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Central visual learning and illusory visual direction after backward head tilts

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When the head is returned to upright after prolonged backward tilt, people who are asked to look straight ahead look higher than they did before the backward tilting. This has been interpreted in terms of hypotheses about central visual learning or by hypotheses about peripheral muscle physiology. According to the learning hypotheses, the illusion of visual direction that occurs after head tilts depends upon the presence of discordant cues about direction. In the present study, the illusion was the same with or without discordant information.

In many activities outside the laboratory, such as piloting aircraft or playing sports, accurate perception of direction is critical during and after head tilts that have been shown to cause illusory visual direction in laboratory test. Figure 1 illustrates some of the effects of head tilts by showing the relationships between (1) the actual direction of gaze, which is determined by a fixation point, (2) the rest position of the eyes, which is operationally defined by the position chosen when a subject is asked to put his or her eyes in the normal straight-ahead position with respect to the head, and (3) the perceived direction of the fixation points. Figure 1 shows a person whose head is upright and whose eyes are uninfluenced by any aftereffects of head tilts. The fixation point is placed in line with the rest position, and the perceived direction of the fixation point corresponds to its actual direction. Notice that the fixation point is in the same location with respect to the head in Figures la, lb, lc, and ld; therefore, the actual direction of gaze is in the same place with respect to the head in all diagrams.

Figure 1b shows a person whose head has been tilted back for about 2 min and whose eyes are therefore under the influence of the doll reflex. The doll reflex is compensatory eye movements which are driven by the gravity receptors. Like the toy dolls with counterweighted eyes, a person's eyes rotate down when he or she is tilted back. It is possible to prevent doll-eye movements simply by looking at a fixation point. However, even when this is done, an extra component of innervation from the gravity receptors is added to the muscles that move the eyes downward. As a result of this, the rest position of the eyes is lower (Ebenholtz & Shebilske, 1975) and the perceived direction of the fixation point is higher (Ebenholtz & Shebilske, 1973). This is called the elevation illusion.

Figure 1c shows a person who has been tilted back for about 5 min and whose eyes have therefore adapted partially to the doll reflex (Shebilske & Karmiohl, 1978). Consequently, the rest position is lowered less than it is in Figure 1b, and the elevation illusion is smaller.

Figure 1d shows a person who has been returned to upright after partially adapting to the doll reflex. The result is a negative aftereffect; the rest position

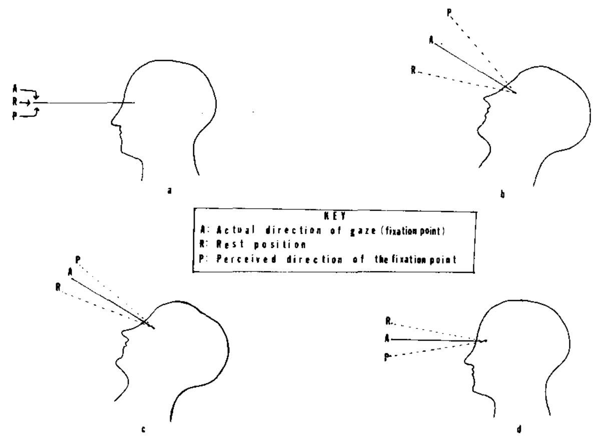

Figure 1. Illusions of visual direction associated with head tilts are illustrated by showing the relationships between the actual direction of gaze (A), which is determined by a fixation point, the rest position of the eyes (R), which is operationally defined by the position chosen when a subject is asked to put his or her eyes in the normal straight-ahead position with respect to the head, and the perceived direction of the fixation point (P). The four diagrams show a person in the following conditions: (a) head is upright before being tilted, (b) head has been tilted back for 2 min, (c) head has been tilted back for 5 min, and (d) head is returned to upright after being tilted for 5 min.

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of the eyes is raised and the perceived direction of the fixation point is lowered (Shebilske & Fogelgren, 1977).

The explanations which have been offered for the adaptation and negative aftereffect can be divided into two classes: those which are based on central visual learning (e.g., Shebilske & Fogelgren, 1977) and those which are based on peripheral muscle physiology (e.g., Ebenholtz, 1977; Shebilske & Karmiohl, 1978). The present experiment was designed to choose between these two classes of explanations.

