CONTROL OF EYE POSITION IN THE DARK

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There have been numerous studies of fixation of visible targets. Much less is known about position control when the eye depends on what MATIN, MATIN, POLA and PEARCE (1968) have called “extraretinal signals,” i.e. position information that does not arise from the relative location of a target-image on the retina. In the few experiments that have examined extraretinal position control (fixation in total darkness), 12 sec was the longest period of time studied (CORNWISHT, 1956); others looked at much briefer periods (NACHMIS, 1961; FIORENTINO and ERCOLI, 1966; and MATIN, MATIN and PEARCE, 1969). These authors agree that the eye rapidly wanders from the position defined by a target previously visible in the primary position. We do not know, however, from these experiments the limits of extraretinal position control or whether eye position becomes stable over long periods of time in the dark. The present experiments examined these questions.

METHOD

A contact-lens optical lever technique was used to record 2-dimensional eye movements. The recording apparatus, described elsewhere (SKAFENSKI, 1965), records rotations of the eye free from contamination by translations of the head and rotations of the eyeball. Features of the method that are important for interpreting records reproduced in this paper are as follows.

A small triangle of infrared light, oriented so that one side was vertical, was reflected from a plane mirror attached to a contact lens worn on the right eye and then focused on a horizontal slit located in front of 35 mm infrared film moving vertically at 5.5 mm sec. as a modified Graflex (Model CRH) camera. The left eye was covered and closed. When S made a horizontal eye movement, the recorded trace displaced left or right on the film. When he looked up or down, narrower or wider portions of the triangle fell on the horizontal slit and the width of the trace changed.

The fixation target was a 16 min arc disc, of uniform-white light (luminance: 0.14 mcd) located 75 m from the right eye. The disc of light was initially placed so that it appeared to be straight ahead of each S in his “primary position.” The target could be moved 10 deg arc to the left or right of this primary position. S initiated each trial, which consisted of an initial period of fixation of the target followed by a long period of total darkness. The target was removed by a relay that operated a shutter, switched-off the current to the target source and fixed an infrared strobe flash that marked the time of target disappearance on the film.

Two Ss, experienced with contact lenses (the authors), participated in these experiments. Both Ss had considerable prior experience “fixating” a variety of visible targets, but neither had previously tried to keep his eye in place for long periods of time in total darkness. Initially, Ss were instructed to use any movement pattern that would keep them in place. They got feedback about their successes in two ways: they noticed the relative position of the target when it reappeared at the end of each trial and they examined their records at the end of each day to get some idea about the way feedback, at the end of the trials, reflected overall performance.

EXPERIMENTS

1. Limits of extraretinal position control

In the first experiment each trial began with 10 sec of fixation of target visible in either the primary or 10 deg arc to the left or right of the primary position. The target was then switched-off and S tried to maintain fixation of the defined position for 38 sec in total darkness, a period similar to that employed in prior studies of maintained fixation of visible targets, e.g. CORNWISHT (1956), NACHMIS (1959) and STINNIS (1965) and in line with a
recent recommendation of DHURBACH and FORBEE-FISHER (1967) that trials of 40-sec duration be adopted as a standard in contact-lens studies of the eye movement pattern. Both subjects participated in 4 sessions during which 72 records were made (24 at each target position). Fifteen records from each of the 3 target positions were exhaustively measured for each S. There were no obvious differences between records made in the first or fourth recording sessions, but, inasmuch as the task was novel and difficult, most of the records measured were taken from the last experimental session. The records were selected for measurement only on the basis that they were free from evidence of contact lens slippage. For each of these records, paired horizontal and vertical eye positions were measured at randomly selected times within successive 1-sec periods. In all, 96 paired position measurements were made for each record (20 at the beginning of the trial when the target was visible and 76 during the 30 sec in total darkness).

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*Errors are not shown for the period when the target was visible because these measures (as defined in the present experiment) cannot be applied to the fixation of a visible target. Errors during fixation of visible targets are usually defined as differences between successive offset position and mean eye position (KRONOVER, 1959 and NAGASOY, 1959) for the standard error of mean fixation point position for independent trials with the same or different targets located in the same special position (STROMSON, 1965). Such fixation errors with visible targets are typically 1-4 min arc.

