

FURTHER PROPERTIES OF THE HUMAN SACCADIC SYSTEM: EYE MOVEMENTS AND CORRECTION SACCADES WITH AND WITHOUT VISUAL FIXATION POINTS

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INTRODUCTION

THE SACCADE is generally regarded as a ballistic eye movement whose trajectory, once begun, cannot be influenced. Voluntary effort or practice, for example, will not alter saccadic velocity. The mean saccadic duration for a given magnitude eye movement is very predictable, with an average standard deviation of 5 msec for magnitudes between 5 and 40 deg. (ROBINSON, 1964). Although several different forms have been observed by various investigators (WESTHEIMER, 1954; YARBUS, 1956; HYDE, 1959; VOSSIUS, 1960; COOK, 1965), saccadic movements, in general, exhibit remarkably reproducible trajectories. It is known that changes in alertness affect the course of a saccade. Alcohol consumption (FRANCK, 1969), intravenous injection of Valium (a well known sedative; ASCHOFF, 1968), natural sleep (FUCHS and RON, 1968) and drowsy states of the diurnal cycle (KRIS, 1960) all result in slower eye movements. However, saccades occurring during the aforementioned states are very likely the product of a depressed oculomotor system. Therefore, except for occasional anecdotal observations (e.g. GOTO, TOKUMASU and COHEN, 1968, in the monkey) the authors are unaware of any reports regarding eye movement trajectory changes in attentive subjects.

The present study shows that the characteristics of saccadic eye movements in alert humans can be influenced by depriving subjects of visible fixation points. Eye movements of 40 deg in the dark or in other homogeneous visual fields exhibit durations 19 msec longer and peak velocities 16 per cent slower than their counterparts executed in looking about at clearly visible targets. If the fixation points are extinguished about 1 sec before the eye movement, the saccade will take on the characteristics of a movement made in the dark. Hence, the oculomotor system is not able to produce a normal saccade on command but must process a visual error signal to create the usual short duration, high velocity trajectory. Attempts to make eye movements in the dark often resulted in two saccades. The paradox of the second corrective saccade in the absence of a visual position error signal was investigated, and a model to account for such eye movements is proposed.

METHODS

The horizontal eye movements of eight persons with normal vision, 24-33 yr old, were measured by recording the electro-oculogram binocularly. The EOG-potentials were d.c.-coupled to an inkjet writer with an upper cut-off frequency of 700 Hz. To reduce head movements the subject rested on a chin holder with a forehead strap providing additional support.

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The experiments described in this paper can be divided into three parts. First, the influence of a homogeneous visual field was investigated by measuring eye movements in the dark. Second, visible fixation points were extinguished at various times preceding and during the saccade to determine the role of the visual error signal on the eye movement trajectory. Third, the target point was made to jump to a new location coincident with the onset or end of a saccade, so that the characteristics of the second corrective saccade could be investigated. Details of the target presentation for each of these cases will be described under the appropriate heading in the Results section.

Precautions were taken to eliminate the various objections against measuring eye movements by the EOG. Results from the subjects used in this study showed at most a ± 5 per cent error in linearity in measuring eye movements between ± 30 deg. Individual experimental runs were kept under 2 min and were always preceded and followed by a calibration. Subjects, preadapted to ordinary room illumination, were allowed to dark adapt for at least 10 min prior to an experiment. Calibration points for eye movements in the dark were provided by very weakly illuminated neon glow tubes, subtending about 0.6 deg at the retina and adjusted to be just perceptible to the subject. In this way the illumination level was essentially unchanged during the calibration and eye movement runs, thus obviating errors due to light and dark adaptation (KRIS, 1958). The diurnal variation in EOG observed by KRIS (1957) played no role in our measurements since the variation of calibrations was, on the average, 1.3 per cent of their mean or just 0.7 deg for a 60 deg eye movement. Finally, as the results will show, saccadic characteristics such as duration, maximum velocity and shape of trajectory agreed well with those published by other authors with other techniques—further evidence that the nonlinear effects reported by BYFORD (1963) were not exhibited by our subjects.

All eye movements were made symmetrically about the primary direction of gaze. Saccadic duration was estimated as the time from the onset of the movement to the next velocity zero; the maximum velocity, as the steepest tangent to the displacement curve.

