THE RESPONSE OF THE OCULO-MOTOR SYSTEM TO VISUAL STIMULI IN THE HORIZONTAL PLANE

DISSERTATION

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By

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Part of the apparatus used in these investigations was built by Dr. Charles R. Stewart and used by him in earlier studies on eye movements. Both in the original construction of the apparatus by Dr. Stewart and in the many and tedious modifications carried out by the author, Professor Merrill J. Allen contributed much helpful advice.

Professor Glenn A. Fry has been my Adviser throughout my graduate studies at the Ohio State University. It is a pleasure to acknowledge the ready manner with which he brought his keen intellect and insight to the discussions in which the questions forming the basis of this dissertation were formulated and their solution sketched.

It is my hope that the results recorded herein constitute a tribute to the atmosphere and facilities for the pursuit of the experimental aspects of our field which Dr. Fry has created in his laboratory and which, I am sure, will have a lasting influence on my outlook.

Gerald Westheimer

Columbus, Ohio
May 1953

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SECTION I

INTRODUCTION: THE RECORDING OF EYE MOVEMENTS

The descriptions of eye movements found in standard works are practically all based on the work of R. Dodge and C. H. Judd which was carried out with the photographic equipment available during the first decade of this century.

Dodge (1901, 1903, 1907) worked with a method which enabled him to secure good resolution in the time dimension but he did not achieve any noteworthy precision in recording the position of the eye. This lack of precision is fatal to any convincing analysis of the data directed toward uncovering the muscular mechanisms subserving these movements. Yet his paper (1903) is classical and many of his findings are corroborated in this report.

Judd's data (1905, 1907) are unfortunately quite unacceptable as a guide to the temporal sequence of events during eye movements. Most of his records were obtained photographically with exposures lasting often as long as 100 milliseconds.

In order to be able to draw correct conclusions concerning the nervous and muscular mechanisms subserving eye movements it seemed in order to investigate again the time relation of the change in position of the eyes in the orbits during various eye movements.

Several methods of studying eye movements are available [Duke-Elder (1942), Carmichael and Dearborn (1947), Taylor (1937), Stewart (1951)] .

The first quantitative method was a subjective one [Helmholtz (1925), *Vol*. *III*, p. 153] and was used successfully by, among others, Lamansky (1869) and Brückner (1902). During the eye movements the eye is intermittently exposed to a bright point source and the retinal separations of the after-images produced by the source give information about the average velocity of the eye during the intervals between successive flashes.

Neither the subjective nature nor the discontinuity of the registration is by itself enough to condemn the method since subjective judgment and discreteness of interval enter into the analysis of even the most continuous objective record.

Leaving aside the mechanical methods [Duke-Elder (1942)] , which by their nature require some interference with the normal physiological processes, there remain the electrical and photographic methods. A good discussion of the electrical method has been given by Marg (1951) recently. Perhaps the outstanding disadvantage of the method is the limitation of its precision; it is estimated that with it the position of the eye within the orbit cannot be determined with an accuracy of more than about one degree.

The photographic method has been widely and variously used and in its most recent forms has been extended to yield continuous records of horizontal and vertical eye movements with a high degree of accuracy. This approach has, however, been applied only to the small movements of the eyes during "steady" fixation and has apparently never been extended to the investigation of the grosser types of eye movements.

The method which provided the data upon which this dissertation is based, appears optional for the purpose. It has been possible, where needed, to secure continuous photographic records of the horizontal movement of both eyes. The resolving power in the time dimension is about one millisecond and the position of the eye is registered with a precision of five to ten minutes of arc.

The apparatus (**figure 1**)consists of an American Optical Company "Ophthalmograph" eye movement camera on which the following modifications were made.

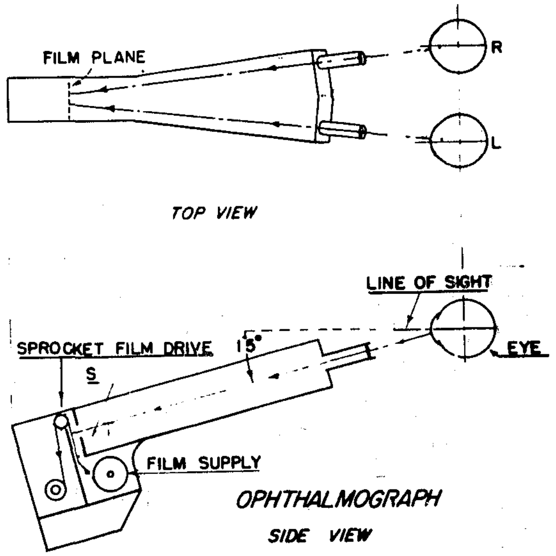


Fig. 1. Diagram of "Ophthalmograph" Eye Movement Camera

(1) The film was moved by a sprocket wheel driven by an assembly designed to keep the motion at a uniform rate and free from chatter. The assembly was driven by an electric motor geared down by a series of pulleys to keep the film moving at the desired speed.

(2) A narrow (less than 1/10 mm) horizontal slit was positioned in front of the film.

(3) The lenses in the camera were replaced by a pair of coated achromats of 26mm aperture and 90mm focal length which were combined with a pair of 1.5D cylinders oriented so that a point object was imaged as a vertical streak in the plane of the film.

(4) The illuminating system consisted of a pair of streak filament bulbs. The images of the streaks, oriented vertically, were focused a little behind the center of curvature of the cornea.

The combined effect of modifications (3) and (4) is to produce in the plane of the film a vertical streak image of the corneal reflex. (In this dissertation the term corneal reflex refers to the reflection of a luminous object in the cornea.) A narrow part of this vertical streak is intercepted by the horizontal slit thus isolating purely the horizontal component of the movement of the streak across the slit.

During most parts of the experimentation the film speed was 87mm per second. The resolution and steadiness in the time direction are illustrated in figure 2a which shows a section of film which was intermittently illuminated by a Strobotac flashing 250 times per second.

In order to test for steadiness in the direction of eye movements, a contact lens was clamped to the subject's bite bar and a record obtained in the ordinary manner. A section of it is shown in figure 2b.

Figure 2c shows the trace of both corneal images of a subject during binocular steady fixation of a light spot 10 minutes of arc in diameter situated in the median line 150cm in front of the observer. It will be seen that the width of the trace is equivalent to an eye movement of about $1/4^{o}$ and that variations in position of the trace of about a half of its own width are clearly discernible and possibly capable of measurement. It is estimated from this that the resolving power in the lateral direction, i.e., at right angles to the time direction, of the apparatus as used is of the order of five minutes of arc, i.e., changes in eye position of about five minutes can be recognized on the record.

Comparison of figures 2b and 2c shows the unsteadiness of the trace during 'steady' fixation. This may correspond to the eye movements during steady fixation which have been so abundantly demonstrated [Adler and Fliegelman (1934), Lord and Wright (1948), Ratliff and Riggs (1950), Ditchburn and Ginsborg (1953),

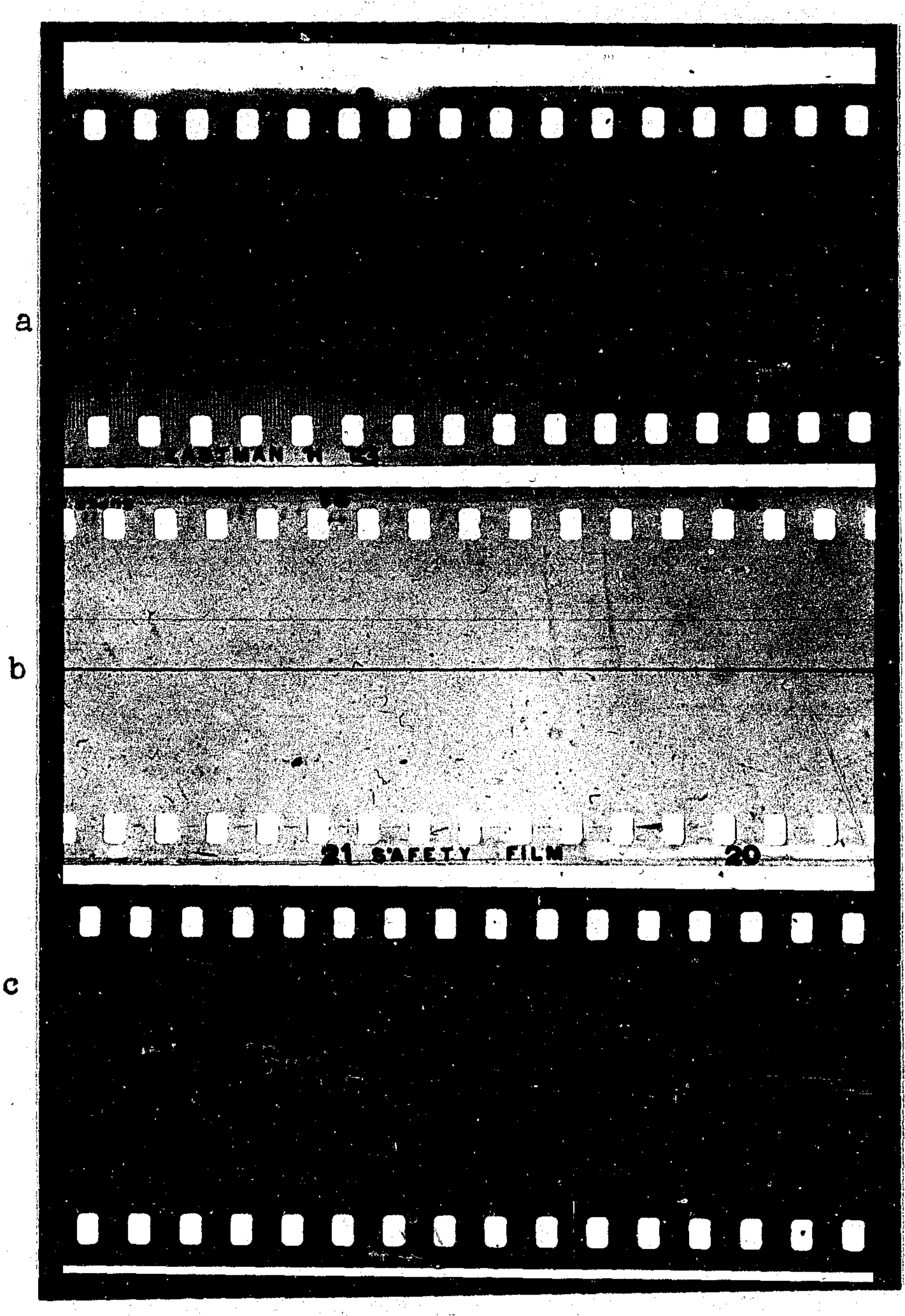


Fig. 2. Performance of modified "Ophthalmograph"

a. Strobotac flashing 250 times per second.
b. Contact lens clamped to subject's bite bar.
c. Trace of corneal reflections from both eyes during 'steady' fixation.