**Mean eye positions, for 2 sec when the target was visible, were calculated for all of the 30 records recorded at the last session. Horizontal and vertical mean eye positions on successive trials differed by more than 1 mm arc; it was observed that the contact lens had slipped and the intervening dark period was not measured. Of the 30 trials summarized in Table 1, 24 came from the last session, and 6 came from the just preceding session.
Error (absolute) distance between mean eye position when the target was visible and mean eye position in the dark) was used to evaluate how well extraneous signals could be used to control eye position. Mean errors are shown in Table 1.

Both S's were able to maintain eye position fairly well in the dark, mean error was less than 1 deg arc at each target position and somewhat less overall. Also, the size of the error was not markedly influenced by where the target was located relative to the subject.

The mean position of the eye in the dark was actually closer to the target than the error measurement suggests, i.e. algebraic mean eye position in the dark (averaged over the 3 target positions) was displaced only 34 min arc for RS and 30 min arc for AS from the positions defined by the visible targets.

Fixation stability at each of the target positions is also summarized in Table 1 where bivariate contour ellipse areas and horizontal and vertical standard deviations are reported. The bivariate contour ellipse area is a 2-dimensional measure of fixation stability. As calculated in the present experiment, the tabulated areas are analogous to standard deviations of eye positions, i.e. they represent where the line of regard was 68% per cent of the time.

Fixation stability, like the error, was not markedly influenced by target position. The variability of the eye about its mean position in the dark (SDs) was about 1 deg arc on the horizontal and vertical meridians, considerably greater (about 6 times) than was found during fixation of the visible targets but a very small fixation of the total range of movements that can be executed by the eye.

The net analysis was concerned with the rate at which error accumulated throughout the 38 sec dark period. Mean error (averaged over the three target positions) was calculated within successive 7-sec portions of the records. Error increased throughout the dark period, but the rate of increase was slow, slightly less than 1 min arc/sec for RS and about 2 min arc/sec for AS (see Fig. 1).

Although both S's eyes were slowly moving further away from the target position as they fixated in the dark, fixation stability about the short term (7sec) mean positions did not show any progressive changes. Immediately after the target was extinguished, the variability of fixation increased to a level that was maintained throughout the dark period, a level

1The algebraic mean position could be misleading if individual trial means were widely scattered in all 2 quadrants. This was not the case, individual trial means fell within 11 deg of target positions.

2Actually, bivariate contour ellipse area is the solid angle in min arc subtended at the eye by an ellipse projected on a plane surface perpendicular to Langen's plane. See Stevens (1958) for a description and the assumptions underlying this measure of bivariate variability.

3Errors from the 3 positions were combined because quantitative differences in error rate were too apparent.
Fig. 2. Mean braking (by rate of change) in the dark for subjects RS and AS. Areas are plotted for the period when the target was within 125·5 sec and at the midpoint of the successive 7·5 sec portions of the 30 sec dark interval. The scale on the left indicates the standard deviation from the mean. The horizontal and vertical standard deviations are equal, and the position measures in the two directions are non-correlated. Data points are based on 15 records for each 7·5 sec target position (left and right target positions). Each area was calculated from 225 paired horizontal and vertical position measures. The variability of the eye during each 7·5 sec period was calculated for both eye position during that interval.

characteristic of extraretinal position control. The abrupt change in variability for extraretinal position control is shown in Fig. 2 where fixation stability (by rate of change contour ellipse area) is plotted for successive 7·5 sec portions of the dark interval. The finding that fixation stability was a flat function throughout the dark interval during which time the eye slowly moved further away from the position previously defined by the target suggests that the progressive accumulation of error in the dark was caused by deterioration of spatial memory rather than a loss of oculomotor control. It is as though the subject forgets precisely where the target is located as time passes but manages to keep his eye reasonably close to where he thinks it is during any successive relatively short period in the dark.

2. Extraretinal position control over protracted periods

In the next experiment RS attempted to maintain fixation of the target for a much longer time after it was removed from view (125·5 sec) in order to find out whether error continued to increase in the dark. Three records (randomly selected from 3 records made at each of the 3 target positions) were measured exhaustively (275 paired position measurements made at randomly sampled times within successive 1·5 sec intervals of each of the 137·5 sec recordings).

