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Extraretinal Eye Position Signals Determine Perceived Target Location when they Conflict with Visual Cues

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To examine the role of extraretinal eye position information (EEPI) in visual perception of target location in normal room illumination, subjects participated in experiments in which EEPI was manipulated using the eye press maneuver with either monocular or binocular viewing. The viewing condition and eye press caused EEPI and retinal information about target location to conflict. Pointing responses in eye press trials were all in the direction of EEPI showing that EEPI is the dominant source of information in egocentric visual space perception. In binocular viewing, version and vergence occur in response to the eye press to maintain fusion and EEPI based on these movements also determine perceived location. An unanticipated finding was that the eye press was variable in its effectiveness in rotating the eye, which contributed to large variability in pointing errors and suggested the method would be a poor choice for future work. © 1997 Elsevier Science Ltd. All rights reserved.

Extraretinal Outflow signals Strabismus Vergence Perception of location

INTRODUCTION

In the experiments described below, we found that subjects pointed to a new position when extraretinal eye position information (EEPI) was manipulated but all other retinal cues to target location were held constant in a normally lighted room. The results support the idea that EEPI is essential to normal visual space perception in spite of claims that those percepts are based on retinal signals alone in normal scenes. The argument that EEPI is a key determinant of visual perception of target location implies that changes in EEPI predict changes in perceived target location. Although this hypothesis has been tested, controversy still exists regarding the role of EEPI in visual localization of targets (Skavenski, 1990; Matin *et al.*, 1982; Bridgeman & Fishman, 1985; Foley, 1985; Morrison & Whiteside, 1984). Some investigators concluded that EEPI is a primary determinant of perceived location when subjects point to targets (Hansen & Skavenski, 1985; Gauthier *et al.*, 1986, 1990) while others claim that EEPI is not important when the experimental conditions require subjects to verbally describe target position (Skavenski *et al.*, 1972; Gogel & Tietz, 1979; Matin *et al.*, 1982). These apparent disparities may be explained by reports that several factors influence the effectiveness of EEPI in perception: visual condition (e.g. monocular vs binocular viewing), visual field structure and the method used to measure space perception (Gogel, 1977; Gogel & Tietz, 1979; Matin *et al.*, 1982; Bridgeman & Fishman, 1985; Stark & Bridgeman, 1983).

Investigations performed to date have been limited to either measuring the effect of EEPI on perceived horizontal location of targets with monocular viewing, or measuring perceived distance of targets with binocular viewing. Investigations limited to binocular viewing reported that extraretinal signals that accompany vergence changes altered depth perception, and that EEPI predominated over either accommodation or parallax cues (Gogel, 1977; Gogel & Tietz, 1979; Morrison & Whiteside, 1984). Monocular viewing experiments report that although EEPI was a determinant of localization, its role was minimized when the background was illuminated (Matin *et al.*, 1982; Bridgeman & Fishman, 1985). Only Stark and Bridgeman (1983) reported that EEPI remained dominant in localization with monocular viewing of single points of light in a structured visual field, but only when pointing was used to measure perceived location. These investigators and others found that EEPI did not influence verbal reports of perceived location, or subjects' judgements of perceived straight ahead position as indicated by either pointing or verbal

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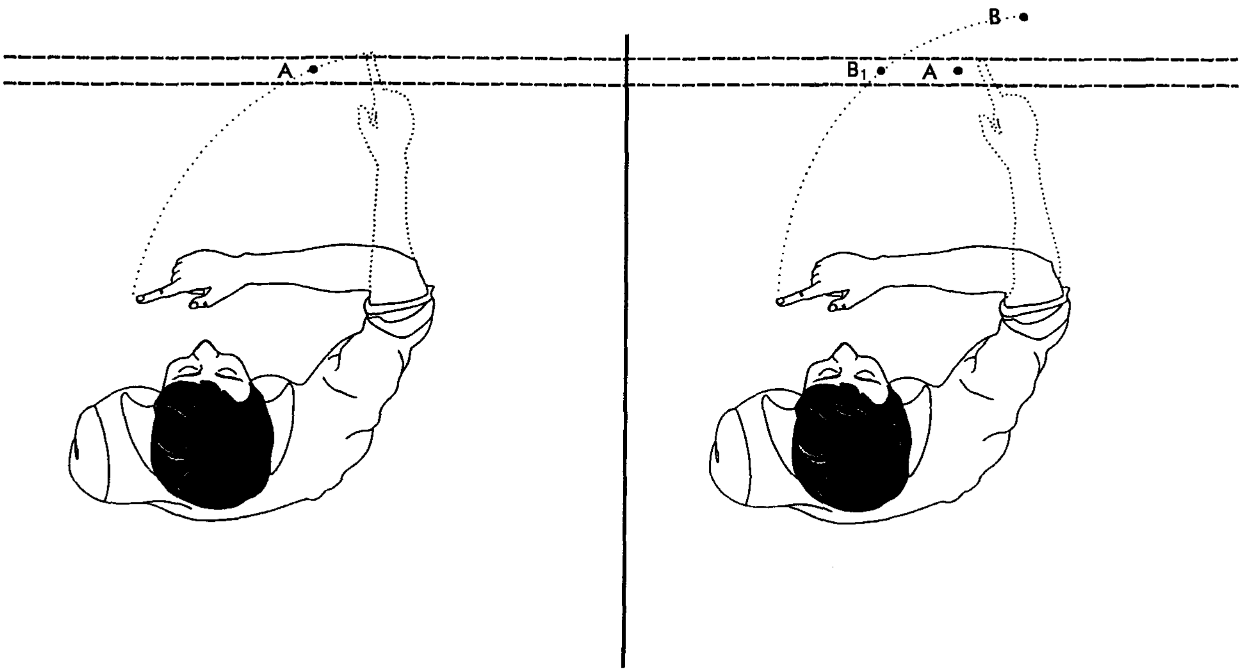

FIGURE 1. Misinterpretation of pointing data. Pointing to a target (point A) presented on a surface which mechanically stops the "pointer", may result in erroneous interpretation of pointing data. As seen in the figure, if point A is perceived to be at location B, but the surface interrupts pointing at location B_1, it can be mistakenly assumed that perception shifted to the left instead of further away.

response (Gogel, 1977; Bridgeman *et al.*, 1979, 1981; Stark & Bridgeman, 1983; Bridgeman & Fishman, 1985; Bridgeman & Graziano, 1989). These results suggest that the visual space perceptual system may have two modes of operation: a motor component that utilizes EEPI and a cognitive component that does not.