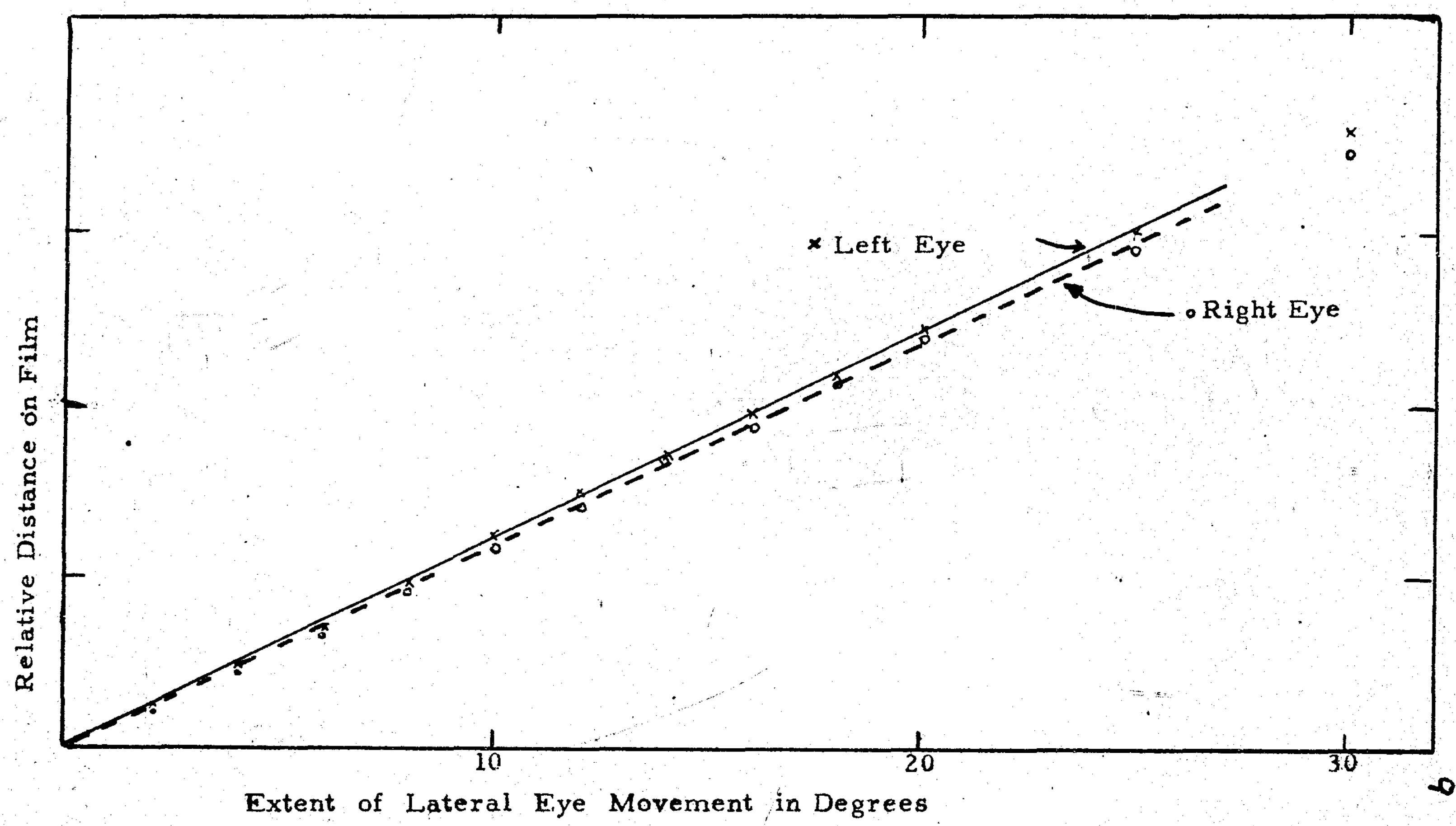
Barlow (1952)]. Not too much attention is being placed on this point in the present dissertation, however, since these phenomena are just about at the threshold of the resolving power of the apparatus and since one cannot be certain that lateral or rotational headmovements of this order are being completely eliminated by using merely a bite bar with a wax impression of the subject's teeth.

Ratliff and Riggs, and Ditchburn and Ginsborg used a contact lens method of recording eye movements which ensures that the record is not contaminated by translational movements of the eye in the orbit as opposed to purely rotational movements. A contact lens probably follows accurately the small involuntary movements during fixation. A contact lens will not, however, follow the eye precisely in its larger excursions.

The correlation between extent of lateral excursion (rotation) of the eyeball and the distance through which the trace moved laterally across the film was established experimentally for each subject. It was found that over a median 25°, i.e., $12\ 1/2^{\circ}$ on either side of the primary position, this relation is linear (figure 3) but falls off sharply from linearity as the extent of the movement increases. Care was taken to use for the purpose of analysis only those parts of the trace falling within this linear range.

FIG. 3

CALIBRATION DATA : SUBJECT D.D.



SECTION II

PROCEDURE AND RESULTS

A. Step Stimuli.

Two neon bulbs N_1 and N_2 were mounted so that they could be moved to any position on a horizontal arc of 150cm radius centered on the midpoint of the base line connecting the centers of rotation of the subject's eyes. They were connected by an electric circuit (figure 4) in such a manner that when the microswitch K was pressed, bulb N_1, would light up and bulb N_2 would be extinguished, and the reverse would occur on releasing the microswitch. A light source S was positioned so that the lens L and the two mirrors M_1 and M_2 would image it on the film plane a little to the side of the trace of the corneal reflex and, like the latter, was intercepted by D, the diaphragm with the narrow slit.

Mirror M_1 was attached to an electromagnet which instaneously (i.e. within about one or two milliseconds) assumed different positions on pressing and releasing the microswitch and in this way the signal line was displaced synchronously with the change-over from one bulb to the other. The bulbs, incidentally, also lit up and became extinguished instantaneously.

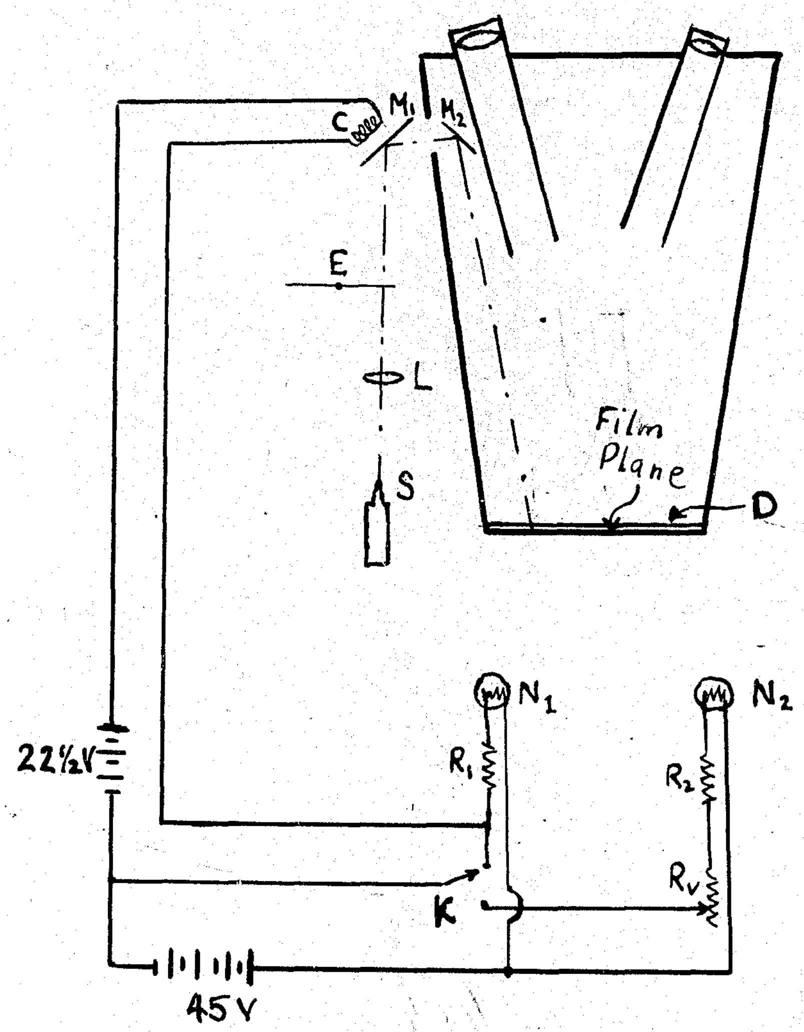


FIG. 4. DIAGRAM OF APPARATUS FOR PRODUCING AND RECORDING STEP AND PULSE STIMULI

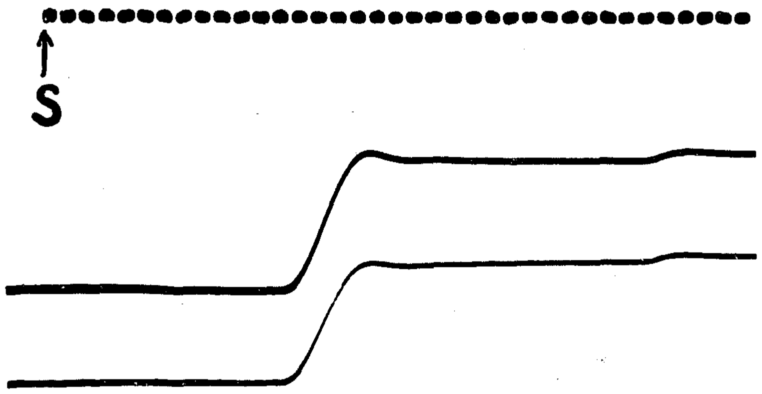


Fig. 5. Typical Record of a 20° Saccadic Eye Movement.

Time line interrupted every 10 milliseconds.

Step Stimulus at S.

An episcotister disc driven by a synchronous motor was placed at E intercepting the light rays constituting the signal line once every one hundredth of a second and in this manner a time scale was established on the record itself.

After securing the calibration record for every subject as illustrated in figure 3, the response of the eye to a step stimulus was obtained in the following manner. The subject was instructed to fixate the neon bulb which was lit up and which was the only target visible in the otherwise dark room and was told to change fixation to the other target immediately it became visible. Both neon lights presented a narrow rectangular filament to the subject measuring approximately 2mm in the horizontal direction and approximately 8mm in the vertical direction. They had a pinkish glow when current was passed through them and their luminance was matched by adjusting the variable resistance R_v.

Responses were obtained for symmetrical positioning of the two targets on either side of the median plane and for angular separations at the nodal point of the eye of 2,4,6,8,10,12,14,16,18,20,25, and 30 degrees. A typical response to a 20^o step stimulus is shown in figure 5.

It exhibits certain characteristics some of which have not so far been described.

There is a reaction time which varies between 120 and 180 milliseconds. The smaller of these values is somewhat less than previously reported. An analysis of the relation between the extent of the separation of the two bulbs and the reaction time has not been attempted. It would require a randomization of the presentation of the stimuli which was not carried out during the experimentation.

Some of the other features to be noted in figure 5 are:

(a) The high degree of simultaneity of onset of the movement in the two eyes.

(b) The rapid acceleration to a velocity which is maintained over a large part of the movement.

(c) The overshoot and small oscillations around the final position. This overshoot is to be distinguished from the overshoot described by previous writers. If the first fixation was beyond the correct point and after another reaction time a further movement was made to a more accurate position, this was often referred to as an overshoot of fixation.

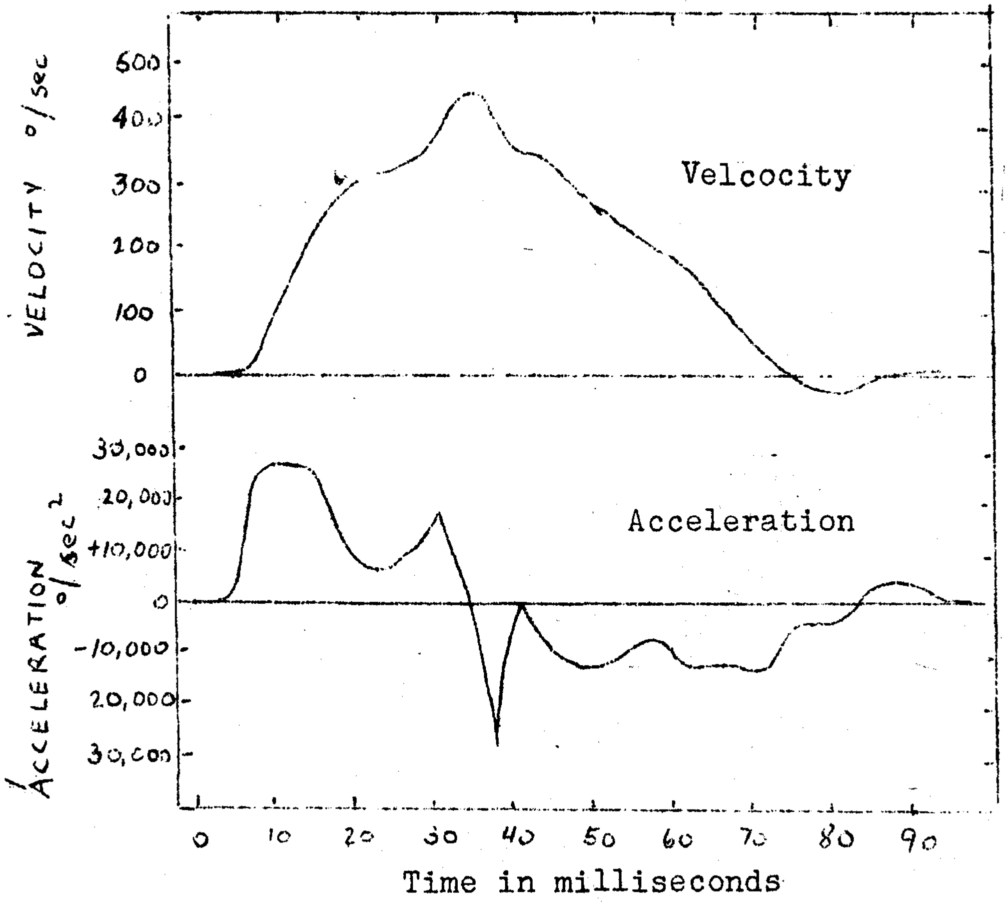


Fig. 6. Typical Velocity and Acceleration changes during a 20° saccadic eye movement.

