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Notes and Comment

Sensory effects of eyepress are due to efference

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The apparent motion of the visual world that results from pressing on the lid of the eye can be used to infer aspects of visual neurophysiology (Descartes, 1664/1972). The classic interpretation of the effect is that the eyepress passively moves the eye without a corresponding oculomotor effort of will (Helmholtz, 1867). In modern terms, there is a mismatch between the moving retinal image and the constant corollary discharge (CD).

In a recent paper in *Perception & Psychophysics*, Stark and Bridgeman (1983) demonstrated that under some circumstances this interpretation is backwards. The perceived image translation comes not from a motion of the retinal image, but from a successful oculomotor effort (and CD) to prevent the eye from rotating. In these instances, the extraocular musculature resists a passive rotation of the eye such that a fixation on a target is maintained while the eye is pressed (Bridgeman, 1979).

The strongest test of the activity of the oculomotor system during the eyepress came from recordings of the position of the fellow eye, occluded and not pressed. This eye underwent a secondary deviation in the same direction as the apparent motion during a press of the seeing eye (Stark & Bridgeman, 1983, Figure 4), proving that the binocular Hering's law innervation had changed with eyepress. The lack of such a secondary deviation in darkness showed that the source of the deviation was outflow rather than inflow. In darkness, the pressed eye moves passively, having no target to elicit stabilization of gaze, so that no change in innervation (outflow) can be generated from a CD. The moving eye should still excite proprioceptors in the extraocular muscles and tendons (inflow). If inflow from those muscles were corrected with an oculomotor innervation, the results of the changed innervation would be apparent in the fellow eye.

A recent comment in *Perception & Psychophysics* (Hershberger, 1984) shows that there is still more to learn about the eyepress maneuver. Hershberger reports that horizontal motion is in phase with the eyepress when the eye is adducted 30°. As Stark and Bridgeman (1983, p. 374) note, the direction of apparent deviation with eyepress is dependent on gaze position; horizontal apparent motion was greatest with a press on the outer canthus of the eye when gaze was slightly elevated, whereas downward and slightly temporal gaze yielded vertical apparent motion. We also find in-phase apparent motion, as Hershberger reports, with 30° adduction if the gaze is directed downward as well, so that one is looking just past the tip of the nose. Our observations do not conflict with Hershberger's, because he did not report the vertical deviation required. (There are also large individual differences in the direction and amount of apparent motion for a given eyepress.)

Hershberger maintains that since out-of-phase apparent motion can be accounted for by retinal image motion or by efference, in-phase motion must be due to extraocular afference. There is no evidence whatever for this assertion, and closer observation shows that it is false.

In fact, inflow theories predict out-of-phase apparent motion. As the fixating eye is pressed, the medial translation of the eye will shorten the lateral rectus. This shortening will elicit an inflow signaling abduction, and the abduction accompanied by lack of motion of the retinal image will create a perception of motion out of phase with the eyepress. (This argument applies regardless of gaze position.)

Nothing that is known about the kinematics of the eyepress suggests that in-phase motion should be due to afference; rather, the direction of the deviating force depends upon position of gaze, direction of eyepress applied, and strength of the eyepress. As gaze position or direction of applied pressure is varied, there is a continuous transition from out-of-phase apparent motion, to vertical motion, to in-phase motion without discontinuities. Unfortunately, existing models of oculomotor kinematics cannot be used to study these effects quantitatively because the eye is translated medially during eyepress (Bridgeman & Stark, 1981; Stark & Bridgeman, 1983), and the models assume a fixed center of rotation.

In order to demonstrate that in-phase apparent motions are elicited by the same mechanisms as out-of-phase motions, we have compared secondary deviations and ocular translations for the two directions of apparent motion. We also present the first illustration of the lack of secondary deviation with eyepress in complete darkness.

Method

Horizontal movements of the right eye were recorded with paired infrared photocells and an infrared LED light source based on the method of Stark, Vossius, and Young (1962). The subject was stabilized with a bite bar. The photocells and LED are attached to the stalk holding the bar, leaving the visual field unobstructed. This method gives better resolution and fewer artifacts than mounting the apparatus on spectacle frames. The system was calibrated to be linear for a 16° range centered about the subject's centerline.

The left eye was pressed under three conditions: (1) out-of-phase apparent motion, structured visual field, (2) in-phase apparent motion, structured visual field, and (3) in-phase apparent motion, complete darkness (downward adducted eye). The only difference between the first two conditions was the position of gaze (upward centered vs. down-

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ward adducted). The third condition should show secondary deviations from inflow, but no deviations if only outflow drives eye positioning.

Translation of the eye in the orbit was determined with the method of Stark and Bridgeman (1983). A millimeter scale was mounted 114 cm from the subject's eye, and a vertical reference line was mounted halfway between the eye and the scale. Apparent deviations of the line with respect to the scale then correspond to translations of the eye in the orbit as it is pressed. Translations were measured for the gaze positions of in-phase motion and out-of-phase motion. Because magnitudes of translation were small for the former position, the eye was moved to 28.5 cm from the reference line, so that 2 mm of translation on the screen represented 1 mm at the eye.