RESULTS

As noted in the Introduction, fatigue and alertness can have a significant effect on eye movement trajectories. In our experiments, day to day variations between saccadic durations of equal angle movements were as much as ± 10 msec. During the course of a 1-hr session, the duration of a 40 deg saccade increased by 6.5 per cent, 12.5 per cent and 24 per cent in three different subjects. These phenomena regarding the effect of attention and fatigue on saccadic eye movements have already been reported in part by KRIS (1957). Their presence necessitated an experimental procedure in which the phenomenon to be investigated was compared to control measures of eye movements obtained within the same run.

Eye movements in the dark

The subjects were instructed to look alternatively at two very dim light spots whose separation subtended, for example, 40 deg of visual angle. After the subject had learned the correct magnitude, the lights were extinguished (leaving no perceptible after-image), and he attempted to continue to make 40 deg movements without benefit of a target.

Eye movements in the dark were obviously saccadic in nature but possessed longer durations and reached smaller peak velocities than those executed between well-illuminated targets (hereafter referred to as visible target saccades).

The difference in duration varied from 10 to 35 msec and the maximum velocity difference from 46 to 108 deg/sec for 40 deg eye movements in the eight subjects studied (Table 1). Since eye movement magnitudes in the absence of visible fixation points vary, all attempts to make a 40 deg saccade were averaged, and if the average magnitude differed from 40 deg the average duration entered in Table 1 was corrected for each subject according to his own curve similar to Fig. 1. The average difference of 19 msec between the visible target and dark mean durations was statistically highly significant ($t=7.73$, $P<0.005$) as was the average maximum velocity difference of 74 deg/sec ($t=9.48$, $P<0.005$). In three subjects who were able to continue making approximately 40 deg movements in the dark, the standard deviations of the dark and visible target

TABLE 1. COMPARISON BETWEEN 40 DEG EYE MOVEMENTS MADE BETWEEN VISIBLE FIXATION POINTS AND THOSE MADE IN THE DARK. MEAN VALUES WITH THEIR STANDARD DEVIATION; SAMPLE SIZE FOR EACH TARGET CONDITION AND FOR EACH SUBJECT WAS > 8

Subject	Duration (msec)			Max. velocity (deg/sec)		
	Visible target	Dark	Diff.	Visible target	Dark	Diff.
BB	96 ± 7.0	113 ± 7.0	17	538 ± 31	448 ± 32	90
UV	131 ± 9.5	149 ± 21	18	442 ± 41	393 ± 39	49
DS	98 ± 4.8	119 ± 20	21	482 ± 29	396 ± 39	86
IH	89 ± 6.0	99 ± 15	10	578 ± 47	532 ± 64	46
AF	114 ± 6.3	133 ± 9.0	19	462 ± 38	375 ± 38	87
OH	132 ± 9.0	148 ± 8.5	16	374 ± 37	320 ± 16	54
TS	123 ± 11	141 ± 21	18	450 ± 45	374 ± 34	76
WP	112 ± 7.5	147 ± 19	35	448 ± 40	340 ± 24	108
Average of individual means	112 ± 15	131 ± 19	19 ± 7	471 ± 61	397 ± 66	74 ± 22

durations were not statistically different. For the remaining five subjects, the standard deviations from the dark duration means exceeded those from the visible target means. The increased variability reflected the five subjects' inability to reproduce a 40-deg eye movement in the dark (range 37–51 deg), rather than an increased variability in averaged eye movement duration due to the absence of fixation points. The overall mean duration (112 ± 15 msec) and maximum velocity (471 ± 61 deg/sec) for 40 deg saccades between visible fixation points agree well with values obtained by other techniques (WESTHEIMER, 1954; ROBINSON, 1964; COOK, 1965; SCHMIDT and KREJCOVA, 1968).

An interesting sidelight was that the saccades of female subjects appeared to be faster than those of males. The first four entries, all female, in Table 1 show an average eye movement duration with a visible target of 104 ± 18 msec, compared to 121 ± 9 msec average for the four male entries. Furthermore, the female maximum velocities were 77 deg/sec faster (510 ± 60 deg/sec compared to 433 ± 40 deg/sec). It should be pointed out, however, that even the fastest woman does not reach the velocities achieved by monkeys (FUCHS, 1967).

