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# Determination of the Stimuli for Involuntary Drifts and Saccadic Eye Movements\*

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Eye movements during monocular fixation were photographically recorded using the contact lens mirror technique. Records were taken during normal viewing and during viewing with a stabilized retinal image. Flicker was used to produce various durations of disappearance of the fixated figure under both conditions. Characteristics of the drifts and saccadic components of the eye movements were compared under these conditions. It was found that, (1) the rate of drift is the same for all conditions, (2) there are many fewer saccades during stabilized than during normal viewing, and (3) the frequency of saccades is independent of the duration of disappearance for stabilized viewing. An analysis of the characteristics of saccadic movements showed that their probability of occurrence, direction, and magnitude are dependent upon the position of the retinal image on the retina. No comparable relationship was evident for the drifts of the eye. Eye movement records taken in the dark indicate that, in the absence of visual control, the eyes are incapable of maintaining their fixation. Proprioceptive feedback, therefore, does not appear to play an important part in the fine corrective movements that serve to maintain ordinary fixation. It is concluded that the primary stimulus condition for involuntary saccadic eye movements is displacement of the retinal image on the retina, and that drift is the result of an instability of the oculomotor system.

## INTRODUCTION

**E**VEN when a subject tries to fixate a point steadily, his eyes are in constant motion. This motion, called involuntary eye movement, has for convenience been categorized into four types: (1) tremor, a very small and rapid oscillation, (2) slow waves of irregular frequency and extent, (3) slow drifts, and (4) rapid flicks, or saccadic movements.<sup>1</sup> A typical photographic record of eye movements taken during fixation contains all of these types (Fig. 1). Since it is often difficult to distinguish between drifts and slow waves on such a record, these are combined under the heading "drift" for the purposes of this paper. All of these movements are extremely small. During fixation, the line of regard rarely moves out of an area ten minutes of arc in diameter (the head of a thumbtack at ten feet).

In the normal course of events, any eye movement produces a corresponding shift of the retinal image of the fixated figure across the retina, and for this reason the influence of eye movements on visual acuity has been a subject of considerable interest. Recently, an optical device has been reported which allows the eye to move normally, but prevents normal excursions of the retinal image.<sup>2-4</sup> (This device will be explained in detail below.) When the image is thus rendered stationary on the retina, the subject reports that the fixation field rapidly fades out and disappears. In other words, the continual displacement of the retinal image by

involuntary eye movements is an essential condition for the maintenance of vision.<sup>3,4</sup>

The purpose of this research was to determine the stimulus conditions that favor the appearance of involuntary drifts and saccadic eye movements. At least three possible stimulus conditions have been suggested in the literature.

### 1. Disappearance

Since, in the absence of retinal image movements, a stationary fixation field will disappear,<sup>3,4</sup> the following may be true during normal fixation. With the eye nearly motionless, the object fixated begins to disappear. This disappearance then triggers a drift or saccade. In other words, disappearance itself may be the condition which initiates an eye movement.<sup>5</sup>

### 2. Displacement

Any discrepancy between the position of the retinal image of the fixation point and a retinal "center of best vision" may trigger a corrective movement of the eye. The correction may be in the form of a drift, a saccadic movement, or both. For example, if, at a given moment, the image of the fixation point is at some distance from the retinal point of best vision, there may be a tendency for a saccadic movement to occur. It might also be true

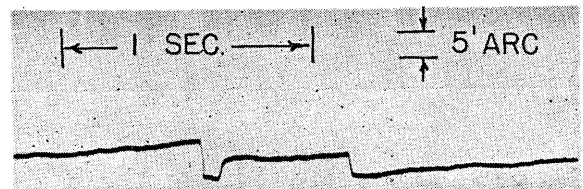


FIG. 1. Typical photographic record of eye movements during fixation. The very small oscillations are tremor. The large, rapid shifts are flicks, or saccades.

\* These experiments were conducted in the Psychological Laboratory at Brown University and were supported by a contract between Brown University and the Office of Naval Research, Department of the Navy. The present paper is based upon research presented in partial fulfillment of the requirements for the Ph.D. degree at Brown University. The author wishes to express his sincere gratitude to Professor Lorrin A. Riggs, the adviser for this research.