These explanations have their roots in studies in which illusions of visual direction have been induced by visual rearrangements through the use of prisms. The effects of prisms have been interpreted in terms of hypotheses about central visual learning (e.g., Epstein, 1975; Craske & Crawshaw, 1978; Howard, 1968; Rock, 1966; Wallach & Frey, 1972; Wallach & Halperin, 1977) or by hypothesis about peripheral muscle physiology (e.g., Ebenholtz, 1974; Paap & Ebenholtz, 1976; Willey, Gyr, & Henry, 1978). On the basis of all the evidence on this issue, Willey et al (1978) concluded that (1) when the eyes are held off-center, illusions of visual direction are induced by changes in muscle responsiveness, and (2) visual learning probably causes illusions of visual direction in some cases, but learning is a more varied phenomenon, depending for its existence on the nature of the information available for learning.

Only direct tests will make it possible to choose between these two classes of explanations for the illusions of visual direction associated with head tilts, because the conditions leading to the illusions are unique. One difference from prism experiments is the fact that the eyes are not held off-center during head tilts. In fact, the illusions have been measured by comparing two groups of subjects who maintained the same eye-in-head position during the exposure period as in Figures la and lb. This does not rule out the possibility that the illusions are caused by peripheral changes in muscle responsiveness, but it suggests that the exact nature of the change is unique. Changes in muscle responsiveness could be caused by the otoliths which alter the pattern of innervation to the eye muscles as explained above, but how the change in muscle responsiveness might occur is not known.

Another unique aspect of the conditions leading to illusions of visual direction associated with head tilt is the nature of the information available for learning. Howard (1968) described three kinds of information that could lead to learning of perceptual-motor adjustments: (1) sensorimotor discordance, which is a difference between the expected and actual sensory consequences of self-produced movement, (2) intramodal discordance, which is a discrepancy between cues within the same sensory modality, and (3) intermodal discordance, which is a discrepancy between cues localized in different modalities. Shebilske and Fogelgren (1977) described how the doll reflex might have introduced sensorimotor and intramodal discordance into their experiment in ways that have not been tested in prism adaptation experiments.

They argued that the doll reflex could have produced sensorimotor discordance by altering the relationship between intended and actual eye movements which would have caused a discrepancy between the expected and actual displacement of the images of the retina. Their argument was based (1) on the possibility that the doll reflex causes the starting position of the eyes to be registered incorrectly before each eye movement, and (2) on the fact that the starting position of the eyes must be registered correctly for eye movements to be accurate. For example, if the starting position of the eyes is registered as an upward direction of gaze when it is actually a straight-ahead direction (as in Figure 1b), then the motor commands for a 5° horizontal eye movement would produce an oblique eye movement, because the oblique muscles would be used inappropriately. This, in turn, would produce a sensorimotor discordance between the expected horizontal displacement of the images on the retina and the actual oblique displacement that would be obtained.

Shebilske and Fogelgren also argued that the doll reflex could have produced intramodal discordance by altering the relationship between two or more visual cues to direction. Their argument was based (1) on the possibility that the doll reflex causes the elevation illusion (as in Figure 1b) by altering the apparent or registered direction of gaze, which is one cue used to see direction, and (2) on the possibility that there are other visual cues to direction that are not altered by the doll reflex because they do not depend upon registered direction of gaze (cf. Shebilske, 1977). For example, if a person knew that a checkerboard pattern was parallel to the plane of the face and the person fixated an object on the checkerboard, the direction of the object would be indicated by the symmetry of the board's retinal image. The image would be symmetrical only when the object was straight ahead, and the magnitude of asymmetry in other positions would indicate the amount of deviation from straight ahead. This symmetry-of-the-background cue would remain accurate despite errors in registered eye position. In the experiments by Shebilske and Fogelgren, there was a checkerboard background that was parallel to the plane of the face when the head was upright and when the head was tilted. Thus, when the head was tilted back, there may have been an intramodal discordance between a symmetry-of-the-background cue which remained accurate and a registered eye position cue which was disturbed by the doll reflex.

While illusions of visual direction associated with prisms are similar to illusions of visual direction associated with head tilts, there are important differences. As the result, the details of possible explanations for the latter are unique and untested, whether one argues from the point of view of peripheral muscle physiology or central visual learning. The literature on prism adaptation can therefore provide a framework for analyzing illusions associated with head tilts, but it cannot support specific predictions. The best a priori statement is that the illusions associated with head tilt may be caused either by peripheral motor adjustments or by central visual learning or by some combination of the two.

The present study was designed to analyze the possible contribution of central visual learning. The opportunity for sensorimotor discordance was manipulated by controlling the presence or absence of eye movements while the head was tilted back; the opportunity for intramodal discordance was manipulated by controlling the background which was either a checkerboard or darkness. The procedure was designed to be as similar to the Shebilske and Fogelgren experiment as possible, which meant, among other things, that subjects were always upright during pre- and posttests and the illusion was measured by comparing two groups who maintained the same eye-in-head position during exposure, as in Figures 1a and 1b.