Bridgeman *et al.* (1979, 1981) proposed that the motor-oriented visual perceptual system, represented by a motor task such as pointing, is dependent on the spatial information obtained from EEPI cues. Conversely, verbal report, representing the cognitive visual perceptual system, is based on conscious awareness of where an object is, and does not use EEPI when it conflicts with retinal information. However tempting it may be to accept this dichotomous resolution it is unsatisfactory because it does *not* explain a very well known phenomenon: the apparent shift of the world everyone can obtain by simply pushing on the eye to change EEPI alone. An alternative analysis, based on egocentric visual direction, attributes the apparent shift to a change in the location of the point of intersection of the visual axes of the two eyes (Ono, 1991). According to Ono (1991), the two oculomotor subsystems of version and vergence work to maintain the object of fixation at the intersection and avoid double vision. Movement of either eye by the eye press results in a change of visual direction, or the location of the intersection of the axes, and thus an apparent shift in the location of the object. However, this hypothesis does not eliminate the problem regarding the discrepancy between pointing and verbal indicators of perceived location. The experiments discussed here used both methods, pointing and verbal response, of assessing perceived direction. We also failed to get good agreement between these methods but the reasons for discrepancy appear to be in the subject's inability to capture the complex movement in the verbal response, and not in the failure of EEPI to participate in spatial cognition.

Although pointing is an intuitively sound method of indicating location, the inherent inaccuracy of pointing responses must be controlled or minimized. For example, pointing accuracy is improved when ballistic, goal oriented arm movements are used (Bock, 1986; Hansen & Skavenski, 1985). We use this method in the measurements which follow. Also, the interpretation of pointing data may be confounded by limitations imposed by a preselected pointing movement pattern (Bard *et al.*, 1985; Bock & Daunicht, 1987; Bock & Eckmiller, 1986). It is possible that limiting mechanical arrangements of the pointing task would produce spurious errors in the subject's indication of perceived target location. For example, if a vergence change caused a subject to perceive a dot to be further away than the surface of presentation, although the subject extends the arm and leans forward to point further away, the pointing hand would be stopped short at the surface of presentation (Fig. 1). The horizontal location of the response would land to the left of target position because the hand is traveling in an arc, and the perception inferred from this response would be erroneously interpreted as having shifted to the left, when in reality, the subject was indicating it shifted only in depth. To eliminate this type of error, and because changes in EEPI have been reported to affect perceived depth as well as horizontal location (Skavenski *et al.*, 1972; Foley & Richards, 1972; Foley, 1985; Morrison & Whiteside, 1984; Fiorentini *et al.*, 1985; Collewijn & Erkelens, 1990), we chose a response that let S indicate perceived location in both horizontal and depth dimensions.

Although several methods have been used to manipulate EEPI, the eye press has been preferred because it is non-invasive to the subject, allows participation of naïve subjects, and permits simultaneous investigation of inflow and outflow sources of EEPI in monocular viewing (Stark & Bridgeman, 1983). Stark and Bridgeman (1983) and Ilg *et al.* (1989) demonstrated that in monocular viewing, the only change in the position of the pressed viewing eye is translation, and not rotation, due to counteractive forces of the extraocular eye muscles. It should be noted that the method used to measure eye movement of the pressed eye in experiments presented here (camera method, see below) cannot discriminate between rotation and translation. The assumption that the movement is translation only is based on Ilg's data. In the unseeing eye, rotation, which is equivalent to the changed extraocular effort, and its accompanying outflow based EEPI occurs. In pilot experiments we found that the eye press was variable in its effectiveness in rotating the eye despite extensive attempts to make the press consistent and practicing our observers. The variable magnitude and direction of force applied to the eye led directly to variability in EEPI, which accounted for variation in the direction of pointing errors. This variation necessitated recording the positions of both eyes on each trial to quantify the change in EEPI and relate that change to perceived target location. In summary, to clearly delineate the role of EEPI in normal visual space perception, we measured visual localization with either monocular or binocular viewing in a well lit area. Perceived location was measured by rapid, open-loop pointing and verbal report. EEPI was systematically manipulated and measured on all trials while all other visual information regarding location of the target indicated the target remained in the same position. The purpose of our experiment was two-fold:

1. To determine the role of EEPI in perceived horizontal and depth location in monocular and binocular viewing with a visible structured visual field; and
2. To establish that in binocular viewing, the eye press results in a vergence change, which predicts a change in perceived depth of the target.

METHODS

Subjects

Three right-handed subjects, 30–48 yr of age with normal uncorrected visual acuity, participated in the monocular viewing experiment. Two of the subjects were naïve participants (AW and SR) and were emmetropic. Subject AS was an experienced participant in similar studies and knew the objectives of the experiment. He was beginning to become presbyopic but had no measurable phoria at the time of the experiments. AS and SR also participated under binocular viewing conditions. None of the subjects knew the results until all experiments were completed.

Procedure

Subjects fixated a target in a normally lighted area, and pointed to that target with their right hand, when cued, as rapidly and accurately as possible during trials with and without an eye press. During eye press trials subjects were instructed to apply a maintained press on the outer canthus of their left eye (the viewing eye in the monocular condition) with their left hand while maintaining fixation on the target. The cue to press on the eye was given 1 sec after the instruction to fixate the target and recording of eye position had begun. One second after the cue to press the eye, the room lights were extinguished, which served as the cue to the subject to point. Lights remained off for the entire pointing act, and until target paper was removed, to prevent subjects from visually guiding their finger onto the target or from receiving visual feedback regarding the accuracy of pointing. No feedback about their performance was provided to subjects until all sessions were completed. In binocular viewing trials, subjects were instructed to inform the experimenter if fusion was not achieved and maintained during the eye press. In those cases, the trial was immediately stopped and restarted.

The target was a black circle, 2 mm or 0.32 deg in diameter, presented on a white paper background at resting arms length for each subject. The target dots were presented one at a time on a horizontal platform just below eye level. Four target locations were used, each presented on 15 trials, both with and without eye press. Locations included: the straight ahead position for the right eye (point location 0), 3.2 deg to the right of 0, 6.4 deg to the left of 0, and 12.8 deg to the left of 0. Subjects were prevented from learning to point to target positions. It should be noted that such an outcome would counter the expected results following manipulation of EEPI. This was achieved by the presentation of target location and eye press in a randomized counterbalanced design, the use of a clean target paper for each trial, and subjects were never permitted to practice responses with any sort of feedback. This was replicated in binocular viewing.