<sup>1</sup> F. Ratliff and L. A. Riggs, *J. Exptl. Psychol.* **40**, 687 (1950).

<sup>2</sup> F. Ratliff, *J. Exptl. Psychol.* **43**, 163 (1952).

<sup>3</sup> R. W. Ditchburn and B. L. Ginsborg, *Nature* **170**, 36 (1952).

<sup>4</sup> Riggs, Ratliff, Cornsweet, and Cornsweet, *J. Opt. Soc. Am.* **43**, 495 (1953).

<sup>5</sup> B. L. Ginsborg, *Brit. J. Ophthalmol.* **37**, 746 (1953).

that this movement would be in a direction such as to reduce that distance.<sup>1,3,6,7</sup>

### 3. Instability

Both drifts and saccades may be a result of a fundamental instability of the oculomotor apparatus, and not influenced by retinal events.<sup>1</sup>

The primary purpose of the present investigation was to evaluate these three suggested stimulus conditions. To accomplish this, eye movements were measured while two variables were manipulated. The first was a temporal variable, namely, the total duration of the disappearance of the fixation figure. This can be best explained by an example. Suppose that the stimulus were presented continuously for one minute and the subject reported that he was seeing the stimulus during twenty seconds of that time. The amount of disappearance would then be represented by the proportion of the total presentation time during which the stimulus was invisible, in this case forty sixtieths, or 0.67. This measure will hereafter be referred to as the disappearance-time fraction.

The variable of disappearance-time fraction was manipulated on the basis of the following considerations. If an image is motionless on the retina, the fixated figure will quickly disappear. The present experiments show, however, that this disappearance may be prevented or overcome by slowly flickering the test object. The rate of flicker is found to determine the disappearance-time fraction. As the flicker rate increases, the amount of disappearance also increases until, at a high rate of flicker, the disappearance-time fraction reaches a value comparable to that for steady illumination.† A similar, but less striking, relationship exists between flicker rate and disappearance-time fraction during normal viewing of a fixation object, that is, when eye movements result in a moving retinal image. The manipulation of the disappearance-time fraction makes possible the evaluation of the first possible stimulus condition mentioned above, namely, that drifts or saccades are elicited by the disappearance of the fixation figure. If such is the case, their frequency of occurrence should increase as the disappearance-time fraction is increased in this way.

The second variable employed was a spatial one, the extent of excursion of the retinal image across the retina. To study this variable, eye movements under two conditions were compared. One was that of normal fixation. The other was the "stopped-image" condition mentioned above, in which, though the eye is permitted to move normally, the retinal image remains stationary

with respect to the receptor units. If, as possibility (2) above suggests, displacement of the retinal image is a stimulus for a given type of eye movement (e.g., saccades), movements of this type should be reduced in number or eliminated under the stopped image condition.

If neither the temporal nor the spatial alteration of the retinal image has any influence on the extent or frequency of the involuntary eye movements, such movements would seem merely error factors, manifesting the instability of the oculomotor system. This is possibility (3) above.

### APPARATUS

To produce a retinal image which remains stationary on the retina in spite of eye movements, an optical system identical in principle to that used in an earlier paper<sup>4</sup> (Condition I) was employed. In Fig. 2, the subject wore, on his right eye, a contact lens into which a plane mirror had been inserted. Rays from a modified slide projector, *P*, were reflected from this mirror, *M*, to a screen, *S*, where they formed an image of a fine dark vertical line bisecting a bright circular background. The subject looked at this image through the contact lens. When optical paths of suitable length are chosen, the retinal image of the stimulus figure will not move with respect to the retina, in spite of movements of the eyeball in its socket. This was the condition of "stopped-image" viewing.

