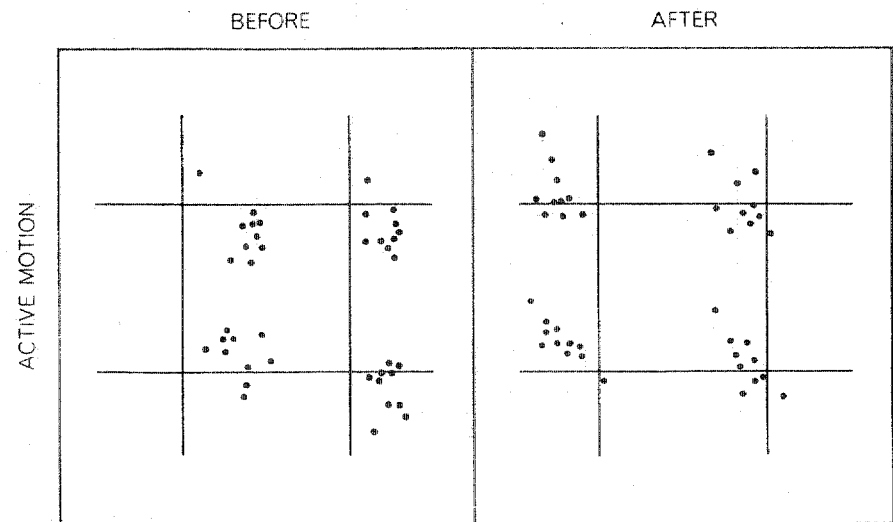
ACTIVE MOVEMENT of subject's hand produced a clear adaptation to displacement of images by prism. Tests showed importance of such movement in sensorimotor coordination.
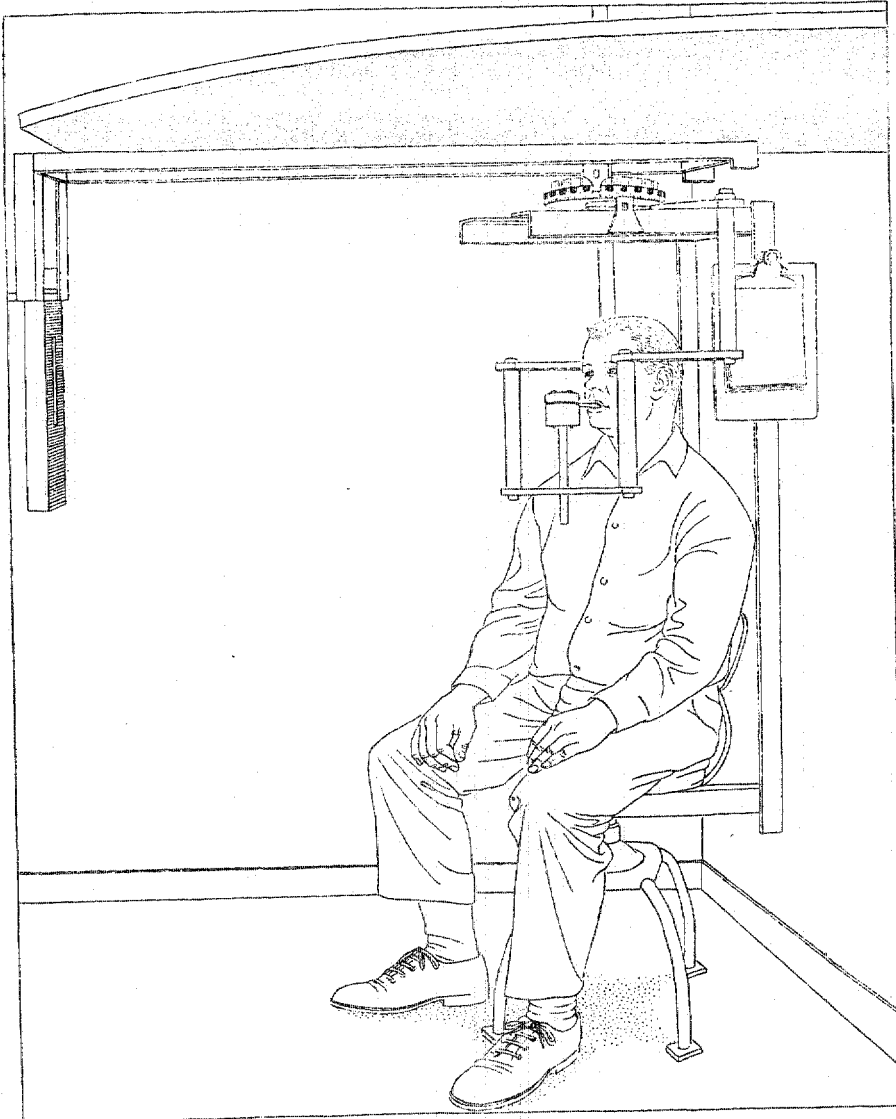
DIRECTION-FINDING by egocentric localization, in which a subject judges the direction of a target only in relation to himself and not to other visual cues, uses this apparatus. Target is randomly positioned at subject's eye level; he then rotates himself so that the target is directly in front of him. He does this before and after wearing prism goggles with which he either walks on an outdoor path or is pushed along the same path in a wheelchair. Change in direction-finding after wearing prisms measures adaptation to the prisms.
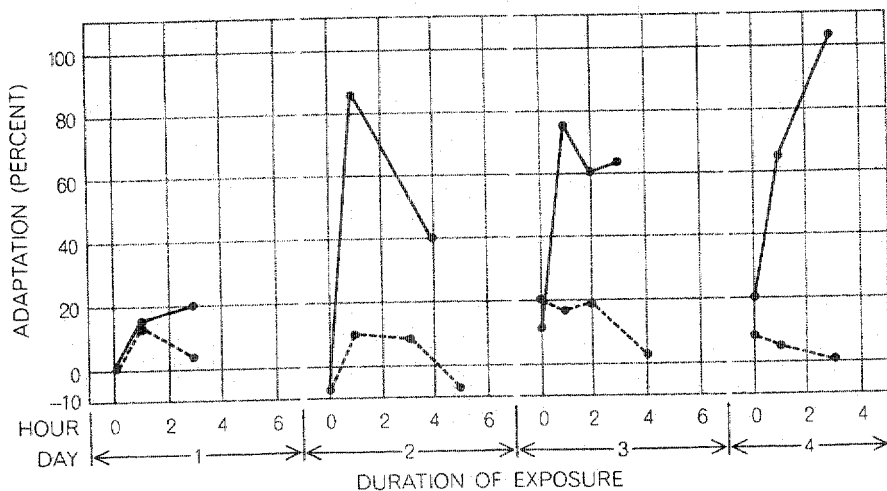
PROLONGED EXPOSURE to prisms produced varying degrees of adaptation to them depending on whether a subject's movement was active (*solid lines*) or passive (*broken lines*).