Perceived target position was measured by rapid radial pointing movement to a target with the subjects' dominant arm. Subjects were seated at a table upon which the platform for target presentation was placed (with *ca* 20 cm between the subject and raised platform). Until cued to point, the subjects' right arm rested on the table at chest level with the elbow flexed. Subjects held a pencil in their right hands with the tip of the pencil as close to the tip of their index finger as possible. When cued, subjects raised the arm and moved the forearm radially to jab the pencil down on the target white paper to make a mark which would record their response. Errors in pointing were adjusted for individual subject's constant error by subtracting the mean error without a press for each target location, from all the responses

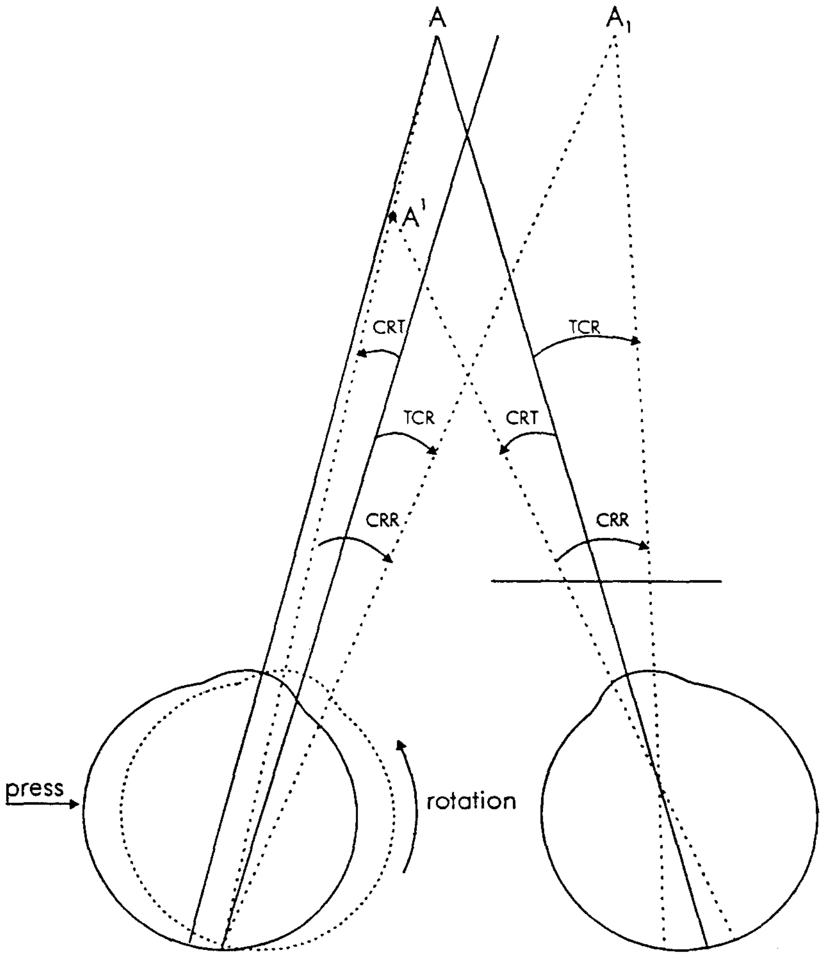

FIGURE 2. Complex response to the eye press in monocular viewing. Eye press on the left seeing eye causes a rightward translation (Tr), and a counterclockwise rotary force. The efferent response is a counter rotation to translation (CRT; efference at A^1) and a counter rotation to the rotary force (CRR). The net change in EEPI is represented by TCR. The left eye is always on A, but has the innervation for A_1. The right eye is on A_1 and has that innervation when the left eye is pressed.

made on eye press trials at that location for each subject. This provided a measure of error due to the press with individual pointing error bias removed. The position of the arm for this manual response was a bit awkward to subjects because it was necessary to adapt to the mechanical arrangement of the Eye Tracker.

At the end of each trial, subjects were asked to verbally report the perceived displacement of the target. The subjects verbally reported whether the perceived location of the target changed, and in what direction(s). However, these reports proved quite inconsistent both within and between subjects. They contributed only in a minor way to the results.

Throughout the testing session, the subjects' heads were stabilized by use of a forehead rest and a tight dental impression bite-board. In addition, they were required to hold their breath for the duration of each trial to avoid breathing translation artifacts in eye position recording made by the DPI Eye Tracker described below.

Eye movement recordings

Simultaneous two-dimensional recordings of the translations of the left eye and rotations of the right eye were obtained on all trials. Recordings began 1 sec before the verbal cue to press on the eye was given, and continued throughout the 4 sec trial (pointing was completed, but room lights were still off). Recording of translation in the pressed (left) eye was obtained from videotapes made on each trial by a Panasonic video camera placed 48 cm from the subjects and focused on the left eye and forehead. A ruler mounted on the forehead rest was visible, and allowed measures to be corrected for magnification and distortion due to the camera lens. During experiments, camera output was recorded and monitored by the examiner on a 12" black and white TV monitor to assure that the pupil was clearly visible throughout the trial. When experiments were completed, videotapes were reviewed frame by frame to obtain the measure of translation (Tr) in millimeters (mm) for each eye press trial. This measure was used to calculate the small counter rotation to compensate for eye translation (CRT) produced by the eye press using the following equation: CRT = Tr/distance.

Horizontal and vertical rotation of the occluded right eye, in response to a press on the viewing left eye, was measured using a Stanford Research Institute Generation V Dual-Purkinje-Image Eyetracker (DPI). Eye position analog voltages were low pass filtered with the cut-off at

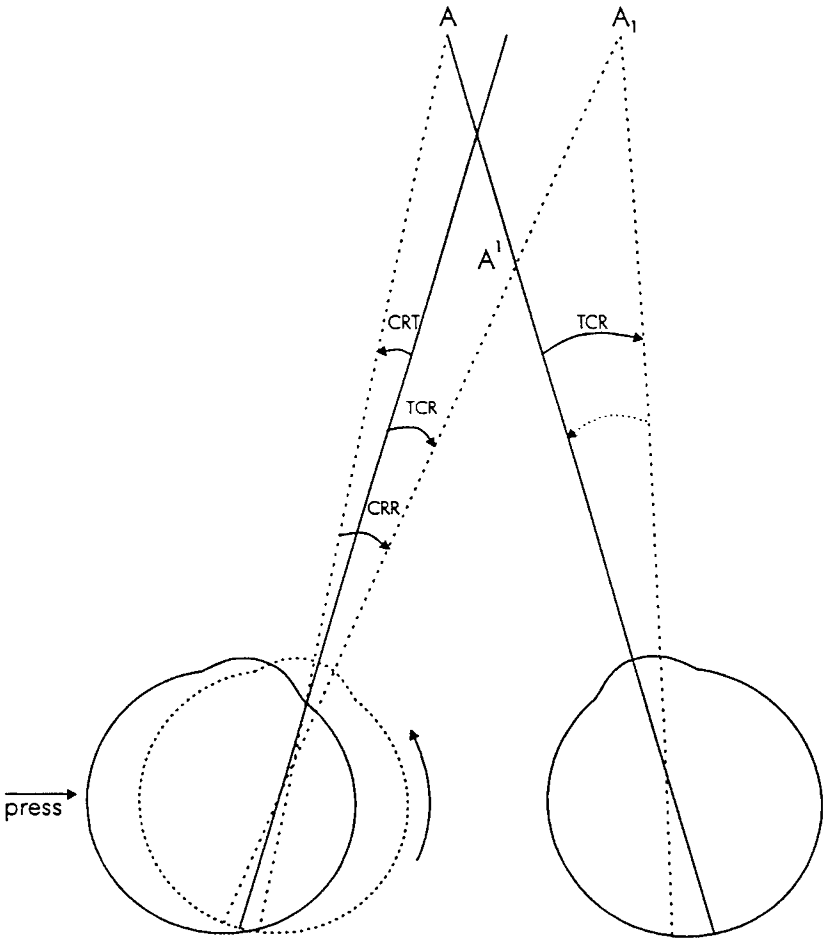

FIGURE 3. Vergence angle change in response to the eye press in binocular viewing. In binocular viewing, initial counter rotation responses are like that described and illustrated in Fig. 2 (component rotations of the right eye are omitted here to avoid clutter and confusion). The left eye has efference indicated by .... but is on A. The right eye is initially shifted to A_1, and must converge back to A by an amount equal to TCR to get fusion. This convergence sets EEPI to A^1 so that the target should appear to move slightly to the right and closer to the subject.