When the contact lens mirror in this system is replaced by a mirror rigidly secured to the apparatus (other conditions remaining the same), the subject sees

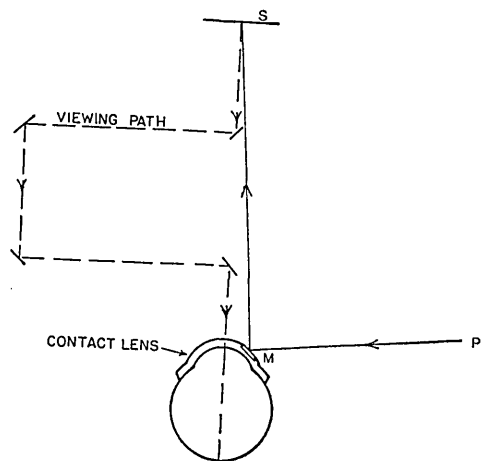


FIG. 2. Diagram of an apparatus used to produce a retinal image which remains stationary on the retina in spite of eye movements. Rays from projector *P* are reflected from mirror *M*, mounted on the contact lens. The rays form an image of a fixation target at screen *S*. The subject views the target through the dashed viewing path. When the eye moves through angle  $\alpha$ , the projected image moves through  $2\alpha$ . Since the length of the viewing path is twice the distance from *M* to *S*, the retinal image enters the eye at angle  $\alpha$ . Therefore the retinal image does not move with respect to the retina. (After Riggs, Ratliff, Cornsweet, and Cornsweet.<sup>4</sup>)

<sup>6</sup> J. ten Doesschate, *Acta Ophthalmol.* 127, 65 (1954).

<sup>7</sup> R. W. Ditchburn, *Optica Acta* 4, 171 (1955).

† Ditchburn and Fender [R. W. Ditchburn and D. H. Fender, *Optica Acta* 2, 128 (1955)] report a somewhat different relationship between flicker rate and disappearance. However, their conditions of flicker were quite different from those used in the present experiment (see section on apparatus).

the same stimulus figure, but eye movements have their normal effect in moving its retinal image. This was the condition of "normal" viewing.

Figure 3 is a schematic representation of the present apparatus. One major modification of the earlier apparatus, introduced in this research, was the substitution of a Mangin mirror,  $M_1$ , Fig. 3, for the screen on which the image was projected. The focal length of  $M_1$  was such that an image of the contact lens mirror was formed at the pupil. Using this mirror instead of a screen, much more (about four log units) of the light reflected from the contact lens mirror actually enters the pupil. Therefore, in order to obtain a test field brightness comparable to that of the previous apparatus, the light incident on the contact lens can be greatly

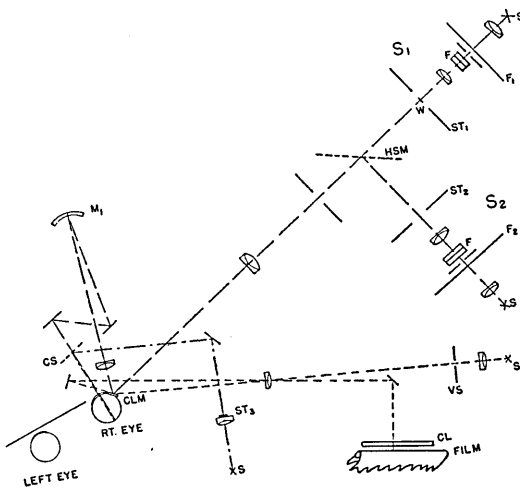
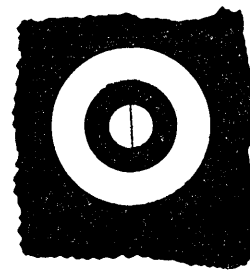


FIG. 3. Diagram of the present optical apparatus.  $S_1$  and  $S_2$  two projection systems;  $S$ 's ribbon filament sources;  $F_1$  and  $F_2$  synchronized flicker vanes;  $P$ 's filter holders;  $ST_1$  and  $ST_2$  stops with circular apertures;  $W$  the stimulus wire;  $HSM$  a half-silvered mirror;  $CLM$  mirror mounted on the contact lens;  $M_1$  a Mangin mirror;  $ST_3$  a circular stop;  $CS$  a microscope cover slip;  $VS$  a vertical slit opening;  $CL$  a horizontal cylindrical lens.

reduced in intensity, with a consequent large reduction in peripheral glare.

