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SENSORY ADAPTATION AND BEHAVIORAL COMPENSATION WITH SPATIALLY TRANSFORMED VISION AND HEARING

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An analysis of spatial transformations of perceived space is made in terms of angular and parallel modifications of the median, horizontal, and frontal planes of O, and the perceptual and behavioral outcomes of such transformations examined. It is argued that there are 2 independent outcomes: behavioral compensation and sensory spatial adaptation with aftereffect. The 1st can be regarded as a special case of motor learning similar to that studied in early investigations with frontal plane transformation (mirror tracing), and the 2nd is essentially similar to spatial adaptation which may occur with appropriate nontransformed stimulation. Both effects can occur simultaneously in the same direction, but the experimental data presented show that they can be studied independently. The effects observed by Ivo Kohler are treated as special instances of sensory adaptation which occur with transformations dependent upon sense-organ position and movement. The felt-position hypothesis and the reafference theory proposed by Held are shown to be reinterpretable in terms of motor learning and transfer of learning. Various methodological issues in the investigation of motor learning and sensory adaptation are examined.

If before entering the eye light is spatially transformed by means of an optical system (prism, lens, mirror), visually guided behavior (reading, walking, card sorting) which is initially disrupted exhibits a progressive return to pretransformation normality. In addition, under certain spatial transformation conditions, visual appearances (shape, size, direction) are also reported to undergo change and to exhibit a tendency to return to pretransformation appearances. Analogous changes also occur when hearing is spatially transformed by means of "pseudophonic" systems. Since Czermak (1855), Helmholtz (1866), and Wundt (1898) drew attention to these effects a variety of explanations have been proposed in terms of perception (Kohler, 1964; J. G. Taylor, 1962), motor learning (Smith & Smith, 1962), reafference (Held & Freedman, 1963), and "felt position" (Harris, 1965). In addition to clarifying the nature of spatial transformations, the purpose of this paper is to show that there are two independent outcomes, sensory spatial adaptations and behavioral compensation, which under some conditions may occur together in the same direction. The first is a purely sensory effect identical to that which occurs without transformation (Gibson, 1933, 1937; Köhler & Wallach, 1944), and the second is a special case of motor learning identical to that investigated in the early mirror-tracing studies (Starch, 1910). The recent interpretation of the second effect in terms of felt position merely deals with learning from a phenomenological viewpoint. It is argued that failure to recognize the simultaneous occurrence of these independent outcomes of transformed vision and hearing has resulted in inappropriate procedures and a tendency to treat both as specific characteristics of transformed conditions rather than as instances of effects which occur under a variety of conditions without transformation.

NATURE OF SPATIAL TRANSFORMATIONS

Despite considerable recent research there has so far been no attempt to describe or to classify the classes, directions, extents, and complexities of transformations. This omission not only makes comparisons of studies difficult, but also obscures relationships between early experiments concerned with motor learning and more recent investigations whose data have been differently interpreted.

Perceived space can be usefully described in terms of three hypothetical planes: the median (sagittal), horizontal, and frontal (or coronal) planes, which for present purposes can be conceived as intersecting at right angles at the center of the head. When the observer is vertical, the median (straight ahead) and frontal (right-left) planes are vertical and the horizontal plane is parallel with the ground plane. Spatial transformations which may vary in class, direction, extent, and complexity can be described in terms of these three planes and those parallel to them, the median, horizontal, and fronto-parallel planes.

Classes of Transformation

There are two classes of spatial transformation, which will be termed angular and parallel. Angular transformation occurs when the optical or pseudophonic system rotates the plane or planes about their transverse or longitudinal axes. A wedge prism with base vertical rotates the median plane right or left about its transverse (i.e., vertical) axis so that objects normally straight ahead now appear laterally displaced. A double Dove-prism system rotates both the median and horizontal planes together about their longitudinal (i.e., horizontal) axes so that normally vertical and horizontal contours appear slanted (see Figure 1). A pseudophone with microphones lying anterior to one ear and posterior to the other serves to rotate the median plane about its transverse axis, and microphone placement above one ear and below the other results in transformation of the same plane about its longitudinal axis. A mirror before the eyes rotates the frontal plane through 180° and the degree of rotation can be varied by slanting the mirror.

Parallel transformations occur when one or more of the three planes are displaced in a linear fashion without rotation about either axis.[1] Thus Weinstein, Sersen, and Weinstein (1964) used a mirror system arranged so that objects at a certain distance appeared to be farther away. Although parallel transformations of auditory space have not been reported so far, they are entirely feasible. Two microphones the same distance apart as the ears but mounted above the head so that both are to the same side of each ear would presumably achieve a parallel transformation of the median plane. Placing both an equal distance above or behind each ear would produce a parallel transformation of the auditory horizontal and frontal planes, respectively.

Direction and Extent of Transformation

Angular transformation can vary between 0° and 360° in either direction about both axes, and parallel transformations can vary to the limits of visual or auditory acuity. The mirror systems used by Kohler (1964) transformed either the median or horizontal plane through 180° so that objects normally right appeared left and those originally above appeared below. Ewert (1930), Snyder and Pronko (1952), and Stratton (1896, 1897) introduced double-convex lens systems so that both median and horizontal planes were simultaneously transformed through 180° about their longitudinal axes. A mirror directly before the eyes transforms the frontal plane through 180° longitudinally so that objects in back appear in front (but objects in front are obscured by the mirror). Stratton (1899) used two mirrors to transform angularly the frontal plane through 90°. In most recent studies, the transformations have been relatively small (10–20°) and most usually of the median plane. The systems used by Young (1928) and Willey, Inglis, and Pearce (1937) transformed the auditory median plane through 180° about its transverse axis, and, more recently, smaller angular transformations of the same plane have been induced (Freedman & Zacks, 1964; Held, 1955).