100 Hz and sampled at 200 Hz by a Data Translation A/D board on a PDP 11/73 computer. A black cloth was draped so that the visual field of the right eye was in total darkness in monocular trials. These eye position data provided the basis for the calculation of total counter rotation response (TCR) during the eye press trials, which coincides with the net change in EEPI.

Ideally, the DPI allows simultaneous measurement of the horizontal and vertical rotations of the eye with an accuracy within 5 min arc (Crane & Steele, 1979). The design of the DPI Eye Tracker allowed track lock with changes in focus values representing as much as 1 cm of head or eye translation in depth. However, such head translations resulted in large rotation artifacts of up to 2.5 deg of horizontal and vertical rotation of the eye. Several trials collected with a subject using a bite board and headrest as done normally, revealed that translations from breathing alone were large enough to produce unacceptable rotation artifacts. It was therefore necessary to request the subjects to remain perfectly still and hold their breath for the duration of the 4 sec trial. The experimenter monitored focus servo output from the tracker and discarded trials (total of 38%) if focus value changes were large enough to cause a rotation artifact >10 min arc.

Prior to the experiment, a calibration procedure was performed to determine linearity over the entire recording field of the tracker as well as the scaling factor for conversion of the arbitrary voltages output from the DPI to rotation angles in degrees. The subject was asked to fixate on a dot of light (0.14 deg diameter) at the straight ahead position for the right eye. The target was produced on an Ikagami TV monitor placed 1 m from the subject in an otherwise dark room. Right eye position was recorded for 2 sec. This was repeated at 1 deg intervals for 442 known positions on a 21×21 deg grid; a lengthy and tedious procedure for subjects. At the beginning of each session, for each subject, a condensed calibration procedure was completed to verify the detailed calibration by using 13 known horizontal positions (straight ahead and six positions to the right and left of straight ahead) and 11 vertical positions (straight ahead as well as five positions up and down from this position). Test–retest reliability of the horizontal and vertical eye rotation positions obtained with the DPI was tested using Cronbach's Alpha and found to be quite high ($\alpha = 0.978$; SD = 7 min arc).

Recordings obtained from the DPI Eye Tracker were converted to min arc using the scaling factors obtained from the calibration procedure. Mean eye position was then calculated for each second of the trial. The mean of the first second of data provided a measure of initial eye position (IEP). The eye that was pressed maintained fixation throughout the second and third seconds of each trial. Mean values of eye position of the unpressed eye during seconds 2 to 3 represent response to the eye press and were used as the measure of final eye position (FEP) during all trials. From these measures, TCR was calculated (FEP−IEP = TCR). The difference between TCR and the measure of CRT was calculated to obtain a measure of counter rotation to the rotation response (CRR = TCR−CRT; refer to Fig. 2). This was calculated for both horizontal and vertical rotations of the eye. Note that in the binocular condition, only IEP and CRT could be quantified because the right eye could also see the target, and to prevent double vision and fuse the target, a vergence movement occurred. That vergence movement canceled any initial counter rotations in that eye (Fig. 3).

RESULTS

Monocular viewing

Eye movement in response to the eye press. In response to the eye press, and as a consequence of Hering's Law, the non-seeing eye usually rotated to the right and down, which was due to CRR being rightward. The amount of translation, and therefore CRT was negligible as was its effect on pointing error. The rotary force exerted by the eye press (and therefore, TCR and CRR) varied in direction and quantity between and within subjects. CRR was rightward in 88, 84, and 66% of the trials for subjects AW, AS, and SR, respectively. The large variation in magnitude and direction of the eye's rotations in response to the eye press is illustrated in Figs 4 and 5. With no press, the eye remained, on average, within a circle of

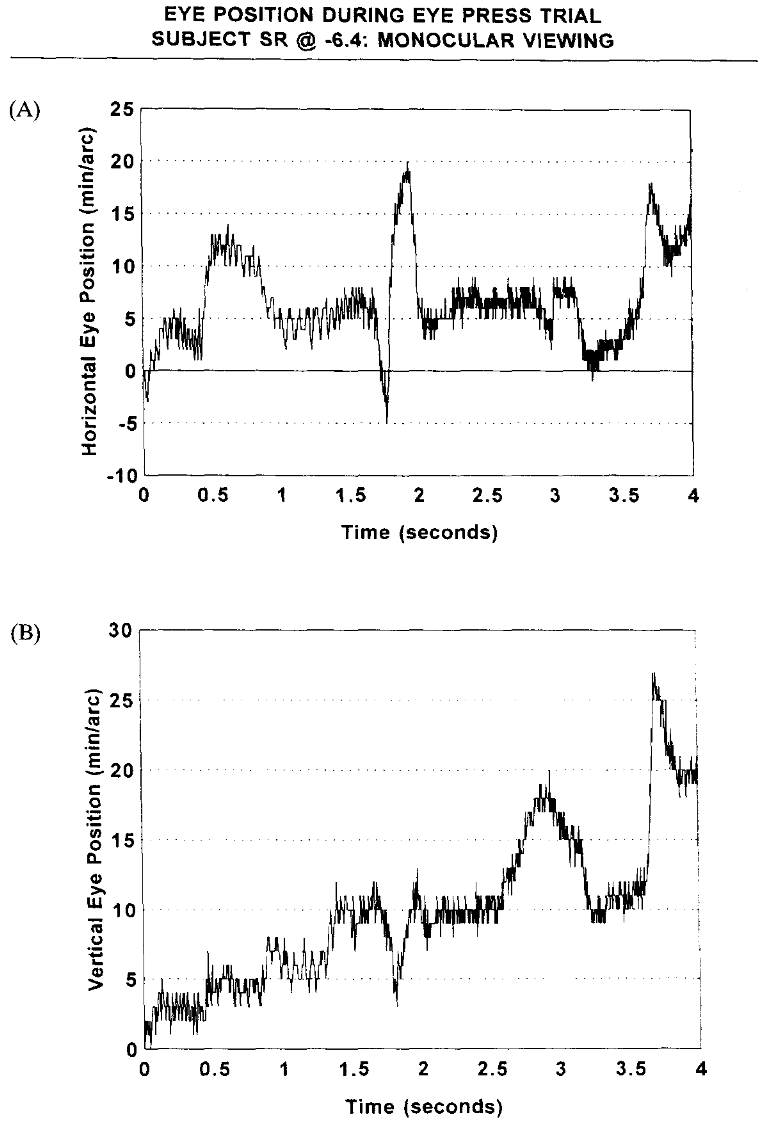

FIGURE 4. Rightward eye position change in monocular eye press trial: subject SR @ location −6.4. Horizontal (A) and vertical (B) eye position of the unseeing, unpressed right eye throughout a 4 sec trial with an eye press. The trial begins at 0 sec, with the press administered at the 1.75 sec mark and lights are extinguished at the 2 sec mark as the cue to point. Short line segments connect eye position samples taken at a sampling rate of 200 Hz.

