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VISUAL ACUITY AND MOVING OBJECTS

by

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PREFACE

What does a pilot look at on the ground when coming in to land ? What does a pilot look at when flying low and fast ? There are as yet no answers to these questions. Many cues are cited as being important but none so proven. The questions are legion and the answers inconsistent.

We learn to fly by example and turn example into skill of varying degree. Whatever visual cues are used in that skill there is one factor which affects them all; these cues have movement and the detail in these cues must be discriminated to permit recognition. High speed flight particularly at low level imparts to all objects seen from the aircraft a movement relative to the observer. Visual acuity under these conditions implies that the detail is seen while the eyes are moving.

It is acuity under these conditions which has been examined to determine man's ability, to determine the physiological mechanisms involved, and to apply the results to the practical problems of flying.

The experiments described were designed and carried

out by me. The requirements of the apparatus and its general form were made by me and the mechanical and electronic detail by members of the staff of the Institute. The work described on the effect of viewing time on ability to discriminate detail in moving targets, the ability when head and eyes are co-ordinated, the co-ordination of head and eye movements in pursuit of a fast moving target, the nature of eye movements during such pursuits, the activation of neck muscle fibres during such pursuits, the contribution to the problem of the function of proprioception in eye muscles, the proving that the second saccadic movement during visual pursuit is a corrective phase, and the description of the moment of perception during pursuit eye movements are believed to be entirely original.

The examination of position error tolerance has frequently been carried out under the description of Peripheral Visual Acuity.

Velocity error tolerance which is the ability to discriminate detail in an image moving across the retina is also considered to be original.

The high speed low level flights were carried out as part of my functions as a medical pilot.

ACKNOWLEDGEMENTS

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I also extend my sincere thanks to my colleagues Mr. Byford, Mr. Williams and their staffs and Mr. N.L. Andrews whose skills and technical abilities turned my requirements into practical electro-mechanical mechanisms; to Mr. Samuel for his aid in statistical evaluations; to Mr. Hills and his staff at the Royal Aircraft Establishment for their production of the Landolt C transparencies and the figures accompanying the text.

I also wish to thank the subjects whose patient tolerance of the vagaries of performance of complex apparatus made the research possible.

Visual Acuity and Moving Objects

Definition of Title

Visual acuity is the term used to describe the ability to discriminate detail in an object. In this thesis the objects viewed have had an angular velocity relative to the observer.

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PART 1

Section 1

Introduction

Aviation has opened many fields of required research in physiology and has involved all the various systems in the body. Not least has been its effect on the visual system which is more critically involved in flight than in any other form of transportation. Vision has always been the dominating sense in aircraft control and visually presented information is received from inside the cockpit and from the outside world. The pilot's attention has to be paid both to the coded information on the instruments in the cockpit and the natural terrain outside, when this is visible.

Modern developments in automatic flight systems have done much to ease the stress involved in flying but there is still a need for the pilot to monitor the automatics by visual reference. Take off and landing are still in the hands of the pilot and will be for some considerable time. The least stressful flight conditions are these in which good visibility of the outside world is available, the most stressful is flight manoeuvre when this world is not visible, as in cloud flying, and the pilot has to accept coded information and integrate it into an appreciation of what the aircraft is currently doing.

To the problems of flight classical vision physiology contributed much of practical value. For example, the effects of brightness, size, colour, contrast and light and dark

adaptation on visual acuity were immediately applicable to the instrument displays and to the external terrain.

The new fields of research opened by the necessity to fly in reasonable safety and carry out flight tasks with efficiency generally received their origins, and the relevant research its impetus, during the second world war 1939-45. Hitherto, in aviation, vision was considered only in terms of visual acuity and depth perception.

Aeronautical achievements and the increasing demand for better performance aircraft for the air forces has made the search for solutions to problems encountered in flight a continuing task.

The effect of supplying oxygen to aircrew at altitudes in excess of 10,000 feet by day and 4,000 feet by night on visual capability was probably the most dramatic achievement and the explanation of 'blacking out' of pilots when accelerations of 4 or 5 times the normal gravitational pull was achieved in aircraft manoeuvres, the most dramatic finding. The latter, however, had no cure but an improvement in tolerance was obtained by applying methods, endogenous and exogenous, to retain an adequate supply of blood, and therefore oxygen, to the light sensitive cells of the retina.

As night flying became more common the problems of obtaining and maintaining dark adaptation to enable the take off run to be seen, the varying targets to be found, and a landing to be made were met and countered by the wearing of red goggles

before the flight while in brightly lit briefing rooms and providing instrument lighting within the aircraft which minimally affected the degree of dark adaptation achieved. The knowledge that in the dark adapted state the most sensitive retinal area was not the central one, the fovea, but some $15-20^{\circ}$ away from it, was applied by aircrew in their never ending search for hostile activity when on bombing missions, or on a night fighter defensive sortie.

Lesser known, but equally important to the safety of aircraft, are the indirect effects of transparencies on visual acuity. Canopies and windscreens have to be carefully designed to ensure that too much light is not lost by the thickness of the material used, that the effect of inclining the windscreen does not further diminish light transmission, and that distortions in the material do not cause embarrassment to the pilot on viewing external objects. The fields of view required, particularly for landing, have been and still are under investigation. As aircraft become faster, indirect visual systems of periscopic type or closed circuit television may become essential if adequate views of the outside world are to be achieved without seriously affecting aircraft performance and actual safety by virtue of failure of transparent material due to the effects of pressure and kinetic heating.

Man is an exceptionally visual animal. (Granit). It might also be said that he is an exceptionally mobile animal. These two qualities are particularly and necessarily interrelated when it is appreciated that when man moves a relative angular velocity

is imparted to all objects in his visual field. If one moving object in the field is to be regarded it is necessary that the angular velocity of the eye and the object should be reasonably similar.

Research in visual physiology has paid scant heed to this important primary biological factor.

The speed at which man can move from one place to another was doubled by the use of the horse, now in 1959 we have aircraft which exceed man's natural speed of movement by 30 to 50 times, and there are signs that 500 to 1000 times this velocity will be only too readily achieved in the future.

High altitude has been shown to adversely affect visual acuity (Whiteside, 1957). High speed per se has also an adverse effect. The generally accepted reaction time of man to a stimulus, under laboratory conditions, is about 200 milliseconds. Mans reaction time to a visual stimulus when flying an aircraft may be ten times as long because the stimulus must withdraw the pilot's attention from his present flight state which in itself is demanding of attention and his responses to the stimulus must be controlled in rate, force and duration. An uncontrolled response may be as dangerous as no response. At a velocity of Mach 1, 200 feet in distance is covered during the laboratory reaction time. Increasing speed of movement is rendering man's reaction time dangerously slow.

To the eyes of pilot or crew of an aircraft, and to the passenger, all objects external to the aircraft have a relative angular velocity by virtue of the movement of the aircraft. From

high altitude or when the external panorama viewed is distant this angular velocity may be at the threshold of movement discrimination. From low altitude particularly, and during the approach to land, these angular velocities may become so great that detail is lost and is replaced by a blurred impression of things moving.

The more general current visual problems in flight are still concerned with lack of oxygen, acceleration, vibration, dark adaptation and orientation. Many other problems are of a more psychological nature. Of these the readability and interpretation of displayed information within the aircraft, the appreciation of the ever changing external panorama, and the interpretation of these changes are of the greatest importance. Failure to interpret accurately the visual clues presented whether inside the aircraft or outside can produce equally disastrous results as can the lack of oxygen or excessive acceleration. The general visual problems have been outlined by many authors either in sections of general treatises of Aviation Medicine or as reviews. The most comprehensive coverage is afforded by Armstrong (1952), Macfarland (1953) and Wulfeck et al (1958). Reviews of more specific natures can be found in the literature of the more aviation minded countries; of these only a few are cited. They are Benchimal and Sebas (1952), Duke Elder and Neely (1953), Berens and Sheppard (1953), Kaffka (1955), Rios Sasiain (1955) and Arner (1957).

With the exception of a limited amount of information presented aurally the pilot of an aircraft is entirely reliant on visual

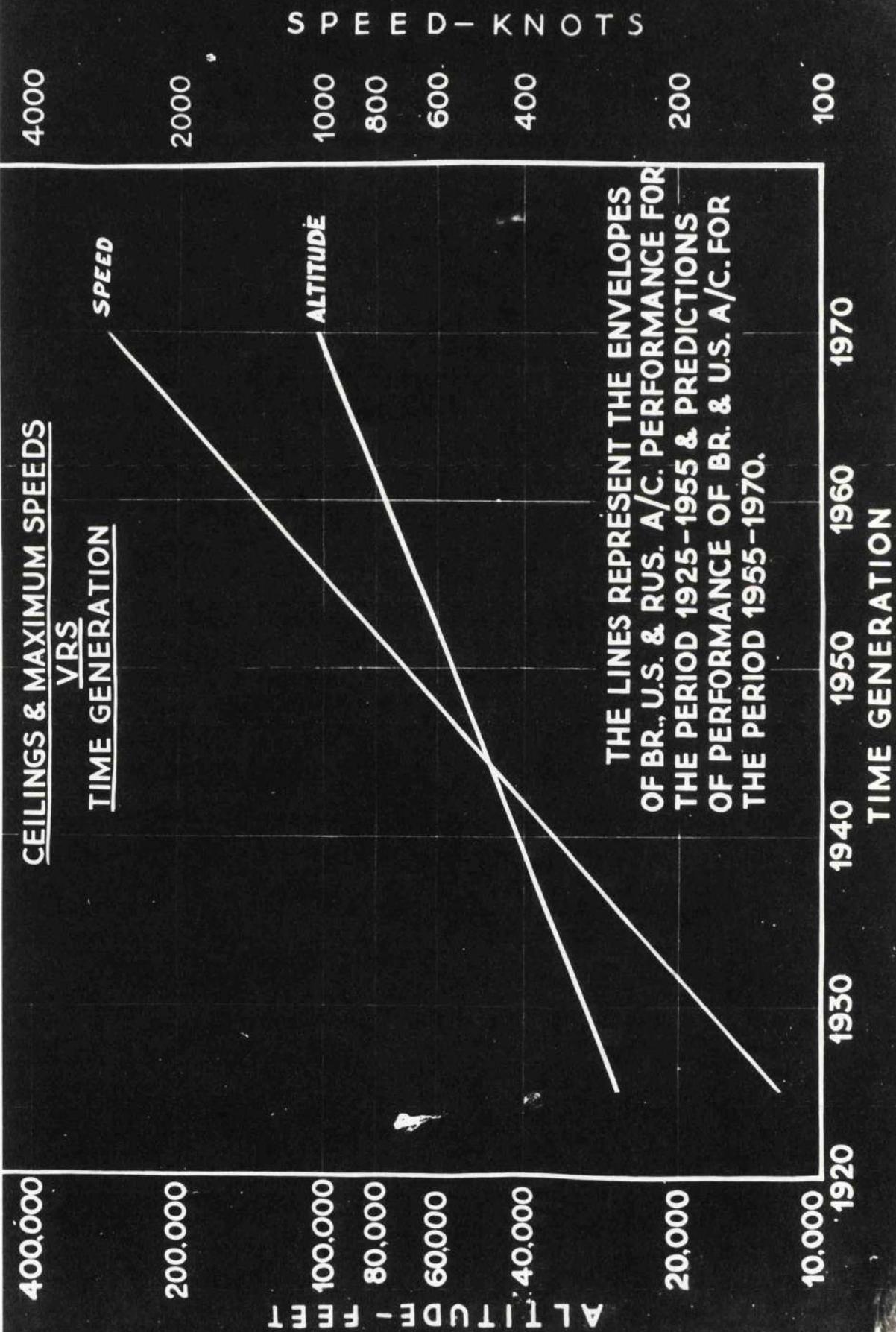


Fig. 1

perception, a perception which can be erroneous because of the adverse environments met in flight.

The purpose of this study is to examine the ability of man to discriminate detail in moving objects and to investigate the functioning of the visual system when presented with moving objects which require to be identified.

Routine examination of pilots in relation to visual acuity is related to static objects. In the Royal Air Force and the Ministry of Transport and Civil Aviation the standard Snellen test letters are used and a normal visual acuity or acuity correctable to normal is required. The aircrew are examined by a static method for a task which is essentially the appreciation of movement and detail in moving objects.

The Aircraft Performance

There is shown (Fig. 1) a graphical appreciation of the past, present and potential future performance of aircraft. The data on which the curves of performance in speed and altitude are based is taken from the performance characteristics of civil, military and research aircraft as described in Janes (1957) and other public sources. The future trend has been obtained in conversations with leading aeronautical research personnel and aircraft designers in Britain, Europe and America.

The general cruising speed of advanced aircraft varies considerably, the approach to land speed however, irrespective of the type, varies by a smaller amount, the general range being 100-180 m.p.h. It is during this phase of landing,

during low level flight, and when other aircraft are in the same airspace that the angular velocities of objects seen tend to be high. It is during such phases that the majority of catastrophic accidents occur. Though these accidents cannot be ascribed to diminution of visual acuity per se it may be a contributory factor.

It is not only in aeronautics that high relative angular velocities of objects viewed are encountered. Any form of locomotion will produce the same situation, high speed flight, however, has made this investigation necessary.

Limitations of Research into the Perception of Movement

The research into the perception of movement forms a very small proportion of the investigations of the functioning of the human eyes. With the exception of relatively recent studies by Low (1947), Ludvigh, Ludvigh and Miller, Miller, Miller and Ludvigh (1947 - 1957), Bhatia (1957) these investigations have entirely ignored the ability to discriminate detail in objects which have angular velocities relative to the observer. The ability to move is a dominant feature of all but the lowest forms of life, and therefore not only is discrimination of movement important, but, so also is the discrimination of the detail in the moving object if the object seen is to be meaningful.

The human eyes (Part 2) with their relatively narrow field of view have developed as organs which have relatively low thresholds for movement perception in all parts of the field of view and fine discriminatory ability only in the central

area. It is to this central area that the stimulus image is brought by eye movement. The presentation to man and animals of sudden peripheral light sources or moving objects will result in involuntary reactions which vary with the phylogenetic state of development of the animal. The higher the species of animal the more logical and intelligent is the reaction to the stimulus. This can be noted in the reactions of immediate flight of some animals and the turning towards the stimulus by other animals. Man is in the latter group and his adverse reaction is not merely confined to the eyes but may affect the whole body orientation. He does, however, still retain the baser reactions of flight or avoidance when the threat is sufficiently stimulating or menacing.

Section 2

History

The Perception of Movement

This may be appreciated in one of two ways. With very slow movement the idea of motion is conveyed by the object viewed having developed a new orientation in relation to another object after an expired interval of time. With fast moving objects there is an immediate impression of actual movement. Duke Elder (1944a) has reviewed the investigations carried out in this field.

The earliest studies reported of movement were made by Tzermak (1857), Exner (1875) and Fleishel (1882). Their studies were concerned with perception of motion and they showed respectively that movement in the periphery of the visual field is phenomenally slower than movement in the central area, that an object could create an indirect perception of movement by change of position, and that a moving object seen while fixating a stationary point moves subjectively faster than when observed during the pursuit movement of the eyes. Aubert (1887) calculated the threshold for movement in homogeneous fields both when seen centrally and peripherally. The Aubert-Fleishel paradox relates to the difference in phenomenal velocity as conditioned by the mode of observing; an object having constant physical velocity appears subjectively faster when viewed with pursuit eye movements against a heterogeneous background than

when viewed against a homogenous background. The explanation of this paradox was considered by Filhene (quoted by Bartley 1941) to be caused by the apparent movement of the background in the opposite direction to that of eye movement. Bartley (1941) also refers to others studies in the 19th century by Metzger who showed that a continuous stream of figures appeared faster than only 3 figures and Dembitz' findings that apparent velocity showed little correspondence with the velocity of the image over the retina. This was also noted by Granit.

More recent studies by Basler (1906) showed that threshold velocity varied with object angular dimensions, the illumination, and the background contrast, and Salaman (1929) detailed the variations in thresholds of movements in the different parts of the retina.

There is a current misconception that the periphery of the eye is the most sensitive area for motion detection. That this is not so was clearly shown by Basler (1906). The fovea has the lowest threshold to movement. The minimum angular velocity detectable is 1-2 minutes of arc per second when stationary objects are also present but this threshold is very much raised, 10-20 times, when no stationary objects are present. The minimum angular displacement perceptible is reported to be 6-20 seconds of arc (Stratton, 1900). Bourdon (1902) showed that for a 10° arc the limiting exposure time to permit perception of movement varied from 79-27 milliseconds which corresponds to angular velocities of 140-350 degrees per second.

At higher velocities there was instantaneous appearance of the stimulus throughout the 10° arc. The literature is quite voluminous on perception of movements.

Dimmick and Scahill (1925) reported on the inability of subjects to differentiate between actual movement of a light and the presentation of two lights successively illuminated under particular experimental conditions of time and distance. In a report with Saunders (Dimmick and Saunders 1929) the former showed that brightness was not a factor except when time is correlated, an increase in time of movement with associated increase of brightness improving perception of movement. The thresholds of illumination for the visual discrimination of direction of movement was further examined by Graham and Hunter (1931).

A major contribution was made by Brown (1931a, b & c) who found six factors of note in the perception of movement.

- 1). As distance from the observer to the object increases from 1 to 20 metres the phenomenal velocity can be maintained by increasing physical velocity by a ratio 1 : 1.56.
- 2). In a homogeneous field - the greater or smaller the field the greater or smaller the physical velocity to maintain subjective velocity.
- 3). The less homogeneous the field the greater the subjective velocity.

- 4). Decreasing either width or length of the field increases apparent velocity.
- 5). Increase in size decreases apparent velocity.
- 6). Objects orientated in line with motion appear to move faster than non-orientated objects.

Neff (1936) has reviewed the previous psychological papers on perception of movement and critically examined the findings which, because of marked variations in methods of examination, demonstrated that few factors were thoroughly explored and not much agreement appeared to exist. Brown (1937) and Brown and Voth (1937) introduced the concept of a vector field, a hypothesis based on size, brightness, velocity, time of and direction of movement which attempted to correlate real and apparent movement. Some years later Hartridge (1950) expressed the view that any explanation of perception of movement must encompass these two types of movement if it were to be acceptable. However, Saucer (1954) postulates two systems to explain real and apparent movement, the former being primitive and the latter isomorphic to detail.

Warren and Brown (1944) and Warren (1946) examined motion acuity at low levels of illumination and in scotopic conditions and found that beyond 10° there is a decrement in acuity which increases linearly with angular distance from the fovea. They noted a considerable variation among subjects.

Brown and Conklen (1954) examined further the effect of exposure times varied from 0.51 sec. to 16.00 sec. and velocities of 1.61 min.

of arc/sec. to 27.37 min. of arc/sec. The most marked rate of improvement was shown to occur up to 4 sec. exposure; an improvement of some 15 times compared to 0.5 secs. exposure.

Smith and Gulick (1956) in studies of perception of movement concluded that within the limits of their particular apparatus the contours of a moving stimulus can be perceived provided time of exposure increases linearly with the velocity of movement.

Gibson (1958) in a general survey has shown errors in all the earlier work caused by having static visible edges to the fields of view used, a situation which is unreal and which actually increases ability to discern the different types of movement examined.

More recent studies by Gemelli (1958) on the visual perception of movement have indicated that objects moving from the left to the right appear faster than right to left, that downward movements appear faster than upward, that vertical movements appear faster than horizontal, and that darts or aircraft shapes appear faster than discs or polygons.

De Silva (1929) in investigations of real and apparent movement noted that at 3° /sec. the object had distinct contour, at 10° /sec. it was slightly blurred, at $14-20^{\circ}$ /sec. it had an after-glow, at $21-58^{\circ}$ /sec. an impression of light rolling up at the end was noted, at $58-116^{\circ}$ /sec. the object filled the whole field with a vibratory movement, and at 116° /sec. the object appeared stationary. He was not studying visual acuity but the

nature of phenomenal movement.

Low (1947b) investigated simple form acuity with a perimeter which moved test objects towards or away from the line of sight at a rate of $15^{\circ}/\text{sec}$. and found that the movement halved acuity in the regions $30-45^{\circ}$ from the fovea and at $45-60^{\circ}$ acuity was unmeasurable in 72% of his subjects. He also reported on peripheral visual acuity under photopic conditions (1943) under scotopic conditions (1946 a, b, c) and the effects of training (1946), and flash presentation (1947).

The Experiments on Dynamic Visual Acuity.

The research programme carried out by Ludvigh (1947-57) is the only large scale investigation of the effects of movement of the object viewed on the ability to discriminate detail within that object. He has shown that there is a progressive decrease in visual acuity as target velocity increases. Using large numbers of subjects Ludvigh and Miller have also demonstrated that the possession of normal visual acuity as measured by the Snellen method or other static display methods gives no indication of the ability of the subject to discriminate detail in moving objects. There was found to be very large differences in the amount of deterioration experienced by different individuals as target angular velocity increased.

In the earlier experiments the subjects viewed the objects through rotating prisms of various strengths thus producing apparent movement of the object in a circular path in the

vertical plane, the orientation of the test object remaining constant. Later experiments were conducted by monocularly viewing via a front silvered rotating mirror a test object for 0.4 secs. Visual acuity with movements of the object in the horizontal plane and also to a smaller extent in the vertical plane was examined.

The authors have used the term Dynamic Visual Acuity to describe this human visual capability and have established a formula to describe this; $Y = a + bx^3$, where 'Y' is the minimum resolvable detail, 'a' is a parameter of 'static' visual acuity in minutes of arc with 0.2 seconds available for attaining fixation and 0.2 seconds for further observation, 'b' is a measure of this 'dynamic' acuity and 'x' is the angular velocity of the object. The visual acuity decrement in his experiments has been shown to be related most accurately to the cube of the angular velocity. Learning plays an important part in these experiments and was found to be substantial at high angular velocities and relatively slight at low angular velocities. The variations found among subjects is thought to be related to the efficiency of the visual and oculomotor system in that foveal vision is not attained and there may also be a movement of the image of the object across the retina. The diminution in acuity with increasing angular velocity is greater than would be expected from extra foveal perception alone. The improvement shown by increasing the illumination far beyond the 30 foot

candles, which gives 90°/o optimum acuity extra-foveally for static targets, to 360 foot candles to give 90°/o optimum acuity for moving targets does indicate that image movement is taking place.

A recent study by Van der Brink (1957) on retinal summation and the visibility of moving objects with specific reference to the possibility of discriminating detail when the image of the object is moving over the retina is particularly relevant to the hypothesis of retinal image movement and its blurred perception.

The only other data pertinent to the visibility of moving objects located has been an article by Langmuir (1938) who as a result of a statement in the Illustrated London News (1.1.38) that the deer botfly could fly at 818 miles per hour showed that a speed of 13 m.p.h. was more probable if the insect was to be seen as an insect and that at 26 m.p.h. it was a mere blur.

Criticism of the dynamic visual acuity studies

The history of research into discrimination of detail in moving objects is in practice confined to the programme of Ludvigh and his associate. This large scale experimental study, of an important aspect of the physiology of vision has shown three important features. The first is the marked deterioration in visual acuity as the velocity of the object viewed increases, secondly it has shown that subjects who all

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have a visual acuity standard of 6/6 Snellen, or better, vary markedly in their ability to resolve detail in moving targets, and thirdly that an improvement in ability can frequently be produced by training.

Unreserved acceptance of these three factors would necessitate a more searching appraisal of medical examination, aircraft flight path parameters, and methods of selecting and training aircrew. The application to motor car driving and sporting activities is also potentially important. Such acceptance is not possible in view of the nature of the experiments.

The following description of the experimental apparatus and procedure is taken from Ludvigh, 1953a.

"The subject with head erect in a head rest and chin in a chin rest monocularly views a Landolt ring test object via a front surface mirror. The optical distance of the test object from the observer's eye is four meters and the illumination on the test object is approximately twenty-five foot-candles (Macbeth). An ample white cardboard background for the test object, one foot wide by two feet high, is provided. The reflection factor of the cardboard is approximately 85^o/o. The mirror is rotated, left to right, about a vertical axis by means of a specially constructed wheel and disc type of variable-speed drive which is designed to supply sufficient torque while main-

taining constant angular velocities. Flexible opaque material can be inserted in the mirror frame so as to cover all of the mirror except a selected vertical strip. By adjustment of this opaque material the duration of the exposure of the test object can be held constant while the rpm of the mirror and, therefore, the apparent angular velocity of the target is varied. A partially etched cover glass was mounted on one half of the anterior surface of the mirror nearest the observer. This substantially blurred the break in the test ring and at the same time did not completely obscure the target area.

"In the experiments the total duration of the observation was 0.4 seconds for all angular velocities. The test objects employed were Landolt rings of various sizes providing so-called "critical detail" at the nodal point of the tested eye. Each size Landolt ring could be rotated into any one of the usual eight positions."

On a basis of the total time of exposure to the moving target of 400 milliseconds Ludvigh has claimed to deprive the oculomotor system of its ability to ensure accurate fixation by exteroceptive feedback from the retina. It was assumed that the initial delay in moving the eyes subsequent to target entry into the field of view is 200 milliseconds and that a second movement of the eyes would require a subsequent 200 milliseconds (Ludvigh, 1955). Thus a corrective phase would not be

accomplished during the target presentation period.

Such temporal aspects do not accord with the findings in the experiments reported here in which eye latency has a range of 150-300 msec. and a mean of about 200 msec. The second or corrective eye movement during pursuit of the target, if required, occurs at varying intervals after the initiation of the first eye movement. These intervals are generally shorter than the latencies of the initial movement no doubt due to complete lack of conscious effort on the subject's part in this fixation reflex. Corrective eye movements can and do occur when exposure time is 400 msec. though such movements more often occur at after 400 msec. It will be shown that the incidence of corrective eye movement increases with increasing target velocity indicating that the initial saccadic movement of the eye is failing in accuracy to a greater extent as the demand for very rapid eye movement occurs. Ginsborg (1953) has shown that the accuracy of the first saccadic eye movement even between stationary points varies considerably in its accuracy as separation of the stationary points is increased. He has also shown the occurrence of corrective movements after a typical intersaccadic interval of time. (120-140msec.)

The results obtained by the American authors are considered to indicate the increasing failure of the initial eye movement to achieve foveal fixation on moving targets and not the ability of man to discriminate detail in moving objects.

The method of observation used, monocular, with the head steady in a chin rest, viewing via a rotating mirror a target which moves over an arc ranging from 8° to 68° appears to neglect the normal adverse movement combination by eyes, head and trunk of the human. This normal behaviour is exemplified in the head and eye movements of spectators at tennis matches. The very presence of areas in the cortex adjacent to the frontal and occipital areas concerned with vision which when stimulated produce such adverse movements indicate the basic nature of such behaviour.

It is not clear in the description of the rotating mirror apparatus whether the eye is expected to move from the central resting position or whether the eye is fixating the target entry point and deviated in the horizontal plane towards that entry point. If the eye is at a central location then the demand at the higher target velocities for eye movements in the horizontal plane during pursuit would require to exceed the field of fixation of the eye which only extends to 50° in either direction on the average.

If on the other hand the eye is deviated towards the point of target entry equal to 50° of the arc through which the target will travel there is an unnatural demand put upon eye muscles. Their reaction to target movement will be complicated with regard to the abrupt reversal of synergistic actions.

It will be shown that the use of the head-eye movement

complex improves significantly the ability of subjects to discriminate detail in moving objects. This pursuit movement which is considered by most writers to be a voluntary action has factors which indicate that its nature may well be reflex or at present in the intangible stratum between reflex and voluntary response.

An investigation of the probable relative velocities of objects which when recognised provide useful or usable information to pilots and other aircrew members shows that it is not recognition of detail in moving objects that is the requirement but recognition of one target or complex navigation pinpoint complex from other relatively similar complexes of natural or man made terrestrial features. These features do not exhibit either linear angular velocities or true horizontal movements but are non linear and generally have downward oblique movement. The extrapolation from the above experiments to the inflight environment is not entirely acceptable.

The term Dynamic Visual Acuity implies that when the eye is regarding a static point the situation is non-dynamic. The research on eye movements while the eye fixates a static object have shown the dynamic nature of such fixations and reason for such minor movements. Specifically these movements have been shown by Adler and Fleigelman (1934), Riggs and Ratliff (1951), Ditchburn and Ginsborg (1952), Ratliff, Riggs, Cornsweet and Cornsweet (1953). The absence of such movements results in diminution of ability to see the object (Ditchburn 1952, Riggs 1958).

Section 3

Outline of the problems and the experimental approach

In the visual tracking of moving objects, if recognition is to be achieved or discrimination of detail attained it is evident that certain conditions must be fulfilled. The angular velocity of the object relative to the eye must be to some critical extent the same as the rotational velocity of the eyeball. The image of the object, if the critical detail is small, must be on or near the fovea of the retina. The image of the object must be on this foveal or parafoveal area for a sufficient duration of time.

Failure to achieve discrimination can therefore be the result of a differential velocity existing between the target movement and eye movement which will be called a velocity error (Part 7). Secondly, it can be the result of an extrafoveal fixation with no velocity error which will be termed position error (Part 7). Thirdly, it can be the result of insufficient exposure time and the concurrent lack of light energy to produce a differentiated image. Fourthly and finally, failure may be due to a combination of these factors.

Whatever the immediate cause of the failure to achieve satisfactory fixation on a moving object there is the greater problem of deciding which part of the visual system (Part 2) was inadequate in the voluntary or reflex task. There has to be considered the adequacy of the retinal organisation and its

receptor fields, the transmission to the cortex from the retina, interpretation of afferent nervous discharges from the retina, the formation of efferent nervous discharges to the muscles, and finally the adequacy of eye muscle response to the efferent volleys.

The whole problem is further complicated by the findings of Ludvigh and Ludvigh and Miller, confirmed in this study, that the possession of a normal visual acuity standard of 6/6 Snellen and freedom from obvious visual or oculomotor defects in no way indicates a subject's ability. The variation among subjects is significant. Three possibilities exist, 1). Some subjects are capable of tolerating greater velocity or position errors than others, 2). The oculomotor system is more efficient in some than others, 3). The relevant muscular system is more adequate in some subjects than it is in others.

Experimentally it was feasible to determine the position errors (Part 8) which can be tolerated without loss of visual acuity and also to determine the degree of loss sustained as the image is displaced from central fovea into the parafovea and near periphery. It was possible to compare the responses of subjects whose ability in discriminating detail was better than others.

It was also possible to examine the velocity error (Part 8) tolerated by subjects and associate velocity error tolerance with the ability to discriminate detail in moving targets. The

simultaneous presentation of position error and velocity error was finally examined and relevant associations made.

The exposure time to view satisfactorily a static object, presented at the fixation point, with no position or velocity error was examined and was found to be adequate with exposure times of 1 msec., the minimum available.

These four experiments indicated the great accuracy demanded of eye movements if object recognition was to be achieved. They showed only minor variations among subjects. These minor variations were not considered adequate to explain the marked difference in individual subjects' ability to discriminate detail in moving objects.

Variations within the retinae of the subjects and in the receptive fields are not readily amenable to experimental procedures. However, it seemed possible that by varying the target entry point while retaining the fixation point, the receptive fields (Part 2 and 5) of varying dimensions which exist in the human eye and which enlarge as the distance from the fovea increases, could be serially stimulated in differing patterns. Thus, by having the target enter the field of view at the fixation point, at 5° , 10° and 15° of arc preceding the fixation point the stimulation would vary, during the period before the eyes moved. At 0° it would change from theoretically optimum at the fovea to poor in the periphery, from poor via optimum to poor at 15° and with intervening grades at 5° and

10°. It seems reasonable to suppose where the greatest number of smaller receptive fields are stimulated the response in terms of eye movement pattern should be potentially more accurate. This accuracy would be shown by the results in terms of discriminatory ability and should occur at 5° and 10° fixation points.

Variations in the neurophysiological network subserving the oculomotor system are also resistant to investigation (Part 5). Time for completion of the afferent-efferent loop measured from stimulus to eye movement reflects some of the activity. Eye movements recordings permitted these to be measured. The types of eye movement could also be noted but only relatively crude methods can be used when large eye movements are to be examined. The eye movement recordings yielded little to aid differentiation between subjects but gave positive and original information on the adequacy of the initial eye movement and gave some entirely new information on the fixation reflex.

Muscular response to efferent volleys from the eye muscle motor system may also be examined indirectly by observing the adequacy of initial eye movements at the previously described 0, 5, 10 and 15° target entry points (Part 5). At 0° the target enters at the fixation point and moves away. The eye movement has to have an overtaking action which is shown by the extremely rapid and powerful displacement of the eyeball. At 15° a gentle movement to attain target velocity only is required. As extrafoveal initial stimulation is the more

normal event in our visual world it would not be surprising if performance was improved.

The effect of increasing the visual pursuit time was examined (Part 4). Increasing the viewing time would permit the eyes to carry out one or more corrective movements to attain a satisfactory fixation and recognition of the gap in the Landolt ring targets.

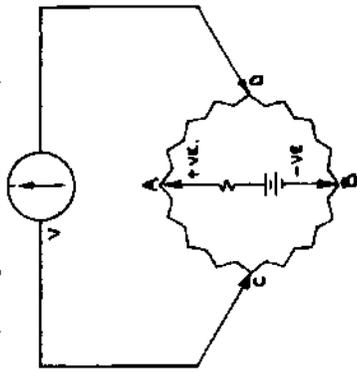
In viewing moving objects, to use the head and body as part of the oculomotor system in the human is natural. The integration of head and eye movement and the activity in muscle in the neck responsible for head movements were examined (Part 9). The combined effort was expected to add further to man's ability to discriminate detail in moving objects (Part 4).

In addition to the horizontal eye movements studied some investigations were carried out of eye movement in the vertical plane. Owing to apparatus limitations the subjects had to lie down on their side. Only limited studies of ability were made owing to an illusion produced by conflict between retinal and proprioceptive position sense organs. The illusion is described (Part 6).

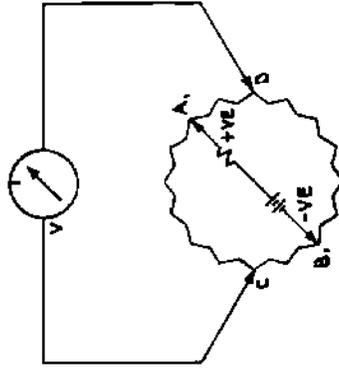
Some observations were made on the presence or absence of position sense of the eyes.

Finally an experiment was conducted to ascertain the moment of perception and its relationship to the eye movement patterns produced during the visual pursuits (Part 11).

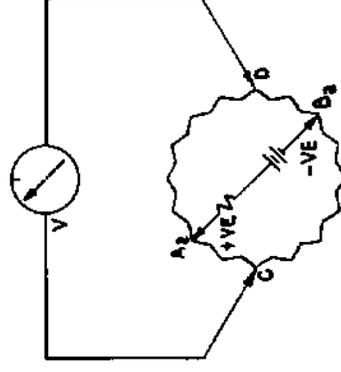
THE CORNEA - RETINAL POTENTIAL - A SIMPLE CIRCUIT ANALOGUE
 EYEBALL - POTENTIAL CHANGE WITH ROTATION.



STATE 1.

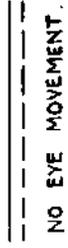


STATE 2.



STATE 3.

PEN RECORDING VOLTAGE CHANGE.
 — D.C. AMPLIFYING SYSTEM
 - - - CAPACITANCE COUPLED AMPLIFYING SYSTEM.



NO EYE MOVEMENT.



MOVEMENT FROM STATE 1 TO 2.



MOVEMENT FROM STATE 1 TO 3.

CHANGES IN THE EYE POTENTIAL AS ROTATION TAKES PLACE IS RECORDED AS A POTENTIAL DIFFERENCE BETWEEN THE STATIC ELECTRODES AT C & D. THE EXTENT OF THE ANGULAR ROTATION & RATE OF ROTATION ARE MEASURED BY VOLTAGE DIFFERENCE & RATE OF CHANGE OF VOLTAGE.

Fig. 2

Flights were conducted at high speed and low level to assess the practical significance of the programme (Part 12).

The cornea-retinal potential and eye movements

All eye movement recording was carried out by this method in this series of experiments.

There exists between the cornea and the retina a potential difference of several millivolts. To achieve pick-up of this potential difference surface electrodes can be positioned at either side of the eye or eyes to record changes caused by eye movements in the horizontal plane and can be placed above and below the eye to record eye movements in the vertical plane. In practice, the changes in the potential recorded at the outer canthi are about 20 microvolts per degree of eye movement, the usual range being 10-30 microvolts. These potentials are amplified and are used to drive conventional pen recorders.

The changes recorded at the outer canthi can be measured and information thereby obtained of total deflection, eye velocity, changes in eye velocity and general patterns of eye movement. Fig. 2 is a diagrammatic representation of the system and its basic principles.

The main difficulty experienced is the elimination of other potentials picked up by the subject or by leads to the amplifier. These stray potentials are seen as 'noise' on the recordings which precluded scoring of the recordings obtained. Elimination

of this 'noise' was frequently obtained by 'earthing' the subject, but on many occasions the experiment planned had to be abandoned because of failure to locate or eliminate the source of the 'noise'. Most of the 'noise' was of 50 c.p.s. which undoubtedly had its origin in the general electrical installations throughout the laboratory.

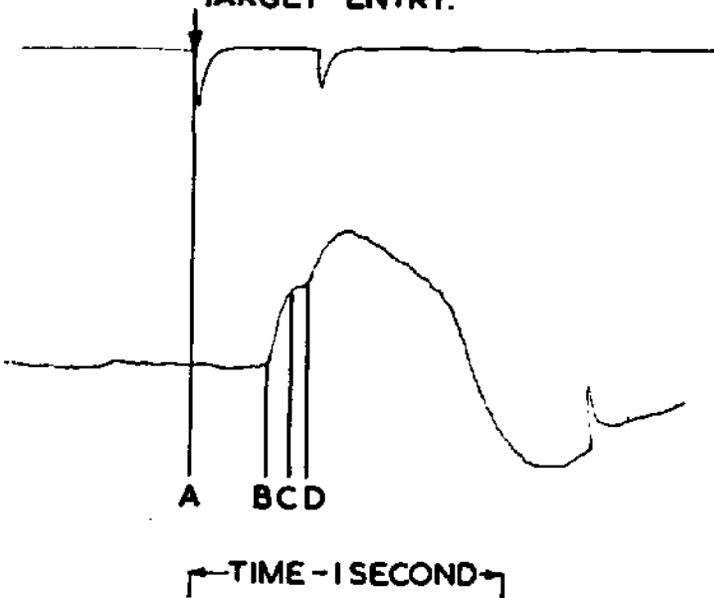
Eye movement recording has been carried out by various means since the original photographic methods of Dodge (1903) and Barnes (1905). The two principal methods are limited, some in extent and some in accuracy.

These methods which involve photography of the eye, of a corneal reflection, of corneal lens, of variously introduced foreign bodies on to the conjunctiva at the cornea scleral junction, of blood vessels of the eye, are all limited to small movements of the eye. The cornea-retinal potential method is unlimited in extent but is limited in accuracy and care has to be taken to ensure that such occurrences as blinks are not misinterpreted as eye movements. All the methods have been reviewed by Duke Elder (1944b), Hartridge and Thomson (1948) and Carmichael and Dearborn (1948), the reliability of photographic methods by Eurich (1933) and Stromberg (1942), the electrical (cornea-retinal potential) method has been reviewed by Marg (1951). A comparison of the methods has been carried out by Hoffman et al (1939). The general trend is now to use photographic and reflection

**EYE MOVEMENT RECORD
(CORNEO-RETINAL POTENTIAL)**

TARGET VELOCITY 100°/SEC

TARGET ENTRY.



CALIBRATION

5°

10°

15°

50µV

100µV

200µV

— T.C. 0.3 SECONDS

A-B EYE MOVEMENT LATENCY - 242MSEC.
 B-D INTERSACCADIC INTERVAL - 127MSEC.
 C-D STEADY STATE - 50MSEC.

GAIN 7

H F CUT 15

Fig. 3.

THE INTERPRETATION OF THE RECORDS OF CHANGE IN CORNEO-RETINAL POTENTIAL DURING EYE MOVEMENTS.

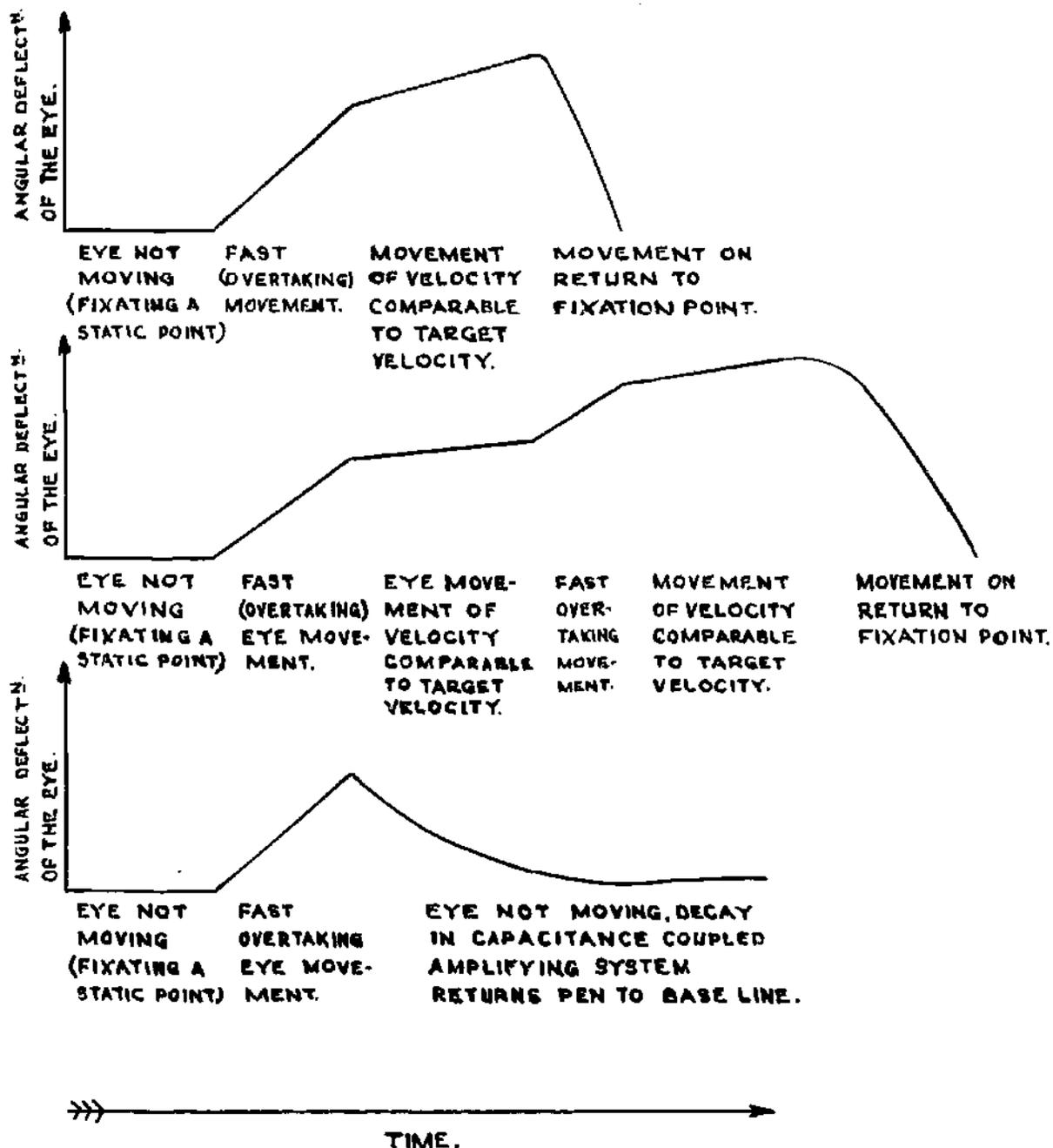


Fig. 4.