Complexity of Transformations

The simplest transformation is small in extent involving a single plane. Complexity

[1] Magnifying and minifying lenses serve to increase and decrease respectively the magnitude of retinal projections thus changing apparent size and distance. In this manner (as when viewing through the eyepiece or mouth of a telescope) parallel transformations of fronto-parallel planes are achieved.

of transformation can vary as a function of class combinations (angular and parallel), number of planes simultaneously transformed, and extents. Probably the most complex transformation investigated so far is that used by Snyder and Pronko (1952) involving 180° angular changes in the median, horizontal, and frontal planes. This was achieved by means of a double-convex lens system and a mirror.

Area of Spatially Transformed Field

In vision, the angle subtended by the transformed field may vary from the total visible field to a small part of it. Prisms worn close to the eyes in spectacle frames transform the total field, whereas a prism set in a screen and viewed from a distance alters only that part of the field bounded by the prism. On viewing into a large mirror the total field is transformed with respect to the frontal plane, but a small mirror held in the hand transforms only that area bounded by the mirror.

In hearing, as in vision, spatial transformations may vary in class, direction, extent, and complexity by suitable positioning of microphones or other devices. Because of the temporal basis of auditory localization, however, the total field is always transformed.

Representative Studies

Helmholtz (1866), using prisms worn before the eyes, angularly transformed the median plane and observed progressive reduction in reaching errors and the occurrence of errors in the opposite direction when the prisms were removed. Wundt (1898), with similar transformation, commented on changes in the apparent direction of objects during and after the transformation period. Wundt observed that whereas objects initially appeared angularly displaced, this effect progressively diminished. In probably the best known of all spatial transformation studies, Stratton (1896, 1897), rotated the median and horizontal planes together through 180° about their longitudinal axes and noted progressive improvement in initially disrupted locomotor and manipulative behavior. The purely perceptual features of this long-term transformation have remained controversial although later experiments (Snyder & Pronko, 1952) have suggested that there were no marked perceptual changes. Later, Gibson (1933) used wedge prisms to give a double median plane transformation about the transverse axis so that straight edges were curved, and he observed that this perceived curvature progressively diminished. On removal of the prisms, straight edges appeared curved in the opposite direction. In later experiments, Gibson dispensed with prisms and established that an inspected field of curved lines results in the same effects as those of prismatic curvature. Subsequent experiments (Gibson & Radner, 1937) showed that essentially similar effects occur with slanted lines, thus confirming an earlier finding by Verhoeff (1902).

Independent of but parallel with these visual transformation investigations were a series of studies of motor learning which used 180° transformations of the frontal plane to produce a novel learning task. Beginning with Starch (1910), the typical "mirror-drawing" or "mirror-tracing" apparatus prevented a direct view of the hand which was viewed in a mirror so that only part of a fronto-parallel plane was rotated through 180°. The observer's task was that of drawing, writing, or tracing a pattern while viewing the hand in the mirror. The task was further developed and used by Siipola (1935) with the mirror arranged so that the median and horizontal planes were also transformed. As in the other studies reviewed, over a number of trials there was a gradual improvement in accuracy.

It can also be noted that while in most experiments it has been found that errors in reaching, pointing, and marking occur in the opposite direction after the transformation period (Held & Hein, 1958; Held & Schlank, 1959), they have also been observed to occur in the same direction as the transformation (Weinstein, Sersen, & Weinstein, 1964). This effect is discussed below.

In summary, investigations of the effects of spatial transformation have variously emphasized the behavioral or perceptual outcomes. While Gibson (1933, 1937) was wholly concerned with visual perceptual phenomena, Starch (1910) and Siipola (1935) were solely interested in changes in motor behavior. Stratton (1896, 1897) reported both perceptual and motor changes as did Kohler (1964).

Visual and Auditory Adaptation

The perceptual outcomes of spatially transformed vision can for the most part be reproduced using appropriate stimulus conditions without transformation. After Gibson (1933) demonstrated apparent diminution of prism-induced curvature with subsequent opposite curvature when the prism was removed, he showed that inspection of curved and then straight lines resulted in the same effects. The prisms induce a double transformation about the longitudinal axis of the median plane so that the retinal projections of straight lines lying in a fronto-parallel plane are curved. A normally viewed curved line of course results in a similar retinal projection. Wundt (1898), however, observed that with the median plane transformed about its transverse axis by means of prisms there was a progressive diminution of the apparent deviation of objects from the straight-ahead. If a field of lines lying in the horizontal plane and parallel to the median plane is viewed through a wedge prism, they appear slanted to one side. With prolonged viewing through the prism the lines appear progressively more straight-ahead. This observation made by one of the authors is essentially that made by Wundt (1898). It has also been observed that a field of lines slanted away from the median plane and lying in the horizontal plane appear progressively more straight-ahead with prolonged normal viewing.

Essentially similar effects to those demonstrated by Gibson (1933) and Wundt (1898) occur with angular transformations of the frontal plane. Wertheimer (1912) used a large slanted mirror so that when an observer stood before it the floors and walls of a room appeared slanted. This apparent slant diminished with prolonged viewing in the mirror. Although Gibson (1952) has disputed this finding, he (Gibson & Bergman, 1959) observed an essentially similar effect with a normally viewed tilted surface. Following inspection of a textured surface a subsequently presented vertical surface appeared slanted in the opposite direction (Gibson & Bergman, 1959).

Köhler and Wallach (1944) showed that following fixation of a figure, the apparent size of a slightly larger figure increased compared with its apparent size prior to fixation. Similarly, the apparent size of a slightly smaller figure was decreased. It would be expected, therefore, that if the retinal projection of an object were reduced in size by means of a minifying optical system, subsequently viewed objects would appear larger. Rock (1965), using a convex mirror to minify retinal projections, has demonstrated that such changes in judged size occur.

In general terms, visual perceptual changes occur with spatially transformed space. If the same stimulus conditions are reproduced without transformation (e.g., actually curved lines as opposed to prismatically curved retinal projections), essentially similar changes occur.