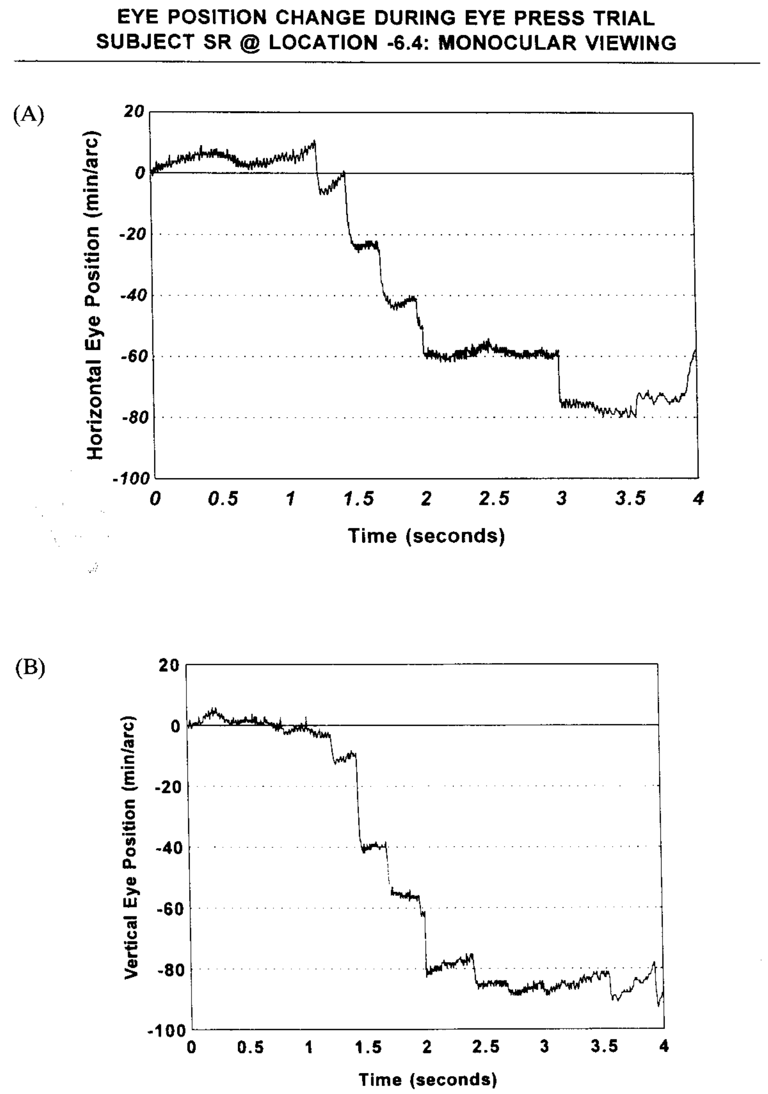

FIGURE 5. Leftward eye position change in monocular eye press trial: subject SR @ location 6.4. Horizontal (A) and vertical (B) eye position of the unseeing, unpressed right eye during a 4 sec trial with an eye press during monocular viewing. Time begins at zero, with the press administered at the 1.25 sec mark and lights extinguished 3 sec into the trial. Short line segments connect eye position samples taken at a sampling rate of 200 Hz.

about 15 min arc diameter, and the eye drifted when lights were extinguished. Figures 4 and 5 represent trials in which difficulties were encountered in inconsistency of the eye press. In Fig. 4, when the press was administered (at 1.75 sec) the eye moved to the right and down. When the lights were extinguished (at 2 sec) the eye appears to move back to the left, close to initial position. In a different trial with the same target position (Fig. 5), this subject's eye was noted to move leftward and down in response to the subject attempting to produce the same eye press. Clearly, overall mean measures would not accurately depict this variation in response to the eye press. This variability necessitated a trial by trial examination of the change in eye position resulting from eye press so that the exact change in EEPI could be compared to the pointing response.

Perception change explained by efference. All subjects indicated a change in perceived depth and horizontal location of the target when they pressed the eye. Though large variability of pointing error was evident, the direction of the shift in pointing error was predicted quite well by EEPI. For example, there was a high correlation of mean pointing error in depth and horizontal location and the efference measures (TCR and CRR, Table 1). This high correlation supports the idea that outflow is the predominant source of EEPI which

TABLE 1. Correlation matrix of averaged pointing error and EEPI measures: monocular viewing condition

	TCR*	CRR†
Hz‡	0.96 $P = 0.04$	0.96 $P = 0.04$
Dp§	0.92 $P = 0.006$	0.91 $P = 0.02$

*Total counter rotation measured in the unpressed eye, in min arc.
†Counter rotation to rotation imposed by the eye press, in min arc.
‡Horizontal pointing error, in mm.
§Pointing error in depth, in mm.

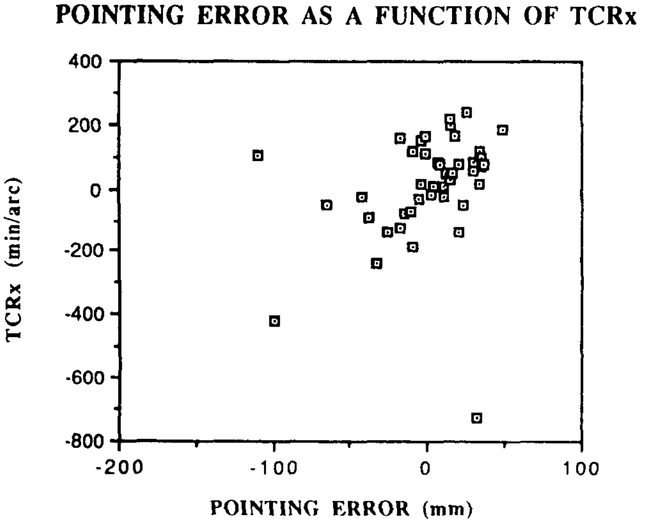

FIGURE 6. Horizontal pointing error and TCR. Horizontal pointing error plotted as a function of the total counter rotation response (TCRx) measured in the unseeing right eye in the monocular viewing condition. Data was obtained from eye press trials for subject SR at three target locations (total of 45 trials). Pointing error measured in millimeters (mm).

determines perceived target location as measured by pointing. Also, Fig. 6 shows the close relation between pointing error and efference (TCR; Fig. 6). The disparity between the amplitude of pointing error and that of efference measures may be explained by the combined effect of EEPI and a change in visual direction secondary to the eye press. The rightward translation of the left, pressed, viewing eye results in a rightward shift in visual direction. The counter rotation to this is leftward. The actual value of TCR is thus reduced by this amount (TCR = CRR+CRT). However, if the absolute value of Tr is added to the rightward CRR, the amount of the expected rightward shift in target position is increased and thus the disparity is reduced.