Results

Figure 1 shows eye movements obtained during the three conditions of exposure. Condition 1 is a replication of Stark and Bridgeman (1983, Figure 4), with similar results. Consistent deviations of the fellow eye are observed out of phase with the eyepress; the fellow eye rotates medially when the seeing eye is translated medially. Condition 2 shows that the oculomotor compensation is in phase with the eyepress if the apparent motion is in phase. In both of these conditions, the direction of psychophysical apparent motion predicts the direction of secondary deviation. Condition 3 shows that an eyepress in darkness with the eye in the in-phase position does not produce a secondary deviation, contradicting Hershberger's assertion that inflow is involved at this position of gaze.

Translation measurements showed that the eye translated in the orbit in phase with the press at both gaze positions. The translation was smaller in the in-phase position (2 mm for the first subject and 1 mm for the second) than it was in the out-of-phase position (3 mm for each of two subjects).

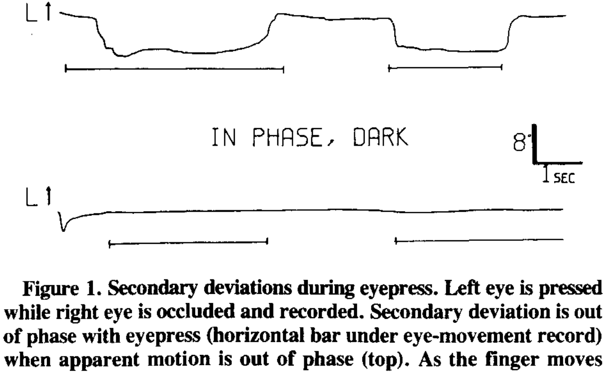

Figure 1. Secondary deviations during eyepress. Left eye is pressed while right eye is occluded and recorded. Secondary deviation is out of phase with eyepress (horizontal bar under eye-movement record) when apparent motion is out of phase (top). As the finger moves to the right to press the left eye, both the apparent motion and the secondary deviation are to the left. For in-phase apparent motion (middle), eye deviation is reversed. In complete darkness (bottom), no deviations are apparent. Note the lack of microsaccades in darkness.

Medial translation of the eye with in-phase motion can be observed directly by looking at a distant object that is nearly occluded by the tip of the nose. An eyepress will occlude the object even while the image appears to move in phase with the press. Direct observation of the eye during in-phase motion suggested that the eye was being pressed back in the orbit as well as medially.

Discussion

Far from implicating inflow, a test of Hershberger's assertions has strengthened the case for outflow as the only source of information contributing to compensation for ocular deviations due to eyepress. Secondary deviations in the fellow eye with a visual target, along with lack of secondary deviations in darkness, indicate that outflow contributes to movement of the fellow eye but that inflow does not.

The need to explain how both in-phase and out-of-phase apparent motion can be elicited along with medial translation of the eye remains. Both our psychophysical evidence and our eye-movement evidence indicate that an eyepress in the in-phase gaze position elicits an abducting rotational force on the eye that is countered by an adducting innervation, with a corresponding adducting apparent motion, and abduction of the occluded fellow eye. Our explanation of this seeming paradox is that the pressed eye, when in a medial position of gaze, cannot easily adduct further because the protuberance of the cornea meets the tissue surrounding the bony orbit. Thus, the eyepress pushes the eye posteriorly in the orbit (because of the roundness of the globe) and exerts an abducting rotational force with its center of rotation anterior to the center of the eye. This hypothesis would also explain the smaller-than-normal translations measured in our psychophysical observations.

The kinematics of the seemingly simple eyepress have turned out to be surprisingly complicated, for the effects of eye translation are influenced by the six extraocular muscles, the suspensory ligaments, the orbital fat, and the distortion of the eye itself. Distortion of the globe is revealed by the deterioration of optical quality as the eye is pressed. The vector of the pressed direction on the eye is also difficult to control, and may contribute substantially to the individual differences in perceptual effects of eyepress. As Bridgeman and Stark (1983) noted, extensive practice is necessary for subjects to bring these variables under control and obtain consistent psychophysical results.

Finally, our results contradict Hershberger's prediction that the results of Skavenski, Haddad, and Steinman (1972) "surely would have" been dependent on gaze position. Since Skavenski et al.'s elegant contact-lens method gives objectively definable rotational forces on the eye, gaze position does not affect the results. Thus, it is understandable that Skavenski et al. preferred to work within the "smaller fixation space" (Hering, 1868/1977) where the relationship of oculomotor effort to gaze deviation is linear and where people keep their eyes most of the time. Our results are in agreement with those of Skavenski et al. The seemingly paradoxical effects of the in-phase eyepress can be completely explained by the abducting force applied in this case, as revealed by both psychophysical and oculomotor measures.

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