Although spatial adaptation and aftereffect have been observed to occur in hearing (Bartlett & Mark, 1922; Flugel, 1921; Krauskopf, 1954; M. M. Taylor, 1962) with a sound source to one side of the median plane, the same effects have not been reported with spatially transformed hearing. There is no reason to suppose, however, that similar effects would not occur if the same conditions were produced by a pseudophonic device. The experiments with spatially transformed hearing reported by Held (1955) and Freedman and Zacks (1964) were concerned with behavioral changes.

Behavioral Compensation

If a wedge prism transforms the median plane 20° right about its transverse axis, the observer reaching for an object quickly will at first move too far to the right. After several attempts, however, accuracy is achieved; and when, without visual guidance, the observer points straight-ahead, his direction of pointing will be to the left of his pretransformation straight-ahead. The leftward compensation for rightward angular transformation persists. Similar effects can be easily demonstrated with a variety of directions, extents, and complexities of transformation. The essential feature of these effects is a change in the direction of responses such as pointing, reaching, marking, walking, or card sorting during the transformation period such that compensation is made for the effects of transformation. The posttransformation responses in the absence of visual or auditory guidance tend to be in the same direction as those developed during the transformation period.

Independent Occurrence of the Two Effects

Gibson and Radner (1937) showed that adaptation to slanted lines achieved a maximum when the field of lines was slanted at 15–20° and was negligible at 45°, a finding which has been confirmed by Logan (1962) and by Morant and Beller (1965) for prismatically slanted lines. In a recent unpublished experiment by the present authors, a physically horizontal line was viewed through a double Dove-prism system (Figure 1) so that the median and horizontal planes were angularly transformed about their horizontal axes. In one condition, the prisms were arranged so that the retinal projection of the line was slanted 20°; and in the other condition, at 45°. The mean aftereffect (difference between pre- and posttransformation adjustments to horizontality with normal viewing) for two groups of 10 observers each was 1.57° ($p < .01$) for the 20° slant and .16° ($p > .05$) for 45°. The transformation period was 3 minutes. Thus the visual adaptation effect is negligible at 45° transformation and significant for the smaller slant.

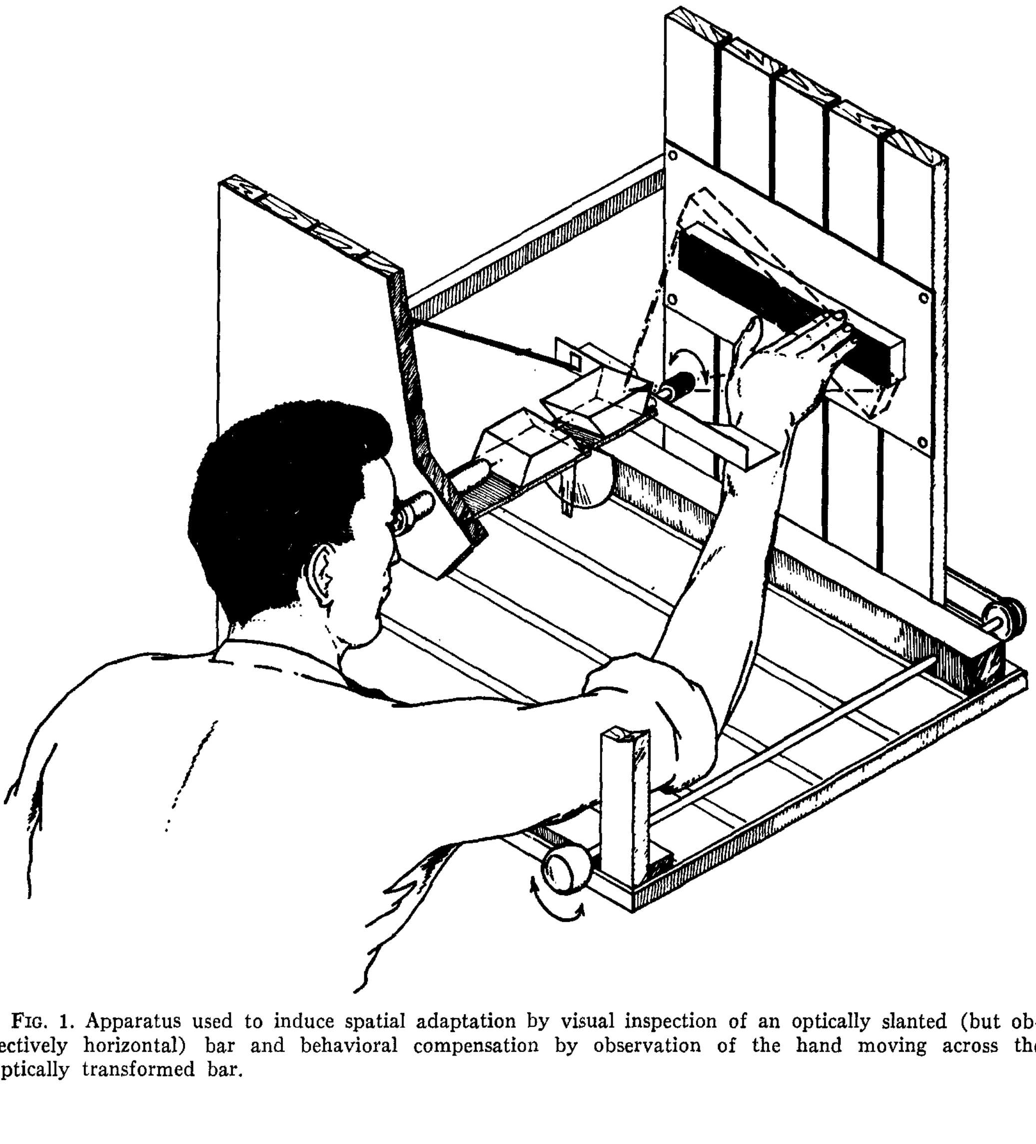

FIG. 1. Apparatus used to induce spatial adaptation by visual inspection of an optically slanted (but objectively horizontal) bar and behavioral compensation by observation of the hand moving across the optically transformed bar.