The rate at which the eye moved away from the target position is shown in Fig. 3 where error is plotted for successive 1·5 sec portions of the dark interval.

During the first 1·5 sec period, error increased rapidly, but during the remainder of the trial, it increased at a much slower rate: about 1·5 of the total error that would accumulate during the 125·5 sec period accumulated during the first 1·5 sec. Also note that the eye stabilized after about 100 sec when error had reached 2 degrees. Although RS's eye slowly moved away from the target position throughout the extended period in the dark, his fixation stability at successive 1·5 sec mean eye positions was uniform throughout the entire dark interval as was the case in the first experiment.

These results were confirmed with the second subject by a similar quantitative analysis of a single long trial randomly selected from 3 recordings made at each of the 3 target positions.
3. Role of conjunctival cues in extraretinal position control

Tactile cues from the conjunctiva could provide extraretinal eye position information in the experiments described above. Such conjunctival cues would be artifacts because the edges of the contact lens and the stalk attaching the mirror to the lens introduce eye position information which would not be available to a normal unencumbered eyeball. Such cues were shown to be unimportant in the next experiment.

This experiment was essentially a replication of the first with one exception, viz. AS's eyes were anesthetized by instilling 2 drops of 0.5 per cent tetraacryl hydrochloride (Akon Laboratories, Inc.) in each eye at 5-min intervals. Fifteen min after the second drop, the contact lens was inserted and 18 records were made (6 at each of the 3 target positions). Anesthesia was profound and subjectively disruptive, i.e. RS reported that he had not been able to keep near the target position after it had been removed from view, he insisted that he was "totally lost in the dark." His records, however, looked similar to those obtained previously without anesthesia. The experiment was repeated and 15 randomly selected records (from the second session) were measured (5 for each of the 3 target positions).

Removal of conjunctival cues had only a slight effect on RS's position control in the dark. His overall error was 50 min arc, not significantly different from that found under the same conditions without anesthesia. There was a small, statistically reliable, increase in the variability of fixation, but on the whole, RS's position control in the dark did not differ

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3Milieu conditions of the Rans type contact lens were worn in the experiments. Such lenses are used to rest on the uninflated and do not slip appreciably when used to steady fixation or mobile targets during which high velocity eye movements of the eye are normally less than 10 mm/sec (McLean and Porter, 1948). Such lenses are rarely of ever worn without anesthesia because they are uncomfortable for 40 min and until the vision (1967) cortical "sucker" which can only be worn for brief periods and always requires an anesthetic because it is held in place by negative pressure and rests completely on the corneal surface.
markedly from that found when their eyes were not anesthetized (overall bivariate contour ellipse area = 7740 mm²) and (c) Table 1 for error and fixation stability when calotte cues were available and Fig. 4 for representative records of performance with and without anesthesia.

4. Does body position define target direction in the dark?

The experiments reported so far have shown that extratemporal position control was not limited to targets in the primary position and did not depend on tactile cues provided by the contact lens. There are at least 3 other ways that the eye could be kept in place in the dark:

1. Stretch receptors; in the extracocular muscles might provide proprioceptive information (inflow) which allows eye position to be adjusted until the "felt position" of the eye in the dark coincides with the "felt position" associated with fixation of the visible target.

2. An eye movement monitor (outflow) might provide information for directing the eye in the dark either (a) by monitoring the size and direction of all eye movements made after the target was removed from view, i.e. the subject knows where the target disappeared (b) by remembering the innervation patterns in the extracocular muscles that was used to fixate the visible target, i.e. the subject keeps his eye in place by maintaining or reestablishing the innervation patterns that placed the visible target in the preferred foveal fixation locus.

3. Body position might provide a reference direction which could be used to define target position in the dark. It is either words, memory for target position may not be necessary at all. But rather, the oculomotor system adjusts eye position to correspond to the subjective "straight-ahead", a direction given by the orientation of the subject's torso relative to the target, i.e. the subject rotates his body until the visible target is "straight ahead" of him and then tries to fixate "straight ahead" when the target is removed from view.