METHOD

Subjects

The subjects were 128 male and female undergraudates at the University of Virginia who did not know the hypothesis being tested.

Design

Sixteen subjects were assigned randomly to each of eight groups that received different treatments during the exposure periods. The eight treatments were defined by the factorial combination of three variables which had two levels each: (1) head tilt (0° or 20° back), (2) eye movements (with or without), and (3) background (darkness or checkerboard). All subjects had the same sequence of events: pretest, exposure, posttest, second exposure, second posttest, third exposure, third posttest. Each exposure period lasted 3 min so that posttests were given after 3, 6, and 9 min of total exposure. The response measure, which was computed separately for each of the three posttests, was the posttest minus pretest shift in the rest position of the eyes.

Procedures

Preliminary procedures. Measures of the apparent upright head position and of the rest position of the eyes were made before the experiment. Head position was measured by an inclinometer (Pro. No. 30) fastened to the head parallel to Reid's baseline, an imaginary line running from the outer canthus to the center of the ear canal. The inclinometer was read after a subject was told to put his or her head in its normal upright position. Since there was variability in the estimations, the subjective upright position was defined as the average of six measures which were taken while subjects stood in front of a blank wall (subjects nodded freely between estimates). The subjective upright-head position averaged across all subjects was 14.72°, with the canthus end tilted up from horizontal.

The instrument used to measure the rest position of the eye was a vertical semicircular perimeter with an array of uniformly illuminated dots which were .67° in diameter with their centers separated by 1°. The dots, which were the only things visible during testing, covered an arc of about 170°, which extended above and below the visual field. The perimeter had a radius of 26.95 cm, and the eyes were positioned at this distance so that they were an equal distance from each dot. To measure the rest position, subjects, whose heads were upright, were instructed to choose that dot which was in their line of sight when their eyes were in the normal straight-ahead position in their heads. The instructions were clarified with a picture of a tilted head illustrating a line of sight perpendicular to the plane of the face; it was emphasized that the same eye-in-head position was called for regardless of head or body orientation. When a dot was selected, it was identified by the experimenter who covered each dot one at a time with a mask until the fixated one was covered. The subjects were instructed to look at the chosen dot continuously until it was covered. During the preliminary test period, six measures of the rest position were taken, with the starting position of the mask counterbalanced 30° above or below center. The subjects closed their eyes between measures while the experimenter recorded the results.

Test procedures. During the experiment, the tests of the eyes' rest position were identical to the preliminary measures except that only two measures were taken during each test period. The head was at the subjective upright position and only the test dots on the perimeter were visible during all the tests.

Exposure procedures. The between-subjects treatment factors were manipulated during the exposure periods as follows:

(1) Half the subjects held their heads at 0°, which was defined as their own subjective upright position; the other half tilted their heads back 20° from their own subjective upright position. The appropriate angles were maintained by chin and forehead rests.

(2) Eye movements were controlled by fixation targets that were 32.4 cm from the eyes. Half the subjects had to move their eyes to follow the targets, which were presented in a repeating sequence of 3 cm (5.3°) left, middle, and 3 cm (5.3°) right. Each fixation target remained on for 1 sec and then was immediately replaced by the next one. The other half of the subjects had to hold their eyes in the middle position, because all the fixation targets were presented in the middle; each one remained on for 1 sec and then was immediately replaced by the next one. In both eye-movement conditions, each time a fixation target was replaced, the subjects had to say whether the new one consisted of two or three dots. The dots were .28° in diameter. In the three-dot targets, the dots were in a horizontal row and separated by .14°. The two-dot targets were the same, except that the middle dot was removed. A pilot test showed that subjects had to look within about 1° of the target to make the discrimination. During the experiment, an average error rate of 1 out of 540 trials was obtained, which left no doubt that subjects were looking in the required positions.

(3) Half the subjects had a homogeneous background of darkness; the other half had the room lights on and a checkerboard background. The fixation targets were luminescent and were the only things visible when the subjects had a homogeneous background of darkness. When the room lights were on, the subjects saw a 11° × 42° checkerboard, which had a slit 1.8° high and 11.5° long; the fixation targets were displayed in the slit. The checkerboard was vertical for subjects whose heads were at 0°, and it was raised and tilted 20° for subjects whose heads were tilted back 20°. As the result, the height of the slit was positioned so that the same vertical eye-in-head position was required in all conditions, and the angle of the checkerboard was such that the board made the same angle with respect to the line of sight in all conditions. This arrangement can be understood by thinking of the slit as being in line with the actual direction of gaze and the board as being perpendicular to the actual direction of gaze in Figures 1a and 1b.