A discussion of the theoretical implications of these findings will be given in Section III.

Figure 6 shows the change in velocity and acceleration of the eye during the course of a typical saccadic eye movement of 20°. The implication of this graph, too, will be discussed in Section III. In this connection it is of interest to note that the maximum acceleration of the eyeball showed no significant differences for saccadic movements ranging from 15° to 50°.

In figure 7 the maximum velocity during a saccadic movement has been plotted against the extent of the movement. It will be seen that the maximum velocity increases as the extent of the movement increases, but that the relation falls off sharply from linearity for more extensive movements.

When an attempt was made to obtain a similar curve for subject L.C. it was found that the maximum velocity was consistently lower when the movement was in the left direction. There was practically no overlapping of the data and figure 8 is a good representation of the two average curves.

This finding is not unique. There are a number of references in the literature to differences in maximum velocity of saccadic movements depending on the direction of movement, or whether the movement is towards the center or away from it and so on (see Tschermak (1931) for a review of the literature and Brockhurst and Lion (1951) for a recent such determination.)

In order to ascertain whether there is any systematic difference in the maximum velocity of a 10° horizontal saccadic eye movement depending on its direction and its relation to the primary position of the eye and the median plane of the body, the following experiment was performed on three young adults with normal vision and with no significant refractive error or oculo-motor imbalance.

One of the two neon bulbs was placed in the median plane and the other 10° lateral to it, first to the right and then to the left. The maximum velocity of saccadic movements from the center bulb to the lateral one was measured for four consecutive movements, both towards and away from the center bulb, and for both lateral positions. The measurement was obtained for each eye and the results for L.C. are set out in table I.

It will be seen that the measurements can be grouped in four classifications each containing two categories:

(a) In and Out (with respect to the primary position of each eye)

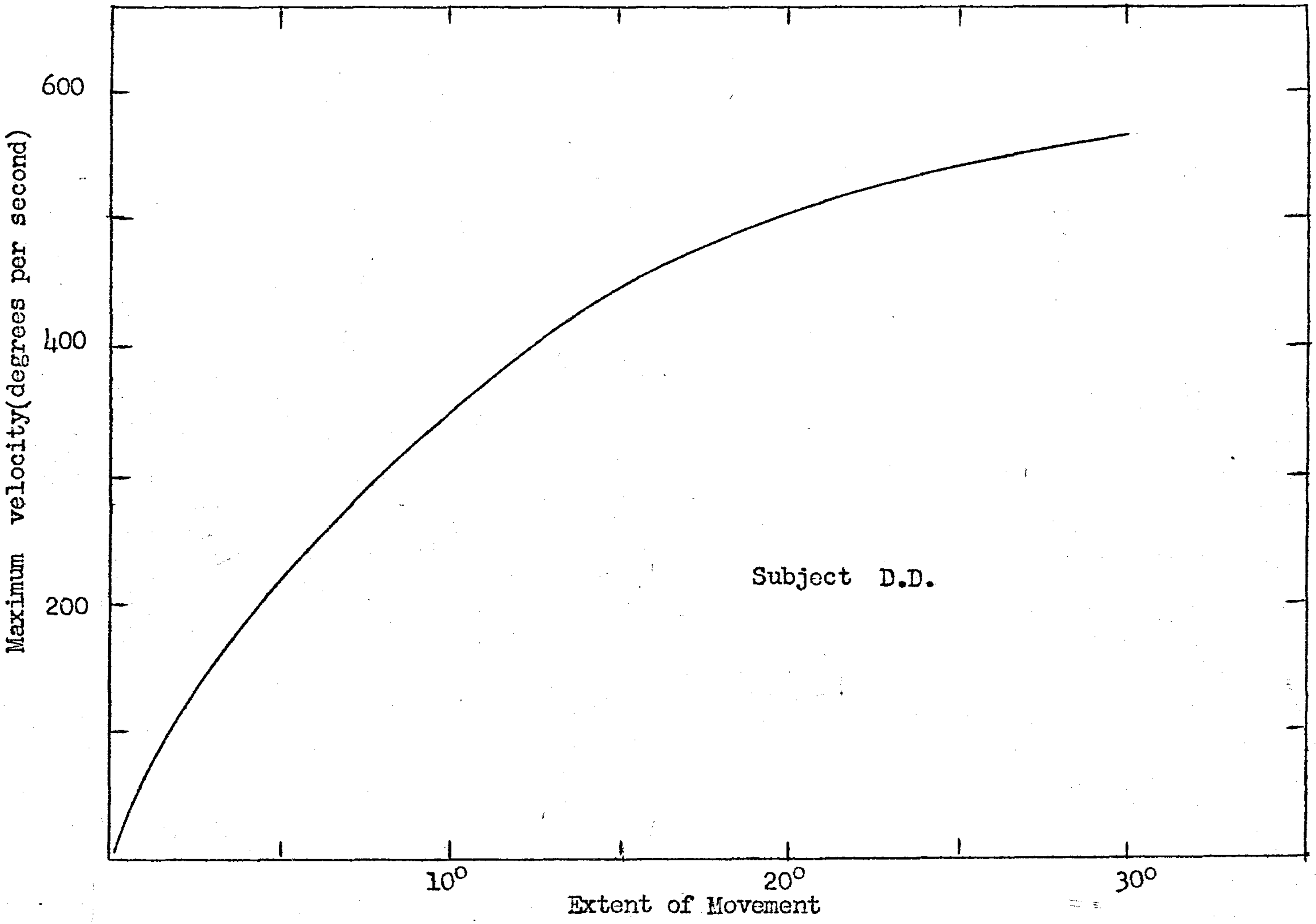


Fig. 7. Relation between maximum velocity during a saccadic eye movement and the extent of the movement (Subject D.D.)

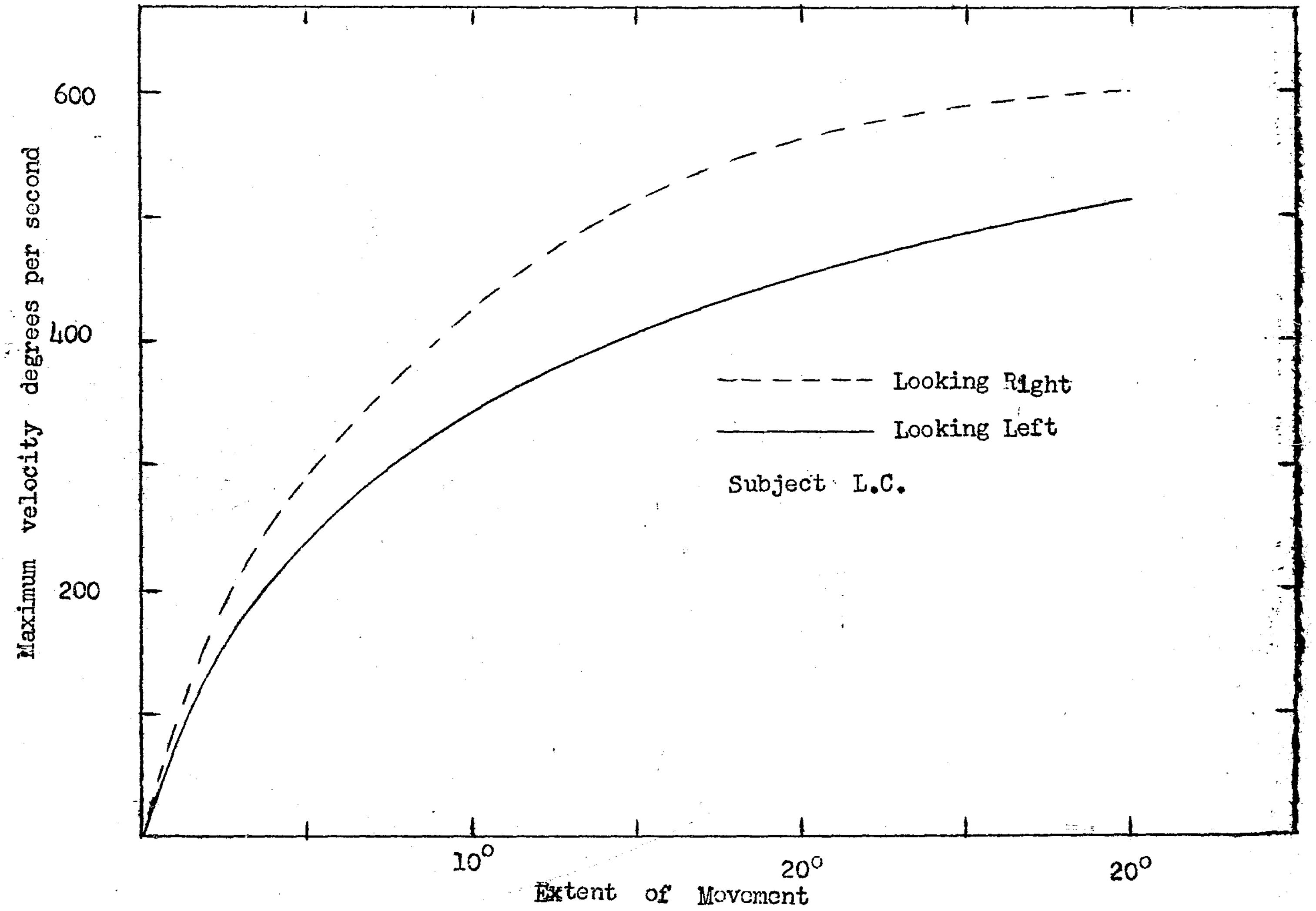


Fig. 8. Relation between the maximum velocity during a saccadic movement and the extent

(b) Nasal and Temporal (with respect to the median plane of the body)

(c) Looking to the right and to the left

(d) Right eye and left eye

The analysis of such data is not a simple matter and it was attempted by setting up a tridimensional analysis of variance for three of the categories. The intragroup variance was used as the denominator for the F ratios. A separate F ratio was then determined for the sum of squares of the remaining category. This is a legitimate procedure since it separately expresses a relation implicit in the interaction terms of the main analysis of variance. Table II shows the analysis of variance of the data of table I,

Under the data in table I the result of the analysis of variance has been summarized. It is seen that in the case of subject L.C. the maximum velocity differs significantly (at the .1% level) depending whether the movement is to the right or to the left. The present manner of analyzing the data makes this a definite conclusion quite independent of variations in maximum velocity with one or more of the other variables.

Table I

MAXIMUM VELOCITIES OF 10° LATERAL SACCADIC EYE MOVEMENTS

Degrees per Second

Subject: L.C.

	Right Eye		Left Eye	
	Looking R Tempor.	Looking L Nasal	Looking R Nasal	Looking L Tempor.
Center-Right	out 337	in 380	out 407	in 395
	395	366	466	352
	337	352	407	366
	366	337	407	352
Center-Left	in 380	out 407	in 428	out 380
	407	447	447	428
	447	407	466	366
	407	337	487	314

<u>AVERAGE</u>:	Right Eye	382	Left Eye	404	Difference significant at 5% level
	Looking R	414	Looking L	374	Difference significant at .1% level
	Nasal	409	Temporal	377	Difference significant at 1% level
	In	398	Out	388	Difference not significant

The experiment was repeated with the other two subjects and the data for these is presented in tables III and IV. An analysis of variance for each of these sets of data was carried out and the results given under the tables.