The increase in saccadic duration and decrease in maximum velocity caused by the absence of visible fixation points occurs at all magnitudes between 10 and 60 deg (Fig. 1). The differences in velocity and duration are most evident for visual angles between 25 and 55 deg. For most subjects, dark saccades finally reach the same saturation velocity as the normal visible target saccades (at a magnitude of 60 deg for the example in Fig. 1). The dark saccadic durations increase in a roughly linear fashion at about the same rate (3 msec/deg in Fig. 1), as their normal counterparts for angles greater than 25 deg. It is often difficult to distinguish between the two saccadic types at angles less than 15 deg.

Dark saccades are slowed down from their inception. A comparison of curves (a) and (c) in Fig. 2 shows that dark saccades have a noticeably smaller initial slope than visible target saccades. However, all parts of the saccade are not equally slowed. For 40 deg saccades, the average time required by all subjects to move the first 20 deg showed a 36 per cent increase, while the time for the second 20 deg increased by 54 per cent in the dark. Whereas 40 deg visible target saccades were just slightly asymmetric (i.e. the second half of the movement was 20 per cent longer than the first half; see also HYDE, 1959),

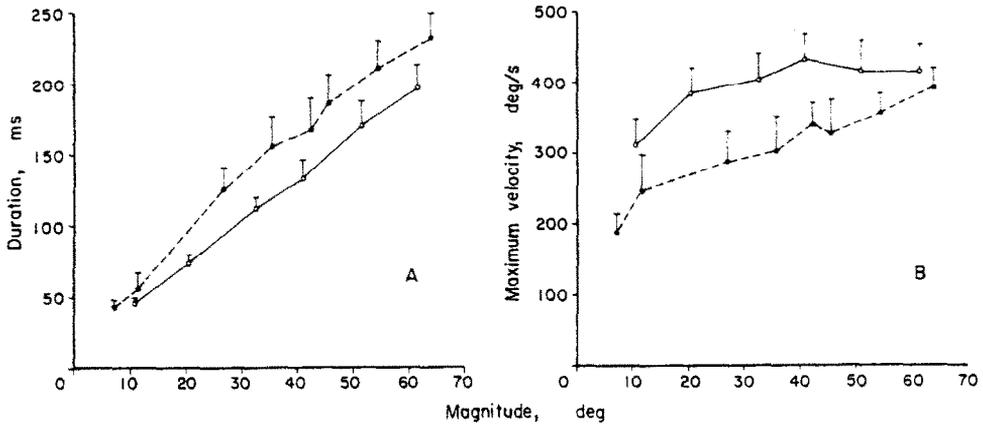


FIG. 1. Saccadic duration (A) and maximum velocity (B) of eye movements between well illuminated fixation points (open circles) and eye movements in the dark (solid circles) for a representative subject. Each point is the mean of at least 10 values; the bars represent the standard deviation of the mean.

movements in the dark had a 36 per cent longer second half.

That the saccadic slowing is due to the eye's having no fixation points in a homogeneous visual field and not simply some peculiarity of eye movements in the dark is shown in Fig. 2d. This eye movement was made while each eye was covered by half of a ping pong ball to provide a homogeneous but well-illuminated field. Its characteristics and those of other movements taken under the same conditions were found to be identical to those of dark movements (Fig. 2c). The similarity of curves 2a and 2b show further that the only requirement necessary to prevent saccadic slowing is the presence of two simple fixation points. An otherwise patterned visual field and the total visual field illumination play no role.

Finally, Fig. 2e shows a typical eye movement that occurs under closed eyelids. The shape of the trajectory under such conditions is extremely variable, but in any case the duration of the eye movement is much longer and the velocities much smaller than those of dark eye movements (the maximum velocity of the trajectory in Fig. 2e is only 150 deg/sec). In fact, the velocities of some closed eye movements intended by the subject to be quick changes in the direction of fixation (i.e. saccades) are comparable to those reached in normal smooth pursuit eye movements.

Each eye movement in Fig. 2 is preceded by a small (about 2 deg) short duration (about 8 msec) potential in the opposite direction of the eye movement. This potential, first observed by BROCKHURST and LION, 1951, was a constant adjunct to all EOG measured eye movements in all subjects and was used to define the onset of the saccade for duration measurements. Since this prepotential is not observed by any other eye movement measuring technique, it clearly does not represent a true displacement of the eyeball, but rather some electrophysiological potential, peculiar only to the EOG, associated with eye movement.