walked for an hour along an outdoor path or sat in a wheelchair that was pushed along the same path for the same length of time. Thereupon he removed the goggles and went back to the target-finding apparatus for more tests. Any error in target-finding after wearing the prism goggles would be a measure of the adaptation the subject had made to the visual displacements produced by the prisms.

Again the degree of adaptation achieved by the subjects who had been involved in active movement was far greater than that of the subjects who had been carried in the wheelchair. This was true both when one subject had been exposed to the active condition and another to the passive and when a single subject had been exposed successively to each condition. Even more striking contrasts appeared in our second test, which involved wearing prisms for several hours at a time under conditions of active and passive movement. In these circumstances several of the subjects who were able to move voluntarily achieved full adaptation, whereas subjects whose movements were passive achieved virtually no adaptation.

In this connection it will be useful to mention an experiment we conducted on directional hearing. The sound emanating from a localized source reaches the listener's nearer ear a fraction of a second sooner than it reaches his farther ear. This small difference in the time of arrival of the sound at the two ears is the first stage in ascertaining the direction from which the sound comes. If, then, a subject's ears could be in effect displaced around the vertical axis of his head by a small angle, he would err by an equivalent angle in his location of the sound. This effect can be produced artificially by a device called the pseudophone, in which microphones substitute for the external ears. Subjects who have worn a pseudophone for several hours in a normally noisy environment show compensatory shifts in locating sounds, provided that they have been able to move voluntarily. In addition they occasionally report that they hear two sources of sound when only one is present. When measurements are made of the two apparent directions of the source, they differ by approximately the angle at which the ears were displaced around the center of the head during the exposure period. I have called the effect diplophonia.

