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Additivity of aftereffects of maintained head and eye rotations: An alternative to recalibration

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Seven groups of 10 subjects each were exposed to various combinations of left and right head and eye rotations for a period of 10 min. Both head and eye produced significant aftereffects of prior position as measured by pointing at a visible target with the unseen hand, but there was no significant interaction. Thus, aftereffects of sustained head and eye rotation were shown to be additive and to account fully for the results of Craske and Crawshaw (1975). Eye muscle potentiation rather than recalibration may be assumed to be the cause of the altered direction of gaze resulting from exposure to displacing prisms.

The thesis recently has been advanced (Ebenholtz, 1974; Ebenholtz & Wolfson, 1975) that the susceptibility of skeletal muscle to aftereffects of sustained innervation, first described by Kohnstamm (1915) and later by Matthaei (1924) and others, is characteristic also of the extraocular muscles. For example, maintaining an asymmetrical ocular posture causes a reflexive deviation of the globes in the direction previously held when the attempt is made to gaze straight ahead (MacDougall, 1903; Park, 1969). The rule applies equally for conjugate positions of gaze as well as disjunctive positions in which the optical axes are maintained at some angle with respect to each other. In the latter case, the aftereffect will be in opposite directions for each eye (Ebenholtz, 1974; Ellerbrock & Fry, 1941). Although these effects have been known for a long time, they have not been previously identified as members of a common class of muscle aftereffects, with a shared set of causal conditions, probably related to the phenomenon of posttetanic potentiation (Hughes, 1958). As a result, there has been a tendency to offer quite disparate and unique explanatory schemata for each individual instance. Thus, Park (1969) suggested adaptation of the system presumed to monitor centrally issued efferent signals to the oculomotor centers, while the work of Ellerbrock and Fry (1941) has led to speculation in terms of the aftereffects of the fusional reflexes (Ebenholtz, 1970). On the other hand, parsimony and the development of theory require consolidation of phenomena and concepts, wherever justified.

Consistent with this point of view, it may be noted that because prisms, which are frequently used in the study of perceptual adaptation, tend to provide asymmetrical ocular postures when worn before the eyes, there are rather direct implications of the eye-muscle aftereffects for an understanding of prism adaptation. This is perhaps especially clear in the link between the registration of ocular position and the appreciation of visual direction and in the role of the oculomotor cues in the perception of distance. In these cases, a misjudgment in the direction of gaze or in the degree of convergence will yield corresponding errors in apparent direction and distance, respectively.

In order to deduce the various perceptual aftereffects of eye-muscle potentiation (EMP), it is necessary to assume that as a result of a period of maintained tension, either isometric or isotonic, there will be a subsequent period of continued innervation of the ocular muscles that will last beyond the point of attempted relaxation. Furthermore, it must also be assumed that the continued innervation is reflexive in the sense that it cannot be compensated for and is the mechanical equivalent of a hidden load attached to the muscles. Because of this hidden load, the innervation pattern utilized to drive the eyes must be abnormal, and it is this abnormal innervation pattern that ultimately leads to the erroneous registration of ocular position.[1] Consider, as an example, the aftereffects induced by a maintained deviation of the eyes to the right. In this case, when fixating a target that is truly straight ahead of the subject, the left lateral and right medial recti must be extraordinarily innervated in order to overcome the reflexive innervation acting to rotate the eyes in the rightward direction. Since the registration of ocular position is dependent only upon the nonreflexive component of innervation, a leftward eye position will be signaled when fixating straight ahead and the eyes actually will deviate to the right when felt to be straight ahead. The latter is precisely the result of position tests taken after exposure to base-left wedge prisms (e.g., Craske, 1967; Kohler, 1964). Consequently, the present formulation represents an alternative to the postulation that prism adaptation entails a recalibration of the mechanism that normally subserves the registration of eye position.

Craske and Crawshaw (1975) have offered a test of the present interpretation of prism adaptation by having subjects view their feet for 6 min through leftward displacing prisms (20 D base right) but with ocular deviation 13.7 deg to the right. The recalibration hypothesis advocated by Craske and Crawshaw entails a change in registered eye position resulting from prism adaptation such that the position of the eye when it is felt to be straight ahead will actually be displaced to the left in the direction of prismatic shift. Thus, after removal of the prisms, the eye will be felt to be to the right of its true location and hence a rightward error is to be expected when pointing at and fixating a visual target truly in the median plane. On the other hand, because of the rightward deviation of the eyes when viewing the feet, and for the reasons already given, the EMP approach requires a leftward error on the same pointing task.

