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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 (CORNSWEET, 1956): others looked at much briefer periods (NACHMIAS, 1961; FIORENTINI and ERCOLES, 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 (STEINMAN, 1965), records rotations of the eye free from contamination by translations of the head and torsions of the eyeball. Features of the method that are important for interpreting records reproduced in this paper are as follows:

A small triangle of infra-red 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 infra-red film moving vertically at 5 mm/sec in a modified Grass (Model C4H) 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 dia. disc of tungsten-white light (luminance, 0·14 mL) located 0·75 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 in total darkness. The target was removed by a relay that operated a shutter, switched-off the current to the target source and fired 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 success 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 a 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. CORNSWEET (1956), NACHMIAS (1959) and STEINMAN (1965) and in line with a recent recommendation of DITCHBURN and FOLEY-FISHER (1967) that trials of 40-sec duration be adopted as a standard in contact lens studies of the eye movement pattern.

Both *S*s participated in 4 sessions during which 72 records were made (24 at each target position). Fifteen records (5 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.[1] For each of these records, paired horizontal and vertical eye positions were measured at randomly selected times within successive $\frac{1}{2}$-sec periods. In all, 96 paired position measures were made for each record (20 at the beginning of the trial when the target was visible and 76 during the 38 sec in total darkness).

TABLE 1. MEAN *Error* (ABSOLUTE DISTANCE BETWEEN MEAN EYE POSITION WHEN THE TARGET WAS VISIBLE AND MEAN EYE POSITION IN THE DARK) AND FIXATION STABILITY, i.e. MEAN BIVARIATE CONTOUR ELLIPSE AREAS (*Area*) AND MEAN STANDARD DEVIATIONS (*SD*) ON HORIZONTAL (*H*) AND VERTICAL (*V*) MERIDIANS ARE SHOWN FOR TARGETS PRESENTED IN THE *Primary*, *Right* AND *Left* POSITIONS. *Error* ONLY APPLIES TO THE 38 sec *Dark* PERIOD.* FIXATION STABILITY IS SHOWN FOR PORTIONS OF THE TRIALS WHEN THE *Targets* WERE VISIBLE AND ALSO WHEN *S*s FIXATED IN THE *Dark*. STANDARD ERRORS ARE GIVEN IN PARENTHESES. EACH MEAN WAS BASED ON 5 RECORDINGS.

		Error (min arc)	*Area* (min arc)^2	*SD* (min arc)	
				H	*V*
					Subject *RS*
Primary	target		244 (25)	4·8 (0·1)	7·3 (0·7)
	dark	29 (10)	4371 (732)	24·0 (1·5)	26·4 (4·3)
Right	target		168 (18)	3·8 (0·4)	6·3 (0·0)
	dark	39 (17)	4891 (750)	31·2 (3·4)	24·0 (2·9)
Left	target		351 (121)	6·4 (0·7)	6·8 (2·4)
	dark	59 (21)	7574 (1297)	35·2 (3·9)	31·1 (4·2)
Overall	target		254	5·0	6·8
	dark	42	5612	30·1	27·2
					Subject *AS*
Primary	target		95 (23)	3·6 (0·3)	4·4 (0·8)
	dark	44 (7)	7012 (757)	27·2 (3·7)	39·8 (4·4)
Right	target		134 (19)	4·0 (0·3)	4·9 (0·7)
	dark	61 (16)	5466 (1052)	37·3 (6·8)	26·5 (5·6)
Left	target		137 (21)	3·8 (0·2)	5·1 (0·7)
	dark	39 (10)	6420 (2545)	31·5 (7·6)	34·4 (5·2)
Overall	target		122	3·8	4·8
	dark	48	6299	32·0	33·6

* *Error* is not shown for the period when the target was visible because this measure (as defined in the present experiments) can not be applied to the fixation of a visible target. "Errors" during fixation of visible targets are usually defined as differences between saccade-offset position and mean eye position (CORNSWEET, 1956 and NACHMIAS, 1959) or as the standard error of mean fixation position on repeated independent trials with the same or different targets located in the same spatial position (STEINMAN, 1965). Such "fixation errors" with visible targets are typically 1 4 min arc.