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methods for small movements and the investigation of the inevitable minute movements of the eyes during steady fixation (Ginsborg 1953, Ditchburn and Ginsborg 1952, 1953, Ratliff 1953, Westheimer 1954b). The cornea-retinal potential is used for examining general trends in eye movement patterns and in this field it is a simple and inexpensive tool which can operate with conventional pen recording apparatus. The type of recording obtainable and its interpretation are shown in Figs 3 and 4.

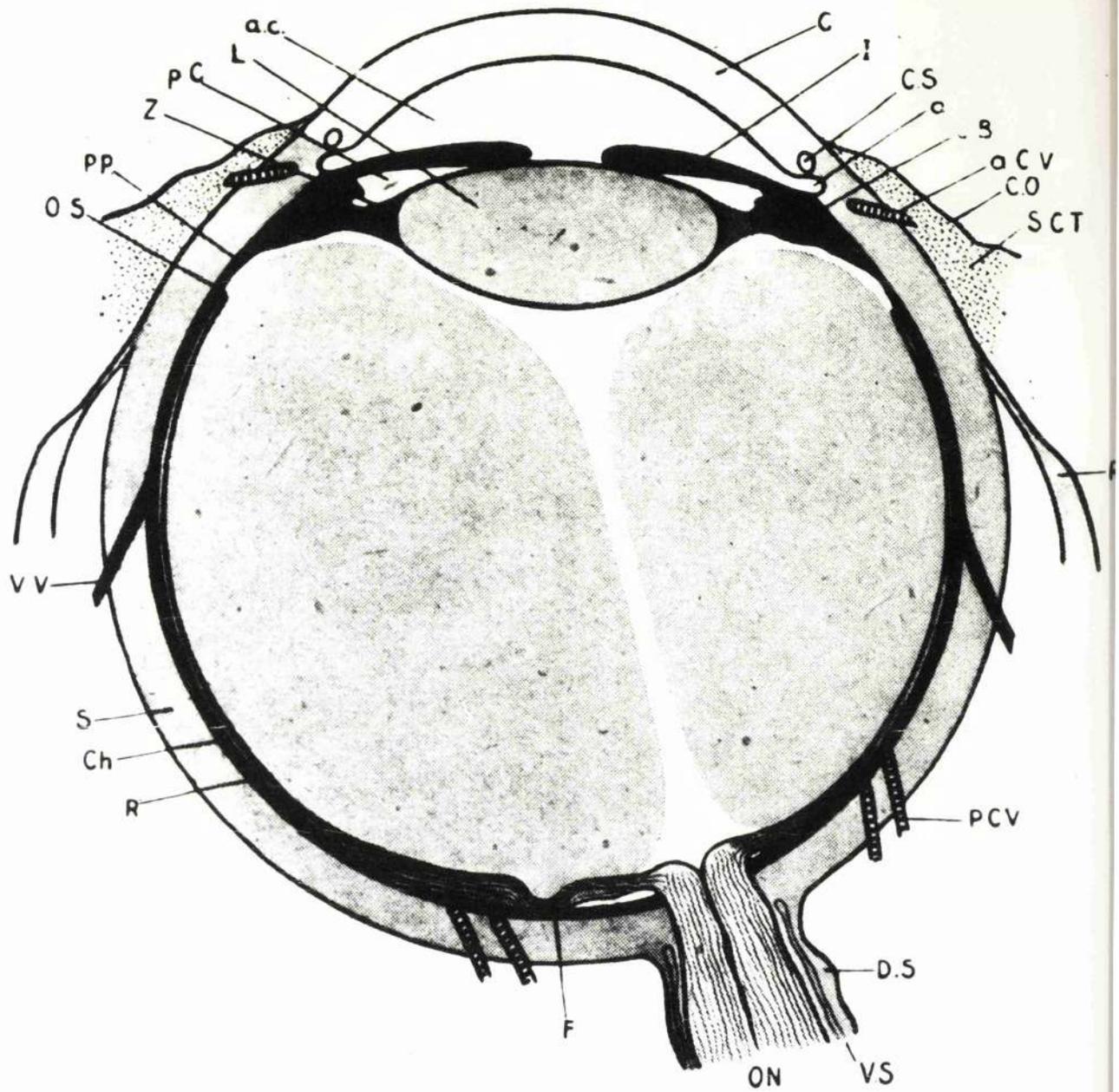


DIAGRAM OF A LONGITUDINAL SECTION OF THE EYEBALL.

- | | |
|---------------------------------|----------------------------------|
| a. Angle of anterior chamber. | O.N. Optic nerve. |
| a.c. Anterior chamber. | O.S. Ora serrata. |
| a.C.V. Anterior ciliary vessel. | P.C. Posterior chamber. |
| C. Cornea. | P.C.V. Posterior ciliary vessel. |
| C.B. Ciliary body. | P.P. Pars plana. |
| Ch. Choroid. | R. Retina. |
| C.O. Ocular conjunctiva. | R.M. Rectus muscle. |
| C.S. Canal of Schlemm. | S. Sclera. |
| D.S. Dural sheath. | S.C.T. Subconjunctival tissue. |
| F. Fovea. | V.S. Vaginal sheath. |
| I. Iris. | V.V. Vortex vein. |
| L. Lens. | Z. Zonule. |

Fig. No. 5

From Duke Elder Textbook of Ophthalmology

PART 2

Anatomy and Physiology

Section 1

The anatomy of the eye

The optical apparatus composing the human eye consists of four major parts, the cornea, the iris, the lens, and a dark chamber (Fig. 5). Its function is to produce a detailed image on the light sensitive nervous layer called the retina. From this structure nervous impulses pass centrally to the cerebral calcarine cortex and thence to consciousness for integration into the concept of space and spatial orientation.

The eyeball is not spherical but is an oblate spheroid being somewhat flattened from above down. Its average diameter is 24.15 mm. in sagittal section, 24.13 mm. in traverse, and 23.48 mm. in vertical section. In circumference it is about 73 mm. Its weight is about 7 grammes and its volume is 6.5 cc.

The eye is surrounded by a fibrous tunic, the anterior 1/6th of which is transparent and is called the cornea and the posterior 5/6th which is white and opaque is called the sclera. The cornea has a greater curvature than the sclera and a shallow groove is present at the cornea-scleral junction. The optic nerve emerges from a point 3 mm. nasal to and about 1 mm. below the posterior pole of the eyeball. Internal to the sclera is a nutrient or vascular layer, which anteriorly forms the greater portion of the iris. Inside the vascular layer is the nervous

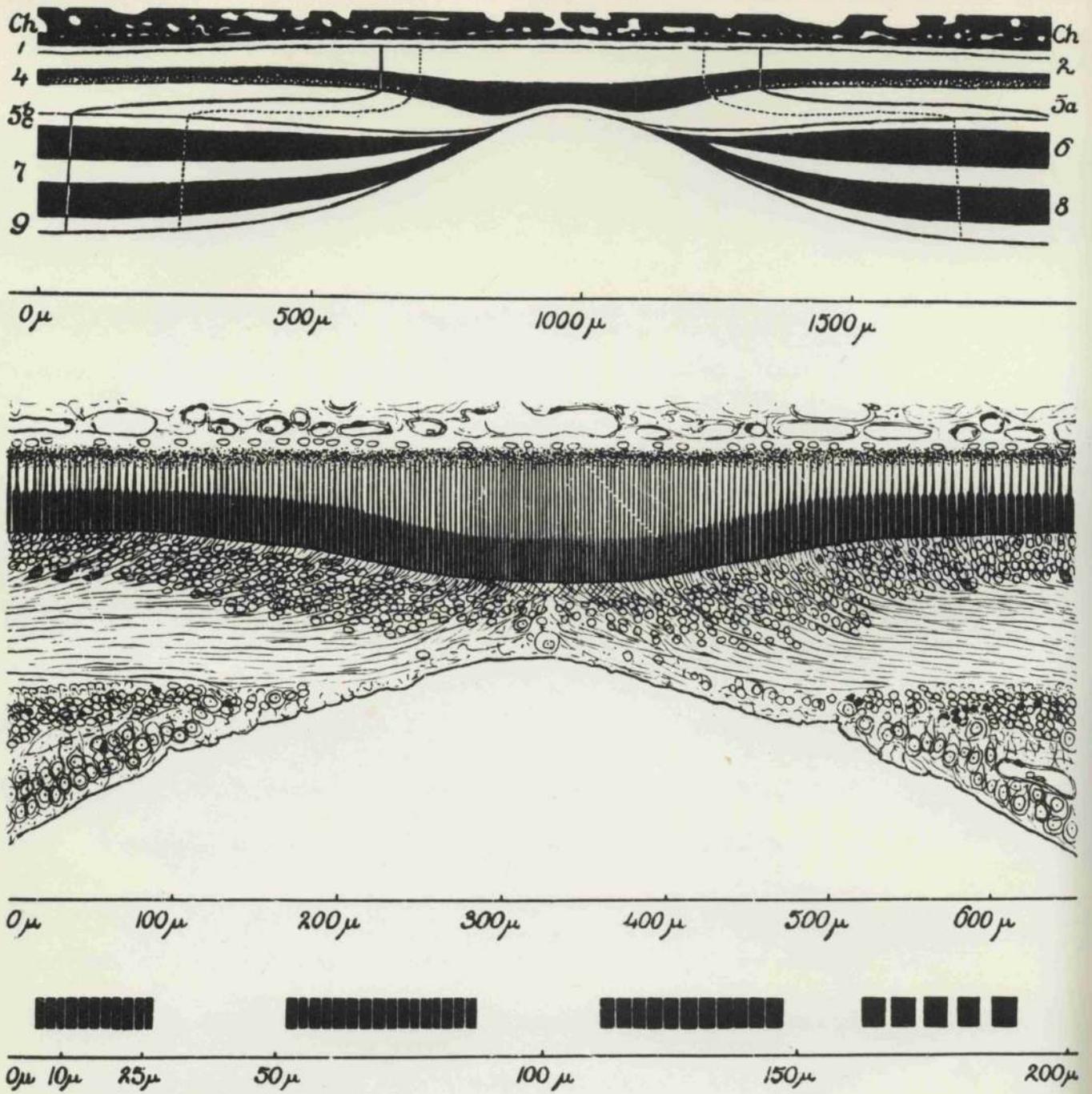
layer or tunic which in the posterior part of the eye forms the retina and in the anterior part of it lines the iris and ciliary body.

The fibrous tunics and vascular tunics are united anteriorly at the junction of the cornea and sclera and posteriorly at the exit of the optic nerve. Anteriorly the space between them forms the anterior chamber and elsewhere it is occupied by the nerves and by the vascular system. The pupil is the rounded opening in the iris and is of changeable diameter while retaining its circular form. Less anteriorly the nutrient layer forms the ciliary body which in addition to its nutrient function in supplying intra-ocular fluid has muscles which adjust the lens.

The lens is supported by a suspension ligament, the Zonule, which is found immediately behind the iris. There is a small space between iris and zonule called the posterior chamber. Anterior and posterior chambers are filled with a clear fluid called the aqueous humour. The rest of the cavity of the eyeball behind the lens is filled with a transparent gel, the vitreous body.

The eyeballs are contained in the bony orbits of the skull where the extrinsic eye muscles and the periorbital fat form controlling and supporting structures.

The sentient layer of the human eye is the retina. It is an outlying part of the central nervous system. This structure has a photosensitive layer of cells, and light from the world



Central fovea of the adult human eye.

Upper sketch shows, semidiagrammatically, changes in the relative thickness and position of the retinal layers brought about by the foveal excavation. It also shows peculiar topical functional relationships of the photoreceptor layer (2) and the deeper layers (4-9) caused by the latter's displacement owing to the formation of the fovea: the broken lines encompass the rodless territory of the bacillary layer and the portion of the foveal pit functionally related to it; the solid lines mark the territory of the thickened portion of the bacillary layer, the "outer fovea," and the extent of the inner layers functionally related to it; white dots in layer 4 indicate rod nuclei; (Ch) portion of the choroid membrane.

Middle drawing represents the outer fovea filled with the thin, elongated cones. The most centrally located rods, in the bacillary layer, correspond with the most central rod nuclei in the outer nuclear layer (shaded). Note the thinning of the mentioned layer and the practical disappearance of the remaining inner layers in the foveal center. Müller's nuclei in the inner nuclear layer given in black.

Lower sketch represents samples from four localities showing relative size and number of cones (inner segments), beginning from the left: center of the outer fovea, slope of the same, edge of the same, and periphery of the central area, or region III.

Upper sketch reproduced at 80 X, middle at 250 X, lower at 700 X magnification. The actual sizes given in $\mu\mu$ on the accompanying scales.

Fig. No. 6

From the 'Retina' by Polyak

around is focussed upon it by the optical system. Walls (1943) has likened the retina to a 'transparent carpet lying upside down on the floor of a well lighted room. The visual cell population then compares with the pile of the carpet. Just as the base cloth of the carpet exists only to support the pile so also the maze of the nerve fibres making up the body of the retina exist only to mediate between the visual cells and the cable to the brain, the optic nerve'.

The complexity of the retina is described in great detail by Polyak (1941) in his massive and elaborate study. The basic features for descriptive purposes have largely been taken from that study.

The cellular structure varies from the central area, the fovea and foveola, to the extreme periphery. The structure varying in such a way that it demonstrates the anatomical basis for the physiological requirement to bring objects of interest to the foveal area where visual cells are the most abundant and fine, and where transmitted light meets the least structural adsorption before reaching the photosensitive cells (Fig. 6).

There are two photosensitive cell systems in the retina, the rod and the cone. They are entirely separate in the rod free foveolar area but are potentially synaptically related in the other regions and undoubtedly share common ganglion cells and therefore optic nerve fibres. The generally accepted hypothesis that the cone system is specialised for use in photopic

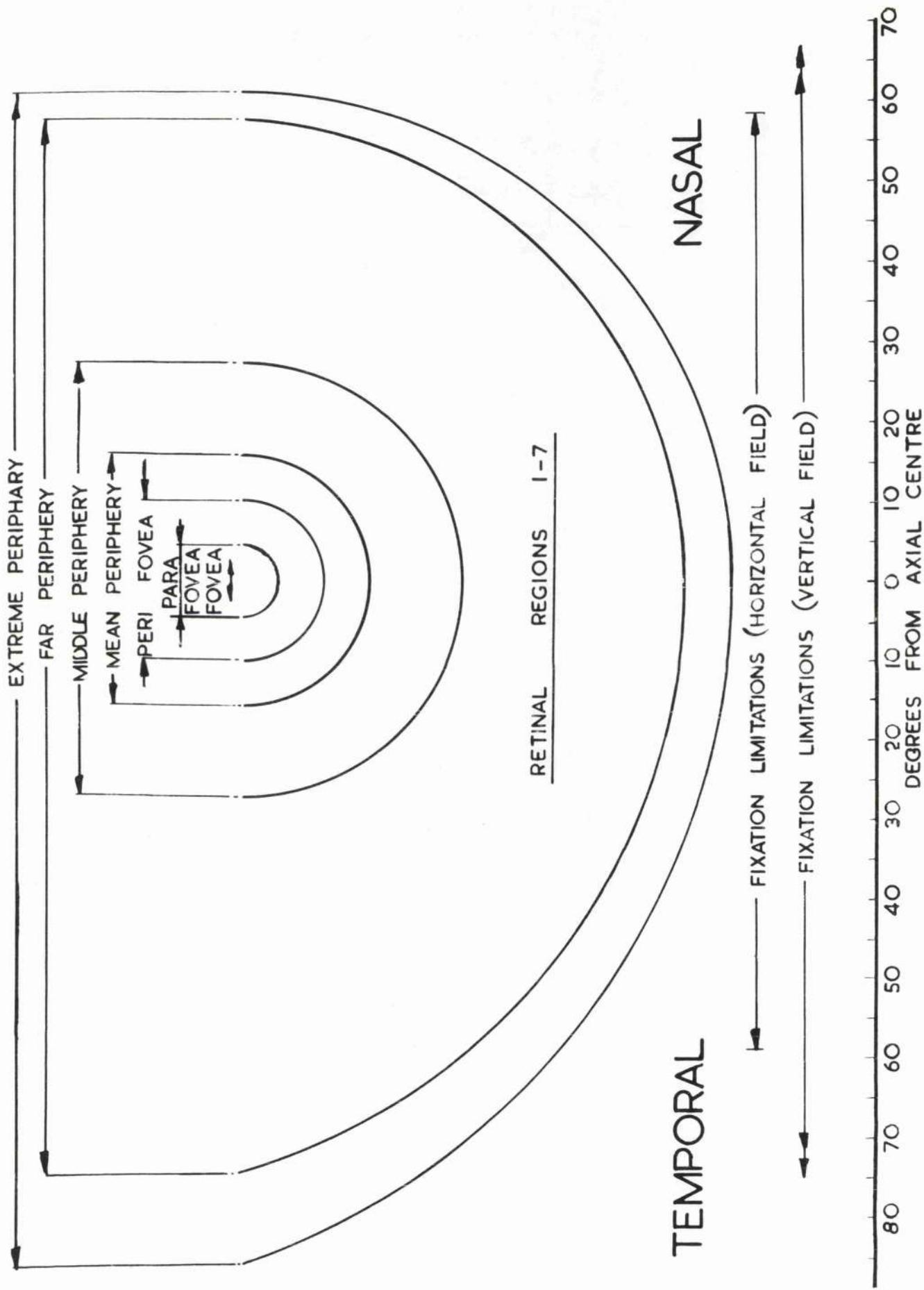


Fig. 7

conditions and the rods in scotopic only is not clear. There is no proof yet that the rods are inactive in photopic conditions.

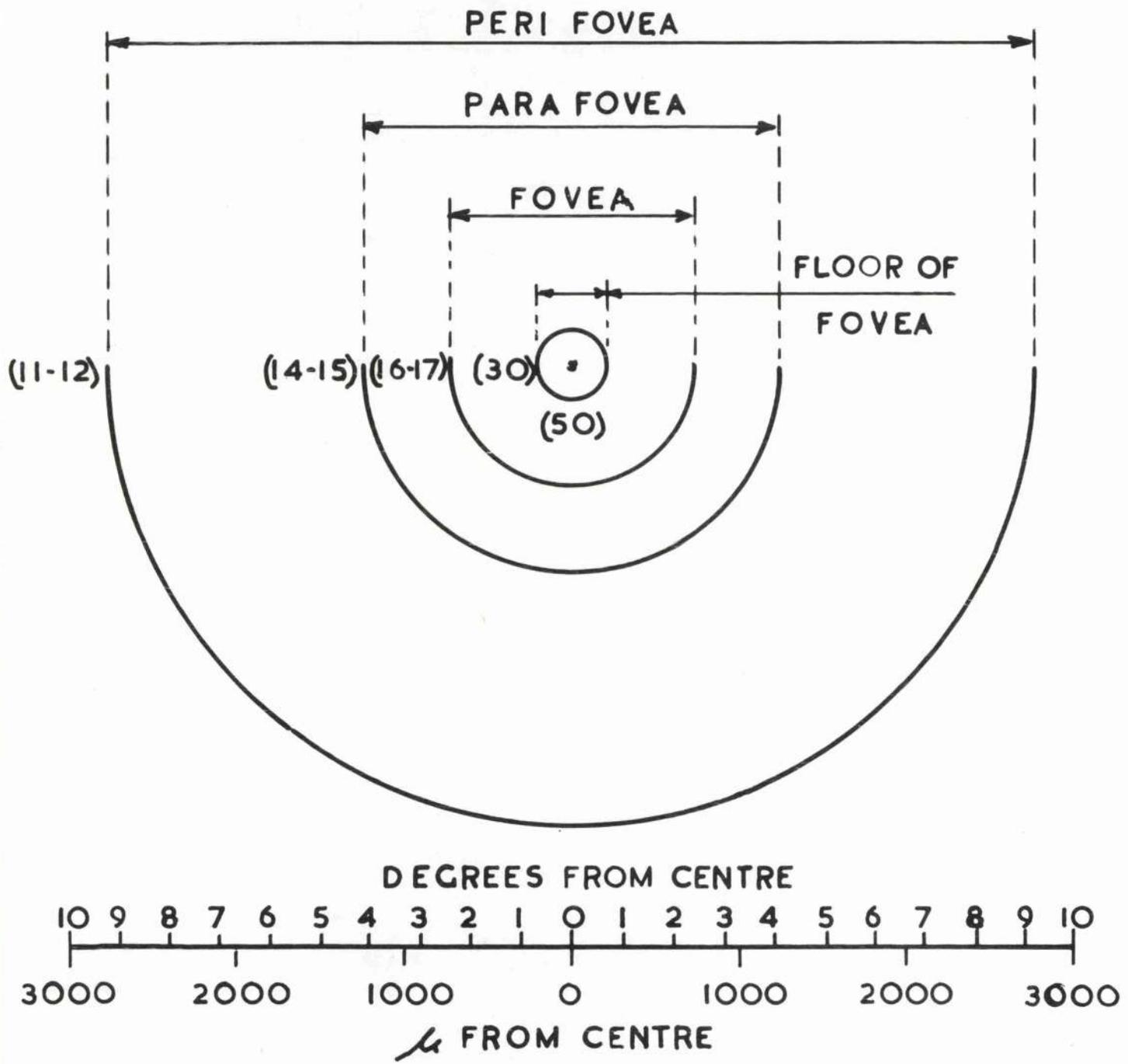
Histological differences within the retina from the central foveolar region to the extreme periphery, the ora serrata, make it possible to subdivide this light sensitive structure into seven concentric areas (Fig. 7). With the exception of the axial centre, where definite margins or boundaries are noted, there are no sudden or abrupt changes from one area to another but rather a gradual change in histological structures.

These subdivisions are :

1. Central Fovea
2. Parafoveal Region
3. Perifoveal Region
4. Near Periphery
5. Middle Periphery
6. Far Periphery
7. Extreme Periphery

The first three form the central area and measure some six millimetres across. The remaining four areas form the extra areal periphery.

The central fovea is a small pit shaped depression on the vitreal surface of the retina. The width from the edge to edge is 1500μ corresponding to $2^{\circ} 30'$ of arc on either side of the central point. The floor of the depression, the foveola, measures 400μ in diameter and corresponds to $1^{\circ} 20'$



RETINAL REGIONS N^o. 1; 2; & 3.
 (BRACKETED NUMBERS INDICATE)
 CONES PER 100 μ .

Fig. 8.

or 40' arc on each side of the central point. It is in this region that the cone photoreceptors find not only their densest population, 50 cones for 100 μ in line, but are also the longest, up to 70 μ , and finest, 1 μ at the tip and 1.5 μ at their base. It is the area where least obstruction to light stimulus occurs. (Fig. 6). This foveola is rod photoreceptors free. The cone population of this foveolar area is estimated at 25,000. In the central part of this foveolar area there is an area 100 μ in diameter corresponding to 20' of arc in which there are estimated to be 2,500 of the finest cones.

Outside this foveolar region, the retina rapidly thickens, the cones become larger, 1.3 μ at the tips and 2.3 μ at their bases, and the cone population diminishes to some 35 per 100 μ in line. At 50' of arc from the central point rods begin to appear. The foveal area is often inaccurately described as the rod free area, only the foveolar area is rod free. (Fig. 8).

The parafovea region II extends to 1250 μ from the central point, an arc of approximately 4°. The cone population diminishes to 15 per 100 μ and the cones measure in their inner segments 4-5 μ and at their bases 1.5 - 2 μ . On the average there is one rod between any two cones. (Fig. 8).

The parafovea region III extends to 3750 μ distant from foveal centre, an arc of approximately 9°. The cone population has diminished to 12 per 100 μ and each cone is separated from any other by an average of 2 rods. (Fig. 8).

The near periphery Region IV extends to 4250μ from the foveal central point, an arc of some 14° , this region is about 1500μ broad. The cones are becoming larger, more dispersed with 2 or 3 rods between cones. The cone population diminishes to 9-10 per 100μ . The rods also show enlargement compared to the more central regions, enlarging to $1.2 - 2\mu$ in diameter from 1.5μ .

In the three remaining peripheral regions structure coarsening continues, cones become less numerous, the number of rods between cones increases to three or more.

In addition to having areal divisions the retina proper can be, when regarded in vertical sections, divided into ten layers.

The cones and rods are found in the second layer and extend downwards to layer four where the cell bodies are found. The efferent fibres from the cell bodies pass through layer five to form synapses with bipolar and horizontal cells in layer six. In this layer a great variety of bipolar cells are found which subserve varying numbers of rods and cones. Horizontal cells and amacrine cells are also found in layer six and freely communicate with one another to permit a lateral spread of nervous activity in the retina. The expansions of these bipolar, horizontal and amacrine cells pass through layer seven in which is found the dendritic processes of the ganglion cells of layer eight. The ganglion cells, arborise with a varying number of bipolar and other cells and further reduce the number of channels

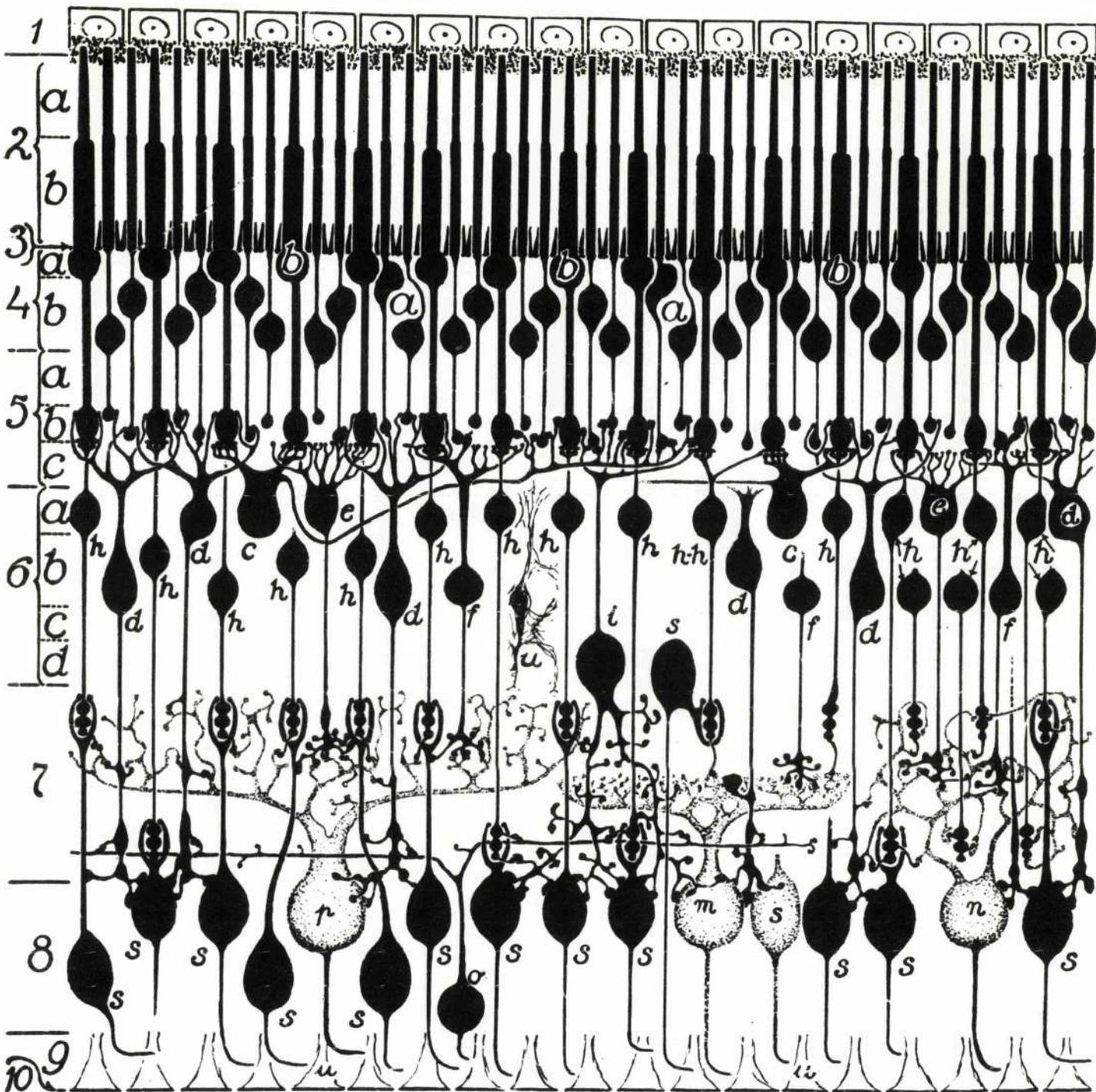
through which afferent impulses from the rods and cones may travel. The axons of the ganglion cells converge and form the optic nerve.

Any message originating in the rods and cones is thus twice elaborated, firstly by the bipolar cell system and secondly by the ganglion cell system. The foveal area which apparently can transmit through to the optic nerve in a one to one basis of cone, bipolar cell, ganglion cell system is still, however, capable of being affected by adjacent cells at the level of layer six.

The coarsening of retinal structure from fovea to periphery, the diminution in the number of bipolar cells, and the diminution in the number of ganglion cells explains known deterioration of visual acuity in the periphery.

In the periphery the more extensive communication from photoreceptors via bipolar and horizontal cells to greatly enlarged ganglion cells permit more ready summation of weak stimuli. They function well in movement perception. Movement perception in this area is attention demanding and is functionally a warning device of visual events occurring outside the field of discrete viewing.

In the preceding descriptions of retinal regions and retinal layers the following cell types have been noted. Cones, rods horizontal, bipolars, amacrine, ganglion and those of Muller. There is a considerable synaptical relationship within the



Scheme of the structures of the primate retina as revealed by the method of Golgi.

The designation of the layers and the zones: (1) pigment layer; (2-a) outer zone; (2-b) inner zone of the rod and cone layer; (3) outer limiting membrane; (4-a) outer zone; (4-b) inner zone of the outer nuclear layer; (5-a) outer zone; (5-b) middle zone; (5-c) inner zone of the outer plexiform layer; (6) inner nuclear layer with its four zones; (7) inner plexiform layer; (8) layer of the ganglion cells; (9) layer of the optic nerve fibers; (10) inner limiting membrane.

The designation of the nerve cells: (a) rods; (b) cones; (c) horizontal cells; (d, e, f, h) bipolar cells; (i, l) so-called "amacrine cells"; (m, n, o, p, s) ganglion cells; (u) "radial fibers" of Müller.

In this scheme the nervous elements are reduced to their essentials, with, however, the characteristic features of each variety preserved—the location of the bodies, the size, the shape, and the spreading of the dendrites and of the axis cylinders—and with the synaptical contacts presented accurately. (Cf. Figs. 37 and 96.)

Fig. No. 9

From the 'Retina' by Polyak

retina which involves cones and rods and which varies in differing areas of the retina and within the different retinal layers.

This arrangement of great complexity, which is as yet not fully understood is seen in Fig. 9 from Polyak's work.

The human retina is rod dominated histologically, the cones accounting for approximately 5% of all the light sensitive cells. The total number of cones is between 6.3 and 6.8 million and the number of rods approximately 110-125 million. As the optic nerve contains an estimated 800,000 - 1,100,000 fibres there must be on average about 100 receptors, rods or cones, subserved by each fibre.

Receptor Fields

Each area containing all the receptors subserved by an optic nerve fibre is called a receptor field. These areas vary in size from the fovea to the retinal periphery, being smallest in the foveolar area. These receptor fields overlap, thus any one rod or cone can be contained within two or more fields. The presence of these fields accounts for the great diminution in the number of optic nerve fibres compared to the number of photosensitive cells. Thus few or many cones or rods may have their discharges modified and subsequently amalgamated into one optic nerve fibre. This, however, does not imply gross degradation in the output because of the overlapping of such fields.

Adrian (1931) was the first in association with Hoagland and Cattell, to define receptor fields in the skin of the frog and as a result of subsequent research it is now clear, as was realised by Adrian, that this overlapping feature is an essential and integral factor in the mechanism of discrimination by sensory systems whether they are touch sensitive, thermal sensitive or photo-sensitive. Visual perception is not a process analogous to photographic reproduction which is reliant upon fineness of grain in the photographic emulsion and the perfection of the lens system. Visual perception is a dynamic act, the dynamics of which are readily demonstrable by the continuous frequency variation in electrical discharge in the optic nerve fibres and by movements of the eye even during steady fixation. However, where fine discrimination is required the receptor fields in the foveal area are to some extent comparable to photographic emulsion grain fineness in that receptor fields are found with a cone to ganglion ratio of one to one.

That these fields have mutual interaction has been shown by Barlow (1953 a & b), in investigations of receptor fields in the frog's retina. He showed that a ring of inhibition existed around receptor fields and that illumination of this inhibited area, which itself does not respond by discharge, inhibits the response from the central area of the field. He suggests that this has a part to play in simultaneous contrast and exemplifies this suggestion by recalling that a white area looks brighter

when surrounded by a black area than when surrounded by grey. The stimulation by the grey inhibiting to an extent, the response to the white centre.

The size of receptor fields has been investigated in various animals, the conger eel in which fields of the order of 1 mm. in diameter were found by Adrian and Matthews (1927 a & b), the frog retina in which similar field sizes were found by Hartline (1940 a & c) and in the rabbit by Thomson (1953). Kuffler (1952) has found fields of up to four millimetres in diameter in the retina of the cat as have also Wirth and Zetterstrom (1954) when the search is undertaken in dark ambient illumination. Hartline (quoted by Granit 1955) has found both large and small receptor fields in the frog's eye and has shown a decrease by a factor of two in the size of these fields when stimulus intensities 100 to 1000 times threshold were used.

Kuffler (1952) also reports that receptor fields shrink with increasing light adaptation which accords with Craik and Vernon's (1941) findings that areas of summation shrink with light adaptation.

Studies of the discharges in optic nerve fibres - the axons of retinal ganglion cells have shown that the electrical discharges from receptor cells modified by the superimposed bipolars and ganglion cells are of three main varieties. There are those which respond to onset of illumination, those which respond to cessation of illumination and those which respond to

onset and cessation of illumination. They are known as on, off, and on-off fibres. On-off fibres are most numerous and there has been shown to be mutual antagonism between on and off elements.

The receptor fields of the retina thus contain two antagonistic systems which discharge, one to one set of illumination the other to cessation. The first point of confluence of on and off discharges is the bipolar cell and it is probably at that site (Granit 1955) that the antagonism is resolved before passing on to the ganglion layer. Kuffler (1952 and 1953) has shown the cat's retinal receptor fields to consist of an inner area which is 'on' in response, an intermediate zone which is 'on-off' in function and an outer zone which is 'off'. He also found the converse, receptor fields with 'off' in the central area, 'on-off' in the middle area, and 'on' in the outer area. By simultaneous stimulation of the 'on' and 'off' areas in the receptor field Kuffler showed that the stronger response will suppress the weaker, but that this stronger response will have been itself weakened. When both areas are equally strongly stimulated both 'on' and 'off' responses are weakened. It has also been reported by Kuffler and Barlow, quoted by Granit (1955), that with dark adaptation of the cat's eye, the whole receptive area is given over to the central response and that the field is no longer one of three zones as described above.

Barlow (1953b) found that 'off' units summate throughout the

field and are unaffected by light outside the field. In his discussion he points out that the 'off' response in the frog's retinal receptor fields probably supply the necessary sensory input to permit appreciation of the movement and position of the frog's prey, i.e. a moving fly, by leaving a trail of 'off' responses as the fly's image moves across the retina.

—EXTRINSIC MUSCLES OF
THE EYE FROM ABOVE.

1. Superior rectus.
2. Levator palpebrae superioris.
3. Medial rectus.
4. Lateral rectus.
5. Superior oblique.
6. Reflected tendon of superior oblique.
7. Annulus of Zinn.
8. Optic nerve.
9. Ophthalmic artery.

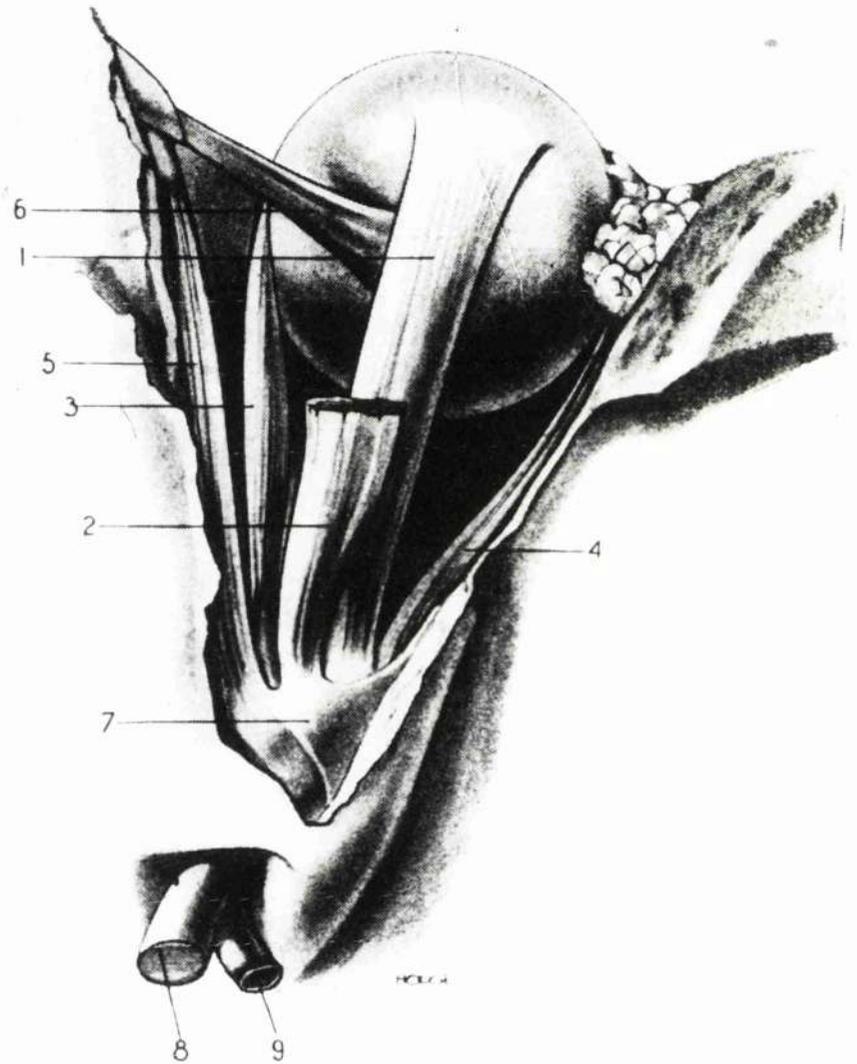
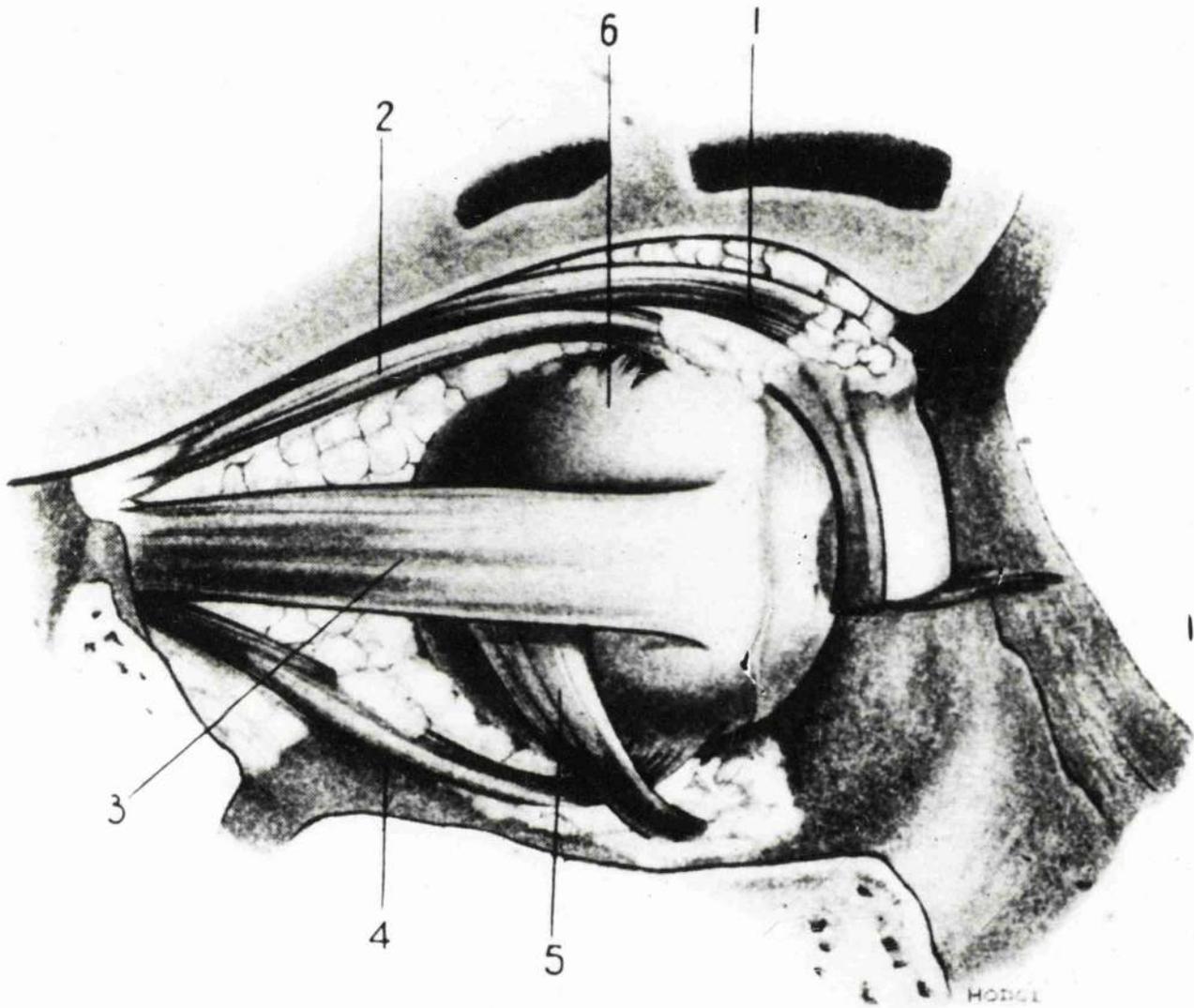
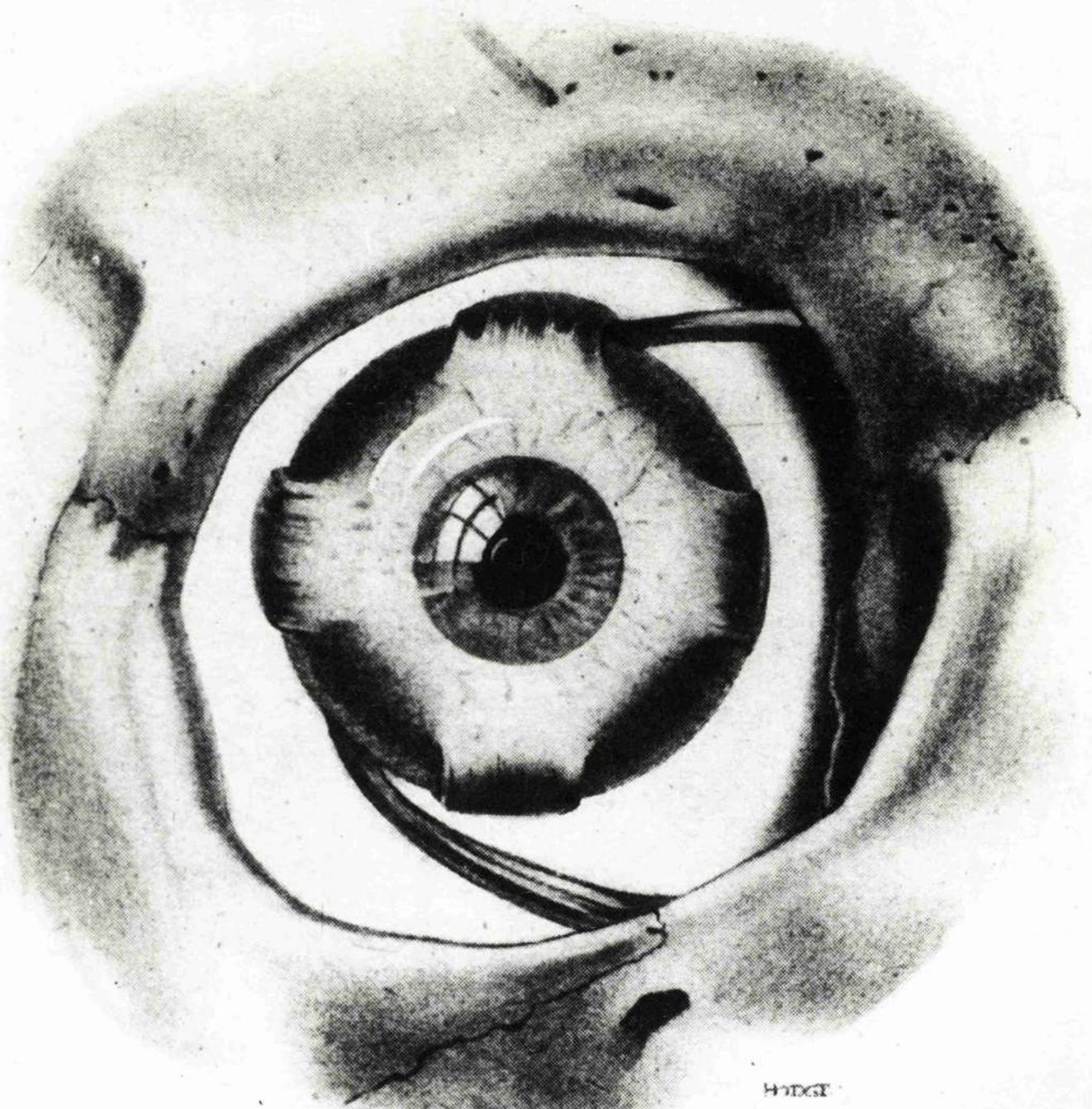


Fig. No. 10
From Duke Elder Textbook of Ophthalmology



—THE EXTRINSIC MUSCLES OF THE EYE FROM THE LATERAL SIDE.

