between the receptors and the ganglia are much shorter. If this is the case, then perhaps the adult structures we have studied are simply vestigial organs.

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Visual Spatial Aftereffect from Prolonged Head-Tilt

Abstract. Subjects with head upright were required to adjust a lighted bar in a dark room until the bar appeared vertical; the task was performed before and after 2 and 3 minutes of lateral head-tilt with their eyes closed. A visual spatial aftereffect was observed which varied as a function of the angle of head-tilt and which was opposite in direction to head-tilt.

The spatial judgments of a subject after he is exposed to visual, kinesthetic, tactile, or auditory stimulation differ from those judgments made before stimulation. Such modifications in judgments of size, shape, orientation, and direction (*1*) are referred to as figural, negative, or spatial aftereffects; these are well established for those sensory modalities which discriminate spatially. However, after one modality is stimulated (vision or kinesthesis) a spatial aftereffect does not occur when judgments are made with the other modality (*2*). Our experiments were concerned with judgments of visual orientation made after the head was tilted; we found that a visual aftereffect occurred when the head was returned to an upright position. Although changes in visual judgments of orientation occur during lateral head- or body-tilt (*3*), changes after prolonged tilt have not been reported. We have conducted two experiments confirming the occurrence of this spatial aftereffect and have shown that the magnitude of the effect is a function of the degree of head-tilt.

In the first experiment there were 30 subjects divided into two equal groups, one group serving as a control for the effects of head movement. Each subject was required to adjust a pivoted bar of light (152 by 0.9 mm) so that it appeared vertical. The bar, which was dimly lighted (2.08 mlam), was 183 cm from the eyes; there was no other source of light in the darkened room. The orientation of the bar could be read to the nearest 0.25 degree by means of a protractor scale. The angle of lateral head-tilt for the seated subject was controlled by a projecting rectangular frame pivoted on heavy uprights. An individual dental-composition biteboard was attached to the frame and was clenched between the subject's teeth throughout each trial. For the experimental group a trial consisted (i) of making, with head upright, five adjustments of the lighted bar to the vertical from each of five random starting positions (vertical and 5 and 10 degrees clockwise and counterclockwise); (ii) a 3-minute period with eyes closed and head tilted 30 degrees right or left; and (iii) a single adjustment of the bar to the vertical with the head again upright from the first of the five starting positions used in the pretilt series (*4*). The difference between the mean of the five adjustments before tilt and the single adjustment after tilt was a measure of the aftereffect. Before and after the tilt, the head was always upright. Each subject underwent one trial with head tilted left and one with head tilted right, the order of these alternating from one subject to another with a 5-minute interval between trials. For the control group the procedure was the same before and after the tilt, but in the intervening period the head was tilted 30 degrees left or right and then immediately returned to an upright position. This control was necessary since differences between adjustments before and after tilt could have been due to movement of the head from a slanted to an upright position with consequent stimulation of the semicircular canal system.

The first group (Fig. 1) showed a visual aftereffect of about 2 degrees in a direction opposite to head-tilt (*5*). Although there was no significant difference in the magnitude of the effect between left and right tilt ($p > .05$), the effect was significant for both when each direction was taken singly ($p < .05$) (*6*). There was no significant effect for the control group ($p > .05$).

In the second experiment eight subjects underwent nine trials similar to those of the first but with head tilted

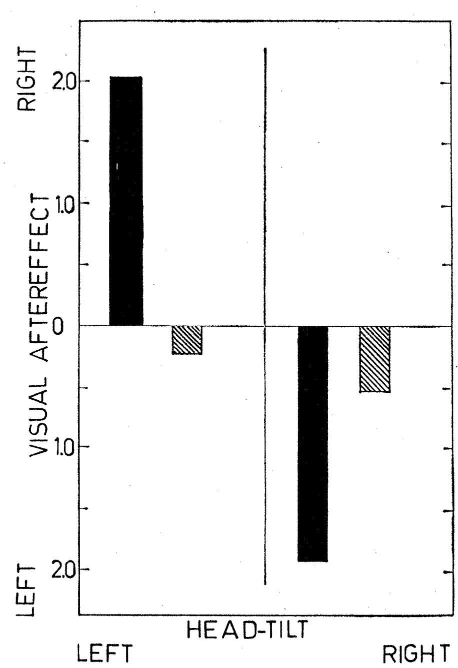

Fig. 1. Magnitude and direction of visual aftereffect resulting from 3-minute head-tilt to the left and to the right, together with control data.

left or right for 2 minutes at 10, 20, 30, and 40 degrees and with head upright (0 degree). The nine trials were presented in a different random order for each subject with a period of 4 minutes between each. The aftereffects for the nine angles of tilt are shown in Fig. 2, as are judgments of verticality during head-tilt. The latter, based on a separate group of ten subjects, were obtained under essentially the same conditions as the aftereffect except that adjustments to apparent verticality were made immediately after the head was tilted. It is clear from Fig. 2 that the visual effect during head-tilt was in the same direction as tilt, an effect referred to as the E-phenomenon (*7*), but that the visual effect following head-tilt (aftereffect) was opposite in direction. Tests of trend (*8*) applied to the aftereffect data indicated that the overall trends for both left and right head-tilt were significant ($p < .001$). Both linear and cubic components were also significant ($p < .01$). It is clear that, in addition to being opposite in direction to the E-phenomenon, the aftereffect increased with the angle of head-tilt and became maximum in the vicinity of 30 to 40 degrees.