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[1] Mean eye positions, for 10 sec when the target was visible, were calculated for all of the trials recorded at the last session. If horizontal and vertical mean eye position on successive trials differed by more than 6 min arc, it was assumed 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 extraretinal 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.[2]

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 experiments, the tabled areas are analogous to standard deviations of eye positions, i.e. they represent where the line of regard was 68·2 per cent of the time.[3] Fixation stability, like *error*, was not markedly influenced by target position. The variability of the eye about its mean position in the dark (*SD*s) was about $\frac{1}{2}$ deg arc on the horizontal and vertical meridians, considerably greater (about 6 ×) than was found during fixation of the visible targets but a very small fraction of the total range of movements that can be executed by the eye.

The next 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 7·6 sec portions of the records. *Error* increased throughout the dark interval, 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).[4]

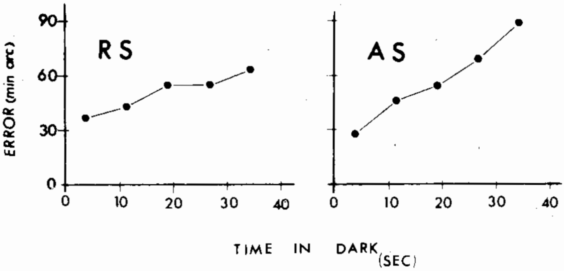

FIG. 1. Short term (7·6 sec) mean *error* during 38 sec periods in the dark for subjects *RS* and *AS*. Each mean is plotted at the midpoint of the short interval. Data points are based on 15 records for each *S* (5 at the primary, right and left target positions). Each mean was calculated from 225 paired horizontal and vertical position measures.

Although both *S*'s eyes were slowly moving farther away from the target position as they fixated in the dark, fixation stability about the short term (7·6 sec) 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

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[2] The algebraic mean position could be misleading if individual trial means were widely scattered in all 4 quadrants. This was not the case: individual trial means all fell within $1\frac{1}{2}$ deg of target positions.

[3] Actually, bivariate contour ellipse area is the solid angle in (min arc)^2 subtended at the eye by an ellipse projected on a plane surface parallel to Listing's plane. See STEINMAN (1965) for a description and test of the assumptions underlying this measure of bivariate variability.

[4] *Errors* from the 3 positions were combined because qualitative differences in *error* rate were not apparent.

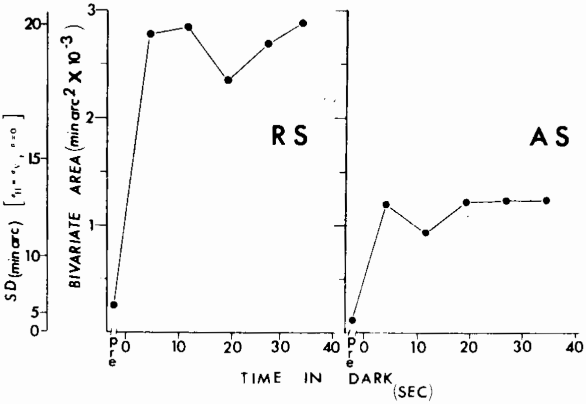

FIG. 2. Mean bivariate contour ellipse areas plotted as a function of time in the dark for subjects *RS* and *AS*. Areas are plotted for the period when the target was visible (*Pre*) and at the mid-points of successive 7·6 sec portions of the 38 sec dark interval. The scale at the left indicates the standard deviation on an average meridian (this measure assumes that the horizontal and vertical standard deviations are equal and that the position measures on the two meridians are not correlated). Data points are based on 15 records for each *S* (5 at the primary, right and left target positions). Each area was calculated from 225 paired horizontal and vertical position measures. The variability of the eye during each 7·6 sec period was calculated for mean eye position during that interval.

characteristic of extraretinal position control. This abrupt change in variability from retinal to extraretinal position control is shown in Fig. 2 where fixation stability (bivariate contour ellipse area) is plotted for successive 7·6-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 farther 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 prolonged periods*

In the next experiment *RS* attempted to maintain fixation of the target for a much longer time after it was removed from view (127·5 sec) in order to find out whether *error* continued to increase in the dark. Three records (1 randomly selected from 3 records made at each of the 3 target positions) were measured exhaustively (275 paired position measures were made at randomly sampled times within successive ½-sec intervals of each of the 137·5 sec records).