The transition between dark and visible target saccades

How long before the onset of an eye movement must the target disappear in order to slow down the saccade? To answer this question, two neon glow lamps separated by 40 deg were turned off simultaneously at various times preceding and during the saccade. The

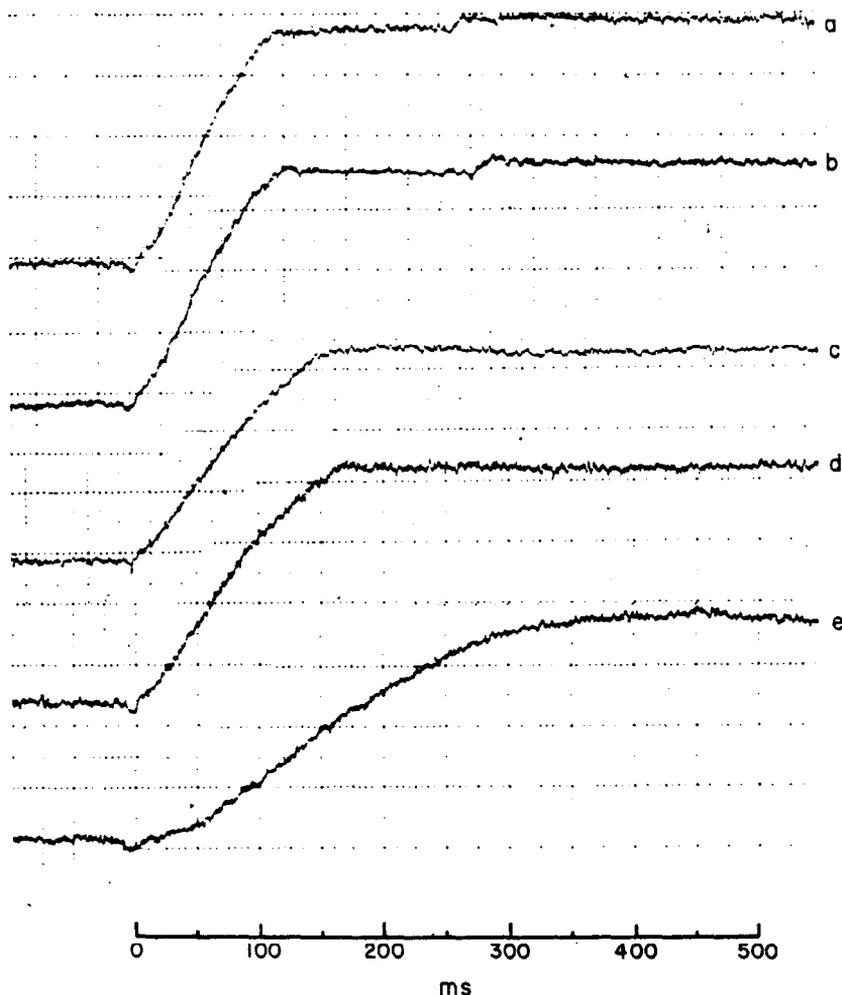


FIG. 2. A comparison of saccadic trajectories obtained with and without visual fixation points. (a) Normal saccade in a well illuminated room. (b) Saccade between two dim fixation points in an otherwise dark room. (c) Saccade in complete darkness. (d) Saccade in a homogeneous, well illuminated visual field. (e) Eye movement with closed eyes. In all cases, 40 deg eye movements typical of each condition were selected.

subject continued fixating the site of, for instance, the left hand lamp after it was extinguished. After a variable time, a click was sounded as the signal to make an eye movement to the site of the right hand extinguished lamp. After the movement, the lamps were re-ignited, the subject fixated the right hand lamp and the process was repeated in the other direction. The delays between the extinction of the lamps and the beginning of the saccade were randomized, and the durations of the visible target saccades were subtracted from those of delayed saccades obtained during the same run. Once again, all saccadic durations were linearly corrected to correspond to movements of equal amplitude.

In three of four subjects tested, the differences thus obtained showed their steepest increase between a delay of zero (extinction at saccade onset) and approximately 1100 msec.

At a delay of 1100 msec, 80 per cent of the difference between delayed and visible target saccades had been reached. For delays greater than 1100 msec, the differences appeared to attain a plateau which extended to the maximum 3 sec delays examined here (Fig. 3).