- | | |
|----------------------------------|----------------------|
| 1. Levator palpebrae superioris. | 4. Inferior rectus. |
| 2. Superior rectus. | 5. Inferior oblique. |
| 3. Lateral rectus. | 6. Superior oblique. |



THE OBLIQUE MUSCLES VIEWED FROM IN FRONT.

Fig. No. 12
From Duke Elder Textbook of Ophthalmology

Section 2

The extrinsic musculature of the eye

The muscles controlling eye movement are six in number. The superior and inferior recti which control up and down movements of the eye are innervated by the third cranial nerve. The medial and lateral recti control side to side eyeball rotations, the medial rectus being innervated by the third cranial nerve and the lateral rectus by the sixth. The remaining two muscles are the superior oblique and the inferior oblique innervated respectively by the 4th and 3rd cranial nerves. Figs. 10, 11, 12.

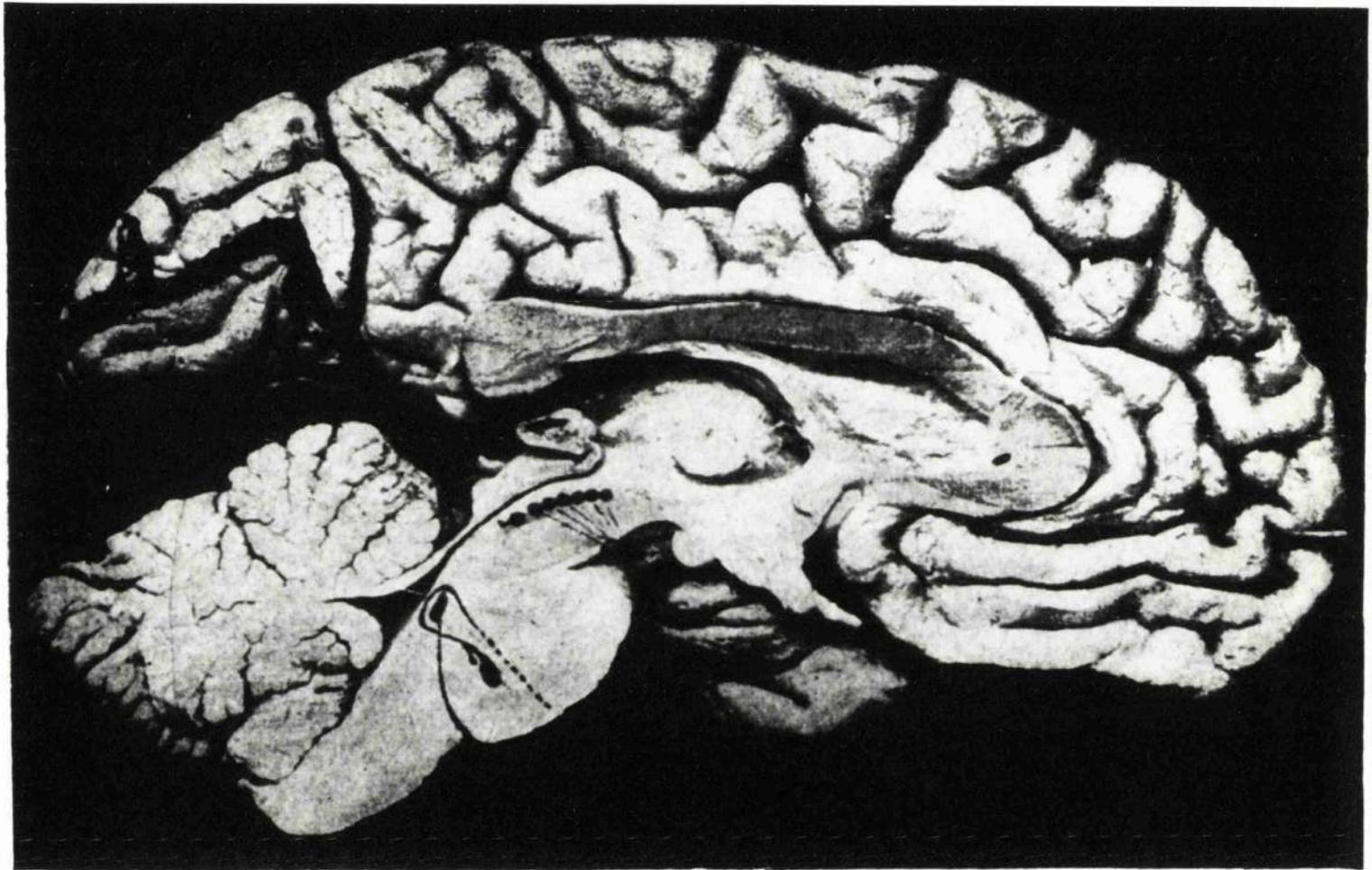
With the exception of the inferior oblique which originates in the antero-medial corner of the floor of the orbit, all the muscles arise from a common origin in an annular ring - the annulus of Zinn at the apex of the orbit. Through this ring, which encircles the optic foramen, passes the optic nerve and the ophthalmic artery. The muscles originating in this annulus form a muscle cone as they extend to their insertions on the sclera of the eyeball. Before its insertion the tendinous extension of the superior oblique muscle passes through a cartilaginous pulley called the trochlea and at this point sharply changes direction backwards, downwards, and laterally. It then runs beneath the superior rectus and is inserted on the postero lateral aspect of the scleral surface of the eyeball. Despite its origin and muscle position by its turning at the pulley its contraction produces an oblique movement of the eyeball.

These muscles are covered with facial sheaths which are continuous with the fibro-elastic tissue of Tenon's capsule which surrounds the eyeball from the cornea-scleral junction anteriorly to the optic nerve posteriorly. Extensions of these sheaths near their terminations spread out to form an intermuscular membrane round the eyeball. From these muscular sheaths check ligaments containing some smooth (involuntary) muscle fibres run to the orbital walls. The function of the ligaments is the checking of overaction of the various extra-ocular muscles. The most fully developed check ligaments are associated with the medial and lateral rectus which are involved in side to side rotations of the eyeball.

The nerve supply to the extraocular muscles

The nerve supply to and from these muscles is contained in the 3rd, 4th, 5th and 6th cranial nerves. The actual distribution among the 3rd, 4th and 6th has been detailed above with respect to the muscles served. It has been shown by Stibbe (1929), cited by Cooper (1951) in an anatomical study that definite connections exist between these nerves and the 5th nerve in man. It appears that motor impulses of central origin travel to the muscles via their respective nerves and that sensory impulses from the muscles travel, not only in these nerves, but have another pathway via the 5th nerves to the brain.

The nuclei or origin of the 3rd and 4th nerves are found in the central grey matter of the mid-brain and are anatomically



THE OCULO-MOTOR NUCLEI.

Mesial section of the left half of the brain showing the position of the nuclei of nerves III and IV represented schematically by the row of black dots; and the position of the nucleus of nerve VI lying within the loop formed by the fibres of nerve VII. The nucleus of nerve VII is seen consisting of a main mass and a small superior facial nucleus. The calcarine fissure is outlined in black (from Whitnall: "Anatomy of the Human Orbit").

—DIAGRAMMATIC SCHEME OF
THE THIRD NUCLEUS AND ITS ASSO-
CIATED CELL GROUPS.

1. Levator palpebræ.
2. Superior rectus.
3. Inferior oblique.
4. Inferior rectus.
5. Superior oblique : Nerve IV.
6. Internal ocular muscles (sphincter of iris and ciliary muscles).
7. Internal rectus : convergence.
8. Internal rectus : inward movement.

1, 2, 3, 4, 8. Cell groups comprising the principal (lateral) nucleus, divisible into :

- 1, 2, 3. The dorso-lateral sub-group.
- 4, 8. The ventro-median sub-group.
5. Nucleus of Nerve IV.
6. Accessory nuclei of Edinger-Westphal.
7. Central nucleus of Perlia.

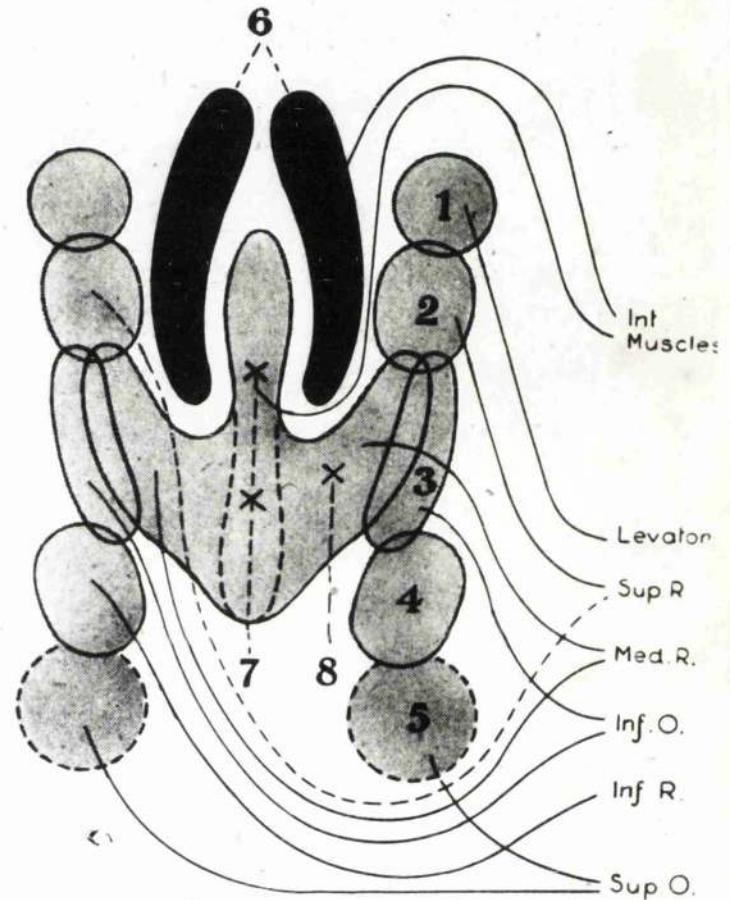


Fig. No. 14

related in general to the aqueduct of Sylvius and the 4th ventricle as seen in Fig. 13. The nucleus of the 6th nerve is found in the dorsal portion of the pons.

The third nerve nucleus is particularly complex as it subserves in addition to four of the six extraocular muscles, the muscle controlling the raising of the upper eye-lid and some intra-ocular muscles (sphincter of iris and ciliary muscles). It is possible to divide this nucleus into various segments which have muscular control as shown in Fig. 14. The nucleus of the 4th nerve is also shown in the diagrammatic display. There is still considerable doubt as to the exact function of each nucleus segment and also as to which nerve fibres are crossed and which are uncrossed, the 3rd nerve is considered to have both types as this is necessary in order that heteronymous muscular actions should be possible despite the oculomotor fibres to the cerebrum being completely crossed. The 4th nerve is also considered to have crossed and direct fibres. The 6th nerve is considered to be direct.

The central connections of the oculomotor system

These form a most complex system much of which is ill-defined. The principal connections only need to be shown. They can be divided into two main groups, the first, the connections in the mid-brain and the second the connections with the cerebrum. According to Duke Elder these connections are:

Group A

1. The three oculomotor nuclei with each other, especially the nucleus of the 4th with the contra-lateral nucleus of the 3rd.
2. With the superior colliculus.
3. With the 8th cranial nerve system.
4. With the cerebellum.

Group B

1. From the cortical centres for eye movements in the frontal lobes.
2. From the visual calcarine cortex.

In addition to these there are other tracts whose functions are not understood and also 'centres' have been hypothecated to control the various eye movements.

The real complexity of the nervous system in its organisation of the control of eye movements is not yet fully unravelled. The correlation and integration of anatomical and physiological findings give an increasingly clear picture of the complex inter-relationships involved when the eyes follow a moving target with the intention of discriminating the detail presented in that target.

Present knowledge, however, leaves many questions unanswerable and inevitably has led to postulation of various 'centres' which carry out the demanded functional integration. The frontier between reflex or involuntary and willed or voluntary

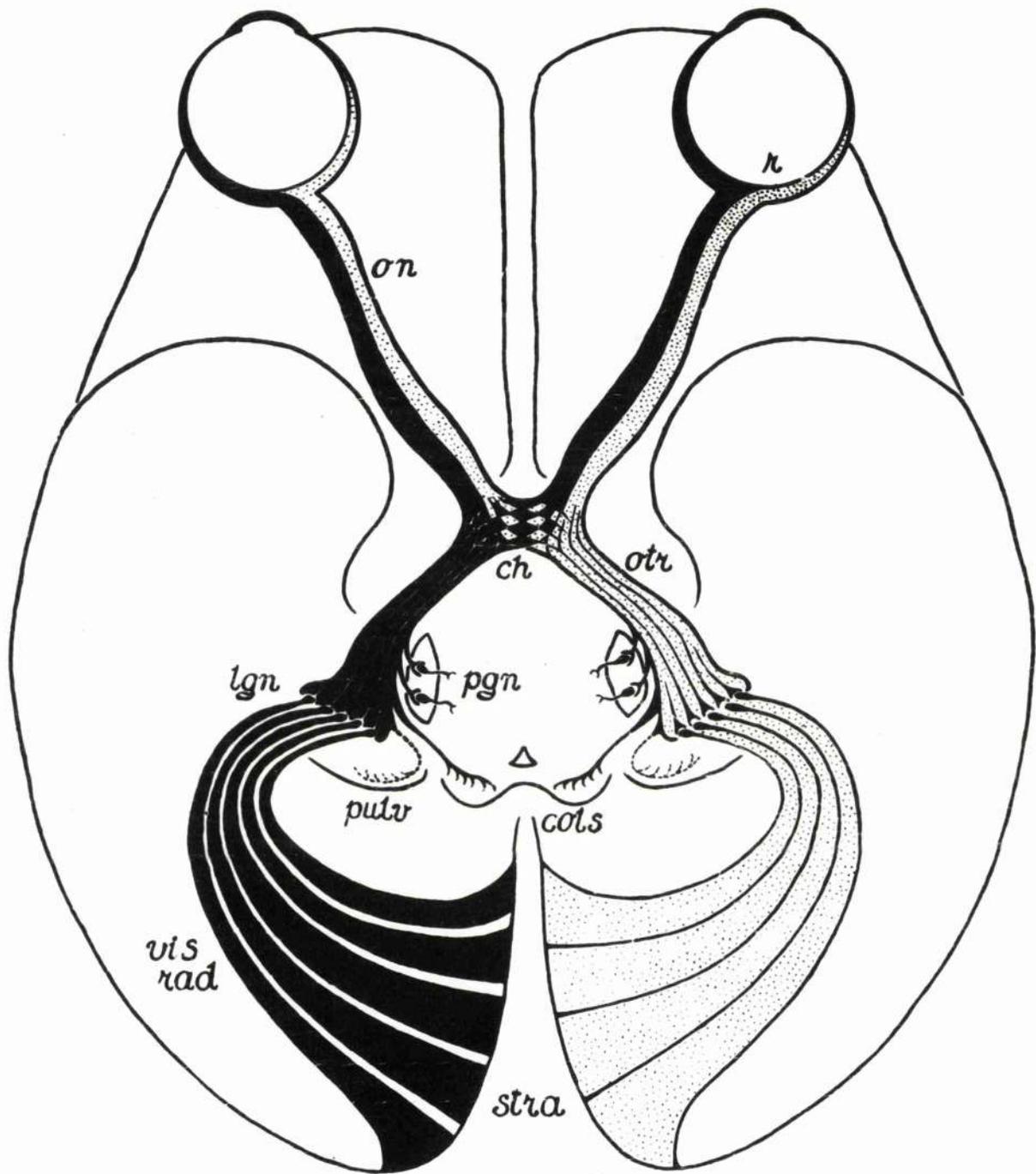
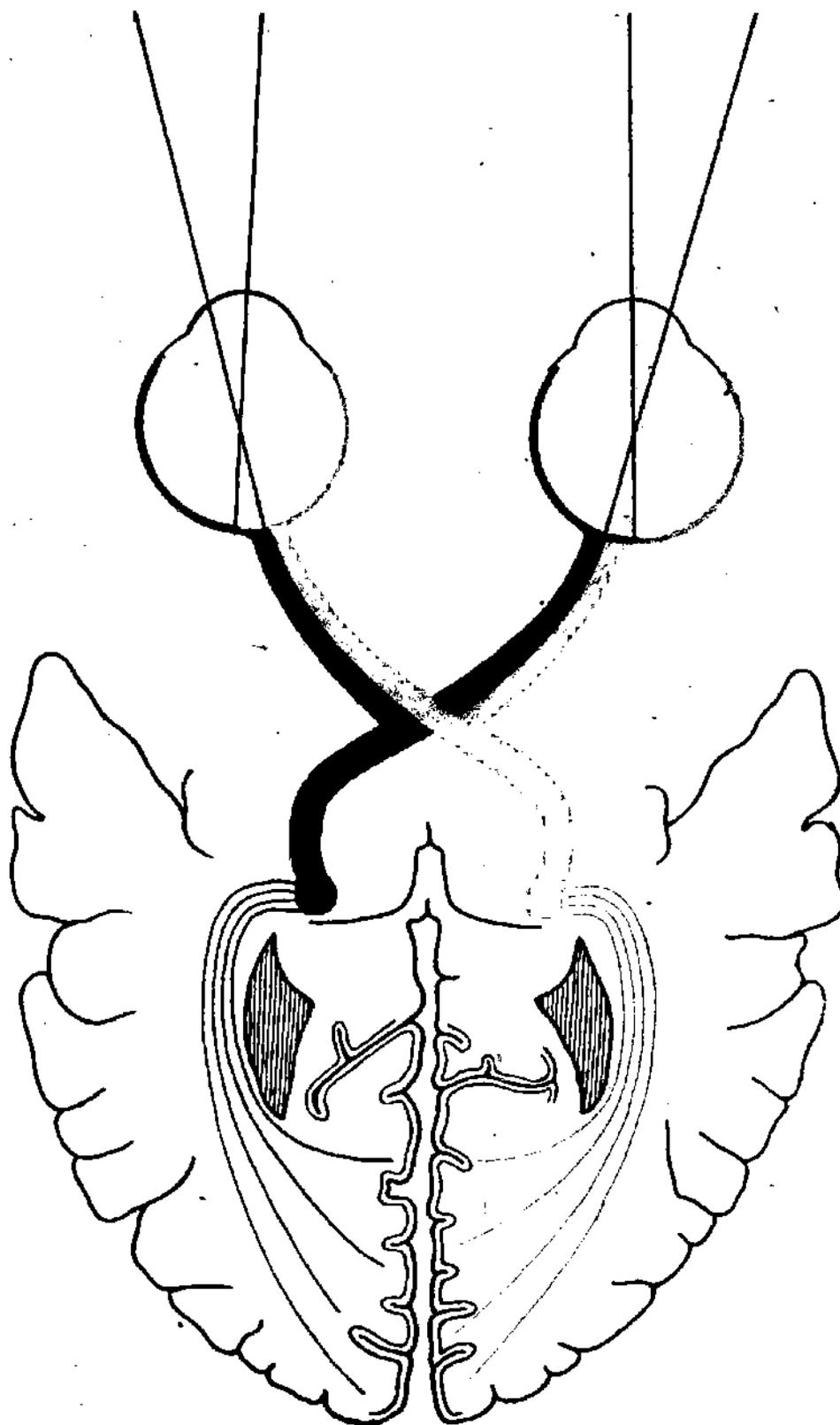


Diagram of the visual system in Primates (Monkey, Ape, Man) drawn in the outline of the human brain. Two-thirds natural size:

The infranuclear division is composed of the eyes, or eyeballs, each inclosing the retina (*r*), of the optic nerves (*on*), and of the optic tracts (*otr*), connected by means of the optic chiasma (*ch*). This division terminates in the subcortical visual centers, of which the principal one is the lateral geniculate nucleus, or lateral geniculate body (*lgn*), the others—the pregeniculate nucleus, or *griseum praegeniculatum* (*pgn*), and the superior colliculus of the midbrain (*cols*)—being subsidiary. A fourth, and a less probable, subcortical visual center is the pulvinar of the thalamus (*pulv*).

The supranuclear division of the visual system is represented by the visual radiation (*vis rad*), a fiber tract originating in the lateral geniculate nucleus of the midbrain (*lgn*) and terminating in a portion of the superficial gray matter or cortex of the occipital lobes of the cerebrum, called "striate area" (*stra*). In the chiasma (*ch*) the nasal or inner halves of the optic nerve fibers, originating in the nasal halves of the two retinae, intercross. In consequence, while each optic nerve (*on*) represents the retina of its own eye, in the visual pathway from the chiasma to the cortical visual centers (*otr*, *lgn*, *vis rad*, *stra*)—each side, right and left, represents the ipsilateral or homonymous halves of both retinae.



THE VISUAL NERVE PATHS SHOWING LINES OF PROJECTION OF THE FIXATION AREA AND THE BLIND SPOT (from Traquair's "Clinical Perimetry").

responses has inexact demarcation. The use of the term fixation 'reflex' is itself subject to criticism in that it is not of the low order of complexity involved in spinal reflexes but has cortical associations and demands the presence of consciousness for its very existence.

The pathways, centres, and cortical areas involved in the experiments reported find their tangible stimulus origin at the retina, their intangible pre-origin is in the will of the motivated subject who voluntarily pursues the object to acquire and describe what is seen. The response of the subject is, therefore in some respects under his control and in other respects is involuntary in that the subject's eye movements to finally bring the object on to the fovea are outside his control.

This present concept of the pathways, centres and areas may be traced in Figs 15A & B. From the ganglion cells of the retina arise the third order neuroses, the first neuroses in the pathway being being the rods or cones, and the second in the bipolar cells within the retina.

The optic tract carries impulses to the lateral geniculate body, the pretectal area and the superior colliculus (Barnes, Ingram and Pearson, 1935). During the course of these fibres there is a partial decussation in the optic chiasma. Fig. 15 B. By virtue of the decussation the fibres from the lateral and medial segments of the two retinae are associated, and in the continuing tract fibres from both retinae are represented. By

this partial decussation a stimulus, moving or otherwise, in the left half of the binocular visual field will be represented in both optic tracts before the decussation, but only in the right tract after decussation.

The main relay station for the tract fibres is the lateral geniculate body through which all fibres to the occipital striate cortex pass. They form the geniculocalcarine tract and at the cerebral cortex the contained impulses give rise to visual sensation.

The optic tract contains nerve fibres of varying size. It is now well known that the larger the fibre the greater the rate of conduction of impulses. Le Gros Clark (1944) has pointed out that the larger fibres in the optic nerve go to the lateral geniculate body where the impulses are relayed to the cortex. Because of the difference in size of the various fibres there would be time for visual impulses to reach the cortex and return by cortico-tectal fibres to the mid-brain before the impulses in the smaller and slower fibres reached the mid-brain directly from the retina.

The pretectal region to which some fibres branch is considered to be concerned only with the pupillary light reflex.

The fixation reflex and the moving target

The accurate correlation of visual stimuli and subsequent eye movement results in a visual fixation. By fixation is meant the maintenance of the posture of the eyes by tonic

contraction of the extraocular muscles so that the retinal images of the object which is fixated falls on the two foveae. Fixation is partly reflex but requires the intervention of consciousness. In this it is distinct from other reflexes which can operate without consciousness being involved. Maintenance of fixation during target movement cannot be accomplished by purely voluntary effort.

Anatomical and electrophysiological studies have shown that multiple sites in the brain stem, mid-brain and cortical regions are involved in fixating an object. Gordon Holmes (1938) had formed the opinion that the occipital cortex was concerned with the fixation reflex and the frontal cortex with voluntary movement of the eyes. The frontal cortex had also an inhibitory action and lesions within the area caused an exaggerated fixation reflex to be operative. Exaggerated to the extent that fixation on an object could not be given up, or only given up by extreme effort. Such pathological fixation resulting from either frontal cortex damage or damage to the pathways to and from the cortex, caused much distress to patients.

The area of the precentral cortex has also been demonstrated to have motor associations with the extraocular muscles. There are therefore known to be in the cortex of man, two distinct areas concerned with the visual system and its movement control - occipital and the precentral motor cortex.

The idea that specific areas of the cortex have specific functions is very old and early work by Fritsch and Hitzig (1870), Ferrier (1886) and others laid down a foundation on which such specifications were built. These foundations no longer support our far from complete knowledge of cortical function, but it is now clear that the nervous system functions as a whole (Lashley 1929, 1931, 1934). Voluntary muscular action may be influenced by thoughtful consideration of the desirability of such action, and its consequences. It may be influenced by many factors which are commonly described as reflex activities, involving many so called centres and nervous pathways. All these various factors will have an effect on the accuracy of control movements of the eyes, or any other anatomical portion, whether they are voluntary or reflex. This more modern concept does not deny that specific areas have localisation, indeed, research has confirmed this, but what is of vital importance is the integrative functions of intercortical areas and cortical subcortical areas, which appear to subserve voluntary movement.

THE HUMAN CENTRIFUGE WITH THE MOUNTED LANDOLT C TARGET

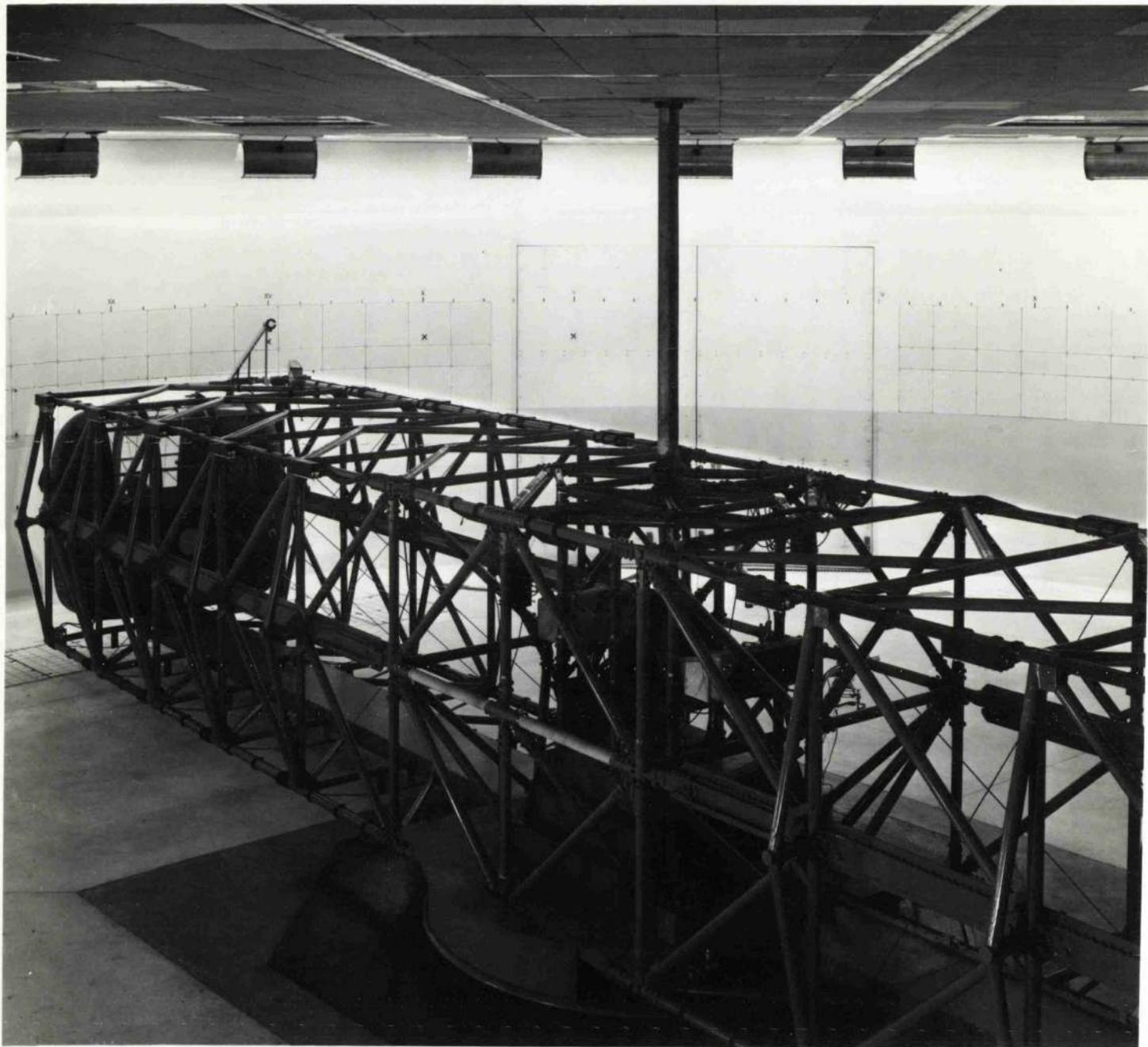


Fig. 16.

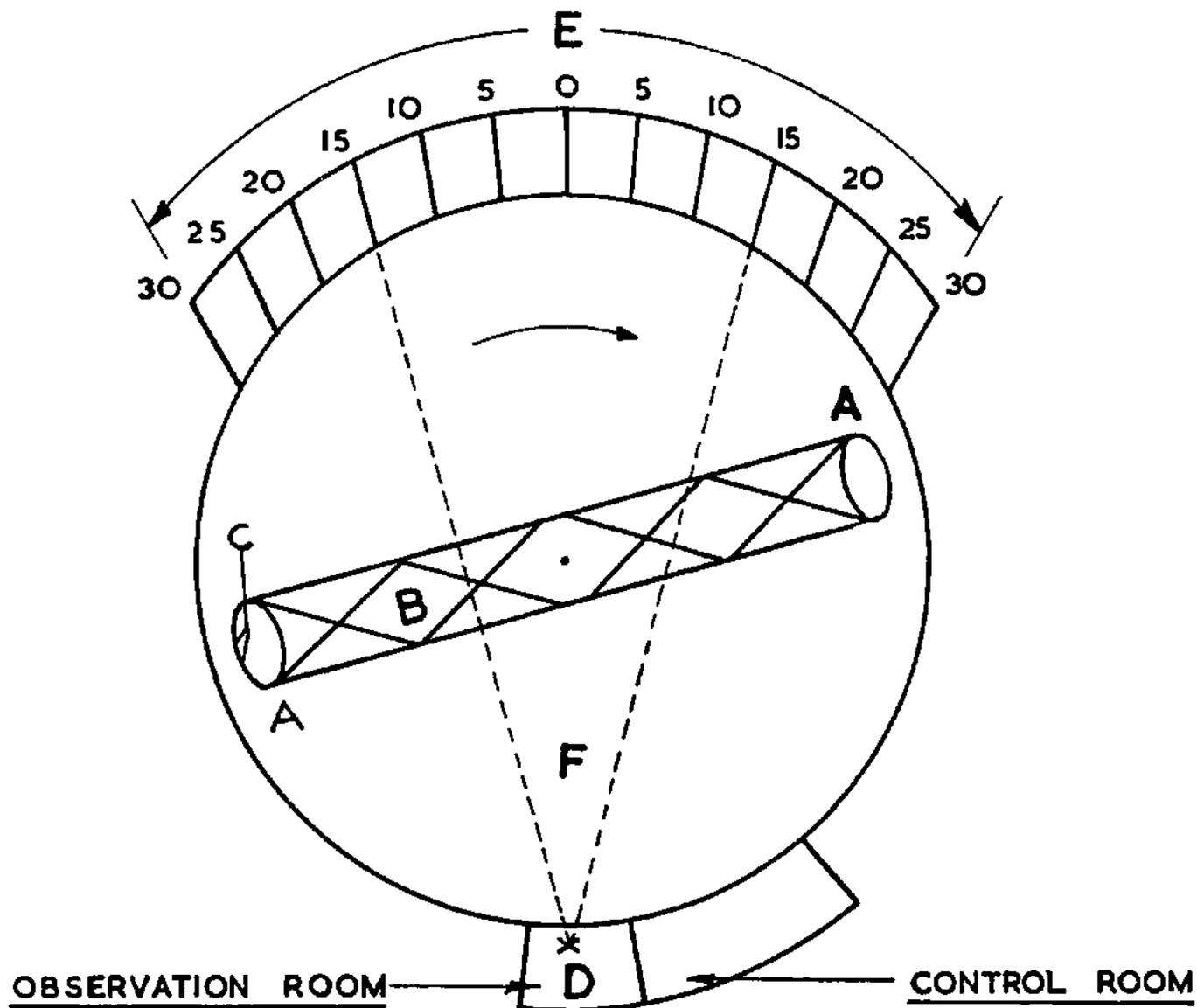
PART 3

The Exploratory Experiments

The rotating arm of the human centrifuge at the Royal Air Force Institute of Aviation Medicine, when viewed from the observation rooms, Fig. 16, provided a means of imparting movement to a simple visual acuity measuring device. This rotating apparatus was available and required no modifications, apart from affixing the system, its remote control and a method of illuminating the device and its background. This apparatus was considered to be adequate for exploratory experiments on which could be based a more searching appraisal of the whole problem of the discrimination of detail in moving objects.

The apparatus and methods

Targets were mounted on the end of the arm of the human centrifuge and consisted of a series of various sized Landolt rings capable of being rotated into the eight standard positions. The rotation was electrically controlled by the observer from an observation room in which the subject was seated, and the subject was required to locate the position of the gap in the Landolt rings, the gaps subtending angles varying from one minute of arc to 2½ minutes of arc at the subject's eye. Movement of the target was from left to right, and the distance of the target from the subject was 70 ft. Fig. 16 shows the



- A**—CENTRIFUGE CAR.
- B**—CENTRIFUGE ARM.
- C**—LANDOLT RING TARGET.
- D**—OBSERVATION ROOM.
- E**—WALL OF CENTRIFUGE CHAMBER MARKED IN DEGREES OF ARC RELATIVE TO SUBJECT.
- F**—ARC USED IN EXPERIMENTS

DIAGRAMMATIC LAYOUT OF CENTRIFUGE CHAMBER

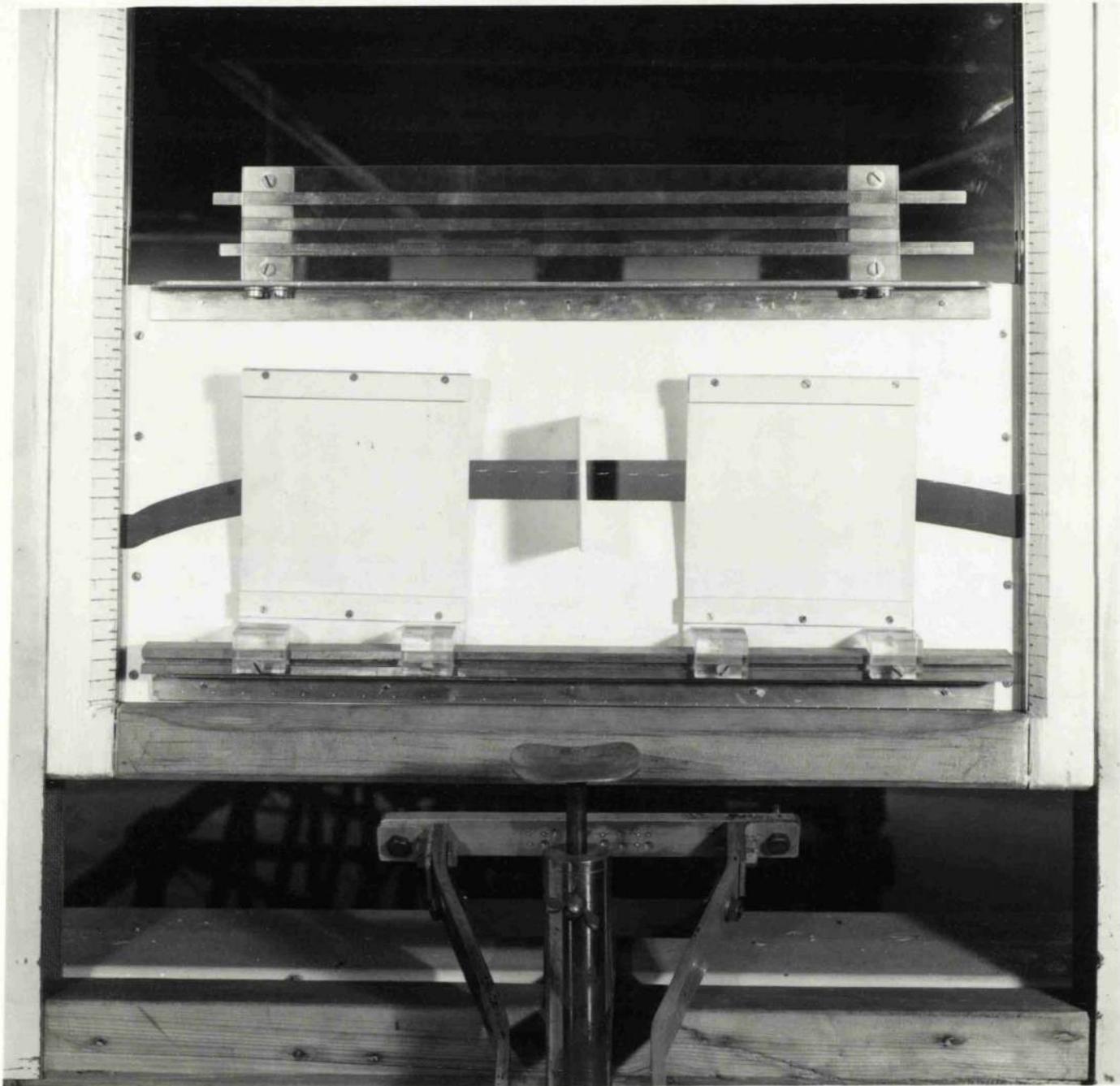


Fig. 18.

target arrangement and Fig. 17 the general layout of the centrifuge. The vertical pillar in the centre of the centrifuge was subjectively unnoticeable during visual pursuit of the Landolt ring.

The technique adopted by Ludvigh of apparently moving the object via a front surfaced mirror was discarded due to our inability to produce an image free from vibration. These very minor vibrations produced by inconstancy of electrical motor performance and gear system performance resulted in just perceptible vibration of the mirror. With an optical lever of magnitude 20, these very minor mechanical non-linearities transmitted to the mirror were considered unacceptable. Recourse was therefore made to the rotatable equipment which was available and which was found to provide vibration-free carriage of an actual object.