The rate at which the eye moved away from the target position is shown in Fig. 3 where *error* is plotted for successive 15-sec portions of the dark interval.

During the first 15-sec period, *error* increased rapidly, but during the remainder of the trial, it increased at a much slower rate: about 1/3 of the total *error* that would accumulate during the 127·5 sec dark period accumulated during the first 15 sec. Also note a *tendency* for the eye to stabilize 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 15-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 trail randomly selected from 3 recordings made at each of the 3 target positions.

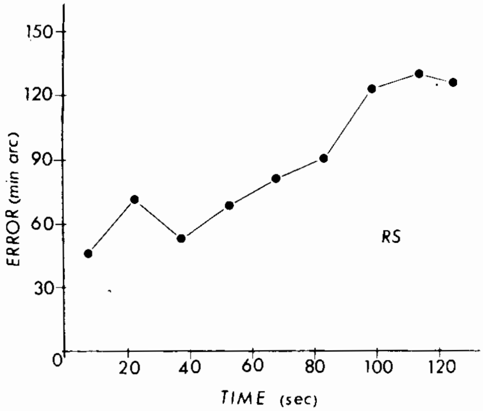

FIG. 3. Short term (15 sec) mean *error* during 127·5 sec periods in the dark for subject *RS*. Each mean is plotted at the mid-point of the short interval. Data points are based on 3 records (1 from the primary, right and left target positions). Each mean was calculated from 90 paired horizontal and vertical position measures.

AS's records were qualitatively similar to *RS*'s, *viz.* he also showed an initial rapid increase in *error* and loss of fixation stability followed by a slow progressive movement away from the position of the target. His fixation stability about successive 15-sec mean eye positions was uniform throughout the dark interval and his *error* also stabilized at about 2 deg, somewhat earlier than *RS* (after about 60 sec) in the randomly selected recording that was measured exhaustively.

3. *Role of conjunctival cues in extraretinal position control*

Tactile cues from the conjunctiva could have provided 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.[5] Such cues were shown to be unimportant in the next experiment.

This experiment was essentially a replication of the first with one exception, *viz.* *RS*'s eyes were anesthetized by instilling 2 drops of 0·5 per cent tetracaine hydrochloride (Alcon 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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[5] Molded versions of the Riggs type contact lens were worn in these experiments. Such lenses are molded to rest on the limbus and do not slip appreciably when used to study fixation of visible targets during which high velocity excursions of the eye are normally less than 10 min arc (RIGGS and SCHICK, 1968). Such lenses are rarely, if ever, worn with anesthesia because they are comfortable for 40–60 min unlike the YARBUS (1967) corneal "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 his eyes were not anesthetized (overall bivariate contour ellipse area = 7740 (min arc)^2; see Table 1 for *error* and fixation stability when tactile 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 extraretinal 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 extraocular 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 he is because he knows how he has moved his eye since the target disappeared or (b) by remembering the innervation pattern to the extraocular muscles that was used to fixate the visible target, i.e. the subject keeps his eye in place in the dark by maintaining or reestablishing the innervation pattern 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. In other 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 (midsaggital) plane passing through the center of the subject. This plane seems to be referenced in the body and not in the head of the perceiver. 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 midsaggital plane as being to 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 deg arc to the left or right of the direction established by the biting board. If our *S*s did rotate their bodies until they perceived the displaced targets as "straight ahead", their control of eye position in the dark could arise from their ability to fixate in the same direction their bodies were pointing.

In the next experiment we found that it was not necessary to orient our bodies towards the target when we kept our eyes in place in the dark: drastic rotations of our torsoes did not preclude reasonable extraretinal position control.