The next experiment was concerned with this last alternative. The logic of this experiment was as follows: Directions of objects in space are perceived in terms of their spatial coordinates with respect to a vertical (mid sagittal) plane passing through the center of the subject. This plane seems to be reference in the body and not in the head of the perceivers. To illustrate, an object is perceived to be "straight ahead" when it is in front of the subject's body regardless of the orientation of his head or eyes. For example, a subject whose head and body are facing the same direction in space will perceive a target placed to the right of the mid sagittal plane to be in his right; if he turns his head to face the target, keeping his body in place, he still perceives the target to his right, but if he turns his body to face the target, the target becomes "straight ahead" even if he keeps his head oriented in the original direction.

Body orientation could have been used in this manner in the experiments described above because the contact lens recording technique requires only that the head be fixed in space leaving the torso free to rotate and point 10 degrees to the left or right of the direction established by the binocular axis. If our subjects did rotate their bodies until they perceived the displaced targets as "straight ahead", then control of eye position in the dark could arise from their ability to rotate in the same direction their bodies were turning.

In the next experiment we found that it was not necessary to orient our subjects towards the target when we kept our eyes in place in the dark; drastic rotations of our torsos did not produce reasonable extratemporal position control.

This experiment was essentially a replication of the first with the exception that the target was always present in front of the fixating eye and the orientation of the torso
Fig. 4. Representative 2-dimensional recordings showing subject RS's retinal and extrastriatal position control with normal and atropinized conjunctiva. The record on the left, labeled NA, was taken from the first experiment where atropine was not used. Records A1 and A2 show position control after atropine had been instilled in both eyes at the first and second recording sessions, respectively. Trials start at the top of the figure where the target is seen fixating a target visible (T) 10 deg to the right of the primary position. The target was switched-off at the time indicated by the arrow and the remainder of the record shows performance during 30 sec in the dark (D) respective horizontal stripes indicate 1 sec periods. The right edge of the recorded trace on each of these records is proportional to the horizontal position of the eye and the width of the trace is proportional to its vertical position. The horizontal bar beneath the records shows a 6 deg arc rotation on the vertical meridian and a 3 deg arc rotation on the horizontal meridian.
Fig. 6. Representative 3-dimensional recordings showing S’s retinal and extraretinal position control when his body and head faced the same direction (A) or when his body was rotated 45 deg wrt to the right (R) or left (L) of his head. Trials start at the top of the figure where this S is seen fixing a target while (F) in the primary position. The target was switched-off at the time indicated by the arrow and the remainder of the record show performance during 30 sec in the dark (D) (negative horizontal stripes indicate 1 sec periods). The right edge of the recorded trace on each of these records is proportional to the horizontal position of the eye and the width of the trace is proportional to its vertical position. The horizontal bar beneath the records shows a 6 deg sec tension on the vertical meridian and a 2 deg sec tension on the horizontal meridian.
Fig. 7. Representative 2-dimensional recordings showing RS attempting to "hold" his eye in place without making saccades (h) and "floating" (f) for 5 sec while the target was visible (T) and for 13 sec after it was switched-off (d). The target was switched-off at the time indicated by the arrow and faint horizontal lines indicate 1 sec periods in the dark. The horizontal bar beneath the records shows a 6 deg arc rotation on the vertical meridian and a 3 deg arc rotation on the horizontal meridian.
Fig. 8. Representative 3-dimensional recordings showing AS "holding" his eye in place without saccades for 5 sec while the target was visible (T) and for 9-5 sec after it was switched-off (d) for each target position, left (L), primary (P) and right (R). The target was switched-off at the time indicated by the arrow and faint horizontal stripes indicate 1 sec periods in the dark. The horizontal bar beneath the records shows a 6 deg arc rotation on the vertical meridian and a 3 deg arc rotation on the horizontal meridian.
relative to the head was varied. 

viz: 21 records were made (6 with the body rotated right, 6 with it rotated left as far as our anatomical arrangements would permit (+45 deg) and 9 records were made with the head and body facing in the same direction). Fifteen records (+ for each body position) were randomly selected and measured exhaustively (see experiment 1).