The over-all results of this group of experiments are summarized in the table V. It will be seen that, while the ratios differ at various levels of significance, no consistent pattern can be found to characterize the variations in maximum velocity with one or other of the categories mentioned. This result is in direct contradiction with the findings of Brockhurst and Lion (1951) who used an electrical method of measuring eye movements.

On the whole the results of the present experiment would support the view that considerable individual variation occurs in this type of data and this would explain the contradictory claims made by the previous investigators.

No ready theory can be advanced for the occurance of these variations. In the case of subject L.C. where the difference between the right and left directions is so highly significant the cause must be placed in a center higher than the motor nuclei. In general however, it is proposed to leave the question of these consistent variations in the maximum velocity of saccadic movements in abeyance until a more definite understanding of the mechanics of rapid eye movements has been achieved.

Table II

ANALYSIS OF VARIANCE OF MAXIMUM VELOCITIES OF 10^{o} LATERAL SACCADIC EYE MOVEMENTS (SUBJECT L.C.)

SOURCE	SUM OF SQUARES	DEGR. OF FREEDOM	ESTIM. VARIANCE	F	SIGNIF.
In/Out	611	1	611	.68	--
Right Eye/ Left Eye	4 028	1	4 028	4.52	5%
Looking R./Looking L.	11 339	1	11 339	12.73	.1%
In/Out - Right E./Left E. Interaction	375	1	375	.42	--
In/Out - Look R./Look.L. Interaction	9 177	1	9177	10.30	1%
R.E./L.E. - Look.R./Look.L. Interaction	8 517	1	8 517	9.56	1%
Triple Interaction	3 886	1	3 886	4.36	5%
	37 933	7			
Intragroup	21 392	24	891		
	59 325	31	1914		
Nasal/Temporal	8 416	1	8 416	9.45	1%

Table III

MAXIMUM VELOCITIES OF 10° LATERAL SACCADIC EYE MOVEMENTS

Degree per Second

Subject: D.D.

	Right Eye		Left Eye	
	Looking R Tempor.	Looking L Nasal	Looking R Nasal	Looking L Tempor.
Center-Right	out 349	in 362	out 404	in 375
	362	389	420	389
	349	389	375	389
	387	404	404	389
Center-Left	in 420	out 437	in 437	out 375
	375	404	389	362
	375	420	404	375
	404	389	404	349

AVERAGE:	Right Eye	385	Left Eye	390	Difference not significant
	Looking R	388	Looking L	387	Difference not significant
	Nasal	402	Temporal	373	Difference significant at .1% Level
	In	392	Out	382	Difference significant at 5% Level

Table IV

MAXIMUM VELOCITIES OF 10° LATERAL SACCADIC EYE MOVEMENTS

Degrees per Second

Subject F.M.

	Right Eye				Left Eye			
	Looking R Tempor.		Looking L Nasal		Looking R Nasal		Looking L Temporal	
Center - Right	out	416	in	416	out	416	in	434
		399		416		434		434
		399		383		399		383
		369		416		369		383
Center - Left	in	416	out	399	in	369	out	399
		383		416		399		383
		369		416		342		399
		369		416		330		399

<u>AVERAGE</u>:	Right Eye	400	Left Eye	392	Difference Not Significant
	Looking R	406	Looking L	386	Difference significant at 1% level
	Nasal	396	Temporal	396	Difference not significant
	In	390	Out	402	Difference not significant

Table V

RATIO OF AVERAGE MAXIMUM VELOCITIES OF 10° LATERAL SACCADIC EYE MOVEMENTS

	Subject D.D.	 L.C.	 F.M.
Right Eye/Left Eye	.99	.95*	1.02
Looking R/ Looking L	1.00	1.11***	1.05**
Nasal / Temporal	1.08***	1.08**	1.00
In / Out	1.03*	1.02	.97

* - Ratio differs from 1.00 at 5% level of significance
** - Ratio differs from 1.00 at 1% level of significance
*** - Ratio differs from 1.00 at .1% level of significance.

B. Pulse Stimuli.

By depressing the microswitch for only a brief period, pulse stimuli were produced in which neon bulb N_2 was lit up for short periods while bulb N_1 was off. Before and after, the reverse held. It was possible in this way to produce pulse stimuli of duration of as low as 40 milliseconds, and the response was studied for pulse stimuli between 40 and 500 milliseconds in duration.

The response consists of a saccadic movement bringing the eyes fully over to the position corresponding to the position of neon bulb N_2. The reaction time for this movement is of the order of 120--140 milliseconds. A return sweep occurs either 200--250 milliseconds after the eye has reached the new position or 120 milliseconds or so after the return of the stimulus to its original position, whichever is the later.

This is illustrated schematically in figure 9.

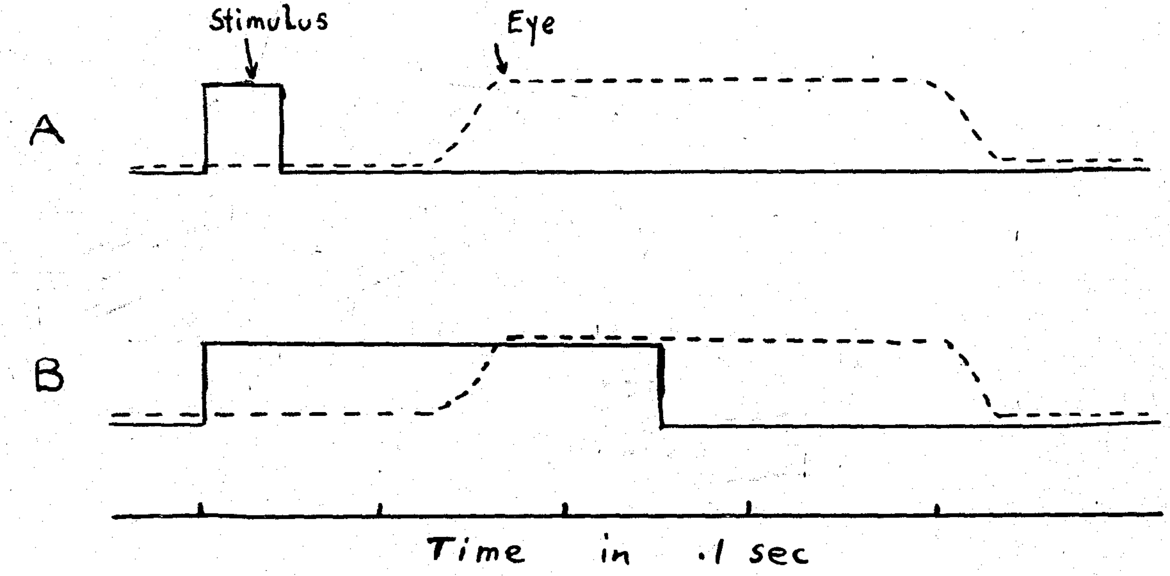


FIG. 9. RESPONSE OF THE EYE TO A PULSE STIMULUS

C. Step Velocity Stimuli.

In order to generate visual stimuli moving with constant angular velocity across the visual field, the following apparatus was constructed.

Light from a projector was reflected by a fixed mirror into a movable mirror and from there onto a large cylindrical screen of 150cm radius, at the center of curvature of which was situated the subject's head. This ensured that the stimulus light was at all times equidistant from the subject's eyes.

The movable mirror was mounted on a base which rotated around a vertical axis. A 12" lever with a roller at its end was attached to the base and the lever was held with a spring so that the roller moved along the edge of a cam, which was rotated at a constant speed for a given run. For different runs, rotation of the cam could be set at various speeds by adjusting the setting of a variable speed torque converter interposed between the cam shaft and a constant speed electric motor. The cam was constructed so that in one of its rotations the mirror was rotated in such a way as to cause the stimulus to move 30° back and forth across the screen with constant velocity throughout each excursion.

As the mirror rotated, a drum mounted on the mirror shaft gave off or took up inextensible string which was wrapped around a rotatable metal cylinder and was held tight by having a weight attached to it. Rotation of the mirror was thus communicated with an extremely high degree of fidelity to the metal cylinder, on which was mounted a small thick piece of glass in the path of light rays emanating from a small streak filament lamp operated on a 1.5 Volt battery and brought to a focus in the plane of the film of the camera by a lens and a mirror. By proper choice of the size of the drum and cylinder, the thickness of the glass plate and the axis of its rotation it was possible to generate on the film a curve which precisely represents the movement that the eyes would have to make in following perfectly and synchronously the movement of the target across the screen. A time scale was established on the film either by interrupting the stimulus beam every 1/100 second by a sector disc driven by a synchronous motor, or by recording the movement of only one eye and using the other eye tube to focus the image of a Strobotac flashing at the rate of 100 per second. In general it was not necessary, however, to place a time scale explicitly

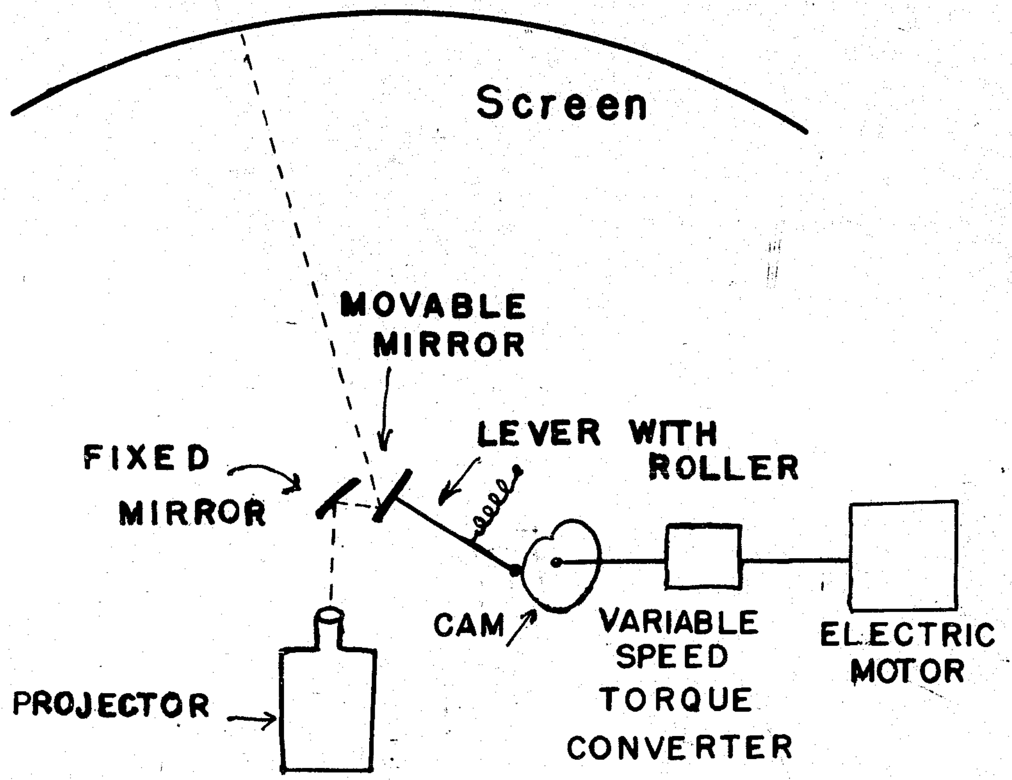


FIG. 10

DIAGRAM OF APPARATUS FOR PROJECTING A TARGET MOVING WITH CONSTANT ANGULAR VELOCITY on the film, since the apparatus was designed and has been repeatedly demonstrated to be highly reliable in the time dimension.

A manually operated mechanical shutter was provided which when raised exposed simultaneously the light stimulus to the screen and the signal beam to the film and when lowered intercepted both beams.

The subject's eye movements were recorded when the subject was instructed to look at the blank (dark) screen and suddenly a light spot appeared somewhere in the central region and moving horizontally with a steady velocity. The spot was rectangular of 10' horizontal width and 20' in the vertical direction. Care was taken to randomize both the velocity of the spot and its position when it first appeared.