The angular velocities of the targets relative to the subject were 0 - 85°/sec. with normal running of the centrifuge and velocities up to 120°/sec. were obtained for short periods when the cabins were not in position. The subject could see the moving target with either or both eyes by manipulating a view restrictor, Fig. 18. This view restrictor consisted of 3 shutters, two of which operated in the vertical plane and two in the lateral plane. By separating the vertically operated shutters the field of view in elevation could be increased, and by separating the lateral shutters variable width fields of

view could be obtained. The 5th shutter which extended from the nose and forehead of the subject and protruded beyond the plane of the other four shutters ensured an equal field of view to left and right eye and also to both eyes when used simultaneously. The field of view was therefore constant for any of the three viewing methods. The distance from corneal surface to the aperture was 3 inches.

The luminance of the background and of the shutters restricting the field was 18 millilamberts, (Holophane Lumeter). The contrast factor between target and background was 85^o/o. (The subject was adapted to the lighting conditions used in the experiment for 2-3 mins. by adopting the viewing position and regarding in general the illuminated field.)

As the lighting condition throughout was constant and the fixation point and target almost equal distances from the subject no change in accommodation or light adaptation was required when the target appeared. The selected angular velocity of the centrifuge target as seen from the observation point varied by 2^o/o from entry point mid-field, being greater at the mid-field position. The angular velocity of the target relative to the eye in the selected 30^o field was 47^o/o of the actual angular velocity of the target from the centrifuge pivot.

A constant size of field of view was selected and with target angular velocities varying from 0^o/sec. to 85^o/sec. the exposure

time was diminished with each higher angular velocity. After a learning period subjects attended six sessions of 40 minutes during which the subject carried out 180 pursuit movements. Six subjects took part in the experiment, but only four completed all sessions. However, as these experiments were primarily designed to find subjects with differing performance for further research experiments the loss of the two subjects was not considered embarrassing.

The subject was seated with his chin in a chin rest and some body stability was provided by forearm rests anterior to the subject. A bite board was not used. Initially with a stationary target in the centre of the field the subject identified the position of the break in the Landolt ring. This was done by clock coding, 12, 10.30, 9, 7.30 etc. The subject responded by calling the various positions, the answers were correct or incorrect.

For the pursuit experiment, a fixation cross at the left periphery of the field of view coincided with the entry point of the moving target. The subject was asked to follow the target and identify the angular position of the break in the ring. A warning period of 1-2 secs. was given before the target appeared. The unlit target passed across the permanently illuminated field once or twice before each trial but was not followed by the subject who maintained fixation on the cross provided. In some experiments employing eye movement recording techniques

SUBJECT I.

ACTUAL ERRORS EXPRESSED AS PERCENTAGES OF POSSIBLE ERRORS FOR EACH VELOCITY.

TARGET SIZE. 1.5 MINUTES OF ARC, 30° FIELD.

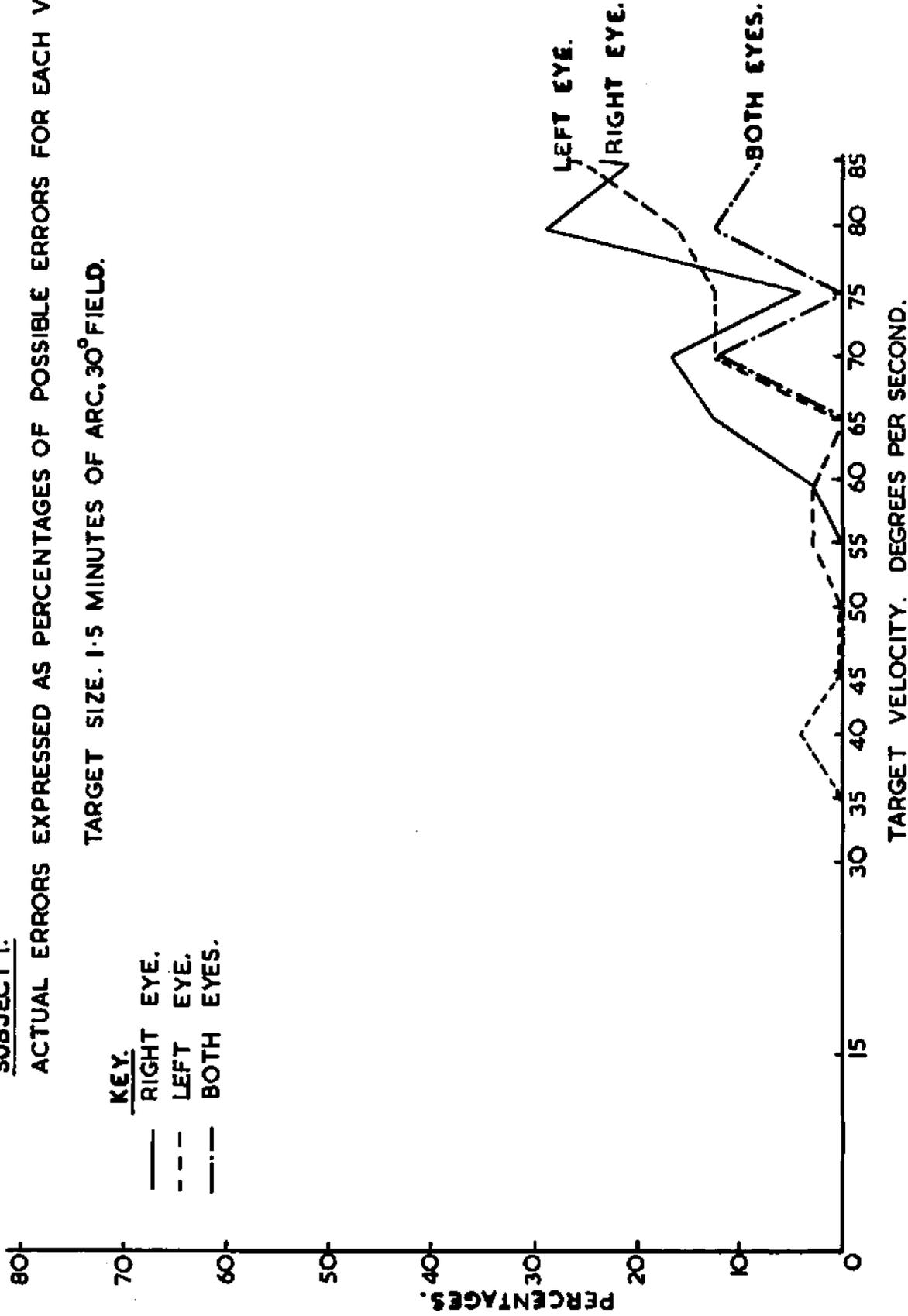


FIG. 19

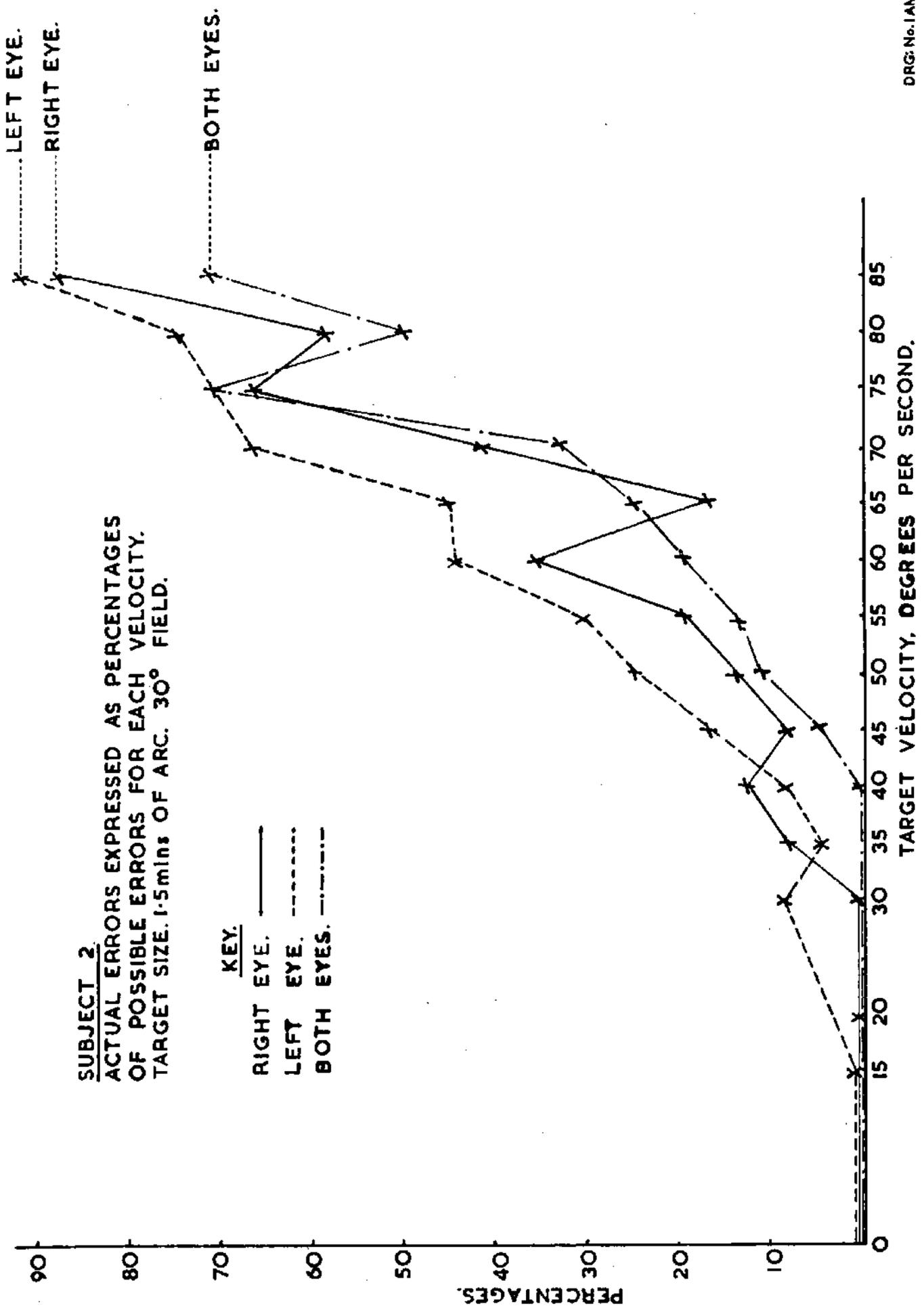
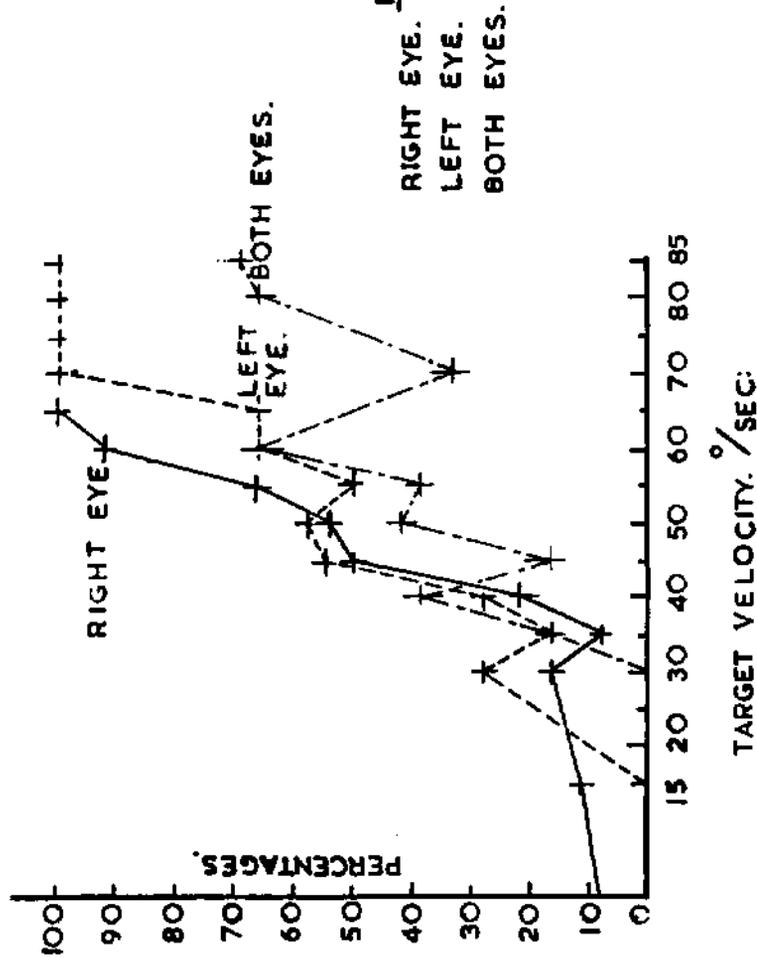


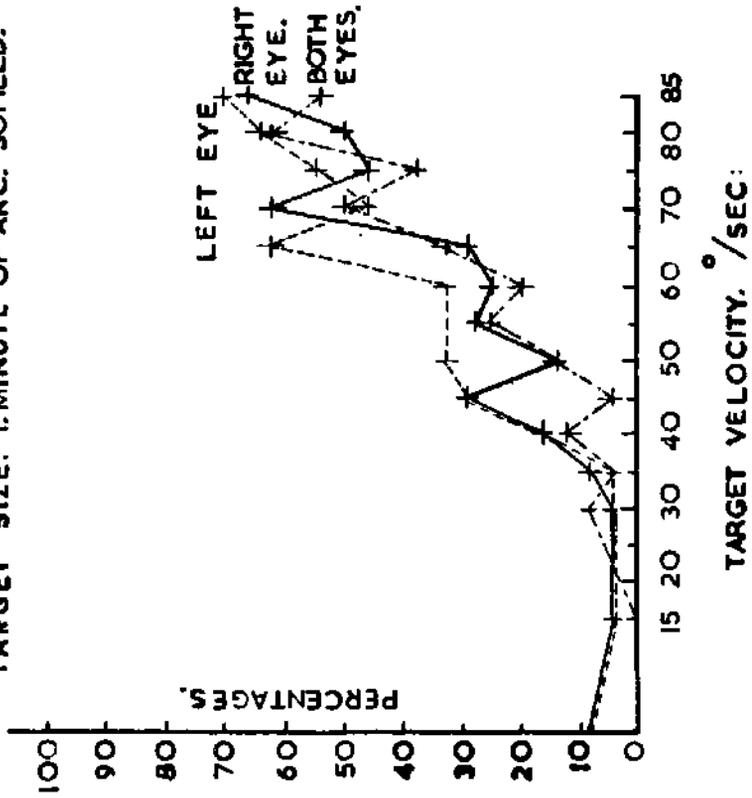
Fig. 19

SUBJECT 3.
ACTUAL ERRORS EXPRESSED AS PERCENTAGES
OF POSSIBLE ERRORS FOR EACH VELOCITY.
TARGET SIZE. 1. MINUTE OF ARC. 30° FIELD.



DRG: No. IAM. 5018

SUBJECT 4.
ACTUAL ERRORS EXPRESSED AS
PERCENTAGES OF POSSIBLE ERRORS
FOR EACH VELOCITY.
TARGET SIZE. 1. MINUTE OF ARC. 30° FIELD.



DRG: No. IAM. 5019

Fig. 21

SUBJECT 5.

**ACTUAL ERRORS EXPRESSED AS PERCENTAGES OF
POSSIBLE ERRORS FOR EACH VELOCITY.**

TARGET SIZE. 2.5 MINS: OF ARC. 30° FIELD.

KEY.

RIGHT EYE. —

LEFT EYE. - - - -

BOTH EYES. - · - · - ·

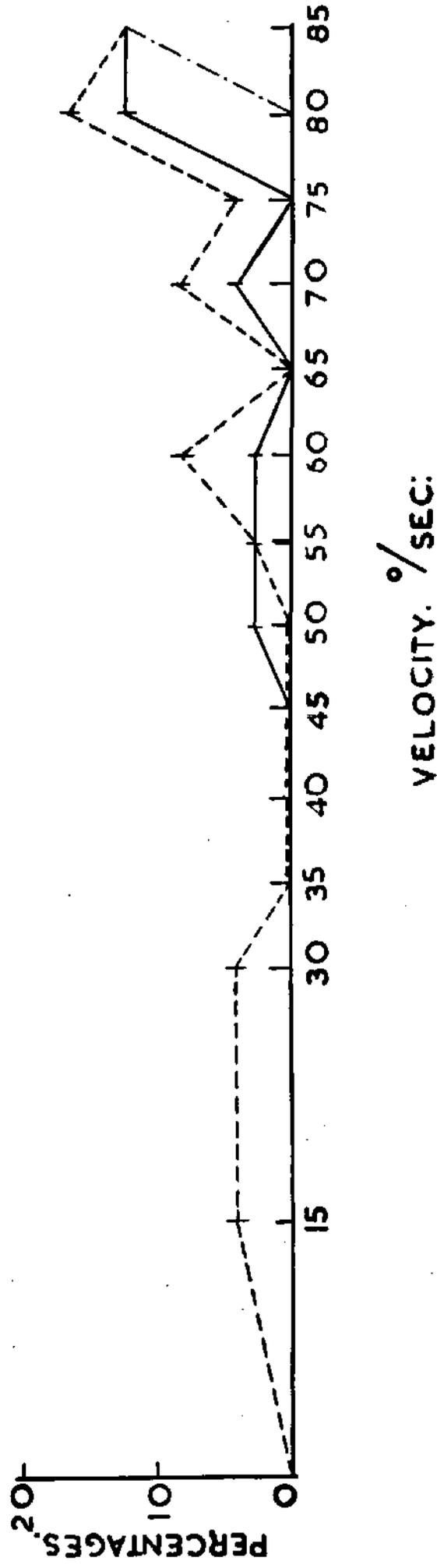


Fig. 22

SUBJECT 6.

**ACTUAL ERRORS EXPRESSED AS PERCENTAGES
OF POSSIBLE ERRORS FOR EACH VELOCITY.
TARGET SIZE, 3.5 mins OF ARC, 30° FIELD.**

KEY.
RIGHT EYE. —
LEFT EYE. - - - -
BOTH EYES. - · - · -

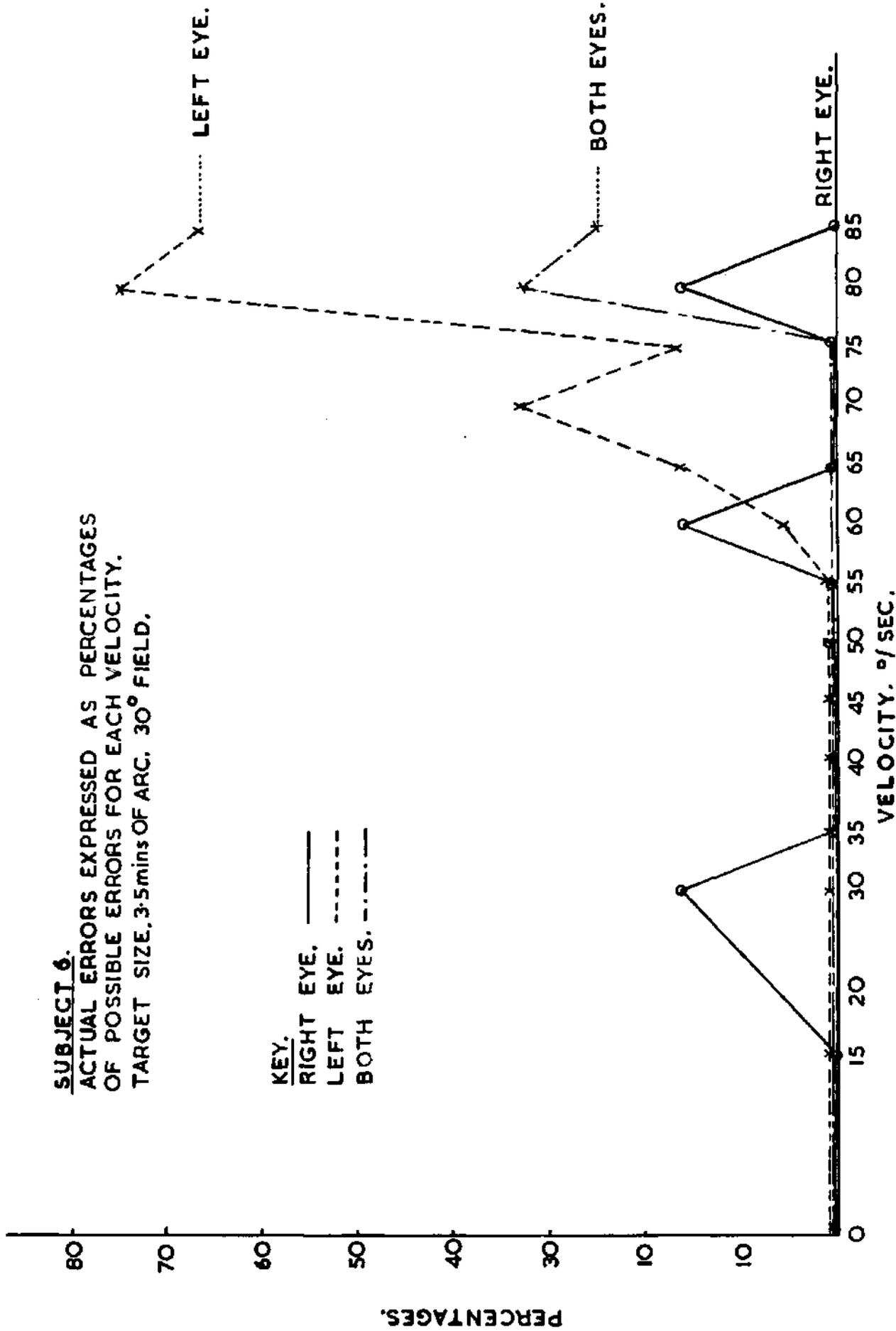


Fig. 23

this fixation could be checked.

The Landolt rings having very large (4-12 minute of arc) gaps were not used as at maximum centrifuge speed the gaps were easily distinguishable. (85° /sec. normal running).

Results in ability to perceive

Subjects 1 and 2 viewed a 1.5 minute of arc target and Subject 1 demonstrated a better ability than Subject 2. These results were not compared statistically as Subject 2 did not complete all six sessions. Figs. 19, 20.

Subjects 3 and 4 viewed a 1 minute of arc target and their results are shown in Fig. 21. Subject 4 performed better than Subject 3 as seen in the graphs and this was confirmed statistically ($P= 0.001$).

Fig. 22 shows the performance of Subject 5 who viewed a 2.5 minute of arc target. The results show only a minor loss of ability to discriminate the detail in the moving target. Subjects 1 - 4 when presented with targets of this size demonstrated an improvement in ability at all velocities compared with their original smaller targets at similar velocities. These improvements were obvious and were not scored.

Subject 6 failed to carry out all the tests required, and his results were graphed only. Fig. 23.

In all subjects and in particular Subject 3, the responses when presented graphically show a trend for binocular vision to

EYE MOVEMENTS OF THE TWO TYPES WITH & WITHOUT 2ND SACCADES.

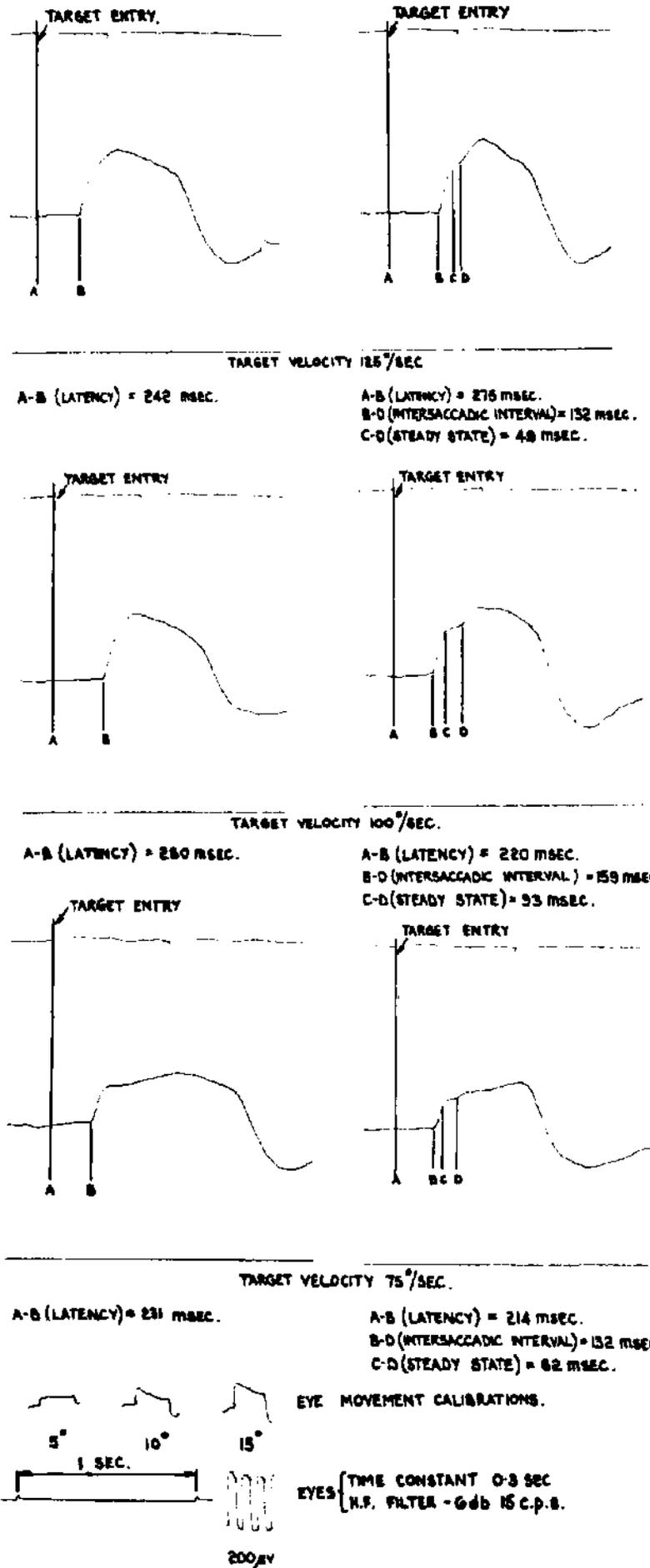


Fig. 24.

be better than monocular. An analysis of the data showed no significant difference to be present nor were there shown significant differences between right and left eyes. The number of errors by Subject 1 and 3 were sufficiently large to permit examination of which positions were seen better than others. The 3 o'clock and 9 o'clock positions were seen better than any others. Subject 1 ($P = 0.01$) Subject 3 ($P = 0.05$). Failure to recognise detail in the moving targets occurred at angular velocities as low as $30^{\circ}/\text{sec.}$ and increased with increasing target velocity.

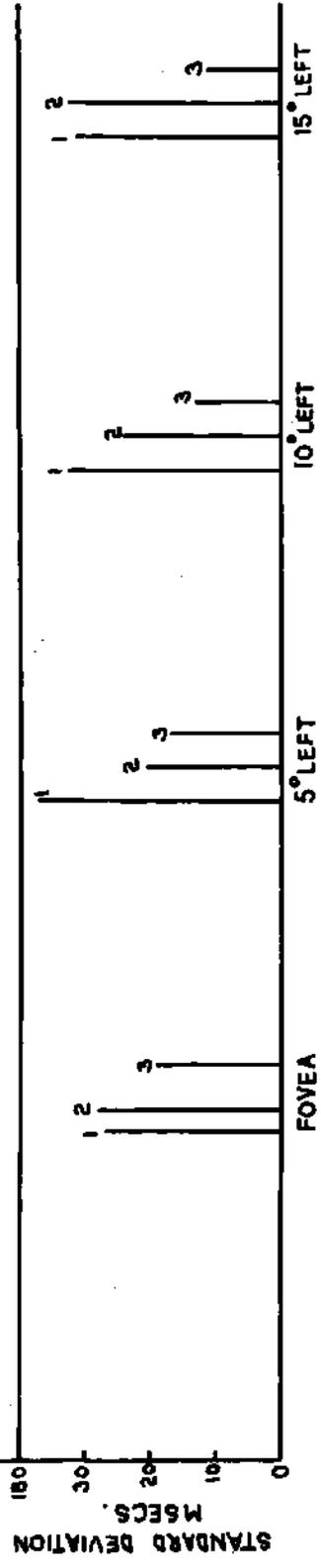
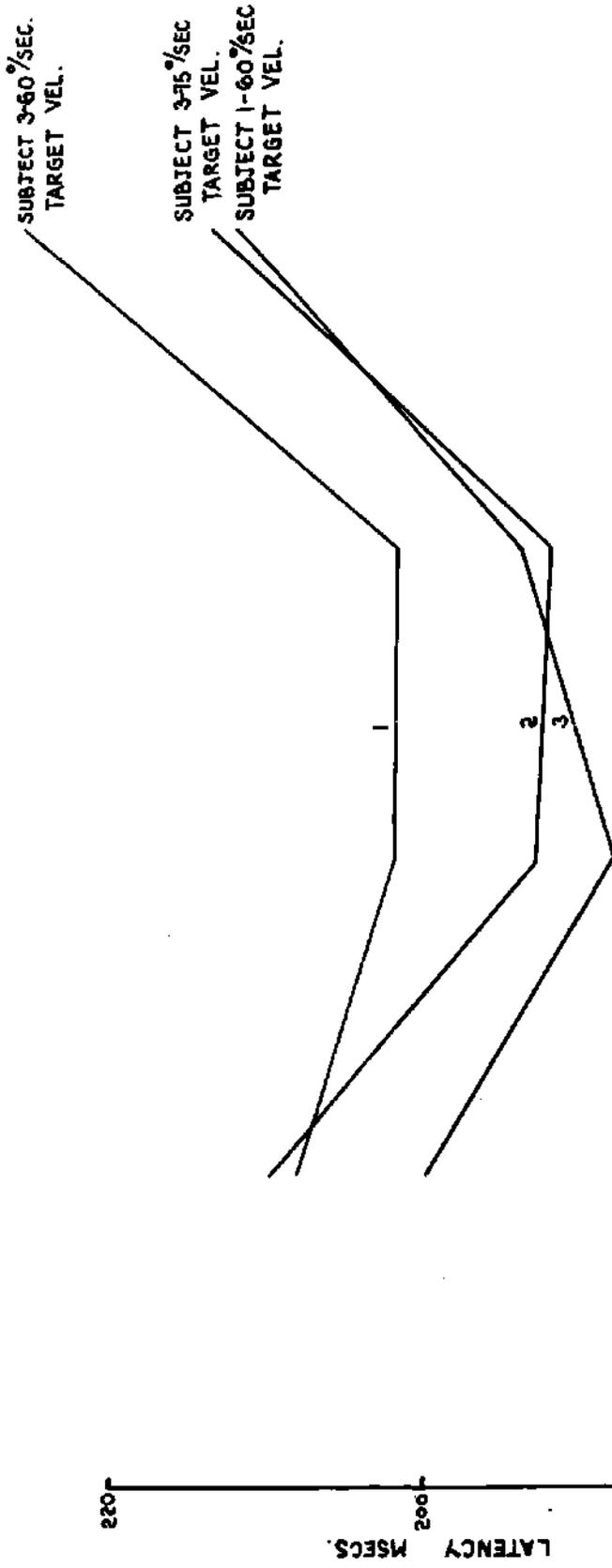
Eye movements

Eye movements were then recorded in Subjects 1 and 3 who varied considerably in ability, to permit investigation of differences in the eye movement patterns and eye movement latencies. Latency is defined as the time delay between target appearance and initial eye movement. Despite the general limitations of the cornea-retinal method of recording eye movements, the time constant in capacitance coupled amplifiers and the 'noise' in the system it was possible to obtain the initial latency of eye movements and to note the occurrence of definite secondary eye movements during the pursuit phase, Fig. 24 (record from later experiments).

Latency of eye movements

There was a wide variation in the initial latencies recorded

VARIATION OF LATENCY WITH AREA OF RETINA INITIALLY STIMULATED.



AREA OF RETINA INITIALLY STIMULATED BY TARGET RELATIVE TO FOREA.

FIG. 25

PERCENTAGE OF 2ND. SACCADIC MOVEMENTS
RELATED TO TARGET VELOCITY.

AVERAGE LATENCY BETWEEN END OF 1 ST. EYE
MOVEMENT TO BEGINNING OF 2 ND EYE MOVEMENT = 136 ms.

KEY
SUBJECT 2. —○—
SUBJECT 4. —X—

MAJOR 2 ND. SACCADDES PER 100
PURSUIT MOVEMENTS

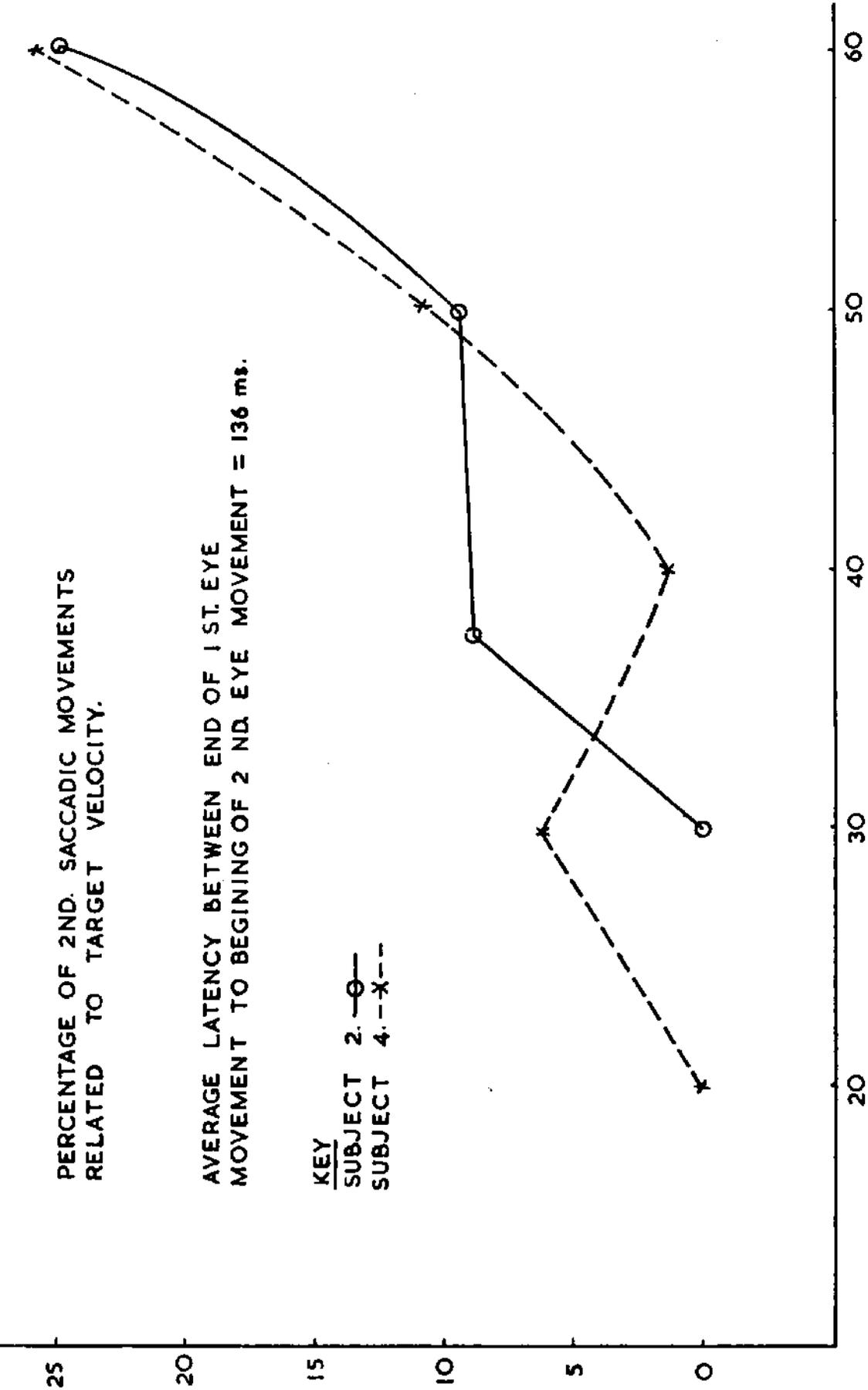


Fig. 26

the general dispersion being in the 150-250 millisecond band with occasional very long ones.

The variation of eye movement latency with variations in the zone of the retina initially stimulated is shown in Fig. 25 and Table 1.

Table 1

Sites of Initial Stimulation in Relation to Target Entry Point and Latencies in Milliseconds with Standard Deviations

	Fovea	5°rt	10°rt	15°rt	Target Velocity
Subject 3	209.5 (28.14)	201.92 (28.34)	202.47 (24.89)	225.6 (32.07)	60°/sec
Subject 1	210.5 (19.55)	188.5 (17.68)	195.8 (12.43)	214.6 (10.91)	75°/sec
Subject 3	200.08 (27.776)	193.675 (37.194)	192.472 (33.125)	215.625 (31.339)	75°/sec

Subject 1 whose ability to discriminate detail in moving targets is better than Subject 3 shows slightly smaller latencies and a substantial diminution in the standard deviation.

Secondary eye movements

These secondary movements occurred more frequently as target velocity increased. Fig. 26 shows the percentage occurrence of these movements related to target velocity and Fig. 24 the type of movement recorded. There is also shown in Fig. 27

RELATION OF OCCURENCE OF 2nd. SACCADES TO FIXATION POINT

FREQUENCY OF OCCURENCE OF 2nd SACCADES WITH VARIATION IN
AREA OF RETINA INITIALLY STIMULATED

TARGET VELOCITY CONSTANT 60°/SECOND

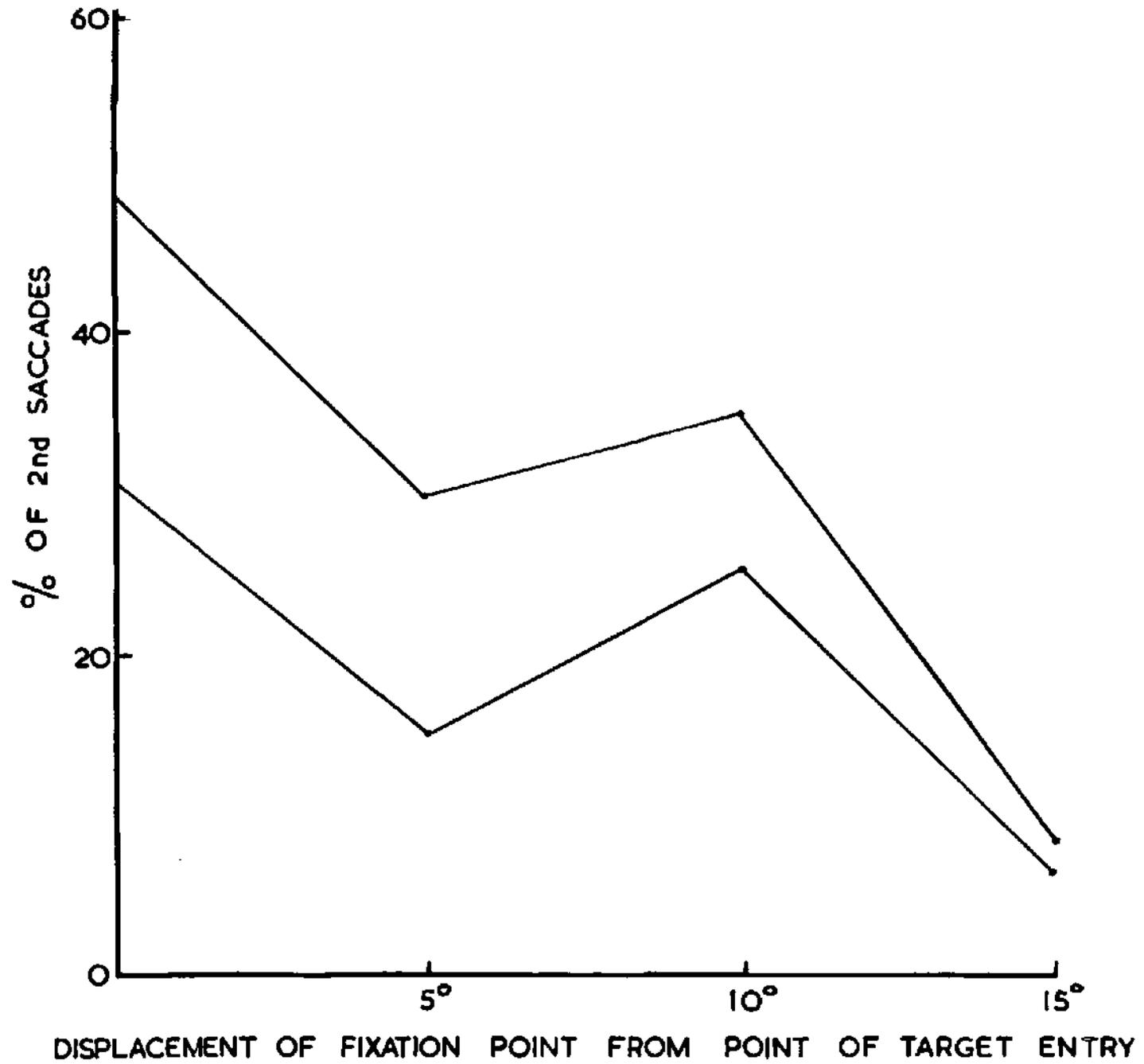


Fig. 27.

the relation of occurrence of these movements to target entry point. The incidence is greatest when target entry and fixation point is coincident.

The latent period of this secondary movement had a mean of 136.28, SD 11.99 for Subject 1 and 135.53, SD 13.56 for Subject 3 when measured from the beginning of the initial sharp saccadic movement to the beginning of the second movement.

The extent of the second movement varied from 2-8° of arc and its direction indicated that the eye in the vast majority of cases was lagging behind the target. Velocity change resulting from the movement was not capable of being measured due to the limitations of the records. The impression was gained that any change which occurred was relatively small.

The total time involved up to the completion of a second movement is about 350-400 msec.

Biphasic eye movements - backward movements prior to pursuit

During the previous exploratory experiment initial movements back to meet the oncoming target were noted at the 10° and 15° points. The type of movement is seen in Fig. 28. An experiment was therefore carried out to determine what peripheral visual field was required to produce this biphasic pursuit movement seen in Fig. 28.

Using the same field of view the subject fixated a black cross in the line of the target movement. This black cross

could be moved into any position in the field from point of entry of the target and was in practice moved from this point in 1° stages to a point 15° from target entry.