Repeated measures ANOVA also supported the hypotheses that perceived horizontal and depth location of the target changed as a consequence of the eye press ($P \leq 0.001$), and that target location affected the accuracy of perceived depth location. The interaction of target location and eye press effects on depth perception made it necessary to perform paired *t*-tests to determine at which locations the manipulation of EEPI was effective in altering perceived depth. The results revealed that, as a consequence of the eye press, either depth or horizontal pointing error was significantly changed at three locations ($P \leq 0.04$; Table 2).

Subjects indicated by both verbal report and pointing that the perceived location of the target changed as a result of the eye press, though the direction of change indicated by these two tasks did not consistently match. For example, the direction of horizontal position change indicated by pointing matched that of verbal report in 62, 35, and 47% of the trials for subjects SR, AW, and AS, respectively. Though perceived depth changes were evident in pointing errors, only two subjects verbally reported changes in depth, and in only 50% of the trials.

The frequency with which the direction of verbally reported perceived position change matched the direction of efference was tabulated. Verbally reported position change matched the direction of TCRx in 70, 67, and 73% in subjects SR, AS, and AW, respectively. In the other 30% for subject SR, TCRx was towards the left (as was pointing error) and verbal report was rightward. For subjects AS and AW, in those trials not corresponding in direction with TCRx subjects either reported no change in perceived location, or as above, the eye rotated leftward, though verbal report was rightward.

With regard to vertical rotations, the concordance rates of pointing and verbal report were poor. Verbally reported position change matched TCR in only 16% of the trials. The verbal responses were quite variable with no trend evident.

Binocular viewing condition

Eye movement in response to the eye press. In response to an eye press in binocular viewing, a second counter

TABLE 2. Effect of eye press on perceived location by target location monocular condition

Localization	N	MN*	SD*	*t* value	Two-tailed *P*
Horizontal					
3.2†	45	−19.9 (−9.9)	35.7 (24.0)	−2.36	0.023
0.0†	45	−11.8 (−8.4)	33.4 (23.2)	−0.77	0.446
−6.4†	45	−21.6 (−14.2)	38.6 (25.2)	−1.18	0.245
−12.8†	45	−28.9 (−9.2)	27.0 (26.7)	−4.35	0.000
Depth					
3.2†	45	−11.9 (−6.7)	30.1 (27.6)	−1.58	0.122
0.0†	45	−14.5 (−11.4)	29.0 (26.8)	−1.07	0.291
−6.4†	45	−18.7 (28.6)	28.6 (29.9)	−2.15	0.037
−12.8†	45	−34.2 (−19.9)	27.9 (28.2)	−4.93	0.000

Mean pointing error (MN) and standard deviation (SD) without eye press provided in parentheses.

*Pointing error in mm; positive numbers indicate errors to the right (horizontal) or overshoot (depth), and negative numbers indicate errors to the left (horizontal) or undershoot (depth) of mean error without an eye press.

†Location of target in reference to straight ahead for the right eye in degrees; negative numbers indicate deviation to the left, and positive numbers indicate deviation to the right.