As's mean error was similar for all positions of the torso (about 70 min arc); RS on the other hand showed a large, statistically reliable, difference in mean error when his torso was rotated left (67 min arc) compared to the straight-ahead (43 min arc) or right (38 min arc) body positions. This error, however, was small compared to the large rotation (45 deg arc) of the torso error was only 5% of body rotation and he was able to stay within 1 deg of the target throughout the dark interval. Fixation stability did not depend on body position for either S (overall binocular corneal ellipse area was 824 min arc) (S.E. = 1445) for RS and 361 min arc) (S.E. = 1054) for AS.

Representative recordings of extraretinal eye position control with the torso in different orientations relative to a target located straight ahead of the eye are shown for each S in Figs. 5 and 6.

We conclude that extraretinal position control does not depend on simple "body-image" direction cues. The perceptual "straight-ahead" could, however, be used to guide the eye in the dark; viz: if the subject accurately estimates the angle formed by the "straight-ahead" of his torso and the target he could keep his eye in the target position by maintaining this angle in the dark. In other words, "body-image" may provide a reference direction for extraretinal position control, but it does not, itself, guide the eye in the dark.

Does extraretinal position control depend on a pattern of eye movements chosen by the subject?

In the experiments reported so far we found that we could keep our eyes four target position in the dark providing we were able to use any eye movement pattern we chose. In the next experiment we were not free to choose our own eye movement pattern: a constraint that allowed us to get some idea of the degree to which the demonstrated control of eye position in the dark depended on self-selected behaviors. We examined this variable by measuring our ability to return to target position after making 30 large saccades in directions specified by the experimenter ("directed" trials) and comparing these measures with performance on alternating trials when we were free to use any saccade eye movement pattern in the dark ("free" trials).

Experimental conditions were as follows: each trial began with 10 sec fixation of a target visible in the left, right or primary position. The target was then switched-off and we attempted to keep our eyes in place for 10 sec. During the next 30 sec in the dark, we were directed to make one large saccade each second in one of four, randomly chosen, directions (up, down, right or left). In the 40th sec we were instructed to fixate the position originally denoted by the target and to remain there for the final 10 sec of the dark interval. Such trials alternated with trials of equal length (10 sec with a visible target followed by 50 sec in the dark) during which, we were free to use any eye movement pattern to keep our eyes in place.

Both subjects participated in 3 recording sessions, each consisting of 5 pairs of "free" and "directed" trials.

The condition in which body position was "straight ahead" in the control experiment was identical to the condition in which the eye was in the primary position in the free trials. Note that error and the variability of fixation were somewhat larger for the "straight-ahead" body position than for the same position (primary) in the free trials (see Table 1). These differences were not statistically reliable and probably represent the fluctuations in performance across subjects.

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"directed" trials, 3 pairs at each target position. Nine pairs of records for RS and 5 pairs for AS were free from evidence of appreciable contact lens slipage and eye position during the last 6 sec of this record was measured exhaustively. 1
Looking in many, arbitrarily chosen, directions in the dark did not lead to large fixation errors when we tried to return to the position defined by the target many seconds earlier. The difference between "directed" and "free" mean error was 0.9 min arc for RS mean "directed" error — 106 min arc, S.E. — 15, and mean "free" error — 87 min arc, S.E. — 15) and 23 min arc for AS (mean "directed" error — 109 min arc, S.E. — 30 and mean "free" error 132 min arc, S.E. 21). We conclude that extraretinal position control does not require a pattern of eye movements selected by the subject.