Typical records obtained are shown in figures (11) and (12). General conclusions concerning the response to this particular type of stimulus in three subjects are the following:

(1) There is a reaction time of 150-250 milliseconds before any response appears. The reaction time seems to be longer when the velocity was slower. No attempt was made to study the relation between reaction

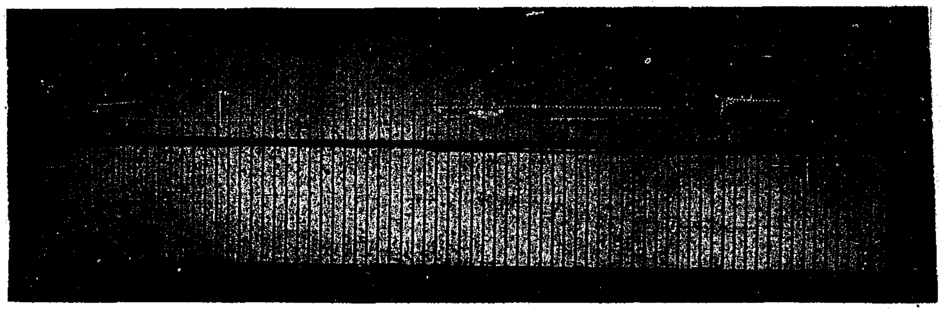


Fig. 11

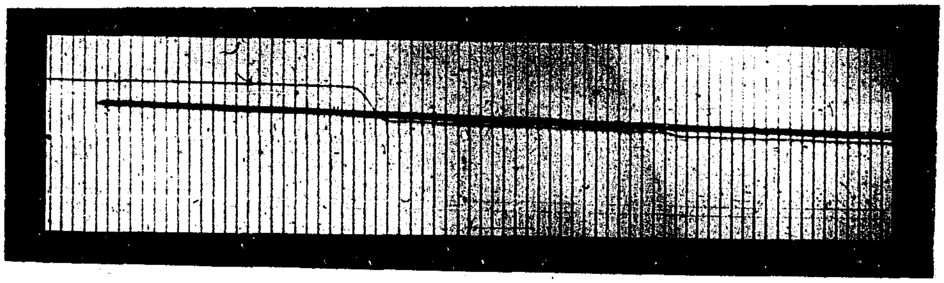


Fig. 12

Fig. 11. Eye movements in response to
a target moving with a constant velocity
of 2° per second.
Heavy trace -- stimulus
Light trace -- corneal reflex
Vertical lines -- time in 10 milliseconds

Fig. 12. The same. Target velocity 5° per sec.

time and difference between the position of the eye and of the spot when it first appeared.

(2) When the velocity is below 25°-30° per second there is usually a saccadic movement at the end of the reaction time which brings the eyes onto the target after which the eyes start to move immediately with a velocity exactly that of the target. During the course of following the target there are often small saccadic movements of 1° or sometimes more back and forth around the target without any subsequent change in the velocity of the eye movements. The movement of the eyes is extremely smooth and constant in velocity in both eyes down to the resolving power of the instrument both in the time and position dimension.

When the velocity of the target is more than about 25°-30° per second, following movements are observed, but they are usually substantially slower than that of the target and more frequently interspersed with saccadic movements.

(3) When the target disappears due to lowering of the shutter, the eyes usually continue the following movement for 100 - 200 milliseconds. In the periods between trials, i.e., when the screen is

completely dark and structureless, eyemovements are usually executed that contained both saccadic and smooth velocity components.

(4) During the course of following a constantly moving stimulus there are usually no changes in the velocity of the following movements. Even if the latter are too slow, the movements continue on at the same speed but are frequently interrupted by saccadic movements to reduce the position error. Occasionally there are changes in the velocity of the smooth movements but they are not always in the direction of reducing the velocity error.

Similar results were obtained when the stimulus was stationary and then suddenly started to move with a constant velocity.

D. Continuously Varying Velocity Stimuli

In order to record the eye movement response to other than constant velocity visual stimuli, a cam was constructed which produced continuous variations of the velocity of the spot moving across the screen. The variations are unpredictable to the subject and contain a number of reversals in direction. The response was recorded for the first few presentations of the cam in three young observers without any visual defects. The results as outlined below were identical in all three subjects and seemed to show no changes even after 20 repetitions.

Essentially the response was charactarized by these features:

(1) The tracking movements consist of constant velocity following movements interspersed with saccadic movements.

(2) Changes in velocity of the smooth following movements are always discrete and occurred at intervals of not less than 100 milliseconds and usually more. These changes are usually associated with small saccadic movements. Occasionally small sections of records look as though smooth and rather slow changes in velocity of following movements had occurred. On careful analysis it is invariably possible to observe stretches of movement of constant velocity separated by "knees", i.e., short periods of the order of 20 milliseconds during which a change had occurred from one velocity to another.

(3) The lag between prominent changes in the stimulus velocity and the concomitant changes in the

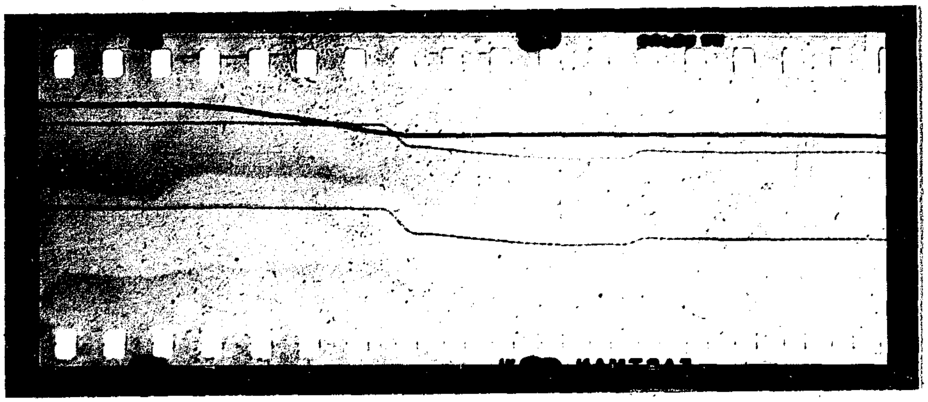


Fig. 13. Binocular eye movement record during visual tracking of a spot moving in an unkbown manner. Length of record one second. Separation of target and corneal reflex traces at beginning of record corresponds to accurate binocular fixation of target.

eye movement response, is usually of the order of 100-150 milliseconds.

Figure 13, a typical example of eye movements during tracking of an unknown visual stimulus, clearly illustrates the above points.

It was possible to produce a horizontal sine motion of the target across the screen by attaching an arm linked to the mirror turntable eccentrically on a rotating disc.

On first following such sine motions, the eye movements show all the characteristics enumerated above. However, records obtained after repeating a sine cycle about 12-15 times show that a considerable amount of learning had taken place. There are then definite stretches of the record during which smooth and slow acceleration or deceleration of the eye movements can be seen and the lag between the stimulus and the response is around zero, sometimes even negative. This is conformity with findings of workers in the U. S. Navy Electronics Laboratory in San Diego (still unpublished).

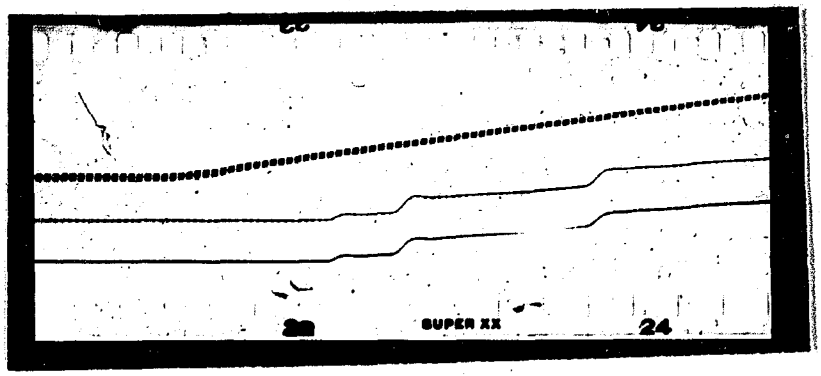


Fig. 14

Eye movements induced by dicontinuously exposed moving stimulus. Stimulus line corresponds to movement which the target would have made had it been continuously exposed. Actually it was exposed for 10 milliseconds every 120 milliseconds. Stimulus line interrupted every 10 milliseconds. Note smooth following movements after target had been moving only about 300 milliseconds, i.e., after at most three short flashes in spatial separation corresponding to movement had been presented. Note also that following movement does not correspond in speed to that of target. Separation of target and corneal reflex traces at beginning of record corresponds to accurate binocular fixation of target.

E. Discontinuously Exposed Moving Stimuli.

The experiment described in the previous section was repeated with an episcotister placed between the stimulus projector and the screen. In this manner it was possible to present the moving stimuli of various kinds exposed for only 10 milliseconds every 120 and 240 milliseconds. At the usual target speeds the 10 millisecond exposure was so brief that no movement of the target could be observed during the exposure time. One may describe the stimulus situation as that of 10-millisecond light flashes at intervals of 120 and 240 milliseconds each separated from the preceding one by the distance dictated by the type of and speed of movement.

Figure 14 illustrates that this stimulus situation can give rise to smooth following movements just as if the target were actually moving. It is to be noted that much more use is made of saccadic movements to reduce the position error than in the situation where the stimulus is continuously present. The results throw further light on the mechanism inducing following movements. They, too, open up a wide field for further investigation.

It would be of interest, for example to know whether the adjustments in velocity and position occur with frequencies clustered around the interval between successive exposures of the stimulus or multiples thereof, Another profitable line of enquiry could concern itself with the study of the effect of changes in rate of interruption of the stimulus on the movement response of the eyes.

Section III

DISCUSSION AND THEORETICAL FORMULATION

A. Introduction.

The records of eye movement responses to visual stimuli which have been described in Section II show the combined effects of all factors contributing to these movements. With some degree of arbitrariness we may classify these under two broad headings: first, all factors initiating and contributing to the change in tension of the eye muscles and, second, the mechanical factors of inertia, friction, and elasticity of the orbital tissues which govern the changes in position of the eyeball in response to change in extra-ocular muscle tension.

There are a number of advantages to this approach. To begin with, we have available a number of physical concepts - inertia, friction, elasticity and so on - capable at best of actual experimental verification and at least of feasible numerical expression from known data of other investigations. It is possible to factor out with some precision these purely mechanical aspects of an eye movement, allowing us to draw definite conclusions concerning the oculo-motor reaction pattern of the central nervous system to visual stimuli. In such a view it is necessary to lump the phenomena of muscular contraction in with the central nervous ones. This is not a serious objection since the eye muscles are singularly well controlled and capable of very delicate adjustment and since in any case we are concerned with the changes in muscle tension and not the manner in which these are brought about.

An illustration of our mode of approach is given in figure 15, taken from Brown and Campbell (1948), which shows schematically the response of a hypothetical system to a command. Let us regard the eye movement as the "output" and let "command" refer to the changes in muscle tension. Our attempt will be to define a system equation relating the two, and this will be done by showing that for a saccadic movement there is good physiological evidence for the postulation of a rather abrupt, or nealy step change in muscle tension. A step input happens to be one input which, when related to the corresponding output, allows the rather ready formulation of a system equation. Once this has been achieved, one can, on the one hand, deduce, on the basis of this equation, the stimulus

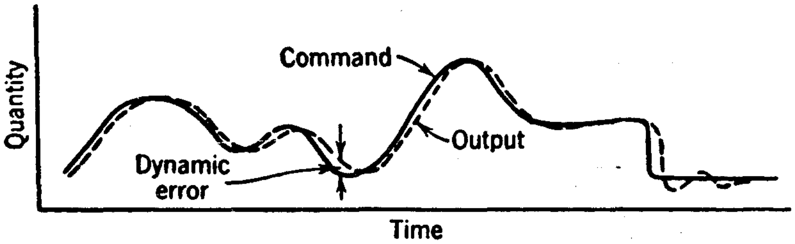


Fig. 15

Comparison between command and output for a hypothetical system with characteristics similar to those postulated to exist in the orbit (after Brown and Campbell).

for a given recorded response and, on the other, predict a response to a given command.

We are then left with the kernel of the problem of this dissertation: the study of the relation of the visual stimulus and the resulting command to the extra-ocular muscles.