One other major change was made. The test object in both this and the earlier study was a fine dark line on a bright circular background. In the present study, however, it was necessary to flicker the test line against its background. For this reason, a second projection system was introduced. The first,  $S_1$ , Fig. 3, projects an image of the complete stimulus figure,  $ST_1$  and  $W$ . The other,  $S_2$ , projects a bright circle,  $ST_2$ , identical with the background of the stimulus line, but containing no such line. With alternating flicker vanes,  $F_1$  and  $F_2$ , these two may be alternately presented at the same place in the visual field. The "flicker," then, refers to the alternate presence and absence of the black line in an otherwise homogeneous field. It appears to the subject



ANNULUS  
O.D.  $4^{\circ} 45'$   
I.D.  $2^{\circ} 36'$   
LUM. 236 FT-L

DISC  
DIAM.  $1^{\circ} 12'$   
LUM. 236 FT-L

LINE WIDTH  
APPROX.  $5^{\circ}$  ARC

FIG. 4. Stimulus pattern and annulus, as seen by the subject. Note that the vertical line is not to scale.

that the dark line is flickered on and off against its bright background.†

In working with the "stopped image," it is necessary to provide some fixation figure which is not "stopped." If such a figure is not provided, the eye will rapidly drift beyond the limits of the optical system. (The reason for this will be clear after a consideration of the conclusions of this research.) Such a fixation figure must not overlap the test figure. If it does, eye movements will produce temporal changes in the retinal pattern of the test figure itself. Therefore, the figure we used was an annulus surrounding the test figure, and having a brightness equal to it. The annulus was formed by lens  $L_1$  and stop  $ST_3$ . The relationship between the functions of the annulus and the central fixation figure will be discussed later.

Figure 4 shows the stimulus pattern and annulus, as viewed by the subject.

Photographic records of the eye movements occurring under the experimental conditions were made. To do this, rays from a vertical slit,  $VS$ , were reflected from the contact lens mirror,  $CLM$ , through a horizontal cylindrical lens,  $CL$ , to a vertically moving film, Fig. 3. In this way, the horizontal components of any eye movements may be recorded. Only the horizontal displacement is of importance when the target line is vertical. (See reference 1 for a detailed description of this recording technique.)

While observing, the subject held a microswitch, which he closed when the stimulus line was visible, and opened when it had disappeared. A continuous indication of the position of the switch was recorded directly on the eye movement film. A time-marker built into the eye movement camera marked the film at one-tenth second intervals. Film speed was 28.6 mm per second. Rotation of the eye through  $99''$  of arc produced a 1-mm deflection on the record. The smallest movement that could be read with reasonable accuracy was about  $12''$  of arc.

#### SUBJECTS

For subjects, it was necessary to use people who could be fitted with tightly fitting contact lenses,

† In the study by Ditchburn and Fender mentioned above, flicker was introduced by turning the entire stimulus figure on and off, rather than flickering the line only.

corrected for good acuity. Considerable training and experience were needed. Two subjects were available in this study. One, LAR, was an observer of long experience in both stopped image and eye movement recording experiments. He was familiar with the purpose of the research, but not with the details of the experimental design. The second, CRC, had not previously been an observer in any eye movement experiments, and was not apprised of the exact purpose of the research. He was given preliminary training in this type of experiment, i.e., in maintaining fixation over long periods of time. Neither subject was informed of the results of the experiment while it was in progress.

**EXPERIMENTAL DESIGN AND PROCEDURE**

For subject LAR, 16 experimental sessions were employed. In 8 of these, viewing was normal, and in the remaining 8 the subject viewed a stopped image. These conditions were alternated in an ABBA order. During any one experimental session, whether normal or stopped-image viewing was employed, there were seven individual runs, one at each of seven flicker frequencies. The light-dark ratio was always 1.0. The order of frequencies was balanced over the 16 sessions. For subject CRC, the design was similar except that only 12 sessions were employed, and 6 flicker frequencies were used.

Each of the individual experimental runs was 45 sec long, with about 30 sec between them. Each session lasted about 20 min, and at least 4 hr intervened between sessions.