The experiment was carried out once again on Subject 1 and 3. Subject 1 was unaware of the purpose and was merely told to view the Landolt ring and recognise the gap as quickly as possible. Target velocities of 20, 30, 40, 50 and 60 degrees per second were used with the 30° field.

By varying the angular position of the initial peripheral stimulation relative to target entry point and by varying the target velocity it was possible to investigate three situations. The first in which the time taken by the target to reach the fixation point was long, 400-500 msec., a backward eye movement would give definite advantage. This was achieved by having a slowly moving target and a large angular displacement between fixation point and target entry point. Secondly, it was possible by adjusting the fixation point and the target velocity to make the time for the target to reach the fixation point so small, that backward movements would be disadvantageous. The third situation is that in which any benefit which could arise from a backward movement would be marginal in respect of the subject obtaining increased time and distance during which to pursue and discriminate the detail in the target.

Backward movement towards the oncoming target occurred as shown in Table 2. This also shows the number of occasions when backward movement could have taken place with advantage but did not occur. No backward movements occurred when the time to be taken by the target from entry point into the field of view to fixation point was less than 200 msec. The frequencies with which advantages and disadvantages accrued from the backward movement is also shown.

Table 2

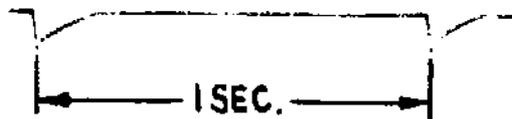
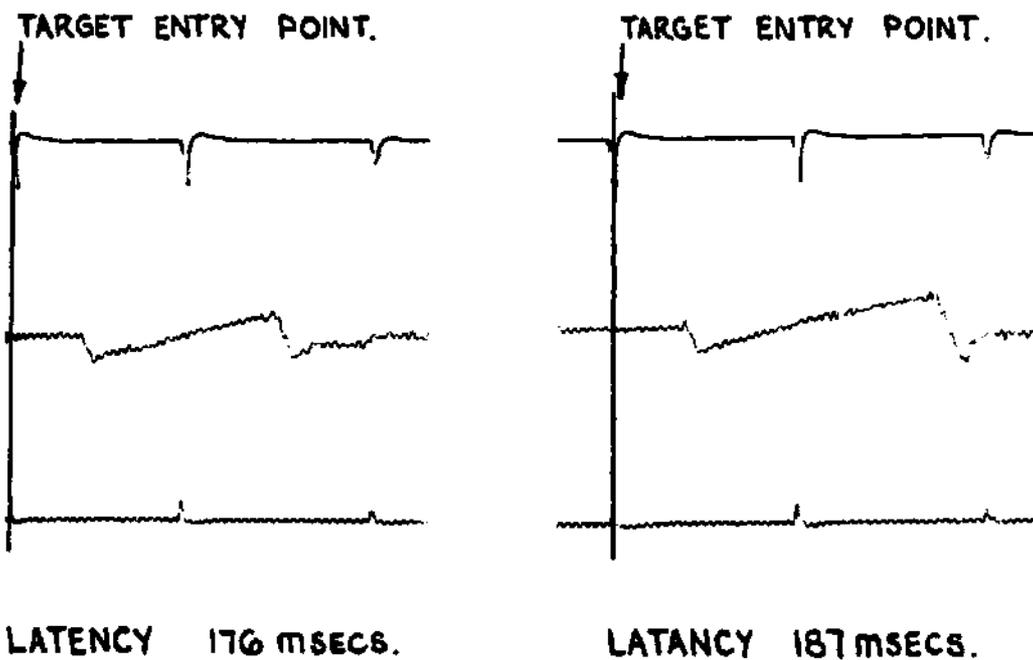
The Advantages, Disadvantages and Missed Opportunities in Biphasic Eye Movements

Subject	Target Velocity °/sec.	No. of Backward Movements	Advantages	Dis-advantages	Missed Opportunity*
1	20	22	22	Nil	Nil
	30	20	19	1	1
	40	13	9	1	3
	50	10	6	1	3
	60	Nil	Nil	Nil	Nil
3	20	15	15	Nil	18
	30	4	4	Nil	29
	40	9	9	Nil	37
	50	5	5	Nil	12
	60	2	2	Nil	24

* A missed opportunity is considered to occur when time for target to travel to the fixation point is more than 200 msec.

The extent of the backward movement varied from 1-5° of arc

THE BIPHASIC MOVEMENT OF THE EYES AND THE
ABSENCE OF AN INTERSACCADIC INTERVAL.



TIME CONSTANT 1.0 SEC.
NO. H.F. FILTER.

Fig. 28.

and the time taken was 22-40 msec. There is no delay measurable in the change from backward movement to meet the oncoming target to movement in the direction of target travel. Fig. 28. The responses of the two subjects are markedly different particularly with regard to missed opportunities.

Two features of note occurred. Firstly, no backward movements to meet the on-coming target occurred when the time taken by the target to reach the fixation point was less than 200 msec., and secondly, no delay comparable to that found with corrective saccadic movements (136 msec.) occurred between the beginning of the backward movement and the beginning of the second movement. The time taken to commence actual pursuit measured from the time of initial backward movement was about 20-40 msec. This suggests that the whole movement was initiated as a biphasic one and not one which resulted from a new mode being impressed on an initial movement.

Discussion

(a) General

In most human activities there is a variation in ability from one person to another. It is not surprising therefore, to find that the discrimination of detail in a moving object is more ably carried out by some people than others, despite the fact that all these people have normal visual acuity. It is surprising, however, that such findings as those of Ludvigh

and Miller had not previously been reported. During flight where high relative angular velocities between the observer and the observed can occur, this variation in human ability may be important to the increase of efficiency of aircraft crews, both civil and military, and thus the safety of passengers, aircrew and aircraft.

Utilising a small number of subjects (6) these variations were noted and confirm the work of the above authors not only in the variability of the human ability but in the increasing decrement in performance found as angular velocity increases.

(b) The ability of subjects with different sized targets and diminishing presentation time

The variation in each subject with regard to ability with right, left and binocular viewing is shown in Figs. 18 - 23. As a result of the experimental design it has not been possible to show significant statistical differences.

The subjects who were given 2.5 and 3.5 minute of arc targets demonstrated the improvement in performance with larger targets and these subjects who failed to recognise small moving targets, found that at the same velocities larger targets were discriminable. However, with even higher velocities, the total time during which the target was visible was reduced to below 300 msec. This time was almost entirely occupied by a latency of eye movement of some 200 msec. and the time to complete an initial

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eye movement to achieve fixation. For example, at 115° /second target velocity when the total exposure time was 260 msec. Subject 5 failed entirely to recognise the position of a gap of 2.5 minutes of arc in the Landolt ring. This failure may have been due to insufficient presentation time or to consistent failure to achieve fixation on a target having such a high angular velocity. A subsequent brief experiment showed that a 1 msec. presentation was adequate for recognition of a static target in comparable conditions. With regard to this gross failure the findings that with increasing target velocities there is an increasing incidence of corrective saccadic movements are pertinent. The total time for initial and corrective saccadic movements was of the order of 350 msec. or more. Thus, time of exposure when a corrective movement is required probably must be at least 350 msec., a time considerably in excess of the exposure time available at 115° /sec. in these experiments.

It was therefore planned to investigate the effect of increasing time of pursuit on ability to discriminate detail in the moving targets.

(c) The latent period of initial eye movements

The variation noted in this time of over 100 msec. between the shortest and longest, demands that consideration be given to causes related to the experimental method itself and to the physiological functioning of the oculomotor system.

With regard to the apparatus, it is possible that as the unlit, but visible target, passed across the field of view once or twice between each trial without being followed, that the subjects estimated the time of the appearance of the target and did not respond solely to its arrival in the field of view. The short latencies of 150 msec. may indicate premature eye movement to have taken place. As the mean latency was about 200 msec. these movements, if premature, would have been the result of an error of judgement of up to 50 msec., which would be a 25⁰/o error in estimating time of target appearance. If this inaccuracy of judgement is also to be applied to how far and how fast the initial saccade should move the eyes, it would not be unreasonable to expect a similar order of error in the initial saccade, which would have been shown by an increase in the number of 2nd or corrective saccadic movements associated with short latencies. This was not noted.

Latencies which are much longer than the mean, can readily be produced by the failure of attention of the subject and also when and if the subject over-estimated the time of arrival of the object.

However, when latencies of the above order are noted and the task required of the visual system is a combined one of pursuit and fixation to discriminate detail, it is possible that the retinal stimulation pattern may affect the latency of the eye movement. The task is more complex than the mere movement of

the eye between two static points when latencies of the order of 150 msec. are expected. Westheimer (1953) in his studies with slowly moving targets found the same scatter in initial latencies, (150-250 msec.) with entirely different apparatus in which learning was not possible. The cause of the scatter found in the results is not explicable.

To aid further discussion it is necessary at this point to refer in broad terms to the anatomy of the retina, described in Part 2, with specific regard to retinal receptor fields, and the stimulus pattern produced by static and moving targets.

The receptors which share a nerve fibre constitute an area called a receptor field. Despite the overlapping of such fields it is probable that a small target stimulating a large field will result in a response which can be related only to the whole receptor field and thus with increasing field size, movements which are intended to bring the object to fovea will be only as accurate as the information available on which the movement is based. The larger the field the poorer becomes the position information. Sensory stimulation in this pursuit and discriminating task is at these retinal fields. The nerve impulses from the retinal photosensitive cells may be modified within the retina itself, in the brain stem, and eventually reach the occipital cortex. The response to such stimulation involves cortical activity in that this pursuit is

a non obligatory function, but accurate fixation is an involuntary or reflex action.

Between static targets the eye is moved from one point to a second point through a variable angle, both points being stationary. For this type of eye movement the retinal sensory system gives information about the initial fixation. The second target when presented then induces a retinal response, the information from which is of purely retinal position character and will vary in its accuracy with the size of retinal fields. The latent period of such reflex movement is reported to have a minimum of 120 msec. and a mean of 150 msec. (Westheimer, 1954).

In the periphery of the retina where receptor units are large the information on position is much inferior to that obtainable at the fovea. An analysis of the visual sensory information must occur and a programmed eye movement of varying accuracy result. If there is an error in fixation, this error is taken out by a gliding movement, or drift, or by a further saccade. An analysis of position change only is required. It may be reasonable to assume that information to modify the movement during the quick phase of the initial saccadic movements is unlikely. The angular velocity of such movements may be as much as 200 to 600°/sec. depending on the angle to be traversed.

When the eyes are required to move from a static position to

one of movement at a given rate the task is quite different. Initial fixation is provided and it is from this point where accurate foveal stimulation is occurring that movement of the image of an object takes place into the parafovea, perifovea and near periphery, Polyak's regions 1, 2, 3 and 4. The object is moving progressively from an area of small receptor fields to an area of larger ones. Nervous impulses from the retina are thus being reduced in rate and in position accuracy as receptor fields increase in size. The change from a steady fixation state to one of a velocity equal to that of the object and to obtain adequate fixation is more complex than the static case. The latent period of such reflex movement has been found to be between 150-250 msec., a much greater latency than the latency of eye movements between static points.

(d) Variation in latency with varying retinal areas

Having regard to the potential accuracy of location within receptor fields and rate of discharge from serially stimulated fields via the optic tract fibres an experiment was conducted to measure any change in the latency of eye movement when the initial retinal stimulation was peripheral to the fovea. It seemed possible that with larger fields, more diffusely placed cones, and bearing in mind the Crawford-Stiles (1933) retinal direction effect that peripheral stimulation might result in a different reaction time.

When the natural visual world is considered it can only be in a small percentage of instances that fixation coincides with the visual origin of a moving object and that the pathway is therefore less well conditioned. This may to some extent account for the reduction in latency shown in the intermediate positions. These reductions are not, however, statistically significant. Arden and Weale (1953, 1954) and Slater Hammel (1955) have shown reaction times to be longer with peripheral stimulation.

The rate of afferent impulses, assuming each field to discharge sequentially, varies as has been stated with target velocity and with receptor field size. Polyak (1941) shows that receptor fields in line vary in number from 144 per degree of arc at fovea to about 25 at 15° peripheral to the fovea.

Theoretical mean rates of impulses per second in the zones $0-5^{\circ}$, and $10-15^{\circ}$ could therefore be - 3,000 and 1,800 respectively at $60^{\circ}/\text{sec}$. target velocity. Increase in target velocity to $75^{\circ}/\text{sec}$. would raise the impulses per second at the $15^{\circ} - 10^{\circ}$ arc to one comparable with the $10^{\circ} - 5^{\circ}$ arc at $60^{\circ}/\text{sec}$. This increase in target velocity did benefit the latency and at all points a decreased time of latency was noted. Fig. 25. The extent of this decrease in latency shown is probably within the day-to-day variation to be expected in such experiments and no significance can be attached to the increase shown in this particular experiment. The interpretation may also indicate

that higher velocity targets may be associated with shorter eye latencies. This cannot be extracted from the data available in these exploratory experiments.

Eye movement recordings when the above mentioned peripheral fixation points are utilised show a much more leisurely initial saccadic movement. The saccadic movement complex is increasingly reduced in the magnitude of each of its phases of acceleration, steady overtaking velocity, and deceleration thus demanding of the extrinsic eye muscles less violent and possibly a better controlled movement, the reduction in the incidence of corrective saccadic movements is possibly due to this effect. Fig. 27. Clarification of these effects, on eye movements and latencies was planned to be carried out at target velocities in which discrimination is more marginally achieved.

(e) The second saccade

A marked feature noted by all investigators of eye movements has been the saccadic nature of such events. Its presence in reading, pursuit tasks, fixation reflex movements between stationary points, its appearance with various labyrinthine stimuli and in pathological conditions among many others shows that this is a basic pattern in eye movements.

In these experiments they occurred firstly as the quick overtaking movement in pursuit of the target and secondly as distinct movements during the pursuit phase.

These second saccades during pursuit are considered to be corrective in nature, the fixation achieved during the ensuing steady tracking phase after the first saccade being inadequate. This corrective saccade is reflex and its existence does not reach consciousness. In extent it varied from 2-8° of arc and occurred after a mean interval of about 136 msec., measured from the beginning of the previous saccade. This interval duration accords well with the findings of Westheimer (1954b).

The increasing incidence of these second saccades was shown in Fig. 26 as target velocity increased from 30° to 60°/sec. This is taken to indicate that fixation is less often achieved by the initial eye movement, particularly when the initial eye movement is of necessity a sharp saccade. Fig. 26 shows the decline in incidence of second saccades when fixation is displaced from target entry point. The initial movements of the eyes are more leisurely, which suggests that it may be muscle response inadequacy which causes the requirement for a second saccade.

The direction of the corrective saccadic movement in all but two pursuits indicate that the eye was lagging behind the target by virtue of not moving far or fast enough - undershooting the position or velocity requirement, or a combination of both. This undershooting is a common finding by many authors in saccades between two fixed points although moving too far - overshooting, is also frequently recorded. It was not possible

to determine whether the subsequent eye angular velocity was greater or less than that occurring before the second saccade owing to the nature of the recording. The time factor involved in such movements up to the completion of the second saccade is of the order of 350-400 msec. (1st latency + 1st saccade + latency of 2nd saccade + 2nd saccade). With a restricted field of view, 30° of arc in these experiments and restricted time in Miller and Ludvigh's experiments, 400 msec., a deterioration might well be expected purely on a basis of insufficient exposure time. This occurrence of corrective movements, however, does not help to explain the difference between the subjects at the target velocities used.

Both subjects (of differing ability) reacted in the same general manner with regard to the incidence of saccades at the relatively low target velocities used.

A further investigation of the incidence of saccades at higher target velocities was considered necessary to permit more adequate correlation of corrective saccades with target velocity and the relationship between diminution of visual acuity and increasing target velocity.

(f) Backward movements of the eyes prior to pursuit movement

During these experiments in which initial retinal stimulation was peripheral, eye movements were recorded and showed that the eyes on occasion moved back towards the oncoming target and

then swiftly reversed their direction to one of pursuit.

One feature of note occurred. No delay comparable to that found with corrective saccadic movements (136 msec.) occurred between the end of the backward movement and the beginning of the pursuit movement. The time taken to commence actual pursuit measured from the time of initial backward movement was about 20-40 msec. which is mostly taken up by the movement itself. This suggests that the whole movement was initiated as a biphasic one and not one which resulted from a corrective mode being impressed on an initial movement.

When marginal conditions were used the vast majority of backward movements, if they occurred benefitted the discrimination task by giving greater time and distance during which to pursue the object. A few backward movements occurred to the detriment of the pursuit task. Under these conditions the control system served by the retina and subserved by the oculomotor system can initiate relatively complex movements in which no delays in the change of phase are occasioned during the programmed movement.

Summary

Exploratory experiments are described on the ability to discriminate detail in moving targets.

The findings of Ludvigh and Miller that visual acuity deteriorates with increasing angular velocities of targets is

confirmed as is also the lack of correlation between static visual acuity and acuity for a moving target.

Eye movement recordings were made by the cornea-retinal potential method.

The target velocities employed were 0-85°/sec. for the majority of experiments and some were conducted at up to 115°/sec. angular velocity.

Discrimination of detail in moving targets is improved with increase in target size.

The latency of eye movements is in the 150-250 msec. zone. The total time from target entry to completion of a corrective saccade is 350 msec. or more.

The latency of eye movements when target entry point and fixation point were not coincident and showed some evidence of shortening at 5° and 10° from fovea and some lengthening at 15°.

There is an increase in the number of second saccades with increasing target velocity. These are considered to be evidence of failure of the initial fixation movement of the eyes.

The duration of the phase from the beginning of the 1st saccade to the beginning of the second had a mean of 136 msec.

When initial stimulation is on the retinal periphery, backward movements to meet the oncoming target were noted. The type of movement indicated that this was a planned biphasic movement and not one in which a corrective saccade is imposed

on an initial eye movement.

When the break in the Landolt C is at the 3 and 9 o'clock positions it is seen more readily than at the 6 and 12 o'clock positions.

Conclusions

To add further to the study of the loss of visual acuity and the ability of man to see detail in moving objects the following programme is required.

1) The position error and velocity error of the eye in relation to the moving target which should warrant a corrective fixation movement.

2) Detailed examination of the second saccadic movement.

3) The investigation of ability at higher angular velocity and the examination of the time factors and movement patterns of the eyes.

4) The effect of increasing viewing time and the effect of permitting freedom of head movement.

5) The co-ordination of head and eye movement.

6) Further investigation of the time factors and patterns of eye movements when the target appeared in the periphery of the retina and tracking towards the fovea.

7) The nature of eye movements when the target moves vertically relative to the eyeball.

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PART 4

The Ability to Perceive Detail in Moving Targets

Method - The Aldis lamp rotation projection system

The limitations in the angular velocities of targets available on the centrifuge system used for the exploratory experiments and the lack of flexibility in its performance necessitated the design and assembly of a new apparatus and electronic control system. This is described in detail in Appendix 'A' and Fig. 1 of Appendix 'A'.

The apparatus basically consisted of an Aldis projector mounted on a power driven turntable. An electric motor with an electronic control ensured that the rate of rotation of the system was accurately matched to the demand.

Slides were made of Landolt rings for the Aldis projector which were mounted in a holder and permitted rotation of the Landolt ring into any position.

The rotation was in either direction through an arc of 270° of which 90° were available for routinely projecting on to a white screen in a laboratory and 160° for the centrifuge chamber, which was used for the study of head and eye movements. The screen was curved and had a radius of 16 ft. A fixation point was provided which could be moved to any part of the curved screen. At the centre of this segment of a circle was placed the projector system. The subjects sat on a chair

immediately behind the projector and by leaning forward their heads were approximately above the centre of rotation of the projector. The angular velocity of the projected Landolt ring was thus to all intent constant throughout its traverse.

Two photocells were mounted on the screen, one at the edge of the screen which gave a record of the time the Landolt ring projection entered the field of view of the subject, and the second placed 50° towards the centre of the screen which permitted calibration of the rotation speed of the Aldis system. It also permitted a physical check of the target velocity at each run.

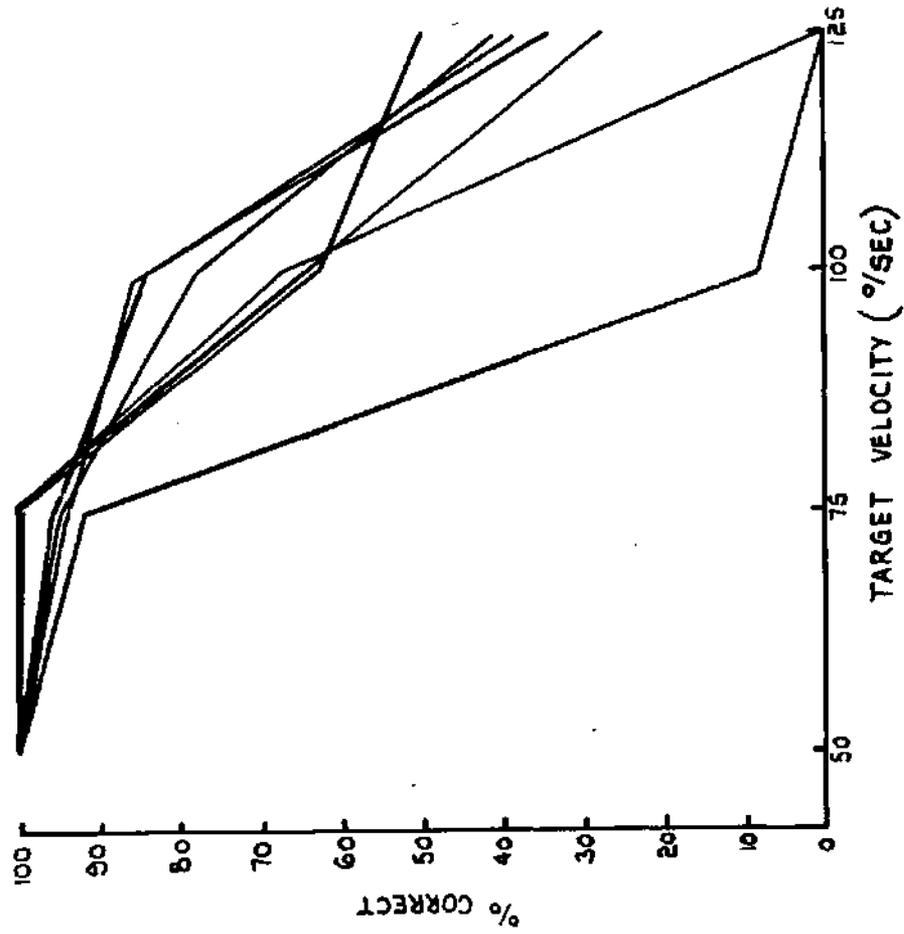
The whole operation was conducted in a dark room, the brightness of the Landolt ring and fixation point was 1 millilambert (Holophane Lumeter).

The presentation of the orientation of the Landolt ring changed with each presentation and the angular velocity of the target varied randomly between 50, 75, 100 and 125° /sec. The time of viewing with each velocity could be varied by a screen which cut off the projected beam at any desired point.

The subject was instructed to regard the fixation point steadily and then, when he saw the moving target, to identify the position of the break in the Landolt ring. Head movement restraint was provided initially by a bite board but it was found that a trained subject who cupped his chin in his hands

THE DECREMENT IN DISCRIMINATION ABILITY WITH INCREASING TARGET
ANGULAR VELOCITY (25 OBSERVATIONS / POINT)

SUBJECT 1.



SUBJECT 2.

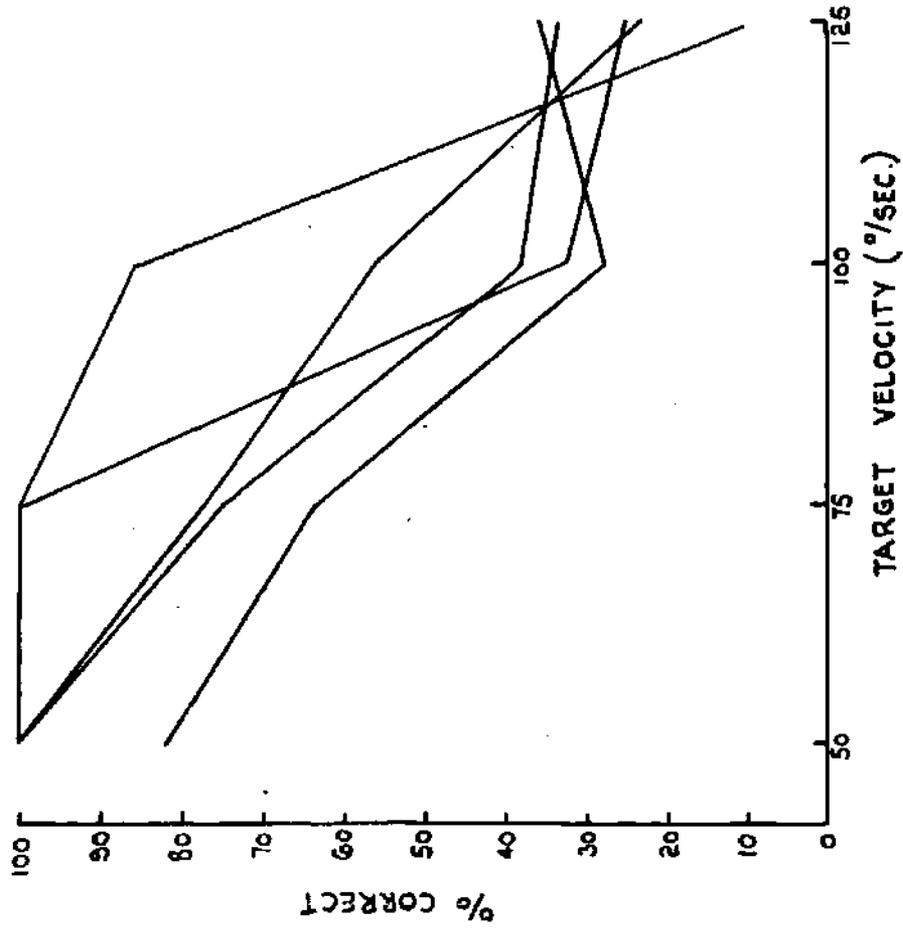
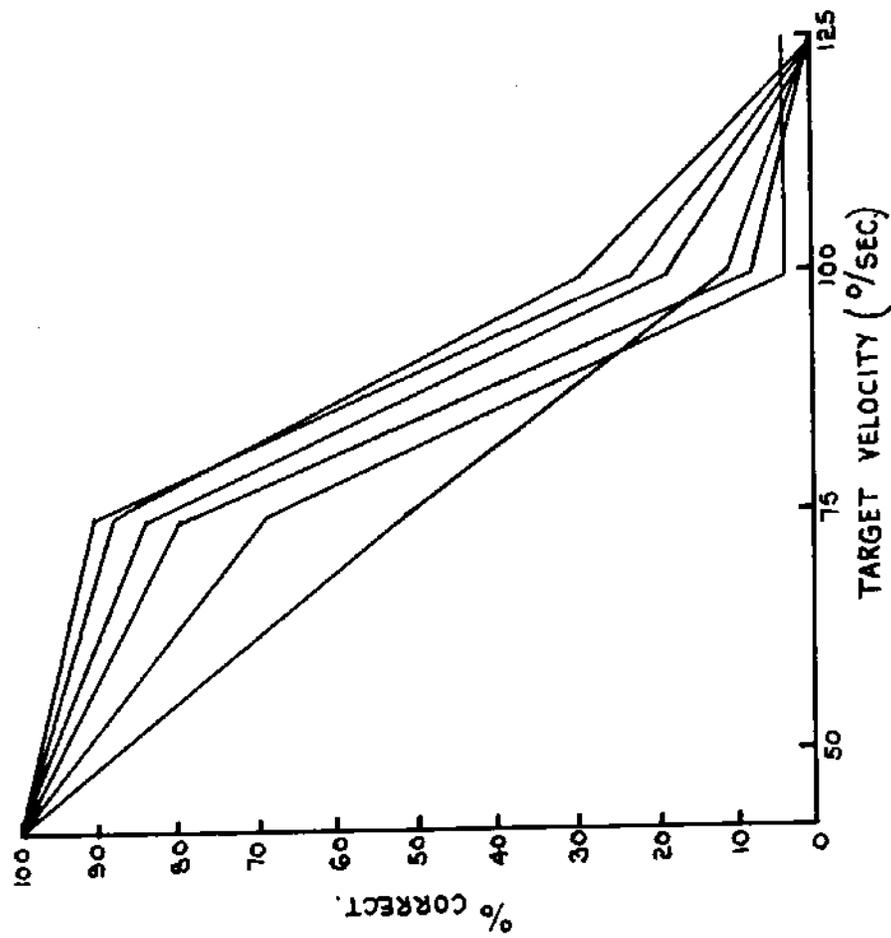


Fig. 29

THE DECREMENT IN DISCRIMINATION ABILITY WITH INCREASING TARGET
ANGULAR VELOCITY (25 OBSERVATIONS/POINT)

SUBJECT 3.



SUBJECT 4.

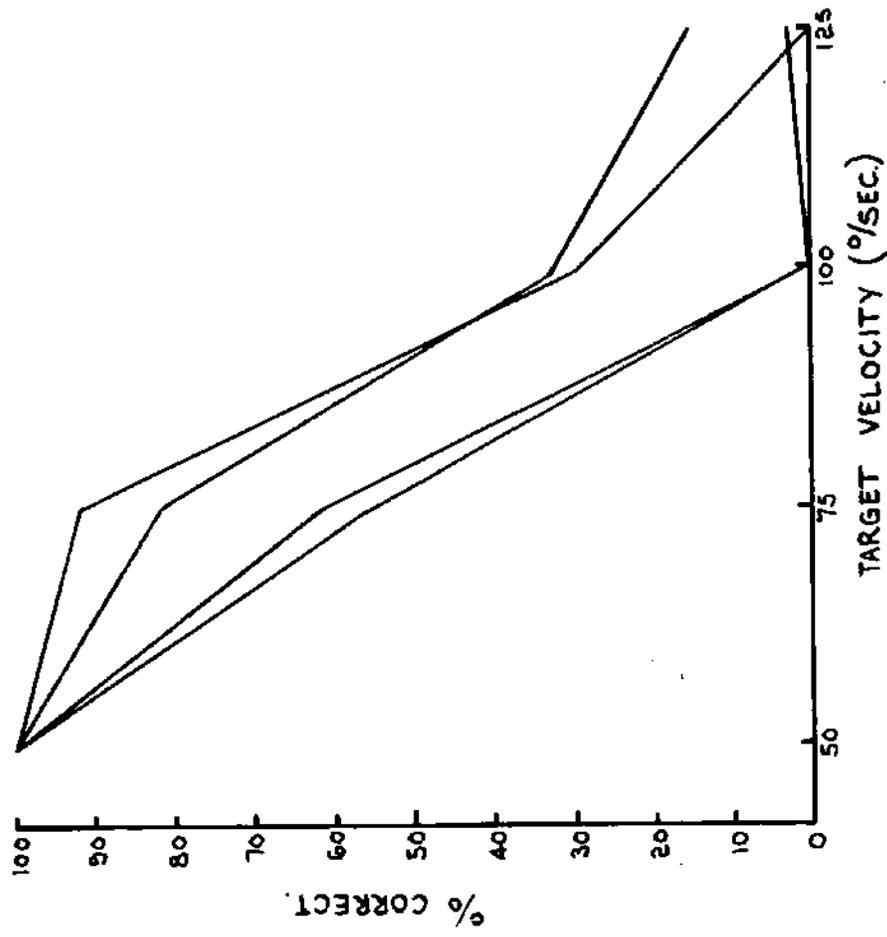
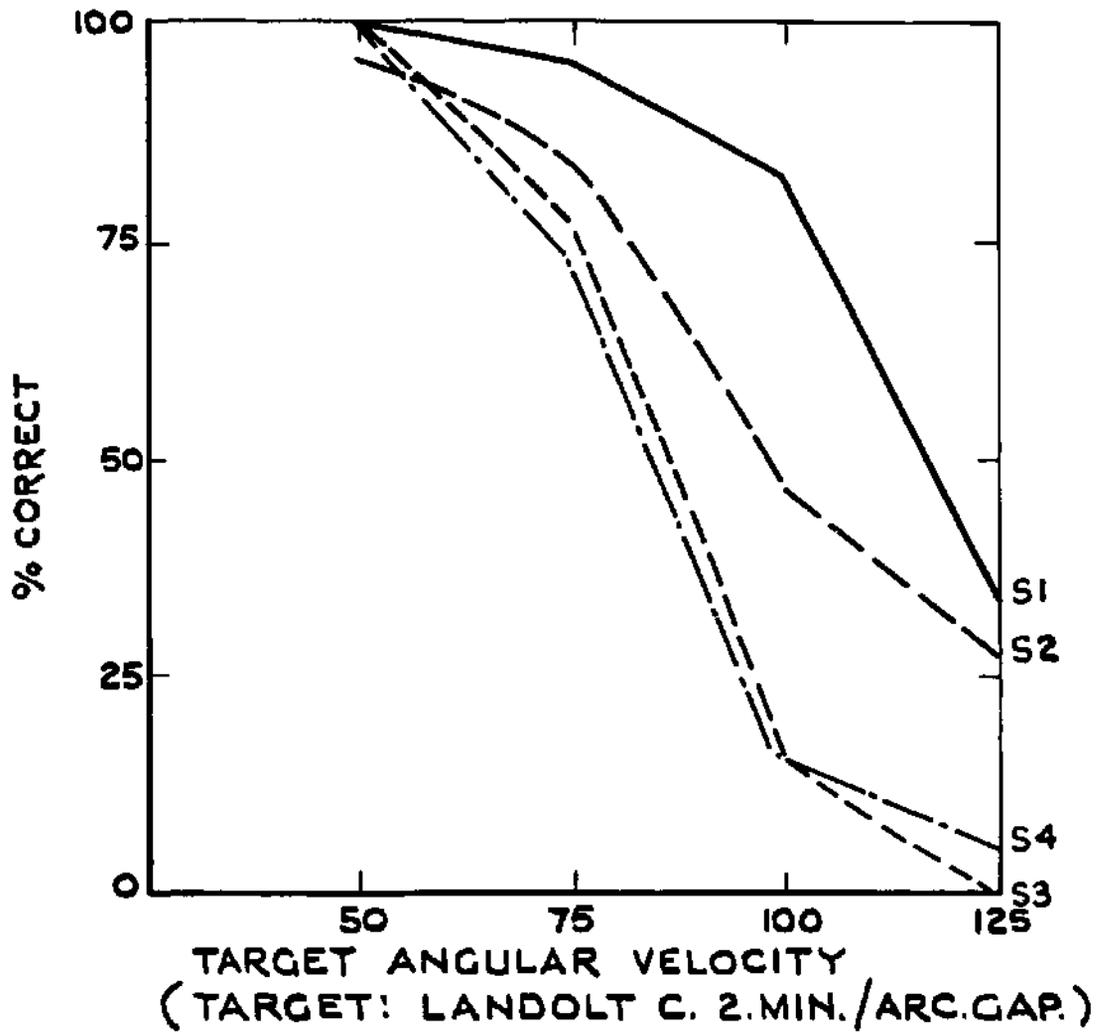


FIG. 30.



SUBJECT AVERAGE ABILITY ON ALL RUNS (HEAD STATIC.)

Fig. 31.

the elbows resting on a table, did not move his head. This was checked by recording head movement. The relief from the need for a dental bite was most welcome. An experimental session consisted of 100 pursuit movements and had a duration of about 60 minutes. The viewing at all times was binocular which is a more comfortable and normal functional condition, one which showed moderate benefit in acuity ability in the exploratory stages, and one which has been shown by Sakiyama (1953) and Sedan et al (1957) to be superior to monocular viewing.

The basic ability of subjects with random velocity targets

The recording of ability was made simultaneously with investigation of eye movements and the results of each subject with a 2 min. of arc target at 50, 75, 100 and 125°/sec. angular velocity relative to the subject shown in Figs. 29, 30, 31.

There is a significant difference in ability demonstrated. Subject 1 had an overall correct response of 61.36°/o; Subject 2, 55°/o; Subject 3, 46.73°/o and Subject 4, 40.65°/o.

The decrement in performance generally commences at 75°/sec. target velocity and at this value Subject 1 showed a small 0-10°/o decrement, Subject 2 showed a decrement varying between 0 and 35°/o and Subjects 3 and 4 showed decrements varying between 10°/o and 50°/o.

At 100°/sec. target velocity Subject 1, with one exception

SUCCESS RATE BASED ON THE ASSUMPTION THAT THE CORRECTIVE PHASE IS NOT COMPLETED.

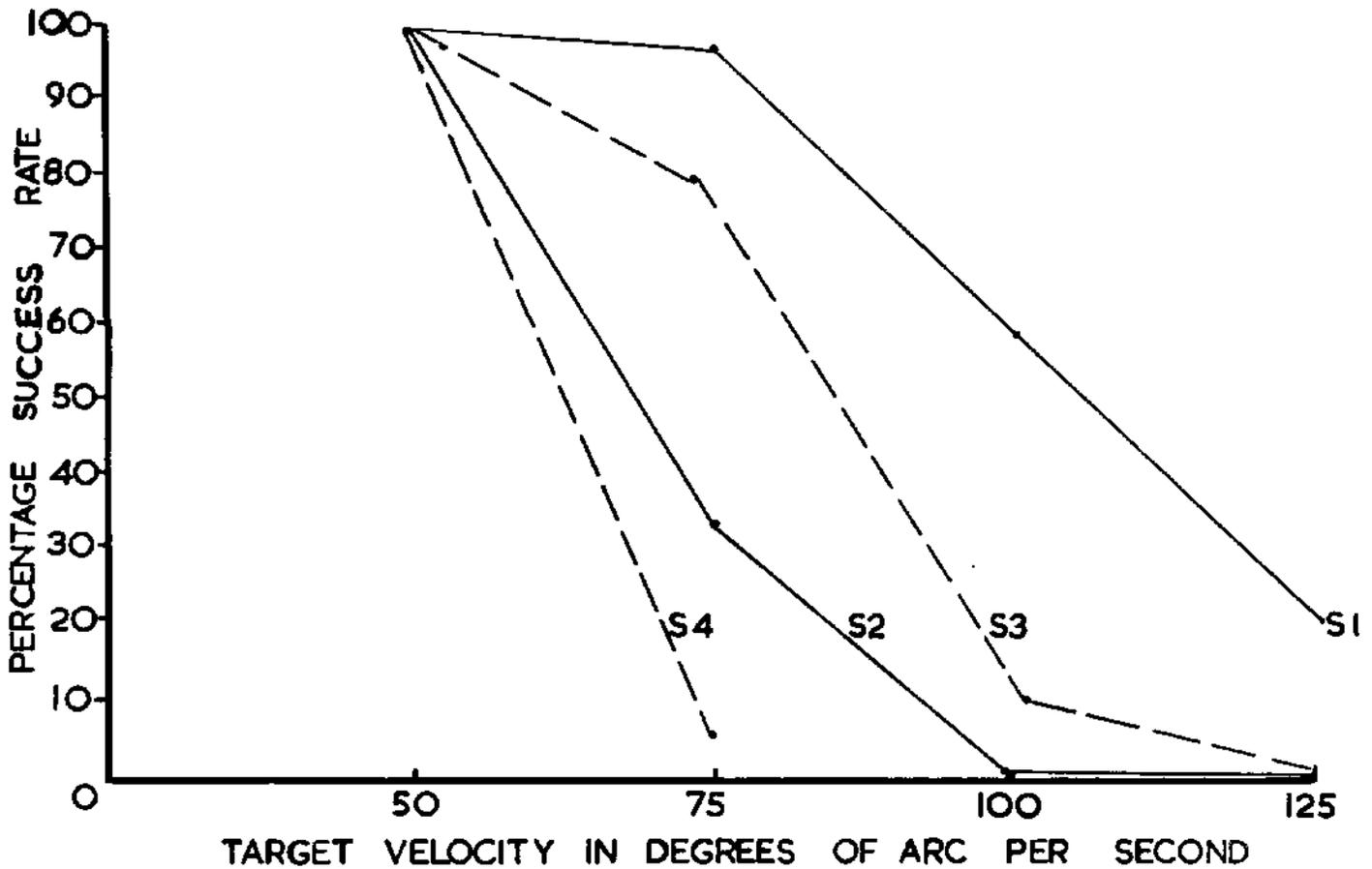


Fig. 32.

retained his ability at 60-85°/o correct value. Subject 2 on one occasion attained 85°/o correct but on the other runs had a correct score of 30-55°/o. Subjects 3 and 4 both attained 30°/o or less and in particular Subject 4 on two runs recognised no targets presented.

At 125°/sec. target velocity Subject 1, with one exception of a zero correct score, retained an ability in the 30-40°/o correct range, Subject 2 was in the same range and Subjects 3 and 4 seldom recognised the gap in the Landolt ring.

In Fig. 32 the success rate the subjects would have obtained on the assumption that the corrective phase would not be completed is shown and can be compared unfavourably with Fig. 31

The relationship of ability to latency of eye movements

The variation in latency during any one, or indeed all, experimental programmes not infrequently exceeded 50 msec. An analysis was carried out to resolve any differences in the incidence of discriminating the detail with variations in the latencies. Target velocities of 75°, 100° and 125°/sec. were chosen; at 50°/sec. the number of errors is very small.

A sample group from each subject was taken and to achieve three equal segments, the mean latency ± 0.43 of the standard deviation was taken as the middle segment, all below was the 1st segment, and all above was the 3rd segment.

Table 3

Percentage Success Rates for Four Subjects with Short, Medium and Long Latencies at 75, 100 and 125°/sec. Target Velocity

Subject	Target Velocity °/sec.	Short Latency °/o Success	Medium Latency °/o Success	Long Latency °/o Success
1	75	100	95	97
	100	58	70	51
	125	35	31	17
2	75	83	83	87
	100	52	43	34
	125	32	25	21
3	75	58	66	40
	100	13	16	0
	125	9	0	0
4	75	86	69	51
	100	22	12	6
	125	0	0	0

A greater percentage of successful target discriminations takes place with average latencies and latencies shorter than average. As latency increases the separation of fixation point and target point is increasing thus demanding greater movements during the initial saccade. The greater the movement the greater the likelihood of inaccuracy of the eye movement.

The effect of increasing viewing time

Eye movement recordings have shown that immediately following the initial eye rapid movement there is frequently another rapid movement. The latency of the initial movement varied from 150 to 300 msec., the interval between the beginning of the first eye movement and the beginning of the second varied from 100 to 180 msec., and the duration of the second eye movement varied from 10 to 20 msec. The total time elapsed before the second movement is complete generally exceeded 400 msec. The second eye movement is considered to be one which reflexly corrects residual errors in fixation after the first eye movement. Given adequate time for the second or even subsequent corrective eye movements to be completed an improvement in ability was postulated.