B. The Contribution of Orbital Mechanical Factors to Observed Eye Movement Characteristics.

The available literature does not contain any records of either the change in nerve impulses to the extra-ocular muscles or the change in tension in these muscles during a saccadic movement.

Labyrinthine stimulation, and particularly the fast phase of nystagmus, produces eye movements which resemble saccadic movements very closely. Figure 16 shows the fast phase of the nystagmus of a patient with congenital nystagmus and, for comparison, a saccadic movement of equal extent in a normal subject. The two movements show very much the same characteristics.

Accurate records were obtained by Lorente de No (1935) of the changes in muscle tension during nystagmus. The fast phase is characterized by a very rapid rise in tension of the agonist, maximum tension being

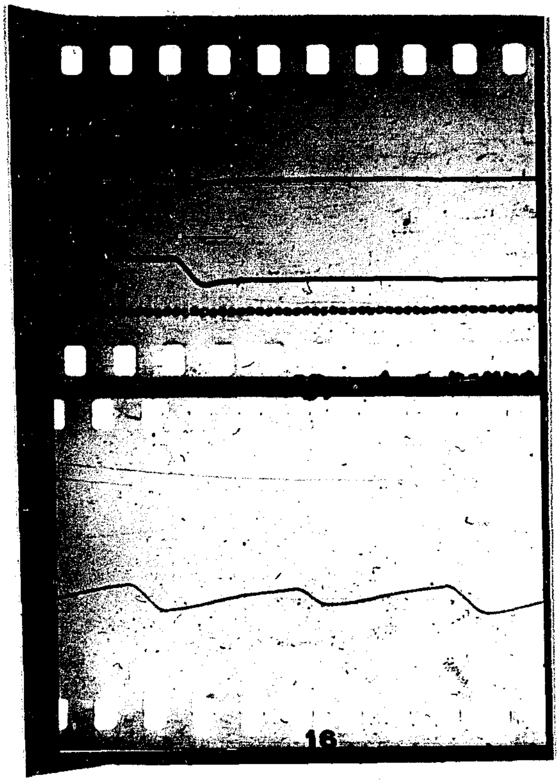


Fig. 16

Comparison of eye movements of subject with congenital nystagmus (lower record) with a saccadic movement of equal extent in a normal subject (upper record - time line interrupted every 10 milliseconds).

achieved in 25 to 30 milliseconds. There is a concomitant relaxation of the antagonist, but the two effects are not always in strict synchrony.

Szentagothai (1952), in a recently published monograph, shows records of the contraction of the eye muscles induced by stimulation of the labyrinth. The reaction time is only 10 milliseconds and the maximum is reached in 20-25 milliseconds. During a tetanic (contraction block (250 stimuli per second) applied to the III nerve nucleus the eye muscle very quickly reaches its peak tension which is held during the whole period of stimulation. The peak contraction is reached without overshoot. Cooper and Eccles (1930) in their classical paper showed that the contraction time of an extraocular muscle for an isolated twitch is only about 7 milliseconds, by far the shortest of any muscle in the body.

McIntyre (1939) studied the action potential of the nerve serving the extra-ocular muscle and the tension of the muscle during caloric nystagmus, recording the two simultaneously. He finds, as did Lorente de No, a rapid contraction of the lateral rectus muscle during the fast phase and a gradual relaxation of the tension in this muscle during the slow phase, if the nystagmus is in a nasal direction for this eye. Similar changes, mutatis mutande, were seen if the nystagmus was in the opposite direction. Evidence from several directions thus indicates that during the fast phase of nystagmus there is an active contraction of the one muscle reaching a high level of contraction quickly and retaining this level until it is gradually reduced during the slow phase. Meanwhile the opposing muscle is relaxed during the fast phase and gradually increases its tension during the slow phase. Earlier work on the eye muscles during nystagmus (McCouch and Adler (1932)) and Lorente de No (1934) have indicated this and Sherrington had originally demonstrated it for skeletal muscle.

It is important to clarify this point since the acceleration curve in figure 6 lends itself to other interpretations which have occasionally been put forward [Stetson (1905)]. In such views the positive part of the acceleration curve is due to active contraction of the agonist during the movement. Later during the movement the agonist ceases to contract and after a variable time, depending on the extent of the movement the antagonist, by active contraction stops the movement. This is often called a ballistic movement. All available evidence is opposed to such an interpretation. Making the assumption that saccadic movements and the fast phase of nystagmus are alike, or even restricting the discussion for a moment to the fast phase of nystagmus, all records show a relaxation of the opposing muscle during the fast phase and a very gradual increase in tension in this muscle during the slow phase. At the same time there is a rapid increase to presumably a steady high level of contraction in the agonist and this is gradually reduced during the slow phase. Such a view represents a full justification of the concept of reciprocal innervation.

Applying this to saccadic movements one can then say with a considerable degree of justification that they are brought about merely by a change in torque which the extra ocular muscles are applying to the eyeball, the latter coming to rest in a position representing an equilibrium of the forces applied. It is helpful to think, and almost certainly correct, that the movements are triggered off as a unit in the central nervous system and that the change in torque takes place very quickly, the eye coming to rest in a position determined by the forces opposing the motion.

A motion such as the one illustrated in figure 5 can be described, with some degree of generality, by an equation of the form

$$A_1\ddot{\theta} + F(\dot{\theta}) + K(\theta) = f(t)$$

which states that if a forcing function f(t), a function of time, is applied to the eye, it is opposed by the inertia of the system, a friction term which is a function of the velocity and a spring term, which is a function of the displacement θ.

The simplest linear system of this kind is one in which the friction is proportional to the velocity and the spring force proportional to the displacement from a given position. This brings the left hand side of the equation into the following form

$$A_2\ddot{\theta} + A_1\dot{\theta} + A_0(\theta - \theta_c)$$

It is not difficult to assign physical meaning to the constants A_2, A_1, and A_o

A_2 is the moment of inertia of the eyeball. A_1 is the coefficient of friction which the eyeball encounters in the course of its movement in the orbit.

A_0 is in a large measure an expression of the force with which the relaxed muscle opposes the extension which the other muscle brings about in moving the eyeball to the new position.

In the solution of this equation we make a further assumption, this time about the muscular forcing function. While all the references cited seem to agree that a movement like a saccadic movement is brought about by a quick change in tension of the muscles, it is unlikely that this change is completely instantaneous. In fact it is quite likely to take 20-30 milliseconds before the peak contraction is reached. This is still only a fraction of the duration of the whole movement which may last 60 milliseconds or more.

In making the assumption that the change in torque is instantaneous we will arrive at physical constants which will overestimate the contribution that these mechanical factors of inertia, friction and elasticity will make to the movement. It will be shown that even then they are small enough not to contaminate our records too much and that we may regard practically all phenomena which our eye movement records demonstrate as genuine changes in innervation and hence accurately reflecting the central nervous response to our stimuli.

We can then write down the following equation

$$A_2\ddot{\theta} + A_1\dot{\theta} + A_0\theta = K \qquad (1)$$

K being a constant. The problem is to evaluate the constants A_2, A_1, and A_0 from curves such as the one shown in figure 5.

It is of value to introduce the following parametic form of equation (1) (Trimmer 1950)

$$\frac{\ddot{\theta}}{\omega_n^2} + \frac{2\zeta\dot{\theta}}{\omega_n} + \theta = K \qquad (1a)$$

where $\omega_n = \sqrt{A_0/A_1}$

$\zeta = A_1/2\sqrt{A_0A_2}$

The solution of (1a) consists of two parts, the complementary function, which is the solution to the equation

$$\frac{\ddot{\theta}}{\omega_n^2} + \frac{2\zeta\dot{\theta}}{\omega_n} + \theta = 0 \qquad (2)$$

and the particular integral which takes into account the particular type of forcing function f(t).

The solution of (2) is

$$\theta = e^{-\zeta\omega_n t}\left(\theta_i \cos \omega t + \frac{\zeta\omega_n\theta_i + \dot{\theta}_i}{\omega}\sin\omega t\right) \qquad (3)$$

and expresses the manner in which the steady state of response to the forcing function is reached. θ_i and $\dot{\theta}_i$ are the values of $\dot{\theta}$ and θ when $t = 0$.

The constants ω_n and ζ characterize the system and approximate numerical solution [Trimmer (1950)] of a number of curves of the type of figure 5 have yielded approximate values as follows:

$$\zeta = .7$$
$$\omega_n = 120$$

A description of the significance and use of these parameters is given in modern discussions of servomechanism [Fitts (1951), James, et. al. (1947)].

It must be fully understood that the assumption underlying the use of equation (3) is that we are, in fact, dealing with a linear system. Unfortunately there is evidence that the oculo-motor system does not in fact fit this description. In a linear system the relation between maximum velocities in the responses to step stimuli of different extents should be linearly related to the stimulus. Figures 7 and 8 show that this is not so in the system under discussion here.

For the time being the nature of the non-linearity remains obscure. It is probable that, for saccadic movements of short extent, lack of instantaneity of onset of changed torque produces a high degree of "guiding" over a considerable proportion of the whole movement.

A very likely cause of the non-linearity would be a friction term proportional to the square of the velocity rather than the velocity itself [Stoker (1950)] a formulation often used when dealing with friction within a fluid. It would, for instance, explain the fall-off from linearity of the maximum velocity curves of figures 7 and 8 since the friction increases with the square of the velocity and thus progressively mitigates against the attainment of high velocities. Guth (1947) shows a tension versus extension curve of muscle which is exponential. It might well be, therefore, that the specification of a spring constant is too simple an assumption; the tension to be overcome in extending a muscle by a given amount would then vary with the initial extension. Since the percentage extension produced by even a large eye movement is quite small, this is probably not an important consideration.

A full analysis of these possible causes of non-linearity, while feasible, has not been attempted in this dissertation.

The derivation of numerical values for the parameters W_n and ζ , while admittedly based on many assumptions of only approximate validity, is, however, of some use. The nature of the central assumption, viz., of a step increase in torque, implies that numerical values arrived by its use will always exaggerate the purely mechanical factors of inertia, friction and elasticity.

In those cases in which the forcing function is a constant or constant rate of charge, i.e., in the case of a step or step velocity forcing function, equation (3) is an expression of the deviations of the system from the position which the function would compel it to assume in the absence of these mechanical opposing forces.

The formulation presented here would give the maximum error due to these mechanical factors and if we make this allowance for these we can deduce with a fair degree of certainty the nature of such forcing functions from the eye movement records.

Equation 3 represents a periodic function and if $\zeta\omega_n$ is positive and real it has an amplitude decreasing with time.

Substituting the approximate values for ζ and W_n obtained earlier and applying equation 3 to the case of a forcing function applied to the eye which will, when

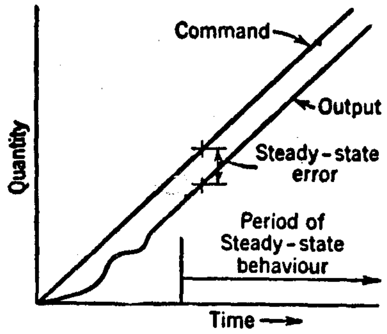


Fig. 17. Response of a hypothetical system to a step velocity forcing function (after Brown and Campbell).

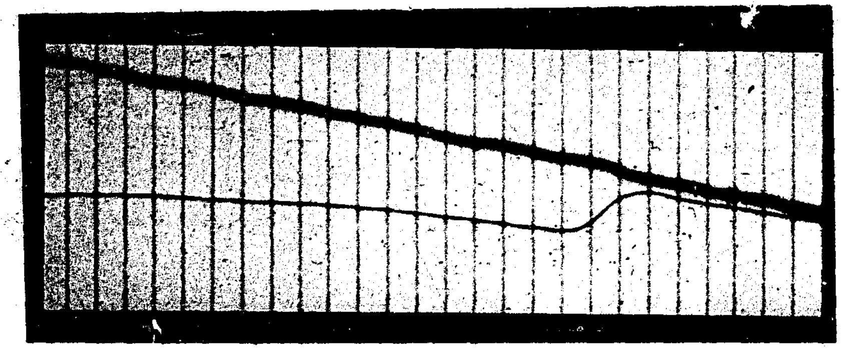


Fig. 18. Onset of steady constant velocity movement in eye. 180 milliseconds before arrow a constant velocity target (heavy trace) appeared on screen. Note gradual assumption, with oscillatory changes, of a constant velocity which is reached about 60 millisecs. before saccadic movement.
Vertical lines -- time in 10 millisecs.

the transients have subsided, cause the eyes to move with a velocity of 20° per second, we find that the transients are small. Within 35 milliseconds of the onset, the transients will have an amplitude of 2' and within 55 milliseconds they will have an amplitude of 36". This means that the maximum error at these times as counted from the onset of the forcing function will not exceed the values given.