**RESULTS**

**1. Stimulus Disappearance as a Function of Flicker Rate**

Table I shows the relationship between the rate of flicker and the disappearance-time fraction, for both normal and stopped-viewing conditions. It can be seen that, for the stationary-image condition, the variation of flicker rate produced a wide range of disappearance-time fractions. For the condition of normal viewing, however, this range was greatly restricted.

TABLE I. Disappearance time-fraction as a function of rate of flicker of the fixation line.

Flicker frequency (cps)	Subject LAR		Flicker frequency (cps)	Subject CRC	
	Stopped	Normal		Stopped	Normal
4.4	0.77	0.19	9.6	0.66	0.45
3.2	0.44	0.03	8.0	0.50	0.43
2.4	0.18	0.01	6.4	0.55	0.35
1.6	0.11	0	4.8	0.40	0.20
1.2	0.02	0	3.2	0.14	0.16
0.8	0	0	Steady on	0.56	0.20
Steady on	0.83	0.07			

**2. Drift**

*Technique of Measurement*

One half-second interval was measured during each two seconds of recording time. The position of the eye was recorded at the beginning and again at the end of these half-second intervals. If a saccade occurred during any of the intervals chosen for measurement, that interval was not measured. The difference between the initial and final positions of the eye during the interval was taken as the amount of drift in that interval. The drift is slow enough so that it almost never reverses direction in a one-half second time sample. This technique yields between 20 and 25 drift samples per 45-sec experimental run. The drift data were thus measured for subject LAR only. No drift analysis was made on subject CRC's data, since inspection of his records showed them to be very similar to those of LAR.

*Experimental Findings*

If a stimulating condition for drift is disappearance of the figure, there should be a high positive correlation between the disappearance-time fraction and the rate of drift. For subject LAR, this correlation was 0.00 for stopped image viewing, and -0.14 for normal viewing. It is concluded that disappearance is not a stimulating condition for drift.

If displacement of the retinal image of the fixation field from some "on-target" position constitutes a stimulating condition for drift, then there should be a higher rate of drift under the normal than stopped-viewing condition. This follows from the fact that there is a greater displacement of the retinal image during normal vision. This prediction was not borne out. The mean rate of drift was actually lower for normal than for stopped viewing. It might also be expected that the drift rate should be greater the farther the eye is from some "on-target" position. To test this, the "on-target" position was taken as the mean position of the eye over each experimental run. While this is not necessarily the "true" "on-target" position, it should be at least near that point. (This question is discussed in greater detail below.) The correlation between the rate of drift in each sample and the displacement of the eye from the mean position at the beginning of each sample was 0.00.

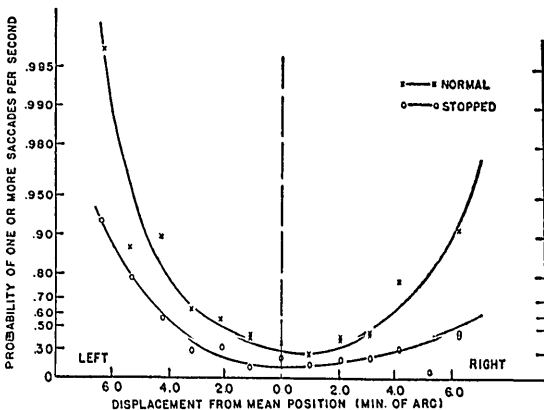


FIG. 5. Probability of occurrence of saccadic eye movements as a function of the position of the eyeball.

Further, on the average, the eye was farther away from its mean position at the end of each drift sample than it was at the beginning of each sample. This means that the drift is more often away from than toward the mean position. Thus, drifts of the eye are not typically "corrective" movements.

If there were any tendency at all for the eye to drift toward its mean position, that tendency would produce a greater *rate* of drift toward, than away from, the mean position during normal vision. The actual difference in these two rates was found to be negligible (5.0% of the total drift rate). It is therefore concluded that displacement of the retinal image is not a stimulus for involuntary drift, and that drift does not serve to bring displaced images "on target."

Since neither disappearance nor displacement produces drift, it is concluded that drift is not under direct visual control, but is, rather, a result of the instability of the oculomotor system. §

### 3. Saccadic Movements

All saccades occurring during the experimental sessions were analyzed for both subjects.