b. Role of drifts and saccades in extraretinal position control
Quite different eye movement patterns have been described in prior research on extraretinal position control, e.g., NAG ano (1961) recorded for 3 sec and reported that his 2 subjects made very few saccades in the dark — both tended to drift in single idiosyncratic directions, FiroRESTI and EroEs (1960) recorded for 4 sec and reported that their 2 subjects made frequent saccades and did not drift in consistent directions in the dark.
Our subjects also showed marked differences in their eye movement patterns despite the fact that their fixation errors and stability were very similar over long periods of time in the dark. To illustrate, in the experiments described so far, AS made many more saccades to maintain the left or right target positions than he used to keep his eye near the primary position, RS, on the other hand, made frequent saccades to maintain his eye at all 3 target positions. When the target was in the primary position (the only condition studied by other investigators), AS performed like one of Nocinitas' subjects while RS' fixation pattern resembled that reported by FiroRESTI and EroEs. This was also the case for both subjects when they tried to maintain their eyes 10 deg arc to the left or to the right of the primary position.
Such variation in occurrence of saccades in the dark might arise from individual differences in drift rates or tendencies to show dominant directional drifts. In other words, different subjects might be required to make a larger or smaller number of saccades to maintain eye position in the dark if their low velocity position control systems do not function in the absence of a visual error signal and muscular imbalances cause their eyes to drift away from the position previously defined by the target. Such imbalances might be idiosyncratic to a given subject's musculature or imposed by asymmetrical leading of the oculomotor muscles when the target is not located in the primary position. We looked at these possibilities in the next experiment by voluntarily suppressing saccades while trying to hold our eyes in place in the dark. 4 We found that extraretinal position control, unlike retinal position control, is accomplished primarily by saccades.

4 Only successive pairs of records were selected for measurement so that a comparison could be made between "free" and "directed" performance at very short time during the recording sessions. Measuring this as well as the selection for contact lens saccades only 1/2 sec before the primary, 1/2 sec before the next from the left target positions for AS, it seems surprising that we found no more successive parts free from evidence of contact lens saccades because large saccades still were too slow to look away from the target position would be expected to disturb the accuracy of the contact lens.

5 Nocinitas, COOHER, Tomasa and MASON (1960) reported that these subjects could suppress saccades while varying stationary targets presented in the primary position and also while tracking constant velocity target movements (Curtis and STAGMAN, 1960). Voluntary saccade suppression did not lead to increased variability of the eye above in mean fixation error; 3 a finding which suggests that low velocity eye movements ("artificial drifts") can maintain the line of regard by making fixation errors induced by " noisy " drifts. In the present experiments we attempted the use of viewing saccade to eye position control to determine whether drifts would also be effective in the absence of a visible target.
In this experiment, Ss held their eyes in place without saccades for 10 sec while the target was visible in the left, right, or primary positions at which time the target was switched-off. When the target disappeared, they tried to stay in place in the dark without making any saccadic eye movements. Both Ss were able to suppress saccades, almost entirely, while the targets were visible and also after the target was removed from view. They could not, however, keep their eyes in place in the dark: both drifted outside the recording limits of the apparatus within 20 sec of target removal. RS, in fact, never managed to stay on the film for more than 5 sec in the dark without saccadic correction. Soon after the target was switched-off, he drifted rapidly downwards and the trace was lost. We tried, over and over again, to record for longer periods in the dark but his downward drifts persisted unchanged throughout several weeks. Representative performance of this subject is shown in the left record reproduced in Fig. 7 where RS can be seen holding his eye in place without saccades while the target was visible followed by a rapid drift downwards (the trace widened) after target removal. The record on the right shows typical performance of this subject when he was instructed to use saccades in the dark. He modulated them frequently and they were corrective, i.e., they tended to return his eye towards the position previously defined by the target.

As's performance is shown in Fig. 8 where a representative record is reproduced for each of the 3 target positions.

There was good retinal position control, without saccades, while the target was visible in the primary and displaced target positions followed by systematic drifts away from target position very soon after the targets were removed from view. When the target was in the primary position (the center record), AS, like RS, drifted downwards (the trace widened). AS's drift was relatively slow, however, and by the 9th sec in the dark he was only about 1.5 deg arc below and 0.5 deg arc to the right of the target. AS always drifted towards the primary position after removal of targets located 10 deg arc to the left or to the right of the primary position. Drifts from these 'off-center' positions also led to relatively small errors after brief periods in the dark, e.g., in the right hand record AS had drifted about 2.1 deg arc towards the primary position after 9 sec in the dark. In the left hand record, his error was 1.8 deg arc just prior to the small 'corrective' saccade (18 min arc) which can be seen in the 8th sec after the target was removed from view.

Systematic drifts of the kind shown in Fig. 8 were never corrected by drifts in any of our records for this subject and error always accumulated to the point where the trace was lost. AS never managed to maintain the position of his eye without saccades within the 4 by 6 deg arc limits of the recording apparatus for more than 20 sec in the dark.