This experiment was essentially a replication of the first with the exception that the target was always presented in front of the fixating eye and the orientation of the torso

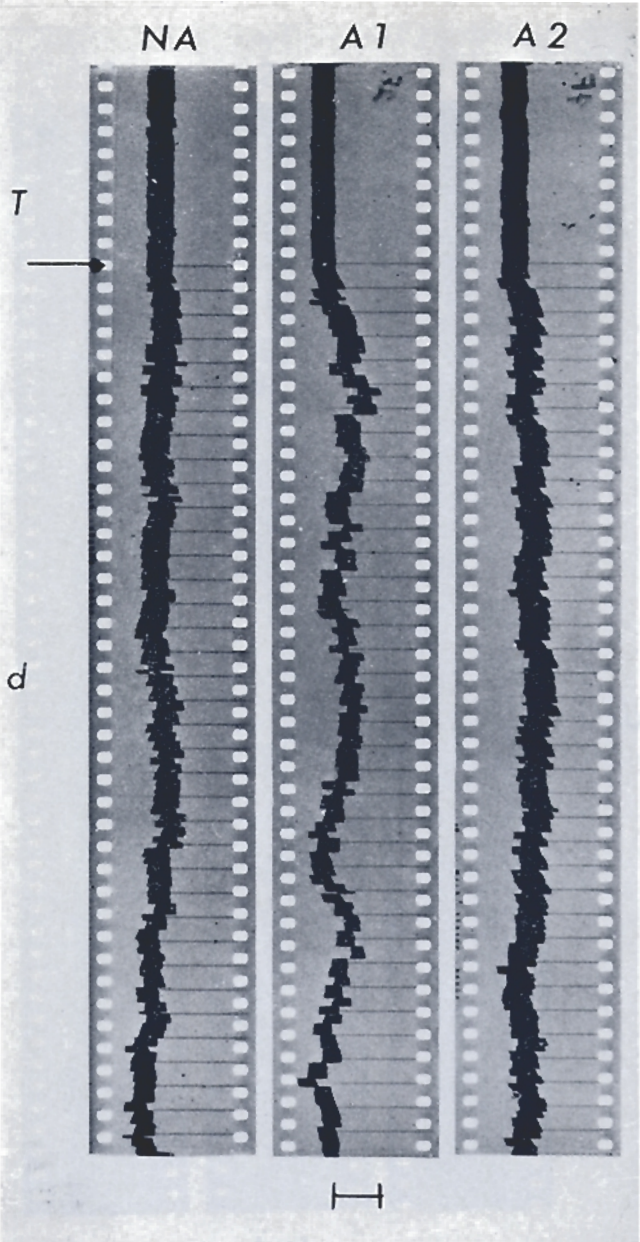

FIG. 4. Representative 2-dimensional recordings showing subject *RS*'s retinal and extraretinal position control with normal and anesthestized conjunctiva. The record on the left, labeled *NA*, was taken from the first experiment when anesthetic was not used. Records *A*1 and *A*2 show position control after anesthetic had been instilled in both eyes at the first and second recording sessions, respectively. Trials start at the top of the figure where this *S* 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 records show performance during 38 sec in the dark (*d*) (repetitive 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.