The Aldis lamp system was modified by screening devices which permitted the target to be exposed for 400, 500, 600 and 700 msec. at angular velocities of 50, 75, 100^o of arc per sec. At 125^o/sec. the maximum viewing time obtainable with the apparatus was 600 msec. Sixteen observations were made at each speed and exposure time. These could not be randomised as resetting for a new exposure in the dark was not possible and even with light available took over one minute.

Increase in viewing time at target angular velocities of 50, 75 and 100^o/sec. resulted in improved ability by all subjects. At 125^o/sec. the improvement was just noticeable in 2 of 5

DISCRIMINATION ABILITY. EYES ONLY MOVING.

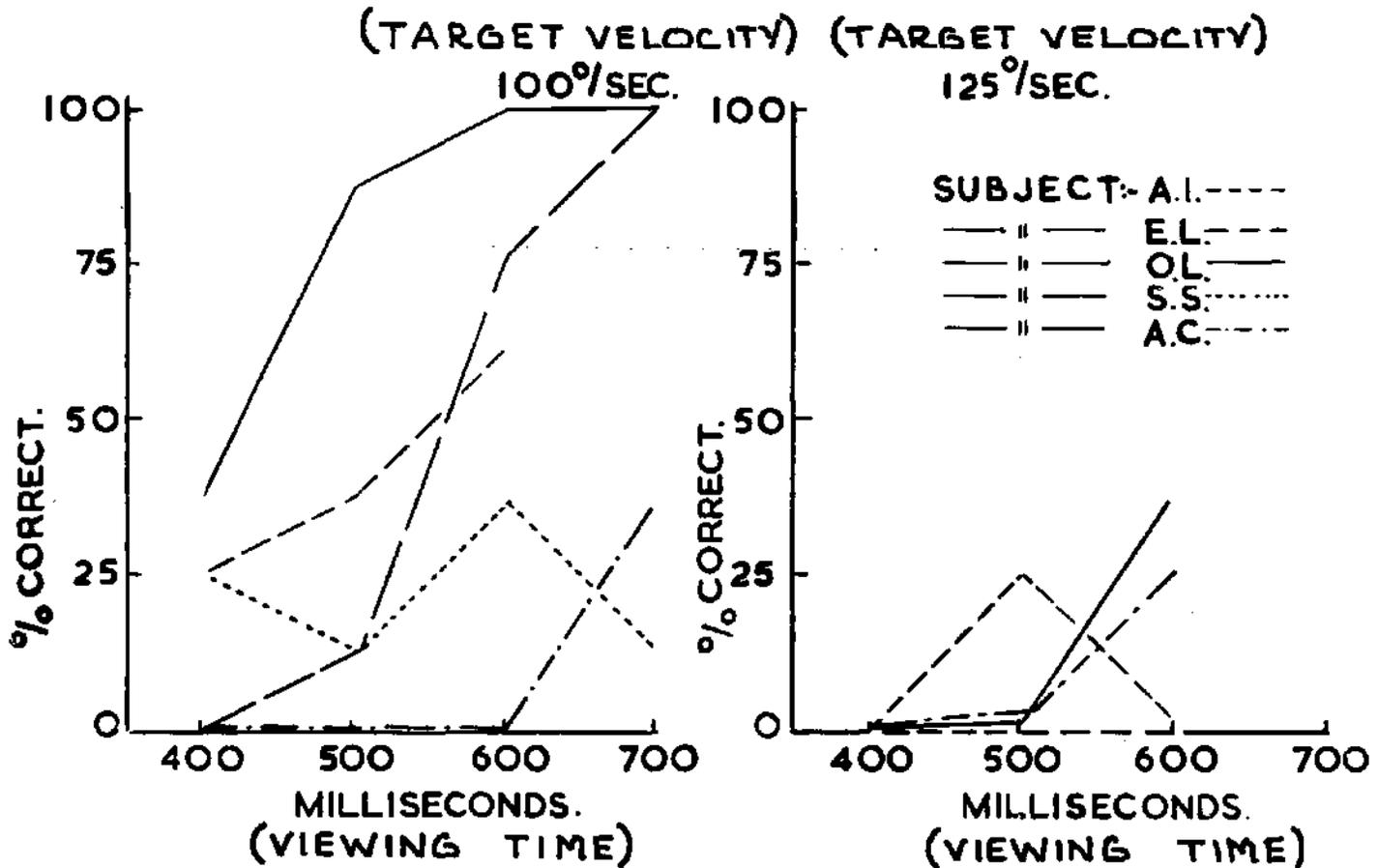
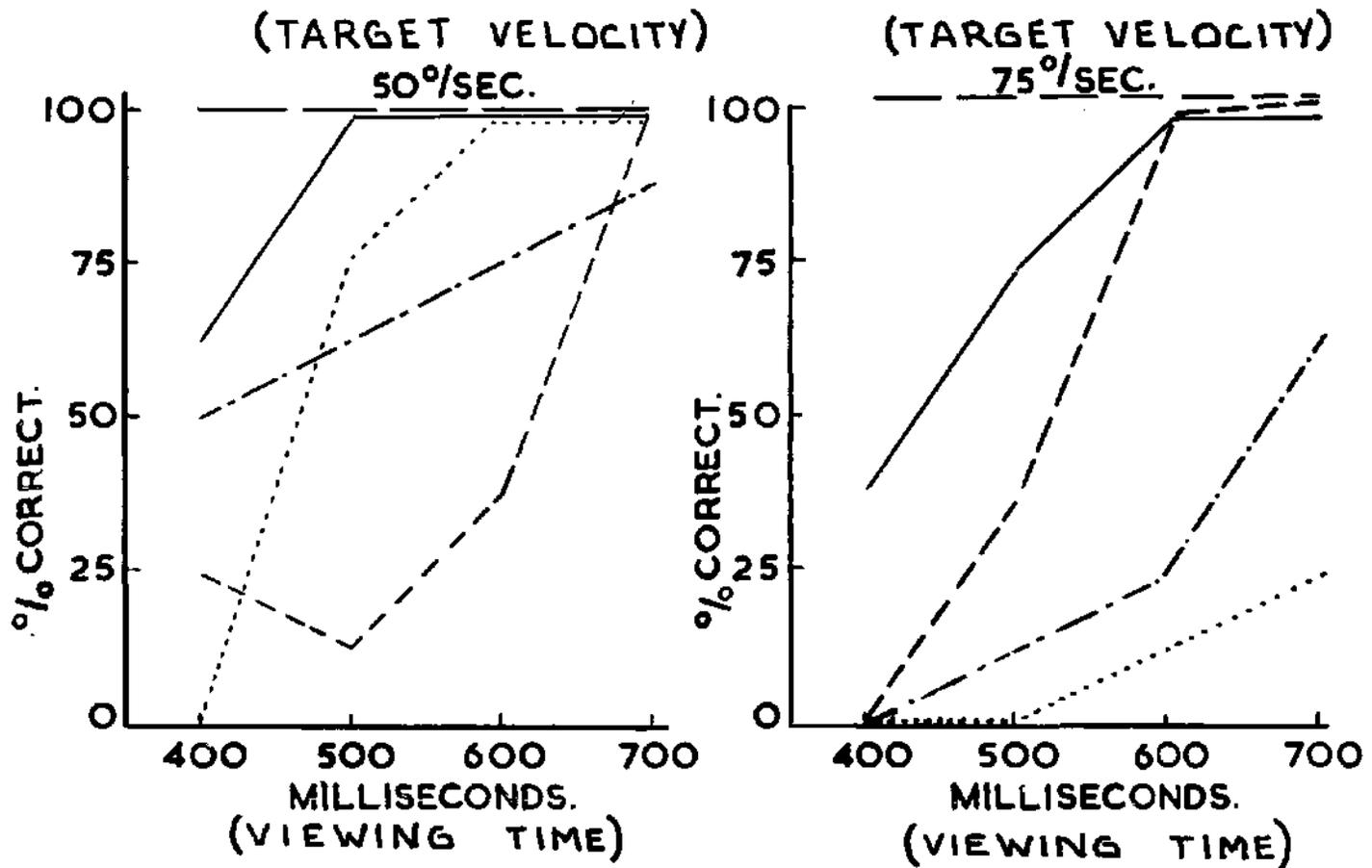


Fig. 33.

subjects with a 600 msec. exposure.

The results for the five subjects are shown graphically in Fig. 33.

It is concluded that the effect of increasing viewing time permitted the completion of the corrective saccade or saccades and thus increased the incidence of accurate fixations and recognitions.

The effect of co-ordinated eye and head movement

The response in viewing a moving object is one of eye and head movement, and if the arc traversed by the object is sufficiently large body rotation will also occur. The spectators at a tennis match demonstrate effectively and clearly this composite movement of head and eye as the ball moves from one end of the court to the other. The eye, head and body rotation is readily observed at Air Displays.

The nature of the nervous mechanism controlling eye movements and the fineness of the extraocular eye muscle fibres suggested that exquisiteness of control is the desired feature and not the ability to achieve and maintain maximal contractions with accuracy. The head is capable of providing a fast moving steady platform on which eye movements are superimposed, thus reducing the need for maintaining gross contractions of extraocular muscles. It is also capable by its rotation of increasing the somewhat limited binocular field of view of man.

DISCRIMINATION ABILITY. EYES & HEAD MOVING.

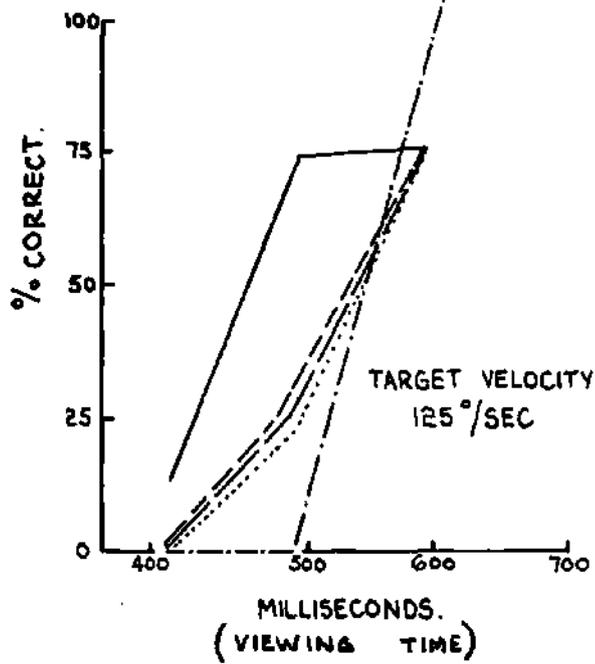
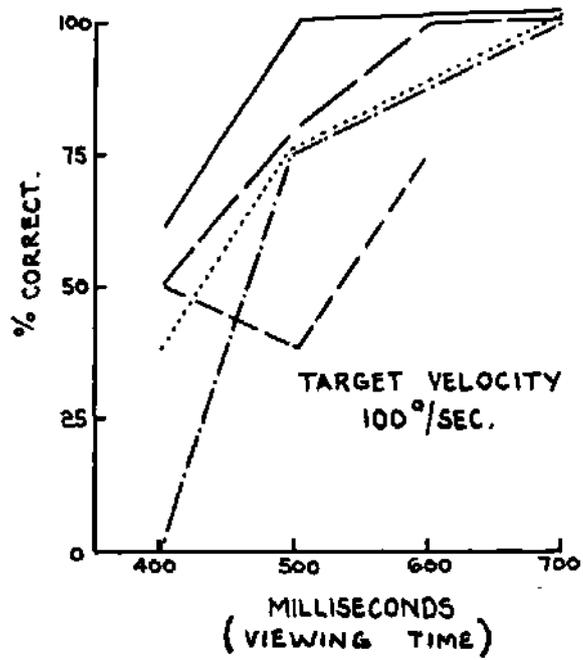
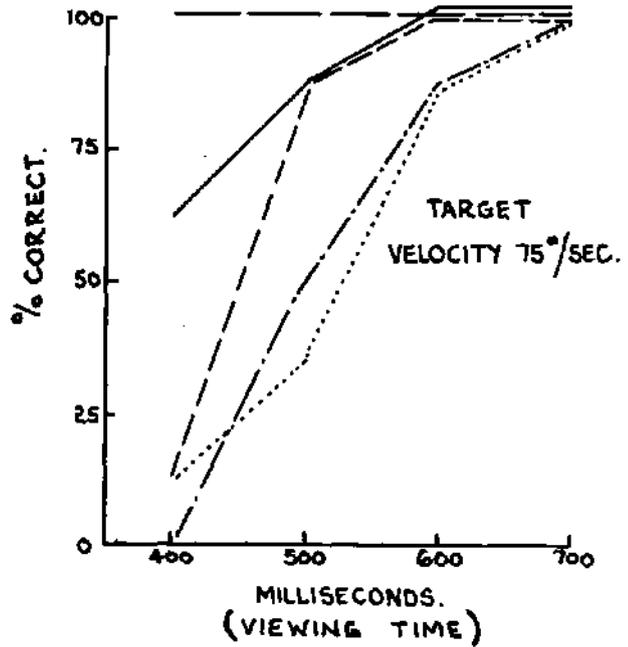
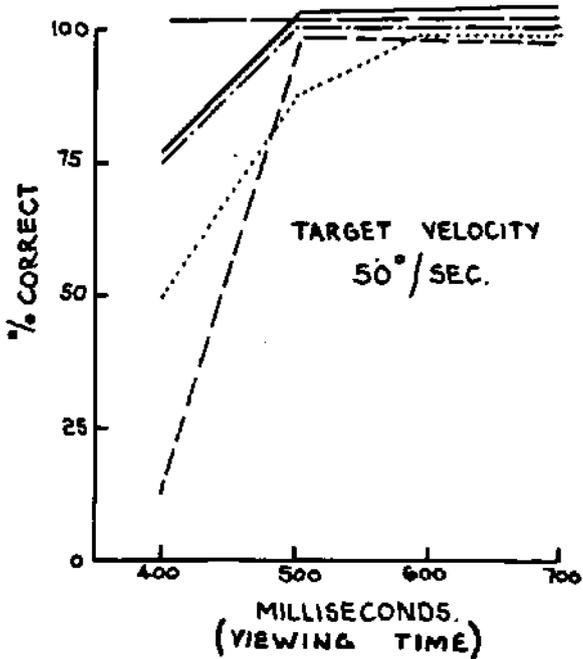


Fig. 34.

DISCRIMINATION ABILITY, COMPARISON OF EYES ONLY
AND HEAD EYE MOVEMENT.

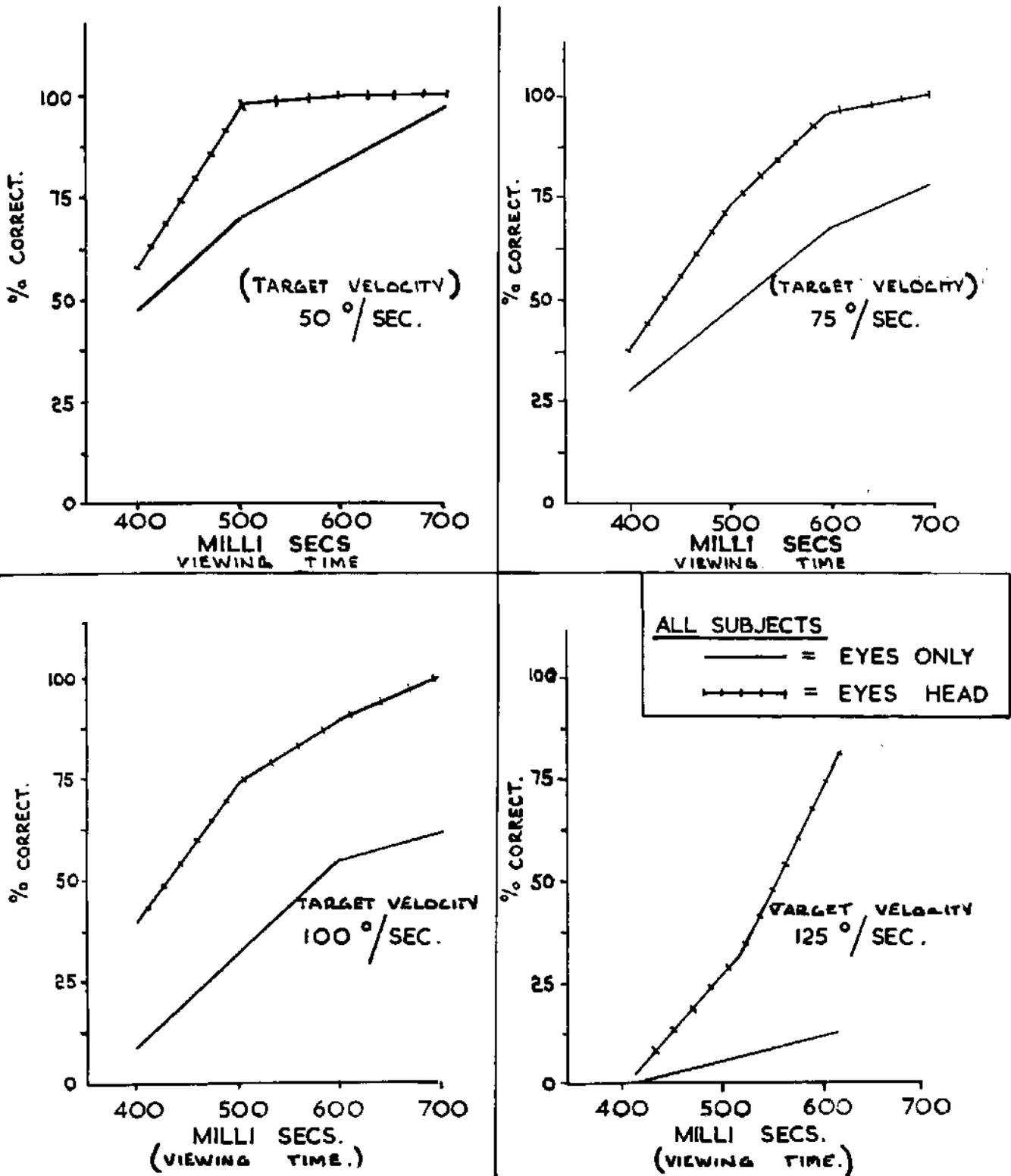


Fig. 35.

The Aldis lamp projector system was modified by the inclusion of screening devices to permit target exposure times of 400, 500, 600 and 700 msec. for targets having angular velocities relative to the viewer of 50, 75 and 100°/sec. At 125°/sec. target angular velocity the maximum exposure time available was 600 msec.

All subjects demonstrated an improvement in ability compared to the 'head still' condition when the time of exposure was 500 msec. or more at all target velocities. The results are shown in Fig. 34 and a comparison of eyes only and head and eye movements in Fig 35 shows the superiority of the combined system.

The ability to use eyes and head in pursuit tasks resulted in improvement in the performance of all the subjects, but this only occurred when the exposure time was at least 500 msec. The inference is that head movement is only an asset when time permits the achievement of a reasonable degree of overtaking of the target by the head and has effectively reduced the rate and amount of rotation of the eyeballs in relation to the head.

Ability with non-random velocity targets

In the basic experiments on the ability to subjects to discriminate the detail in the presented and moving Landolt ring, the velocities of the object had been randomised between 50 and 125°/sec. By this means the subject did not know, nor

could he anticipate target velocity and could not learn to what extent and what velocity the eyes would have to be moved to achieve fixation.

By presenting a series of targets at a constant velocity if learning takes place then it would be expected that there would be fewer errors of discrimination in the later presentation of any series.

Subjects 2 and 3 carried out a series of 100 and 200 pursuits respectively with a target velocity of $100^{\circ}/\text{sec.}$ and $125^{\circ}/\text{sec.}$ The interval between pursuits was approximately 5 seconds.

Table 4

Occurrence of Errors in Series of Constant Velocity Target Presentations

Subject	Target Velocity $^{\circ}/\text{sec.}$	Errors in Presentation Numbers				
		1-20	21-40	41-60	61-80	81-100
2	100	3	4	4	3	2
3	100	3	4	4	4	4
2	125	14	16	14	17	15
3*	125	8	9	7	10	10
3*	125	5	7	5	7	8

* Subject 3 (writer) at this stage in the experimental programme had been conducting all the experiments and had developed a much improved performance, not only relative to his original ability but to that of Subject 2, i.e. considerable learning had taken place.

05

The number of errors was evenly distributed throughout the series as shown in the above table, and this suggests that either no learning takes place, which would be unusual in the field of human psycho-motor accomplishments, or that despite learning in opto-motor neural integrations the muscular response is variable in response to a constant velocity demand.

Although the retinal stimulation pattern was the same throughout these series the latent period of eye movement varied with each presentation. These variations would require the overtaking phase of the first saccade to vary also. The longer the latency the faster would be the overtaking velocity and the larger the arc to be traversed before a steady state is reached with equalised eye and target angular velocities.

The effect of initial peripheral retinal stimulation

The increase in the size of retinal receptive fields in the retinal periphery and the corresponding diminution of fields per degree of arc suggested that the accuracy of information about target position and velocity at any one moment would depend on receptive field size. The smallest fields are in the central fovea and the largest is the periphery.

It is assumed that the eye movement is completely planned and irretrievably organised and ordered some time before an actual eye movement begins. This is shown in one of Westheimer's (1954a) experiments in which with a displacement of a

THE RETINAL AREAS STIMULATED BY MOVING TARGETS OF 50-125 %/SEC, VIEWING DURATIONS OF 100 & 200 M.SEC. AND SEEN FROM VARIOUS FIXATION POINTS WITHIN THE ARC OF MOVEMENT.

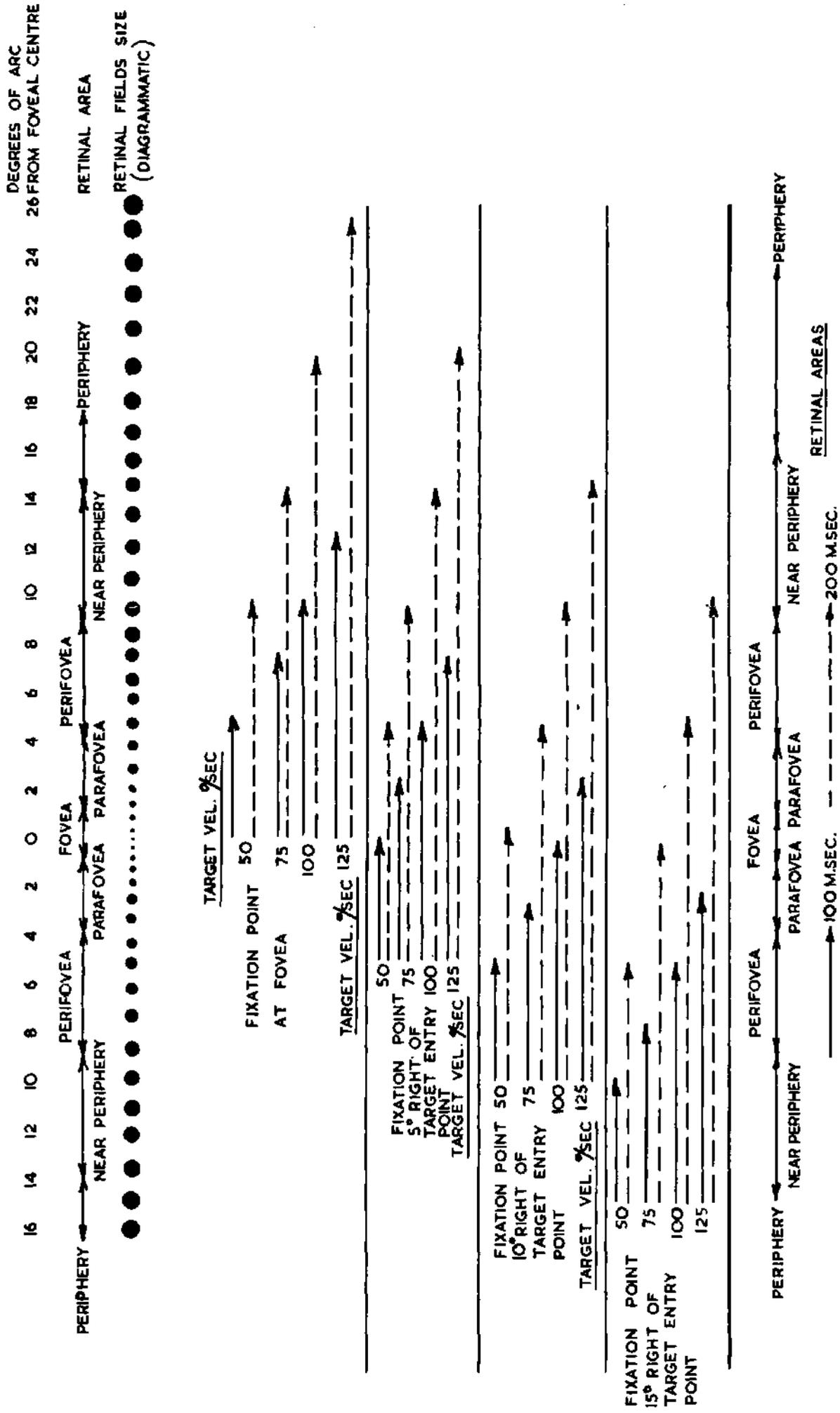
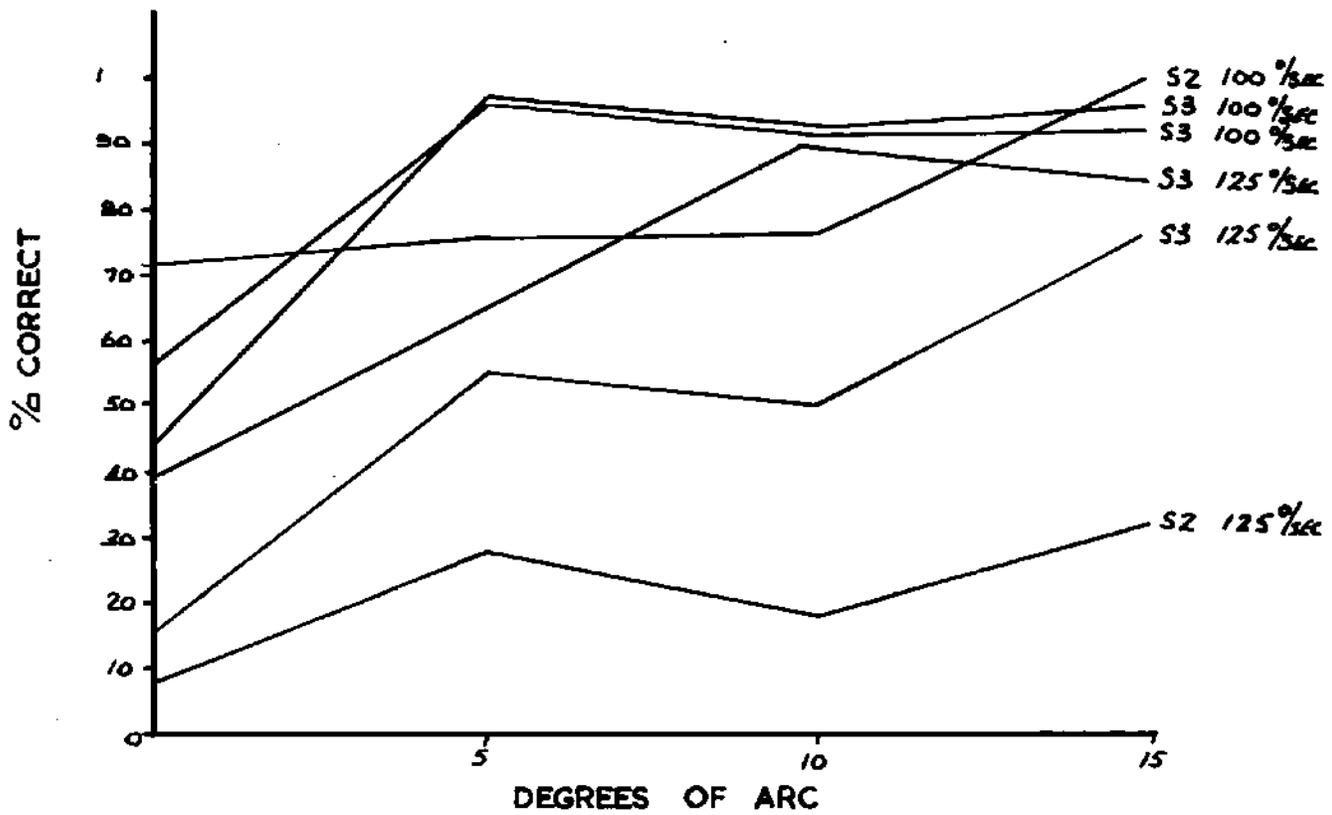


Fig. 36

moving spot for only 40 msec. followed by its return to the originating position, the eye, after a typical reaction time moved to a position which the object might have occupied had it not returned after the 40 msec. The subsequent eye movement had a latency of 120-150 msec. The latest information on which the movement is based may therefore not be the best. In Fig. 36 this is schematically presented.

In Fig. 36 there are depicted the foveal regions described in Part 2 and Figs. 7 and 8, a representation of retinal field sizes and the arcs through which a target would move at 50, 75, 100 and 125°/sec. angular velocity during 100 and 200 msec. of fixation. The arcs are related to the fixation points, 0°, 5°, 10°, 15° to the right of target entry point. The arrows indicate the retinal areas through which the target will pass prior to eye movement and it can be seen that these vary with fixation point.

At 0°, i.e., fovea as target entry point, the retinal areas stimulated become steadily more coarse for all speeds and durations. At 5° the retinal areas become finer and then coarsen. This process continues at 10° when target velocity is 75°/sec. or more but at 50°/sec. target velocity and 100 msec. of target travel the information continually improves. If however, 200 msec. target travel is utilised in assessing eye movement requirements information again deteriorates during



DISCRIMINATION ABILITY WITH TARGET ENTRY VARIED FROM 0°- 15° OF ARC PRECEEDING FIXATION POINT.

the second 100 msec. At 10° with 100 msec. utilised for assessing eye movement requirements the potential information is improving at 50, 75 and $100^{\circ}/\text{sec}$. target angular velocity. At 200 msec. a coarsening of retinal areas stimulated again occurs at 75, 100 and $125^{\circ}/\text{sec}$. but not at $50^{\circ}/\text{sec}$. At 15° with 100 msec. utilised for eye assessing movement requirements the potential information improves at all speeds during the traverse but never reaches the optimum available. At 200 msec. at 75, 100 and $125^{\circ}/\text{sec}$. target velocities an optimum rates is more nearly obtained.

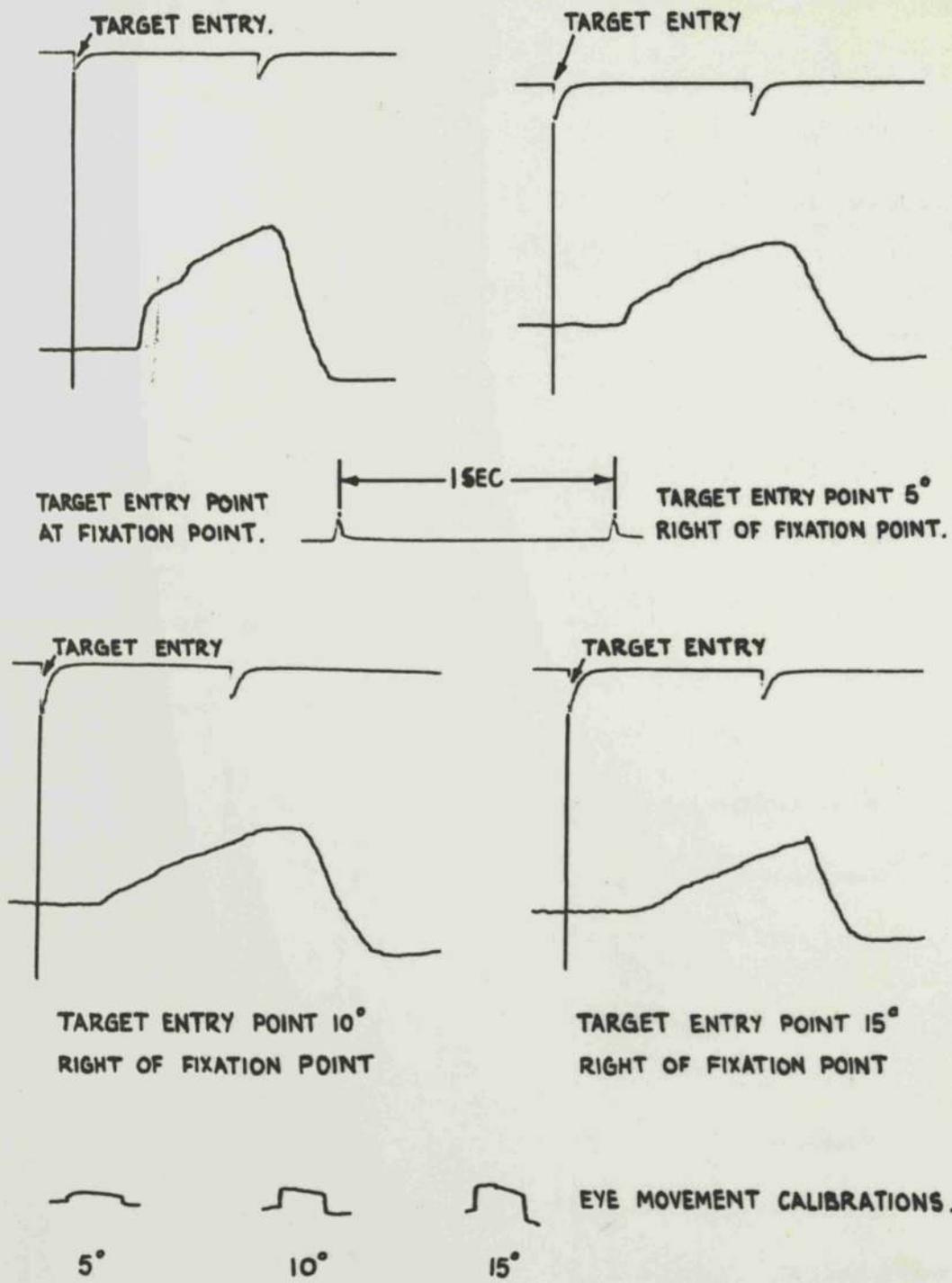
It is more likely that the 100 msec. utilisation rate is the one more likely to be utilised and on this basis the best assessment of eye movement pattern requirement should occur at 5° and 10° peripheral initial stimulation.

The results (Fig. 37) however, show that the 15° point was the best at 100 and $125^{\circ}/\text{sec}$. target velocity. With varying target velocity and varying peripheral initial stimulation it is unlikely that the benefit entirely accrued from the improved information.

The eye movement patterns were quite different when initial peripheral stimulation was employed. The magnitude of the first saccade was reduced irrespective of target velocity. The fast over taking phase became less necessary and thus the muscle contraction in both rate and amount is reduced.

THE VARIATION IN EYE MOVEMENT PATTERNS WITH CHANGE OF INITIAL STIMULATION SITE ON THE RETINA.

TARGET MOVEMENT LEFT TO RIGHT.



500 μ v

EYES { TIME CONSTANT 1.0 SEC.
H.F. FILTER -6db 75 cps.

Fig. 38.

Hammond Merton and Innes have already been referred to as having shown that the accuracy of muscular contraction diminishes as demand increases thus with peripheral stimulation the requirement for accurate muscle contraction is met with a smaller actual error, though not necessarily a smaller percentage error. The improvement in ability with peripheral stimulation may be in the major part due to the less exacting demand on eye muscles. The demand is least with the maximum peripheral stimulation and the results were best at this point.

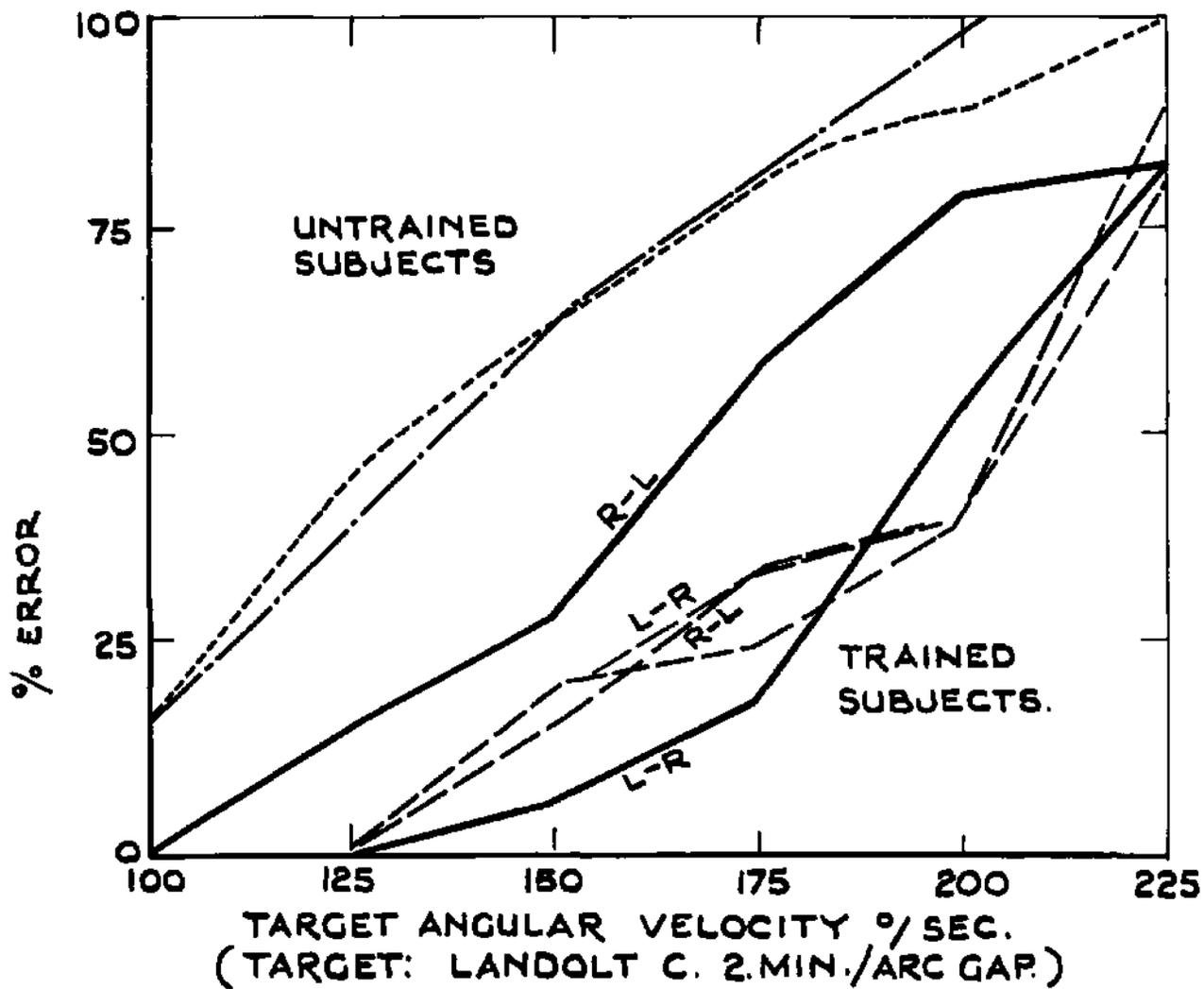
In addition the incidence of corrective saccadic movements was reduced as was also the extent of the correction required.

Fig. 38 shows eye movements at 75° /sec. target velocity with 0, 5, 10 and 15° peripheral stimulation.

A comparison of trained and untrained subjects.

As a final experiment on ability two subjects (author and assistant) who had been present at all previous runs of all types, used the centrifuge chamber system to assess their maximum achievement. This system is described in detail in Part 9 in which there was an arc of 160° available for pursuit. Two new subjects, both pilots, were also tested.

The arc used for target traverse was 150° , head and eye movement was employed, other factors were as previously described, and the target Landolt ring had a 2 minute of arc gap. Runs were carried out to left and right and the angular velocities



MAXIMUM ABILITY OBTAINED BY TWO TRAINED SUBJECTS AND THE ABILITY OF TWO UNTRAINED SUBJECTS (EYE & HEAD FREE TO MOVE.)

Fig. 39.

utilised were 100-225°/sec., the maximum obtainable, in steps of 25°/sec. 20 observations were carried out at each successively greater angular velocity.

Results. No errors were recorded until 150°/sec. angular velocity of the target was obtained, at 200°/sec. the errors amounted to about 50% and reached 85% at 225°/sec. The results are reasonably similar in both directions for the author but the assistant showed a poorer performance, at all velocities except 100°/sec. The results are shown in Fig. 39. The time of presentation varied with target velocity being 1.5 sec. at 100°/sec. to 0.66 secs. at 225°/sec. The new subjects gave a much poorer performance, and substantial failure rates, 50% or more occurring at 150°/sec. (see Fig. 39) and almost complete failure at 200°/sec.

Discussion. The complete freedom of movement afforded to subjects and the time available for visual pursuit demonstrates an ability in excess of that previously shown. The failure at the higher velocities is probably partly due to the velocity of the target and also to lack of time. It is unfortunate that a wider viewing arc could not be obtained to permit times up to 1 second to be available at 200 and 225°/sec. The subjective impression, however, of all subjects was that they had reached a maximum capability.

The new subjects' performances which were poorer than the practiced ones are considered to be largely ascribed to lack of training

Conclusions

The results achieved by Ludvigh and Miller have been previously criticised for limiting with potentially adverse effects, the time of viewing of the moving object, monocular presentation, and the lack of co-ordinated activity of the head and eyes. It has been shown that increasing the viewing time resulted in an improvement in man's ability and that this improvement is due to the ability to complete a corrective movement of the eyes. This corrective movement is necessitated by the inadequacy which is physically demonstrated by the occurrence of these second saccades (corrective movement) which increased in incidence as target velocity increased.

That the decrease in visual acuity was best related to the third power of the target velocity when the eyes only are permitted to move as in Ludvigh's formula - Visual Acuity = $a + bx^3$, where 'x' is the target velocity, was confirmed. However, when the viewing time was increased beyond the 400 msec. used in the Ludvigh experiments this third power deterioration is difficult to retain. When, in addition to increasing viewing time, the head is allowed freedom to fulfill its normal contribution to the task the decrement in visual acuity is of more linear character with reference to target velocity. The ability to discriminate detail in moving objects is dependent not only on the size and brightness of the object but is

dependent on the completeness of the activated adverse system of eyes, head and probably body and the duration of time available for viewing.

The variations found in individuals was confirmed, variations which bore no relationship to visual acuity measured in a conventional manner. It became evident also that training in this task benefitted the subjects and in particular the author and his assistant, who were present at each session, became very experienced. The amount of improvement was briefly examined but no critical investigations were carried out.