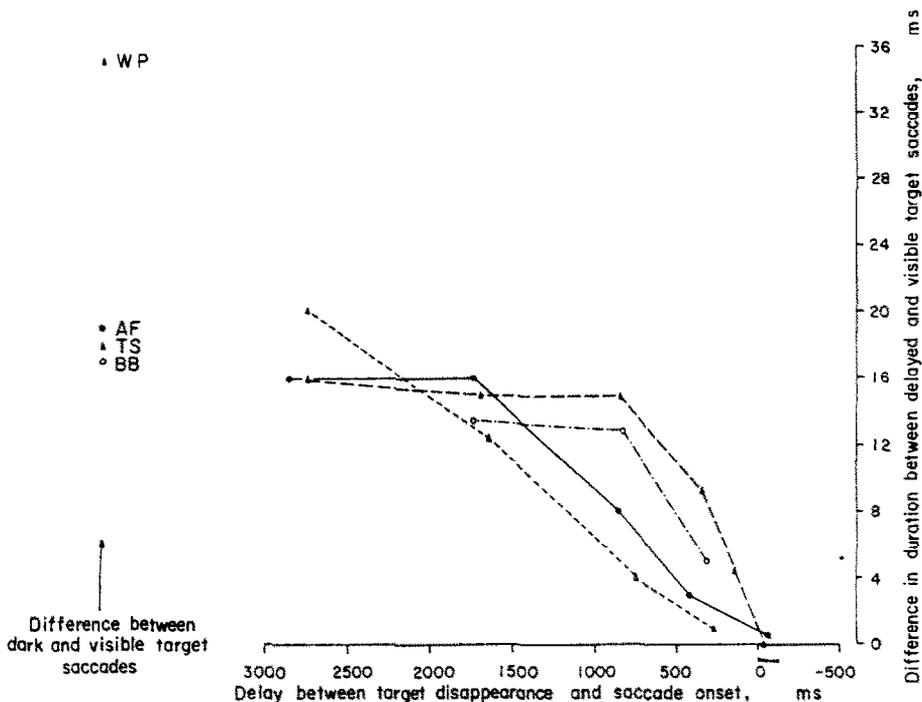


FIG. 3. The effect on saccadic duration of extinguishing target lamps at various delay times prior to the onset of a saccade. All saccades were 40 deg; 4 subjects are represented. The horizontal bar from 0 to -120 msec represents the duration of a typical 40 deg movement between visible targets.

The remaining subject showed no saturation within this period.

Characteristics of the second corrective saccade for large angle movements

In order to fixate a target at an angular distance of 40 deg, most subjects require two saccades: a large initial saccade which travels about 90 per cent of the distance followed, after a short latency, by a second smaller saccade which brings the eyes on target. Subjects who normally made this second saccade in looking between two visible fixation points also made a second saccade in the dark. In the case of well illuminated fixation points the second saccade is, in fact, a correction elicited by the position error remaining after the initial saccade, since the second saccade magnitude increases if the first saccade magnitude decreases. What, however, is the stimulus for a second saccade in the dark?

The initial few dark movements after the target lights are extinguished are of approximately the correct amplitude. Thereafter, a subject's performance usually deteriorates and results in initial saccades greater than 40 deg; hence, it is meaningless to ask if the second saccade is corrective or not. However, it is remarkable that the second saccade is

always in the same direction as the initial saccade. Furthermore, the mean latency of the second saccade in the dark (130 msec) is not statistically different from that elicited by visible fixation points (127 msec). Lastly, the latency of the second saccade under both light and dark conditions (approximately 130 msec) is always less than the latency of the first saccade (approximately 230 msec from WHEELLESS *et al.*, 1967). These three observations suggested that large fixation changes may be preprogrammed as a package composed of two movements: a first, large movement which almost always falls short and a second, smaller movement to acquire the target. Since the direction and the approximate amplitude are already built into the "package", the usual error sampling time can be significantly reduced, accounting for the observed decrease in latency of the second saccade.

To investigate this package hypothesis further, the target was made to change position between the first and second saccades, and the resulting eye responses were examined in somewhat the same way as WHEELLESS *et al.* did (1966) with their pulse-step stimuli for the first saccade. Two neon glow lamps (extinction time $\ll 1$ msec) were positioned to subtend a 40 deg visual angle. At a horizontal distance of 5 deg on either side of the right hand lamp, additional lamps were placed to subtend 35 deg and 45 deg. The subject was instructed to first fixate the left hand lamp and then move his eyes as rapidly as possible to that right hand lamp which was illuminated. As long as the subject fixated the left hand lamp, only the right hand lamp at 40 deg was visible. Upon executing a rightward saccade, the subject's eye movement actuated a trigger device causing one of three possible changes in the right hand lamps: (1) the lamp at 40 deg remained on; (2) the lamp at 40 deg was extinguished and simultaneously the lamp at 35 deg was ignited, resulting in a 5-deg step back in target position; (3) the lamp at 40 deg was extinguished and the lamp at 45 deg ignited, resulting in a 5-deg step ahead in target position. The time at which the target jumped from 40 to 45 or to 35 deg was varied so that the jump could occur near the onset of the saccade, at the end of the saccade or at a fixed time after the end of the saccade. The variable latency and variable jump conditions were mixed together to create a program of random end positions. Three of the seven subjects who usually required two saccades for a 40 deg visible target movement were studied.