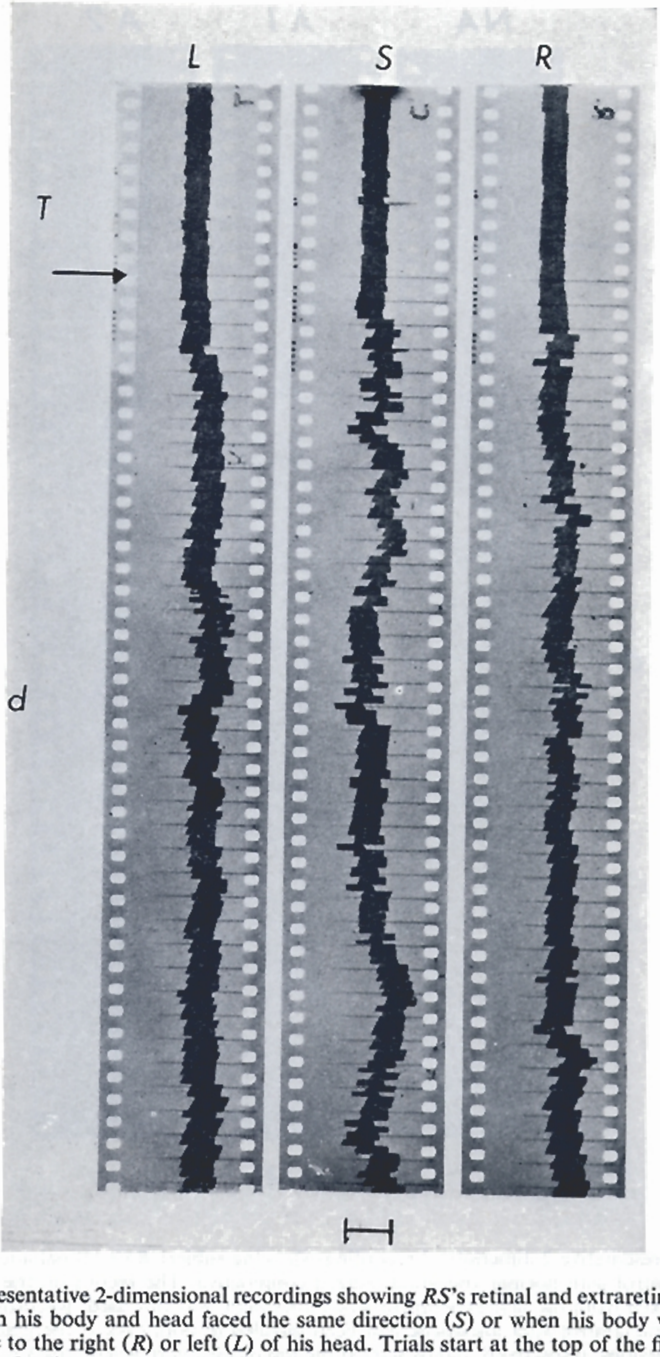

FIG. 5. Representative 2-dimensional recordings showing *RS*'s retinal and extraretinal position control when his body and head faced the same direction (*S*) or when his body was rotated ~45 deg arc to the right (*R*) or left (*L*) of his head. Trials start at the top of the figure where this *S* is seen fixating a target visible (*T*) in the primary position. The target was switched-off at the time indicated by the arrow and the remainder of the records show performance during 38 sec in the dark (*d*) (repetitive 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.