The reports of doubled localization

following adaptation suggest that compensation for rearrangement consists in the acquisition of a new mode of coordination that is objectively accurate for the condition of rearrangement but that coexists along with the older and more habitual mode. If this is true, the gradual and progressive course of adaptation usually found in experiments must be considered the result of a slow shift by the subject from the older direction of localization to the newer direction.
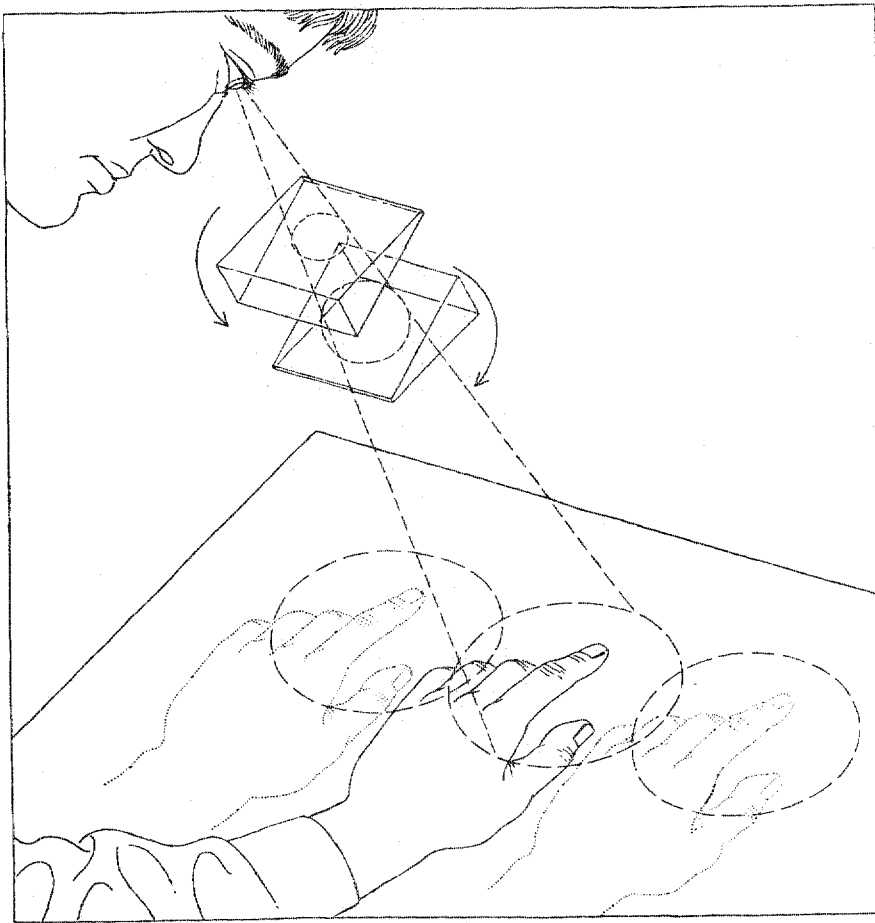
All these experiments strongly suggested the role in adaptation of the close correlation between signals from the motor nervous system, producing active physical movement, and