If saccadic movements are triggered by the disappearance of the fixation figure, there should be a high positive correlation between the disappearance-time fraction and the frequency of these movements. This was found not to be the case. For subject LAR, this correlation was +0.05 for normal and -0.13 for stopped viewing. For CRC, both correlations were negative. It is concluded that disappearance does not trigger saccadic movements.

If displacement of the retinal image triggers saccades, there should be significantly fewer saccades during stopped than normal viewing, since there is no displacement during stopped viewing. This was indeed true. For LAR, the mean number of saccades per 45-sec run was 18.2 for stopped and 39.0 for normal viewing. For subject CRC, the equivalent values were 44.6 and 70.0, respectively. Both of these differences are statistically significant beyond the 1% confidence level.

Since displacement of the retinal image does trigger saccadic movements, it is of some interest to determine the characteristics of the saccades as influenced by the position of the retinal image on the retina. For this purpose, the mean position of the eye on each 45-sec run was again used as a reference position. However, in this case no particular physiological implications of this mean position need be assumed, since the choice of any other reference point (e.g., the edge of the recording paper) would only affect the variability of the results, and would not change the mean values.

Figure 5 shows the relationship between the displace-

§ Another experiment, to be discussed later, corroborates the conclusion that drift is independent of visual control. Eye movements were recorded first with a fixation point and then in total darkness. While the over-all record looked considerably different in the two cases, the drift rates were essentially identical.

ment of the eye from its mean position and the corresponding probability of occurrence of saccadic movements. If the eye is as far away as 7 min of arc from its mean position, the probability of occurrence of one or more saccades in any given second of time approaches 1.0 for normal vision. For vision with a stopped retinal image, the curve is flatter. That is, the relationship between displacement and the probability of occurrence is materially reduced. This is to be expected, since, in the stopped image condition, there is no displacement of the retinal image with displacement of the eye. There are two possible reasons for the fact that the curve is not completely flat. The first is that proprioceptive factors enter here, that is, that the stretching of the eye muscles tends to produce saccades. Evidence to be presented later indicates that this tendency, if it exists at all, is negligible. A second explanation is more likely. In the stopped-image condition not all of the image is "stopped." The image of the fixation annulus does exhibit displacements across the retina with eye movements. Thus, the difference between the two curves in Fig. 5 may be interpreted as reflecting the difference between a condition in which there is the normal displacement of the retinal image of the whole fixation figure and a condition in which there is displacement of only a part of the fixation figure. Under these conditions of "stopped" viewing, the visual feedback from eye movements is reduced but not eliminated.

Since saccadic movements are triggered by a displacement of the retinal image from its "on-target" position, it would seem likely that they serve to keep the eye on target. If this were true, two further predictions can be made. First, each saccade should be in such a *direction* that it returns the eye toward the "on-target" position. Second, each saccade should be of a *magnitude* such that it returns the eye to its "on-target" position. The following three figures serve to illustrate the extent to which these relationships hold.

Figure 6 shows the direction of saccadic movements

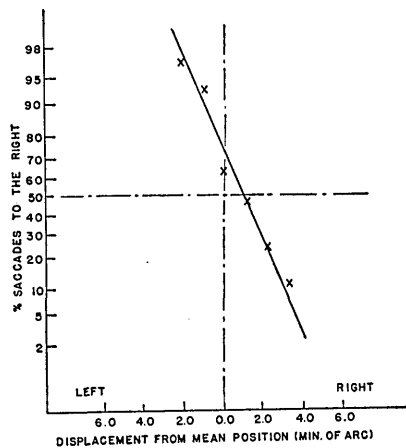


FIG. 6. Direction of saccadic eye movements as a function of the position of the eyeball, normal vision.

as a function of the position of the eye at their onset, during normal viewing. This figure is for LAR. Subject CRC showed an identical relationship. This curve can be interpreted as follows. When the eye is 4 min of arc to the left of its mean position, about 98% of the saccades will move the eye to the right, that is, toward its mean position. When the eye is at its mean position, about 70% of the saccades move the eye to the right. The "neutral" position, that is, the position at which a saccade is equally likely to move the eye to the right or to the left, is one minute of arc to the right of the mean position. This "neutral" position might be considered the "on-target" position, or, in the parlance of servomechanics, the point of minimum error signal. It should be noted that the curve is very steep, so that, when the eye is more than 5 or 6 min of arc off target, any saccade that occurs is almost certain to move the eye back toward the "on-target" position. Analysis of the data showed, moreover, that there were significant differences (beyond the 1% level of confidence) among the obtained percentages between all the displacement values.

