Visual Adaptation to an Altered Correlation between Eye Movement and Head Movement

Abstract. *A visual target was moved left and right in exact synchrony with vertical movements of the head. A few minutes' exposure to this novel head-movement feedback led to a change in the visual discrimination of head movement from object movement. The critical factor in the adaptation is the novel correlation of eye and head movement elicited during the period of exposure.*

Vision discriminates remarkably well between movements of the observer and movements of the thing observed (*1*). This discrimination is influenced by past experience. A subject wearing inverting spectacles (which reverse the normal optical displacement during head movement) or wedge prism spectacles (which tilt and compress the visual field during head movement) at first mistakes the altered feedback from his head movement for motions of viewed objects. After a period of wearing the spectacles, however, these illusory movements of objects diminish. When the spectacles are removed, the restored normal feedback from head movement elicits opposite illusions of objects' movement (*2*).

In their theory of perceptual adaptation, Hay and Pick (*3*) note that an altered optical displacement during head movement is ordinarily accompanied by an altered pattern of eye movement. That is, even if the optical direction of an object shifts in a novel way during a head movement, the eyes manage to follow it. This happens because the eye movements are governed by movement of an image on the retina as well as by other processes accompanying head movement (*4*). When spectacles are worn, this new correlation between eye movement and head movement is required. The new correlation may become perceptually neutral, in that it no longer contributes to the perceptual impression of object movement. To the extent that the eyes' new movements keep the retinal image stationary, there is no longer any visual stimulus for the perception of an object moving.

This theory has two main implications. (i) Adaptation to a new optical feedback from head movement should occur if and only if a new correlation between eye and head movement is required. (ii) If the new optical feedback involves anything other than an added rotation of the visual field, an exactly matching adaptation is impossible, since eye movements are limited to rotations.

To test this theory, an electromechanical apparatus was devised to rearrange systematically the optical feedback from head movement (*5*). The subject's head movement was constrained to vertical nodding by means of a biteboard that was offset from a rotational axis centered on his neck. The head movement was registered by a low-torque linear potentiometer. The head-movement signal thereby generated was fed through a d-c amplifier-recorder and thence, through suitable gain-control devices, to a cathode-ray oscilloscope (CRO). The CRO trace was projected through an $f/4.5$ enlarger lens onto a rear-projection screen (0.61 by 0.99 m). The subject viewed the projected trace from the other side of the screen, and this served as the visible "object" in the experiments. The object's brightness was about 0.1 mlam, and it moved in exact synchrony with the head by as much as 28 degrees of visual angle, depending on the arrangement of the CRO input circuit.

The eye-head recorrelation theory was first tested by checking whether a perceptual adaptation was induced by a hitherto untried feedback rearrangement. The CRO projected a single spot (about 5 mm in diameter) on the screen, in an otherwise dark room, and this object moved left and right in synchrony with the up and down movements of the subject's head. Thus, the subject's eyes were required to move diagonally during vertical head movement, in order to keep the image of the object centered on the retina (condition 1, Fig. 1). Periods of exposure of 1 and 10 minutes were tested, during which the object moved 28 degrees horizontally (relative to the head) for each 40 degrees of vertical head movement. The subject's head movement was paced by a metronome set to ½ hz.

After as little as one minute's exposure, a perceptual adaptation could be measured by holding the luminous object fixed while the subject kept nodding his head. In this case, the subject reported that the object moved left and right in synchrony with his head, but with left-to-right directions reversed from the exposure condition (aftereffect, condition 1, Fig. 1). Eleven of 12 subjects tested in this manner reported this effect. The magnitude of the aftereffect was measured by allowing eight different subjects to adjust the

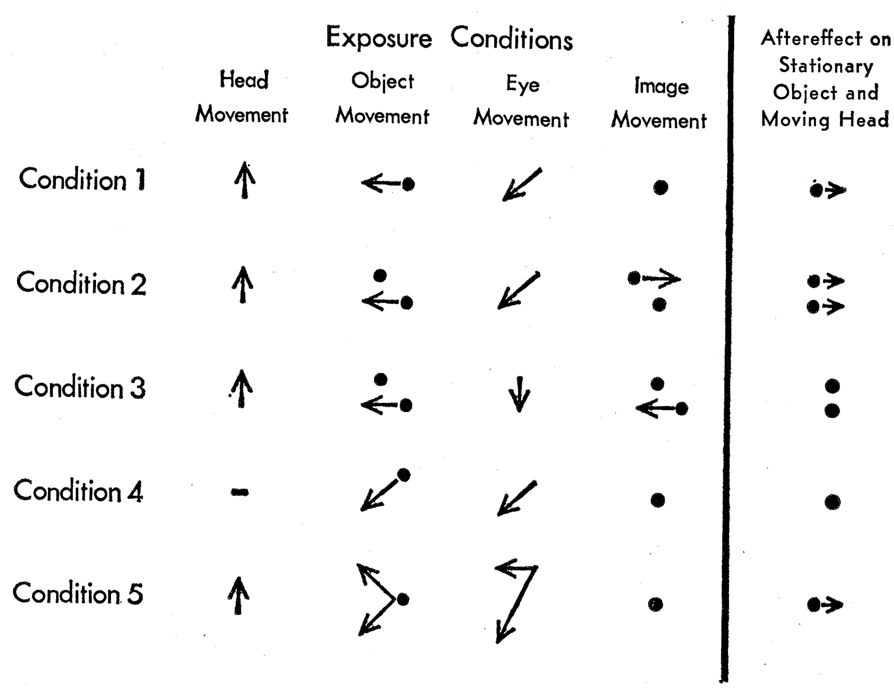

Fig. 1. Exposure conditions that induce adaptation (1, 2, 5) and those that do not (3, 4). The vector sum of head movement and object movement determines the vector sum of eye movement and retinal image movement. Only the conditions for upward head movement are illustrated; those for downward head movement are the reverse. In condition 5, the vertical movement of the object varied over time, independently of head movement, as did the vertical component of eye movement. The critical condition for adaptation is that a vertical head movement be paired with a horizontal component of eye movement.