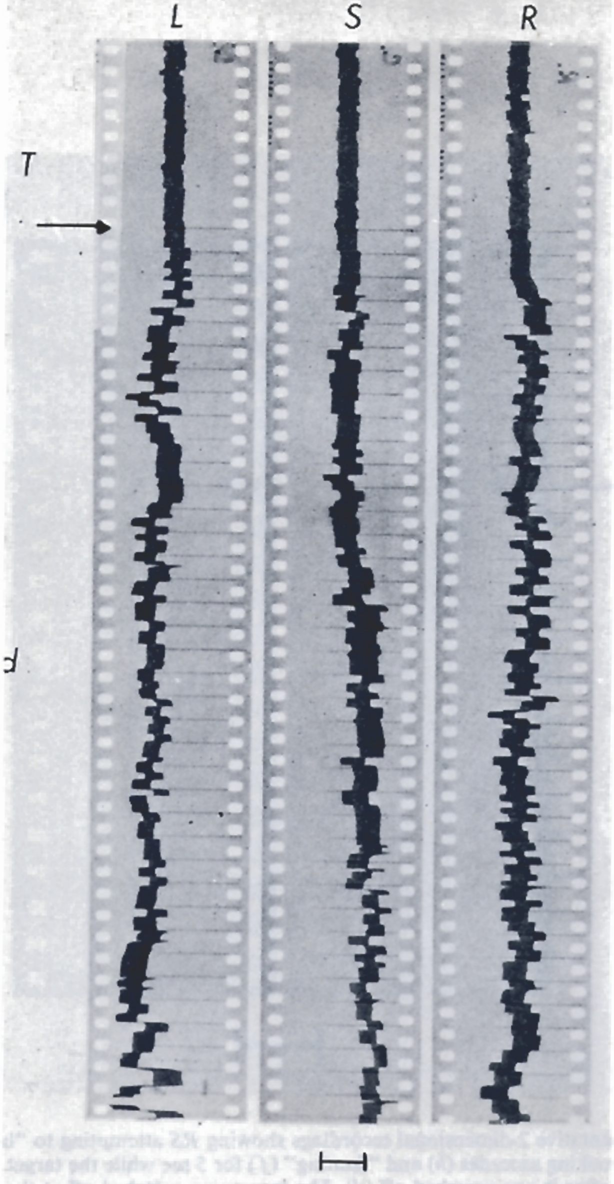

FIG. 6. Representative 2-dimensional recordings showing *AS*'s retinal and extraretinal position control when his body and head faced the same direction (*S*) or when his body was rotated ~45 deg arc to the right (*R*) or left (*L*) of his head. Trials start at the top of the figure where this *S* is seen fixating a target visible (*T*) in the primary position. The target was switched-off at the time indicated by the arrow and the remainder of the records show performance during 38 sec in the dark (*d*) (repetitive 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.

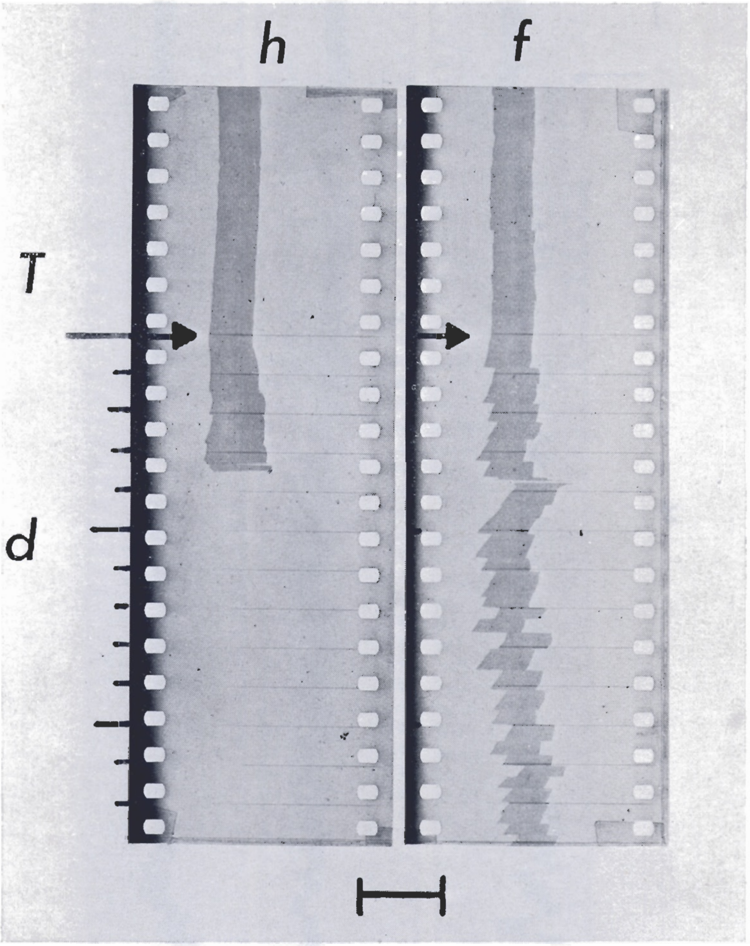

FIG. 7. Representative 2-dimensional recordings showing ***RS*** attempting to "hold" his eye in place without making saccades (*h*) and "fixating" (*f*) for 5 sec while the target was visible (*T*) and for 13 sec after it was switched-off (*d*). The target was switched-off at the time indicated by the arrow and faint horizontal 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.