In summary, extraretinal position control over long periods of time required periodic high velocity eye movements to correct errors introduced by 'noisy' drifts. All drifts in the dark were 'noisy' and the eye could not, therefore, be held in place without saccades. Position control was quite different when a retinal error signal was available, viz., the eye could be held in place, without saccades, when a target was visible despite asymmetrical loading of the oculomotor muscles. This finding adds further support to the suggestion that 'corrective drifts' contribute importantly to eye position control with visible targets (Nachmans, 1959; Stempson, Cunez, Timberlake and Heiman, 1967).

IMPLICATIONS
Prior investigators concerned primarily with the fixation of visible targets left open the possibility of effective extraretinal position control despite their subjects' inability to keep their eyes near the primary position for very short periods of time in the dark. For example,
Navarro (1961) found that "the eye moved farther and farther away from initial position," during the first 3 sec after the fixation target was removed, but points out that "there is no evidence to indicate whether or not it attains some such, stable position." Also, Cornsweet (1956), who recorded for a longer period, reported data for one subject which looks as though the eye was beginning to stabilize about 2 deg arc away from the former target position. His graph of "net displacement" (four error) as a function of time in the dark shows error accumulating at only 4 min arc after the second 1 sec trial as compared with 14 min arc during the earlier portion of the dark period.

More recently Mathin, Mathin, and Peare (1970) studied position control for 3 sec immediately following removal of a target in the primary position and found that the eye followed a "nearly-random walk." These authors point out, however, that there were statistically reliable "corrective tendencies" but "such tendencies are small relative to the large random component in the sequence of displacements in the dark." Mathin et al. (1969) suggest that their demonstration of a "nearly-random walk" following removal of the target may describe a transitory state: the period during which the oculomotor system switches from retinal to extraretinal position control. We agree with this suggestion and believe that our measurements show that once this transitory period is over there is an extraretinal signal of considerable fidelity which can be used to maintain the eye near the primary and other orientations for very long periods of time in the dark. The nature of this signal is still to be determined.

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REFERENCES


Two-dimensional eye movements were recorded for long periods in total darkness while 2% acetylpromazine was added to their eyes in the primary position or 10 deg arc in the left or right. Effective position control of the eye was obtained by a visual signal (the eye was maintained 2 deg arc or more in the dark and at least 2.5 deg closer during brief periods). Effective position control of the eye did not depend on the ratio of retinal light stimulating the eye, the orientation of the eye, or the refractive error in the eye. The eye was not moved during periods when the eye moved after the target was removed or the eye was closed.

Forced movements were initiated in two dimensions of the eyes by adding frequent periods of darkness to the experimental situation. The eyes were moved from one position to another without prior warning. The eyes were moved during periods when the eye moved after the target was removed or the eye was closed.


Die Augen waren während langer Zeiträume in totaler Dunkelheit registriert, während 2% Acetylpromazin in der primären Stellung oder 10 deg zur Rechten oder zur Linke fortwährend verabreicht wurde. Tatsächliche Stellungskontrolle konnte während der Abwesenheit eines Schattenbildes beobachtet werden (das Augenbild blieb im wesentlichen von vorne in der Dunkelheit und nach einigen Minuten in der Dunkelheit in der Dunkelheit blieb erhalten). Die tatsächliche Stellungskontrolle hing mit der Dunkelheit nicht von künstlichen Augenbewegungen ab. Sollten sie während der Dunkelheit hervortreten, blieb das gleiche Muster erhalten. Tatsächliche Augenbewegungen wurden beobachtet, dass die Augen im Dunkeln in der Nähe des Zieles zu bleiben: die Stellungskontrolle für niedere Geschwindigkeiten (Korrekturnachteilen) wurde unterdrückt; sobald das Ziel der Augen entfernt worden war.

In the dark, the eyes were moved during periods when the eye moved after the target was removed or the eye was closed.

The control of the eye position in the dark was achieved by a visual signal (the eye was maintained 2 deg arc or more in the dark and at least 2.5 deg closer during brief periods). Effective position control of the eye did not depend on the ratio of retinal light stimulating the eye, the orientation of the eye, or the refractive error in the eye. The eye was not moved during periods when the eye moved after the target was removed or the eye was closed.

Control of Eye Position in the Dark