The exact shape of the response curve can be deduced from an analysis of the equation. Schematically it would look like figure 17, reproduced from Brown and Campbell (1948). Comparison may be made with figure 18, which is taken from an actual record in which a steadily moving stimulus was presented to the eye about 180 milliseconds before the arrow.

The trace of the corneal reflex of the eye clearly shows the transition period between zero velocity and a steady velocity which is maintained for about 60 milliseconds before the steady state error, including a difference in zero position, is compensated for by a saccadic movement.

The transient period in the record is characterized by oscillatory changes and the constant velocity is reached somewhat more slowly than this formulation would predict for a step velocity input. One is probably entitled to conclude that the latter assumption is too idealized.

In general, then, we may conclude that for a reasonably slowly changing forcing function the eye follows the forcing function with considerable fidelity. In particular we may conclude that the discrete changes in eye velocity exhibited during visual tracking of an unknown task are in fact expressions of a discretely changing motor input.

C. The Mechanism of Saccadic Eye Movements.

It is of interest to compare the actual position, velocity and acceleration characteristics of a saccadic movement with that to be expected on the basis of the assumption of a ballistic movement. The left hand side of figure 19 gives in a schematic way these curves based on the assumption that a movement is started and stopped by sudden and individual bursts of contraction of the agonists and antagonists respectively. The right hand side shows the curves actually obtained. The movement is obviously not stopped in this manner since the negative acceleration comes on relatively early in its course.

Considerable variations exist in the details of the acceleration curve of various movements even of the same extent in one individual. However in general features they are quite alike and almost all of them show a second burst of positive acceleration.

It is likely that this doubling of the positive part of the acceleration curve is due to a possible asynchrony in the onset of the contraction in the agonist and the relaxation in the antagonist. This was found by Lorente de No (1934) in the fast phase of nystagmus. The evidence adduced in the previous subsection seems to show that without a doubt a saccadic movement is a single change in tension occuring more or less simultaneously and in opposite directions in the two muscles concerned.

Such a view leads also to a most parsimonious explanation of all eye movement phenomena. It may be postulated that a biunique relation exists between innervation sets to the eye muscles and positions of the eye in the orbit. A saccadic movement would then be no

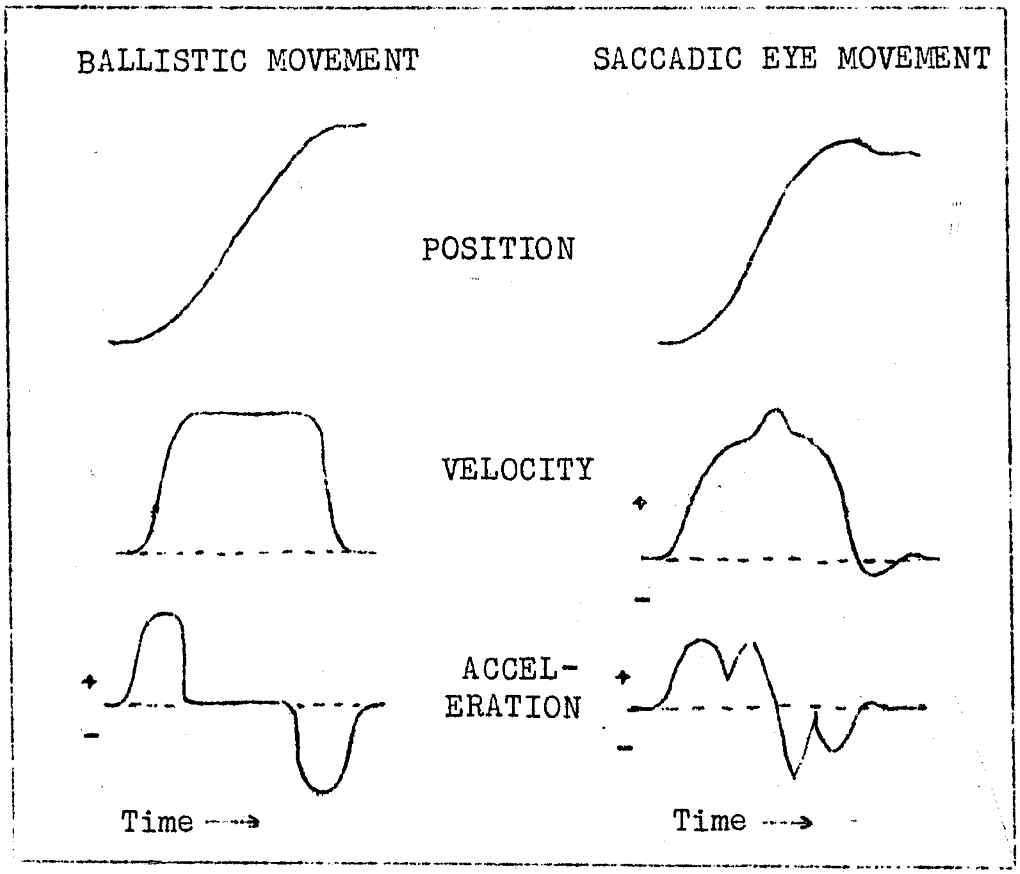


Fig. 19

Schematic diagram of position, velocity and acceleration changes during a hypothetical ballistic movement (left) and a typical saccadic eye movement (right).

more than a practically instantaneous change-over from one innervation set (one position) to another one. This would occur as a unitary phenomenon in which instructions for all necessary change in muscle tension are issued and effected practically instantaneously and the eyeball comes to a stop in the equilibrium position dictated by the new forces. A discussion of the implications of this view from the standpoint of the mechanics of the orbit was presented in the previous subsection.

Problems such as to the manner in which the vertically acting muscles are re-aligned during a saccadic movement, solve themselves in such a formulation: the innervation corresponding to the new position reaches them just as the more immediately concerned muscles.

Such an explanation would have the advantage of eliminating the necessity of the careful timing of the contraction of the opposing muscle to stop the muscle that is inherent in the hypothesis of a ballistic movement and, moreover, it has all the physiological evidence on its side.

This unitary concept of a saccadic movement is particularly appealing since it identifies eye position with a particular set of innervations and fits in with a new rational view of the oft-discussed problem of proprioception in the extra-ocular muscles. This will be further elaborated in a subsequent subsection.

In connection with the mathematical formulation presented in the previous subsection it is of interest to point out that the root means square error of the response of the system to a step stimulus would be just about minimized with a system of the characteristics we have found it to possess. This means that the mechanical system of the orbit works in such a way as to reduce the total error involved during the process in shifting from one position into another to a minimum.

While the evidence points to an independent initiation and elaboration of saccadic movements, the question arises whether a sequence of saccadic movements can be carried out in intevals shorter than that of visual reaction times. Figure 9 shows that the return sweep in the response to a pulse stimulus seems to be visually induced, i.e., its delayed onset suggests that the detection of the absence of the original target (in the case of short pulse stimuli) or the cessation of the return sweep. This is a definite conclusion here, but it is in contradiction to experiments carried out by Cobb who showed that a sequence of saccadic movements can be organized beforehand and that such saccadic movements are separated in time by intervals shorter than a visual reaction time. That the latter situation can exist is not denied. In fact, a sequence of small saccadic movements during apparently steady fixation was observed in subject L.C. and is reproduced in figure 20. It will be observed that the pauses between the movements are only about 50 milliseconds -- far shorter than any observed visual reaction time. Occasionally during tracking there are sequences of saccadic movements separated by intervals of less than 100 milliseconds. An example of this can be seen in figure 14.

From this we may draw the conclusion that although saccadic movements are indivisible innervational units and are usually brought into operation by specific visual stimuli, they can be elaborated in sequences at intervals shorter than a visual reaction time. Apparently such a sequence is not induced by a pulse stimulus as described in Section 2B, and this raises a number

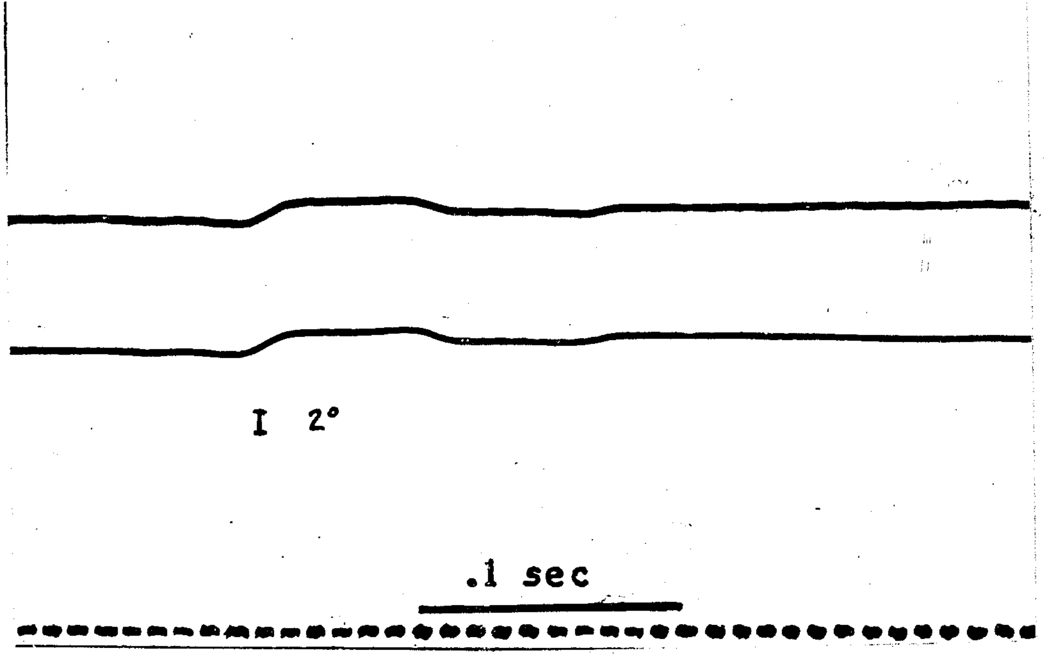


Fig. 20

Sequence of small saccadic movements during apparently steady fixation. Intervals between movements are only about 50 milliseconds, less than half the shortest reaction time to a visual stimulus.

of points about the manner of visually responding to more complex pulse stimuli consisting of several components. Yet the thesis of the unitary and independent initiation of a saccadic movement seems fully justified.

D. The Mechanism of Visual Tracking.

The interpretation of the data of subsections C, D, and E of Section II allows us to set up a clear cut formulation of the mechanism by which eye movements are induced by horizontally moving visual stimuli.

It is to be pointed out explicitly that the stimulus situation was designed thoughout to study the mechanism of tracking when the subject had no clues with which the predict the movement. Care was taken to keep the subject unaware of the type of movement to be presented and the speed and starting position of the target which he was to track.

On three occasions a deliberate attempt was made to determine the effect of repetition of the stimulus on the response. In one case a regular "square wave" of stimulation was presented, i.e., the stimulus effectively jumped back and forth from one position to another at regular intervals which were varied from two per second to one every three seconds. In the second instance the target moved across the screen back and forth horizontally with the velocity changes dictated by a sine motion.

In both cases it was found that within a very few presentations, half a dozen or so, the subject was no longer tracking the target, i.e., following it, but was actually anticipating the movement with the result that the lag between the stimulus and the response was reduced to a value of about zero and sometimes the response actually preceded the stimulus. It is clear that anticipation plays a major role in the visual response and all was done in this experiment to eliminate it, for our interest lies in the mechanism with which purely visual stimuli per se produce movement responses.

The third case of repetition was that of the "problem" cam which contained unpredictable velocity and acceleration changes. No learning was demonstrated in its case in as many as 20 presentations.