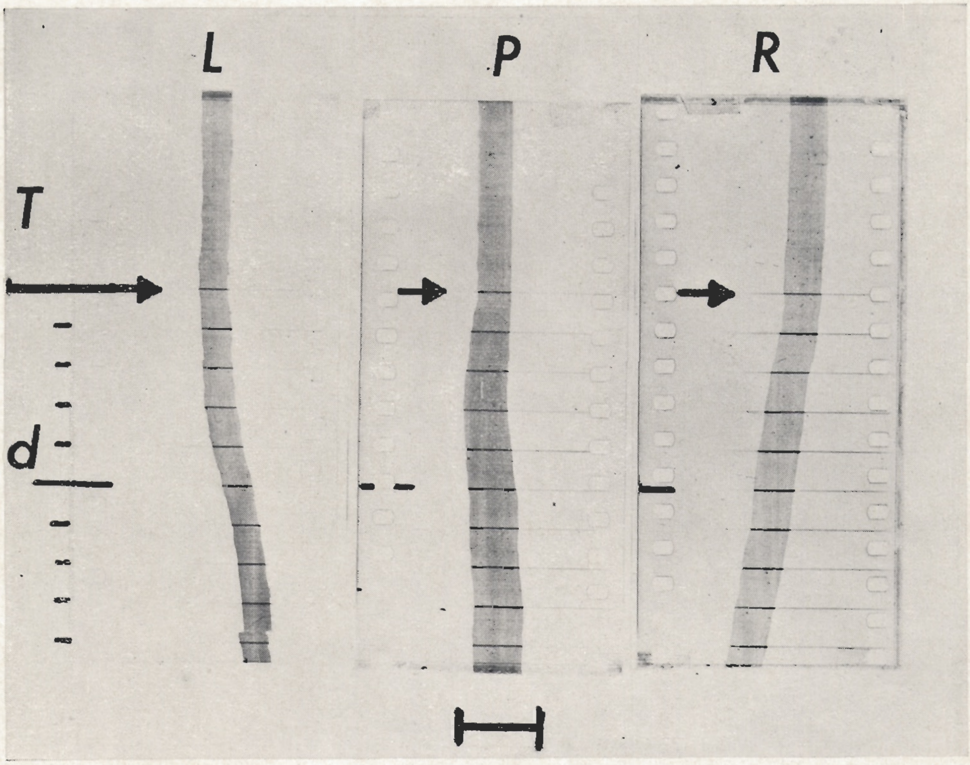

FIG. 8. Representative 2-dimensional recordings showing *AS* "holding" his eye in place without saccades for 5 sec while the target was visible (*T*) and for 9·5 sec after it was switched-off (*d*) for each target position, left (*L*), primary (*P*) and right (*R*). The target was switched-off at the 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 (5 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 (87 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 his torso (*error* was only 3 per cent of body rotation) and he was still able to stay within $1\frac{1}{2}$ deg of the target throughout the dark interval. Fixation stability did not depend on body position for either *S* (overall bivariate contour ellipse areas were 8244 (min arc)^2 (S.E. = 1445) for *RS* and 10418 (min arc)^2 (S.E. = 1054) for *AS*).[6]

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, in itself, guide the eye in the dark.

5. *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 near target position in the dark providing we were allowed 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 behaviours. 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 saccadic 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 defined 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 9 pairs of "free" and

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[6] The condition in which body position was "straight ahead" in this control experiment was identical to the condition in which the eye was in the primary position in the first experiment. Note that *error* and the variability of fixation were somewhat larger for the "straight ahead" body position than they were for the same position (primary) in the first experiment (see Table 1). These differences were not statistically reliable and probably

"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 slippage and eye position during the last 5 sec of these records was measured exhaustively.[7]

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 *errors* was 19 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.

6. *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. NACHMIAS (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. FIORENTINI and ERCOLES (1966) 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 Nachmias' subjects while *RS*'s fixation pattern resembled that reported by Fiorentini and Ercoles. 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 variations in occurrance of saccades in the dark might arise from individual differences in drift rates or tendencies to show dominant directions of drift. 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 loading 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.[8] We found that extraretinal position control, unlike retinal position control, is accomplished primarily by saccades.

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[7] Only successive pairs of records were selected for measurement so that a comparison could be made between "free" and "directed" performance at very similar times during the recording sessions. Meeting this as well as the criterion for contact lens slippage (see Note 1) left only 1 pair from the primary, 3 from the right and 1 from the left target positions for *AS*. It is not surprising that we couldn't find more successive pairs free from evidence of contact lens slippage because large saccades made when *Ss* were asked to look away from the target position would be expected to disturb the orientation of the contact lens.