If, on the other hand, the observer moves his extended hand across a physically horizontal bar while viewing both hand and bar (Figure 1) and sets it so it seems horizontal at 15-second intervals during the 3-minute period, he will adjust it to compensate for the visual transformation in the opposite direction to the slant. This compensation for visual transformation persists so that it occurs when the observer makes an adjustment to apparent horizontality without visual guidance after the transformation period. In an extension of the experiment, two groups of 12 observers adjusted the bar so that it seemed horizontal at 15-second intervals during the 3-minute transformation period, observing the bar and their hand moving across it. The prisms were arranged so that the retinal projection of the horizontal bar was slanted 20° for one group and 45° for the other. The aftereffect (difference between pre- and posttransformation adjustments without visual guidance) was 6.86° for the 20° transformation and 8.23° for the 45° transformation.

This latter finding is similar in principle to that reported by Harris (1965) in which the observer moved his viewed hand across a prismatically curved (but physically straight) line.[2] It is clear from the data reported here, however, that the visual and behavioral effects are independent. Whereas visual adaptation with aftereffect is negligible at 45° of prismatically induced slant, the behavioral effect is substantial. At 20° slant, the visual effect is larger than at 45°, while the behavioral effect is larger at 45° than at 20°. Since there is no visual effect at 45°, it seems unlikely that this phenomenon is due to changes in the registration of eye movements as suggested by Harris (1965) for prismatically induced curvature. Such a hypothesis would predict that the visual effect would be greater at 45° than at 20°. There is, of course, no essential difference between visual adaptation deriving from the inspection of prismatically curved and prismatically slanted lines.

[2] Learning to move the hand across an objectively straight but prismatically curved line is, of course, essentially similar to a mirror-tracing task. Whereas mirror tracing usually involves a 180° transformation of the frontal plane, Harris's task involved a double median plane transformation about its longitudinal axis.

Simultaneous Occurrence of the Two Effects

Under a variety of spatial transformation conditions, sensory adaptation and behavioral compensations can occur simultaneously in the same direction. Consider a wedge prism which transforms the median plane through 20° to the right set into a sheet of plate glass with the prism surface flush with the glass and the whole forming the top of an open-sided box. If a rod is placed a few inches below the underside of the glass, that section directly beneath the prism is displaced to the right so that the rod appears to be discontinuous. A cover with a line the same width as the rod and coincident with it can be placed over the glass and prism. With fixed head position, the observer fixates the rod at the center of the prism for 2 minutes, after which the cover is quickly replaced and the line fixated at the point coincident with the previous fixation point. Since the central section of the rod was prismatically displaced right, the same section of the line appears displaced left. This is a typical visual spatial aftereffect. Now, if while viewing the rod the observer quickly reaches beneath the glass and touches the section beneath the prism 10 times during a 2-minute period, he will at first reach too far right. After several responses, accuracy will be achieved; and when the cover is replaced and the observer is required to touch its underside directly beneath a point coincident with the center of the prism, his response will be too far left. That is, compensation for transformed vision during the transformation period persists and is revealed in posttransformation responses without visual guidance. The point to note is that the visual spatial aftereffect and behavioral aftereffect both deriving from median plane transformation are in the same (leftward) direction.

The independence of these two effects can be demonstrated by requiring the observer during the second part of the experiment to reach out quickly and touch the rod, allowing about 3 seconds for the response and closing his eyes for about 20 seconds between each response. In this case, behavioral compensation will be marked but the visual effect negligible since there is insufficient time for it to develop fully and what does develop will dissipate during the periods when the eyes are closed (Hammer, 1949; Oyama, 1953). With spatial transformation of the total visual field by means of prisms worn before the eyes for a long period, both visual and behavioral adaptation with subsequent aftereffects on removal would be expected to occur.

Whether or not visual adaptation occurs in addition to behavioral compensation depends on the type and extent of spatial transformation. For example, for the reasons already outlined, visual adaptation with aftereffect would not be expected with the median plane angularly transformed 45° about its longitudinal axis. Since with 180° transformations of the median or horizontal planes (or with both, as studied by Stratton, 1896, 1897), the straight-ahead remains straight ahead and vertical and horizontal edges remain so; adaptation with aftereffect would not be expected.

Behavioral Compensation and Kinesthetic Aftereffect

In addition to vision and hearing, sensory spatial adaptation with consequent aftereffect occurs following prolonged kinesthetic stimulation (Day & Singer, 1964; Gibson, 1933; Köhler & Dinnerstein, 1947). Under certain conditions a kinesthetic aftereffect and behavioral compensation may occur together in the same direction. For this reason it is necessary to distinguish between them.

If a blindfolded observer moves his extended hand from side to side across a slanted edge, a subsequently presented horizontal edge is judged to be slanted in the opposite direction. If, however, the observer is required to adjust the edge so that it feels horizontal, he will set it in the same direction as the original slant. Movement across an objectively horizontal edge does not result in an aftereffect if the poststimulation task is that of adjusting the edge to apparent horizontality (Day & Singer, 1964). With the apparatus shown in Figure 1, the actual slant of the bar and optical slant (i.e., median and horizontal plane transformation) can be varied independently. In a recent series of experiments[8] in which bar slant and optical slant were independently varied in both directions, the observer moved his hand from side to side across the bar while viewing it, after which a nonvisual posttransformation adjustment to apparent horizontality was made. The results from these experiments show that the kinesthetic aftereffect and behavioral compensation may summate or cancel as a function of the extent and direction of bar and optical slants. If, for example, the bar was slanted left and optical slant was right, the two effects summed. If both bar and optical slant were in the same direction, the net effect was zero since the kinesthetic aftereffect and behavioral compensation occur in opposite directions, as Harris (1965) has implied. If the bar was objectively horizontal but optically slanted, a pure measure of behavioral compensation was obtained since, as pointed out above, the kinesthetic aftereffect does not occur under this condition.