the consequent sensory feedback. This correlation results from the fact that the feedback signals are causally related to movement and that in a stable environ-
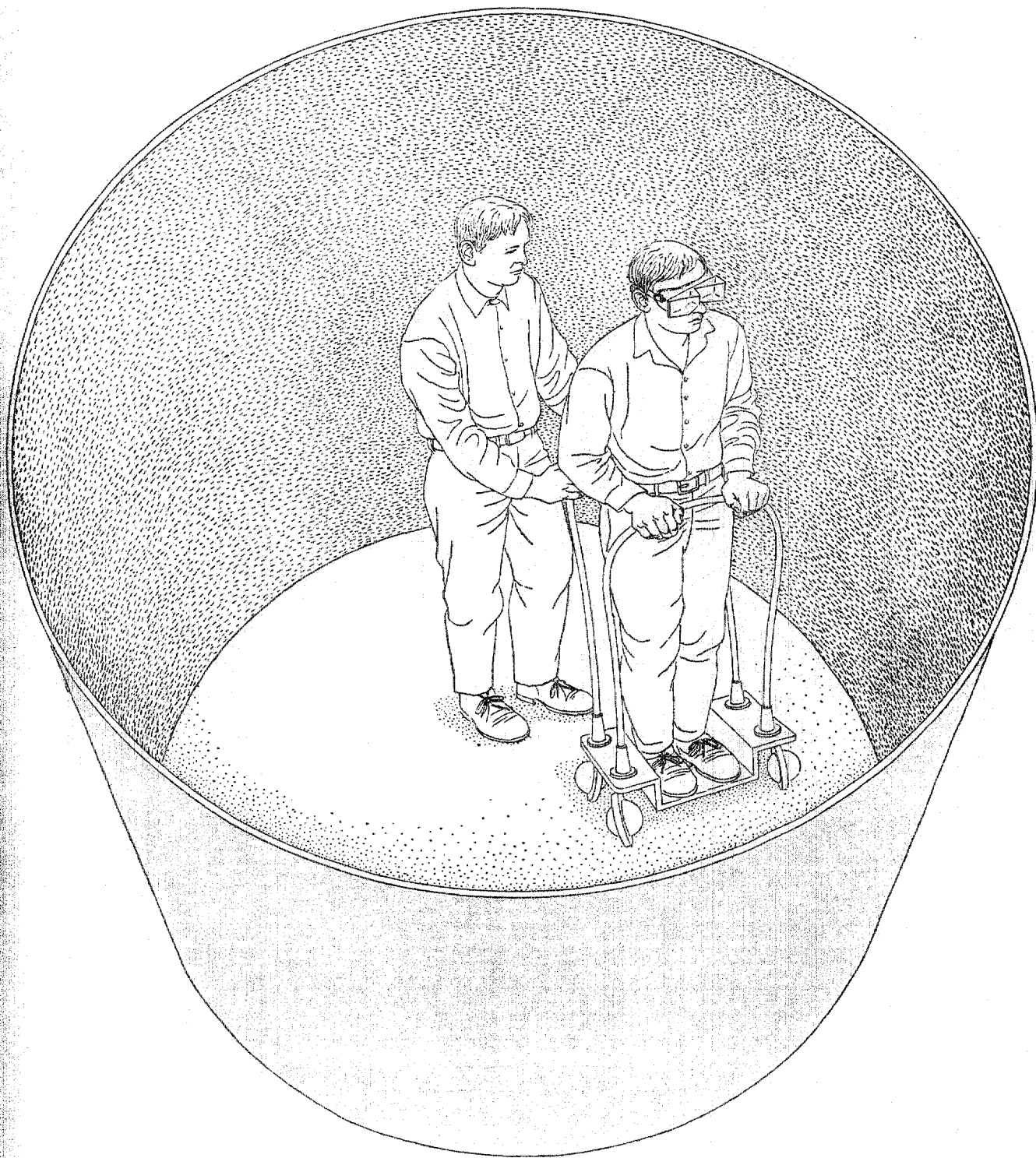
PASSIVE TRANSPORT of a subject wearing prism goggles while viewing a random scene is depicted. Purpose of the apparatus was to test the hypothesis that subjects moving actively through such a scene, which looks the same with or without prisms, would show a degree of adaptation to the prisms whereas subjects moved passively would not. That is what happened. Tests showed a link between visual and motor processes in the central nervous system by altering the correlation between motor outflow and visual feedback.