Figure 4 is a summary of the various response types obtained from all subjects. When the target stepped to a new position at the beginning of the first saccade, the eye waited about one normal reaction time (average 233 msec) before jumping on target with one additional saccade (Fig. 4 c, d). If, however, the target jumped 70 msec after the end of the saccade, two possible eye movement responses resulted. In the majority of cases (53 per cent), a second saccade moved the eye to 40 deg after a very short latency (162 ± 10 msec), although approximately 100 msec previously the target had jumped to either 35 or 45 deg (Fig. 4 a, b; upper curves). Only after a normal reaction time of 240 msec did the eye make a third saccade to the correct target location. The second type of response (Fig. 4 a, b; lower curves) occurred about 36 per cent of the time and was composed of only two saccades; a first saccade which fell short of 40 deg, followed, after an average interval of 389 msec, by a second, which moved the eye to the correct angle. If the target remained at 40 deg, the average latencies for three subjects to the second saccade were 150, 166, and 241 msec, yielding an overall mean of 186 ± 49 msec. When the subject looked between two permanently fixed points, it will be recalled that the latency of the second saccade was only 130 msec, so that the latency increased somewhat with the additional uncertainty that the target might jump to a new location. In two subjects, this increase was modest (43 msec maximum), but the third subject exhibited a 109 msec increase.

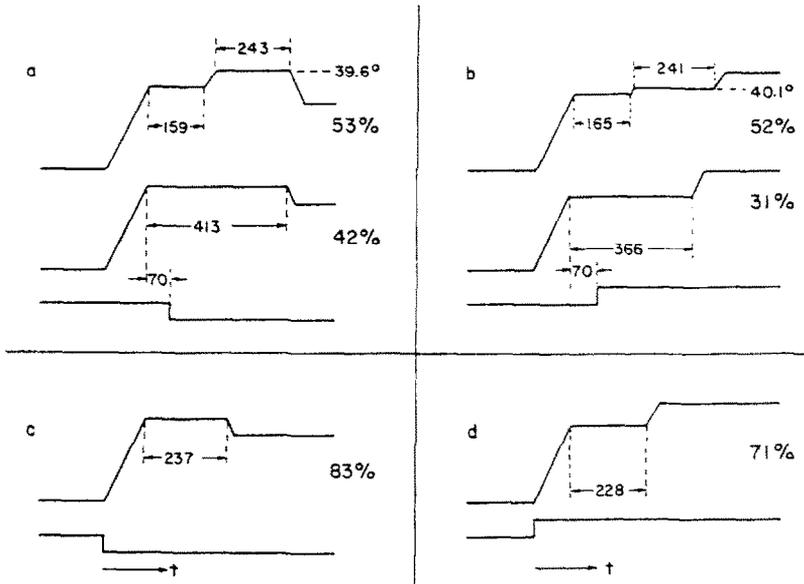


FIG. 4. A schematic of the most frequent types of eye responses obtained when a target originally located at 40 deg jumped to either 35 deg (a, c) or 45 deg (b, d). The lowest trace in each case represents the target position which jumped either 70 msec after the end of the saccade (a, b) or coincident with the onset of the saccade (c, d). All times in msec.

On the basis of the first two subjects, we feel that the third subject showed an atypical increase that was too large and therefore that a figure closer to 160 msec would be more appropriate as the average latency for the three subjects.

The target jumps studied here occurred only at the onset, end or 70 msec after the end of the saccade. Had the target jumped after a delay greater than 70 msec, we would have expected more than 50 per cent of the responses to have had three saccades (Fig. 4 a, b—upper curves). Because of the variability in triggering a target displacement from an eye movement, the target occasionally jumped 100 msec after the first saccade. In almost every case, such target movements elicited a response which first corrected to 40 deg. Had the target jumped within the 70 msec following the end of the saccade, less than 50 per cent of the responses would have had three saccades.