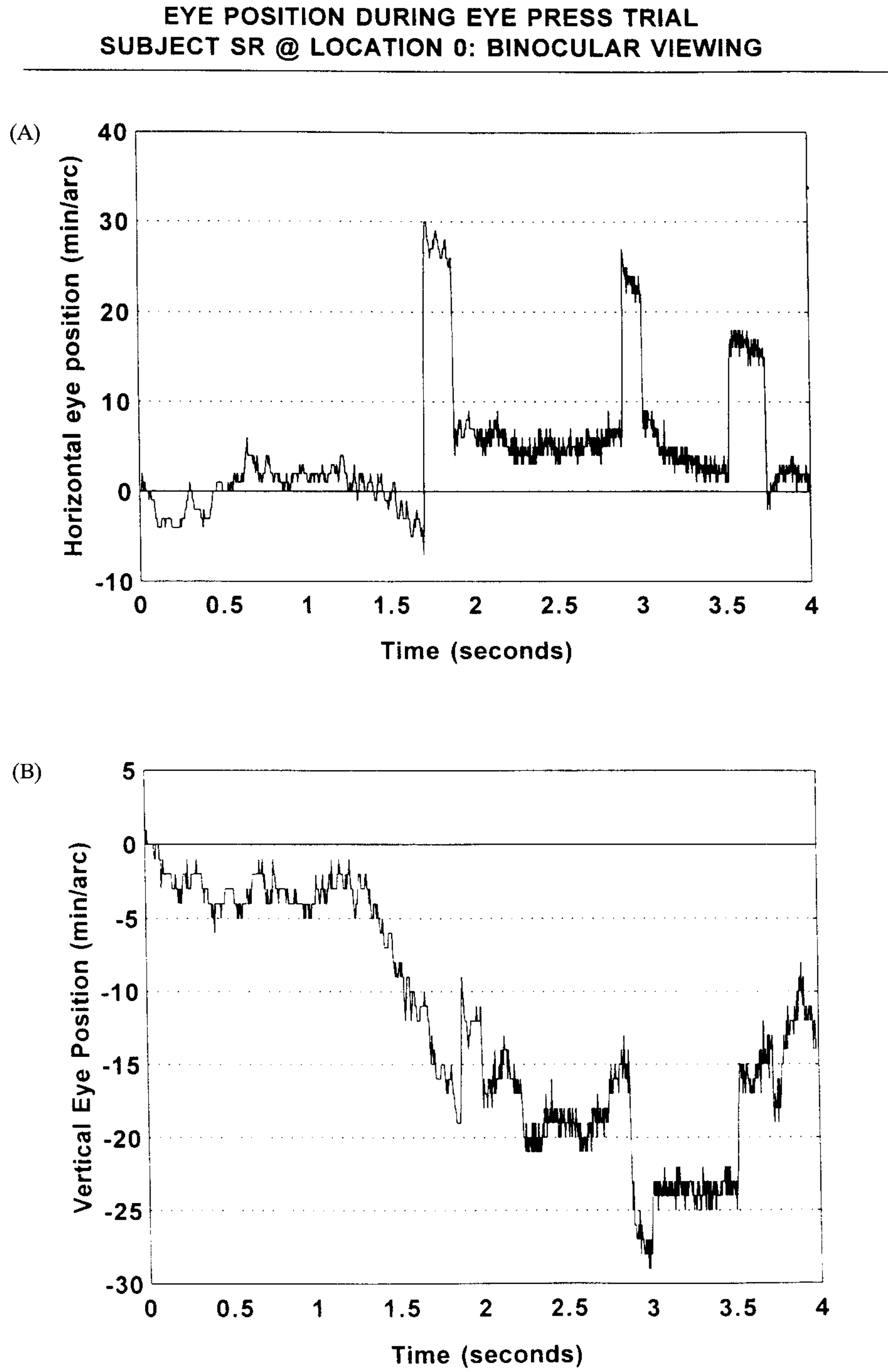

FIGURE 7. Right eye position change during eye press trial in binocular viewing. Horizontal (A) and vertical (B) eye position are plotted throughout a 4 sec eye press trial for subject SR during binocular viewing. Trial begins at 0 sec. Short line segments connect eye position samples taken at a sampling rate of 200 Hz. Positive numbers indicate position change to the right (horizontal plot) or upward (vertical plot). It is evident that following an initial counter rotation rightward and down, a second counter rotation leftward occurs in the right eye.

rotation occurred (vergence) that minimized or negated the TCR, thereby preventing its direct measurement. As a consequence of the vergence and the large trial to trial variability in the effectiveness of the eye press, only a descriptive or qualitative analysis could be performed with this data set. The sample plot in Fig. 7 shows that once the press was imposed on the left eye (just after 1 sec), the right eye started to change position (rightwards), but quickly rotated back (0.2 sec later) towards the initial position. The result was extraocular muscle tension and EEPI equivalent to convergence of the two eyes. In other trials the initial counter rotation was leftward followed by a motor pattern equivalent to divergence, despite the eye press being administered in the same way. Quantitative measures of the EEPI accompanying the vergence change requires either

TABLE 3. Effect of eye press on perceived horizontal and depth location by target location: binocular condition

Localization	N	MN*	SD*	t value	Two-tailed P
Horizontal					
3.2†	30	−25.6 (2.4)	29.5 (23.8)	−6.48	0.000
0.0†	30	−22.4 (−0.9)	26.1 (23.7)	−3.00	0.005
−6.4†	30	−27.1 (−5.4)	25.4 (20.1)	−4.79	0.000
−12.8†	30	−23.9 (−18.7)	35.6 (26.6)	−0.63	0.531
Depth					
3.2†	30	19.0 (11.4)	34.2 (21.4)	−1.39	0.176
0.0†	30	09.8 (15.8)	32.8 (20.4)	−1.37	0.182
−6.4†	30	24.4 (16.1)	27.7 (18.5)	2.21	0.035
−12.8†	30	−23.1 (12.9)	29.9 (20.9)	2.50	0.018

Mean pointing error (MN) and standard deviation (SD) without eye press provided in parentheses.

*Pointing error in mm; positive numbers indicate errors increased to the right, and negative numbers indicate errors shifted to the left with an eye press.

†Location of target in reference to straight ahead for the right eye in degrees; negative numbers indicate deviation to the left, positive numbers indicate deviation to the right.

accurate measurement of vergence or use of a consistent force in the eye press. Neither was possible in this paradigm. However, support for our interpretation is provided by the direction of pointing errors, noted below.

Pointing error explained by efference. Perceived depth and horizontal location of the target indicated by pointing was altered significantly by the eye press ($P \leq 0.05$) during binocular viewing. The effects of target location and eye press interacted ($P \leq 0.03$), so paired t-tests were performed. Eye press produced significant shifts in perceived horizontal or depth location at all locations (Table 3). Both subjects tended to point consistently to a location to the left and further away than target position, though initial counter rotation was left and downward. This trend is illustrated in Fig. 8. The results indicate that the second counter rotation which occurred in binocular viewing is a vergence and predicts the difference in perceived depth change in the two viewing conditions.

Variability of pointing errors were similar to those noted in monocular trials, as can be seen in the representative plot of two-dimensional pointing errors for one subject in Fig. 8. In spite of the variability of pointing errors, it is clear that the eye press caused the subject to point to a location to the left and further away than in the no eye press condition.

Verbal report of the direction of horizontal and depth error matched the direction of pointing error in <50% of the binocular trials for both subjects. Subjects verbally reported that they perceived that the target moved but they were often unsure about the direction of the perceived location change in binocular viewing.

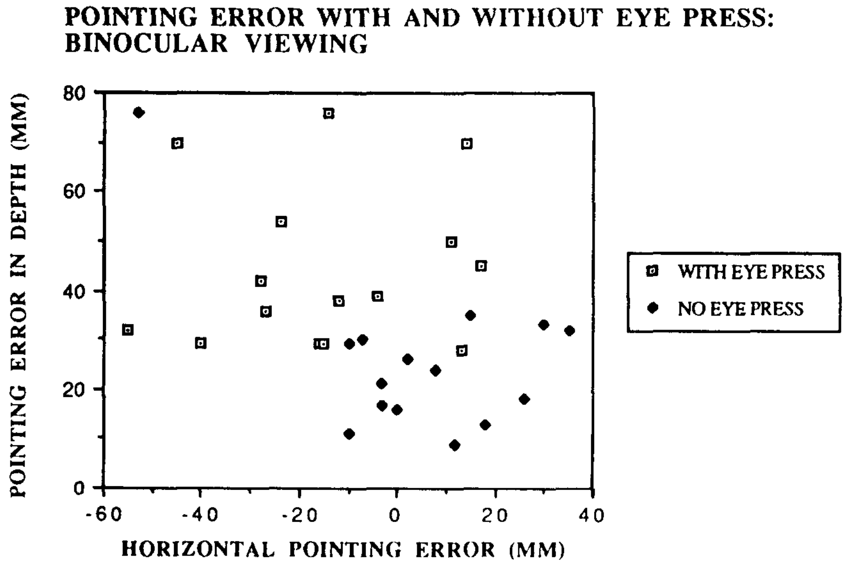

FIGURE 8. Pointing error with and without eye press in binocular trials. Overhead view of the two-dimensional pointing errors in millimeters (mm), both with and without an eye press, are plotted for all trials at one target location for subject SR. Actual target position is located at point (0, 0). Increased variability of pointing accuracy is evident in eye press trials, as compared to no eye press trials, and pointing error shifted (leftward and overshoot) as a result of the imposed eye press.

