

Motor-Sensory Feedback and the Geometry of Visual Space

Abstract. Normal surroundings appear curved when viewed through wedge prism eyeglasses. But prolonged viewing of uniformly curved lines makes them appear less curved. An environment specially patterned to prevent the appearance of curvature when viewed through a prism made possible the demonstration of change in apparent curvature wholly dependent upon the visual feedback accompanying self-produced movement of the prism-wearer.

A wedge prism placed in front of the eye results in a number of alterations of the visual field including the apparent curvature of what would appear as straight lines to the uncovered eye. Many investigators, following Wundt (1), have reported adaptation in the form of diminished curvature during prolonged wearing of the prisms. Upon removal of the prisms, they noted a transient aftereffect that makes objectively straight lines appear to be curved in the opposite direction. Gibson's report, that merely staring at objectively curved lines with the naked eye makes them appear to straighten out (2), made it plausible to attribute the prism-wearer's adaptation solely to his prolonged viewing of the optically-induced curvature of contours in his field of vision. However, new evidence suggests that exposure to an atypically patterned field, such as a set of curved lines, is not necessary for producing these effects (3).

Self-produced movement of the head and body with the accompanying feedback of visual stimulation is required for full and exact compensation for the errors of localization induced by several forms of optical rearrangement (4). These findings suggest that adaptation to any of the optical changes induced by a prism may be generated solely as a result of exposure to the transformed relation between active movement and its dependent sensory feedback. The apparent curvature of straight lines after the wearing and removal of a wedge prism might then be produced even though the environment viewed through the prism did not contain a configuration which was discriminably curved by the prism. Since this curvature aftereffect would represent an

alteration of the spatial relationship among points within the visual field, its demonstration would constitute proof that the subjective geometry of the visual field can be altered by movement-dependent feedback. A link between motor and visual mechanisms in the nervous system would be revealed: one that could not readily be interpreted as a mere shifting of orienting or localizing responses in the absence of any change in visual space (5).

In previous studies of adaptation to curvature, subjects have worn wedge-prism goggles in typical environments, such as urban streets, that provide many continuous and well-defined contours. Under this exposure condition, Gibson's aftereffect, which follows mere scanning of the curved lines that are produced by the prism transform, is confounded with the hypothesized movement-determined aftereffect. To prevent this confusion, the visual field of the prism-covered eye must have no more and no less curvature than it would if the eye were uncovered. This effect was produced in the present experiment by an environment consisting of an array of small spots of irregular shape and distribution which encompassed the subject's normal field of view. If the positional relations among the images of these spots on the retina at any instant are assumed random, then they will remain random even when changed by the differential displacements produced by the prism. This assumption was borne out by the finding that no curvature aftereffect is produced after the prism-wearer has scanned this sort of field solely by eye movements (3). On the other hand, since the spots are fixed in position in space (their motion is not random), the relative rates of displacement (velocities) of their images on the retina are systematically changed by the placement of a prism in front of the eye of a moving observer. This information is always available to the moving prism-wearer but should, according to our hypothesis, produce a curvature aftereffect only after self-produced movement. Before and after viewing this surround through the prism under conditions to be described, the subject's perception of the straightness of a vertical line was tested by having him vary optically the curvature of a grating of bars until they appeared straight.

In the testing procedure, curvature was varied and measured by a rotary prism consisting of two wedge prisms of 20 prism diopter (pd) power mounted in tandem so that they could be rotated at equal speeds but in opposite directions. The powers of this variable prism ranged from 40-pd base left to 40-pd base right. Through it the subject viewed with his right eye (left eye occluded) a grating of straight vertical bars transilluminated by diffused fluorescent light. Increased base right power made the bars appear more convex to the right; increased base left power, more convex to the left. The target was viewed through a narrow band filter (Kodak Wratten No. 61) which transmitted wavelengths in the green region of the spectrum, thereby eliminating the color fringes caused by dispersion through the prism. Ten adjustments were made by the subject both before and after exposure. The starting settings of the measuring prism were randomly distributed throughout the range of 10 to 20 pd and of the same base orientation as that of the prism worn by the subject during exposure. The subject was instructed to rotate the prism until the bars appeared perfectly straight. The difference between the means of the pre- and postexposure adjustments measured the effects of exposure.

During exposure each subject (college students) wore a goggle which occluded his left eye and which placed in front of his right eye a 20 pd prism, either base right or base left, giving him a field approximately 70° in extent. He was placed inside a drum 1.83 m (6 ft) in diameter and 1.83 m (6 ft) high, with its axis vertical and its lower edge 0.76 m (2.5 ft) above the floor. The inside surface of the drum was covered with the irregular pattern mentioned above and illuminated by ordinary room lighting. The subject was instructed not to view any part of his body and to keep his hands at his sides. His visual field then contained only spots whose greatest diameter did not exceed a fraction of an inch. These spots appeared to have the same patterning when viewed with or without the prism.