It remains to be noted that in order to satisfy their viewing requirements, subjects had to turn their heads to the left by 25 deg, a condition that Craske and Crawshaw regarded as unlikely in itself to produce aftereffects. The results showed a significant pointing error of 2.44 deg to the right, and the authors therefore claimed support for the recalibration concept. Actually, aftereffects of maintained asymmetrical head position do occur. Howard and Anstis (1974) showed that as a result of holding the head 24 deg to the right, the head felt straight ahead when rotated 6 deg to the right.[2] Similar effects of pointing with the unseen hand at a position regarded as straight ahead of the nose also were obtained. Thus it is possible to interpret the outcome of Craske and Crawshaw (1975) in terms of the algebraic sum of the aftereffects of head and eye position on the assumption that the aftereffect of a 25-deg leftward head turn is greater than the aftereffect following a 13.7-deg rightward eye turn. However, empirical support is required for this conclusion for two reasons. First, although Howard and Anstis (1974) showed a proprioceptive change in head position, no effect on the location of a visual target was demonstrated. Second, there is no evidence that aftereffects of eye and head position are additive or that they could cancel when in opposed directions. The experiment reported below treats these issues by examining the aftereffects of combinations of head and eye rotations.

METHOD

Seven groups of 10 subjects each were tested before and then after a 10-min exposure to asymmetrical eye (E) and head (H) positions, either to the left (L) or to the right (R). Head position was specified relative to the median plane of the trunk, while eye position was taken relative to the head. The six conditions to which subjects were assigned alternately were HL-25°, EL-25°; HL-25°, E-0°; HL-25°, ER-25°; H-0°, EL-25°; H-0°, E-0°; and H-0°, ER-25°. The seventh condition, HL-25°, ER-13.5°, was run after completion of the others. Testing was accomplished in the dark with the eyes in primary position and the head held straight ahead and secured with a strap in a chin- and foreheadrest.

The subjects fixated the center dot of a dim visible target surrounded by a ring of six additional dots with a diameter of about 1.5 cm. The target produced a visual angle of 2.9 deg of arc. The target was at 30 cm from the vertical axis around which the head and headrest pivoted in the exposure conditions. This axis was in the plane that was tangent to the anterior surface of the corneas and was perpendicular to the interocular axis at its midpoint. While fixating the target, the subjects moved the left index finger in a thimble-like device that could be moved in a track along a 45-deg arc, 22.5 deg left and right of center, at a radius of curvature of 30 cm. The task was to place the finger at a position felt to be directly below or in the same radial direction as the visible target. One setting was made at each of two starting positions, 15 deg on either side of the true position. Prior to the two pretest matches, the subjects dark-adapted for 3 min and made two practice settings of the slide. The difference between the means of the two settings taken before and again after the exposure period constituted the data of the study. During the exposure period, eye position was controlled by having the subjects fixate a small red-light-emitting diode placed in position according to the required eye and head rotation.

RESULTS AND DISCUSSION

The data of the initial six groups were analyzed in a factorial analysis of variance with two levels of head position (25 deg left and undeviated) and three levels of eye position (25 deg left, primary position, 25 deg right). Head position was significant, $F(1,54) = 22.80$, $p < .01$, as was eye position, $F(2,54) = 8.81$, $p < .01$. There was, however, virtually no sign of an interaction, $F(2,54) = .04$, $p > .05$.

These results, represented in Figure 1, provide clear answers to the issues posed earlier. First, aftereffects of maintained head rotation are indeed manifest in altered visual positions of the fixated target. The aftereffect of a pure head rotation of 4.41 deg was surprisingly large, given the modest 10-min inducing period and the 25-deg left head turn, and amounted to 17.6% of the theoretical maximum of 25 deg. The corresponding pure ocular rotation