Figure 7 illustrates the effect of position of the eye upon magnitude of consequent saccades, for normal viewing, in subject LAR. In this curve, the position of the eye at which saccades are of minimum size, that is, the position of minimum error signal, is about one minute of arc to the left of the mean position. It should be noted that this minimum falls at a point two minutes of arc to the left of the 50% position in Fig. 6, where saccades to the left and to the right are equally likely to occur. There is a significant difference between the magnitude of saccades at this minimum point and the magnitude at a position one minute to the right of the mean position. In other words, it is highly improbable that the retinal position characterized by saccades of minimum size coincides with the retinal position from which saccades to the right and to the left are equally likely to occur. That is, the "points of minimum error



Fig. 7. Mean magnitude of saccadic eye movements as a function of the position of the eyeball, normal vision.

signal" for the *direction* and *magnitude* of saccadic movements are not coincident.

For subject CRC, the above relationship is similar, except that the minimum for his magnitude curve is not so sharply defined.

A further finding evident in Fig. 7 is that the minimum size of saccades is 3 min of arc. When the eye is near its mean position, or its "on-target" position, saccades on the average widely overshoot that position.

Figure 8 illustrates the over-all average effect of various saccades in normal vision. This includes the effects of both magnitude and direction of saccades. For example, if a saccade begins when the eye is 6.3 min of arc to the left of its mean position, it will, on the average, leave the eye 0.6 min to the right of its mean position. Displacement values representing one standard deviation on each side of the mean final position are indicated by short vertical lines. These standard deviations are very large, so that the final positions

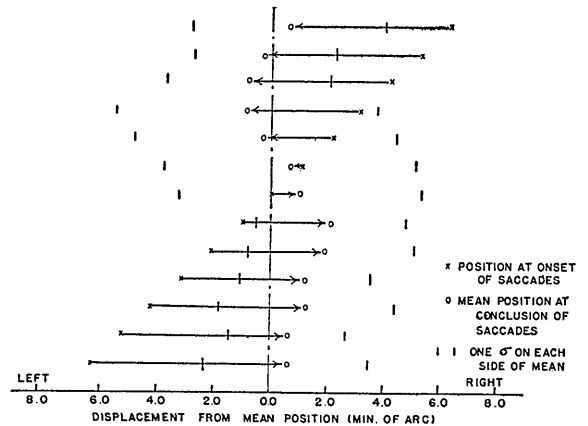


FIG. 8. Over-all effect of saccadic eye movements on the position of the eyeball, normal vision.

indicated in this figure do not at all represent each saccade that occurred, but only an average of many saccades in both directions.

### DISCUSSION

The data presented above lead to the following general conclusion. During normal fixation, the instability of the oculomotor system permits the eye to drift, and, consequently, the retinal image drifts across the retina. As the retinal image drifts farther and farther away from some particular region of the retina, it becomes more and more likely that a saccadic movement will occur, tending to return the retinal image to that particular region.