We soon discovered that movements of the head alone, if of sufficient amplitude and duration, sufficed to produce an adaptive change in the settings of the measuring prism (6). However, our purpose was to demon-

strate the role of information available only through the mediation of the motor-sensory feedback loop. Previous experiments have achieved this end by showing that greater compensation is achieved after self-produced movement than after equivalent passive movement, with sensory input equated under both conditions (4). But the head is not easily subjected to passive movement because of the difficulty of relaxing the neck musculature. Consequently, we chose to compare the effects of locomotion with equivalent passive transport of the body.

Each of eight subjects was exposed under two conditions of movement. During the "active" condition the subject walked inside the drum for one-half hour while viewing its surface. During the "passive" condition he viewed the surface while being wheeled around a similar path, for the same duration, standing on a specially designed cart. Each subject was run under each of the two conditions with both base right and base left prisms, making four runs per subject. All subjects were instructed to minimize movements of their heads in relation to their bodies and periodic inspections by the experimenter checked on this factor. The sequence of conditions was randomized among the eight subjects. Comparison of the aftereffects following the two conditions provided a test of our hypothesis that the transformed rates of displacement of parts of the retinal image will produce the aftereffect only after self-produced movement. In addition, the absence of an aftereffect following passive motion would confirm the assumption that the exposure field was not patterned in a manner that could generate the curvature aftereffect on mere scanning. As a further check, three additional subjects were run under both conditions without prisms. With the measuring procedure described above, theoretical full compensation for the curvature induced by a 20 pd prism should result in a difference between pre- and postexposure means of 20 pd of the same base orientation as the prism. This difference would indicate that what is then seen as a straight line is objectively a line either convex to the right or convex to the left, the curvature induced by the prism during exposure.

The aftereffects for the eight subjects exposed under the active condi-

tion with base right prism averaged 3.3 (range from 2.0 to 4.9) pd base right; with base left prism, 3.4 (range from 2.2 to 6.5) pd base left. They were compensatory without exception. When released from the measuring apparatus, after this condition, most of these subjects immediately noticed an apparent curvature when fixating points on straight vertical contours in their normal surroundings. After the passive condition with base right prism the mean aftereffect was 0.1 pd base left (range from 0.8 pd base right to 0.9 pd base left); with base left prism, 0.0 (range from 0.7 pd base right to 0.9 pd base left). None of the three subjects run without prisms showed a significant aftereffect under either active or passive conditions.

These results show that the presence of curved patterning in the visual field is not a necessary condition for generating the curvature aftereffect. Visual space can be warped solely as a result of transforming the relation between self-produced movement and its concurrent sensory feedback. Patterns of change in retinal stimulation are normally correlated with the movements that produce them. A prism placed in front of the eye will change the terms of the correlation but not the order entailed in it. Consequently, with exposure to the transformed condition, the central nervous system becomes in-

formed of the new correlation which is a prerequisite for adaptation. This demonstration is consistent with our contention that the plasticity underlying adaptation to rearrangement is not attributable to changes in either response systems alone or in sensory processes alone but rather to a complex interaction between the two (4). The importance of this plastic process for the maintenance of stable visuospatial behavior and its development are discussed elsewhere (7; 8).

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References and Notes

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Dialysis Studies in Rats on the Long-Acting Antimalarial CI-501

Abstract. *Through the use of dialysis sacks, containing the repository anti-malarial CI-501, implanted intraperitoneally into rats, evidence has been obtained indicating a local rather than a systemic reservoir of the drug. These results suggest that the repository activity of CI-501 is due to drug release from the injection site and that the probability of toxic effects resulting from storage or accumulation of the drug in vital organs is remote.*

A pamoic acid salt of 4,6-diamino-1-(*p*-chlorophenyl)-1,2-dihydro-2,2-dimethyl-*s*-triazine, CI-501, is a long-acting, parenteral, antimalarial drug in mice (1), monkeys (1, 2), and man (3). This drug also shows repository action in rats: a single subcutaneous dose (100 mg/kg) gave protection for 10 to 11 weeks (4). The salt, sparingly soluble in water (0.003 percent), is slowly released from the subcutaneous or intramuscular injection sites in quantities sufficient for both protective and therapeutic activity (1).

The purpose of this study was to determine whether CI-501 might be stored elsewhere after release from the injection site and then released from this second site in sufficient amount for activity against the malaria parasite.

We suspected that this point could be clarified by injecting the drug and then removing it before challenge with parasites. Surgical excision of the drug mass (5) was considered, but dismissed in favor of intraperitoneal implantation of the drug in dialysis sacks, followed by removal prior to challenge. An