Movement of the target across the retina or the illusion of movement as produced by short bursts of retinal stimulation in the temporal and spatial sequence of a typical movement stimulus but separated by reasonably short time intervals, induces a regular constant

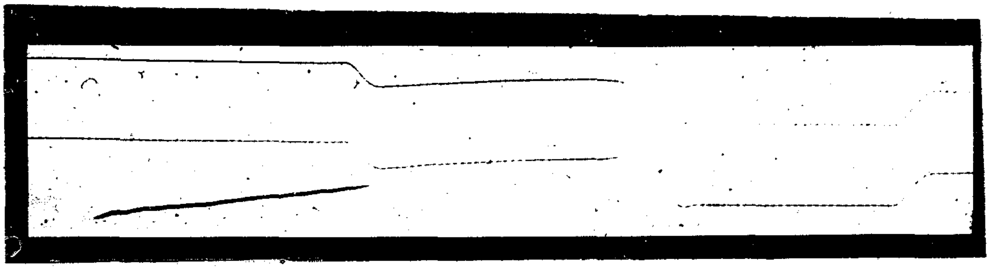


Fig. 21

Eye movements in response to a brief (200 milliseconds) constant velocity stimulus velocity movement in both eyes. The velocity of this movement is generally but by no means always closely related to the speed of the target and within a reasonable span of velocities the eyes start moving with the correct velocity after a reaction time of often less than 200 milliseconds. After the stimulus has ceased to move or has disappeared from view, the eyes continue to move for 100 milliseconds or more.

This is well illustrated in figure 21, which shows the response to a brief constant velocity stimulus which has already disappeared before the eyes started responding. There is a saccadic movement to a position which the target would have occupied had it not been withdrawn from view. The smooth following movement induced is of the correct velocity and persists for nearly 200 milliseconds before it is checked. Several hunting saccadic movements follow.

During tracking, adjustments to errors are carried out by discrete changes in the velocity of the following movements and by saccadic movements. A great deal of the adjustment of errors due to an incorrect velocity of the constant velocity following movements as well as the adjustment of all position errors takes place by means of saccadic movements.

It has been shown in a previous subsection that an ophthalmograph record of a smooth constant velocity following movement may in fact be regarded as an expression of an innervation to this end, mechanical artefacts being of a smaller order of magnitude.

This means that innervation to produce a smooth following movement can be induced as a unit as a result of the perception of movement and that these movements are not always fully correlated in velocity with that of the stimulus. One pictures the mechanism of tracking then as a perception of movement, the putting into operation of a well-integrated train of impulses designed to impart to the eyes a constant velocity movement, the correction of position errors by saccadic movements and the modification of the speed of the following movements in discrete steps as the need may arise. The corrections lag behind the stimulus by an interval of the order of a reaction time.

This may perhaps be called a closed loop circuit in which errors are used to modify the performance, but it is a closed loop circuit of a higher order which uses both jump responses and smooth following responses all of which are used and modified discretely and at intervals.

In general the results give support to the view of looking at the human tracking response as a closed loop circuit reacting discretely and further studies seem in order. For example, it would undoubtedly be of interest to investigate the magnitude of the errors which induce certain responses and, in a more general way, to cross correlate the stimulus with the eye movement response.

E. The Components of the Reaction Time to Visual Stimuli.

There are several clearly distinguishable stages in the response of the oculo-motor system to visual stimuli: the sensory aspect involving the eye as a sense organ and the optic nerve as a transmitting agent, the central stage involving the various cerebral areas, and the motor stage involving the pathways to the oculomotor nuclei and the transmission and putting into effect of the motor impulses originating there.

It is of interest to assign approximate fractions of the total reaction time to a visual stimulus to the three stages involved.

Szentagothai (1952) found that the interval between the onset of a direct stimulation of the labyrinth in cats and dogs and the onset of a reflex contraction of an eye muscle (which would produce vestibular nystagmus) is about 10 milliseconds. This leads him to postulate a three neuron pathway between the labyrinth and the eye muscles. The delay introduced by the oculomotor nuclei is very small indeed. Lorente de No (1935) found a synaptic delay in the third nerve nucleus of .5 to .9 milliseconds. It is then reasonable to assume that the interval between the sending out of the innervation by the center immediately preceding the oculomotor nucleus and the beginning of the contraction in the extra-ocular muscle is also of the order of 10 milliseconds.

There has been a number of estimates of the time interval between the onset of a light stimulus and the arrival in the visual cortex of stimuli induced by it. Monnier (1952) reviewing his own work in man and mammals as well as that of others concludes that this interval is of the order of 33 to 42 milliseconds.

The reaction time of eye movements to visual stimuli is often as low as 120 milliseconds. Deducting the upper estimates of 50 and 15 milliseconds for the purely sensory and the purely motor aspects respectively of the response we are left with a minimum cortical integration time of the order of 60 milliseconds. If we assume that each intervening neuron takes up as much as three milliseconds in synaptic delay and transmission time, we are left with an estimate of 20 or more neurons as intervening cortical and higher central stages in the sequence of events commencing with the light rays entering the eye and ending with a change in state of contraction of the extra-ocular muscles. This effectively removes the eye movement response studies in this dissertation from the realm of simple reflexes and helps to pave the way to a re-evaluation of the concepts of voluntary and involuntary eye movements.

F. Proprioception and Eye Movements.

The argument on whether proprioceptive impulses arising from the eye muscles play a part in the guiding of eye movements has been protracted and not always decisive (seeLudvigh, (1952) for a review and recent formulation). Most of the evidence tends to contradict the view that proprioception plays a role in eye movements. The work presented in this dissertation seems to show fairly clearly that when visual stimuli operate their manner of producing eye movements is definitive and can account by itself for all observed phenomena.

This is not enough, however, to negate the existence of proprioception since the possibility of it being overridden by visual impulses cannot be overlooked.

Ludvigh (1952) ably reviews the problem and in the light of all known facts, including the existence of sensory end organs in eye muscle tendons, the lack of existence of a sensory pathway separate from a motor pathway, and the many experimental verifications of the thesis that a proprioceptive sense does not exist for the eyes, postulates a parametric feed back between the eye muscles and the oculo-motor nuclei. Thus the end-organs in the muscle tendons would send their impulses by way of the motor nerves to the oculo-motor nuclei and no further. The information which they convey would concern itself with the state of tonus, nutrition etc. of the muscle and this would be used to modify the innervation sent out by the motor nuclei so that a desired movement (as determined by the higher centers and sent down as an innervation to the nuclei) would in fact be carried out as such.

This formulation appears adequately to account for all known facts. The function of the end organs would then be merely to communicate with the motor nuclei and not any higher centers and awareness of the position of the eyes through this channel would not be expected.

The view expressed in this dissertation that a given set of innervations normally corresponds to a given eye position would fit in well with Ludvigh's thesis. The parametric feedback circuit between muscle and motor nuclei would then take care of minor variations in muscle tension and no allowance is made by the higher centers for any variations in normal tension. The past-pointing of fresh paresis bears this out.

When viewed in this manner, a change in eye position would correspond to a change over from one impulse pattern to another and, if this involves the higher centers, a collateral impulse pattern is sent to the space perceiving centers. The information thus gained by the latter is integrated with others for the purpose of egocentric localization and would according to the present view constitute the only source of available information concerning eye position in the orbit.

Section IV

Summary and Conclusions

The experiments were designed to study the nervous and muscular mechanisms that initiate and execute eye movements in response to visual stimuli in the horizontal plane.

To achieve this there was developed a method of photographically registering horizontal eye movements with a precision of about one millisecond in the time dimension and about five to ten minutes of arc in the dimension of the eye movement. The stimulus throughout was a small light spot in an otherwise structureless surrounding, except on one occasion when a pair of such spots was used.

The response to a step stimulus, i.e., the instantaneous displacement of the light spot from one position in the visual field to another one in the same horizontal plane, consists of a saccadic movement. Such a movement, when studied with the high magnification in the time dimension which the resolving power of the instrument permitted, shows certain characteristics not previously described. There is a high degree of simultaneity of onset of the movement in the two eyes; there is a rapid acceleration to a maximum velocity which is a non-linear monotonically increasing function of the extent of the movement; and the eyes come to a stop after a significant overshoot and with minute oscillations around the final position.

It is concluded from the present findings and in the light of physiological evidence from other sources that a saccadic movement is initiated as a single, unitary step by means of a single change in innervation to each of the muscles involved. This produces a change in the tension of the various muscles which may be considered to be effected extremely rapidly. The eyeball then assumes its new position in the orbit as dictated by this torque produced by the changes in muscle tension and the forces opposing it, friction, inertia and elasticity. A mathematical treatment of an idealized physical system of such characteristics suggests that these purely mechanical orbital factors play a relatively minor role in eye movements particularly in the case of slow, smooth following movements which may be regarded as clear expressions of changes in innervation directed to produce such movements.

Many previous investigators have found differences in maximum eye velocities during saccadic movements,depending on the direction of movement and whether it was in or out with respect to the median plane of the body or the primary position of the eye. A detailed statistical study in three subjects showed that such variations do indeed occur at statistically significant levels but that these variations do not present a consistent pattern from one individual to another.

When the visual stimulus is moved horizontally with a constant angular velocity, smooth following movements are induced. There is a reaction time of nearly 200 milliseconds after which a saccadic movement occurs which brings the eyes directly onto the stimulus and the eyes immediately commence to move with a constant velocity. The latter is usually closely related to the stimulus velocity particularly when this is small; for high stimulus velocities the velocity of the smooth following movements lags considerably and the position error thus introduced is reduced by saccadic movements. Substantially similar results are obtained when the stimulus is only intermittently exposed. When as few as four stimuli of 10 millisecond duraction each are presented every second in the spatial sequence dictated by a target moving with a constant velocity, smooth constant velocity following movements are induced, although the latter are usually inaccurate in velocity and frequently interrupted by saccadic movements.

When a moving target is following a course which is unknown and unpredictable to the observer, the visual tracking mechanism makes use of only saccadic and smooth constant velocity movements. The latter are modified in discrete steps at intervals of not less than 100 milliseconds. Changes in position or velocity of the stimulus precede concomitant changes in response by an interval equal to the reaction time to such visual responses.

The conclusion is drawn that smooth constant velocity movements constitute a basic response pattern and that they may be induced by the perception of movement.

When a relatively simple movement pattern is used, such as a stimulus moving horizontally with velocity changes corresponding to a sine wave, it is found that the usual tracking mechanism operates for only a few cycles after which learning and anticipation becomes evident: there is little or no time interval between stimulus and response changes and smooth changes in the velocity of following movements are observed for the first time.

A dissection of the time interval between the onset of a visual stimulus and the beginning of the eye movement response into its various phases enables the conclusion to be drawn that a minimum of 20 neurons seems to be interposed between the first line of receiving neurons in the visual cortex and the oculo-motor centers in the brain stem. This effectively removes the eye movement responses studied here from the realm of simple reflexes.

The concept of a biunique relation between innervation sets to the eye muscles and eye positions in the orbit may be viewed as fully in accord with modern theories of proprioception and the eye muscles. Thus any efferent impulses originating in they eye muscles or their tendons would travel by way of the motor nerves only as far as the oculo-motor nuclei and there exert a regulating influence over the actual innervation sent out by them to produce a given movement. The position of the eyes in the orbit would then be controlled by an invariant impulse pattern from the higher centers to the motor nuclei and this impulse pattern would in the absence of visual stimuli be the sole extent of the higher centers source of information of eye position.

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AUTOBIOGRAPHY

I, Gerald Westheimer, was born on May 13, 1924 in Berlin, Germany, where I received my primary and secondary education. In 1940 I entered the Sydney Technical College. In 1943 I received my Associateship Diploma from this institution in Optometry with Honors and was awarded the Sydney Technical College Medal. From 1944 to 1947 I attended the University of Sydney, graduating B.Sc. in 1947. In 1950 I was awarded the Fellowship Diploma of the Sydney Technical College for a thesis "Studies in the Optical Theory of Contact Lenses". From 1945 to 1951 I was in part-time and later in full-time optometric practice in Sydney, N.S.W. Since September 1951 I have attended the Graduate School of the Ohio State University. In the academic year 1951-2 I held the position of Associate in Optometry in the Ohio State University and for the academic year 1952-3 I received an appointment as a Research Fellow.