[8] These experiments were conducted by Mrs. Margaret Austin, University of Sydney, 1966.

It seems likely that in some studies the occurrence of a kinesthetic aftereffect has affected the results which have been interpreted in terms of "negative behavioral compensation." Weinstein, Sersen, and Weinstein (1964) attempted to repeat an experiment by Held and Schlank (1959) and obtained posttransformation responses opposite in direction to those originally obtained. A mirror system was arranged to give a parallel transformation of the frontal plane so that when the resting hand was viewed it appeared at a greater distance from the body than when normally viewed. During the transformation period, the hand was moved rapidly (68 movements per minute) toward and away from the body. Before and after this 6-minute period the observer was required to mark a point without viewing his hand. The range of movement of the hand and the position of marking strongly suggest that a kinesthetic aftereffect occurred in a direction opposite to behavioral compensation.

Nature of Sensory Adaptation and Behavioral Compensation

Sensory Adaptation

The essential effects of optical and pseudophonic transformation are changes in the spatial properties of stimulation similar to those which can be achieved by appropriate patterns without transformation. The processes underlying the effects of protracted stimulation produced by either means, however, are far from clear. Although a number of theories have been proposed to explain spatial aftereffects (Gibson, 1937; Köhler & Wallach, 1944; Osgood & Heyer, 1952), none is entirely satisfactory. It is sufficient to note for present purposes, however, that spatial aftereffects in vision occur with retinal stabilization of the projected image (Ganz, 1964), thus ruling out ocular movement as a determinant. Howard and Templeton (1964) demonstrated that effects from slanted lines cannot be attributed to ocular torsion as proposed by Ogle (1950).

Interocular transfer. It is well established (Gibson, 1933; Köhler & Wallach, 1944) that following appropriate stimulation of one eye with the other occluded, a spatial aftereffect occurs when the occluded eye is used for testing. The occurrence of the effect in the previously nonstimulated eye is generally referred to as interocular transfer. It would be expected that if spatial adaptation with aftereffect consequent upon transformed vision represents the same effects as with appropriate nontransformed vision, interocular transfer would also occur with transformed stimulation. That this is so has been demonstrated by Ebenholtz (1966), Hajos and Ritter (1965), and Pick, Hay, and Willoughby (1966). The question of whether or not such demonstrations of interocular transfer provide evidence for the central origin of the processes involved remains unsettled (Day, 1958).

Behavioral Compensation

It is argued here that changes in behavior concomitant with transformed visual and auditory input are a special case of motor learning essentially similar to and exhibiting the same characteristics as the learning process observable with the pursuit-rotor, finger-maze or mirror-tracing apparatus. To this extent it seems unnecessary to attribute special properties to behavior deriving from transformed sensory input as has been common in recent contributions (Harris, 1965; Held & Freedman, 1963). That is, it seems unnecessary and unparsimonious to regard changes in behavior deriving from transformation as essentially different from changes occurring in a variety of alternative motor-learning situations.

If an observer wearing wedge prisms which transform the median plane transversely 20° right regards an object which is objectively straight-ahead, it appears 20° to the right. In reaching quickly for the object, the observer may at first miss it but after several attempts he will reach accurately. If reaching is continued, proprioceptive information for a particular direction of limb movement (previously associated with the nontransformed median plane) and visual information become associated. In brief, an appropriate response pattern to the spatial properties of stimulation is learned. When the prisms are removed and the observer reaches straight ahead without visual guidance, the response deviates left of the actual straight-ahead point. Since the original proprioceptive information for straight-ahead has become associated with 20° right, the new nontransformed straight-ahead (without visual guidance of the limb) must of necessity be to the left. In this sense, behavioral compensation is representative of the learning process which occurs in a wide variety of situations and is subjected to extensive enquiry. An appropriate response pattern develops in relation to a certain pattern of stimulation. Presented with a target moving rapidly in a circular path, as with the pursuit-rotor, the individual, after initial inaccuracies, exhibits an appropriate response pattern which improves with practice. If the frontal plane is transformed through 180° by means of a mirror placed before the observer and he is required to trace a star pattern while observing his hand in the mirror, a typical learning curve can be plotted on the basis of either time taken or number of errors per trial. If the median plane is less drastically transformed through 20° and the observer is required to reach for an object while observing his hand, a typical learning curve results (Hamilton, 1964). The main difference between early studies of this process (Siipola, 1935; Starch, 1910) and more recent investigations (Held & Freedman, 1963) is that the early experiments did not make use of pre- and posttransformation tests to measure the transfer of learning to nontransformed conditions, and the term "sensorimotor adaptation" has been coined in referring to the change. Further, in recent investigations there has been a failure to distinguish clearly between the purely sensory (adaptive) phenomena and learning or to recognize that the frequently used median plane transformations achieved by wedge prisms are identical in principle to the frontal plane transformations deriving from mirrors. The classical mirror-tracing procedure is a standard procedure for demonstrating the course of motor learning and bilateral transfer of learning. Although the learning is more rapid (since the transformation is smaller and less complex), median plane transformations or any other spatial transformation would serve as well. Although the evidence strongly suggests that changes in behavior with transformation represent a motor-learning process, the term "behavioral compensation" can be conveniently used in referring to learning under these conditions.

Rate of behavioral compensation. The evidence suggests that the rate of motor learning with transformed input varies as a function of both the extent and complexity of transformation and the nature of the responses. In those studies involving 180° transformations of median and horizontal planes about longitudinal axes (Ewert, 1930; Snyder & Pronko, 1952; Stratton, 1896, 1897) and involving complex response patterns such as perambulation and card sorting, the time to achieve pretransformation efficiency was protracted, taking up to 2 or 3 days. Learning with simpler and less extensive transformations involving less complex responses such as reaching or marking is relatively rapid, occupying a few seconds (Hamilton, 1964). So far, there has been no systematic study of the effects of extent, direction, and complexity of transformation on motor learning, although Siipola (1935) investigated the effects of 180° transformation of the frontal and horizontal planes singly and together. She found no difference between the three conditions. The accumulated data from a number of studies indicate, however, that the extent of transformation may be a critical variable affecting rate of learning to a set criterion.