DISCUSSION

In these experiments, the eye press maneuver was used to manipulate EEPI while subjects fixated a target in a well lit area. In this condition, all visual cues indicate the target's correct location but EEPI based processing would cause subjects to mislocalize the targets. The data indicate that visuo-motor perception of depth and horizontal location of targets, as measured by pointing, was altered in a way that could be predicted by the change in EEPI caused by the eye press. These shifts in pointing location occurred despite the availability of retinal information that indicated there was no change in target location in any of the trials. Therefore, it may be concluded that under normal viewing conditions, when retinal and extraretinal information about target location conflict with regard to egocentric localization of a target, EEPI information is predominant in the perception of location when the subject actually tries to hit the target.

Vergence changes predicted changes in perceived depth

As suggested by previous investigators (Alpern, 1969; Erkelens *et al.*, 1989a,b; Ono, 1991), the response of the eye to the eye press in binocular viewing is a counter rotation (vergence) to allow the subject to maintain fusion and prevent double vision (refer to Fig. 3). Several investigators (Gogel, 1977; Gogel & Tietz, 1979; Morrison & Whiteside, 1984) have reported that a change in vergence angle results in a change in perceived depth, though vergence was not measured nor systematically manipulated by Gogel and Tietz (1979) and Morrison and Whiteside (1984). Those experiments were performed in visually impoverished environments. Ilg *et al.* (1989) reported that in response to a mechanical displacement of one eye during binocular experiments, either both or neither eye moved. Ilg's subjects said they did not perceive a change in depth location, but perceived location was not measured as part of the experiment. In our paradigm, perceived changes in depth were measured, but the vergence response and variability in the effect of the eye press made it impossible to quantify EEPI which required that different analysis be performed on eye position data. Visual inspection of plots of eye position throughout eye press trials revealed that either:

1. The unpressed eye was initially displaced leftward (TCR), but immediately rotated back to the right; or
2. The initial displacement was rightward (TCR), and the eye rotated back to the left.

If the second rotation was vergence (divergence and convergence respectively as described above), predicted pointing error would be an overshoot to the left or an undershoot to the right. This prediction was substantiated in 75% of the trials. These results were in concordance with the claim that vergence and version movements occurred and predicted errors in perceived depth localization in normal illumination.

This conclusion was possible despite complications arising from the second major finding of this experiment which is large variability in pointing error (in both direction and magnitude) between trials, that was caused by variation in the effectiveness of the eye press in rotating the eye, and was contrary to the consistency reported by Bridgeman *et al.* (1979) and Stark and Bridgeman (1983). This variation in *direction and magnitude* occurred despite the fact that:

1. Subjects were instructed to press with a consistent force at a consistent location on the outer canthus of the left eye while maintaining fixation on a target; and
2. The subjects were careful and conscientious in following these instructions.

The variation in *direction* of CRR may in part explain the smaller mean values of TCR in our data as compared to previous reports in which only experienced subjects participated and all counter rotations were in the same direction. If absolute values of the data from our one experienced subject are used, the mean values of TCR are comparable to those in previous reports.

It is unfortunate that evidence for an EEPI contribution to perceived depth must be based on such qualitative observations. Quantitative support for this argument would require that vergence be measured, or that a known consistent force be applied to the eye. However, we found variation in the effectiveness of the eye press in rotating the eye. The requirement of consistency indicates that effectual use of the self-imposed eye press has reached its upper limit in these experiments. In retrospect, the inconsistency in eye rotation may have been anticipated. The eye has a spring constant of about 1.25 g/deg (Robinson, 1964). This means that a force of 1.25 g can rotate the eye by 1 deg. There are no guides to precisely position the finger on the globe in the eye press maneuver. Consequently, some variability would result exactly where the pressure falls on the globe, which results in variation in rotational force on the eye. A report by Steinbach and Skarf (1985) supports this mechanical explanation for the variable effects of the eye press.

Additional technical problems were identified in these experiments which may have contributed to the large variability of pointing errors. The constraints placed on the arm and head by the mechanical arrangements required by our eye movement recorder may have increased pointing variability. The arm movement constraints made the pointing response somewhat unnatural to subjects, and undoubtedly contributed to variability of pointing accuracy. Also, Biguer *et al.* (1984) reported that limiting head movement reduced the accuracy of pointing and that location of targets away from center position exacerbates the inaccuracy. In experiments presented here, head movement was severely constrained by use of the forehead rest and bite board to obtain accurate eye position measures. The restricted movement and requirement that subjects hold their breath during trials were quite demanding and exhausting to subjects. The large number of additional trials that were necessary to assure accuracy in eye position data was also tiring. Subjects could only tolerate completing 8–10 trials in any one sitting (usually lasting 45 min–1 hr). It may be that pointing error and its variability was increased as a consequence of the strain.

In spite of the variability in pointing and in eye rotations, several conclusions regarding the role of EEPI in egocentric space localization can be inferred from these results. Specifically, in both monocular and binocular viewing, a change in EEPI predicted pointing error in depth and horizontal location, with all other visual cues constant in a fully illuminated visual field. In monocular viewing, horizontal and vertical version movements occur as a consequence of the eye press and predict changes in perceived location. In binocular viewing, vergence and version occur in response to the eye press and predict changes in depth and on the horizon. Our data do not agree with the idea that the presence of a clearly visible, structured visual field obviates the use of EEPI in perception of location.

Effect of task selection and visual field structure

Results indicate that in monocular viewing, EEPI affects both visual motor pointing and the more cognitive verbal report of perception of location. In binocular viewing, though subjects reported that the target did change in location, they were unable to describe that movement. The subjects' inability to accurately describe the direction of perceived location change may be due to the complex response to the eye press in binocular viewing. For example, AS noted the target often "wiggled" so much as the eye press was being applied he could not keep track of where it started. These results indicate that verbal report of perceived location is not a reliable or valid method of measuring perceived location and should not be used in experiments.

These results do not dispute findings that other types of perception (e.g. perceived straight ahead) are not affected by EEPI. Bridgeman and Fishman (1985) reported that when visual information was available (experiments were performed in a lighted area), pointing error was affected by EEPI, but the perception of straight ahead was not. Perception of straight ahead may be referenced differently than verbal report of target location. Perception of this forward, central position is based on proprioceptive information from the head and neck. When the eyes move in the head, and EEPI changes, proprioceptive information about head position does not change, and neither does perception of where straight ahead from the head is. Pointing to a target's location, or verbally reporting where it is, is a measure of the perception of an object's location in relation to the body which would be affected by eye position (and EEPI). Therefore, measures of the effect of EEPI on the straight ahead location and measures of the effect on perceived location of an object are not comparable since they are referenced differently (relation of object to self vs central location of self).

CONCLUSIONS

The goal of establishing that EEPI is the predominant source of information in visual motor pointing to the location of targets in depth and on the horizon, in both monocular and binocular viewing in normal illumination was achieved in these studies. Future studies should attempt to provide quantitative support to the idea shown qualitatively here that changes in vergence angle result in altered perceived depth location of a target.

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