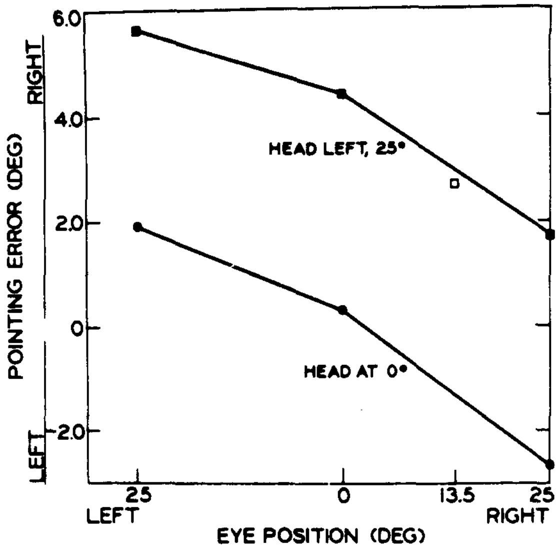

Figure 1. Aftereffect magnitude as a function of eye position for two levels of head rotation. The unfilled square represents results obtained by approximating the head and eye rotation used in the prism adaptation study of Craske and Crawshaw (1975).

yielded an aftereffect of 1.94 deg, or only 7.8% of maximum. Assuming both effects reflect the muscle potentiation phenomenon, then the greater effects of neck muscle over eye muscle may be related in part to the greater size of the former over the latter. This would accord with the early observations of Matthaei (1924) on the relation between muscle size and aftereffect magnitude.

The second issue concerning the additivity of head and eye aftereffects also has a clear answer. Within the range of values tested, the two aftereffects are quite independent and an additive model yields excellent predictions. The results of the seventh group using values close to those used by Craske and Crawshaw (1975) also demonstrate the validity of this approach. A 10-min head turn of 25 deg left together with an ocular rotation of 13.5 deg right produced a net aftereffect of 2.72 deg right, which differed significantly from zero, $t(9) = 3.49$, $p < .01$. This is in favorable comparison with the mean value of 3.00 derived by interpolation from the graph itself. The main point, however, is that the results of Craske and Crawshaw (1975) can be fully accounted for and therefore are best interpreted in terms of the additivity of the aftereffects of head and eye rotation and not as evidence for the recalibration notion.

Previous research (Ebenholtz, 1974; Ebenholtz & Wolfson, 1975) has presented evidence that EMP effects may underlie several forms of prism adaptation in that EMP is capable of producing eye-specific aftereffects of opposed direction and also aftereffects that are manifest as an error in the convergence cue to distance. The present work makes it feasible to assume that EMP underlies the visual aftereffects obtained as a result of exposure to laterally displacing prisms as well. Because of the importance of the notion of adaptation in a theory of visual perception, special care should be taken in determining whether, in cases of prism exposure, oculomotor recalibration has in fact occurred. This requires control methods for EMP in which both stimulus conditions and measurement procedures are applied equally to prism and EMP control groups, respectively. This is particularly critical because so little is known about muscle potentiation, especially as applied to eye muscle, but an example of this point is available. It is related to the role of muscle inhibition as a probable source of release from the effects of EMP.

The rationale is simply that if muscle tension causes the aftereffect, then if tension is reduced during the exposure period the aftereffect will be lower than otherwise or will take longer to develop (Ebenholtz & Wolfson, 1975). Furthermore, even if the aftereffect has been attained, its magnitude may be attenuated by relaxing the muscles in question. Since the extraocular muscles operate according to Sherrington's law of reciprocal inhibition, there exists a "natural" method to reduce muscle tension and hence the aftereffect itself, namely to rotate the eyes in the direction opposite that used during the induction interval. Since innervation of the agonist requires inhibition of the antagonist, the aftereffect will dissipate rapidly when measured under conditions that permit or encourage eye movements. The failure to detect aftereffects of sustained ocular deviation (Craske, 1967), their rapid decay relative to the effects of prism exposure (Craske & Templeton, 1968), and the poor effects of eye centering (i.e., moving the eyes until they are felt to be straight ahead), relative to the results of measuring the resting position of the eye, i.e., the momentary position of the eye when its eyelids are opened and with no attempt at voluntary positioning (Craske, Crawshaw, & Heron, 1975), may all be explained in terms of the differential presence of uncontrolled eye movements.

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NOTES

1. The same conclusion holds whether an inflow or an outflow model of ocular registration is proposed, since in both cases the reflexive component of the innervation pattern is ignored. In the former case, the muscle feedback would be abnormal, and in the latter case, the monitored efference would be abnormal, for the actual ocular posture assumed.

2. Subjects in the Craske and Crawshaw (1975) study tipped their heads forward to view the feet and then rotated the head, chin toward the left shoulder. In the present study and in Howard and Anstis (1974), subjects rotated the head in the horizontal plane. This difference is not critical since informal observations on several subjects revealed similar head-position aftereffects when the posture of the Craske and Crawshaw subjects was followed.

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