It was also noted that when the initial stimulation of the retina by the target preceeded the fixation point in the target's traverse an improvement in ability occurred. Eye movement recordings showed that as this peripheral warning increased in time and extent there were two notable changes in the patterns of eye movements. In the first place the initial saccade was reduced in extent, maximum velocity, and accelerations and in the second place the incidence of second saccades fell. This improvement in ability and reduction in corrective movements of the eyes can be ascribed to one of two reasons. Either the information on which the eye movement was based improved or the muscular response more accurately matched the demands on it by the relevant nervous system components. The results obtained suggest that it was not improvement in information which

contributed to the improvement but the reduction in the amount and rate of contraction required of extraocular eye muscles. When viewing time permits the coarse and powerful neck muscles take away from the extraocular muscles the requirement to sustain a massive contraction and leave to the latter muscles the finer responses for which anatomically and physiologically they are suited.

Summary

The method of examining the ability to perceive detail is described and the results show a degradation in ability as target velocity increases.

Ability is improved when the latency of eye movement is of mean or less than the mean duration, by increasing viewing time, by permitting head and eye movement, when the target enters the visual field at points preceding the fixation and by training.

Errors in perception when non random velocity targets are used were evenly distributed and did not show more errors at the beginning than at the end of a series of runs.

EYE MOVEMENTS OF THE TWO TYPES WITH & WITHOUT 2ND SACCADES.

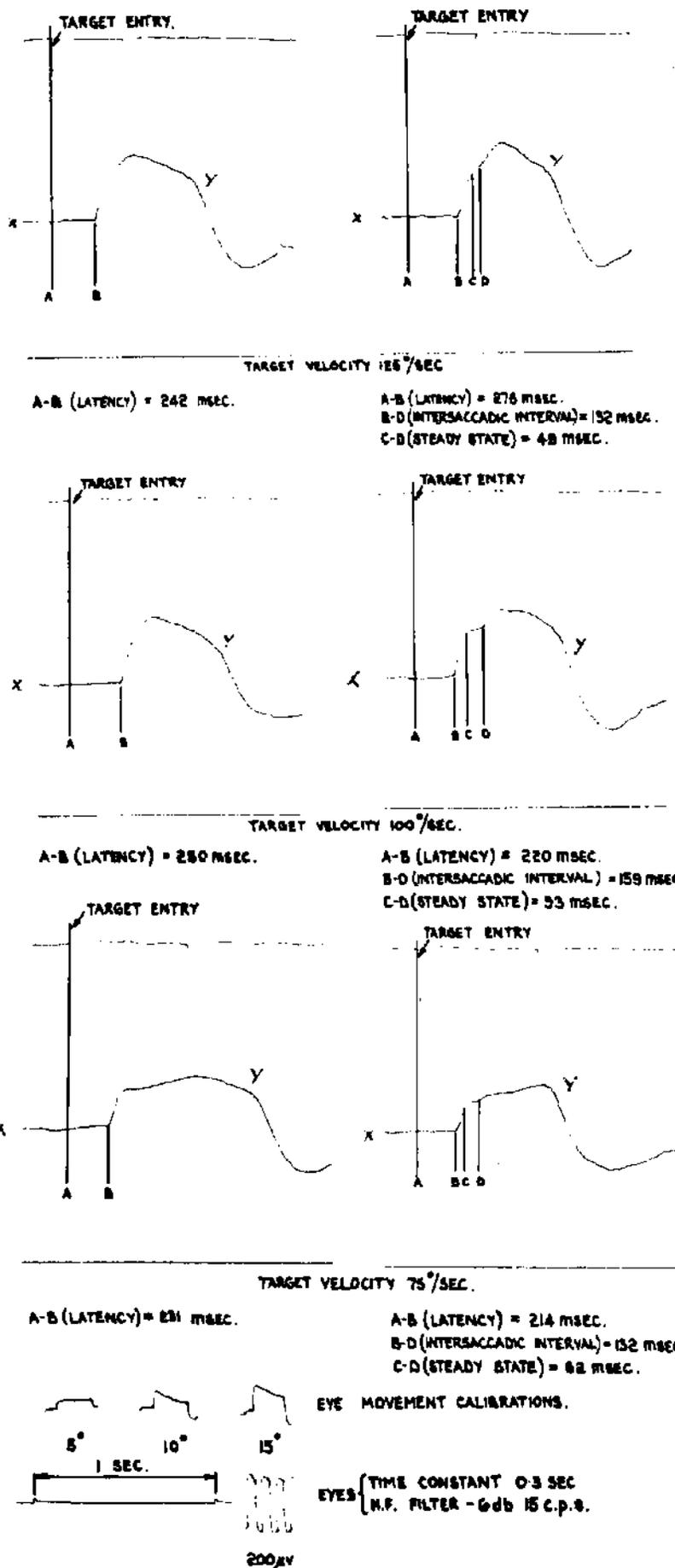


Fig. 40.

PART 5

Eye Movements in Pursuit of a Moving Target

The two basic types of eye movements

Two principal types of eye movement were noted. The first in which the eye accelerates to obtain an overtaking velocity, decelerates to attain a velocity comparable to that of the target and subsequently demonstrates a smooth pursuit movement. The second type demonstrates the same eye movement initially, but the pursuit phase is intercepted by jerky movements known as saccades. Fig. 40 and Fig. 24 B illustrate the movements.

In both types the eyes are fixating the point of entry of the moving Landolt ring, and as it appears it activates a photocell which is noted as a mark on the recording paper at A1. A perpendicular dropped from A1 to A on the eye movement trace indicates the beginning of visual stimulation.

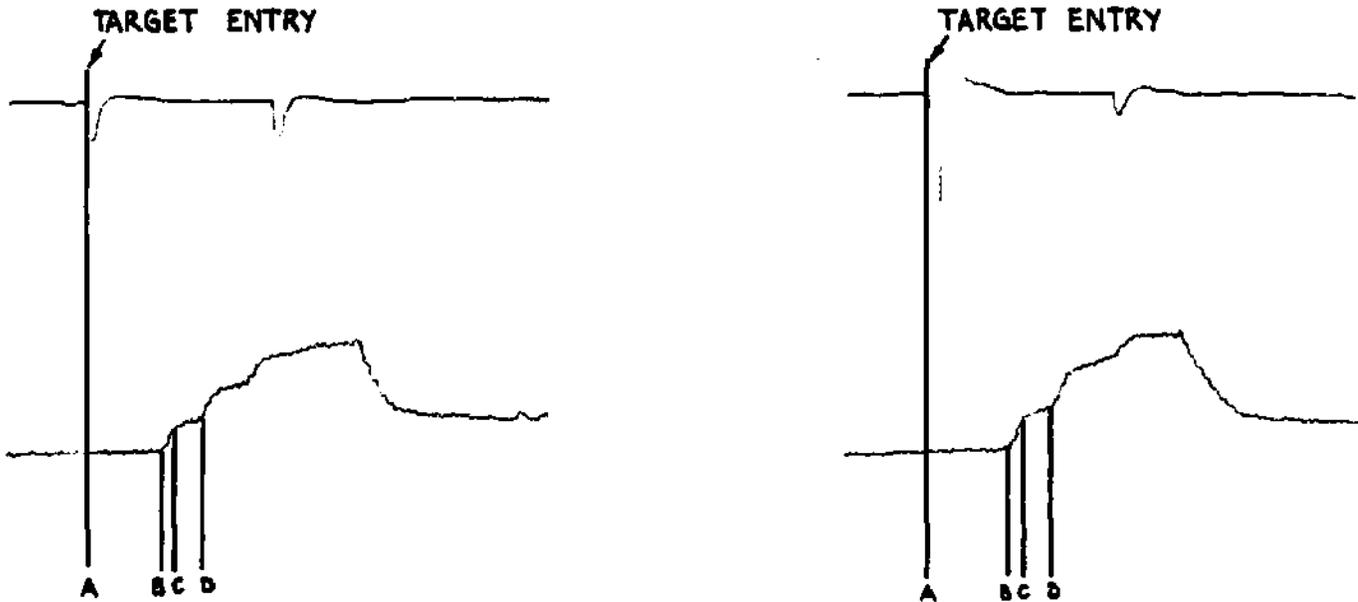
Fig. 40 can be divided into four phases.

X - A indicates a steady regard by the eyes of the fixation point prior to target entry.

A - B indicates the time elapsed from target entry until an eye movement is commenced.

B - C indicates the rapid jerky movement of the eyes during an essentially overtaking phase which should terminate with the eyes having traversed the same angle as the moving target, and having obtained a similar angular velocity. This rapid

EYE MOVEMENT TRACE SHOWING MULTIPLE SACCADES.



A-B (LATENCY) = 198 msec. 1SEC A-B (LATENCY) = 210 msec.
 B-D (INTERSACCADIC INTERVAL) = 110 msec. B-D (INTERSACCADIC INTERVAL) = 110 msec.
 C-D (STEADY STATE) = 77 msec. TARGET VELOCITY 100°/SEC. C-D (STEADY STATE) = 66 msec.



0.100
 0.050
 500 μ v

EYES { TIME CONSTANT 1.0 SEC.
 H.F. FILTER -6db 15cps.

Fig. 41.

type of movement is called a saccade.

C - Y indicates the smooth pursuit eye movement during which the target is considered to be identified by the subject. Fig. 24 has the corresponding phases but shortly after position C has been reached and the smooth pursuit phase has begun another rapid saccade appears. At the end of this the smooth pursuit phase reappears. This additional phase occurs between D and E. The smooth pursuit phase is shown as E - Y. The saccades may be repeated as shown in Fig. 41.

The time between A and B is called the latency of eye movement.

The interval B - C is called the 1st saccade and its measurement permits appraisal of the magnitude and velocity of the eye movement accomplished.

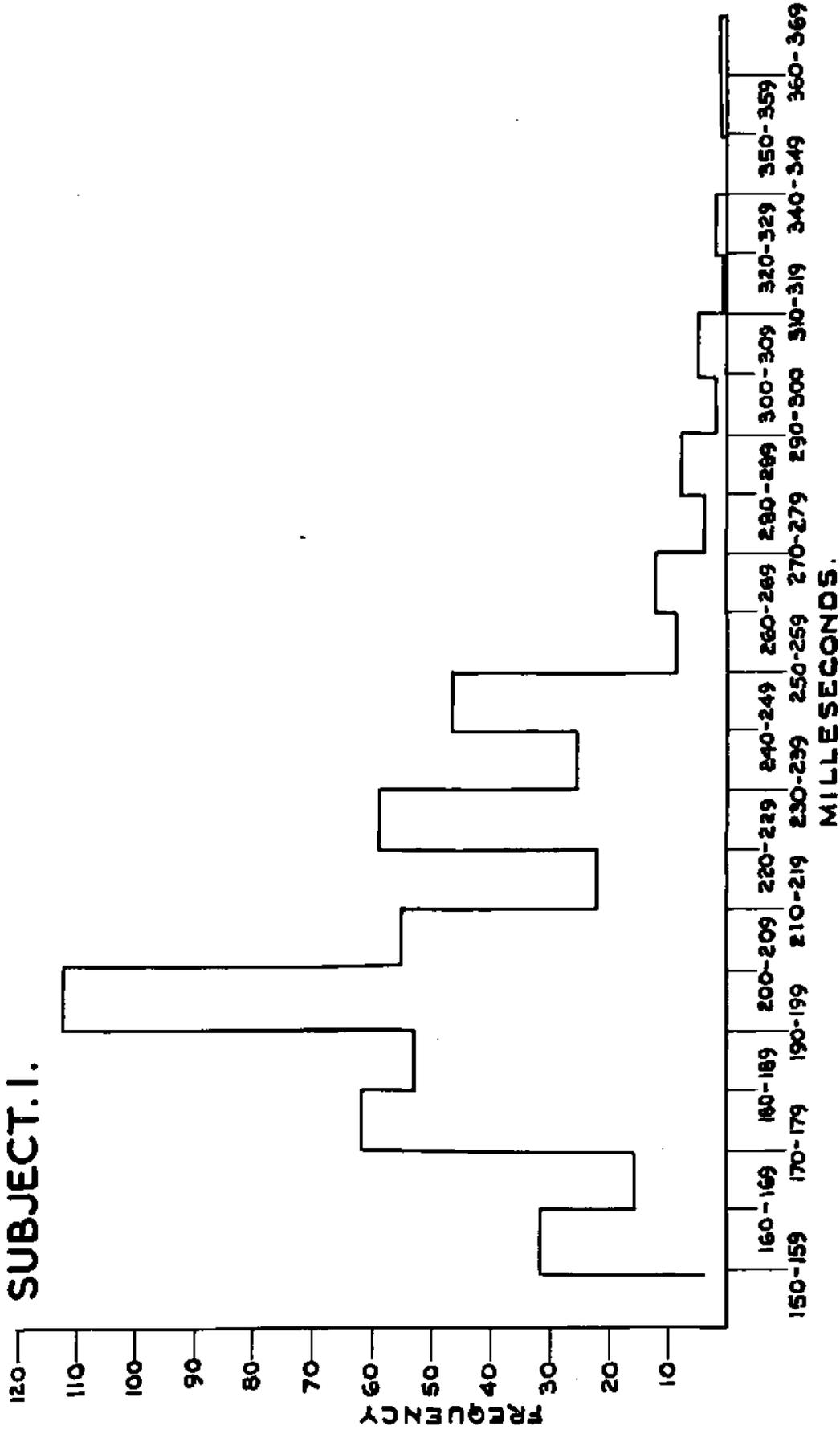
The interval C - D is called the steady state and indicates that tracking is taking place prior to a subsequent saccade.

The interval D - E is called the second saccade and is similar to phase B - C.

The presence of a second saccade is interpreted in all the records obtained as indicating that during the steady state at the termination of the first saccade B - C an unacceptable error in fixation is present and that recognition did not take place.

The intervals A-B, B-C, B-D and C-D were measured. The

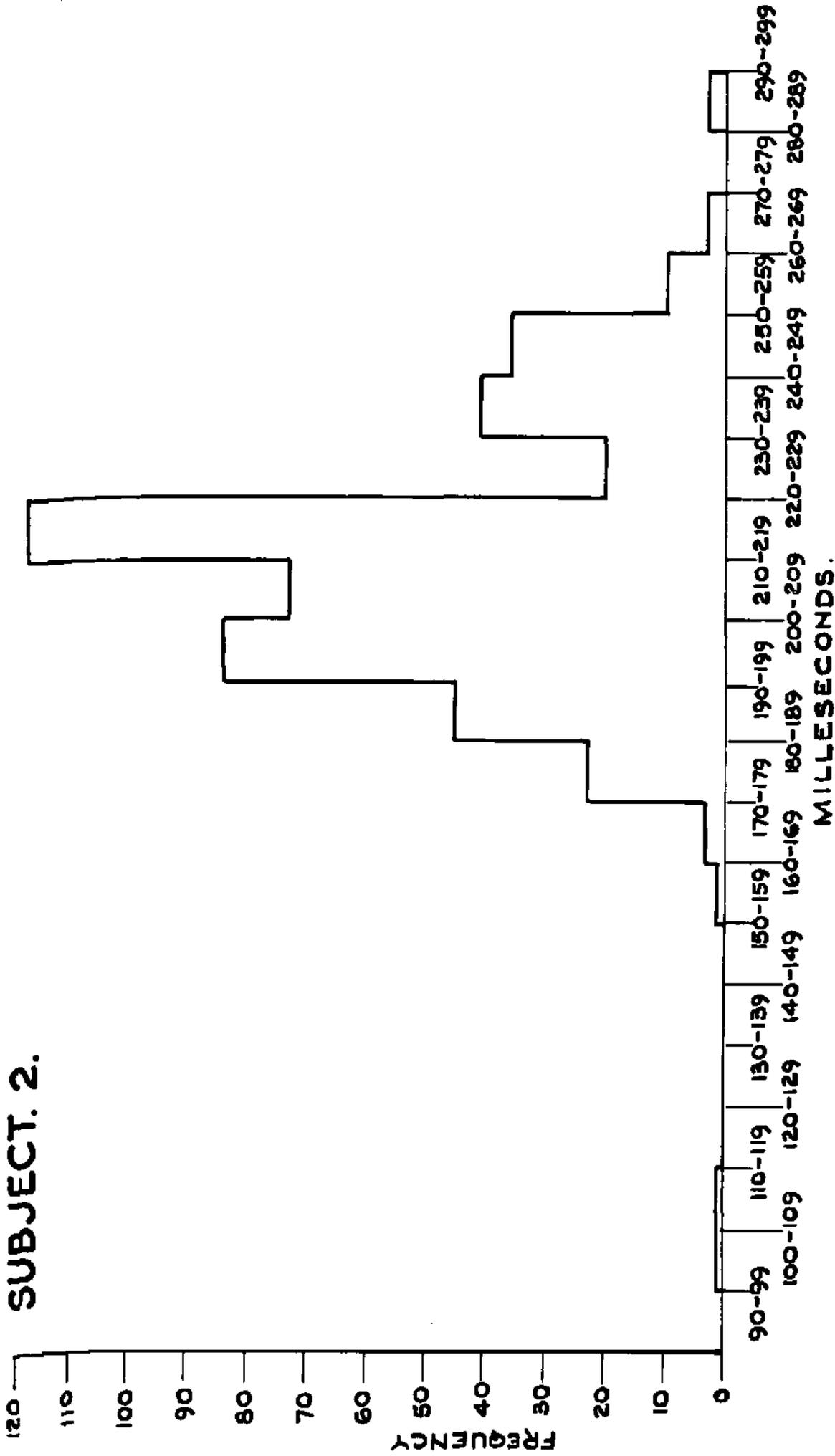
SUBJECT. I.



HISTOGRAM OF INITIAL EYE
MOVEMENT LATENCY.

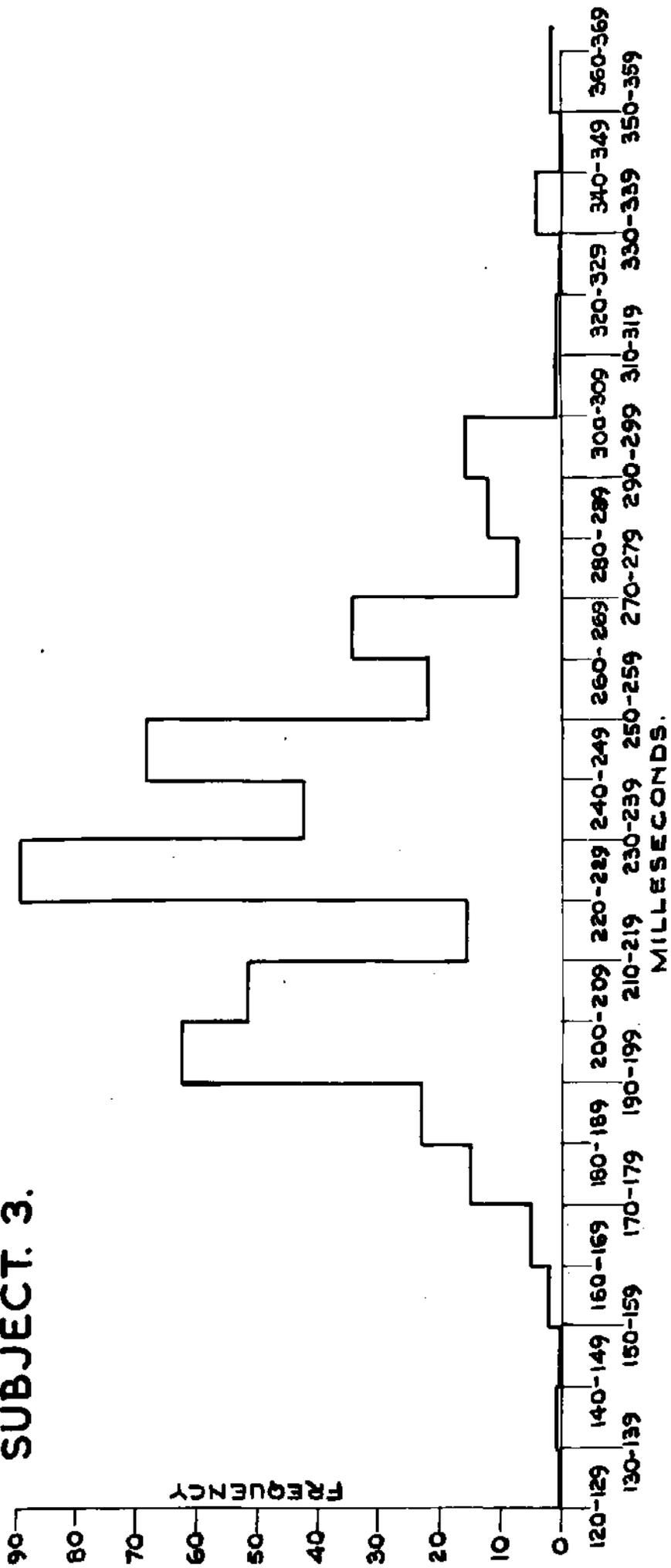
Fig. 42

SUBJECT. 2.



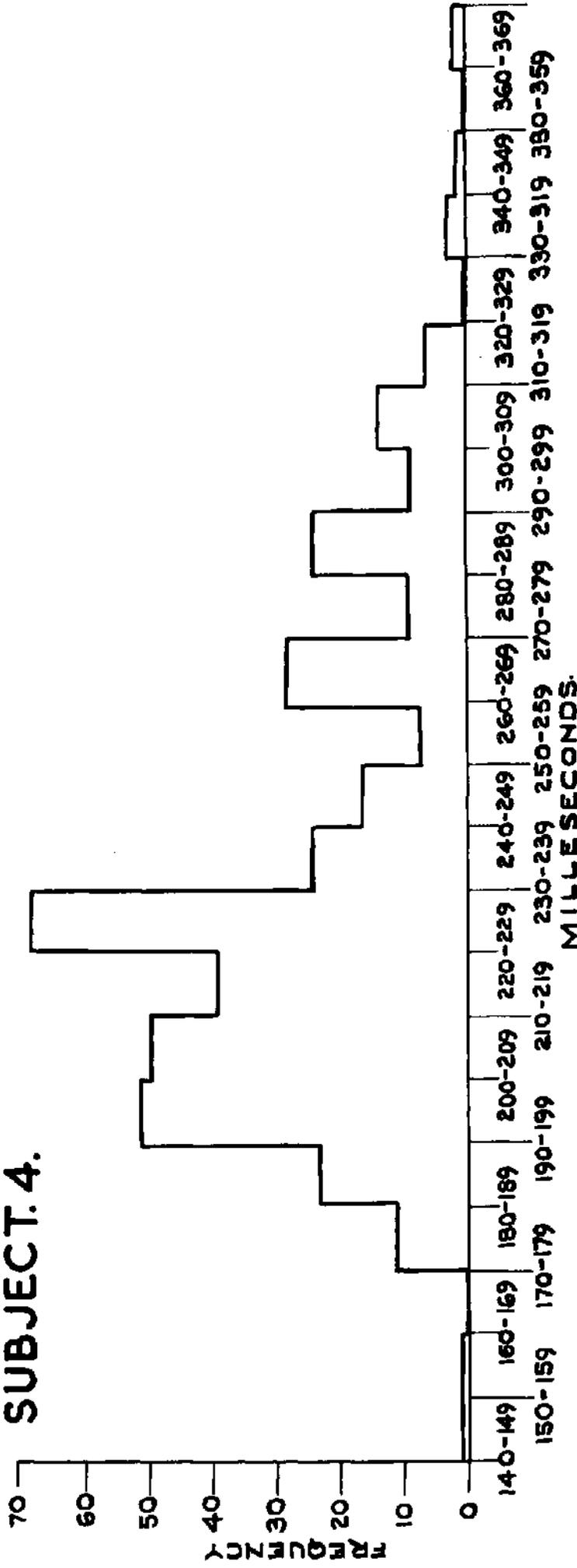
HISTOGRAM OF INITIAL EYE
MOVEMENT LATENCY.

SUBJECT. 3.



HISTOGRAM OF INITIAL EYE MOVEMENT LATENCY.

SUBJECT. 4.



**HISTOGRAM OF INITIAL EYE
MOVEMENT LATENCY.**

Fig. 45

HISTOGRAMS - STANDARDISING OR NORMALISING LATENCY

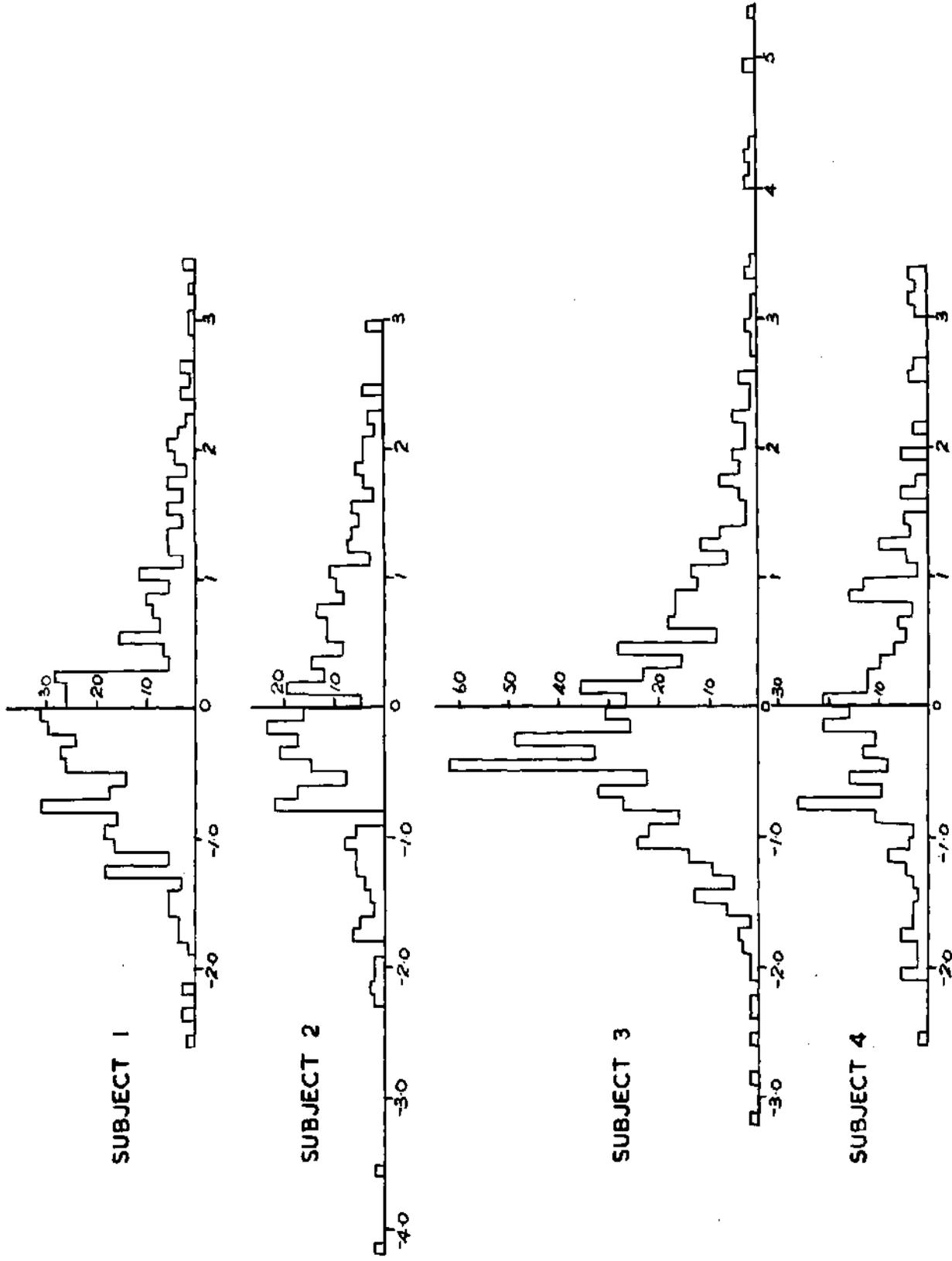


FIG. 46

HISTOGRAM OF STANDARDISING OR NORMALISING LATENCY (SUBJECTS 1,2,3,&4 COMBINED)

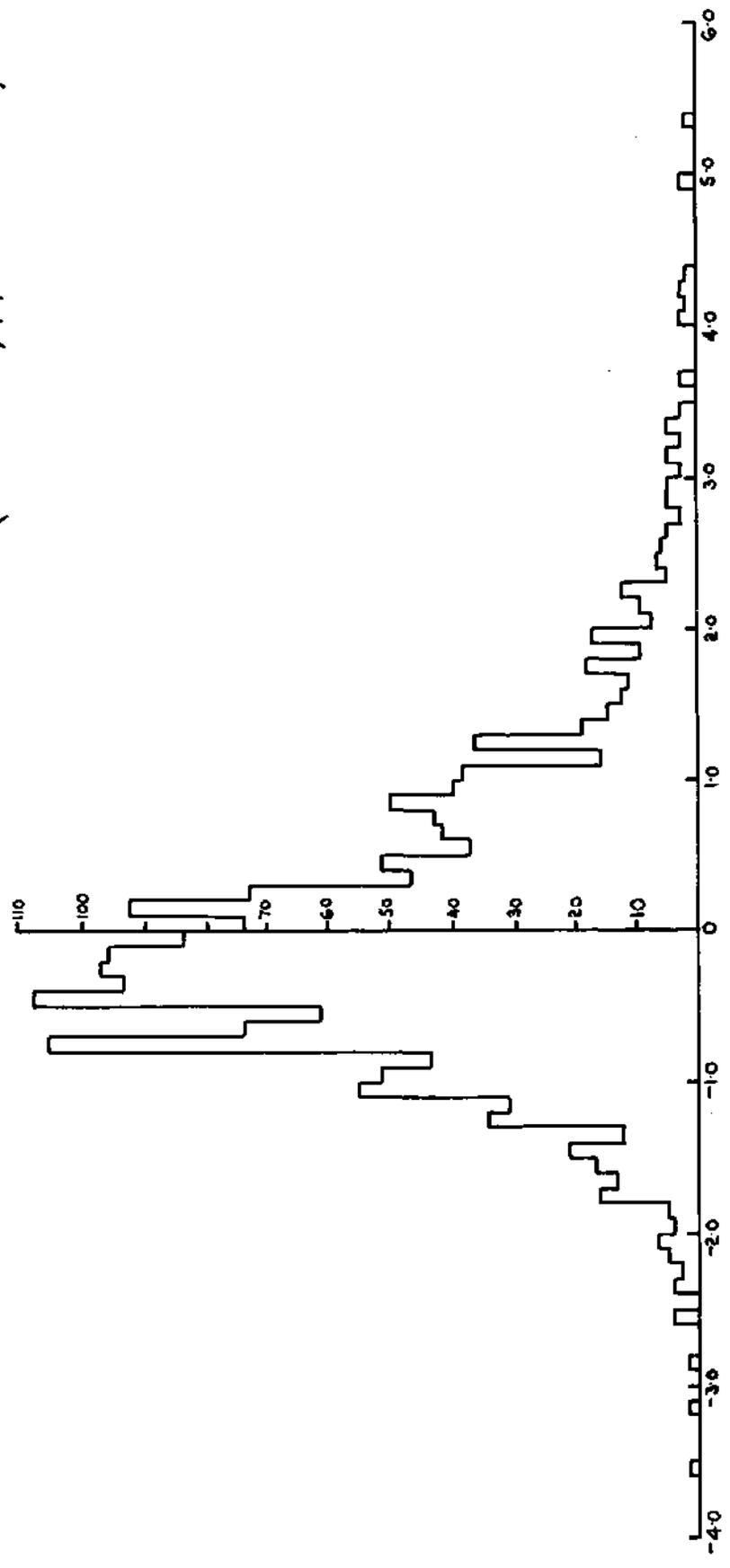


Fig. 47.

accuracy of measurement is correct to certainly less than 10 msec. and probably to 5 msec., which on the recording paper are represented by distances of one half and one quarter of a millimetre respectively.

The latency of eye movements

The vast majority of latencies were in the range of 150-250 msec., the shortest one recorded was 140 msec. and the longest over 300 msec. The distribution of these latencies is shown in Figs. 42-45 for the four major subjects and Figs. 46 and 47 are histograms of normalising the latency.

There is a daily variation in individual subjects. There is only one significant variation with varying target velocities, R 50 being longer than all the others ($P=0.05$). Generally the temporal features in any one day were not dissimilar. This was noted with all subjects and is typified by the responses shown by Subject 1 in Table 5.

The latencies recorded are somewhat longer than those which occur when the eyes have to move from one static object to another which are normally about 120-180 msec. They are comparable to those in the exploratory experiments described and discussed in Part 3. There is no doubt that a pursuit task demands more of the visual and oculomotor system than a mere transfer of gaze from one static point to another. The pursuit task requires the eye to achieve not only a subjectively

satisfactory position, but also a reasonably similar angular velocity to that of the target. Not only has the neural organisation to predict where the target will be after an interval of time such as the latent period but has to predict where it will be by the time the first saccadic movement is complete. A successful prediction is therefore to some extent based on the eye movement obtained being similar to that demanded. That this accuracy is unlikely to be obtained is noted in Part 4.

Table 5

Mean Latencies at Varying Velocity on Different Days

Experimental Run No.	Latencies and Standard Deviations at			
	50°/sec.	75°/sec.	100°/sec.	125°/sec.
1	240.68 27.80	236.79 21.65	235.68 21.04	265.17 24.76
2	212.25 32.45	190.76 23.69	182.00 19.40	180.00 12.27
3	217.43 30.08	195.95 19.71	198.80 20.18	193.59 23.52
4	262.36 64.59	214.94 21.49	212.00 19.25	219.30 21.21
5	214.38 30.92	199.26 12.92	200.24 17.57	196.74 20.34

The first saccade, its duration and velocity

The first saccade begins at the end of the latent period and ends when the eye movement slows down to a velocity comparable to that of the target. Although the records cannot show the character of the eye movement clearly, it is obvious that there must be three phases in the movement; an accelerating phase to attain velocity adequate to overtake the target, a maintenance of the overtaking velocity for some duration of time and a deceleration to a velocity comparable with the target. If the predicted and obtained movement pattern is adequate a smooth pursuit eye movement as in Fig. 40 A will result. However, the high incidence of second saccades found with target velocities of $50^{\circ}/\text{sec.}$ and faster is evidence in favour of a failure to secure with the first saccade an adequate fixation. The angular movement of the eyes was in the vast majority of occasions insufficient, the eyes undershot the target. Only 4 of the thousands of eye movements examined showed signs of the angle through which the eyes move during the first saccade having been too great. With a capacitance coupled amplifying system it was not possible to accurately measure the extent of the first saccade, but there are many indications that the extent of the eye movement was sometimes only half that which would have been necessary to achieve accurate position. Such measurements as were recorded show

variation with identical stimuli, which indicates that some part or parts of the whole system underlying eye movement does not always give the same response to identical stimuli.

The duration of the initial saccade varied with subjects and in all subjects increased significantly in duration between 50 and 75°/sec. and 100 and 125°/sec. target angular velocities. The difference between 75° and 100°/sec. targets did not show this statistically but the table shows the same trend to be present.

Table 6

The Duration of the Initial Saccadic Movement in
Msec. at Various Target Velocities

Angular Velocity of Target °/sec.	Subject 1	Subject 2	Subject 3	Subject 4
50	42.92	24.73	49.69	35.45
75	52.58	30.17	62.68	44.39
100	63.58	35.57	68.97	47.79
125	78.43	37.09	86.33	54.23

Mean Values at 50°/sec. = 38.2, at 75°/sec. = 47.46
at 100°/sec. = 53.98 at 125°/sec = 64.02

Critical Difference = 8.47

R 50 is less than 75
R 100 is less than 125

The mean velocities of eye movements are not capable of being accurately measured in the recordings obtained, but it was noted that as target velocity increased to 100°/sec. the velocity of eye movements increased. Only in Subject 2 did the mean angular velocity continue to increase at 125°/sec. These inexact results are shown in Table 7.

Table 7

The Mean Velocities of Eye Movements in °/sec. at Various Target Velocities

Angular Velocity of Target °/sec.	Subject 1	Subject 2	Subject 3	Subject 4
50	185	223	200	190
75	268	318	250	217
100	314	417	350	250
125	309	569	350	250

A perusal of these tables indicates that eye movement duration and velocities increase as the required displacement of the eye and final angular velocity increases. The velocities are mean velocities during a movement which of necessity commences with a very slow period, reaches a maximum somewhere about the mid-phase and is then reduced to one approximating

THE EFFECT OF TARGET ANGULAR VELOCITY
ON THE INCIDENCE OF SECOND SACCADES.

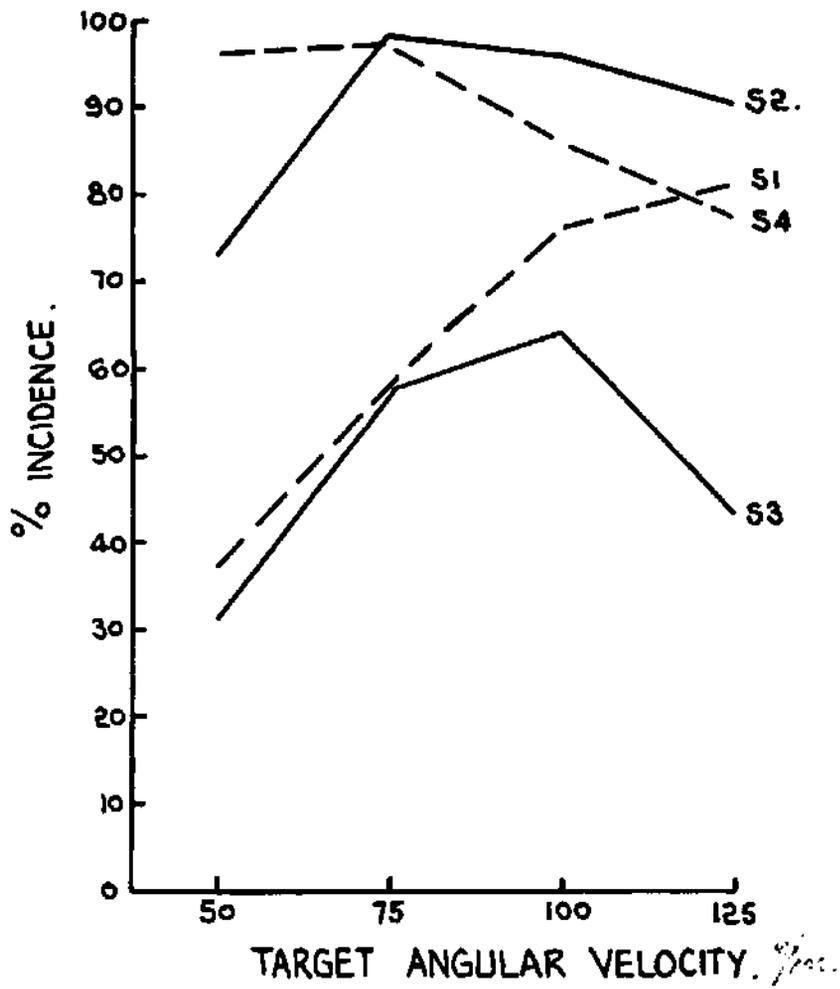


Fig. 48.

90

to target angular velocity. The eye movement velocities, in degree/sec., must reach greater maximum values than are tabulated here. The velocity of eye movement is known to increase when the required angular movement between static targets enlarges (Duke Elder 1944b), with increasing target velocity this also was noted to occur.

The descending order of ability to perceive detail in moving targets for the subjects is 1, 2, 3 and 4. The subject with the fastest eye movements, and smallest duration of eye movement is not the most capable. The subject with the slowest eye movement in these experiments is the least capable.

Any conclusions as to the relationship of ability to eye movement velocity would be unjustified.

The incidence of second saccades

This incidence varied in all the subjects. The only common factor being the high incidences reached of 50 to 100^o/. Subject 1 showed a steady increase as target velocity increased, Subject 2 showed a very high incidence which slowly decreased as target velocity increased, Subject 3 showed an increase up to a target velocity of 100^o/sec. and then a decrease, Subject 4 showed an increase up to 75^o/sec. and then a decrease at 100^o/sec. and 125^o/sec. Fig. 48 shows the incidence of second saccades by subjects.

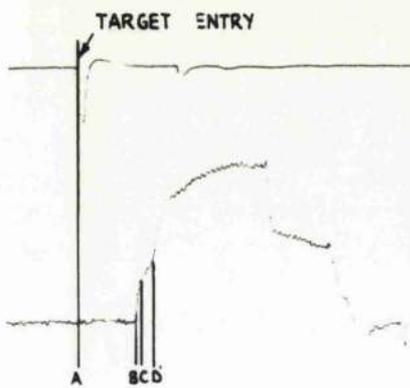
The incidence of second saccades in these experiments showed,

with the exception of one subject, a fall off at $125^{\circ}/\text{sec.}$, at $100^{\circ}/\text{sec.}$ in two subjects and at $75^{\circ}/\text{sec.}$ in another. This may be the result of complete failure of the system to carry out an effective initial saccade, the error being so large that the sensory stimulus on which a corrective move is based cannot be assimilated and processed. If the lack is one of time of stimulation then a second saccade could still be expected after the target had disappeared but no saccade occurred even with 300 msec. or more of target presence remaining after the initial saccade. It is considered that the stimulus is not one which is lacking in duration but is one which is at or beyond the capability of the oculomotor system to contain.

The intersaccadic phase

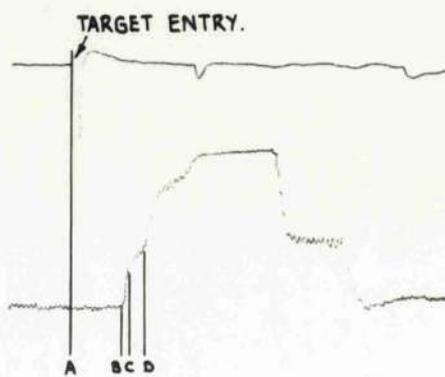
The intersaccadic phase includes the first rapid eye movement and the subsequent tracking period which had been designated the steady state. Such phases occur more frequently in some subjects than others and may occur in all pursuit movements when the target angular velocity is high. This intersaccadic phase has been generally described since the days of Dodge (1903) to last some 200 msec., more recently Ginsborg (1953) and Westheimer (1954a) have reported durations as short as 130 msec. The stimuli these research workers used were either slowly moving or were interstatic, i.e. from one static object to another. When the stimulus angular velocity was 50, 75, 100

TRACES SHOWING SHORT INTERSACCADIC INTERVALS.