Intermanual transfer of behavioral compensation. Kalil and Freedman (1966) found that after viewing one hand with transformed vision behavioral compensation occurred in the other hand in a nonvisual posttransformation test. This finding was not confirmed by Harris (1963) or Mikaelian (1963). Hamilton (1964) noted intermanual transfer with unrestricted head and body movement but found that it did not occur with restricted movement. Intermanual or, as it was called earlier, bilateral transfer, is well established with 180° transformation of the frontal plane in the typical mirror-tracing experiment (Ewert, 1926; Siipola, 1935). In fact, it has also been found to occur between hand and foot (Bray, 1928). Since the recent investigations of intermanual or bilateral transfer have been restricted to relatively small spatial transformations usually of the median plane whereas the earlier studies employed 180° changes, it seems that transformation extent may be a determinant of such transfer. A further point of difference between early and recent studies concerns the procedure for measuring transfer. The older procedure (Ewert, 1926; Siipola, 1935) involved a series of trials viewing one hand with transformed vision followed by trials with the other hand under the same conditions. More recent studies (Harris, 1963; Mikaelian, 1963) have investigated transfer from transformed vision of one hand to a nonvisual test with the other. A double transfer is involved in this procedure—transfer between a transformed visual condition and a nonvisual condition and transfer between one hand and the other. It is probable that the earlier transfer studies constituted a more sensitive test of transfer of motor learning between limbs and were sounder in terms of experimental design. The "double transfer" procedure must lead to a confounding of transfer from visual to nonvisual conditions with transfer from one limb to the other.

Intermodal transfer. Harris (1963) demonstrated that following behavioral compensation for median plane transformation, the compensation occurred in pointing to the direction of a sound source. Since visual and auditory directions are normally in accord (e.g., the telephone is both seen and heard to the left or right), it follows that if new motor responses are learned with transformed vision they would also be manifest during a nonvisual posttransformation test with an auditory stimulus. So far, the opposite transfer from hearing to vision has not been demonstrated although it would clearly be of interest to do so.

Further Evidence for Behavioral Compensation as a Special Case of Motor Learning

In a recent experiment (Day & Singer, 1966) using the apparatus shown in Figure 1, the number of trials during the transformation period and during the posttransformation phase were systematically varied. The bar which was objectively horizontal was optically transformed through 20° and the observer's task was that of adjusting it to the apparent horizontal. Nonvisual posttransformation adjustments were compared with those made similarly before transformation. Three groups made a single adjustment to the horizontal while viewing the angularly transformed bar, and three further groups made seven adjustments. While two groups (1 and 7 trials) made 15 posttransformation adjustments at 1-minute intervals, two further groups (1 and 7 trials) made a single adjustment after 7 minutes, and the remaining

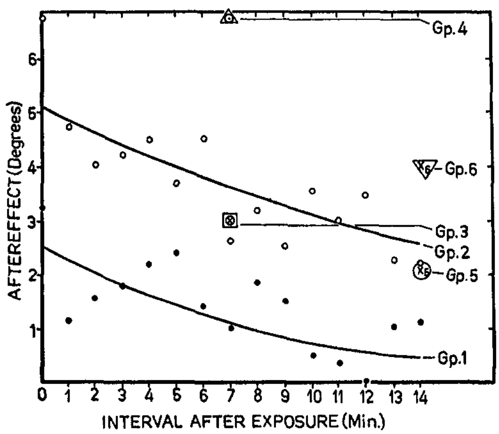

FIG. 2. Dissipation of behavioral compensation under two conditions of transformation (1 and 7 trials) and three conditions of posttransformation (15 trials at 1-minute intervals, 1 trial after 7 minutes and 1 trial after 14 minutes).

two groups (1 and 7 trials) made a single adjustment after 15 minutes. The data from this experiment are plotted for the six conditions in Figure 2. It is clear from the graph that the frequency of transformation trials determines the degree of learning and that dissipation of the learned response during the posttransformation period is accelerated as a function of the number of posttransformation trials without visual guidance. If the transformation period is regarded as a training period during which new relationships between stimulus and response are learned, then the posttransformation phase can be treated as an extinction period. During this latter period it would be expected that in the absence of transformed stimulation the recently acquired responses would give way to previously learned and more firmly established responses.

METHODOLOGICAL ISSUES

By far the most common procedure in investigating sensory spatial adaptation and behavioral compensation is that involving tests before and after a period of spatial transformation. The difference between pre- and posttransformation measures serves as an index of either visual or auditory adaptation or of behavioral compensation. The use of this procedure raises two questions—that concerning the appropriateness of the tests to reveal one or the other effects, and that concerning transfer of learning from the transformation period to the posttransformation test.

Appropriateness of Pre- and Posttransformation Tests

It has been pointed out that both sensory spatial adaptation and behavioral compensation may occur simultaneously. Whether one or both effects are revealed depends on the nature of the pre- and posttransformation tests. If after a period of wearing wedge prisms to transform the median plane through its transverse axis the observer is required to point straight ahead without viewing his hand and arm, then behavioral compensation will be exhibited. If, on the other hand, the observer is required to report when a field of lines in the horizontal plane appears straight ahead, then a perceptual change will be revealed.