gain of the CRO input until the object no longer appeared to move. For the object to appear stationary immediately after 10 minutes' exposure, it had to undergo 12.0 percent of the motion experienced during exposure (S.E. = 0.9 percent). The aftereffect was also found to persist if a stationary luminous frame was placed around the luminous spot, thereby distinguishing it from the spontaneous movements luminous spots sometimes appear to undergo in wholly darkened rooms.

The next step in testing the theory was to see if this new perceptual adaptation required the recorrelation of eye and head movement. A second, stationary spot was added to the screen (by using the second channel of a dual-trace oscilloscope). During exposure the subject could now be told to keep his eyes trained on either the moving spot (condition 2, Fig. 1) or the stationary spot (condition 3, Fig. 1). An adaptation was found only in condition 2, where the correlation of eye and head movement had been rearranged. Ten of the 12 new subjects tested reported the aftereffect shown in row 2, Fig. 1. This aftereffect surprised the subjects, since the two spots moved together, rather than separately as in the exposure period. The exposure condition could not be compensated for by a rotation of the eyes; the aftereffect indicates that the adaptation was a rotation of the visual field, a compromise between what the exposure condition required and what eye movements could achieve. In condition 3 (tested in counterbalanced order with condition 2), where the correlation between eye movement and head movement had not been rearranged, only one of the 12 subjects reported an aftereffect, and that was of the form found in condition 2. The difference between the two conditions is significant at the .01 level ($\chi^2 = 7.13$).

The final tests of the theory were designed to determine whether diagonal eye movements, as occurred in conditions 1 and 2, were important in themselves for the adaptation. In condition 4 (Fig. 1) the subject's head was held stationary during the exposure period, and the spot on the screen was made to undergo the same diagonal movement relative to the head as in condition 1, by applying a ½-hz sine wave to both the horizontal and vertical amplifiers of the oscilloscope. None of the 12 subjects reported an aftereffect, after exposure for 7 minutes, when given the usual test of nodding their heads while gazing at the stationary spot.

The same group of 12 subjects was tested, in counterbalanced order, on condition 5 (Fig. 1), where the regular diagonal eye movement was eliminated, but the correlation between eye and head movement was preserved by moving the spot vertically on the screen asynchronously with the head movement, while allowing it to move horizontally in synchrony with the head. The spot moved in a varying Lissajou's pattern during head movement, and the tracking eye movements were correspondingly varied. However, the horizontal component of eye movement was still exactly correlated with vertical head movement. After 7 minutes' exposure, 11 of the 12 subjects reported the same aftereffect as in condition 1. The difference between conditions 4 and 5 is significant at the .005 level ($\chi^2 = 9.09$). Eight of the subjects showing an aftereffect reported not having been aware, during the exposure period, of the correlation between spot movement and head movement.

These results are consistent with recent findings on perceptual adaptation to a fixed displacement of optical directions from the head, which indicate that eye-positioning responses play an important role (*6*). The results offer a contrast to another type of visual-movement adaptation, the "waterfall aftereffect" that follows prolonged viewing of unidirectional movement. For the latter, movement of the image across the retina, rather than eye movement, seems to be the inducing factor (*7*).

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References and Notes

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Adaptation and Negative Aftereffect to Lateral Optical Displacement in Newly Hatched Chicks

Abstract. *Chicks wearing hoods containing 8.5-degree wedge prisms from the day of hatching showed both significant reduction in the average lateral displacement of pecking (adaptation) and significant pecking overcompensation in the direction opposite to the original displacement (negative aftereffect) when matched 0-degree plates were substituted for the prisms on the 8th day.*

Domestic fowl reportedly lack the capacity to adjust to altered visual input. Pfister (*1*) has reported that two adult hens were unable to adapt to monocular left-right reversal after a period of 3 months. Hess (*2*) reported that newly hatched Leghorn chicks were unable to adapt to 7° of lateral optical displacement during the first 4 days after hatching; but they did show a reduction of their pecking errors comparable to that of hooded chicks for which no displacement occurred.

The negative results reported in these two studies have been used as support for the position that the ability to adapt to displaced visual direction is limited to the higher primates (*3*) or at least to mammals (*4*). Hess (*2*) predicts that no negative aftereffects would occur after removal of the prism displacement since this would involve performing a response which is antagonistic to an instinctive one.

I have tried to determine whether chicks could adapt after more extended exposure to displacement, and, if they can, to demonstrate a negative aftereffect to lateral optical displacement. Positive results would require reexamination of the prevailing current theory concerning the phylogenetic limitations of adaptation to altered visual input.

Twenty-eight newly hatched White Leghorn cockerels were fitted with latex hoods with 8.5° (15 diopter) prisms mounted binocularly in the hoods (Fig. 1). Half of the chicks had base-right