The effect may be explained by apparent inclination of the upright head after protracted tilt. Some subjects reported that after the head was tilted to the right and returned to the upright position they felt as if the head were tilted to the left and vice versa. Ten subjects were required to adjust their heads to the upright after left or right head-tilt for 3 minutes at 30 degrees. All but two subjects exhibited an aftereffect of head position in the direction opposite to previous head-tilt. The mean aftereffect was 1.99 degrees. If the apparent tilt of the head was slightly opposite to the direction of previous prolonged tilt, the visual aftereffect could be the E-phenomenon resulting from apparent head position. But this explanation is doubtful since the apparent tilt of the head after 30 degrees inclination for 3 minutes was only 1.99 degrees. According to the E-phenomenon data shown in Fig. 2 this alone could not account for a visual effect as great as that found.

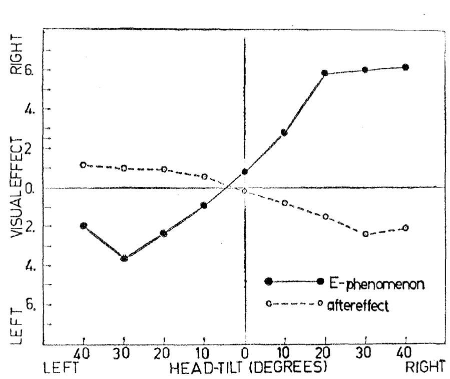

Fig. 2. Visual aftereffect and E-phenomenon as a function of angle of head-tilt.

The occurrence of a visual spatial aftereffect after prolonged head-tilt raises related questions concerning the mechanisms involved and the adequacy of current theories to explain the effect. Experiments (*9*) show that the aftereffect occurs when the observer is supine and the bar of light is directly above. This finding eliminates the possibility that the otolith system of the vestibular utricle, which is associated with the Aubert effect (*3*), is directly involved. Gravitational receptors of the vestibule do not respond to head- or body-tilt in the supine posture (*10*). One possible interpretation is that receptors in the joints and ligaments of the first three cervical vertebrae—these receptors affect the extraocular muscles (*11*)—are stimulated by lateral head-tilt.

Current theories which attribute visual spatial aftereffects solely to processes in the visual system (*1*) would require some modification to explain our data. A recent explanation proposed by Ganz (*12*), which treats spatial aftereffects as special instances of simultaneous illusions, would also require extension and modification to deal with a visual effect which does not derive from visual stimulation. Since the theory proposed by Gibson (*1*) is more general and makes no assumptions concerning the neurophysiological processes associated with aftereffects, it would have less difficulty in explaining these data. Both the visual and postural aftereffect from prolonged head-tilt can be attributed to Gibson's postulated changes in the norm of verticality. Clearly, then, the occurrence of an intermodal aftereffect requires some revisions of those theories which seek to explain spatial aftereffects.

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5. In adjusting the bar so that it appeared vertical, subjects set it in the same direction as previous head-tilt. It is inferred, therefore, that if the bar had remained vertical it would have been judged as slanted in the direction opposite to head-tilt.
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Segregation of Sister Chromatids in Mammalian Cells

Abstract. *Segregation of sister chromatids in embryonic mouse cells in primary tissue culture is not random. In mitosis those chromatids replicated on a DNA template synthesized during the preceding division cycle are separated from those constructed on a template synthesized two division cycles previously. Segregation in cells of the Chinese hamster follows a similar, but less pronounced, pattern.*

In bacteria, the products of chromosome replication, analogous to sister chromatids in higher organisms, are segregated into daughter cells in such a manner as to distinguish a chromatid containing a template strand synthesized in the previous division cycle from one containing a template strand synthesized in an earlier division cycle (*1*, *2*). This distinction between chromatids containing "parent" and "grandparent" templates has been explained with a model in which a polynucleotide strand attaches permanently to a subcellular segregation structure (membrane) when it is first used as a template in replication (*1*). When bacteria contain two linkage units or replicons, these segregate together. The replication products of chromosomes and episomes segregate so that units containing "grandparent" polynucleotide