In a recent experiment, Mikaelian and Held (1964) used a dual prism system to transform spatially the median plane through its longitudinal and transverse axes and the horizontal plane through its transverse axis. The outcome of this complex transformation was that a point normally straight ahead was displaced left and upward and a normally vertical line was rotated into a slanted position. There were two tests before and after transformation: adjustment of the line to apparent verticality and rotation of the body by leg movement until a point of light appeared straight ahead. The first is a perceptual test and the second is a behavioral test. Using the conditions of Mikaelian and Held (1964), it would be possible to devise a behavioral test in relation to the slanted line (e.g., pointing to the top of the line) and a perceptual test for the straight-ahead (e.g., adjusting a point to appear straight ahead). As a matter of fact, McLaughlin and Rifkin (1965) have shown that following transverse angular transformation of the median plane, a spatial aftereffect occurs in adjusting a pointer to the straight-ahead. It is clear that appropriate behavioral and perceptual tests could be devised for the complex transformation used by Mikaelian and Held (1964) such that behavioral compensation and sensory spatial adaptation could be shown to occur for the two aspects of transformation separately investigated.

In a large number of recent investigations, perceptual tests have preceded and followed a transformation period during which the observer was required to engage in various activities. Thus, Ebenholtz (1966), using angular transformation of median and horizontal planes, required observers to walk through long corridors and to undertake various manipulative tasks (jigsaw puzzles, dart throwing). The pre- and posttransformation tests involved judgments of verticality. It is highly likely that if the observers had merely inspected a field of vertical lines for the same period of time the same results would have been obtained since spatial adaptation is dependent on stimulation rather than motor activity during the transformation period. The same argument applies in the case of an experiment by Freedman and Stampfer (1964) in which judgments of the auditory straight-ahead were made before and after a period of pseudophonically transformed hearing during which the observer walked about. Had the observer been seated for the same period the same results probably would have occurred.

Transfer from Transformation to Test Phase

The experimental situation in which an observer learns to make certain responses with spatially transformed vision or hearing followed by responses with normal sensory input (but usually with his responding limb occluded) is similar in many respects to many transfer-of-learning experiments. The observer learns to make appropriate responses with one form of sensory input and later responds with another. The posttransformation responses (reaching, pointing, marking) tend to be in the direction of those developed during the transformation phase. That is, responses learned under one condition transfer to another. In this sense, it would be expected that the magnitude of behavioral compensation as revealed by the difference between pre- and posttransformation tests would be a function of those variables known to affect transfer of learning. The relationship between transformation and posttransformation phases in terms of task similarity, relative task difficulty, degree of learning in the transformation phase, and time interval (Ellis, 1965) would be expected to affect compensation. The data from Day and Singer (1966) which indicated that one trial during the transformation phase resulted in less compensation than seven trials are in agreement with a transfer-of-learning interpretation. Further evidence in support of this view was provided by Freedman, Hall, and Rekosh (1965) who showed that similar activities during transformation and posttransformation phases resulted in greater transfer than dissimilar activities.

Theoretical Issues

In view of the distinction which has been made between sensory adaptation to and behavioral compensation for spatially transformed vision and the identification of the latter as motor learning, the role of active and passive responding (Held & Freedman, 1963) and the felt-position hypothesis (Harris, 1965) can be considered.

Active and Passive Responding during Transformation

Held and his associates (Held & Freedman, 1963; Mikaelian & Held, 1964) proposed that the self-induced movement is a fundamental determinant of what they called sensorimotor adaptation to spatially transformed input. Recent experiments have shown, however, that for some conditions of transformation, externally induced or "passive" movement during transformation is as effective as self-induced or "active" movement (Pick & Hay, 1965; Singer & Day, 1966b; Templeton, Howard, & Lowman, 1966). In a recent study, (Singer & Day, 1966a) it was shown that when the passive, resting limb was viewed through a wedge prism, behavioral compensation occurred if the observer was required to *judge* the position of his limb in terms of a moving scale located between prism and eye. If, on the other hand, the observer merely viewed his limb without judging position, compensation was negligible.

If, as argued here, changes in behavior with spatial transformation represent learning, it follows that the observer, in order to compensate for the altered spatial input, must be given an opportunity to learn. Although *some* learning would be expected to occur as a result of merely observing the resting limb or through observing another individual learning (Siipola, 1935), maximum learning would be more likely to occur when the observer actually responds. It does not seem at all surprising that when the observer's responses are restricted, as when he is moved about in a wheelchair (Held & Bossom, 1961), or when the movements are induced by an external force, he learns less. It has been pointed out that the occurrence of responses learned during the transformation phase in the posttransformation phase can reasonably be regarded as an instance of transfer of learning. If little learning takes place during transformation as a consequence of "passive" movement (i.e., limited opportunity to learn) and the responses in the two phases are markedly different, it is to be expected that little or no transfer would be manifested.

There is a further point which arises in connection with Held's theory. Proprioceptive feedback, which is central to his argument, is by no means dependent on self-induced movement as implied in the theory. Stimulation of receptors mediating the sense of position and movement occurs with passive as well as active movement (Mountcastle & Powell, 1959). Only the muscle spindles rely on self-induced movement for their stimulation. Thus, following passive movement during the transformation phase, transfer would be expected to occur to a passive posttransformation task. Less transfer of learning would be likely to occur from a task requiring passive movement to one demanding active movement, as is common with tasks dissimilar in the type of responses involved.

Felt-Position Hypothesis

Harris (1965) has proposed that changes occurring with spatially transformed input can be largely attributed to changes in the position sense. He called the perception of position "felt position" but made clear that the hypothesis applies when position information is unconscious.

In discussing his own experiments, Harris contended that since the observer was not allowed to make any active movement with his viewed arm during transformation, a simple motor-learning interpretation is inadequate to explain the changes which occurred. But it is well established that even inspection of a pictorial representation of a motor task affects the learning of that task positively (Gagné & Baker, 1950). In fact, Siipola (1935) showed that subjects who observed others performing the mirror-tracing task benefitted from such perceptual pretraining. In other words, it is not absolutely necessary to perform the task to learn it; merely observing the arm or hand with spatially transformed vision is sufficient to result in some learning. The argument advanced by Harris that the elimination of active movement while viewing the hand through a prism attests to the inadequacy of a motor-learning explanation ignores the role of perceptual pretraining in motor learning.