DISCUSSION

Since eye movements executed without fixation points are statistically slower than normal saccades, a visual position error signal must be necessary to elicit the optimal (i.e. fastest) oculomotor response. This signal can be stored for about 350 msec, since for delays less than this the average increase in saccadic duration is less than 5 msec (Fig. 3), making it impossible to statistically distinguish the delayed from the visible target saccades. In any case, for a delay less than 100 msec, it is certain that the saccadic duration is not increased. This finding may be anticipated from the results of WHEELLESS *et al.* (1966) whose data suggest that the measurement of visual error is concluded about 100 msec to 150 msec before execution of the saccade. When the target disappeared during the course of the movement, there was an even smaller difference in saccadic durations (0.3 msec) supporting the view that while the saccade is being executed no visual input is processed to influence the saccadic trajectory.

YOUNG (1962, 1968) has demonstrated that saccadic responses can be modelled by a sampled data control system. Every 200 msec, the visual error is sampled for a brief instant (certainly less than 10 msec) by an impulse modulator, and the system is refractory to target movements occurring between samples. In 1966, WHEELLESS *et al.* presented a target that stepped 6 deg horizontally to one side for T msec, after which it stepped 12 deg in the opposite direction. For values of T less than 200 msec, the Young model predicts a 6-deg saccade after 200 msec, followed by a 12-deg movement in another 200 msec. WHEELLESS *et al.* (1966), however, found that for $T = 100$ msec, 77 per cent of the responses were composed of a single saccade to the second target position. Such results suggest that information regarding target behavior is accepted up to about 100 msec before a saccade, so that a finite width, rather than an impulse sample, is more appropriate. Let us arbitrarily define the sample width as that interval after an initial target movement during which, should the target move again, the eye will respond to the second target movement 50 per cent of the time. From Table 1 of WHEELLESS *et al.* (1966), the typical sample width would then be about 150 msec. In our Fig. 4, less than 50 per cent of the responses follow a step occurring only 70 msec after the first saccade, suggesting that the sample width for second saccades is much smaller.

The notion that, for large angles, the total eye movement response is prepackaged as two saccades helps to interpret the results of the target jump experiments. We suggest that the following sequence of events may occur in response to target steps larger than 15 deg:

- (1) After a visual reaction time of 230 msec, a large saccade travels approximately 90 per cent of the distance to the target.
- (2) At the end of the saccade, the remaining error is observed (sampled) by the oculomotor system for approximately 70 msec.
- (3) A decision is made either to continue the package program or to cancel it. The oculomotor system anticipates an error whose magnitude is about 10 per cent of the original target displacement and whose direction is the same as the first saccade. The program is cancelled if the error is too large or in a direction opposite to that expected.
- (4) If the program is accepted, a second saccade moves the eye after 160 msec to the correct position.
- (5) If the program is cancelled:
 - (a) when an inappropriate error is already present at the beginning of the 70 msec sample, the package response is abandoned for a normal latency response, i.e. the next saccade occurs in about 230 msec.
 - (b) when the inappropriate error first occurs at the end of the sample period, the short package latency is allowed to elapse and is then followed by an additional normal reaction time before a saccade occurs, i.e. the next saccade occurs in $160 + 230 \approx 390$ msec.

In Fig. 4 a, b, two types of response occurred. In both upper curves, the target remained at 40 deg for the entire sampling interval of 70 msec, so that the step change in target position occurred too late to influence the package decision to correct to 40 deg. The eye then waited a full visual reaction time before making a saccade to the correct target position. If the target did not jump, but remained at 40 deg, a two saccade response occurred, similar to the first two movements in the upper curves. Apparently also in both lower curves, the target jumped after the 70 msec sample, so that a correction to 40 deg

would have been appropriate; however, the eye made no saccade after 160 msec and waited for what appeared to be an additional full reaction time of 230 msec before responding. The results of WHEELLESS *et al.* (1966) make it clear that the width of a sample cannot be sharply defined; that the occurrence in time of the end of a sample is probabalistic. Hence, it is likely that in the lower curves the target stepped just before the end of the sample, causing an unexpected error, which resulted in suppression of the second saccade in the package. Since the decision to cancel was made so late, the short package latency had to run its course before a normal latency response was permitted to occur.