VERIFICATION EXPERIMENT sought to show role of correlation of sensory feedback and active physical movement by impairing it. Means of decorrelation was the rotating-prism apparatus shown here. It produces apparently continuous movement of subject's hand in one dimension, thus breaking the link between actual movement and visual feedback.

RESULTS OF DECORRELATION are shown in markings made by a subject before and after looking through rotating prism. In one condition (*left*) prisms displaced images vertically; in another (*right*), horizontally. Markings after long exposure are spread out in the direction of displacement, showing a loss of precision in visual-motor coordination.

ment there is a unique feedback signal for any particular movement. The correlation is reduced by environmental instability: the presence either of objects that themselves move or of passive movements of the body that are produced by external forces. Under these conditions more than one feedback signal may accompany any particular movement.

From a theoretical point of view the importance of body movement and particularly of self-produced movement derives from the fact that only an organism that can take account of the output signals to its own musculature is in a position to detect and factor out the decorrelating effects of both moving objects and externally imposed body movement. One way to verify the importance of the correlation would be to set up an experimental situation in which the correlation was impaired or deliberately decorrelated. If the consequence was a loss of coordination, evidence for the role of normally correlated reafference in maintaining normal coordination would be strengthened.

We conducted such an experiment in visual perception by means of an apparatus that provided a prism effect of continually varying power [*see top illustration at left*]. In such an apparatus an object such as the hand seems to move constantly, and the movement perceived is wholly independent of whatever actual motion may be taking place. The same arm movement made at different times will produce different retinal feedbacks. Since the subject does not control the continual changes in his visual input that are produced by the prism, his nervous system has no means of distinguishing these changes in the input from those that are self-initiated.

With this apparatus we conducted various experiments, again including active and passive arm movements of the type described previously. We found that the coordination between eye and hand was significantly degraded under conditions of active movement but not under conditions of passive movement. Similar results appeared in tests made by Sanford Freedman of Tufts University of the effect of decorrelation on hearing. Again the performance of subjects who were allowed to move actively during decorrelation deteriorated badly, whereas the performance of subjects whose bodily movements were restricted did not deteriorate. Both the visual and the auditory experiments confirmed the importance of the correlation between

movement and sensory feedback in maintaining accurate coordination.

In another test of our hypothesis about reafference we undertook to see what would happen when subjects looked through prisms at a random scene, lacking in the lines and curves that provide normal visual cues. The straight lines characteristic of normal scenes look curved when viewed through a prism. When the prism is removed, such lines seem to curve in the opposite direction. What if straight lines looked curved after a subject had removed prism goggles through which he had viewed a random scene?

Our hypothesis was that such an effect would be produced in subjects who moved actively while viewing the random field but not in those whose movements were passive. If such a result occurred, we would have shown that the subjective geometry of the visual field can be altered by reafference. This finding would have the surprising implication that a motor factor is involved in a process traditionally regarded as purely visual. We would have demonstrated in another way the close, one-to-one correlation between movement and visual feedback and would have further evidence of a link between motor and visual mechanisms in the central nervous system.

Our apparatus for testing this hypothesis consisted of a large drum that had on its inside surface an irregular array of small spots [see illustration on page 91]. These spots looked the same whether viewed with a prism or not. Each subject, before putting on prism goggles and entering the drum, was tested for his perception of a vertical line; we did this by having him indicate when a grating of bars given varying curvatures by prisms appeared straight. Thereafter, entering the drum with the goggles on, the subject either walked around in the drum or was transported on a cart. He stayed in the drum for half an hour and then, after removing the goggles, again took the test with the grating of bars. Without exception the active subjects perceived curvature when looking at lines that were actually straight, whereas the passive subjects perceived little or none.

Having established by these various means the role of reafference in adaptation to changed sensory inputs, we decided to examine its role in the development of visually controlled coordination in the newborn. The contribution of experience to the development

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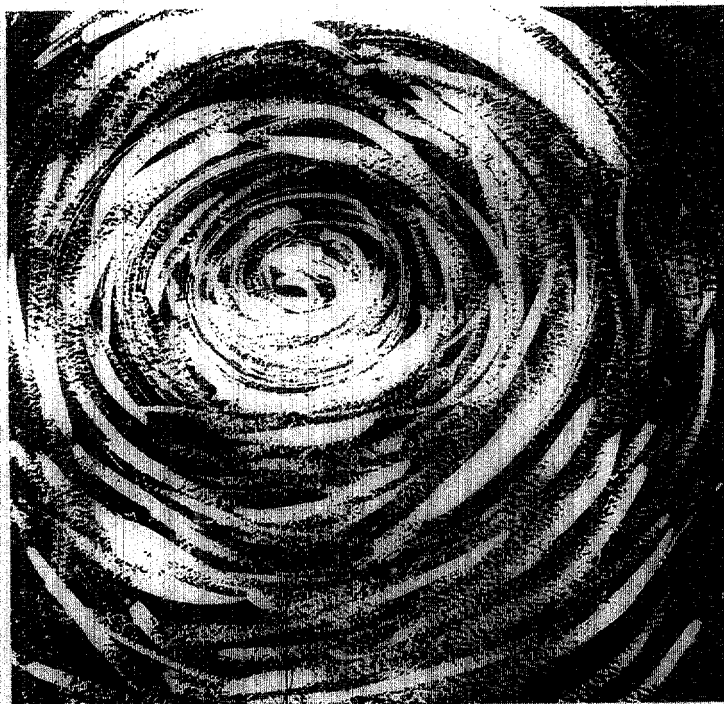
This is the second in a series of ads featuring art by students in the Los Alamos School System. This painting is by Carolyn B. Wilder, who was a senior at Los Alamos High School when it was painted.