The second point, although more abstract, is more fundamental in evaluating Harris's explanation in terms of the felt position of limbs or body parts. The study of perception has long been as equally concerned with phenomena as it has been with responses. Descriptive phenomenology and behavioral psychophysics represent the extremes of a continuum of viewpoint with shades of approach between. The study of learning, on the other hand, has been almost exclusively concerned with the objective observation, recording, and measurement of responses. Subjective data are seldom sought. But, and this is the core of the argument, responses are accompanied by sensory stimulation. The proprioceptive end-organs function in the maintenance and control of posture and movement. If a new set of responses is learned, a new set of proprioceptive perceptual phenomena must also occur. If after many months of reaching to the right to pick up the telephone, the position of the telephone is altered to the left, the individual tends to continue reaching right. Gradually, he learns to reach left and the right-reaching response disappears. At the same time there is a change in the proprioceptive "sensation" accompanying the movements. Reaching left is accompanied by different felt-positions and felt-movements than reaching right. If with median plane transformation the observer learns to reach right to pick up an object which is actually straight ahead, the learning which occurs has its sensory component. To argue that changes in behavior with spatially transformed input are due to changes in proprioception is merely to offer an explanation in terms of the proprioceptive accompaniments of learning. If, as Harris (1965) has indicated, this interpretation applies when position information is not available to consciousness, then there would seem to be little difference between the felt-position hypothesis and one couched in terms of motor learning.

Interaction between Sensory and Motor Processes: Direction-Contingent Effects

The data treated so far strongly suggest that under conditions of visual and auditory transformation, independent sensory effects and learning occur. While sensory spatial adaptation is essentially similar to that occurring with appropriate nontransformed stimulation, the learning effects are the same in principle to those observable in a variety of alternative situations involving perceptual-motor coordination. There is, however, a third group of phenomena which, although apparently related to the sensory effects, has a motor component. These have been termed "gaze-contingent" effects by Pick and Hay (1966) and were first observed and intensively studied by Kohler (1964).

The refraction of light passing through a prism is a function of the angle at which light enters the prism. If when viewing through a prism the eyes are turned right, the transformation is different from that when the eyes are turned left. The light falling on the eye enters the prism at a different angle for each direction of regard. Similar variations in the characteristics of transformation occur when the eyes remain in a fixed position and the head is turned from right to left. Kohler (1964) has shown that with prolonged wearing of prisms and other devices, adaptation to these gaze-contingent transformations takes place but that on removal, the consequent aftereffect varies with direction of regard. That is, if the eyes are turned one way, the aftereffect is different from that when the eyes are turned another. It is also claimed that if spectacles whose eyepieces consist of half blue and half yellow glass are worn for a sufficiently long period, chromatic aftereffects which are gaze-contingent also occur. This latter observation was not confirmed by Harrington (1965), one of whose observers wore the bicolor lenses for 146 days with no marked changes.

Spatial aftereffects of the type studied by Verhoeff (1902) and Gibson (1933) can be induced either by transformation or by suitable nontransformed stimulation. The question immediately arises concerning whether gaze-contingent effects might also occur with nontransformed stimulation. Both Carlson (1964) and Hein and Sekuler (1959) reported that adaptation to curved and tilted lines can vary as a function of eye position and head position with nontransformed vision. Carlson (1964) proposed that perceptual adaptation is basically an immediate localized consequence of stimulation but can become generalized through a process of conditioning by temporal contiguity. Thus the data reported by Kohler (1964) with transformed vision and by Carlson (1964) and Hein and Sekuler (1959) with normal viewing indicate that sensory spatial adaptation with aftereffect under conditions of varying direction of gaze may become associated with visual direction.

Another question concerns the possible occurrence of direction-contingent effects in senses other than vision. Since sensory spatial adaptation and aftereffect occur in the auditory modality, it is conceivable that direction-contingent auditory effects might also occur. A pseudophone with a fixed sound source would presumably result in variations in spatial and other properties with movements of the head. In view of the possibility of such effects occurring with sensory stimulation other than vision, the term "direction-contingent" is preferable.

Conclusions

Over 50 years ago a 180° rotation of the frontal plane about its longitudinal axis was used by Starch to demonstrate the course of what he called "trial-and-error learning." This technique has since been used in a large number of studies to demonstrate numerous features of the learning process, including that of bilateral transfer. More recently, other classes, directions, and extents of visual and auditory transformation have been used to study similar changes in behavior. For the most part, recent investigations have tended to regard these behavioral changes as unique. An analysis of spatial transformation in terms of angular and parallel shifts in the median, horizontal, and slanted planes shows that there is no difference in principle between frontal plane transformations induced by mirrors and median and horizontal plane changes induced by prisms, lenses, and other optical systems. In addition to motor learning under these conditions, however, there also occur sensory adaptive effects of a type essentially similar to those which take place with appropriate nontransformed stimulation. With spatial transformation, both effects may occur simultaneously and in the same direction. The basic argument proposed here is that these effects are independent but since they occur together under conditions of optical and pseudophonic transformation of space they have been confused. Perceptual tests have frequently been used to index motor learning, and behavioral tests have been used to demonstrate perceptual changes. To further complicate the picture, Ivo Kohler and his colleagues have shown and others (Pick & Hay, 1966) have confirmed that varying visual transformation with eye movement results in gaze-contingent adaptation with aftereffect. Such direction-contingent effects may also occur with appropriate nontransformed stimulation. It is also conceivable that such effects may take place in hearing as well as vision.

Since behavioral compensation represents a special case of motor learning, it is to be expected that amount of practice, task difficulty, and other factors determine its cause and dissipation. Experimental data have been reported to show that this is so and that the method of studying the learning process is essentially a transfer-of-learning paradigm.

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