If the target moved prior to the onset of the sample, as in Fig. 4 c, d, the oculomotor system quickly recognized that the second saccade of the package was inappropriate for the observed error. Because the error was much larger (Fig. 4d) or in the opposite direction (Fig. 4c) than expected, the package response, in most cases, was abandoned in favor of the normal latency response to a new stimulus. Since the decision to cancel was made very early in the sample period, it was still possible to obtain the normal saccadic latency.

When the target jumped just at the end of the saccade, the eye movement response also usually showed only one corrective saccade, with a latency of 290 msec for a step to 45 deg and 307 msec for a step to 35 deg, i.e. the latencies fell between those of Fig. 4 a, b (lower curves) and Fig. 4 c, d. These results are difficult to explain with our model and imply that preliminary information received during the saccade influences the subsequent eye response. However, it is already known that vision is at least partially suppressed during a saccade (MICHAEL and STARK, 1967; GROSS *et al.*, 1967) so that such a hypothesis remains tentative.

If, for illuminated targets separated by large visual angles, the response is prepackaged as two saccades, one might also expect a second movement in the dark. The input to the oculomotor system would be, for example, an imagined 40 deg target displacement. All responses to a 40 deg error are preprogrammed as two saccades, so that, even lacking a visual error after the first saccade, a second saccade occurs. If the second saccade usually corrects for about 10 per cent of the angle, it will also do so in the dark.

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Abstract—The execution of normal saccadic eye movements was found to depend upon clearly visible fixation points. Eye movements made in the dark or in an otherwise homogeneous field exhibited 10% longer durations and 16% slower maximum velocities than those between well illuminated targets. An increase in duration is already noticeable when the fixation points disappear 350 msec before the saccade. A second saccade often occurs despite the absence of fixation points. This phenomenon led to experiments which suggest that for large angles, the eye movement response is preprogrammed as two movements and that the second saccade in the package is determined by a position error sample of 70 msec.

Résumé—L'exécution normale de mouvements rapides des yeux (saccades) dépend de l'existence, dans le champs visuel, de points de fixation. Dans le noir ou dans un champs visuel autrement homogène les saccades montrent une augmentation de durée de 10% et une réduction en vitesse maximale de 16% par rapport aux valeurs normales. Une augmentation de durée se fait déjà remarquer si les points de fixation disparaissent 350 ms avant le début de la saccade. Même en l'absence de points de fixation les mouvements se terminent souvent par une saccade secondaire. Ceci a mené à des expériences qui, par leurs résultats, suggèrent que les larges mouvements oculaires sont préprogrammés comme volée de deux saccades dont la 2^{ième} est déterminée, quant à son amplitude, par une mesure d'erreur d'une durée de 70 ms.

Zusammenfassung—Voraussetzung für die Ausführung normaler sakkadischer Augenbewegungen sind gut sichtbare Fixationspunkte. Augenbewegungen im Dunkeln oder in einem in anderer Weise homogenen Gesichtsfeld zeigen eine um 10% erhöhte Dauer und um 16% verlangsamte Maximalgeschwindigkeit gegenüber Bewegungen zwischen gut sichtbaren Zielpunkten. Ein Zuwachs der Dauer ist bereits bemerkbar, wenn die Fixationspunkte 350 ms vor Sakkadenbeginn verschwinden. Sekundärsakkaden treten oft auch auf, wenn keine Fixationspunkte sichtbar sind. Diese Erscheinung führte zu Experimenten, deren Ergebnisse vermuten lassen, daß Blickrichtungsänderungen über große Winkel als Bündel von 2 Sakkaden vorprogrammiert sind und daß die 2. Sakkade des Bündels auf Grund einer Fehlerabtastung von 70 ms Dauer ausgeführt wird.

Резюме — Было найдено, что выполнение нормальных саккадических движений глаза зависит от того, насколько ясно видны точки фиксации. Глазные движения делаемые в темноте, или при том условии, что имеется другое гомогенное поле, обнаруживают увеличение длительности на 10% и замедление максимальной скорости на 16%, по сравнению с тем, что наблюдается при хорошей освещенности тестов. Увеличение длительности становится уже заметным, когда фиксационные пункты исчезают за 350 мсек до саккады. Несмотря на отсутствие фиксационной точки часто появляется вторая саккада. Это явление привело нас к постановке таких экспериментов, результаты которых говорят о том, что вторая саккада в послылке определяется ошибкой положения в пределах 70 мсек.