of perceived space and of spatially oriented behavior has been debated for some centuries. During the past few decades a number of experimental approaches to the issue have been made. The technique most often used involves depriving very young animals of sensory contact with the environment. It has been hoped that the procedure would decide whether or not sensory experience, as opposed to maturation alone in the absence of such experience, is required for the development of spatial discrimination.

In certain species of higher mammals, including man, various forms of visual deprivation ranging from total absence of light to mere absence of gross movement in a normally illuminated environment have all resulted in deficiencies in visually guided behavior. Unfortunately these deficiencies are not easily interpreted. They can be attributed, at least in part, to several alternative causes, including pathological changes in the anatomy of the retina and its projections to the brain. Since our findings implicated movement-produced stimulation, they enabled us to test this factor without depriving animals of normal visual stimulation.

The experiments my colleague Alan Hein and I have performed to study the earliest development of vision originated from observations made by Austin H. Riesen of the University of California at Riverside and his collaborators. Riesen's research demonstrated that kittens restrained from walking from the time of their earliest exposure to light develop marked deficiencies in the visual control of behavior compared with unrestrained animals reared normally. The deficiencies of Riesen's animals may have resulted either from the lack of variation in visual stimulation, which was the explanation he preferred, or from the lack of visual stimulation correlated with movement, which was our own hypothesis.

To decide between these alternatives we devised an apparatus in which the gross movements of a kitten moving more or less normally were transmitted to a second kitten that was carried in a gondola [see illustration on page 85]. These gross movements included turns to left and right, circular progress around the center post of the apparatus and any up-and-down motions made by the first kitten. The second kitten was allowed to move its head, since prior experimenters had reported that head movement alone was not sufficient to

produce normal behavior in kittens, and it could also move its legs inside the gondola. Both kittens received essentially the same visual stimulation because the pattern on the walls and the center post of the apparatus was unvarying.

Eight pairs of kittens were reared in darkness until the active member of each pair had enough strength and coordination to move the other kitten in the apparatus; the ages at which that state was attained ranged from eight to 12 weeks. Two other pairs were exposed to patterned light for three hours a day between the ages of two and 10 weeks; during exposure they were in a holder that prevented locomotion. Thereafter all 10 pairs spent three hours a day in the apparatus under the experimental condition; when they were not in the apparatus, they were kept with their mothers and littermates in unlighted cages.

After an average of about 30 hours in the apparatus the active member of each pair showed normal behavior in several visually guided tasks. It blinked at an approaching object; it put out its forepaws as if to ward off collision when gently carried downward toward a surface, and it avoided the deep side of a visual cliff—an apparatus in which two depths, one shallow and the other a sharp drop, appear beneath a sheet of glass [see "The 'Visual Cliff,'" by Eleanor J. Gibson and Richard D. Walk; SCIENTIFIC AMERICAN, April, 1960]. After the same period of exposure each of the passive kittens failed to show these types of behavior. The passive kittens did, however, develop such types of behavior within days after they were allowed to run about in a normal environment.

In sum, the experiments I have described have led us to conclude that the correlation entailed in the sensory feedback accompanying movement—reafference—plays a vital role in perceptual adaptation. It helps the newborn to develop motor coordination; it figures in the adjustment to the changed relation between afferent and efferent signals resulting from growth; it operates in the maintenance of normal coordination, and it is of major importance in coping with altered visual and auditory inputs. The importance of the correlation in all these functions has been revealed by experiments that tamper with its normal operation. In the process these experiments have uncovered a fundamental role of the motor-sensory feedback loop.