This conclusion suggests certain predictions about the behavior of the eye in the dark. First, the rate of drift of the eye should be identical with or without a fixation point. Second, since any saccades that occur in the absence of a fixation point should be essentially random in direction and amplitude, the eye should gradually



move farther and farther away from its initial position.||

In order to test these predictions, eye movements were compared, in a dark room, with and without a fixation point, as was mentioned in a foregoing reference. The drift rates in the two cases were indeed found to be virtually identical. Further, in the absence of a fixation point, the eye did move farther and farther away from its mean position when the fixation point was present, as shown in Fig. 9. The data for this figure were computed as follows. The mean position of the eye with a fixation point was calculated, as was the standard deviation of that mean. The displacement of the eye from the mean position was measured at each second of time after the fixation point had been extinguished. This procedure was followed for each of ten 15-sec runs, and the displacements were averaged without regard to their direction. These averages, and the over-all standard deviation with a fixation point, were plotted in Fig. 9. It is very clear from this figure that a fixation point is essential if the eye is to maintain its position, that is, that saccadic movements are under visual and not proprioceptive control. And, since the drift rate was not changed when the fixation point was extinguished, it is also clear that it is not drift, but rather saccades, that do the work of holding the eye on target.

It is evident from these data that there is no such thing as a visually "controlled" *smooth* eye movement *during monocular fixation*. That is, the only controlled movements are saccadic. It seems possible, then, that the eye is incapable of moving smoothly in a controlled way. The literature on pursuit movement indicates that the eye does indeed move smoothly to follow a smoothly moving object. However, this author was unable to find any records of pursuit movement which had sensitivity great enough to discriminate saccadic movements as small as those recorded in the present research. It seemed possible that pursuit movements which appeared to be smooth were actually composed of rapid series of very small saccadic movements, with random drift interspersed between them. Pursuit movements were therefore recorded using a sensitivity identical with that used in the main experiment above. Under these recording conditions, it was very clear that the eye does indeed move smoothly while pursuing a moving target. Therefore, it must be concluded that, although the eye does not exhibit any smooth controlled movement during fixation of a stationary target, it is capable of such movement under different conditions of stimulation.

|| This statement follows from a generalization of the "law of statistical behavior," better known as the "law of the drunkard's walk." The law states that, if an object (or a drunkard) moves in discrete steps of random direction, its (his) most probable displacement from its initial position increases with time.

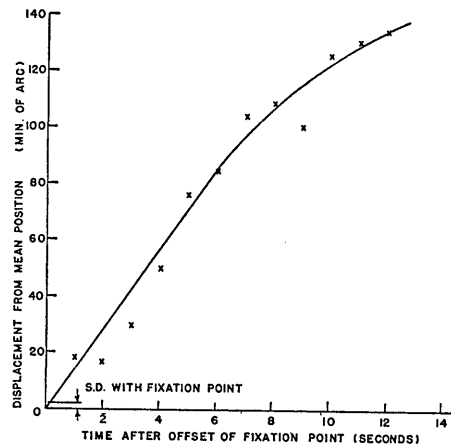


FIG. 9. Effect of eye movements on the position of the eyeball when there is no fixation field. The origin is the mean position of the eye before the fixation point is extinguished.

In a paper published during the preparation of this report, Ditchburn<sup>7</sup> reported a series of studies of eye movements under conditions similar to the present ones.

From some of his data, Ditchburn concludes that proprioceptive signals, or other signals not derived from the retina, play an important part in the maintenance of fixation.<sup>7</sup> We cannot account for the difference between this conclusion and ours.

The question of what is an "on-target" position remains a difficult one, since for at least one subject there appear to be two different "on-target" positions, separated by two minutes of arc. (For the second subject, CRC, the separation between these two positions appears to be present, but is not so sharply defined by these data.) This question seems to be easier to deal with if saccadic movements are conceptually treated as a resultant of three different aspects. The first is that a saccade has some particular probability of occurrence. The second, that the saccade will have some particular direction. And the third, that the saccade will have some particular magnitude. Each of these aspects of a given saccadic movement could, theoretically, be controlled by a different nervous mechanism. If saccades are considered in this way, the curves in Figs. 5, 6, and 7 represent the characteristics of each of these three mechanisms, respectively. The fact that there appear to be at least two different "on-target" positions (Figs. 6 and 7) can now be rephrased as follows: The "on-target" position for the directional control mechanism is two minutes of arc to the right of the "on-target" position for the magnitude control mechanism.

The suggestion that there are at least two, and possibly three, separate physiological control mechanisms for saccadic movements may be tested. The use of drugs might inactivate one of these mechanisms while leaving the others in working order. Such a dissociation would result in a flattening of one of the curves above, without affecting the others.