[8] STEINMAN, CUNITZ, TIMBERLAKE and HERMAN (1967) reported that these subjects could suppress saccades while viewing stationary targets presented in the primary position and also while tracking constant velocity target motions (PUCKETT and STEINMAN, 1969). Voluntary saccade suppression did not lead to increased variability of the eye about its mean fixation position: a finding which suggests that low velocity eye movements ("corrective drifts") can maintain the line of regard by nulling fixation errors induced by "noisy" drifts. In the present experiment we adopted this mode of viewing (saccade-free position control) to determine whether drifts would also be corrective 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 made 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 (NACHMIAS, 1959; STEINMAN, CUNITZ, TIMBERLAKE and HERMAN, 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, NACHMIAS (1961) found that "the eye moved further and further 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 new, 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" (our *error*) as a function of time in the dark shows *error* accumulating at only 4 min arc/sec during the last 2 sec of his 12 sec trials as compared with 14 min arc/sec during the earlier portion of the dark period.

More recently MATIN, MATIN and PEARCE (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". MATIN *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 transition 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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Abstract—Two-dimensional eye movements were recorded for long periods in total darkness while 2 *S*s attempted to keep their eyes in the primary position or 10 deg arc to the left or right. Effective position control was observed in the absence of a visual error signal (the eye stayed within 2 deg arc of previously defined target positions after more than 2 min in the dark and much closer during briefer periods). Effective position control in the dark did not depend on tactile cues from the conjunctiva, the orientation of the *S*s' torsos or a self-selected eye movement pattern. Saccades were used to keep the eye near target position in the dark: low velocity position control (corrective drifts) dropped out soon after the target was removed from view.

Résumé—On enregistre les mouvements à deux dimensions des yeux pendant de longues périodes d'obscurité totale, tandis que les deux sujets essayaient de laisser leurs yeux soit dans la position primaire, soit à 10 degrés à gauche ou à droite. On observe un contrôle effectif de la position en l'absence de signal visuel d'erreur (l'oeil consevait à mieux que 2° la position de la cible précédemment définie après plus de 2 min d'obscurite, et avec une bien meilleure précision pour des périodes plus courtes). Le contrôle effectif de position dans l'obscurité ne dépend pas de données tactiles de la conjonctive, ni de l'orientation du torse des sujets, ni d'un type de mouvement des yeux choisi par le sujet. Les saccades servent à garder les yeux au voisinage de la cible dans l'obscurite: les contrôles de position à faible vitesse (dérives correctrices) disparaissent peut après que la cible cesse d'être vue.

Zusammenfassung—Zweidimensionelle Augenbewegungen wurden während langer Zeiträume in voller Dunkelheit registriert, während 2 Vp ihre Augen in der Primärstellung oder 10° zur Rechten oder zur Linken festzuhalten versuchten. Tatsächliche Stellungskontrolle konnte während der Abwesenheit eines Sehfehlersignales beobachtet werden (das Auge verblieb innerhalb 2° von früher festgesetzten Zielstellungen nach mehr als 2 Min im Dunkeln und sogar näher in kürzeren Zeiträumen). Die tatsächliche Stellungskontrolle hing im Dunkeln nicht von haptischen Aussagen der Bindehaut, der Stellung der Vp oder selbstgewählten Augenbewegungsmustern ab. Sakkaden wurden benützt, um die Augen im Dunkeln in der Nähe des Zieles zu behalten: die Stellungskontrolle für niedrige Geschwindigkeiten (Korrektionsgleiten) wurde unterdrückt, sobald das Ziel den Augen enthoben worden war.

Резюме — Регистрировались двумерные движения глаз, в то время как 2 исп. в течение длительного времени в полной темноте пытались удержать глаза в первичном положении, или на 10° правее, или же на 10° левее этого положения. В отсутствие зрительной обратной связи отмечен эффективный контроль положения глаз (глаза оставались в пределах 2° от ранее заданного положения — более чем через две минуты в темноте). При более кратком затемнении положение сохранялось намного точнее. Эффективность контроля положения глаз в темноте не зависела от тактильных сигналов с конъюнктивы, не зависела от положения тела исп., или от произвольно выбираемого испытуемым типа движений глаз. Положение глаз в темноте регулировалось с помощью саккад; коррегируюший дрейф прекращался вскоре после наступления темноты.