RESULTS

The posttest minus pretest shift scores were analyzed by an analysis of variance which included three between-subjects factors (head tilt, eye movements, and background) and one within-subjects factor (total exposure time). The results were as follows: (1) The effect of head tilt during exposure was highly significant [$F(1,120) = 55.32$, $p < .001$]; for subjects who were tilted back during exposure, the rest position of the eyes shifted 3.0° upward, while the rest position of subjects who held their heads upright during exposure shifted a negligible .1°. (2) The shift was .2° higher without eye movements and .2° higher with the checkerboard background, but neither of these slight differences was significant ($F < 1$). (3) Total exposure time had a significant effect [$F(2,240) = 4.06$, $p < .05$], which was marginal and unimportant. (4) No interactions were significant.

Figure 2 shows the results in a way that facilitates comparisons with the results of Shebilske and Fogelgren (1977). In four graphs, the shift in the rest position of the eyes in degrees is shown as a function of total minutes of exposure for subjects who held their heads upright during exposure (circles) and subjects who tilted their heads back 20° during exposure (squares). The graphs are shown in a 2 by 2 matrix, which is defined by the factorial combination of the two most important treatment variables of this study: eye movements (sensorimotor discordance) and background (intramodal discordance). The graph in the upper left-hand corner shows the conditions that were almost identical to those of Shebilske and Fogelgren; eye movements provided the opportunity for sensorimotor discordance and a checkerboard provided the opportunity for intramodal discordance. The results of this condition were virtually the same as those of the previous study. The other three graphs show that the opportunity for sensorimotor discordance and intramodal discordance made no difference whatsoever.

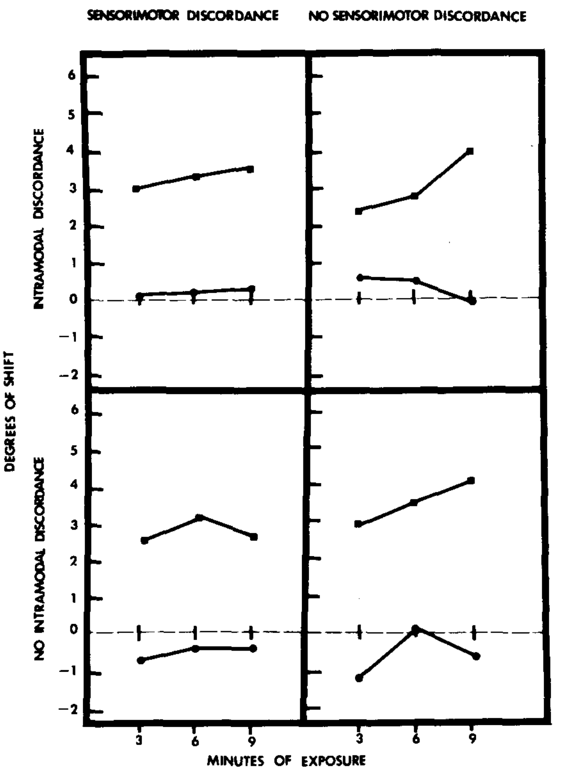

Figure 2. The posttest minus pretest shift in the rest position of the eyes in degrees is shown as a function of total minutes of exposure for subjects who held their heads upright during exposure (circles) and subjects who tilted their heads back 20° during exposure (squares). Four graphs are shown in a 2 by 2 matrix, which is defined by the factorial combination of two levels of sensorimotor discordance and two levels of intramodal discordance.

DISCUSSION

Often, such null results are uninteresting, but in this case they are important, because they establish that central visual learning is not an influential factor in the illusion of visual direction, which was first observed by Shebilske and Fogelgren. This eliminates one of the two major classes of explanations of illusions of visual direction related to head tilts, and it suggests that the illusions should be interpreted by hypotheses about peripheral muscle physiology.

While this leaves us closer to understanding the illusions, a number of specific hypothesis about muscle physiology remain to be tested. Many possibilities exist, because electrophysiological phenomena such as neuromuscular depression and facilitation have undetermined roles in normal synaptic integration. In addition, local intramuscular temperature related to circulation and metabolic levels have been implicated in neuromuscular variability but its exact effects remain obscure (Hayes, 1975). Another possibility is post-tetanic potentiation, which is a relatively long-lasting increase in muscle responsiveness following repetitive stimulation (cf. Ebenholtz, 1977; Shebilske & Karmiohl, 1978). Finally, adaptation of the otolithic innervation of eye muscles cannot be ruled out with certainty.

Whatever the specific explanation, however, it is clear that the oculomotor system is labile in the face of ordinary head tilts. Current research is following theoretical (Shebilske, 1977, 1978; Note 1) and practical (Shebilske & Karmiohl, Note 2) implications of this lability.

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