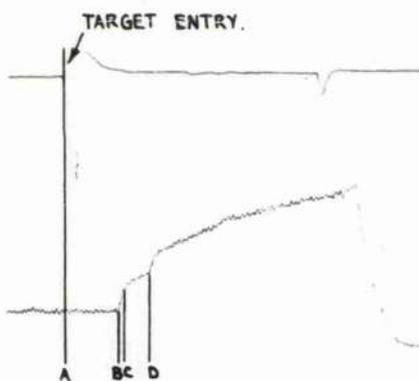
TARGET VELOCITY 125°/SEC.

A-B (LATENCY) = 220 msec.
 B-D (INTERSACCADIC INTERVAL) = 77 msec.
 C-D (STEADY STATE) = 55 msec.



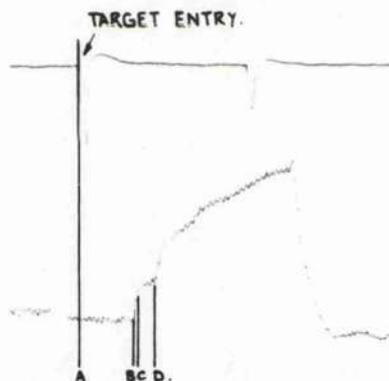
TARGET VELOCITY 100°/SEC.

A-B (LATENCY) = 203 msec.
 B-D (INTERSACCADIC INTERVAL) = 88 msec.
 C-D (STEADY STATE) = 66 msec.



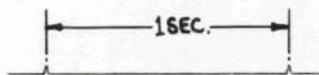
TARGET VELOCITY 50°/SEC.

A-B (LATENCY) = 220 msec.
 B-D (INTERSACCADIC INTERVAL) = 110 msec.
 C-D (STEADY STATE) = 93 msec.



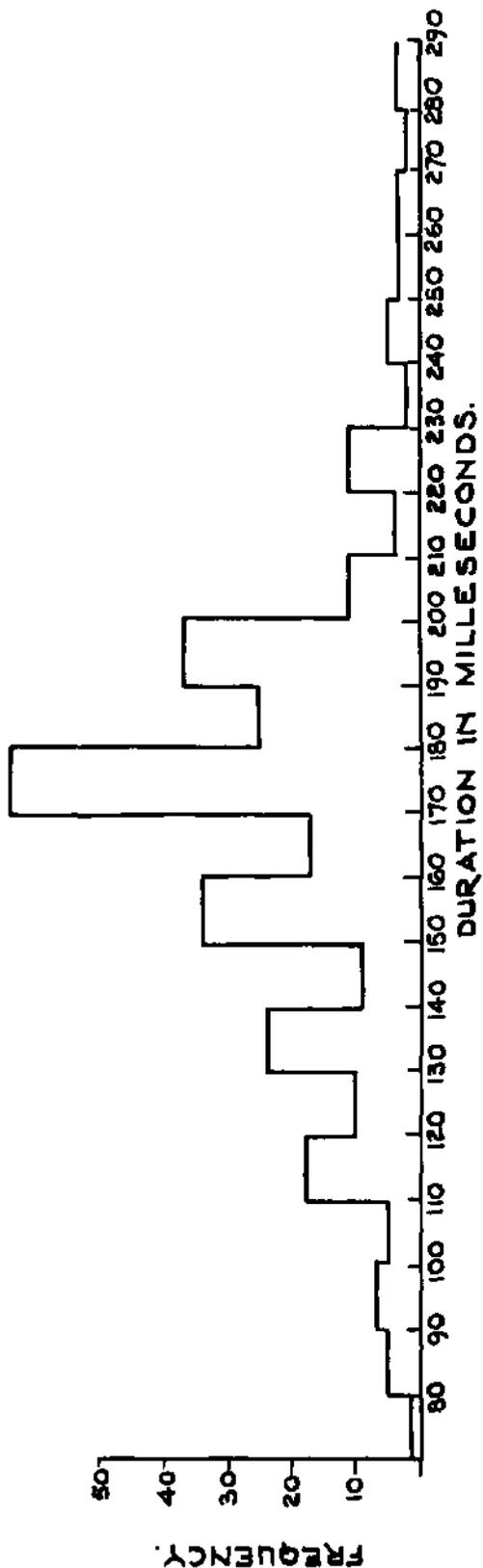
TARGET VELOCITY -75°/SEC.

A-B (LATENCY) = 215 msec.
 B-D (INTERSACCADIC INTERVAL) = 88 msec.
 C-D (STEADY STATE) = 66 msec.

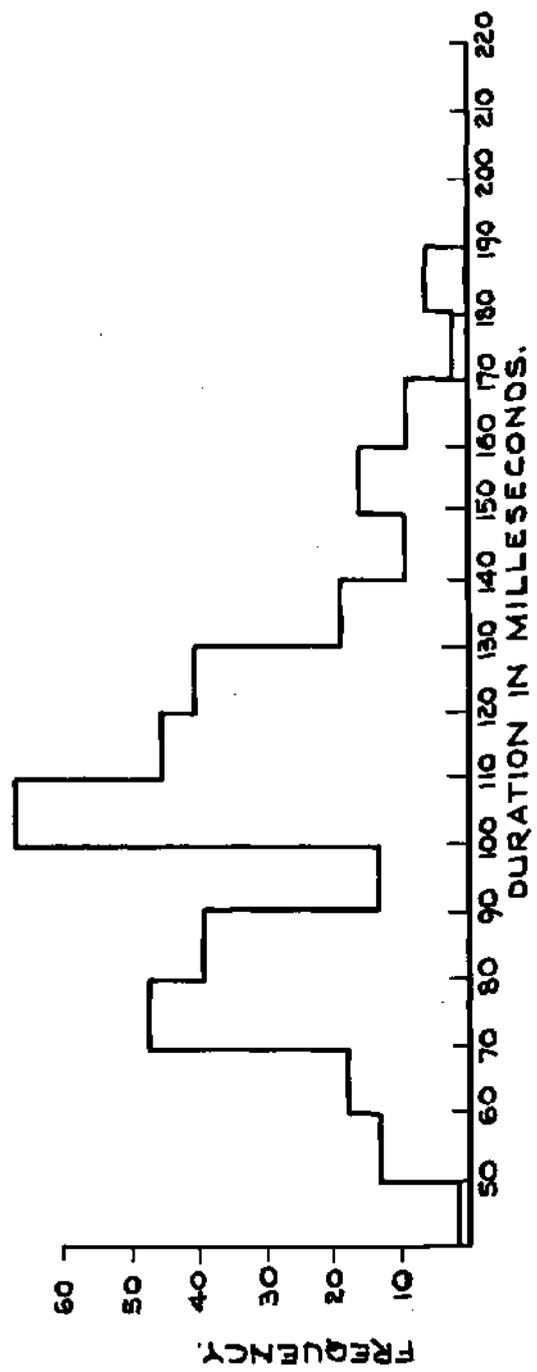


200μV. EYES { TIME CONSTANT 1.0 SEC.
 H.F. FILTER -6db 15 c.p.s.

Fig. 49.

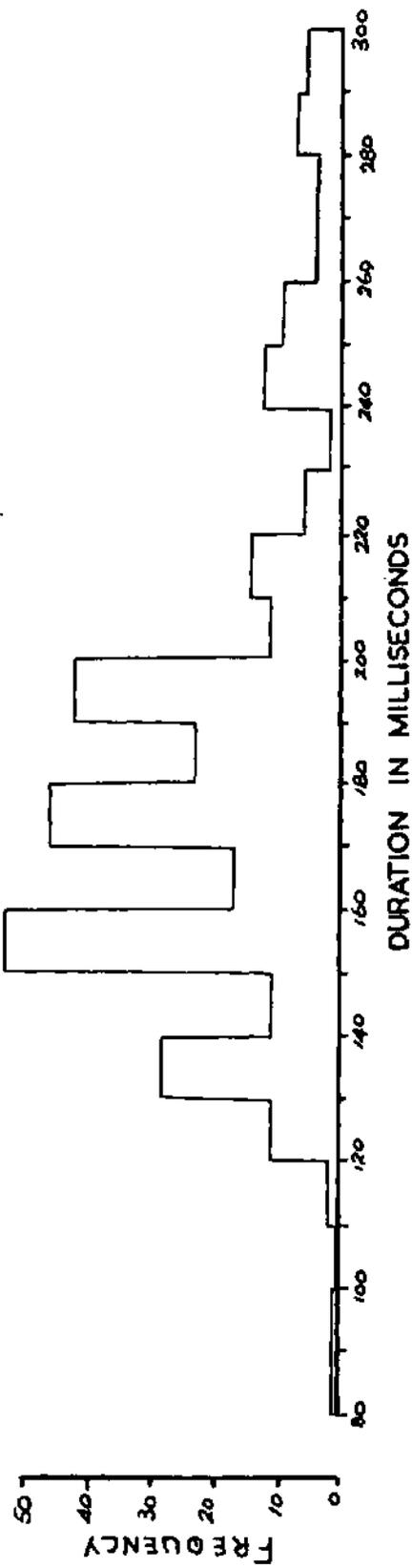


COMBINED HISTOGRAM OF THE DURATION OF THE INTERSACCADIC INTERVAL FOR SUBJECT 1. AT ALL TARGET VELOCITIES.

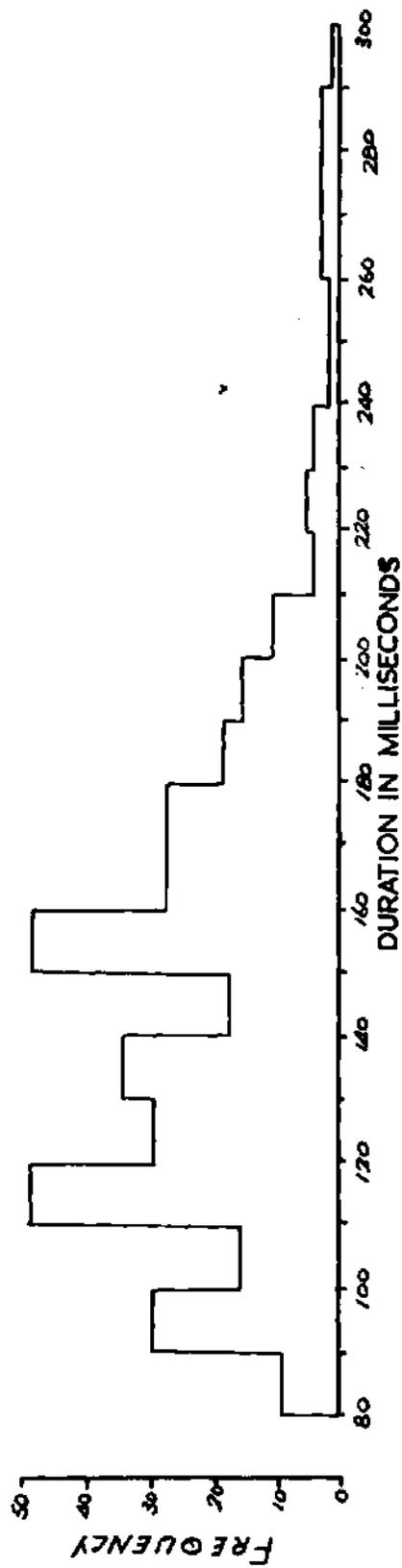


COMBINED HISTOGRAM OF THE DURATION OF THE INTERSACCADIC INTERVAL. FOR SUBJECT 2. AT ALL TARGET VELOCITIES.

Fig. 50.



COMBINED HISTOGRAM OF THE DURATION OF THE INTERSACCADIC INTERVAL FOR SUBJECT 3 . AT ALL TARGET VELOCITIES.



COMBINED HISTOGRAM OF THE DURATION OF THE INTERSACCADIC INTERVAL FOR SUBJECT 4 . AT ALL TARGET VELOCITIES

INTERSACCADIC INTERVAL ALL SUBJECTS.

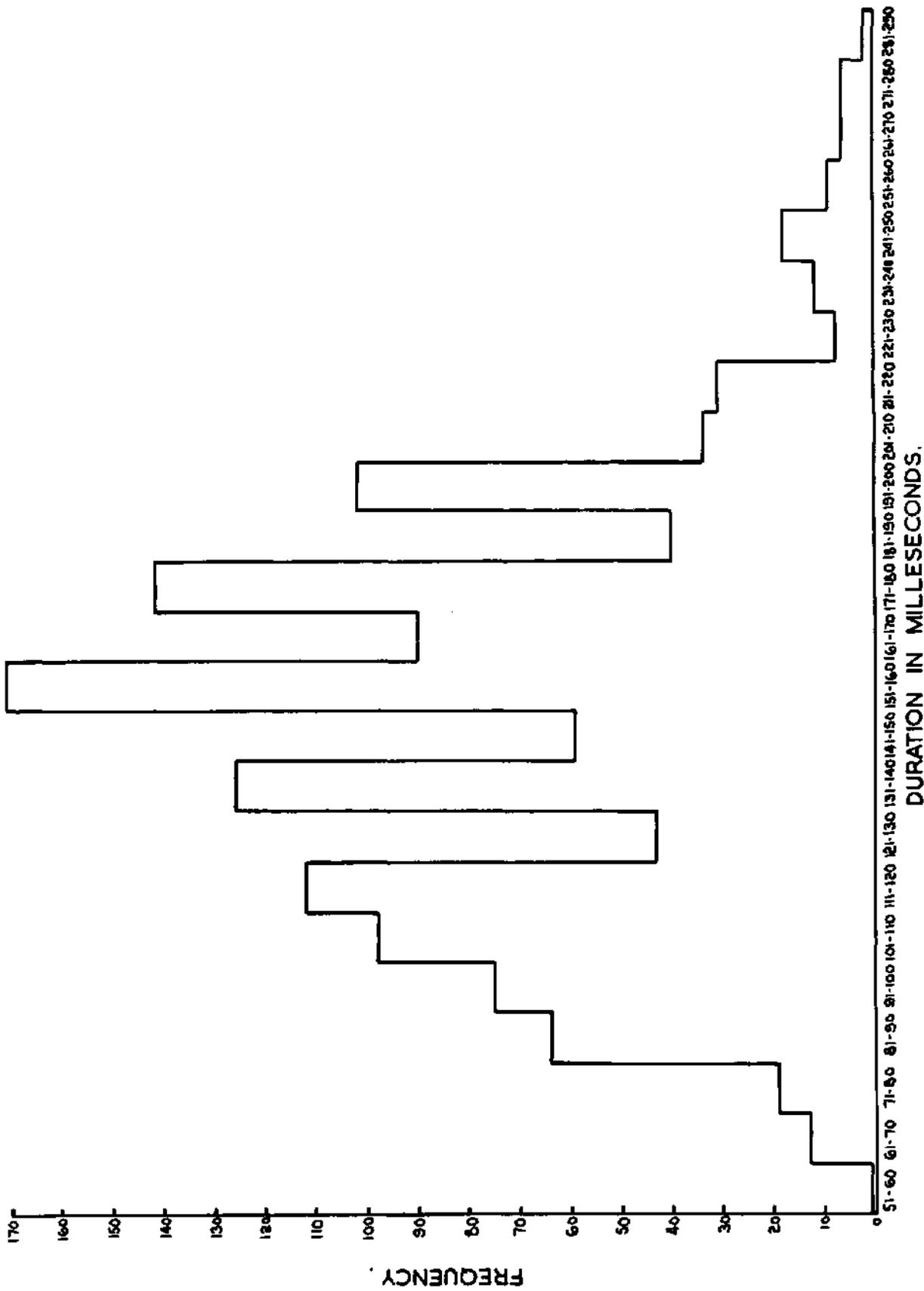


Fig. 52.

and 125°/sec. randomly presented intersaccadic phases were found which were substantially less than the 130 msec. minimum duration previously reported. Some relevant traces are shown in Fig. 49. These occurred on 382 occasions in 1198 pursuit movements (31.9%). The minimum recorded was 56 msec. Histograms of each of the four subjects are shown (Figs. 50, 51) and a composite for all subjects in Fig. 52. The intersaccadic period became shorter as target velocity increased, as seen in Table 8. Subject 2 demonstrated more intersaccadic periods than the others and also more short ones.

Table 8

Mean Durations and Significant Differences of the Duration of the Intersaccadic Interval. (All Subjects)

Target Velocity	50	75	100	125
Mean Duration	180.41	156.32	144.37	151.10

R.50 is significantly greater than all others (P = 0.001)

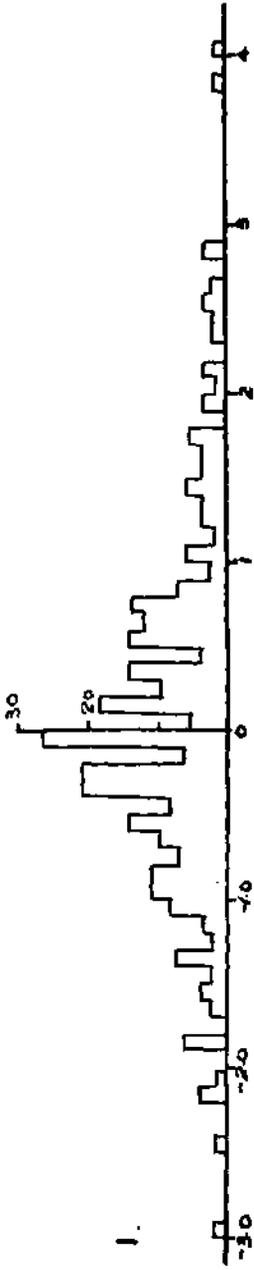
R.75 is significantly greater than R.100 and R.125 (P = 0.05)

There was no significant difference between R.100 and R.125.

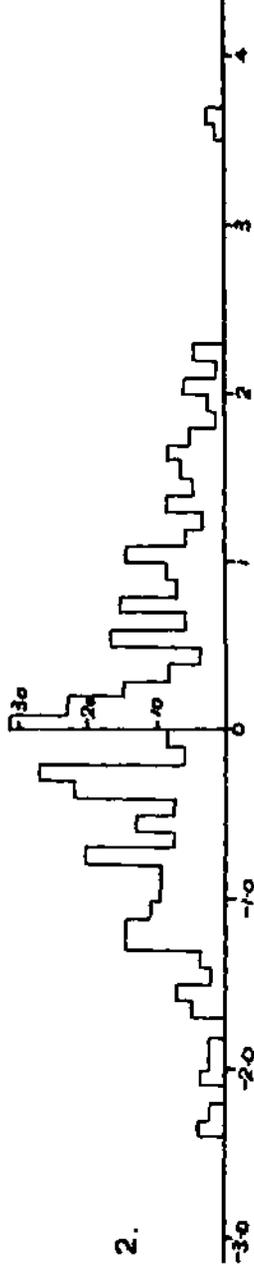
Such results were obtained with or without using a dental bite to ensure head immobility. A head movement of 5° or more would be required to produce the changes in eye movement recording seen in Fig. 49. The head can be kept from rotation

HISTOGRAMS OF STANDARDISING OR NORMALISING 2nd. MOVEMENTS

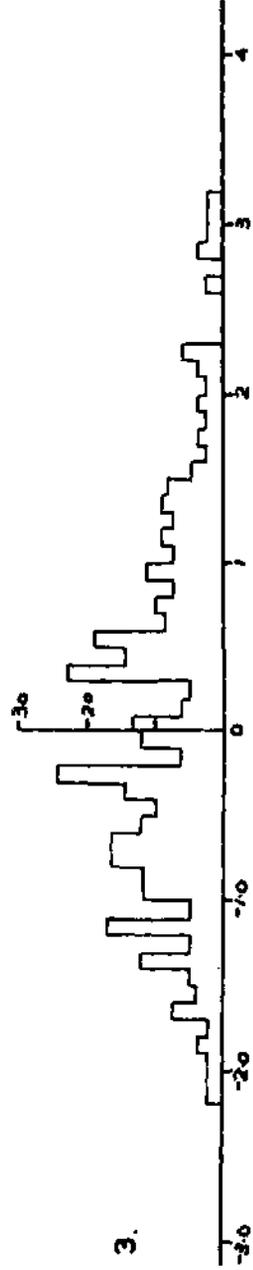
SUBJECT 1.



SUBJECT 2.



SUBJECT 3.



SUBJECT 4.

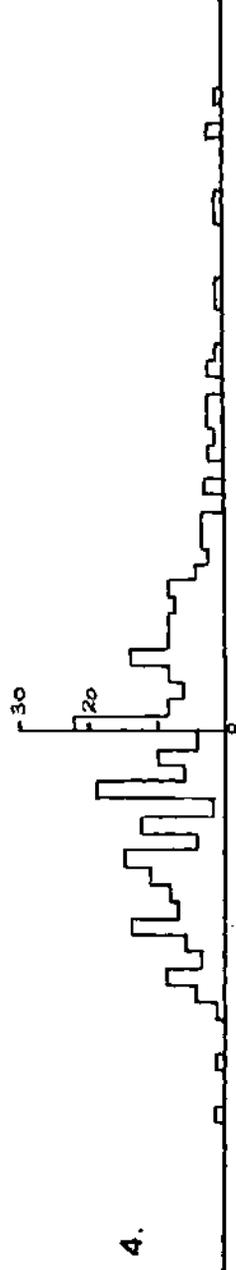


Fig. 54.

by simply resting the chin in the cupped hands. Head movement is definitely a voluntary process in such experiments. A recording of eye movements (Fig. 53) when the head was supported by cupped hands only, shows the complete lack of movement when voluntary inhibition of movement is undertaken.

The wide variation in the duration of the intersaccadic interval seen in the relevant histograms were examined to show the presence or absence to two modes, the one being shorter in duration than the other. This was done by normalising each interval using the formula $\frac{x - \bar{x}}{S.D.} = \frac{(\text{Duration} - \text{Mean Duration})}{(\text{Standard Deviation})}$ Fig. 54. This failed to show two modes which may mean that only one neural process is involved; a process which has a great variability in its operative time.

The finding of such short intervals during which a rapid eye movement has taken place and during which exteroceptive feedback from the retina is reputed to occur is of importance in any discussion on the nervous pathways in the visuo-oculomotor systems. Such discussion follows after a description of the 'steady state' and second saccades during eye movements.

The relationship of latency duration and second saccadic movements

Some consideration was given to the possibility that the second saccade may have been planned during the latter stages of the latent period of the eye movement. It seemed not unreasonable to assume, as Westheimer (1954a) showed and to which

reference has already been made, that the eyes become committed to a move before the latent period is complete. During the latter part of the latency, as further retinal stimulation occurs a corrective phase may be planned to some extent. Short intersaccadic intervals associated with long latencies would lend some weight to this possibility. It is not, however, until the eye movement first saccade is complete that actual position and velocity errors can be finally gauged. A survey of the short intersaccadic intervals showed that they were not associated with either short, average, or long latencies but occurred in any grouping.

The latencies of eye movements with peripheral retinal stimulation.

In the exploratory experiments the non significant results in variation in latency were described. A further series of experiments were conducted at 50, 75, 100 and 125^o/sec. and the latencies examined. Scoring of the latencies was difficult owing to the lack of sensitivity in the corneo-retinal potential method. The inaccuracy particularly when the target entered at 10^o and 15^o from the fovea cannot be estimated. Because of this no statistical evaluation was deemed worthwhile.

The type of eye movement has already been described in discussion of ability when the target enters the peripheral visual field before reaching the fixation point.

The results showed that latency tended to increase as peripheral retinal stimulation was increasing further from the fovea. The results are shown in Table 9 as mean values only.

Table 9
Mean Latencies of Pursuit Eye Movements with Varying Initial Retinal Stimulation Area.

Target Velocity °/sec.	Initial Retinal Stimulation Point			
	Fovea	5° Right	10° Right	15° Right
50	249.40	207.80	267.08	259.80
	246.20	207.70	264.80	
75	195.75	256.60	268.50	310.70
	220.79	272.40	270.50	281.50
		273.64	262.08	294.00
100	174.09	215.20	248.10	275.00
		256.40	246.40	275.40
	235.80	241.17	228.64	253.96
125	174.40	236.60	292.90	237.40
	222.96	192.90	189.70	222.80
	198.16	193.50	198.70	221.30
	252.10	246.80	270.70	242.80
Overall Mean	214.80	240.60	250.60	261.30

This trend to have greater latencies when the movement arises from peripheral stimulation may be due to one or both of two factors. The first being a lengthening of latency resulting from peripheral stimulation and the second a deliberate delaying

DISTRIBUTION AT 50, 75, 100 & 125°/SEC STEADY STATE DURATION
 SUBJECT I.

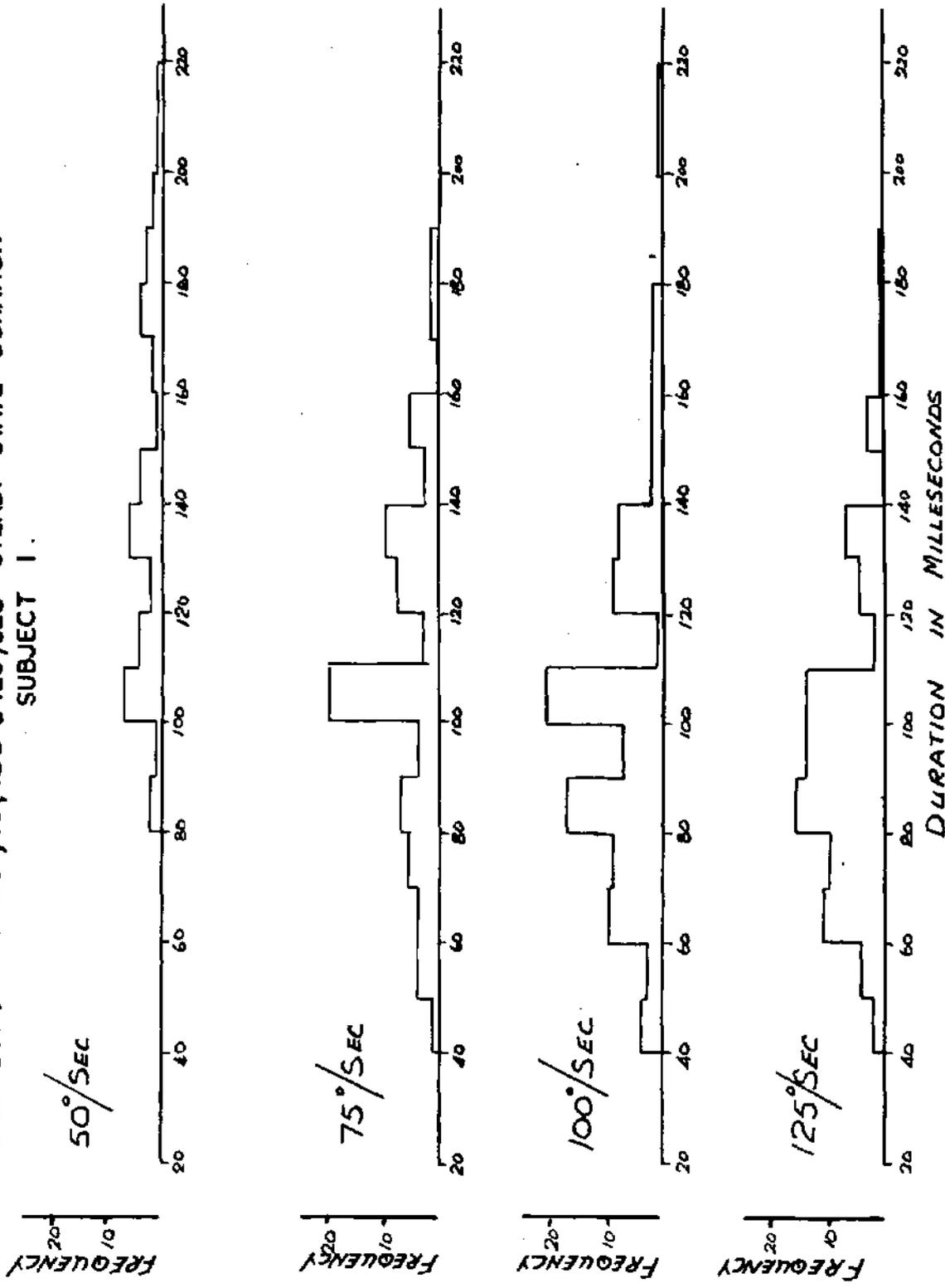
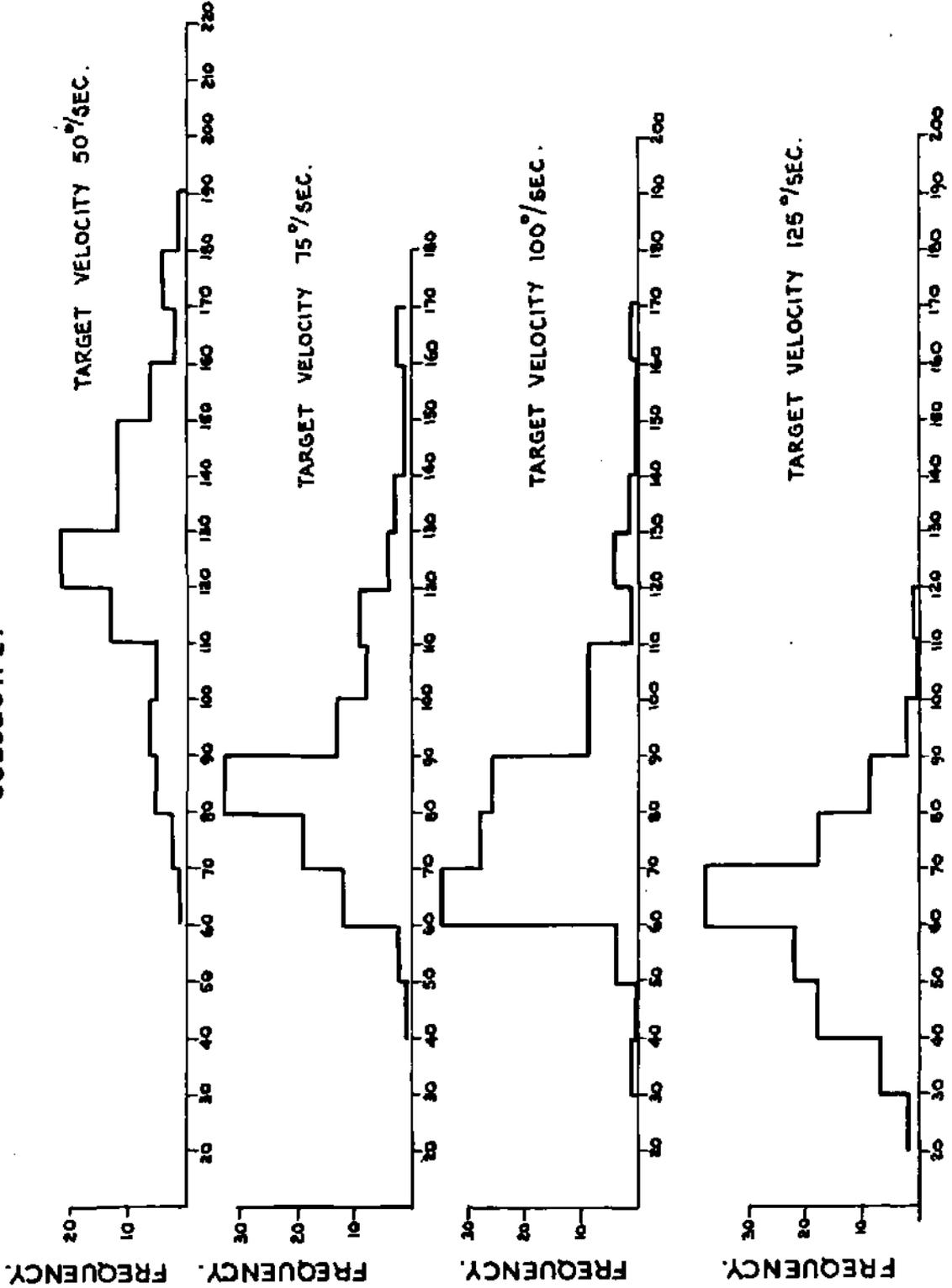


Fig. 55.

DISTRIBUTION AT 50, 75, 100, AND 125°/SEC. STEADY STATE DURATION.
SUBJECT. 2.



DURATION IN MILLESECONDS

Fig. 56

DISTRIBUTION AT 50, 75, 100 AND 125°/SEC.
SUBJECT 3.

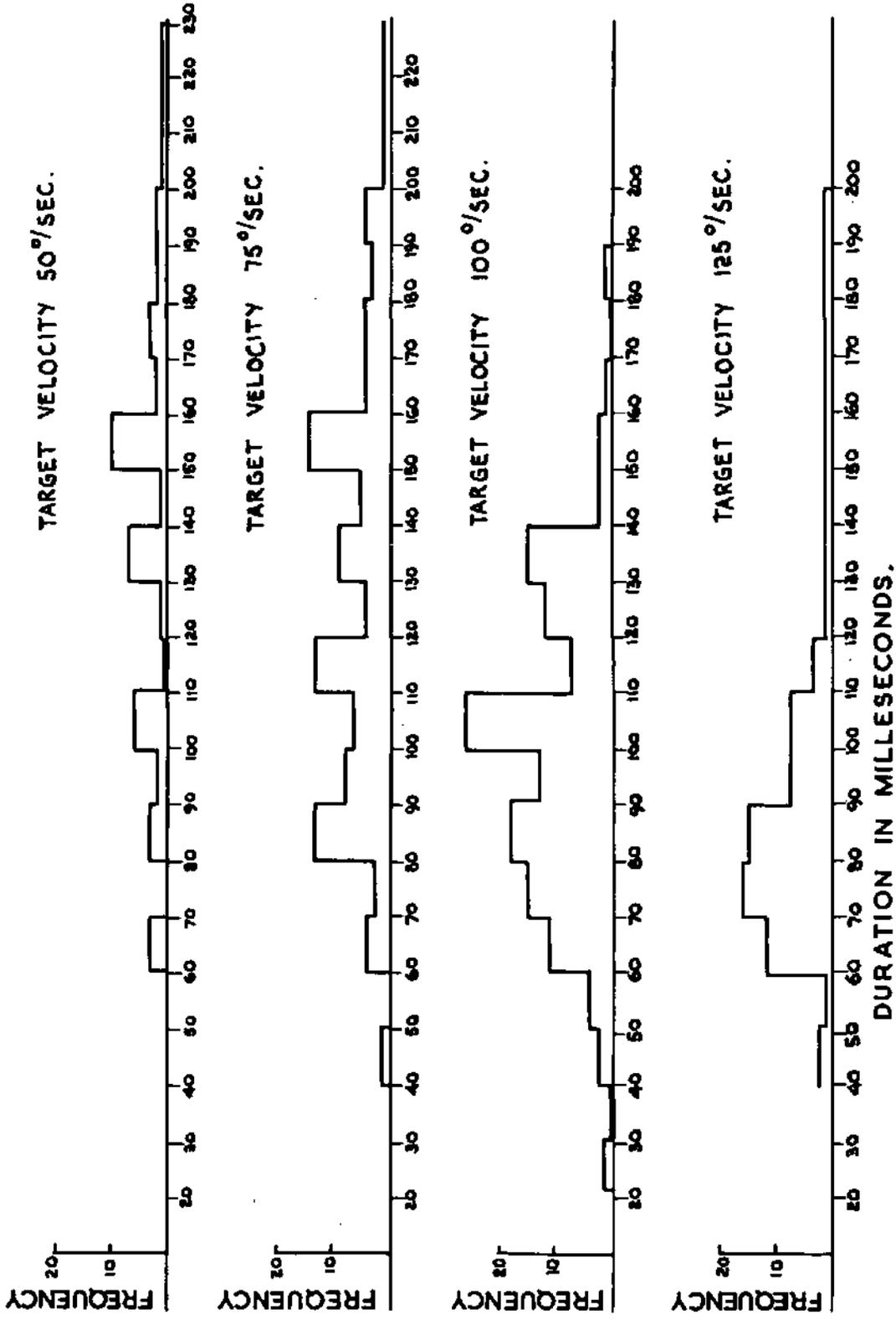


Fig. 57

DISTRIBUTION AT 50, 75, 100 & 125°/SEC STEADY STATE DURATION.

SUBJECT 4.

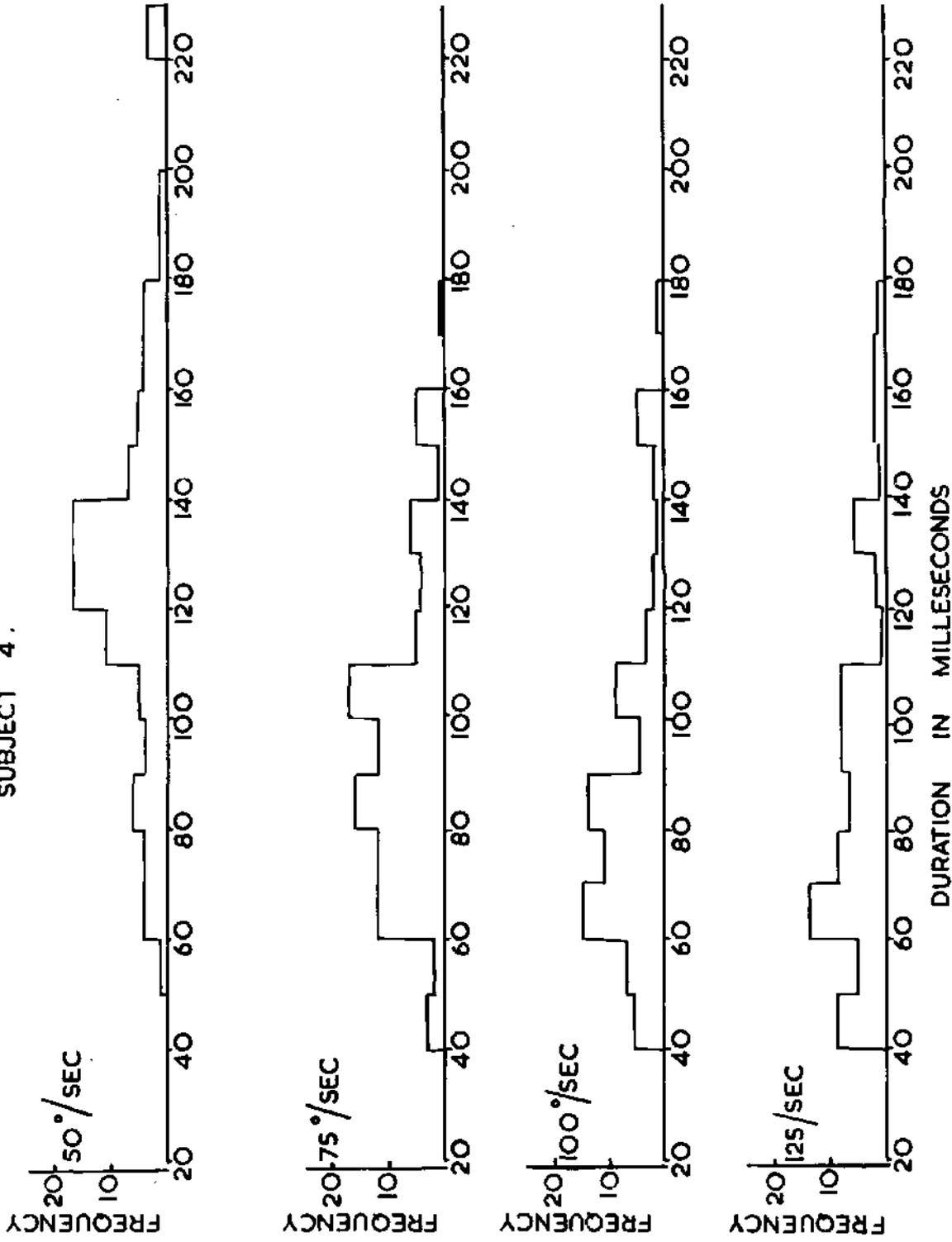
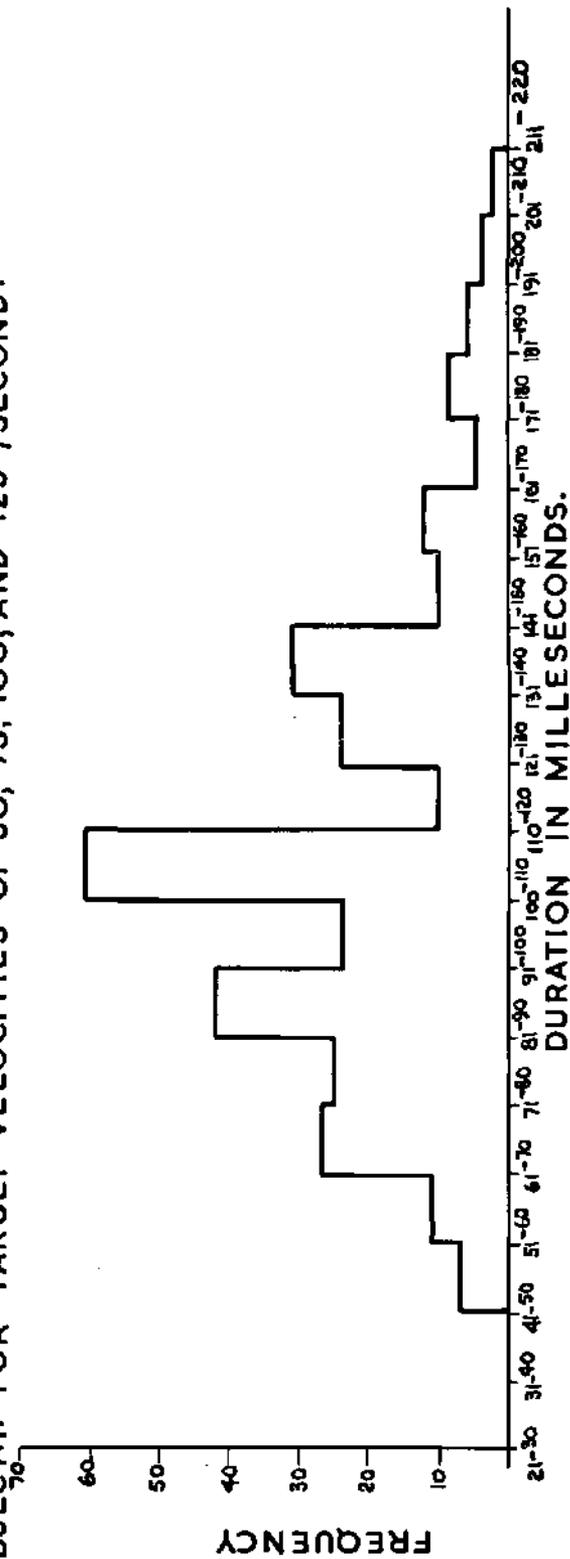


Fig. 58

COMBINED HISTOGRAM OF THE DURATION OF THE STEADY STATE.
 SUBJECT 1. FOR TARGET VELOCITIES OF 50, 75, 100, AND 125°/SECOND.



COMBINED HISTOGRAM OF THE DURATION OF THE
 STEADY STATE. SUBJECT 2. ALL VELOCITIES.

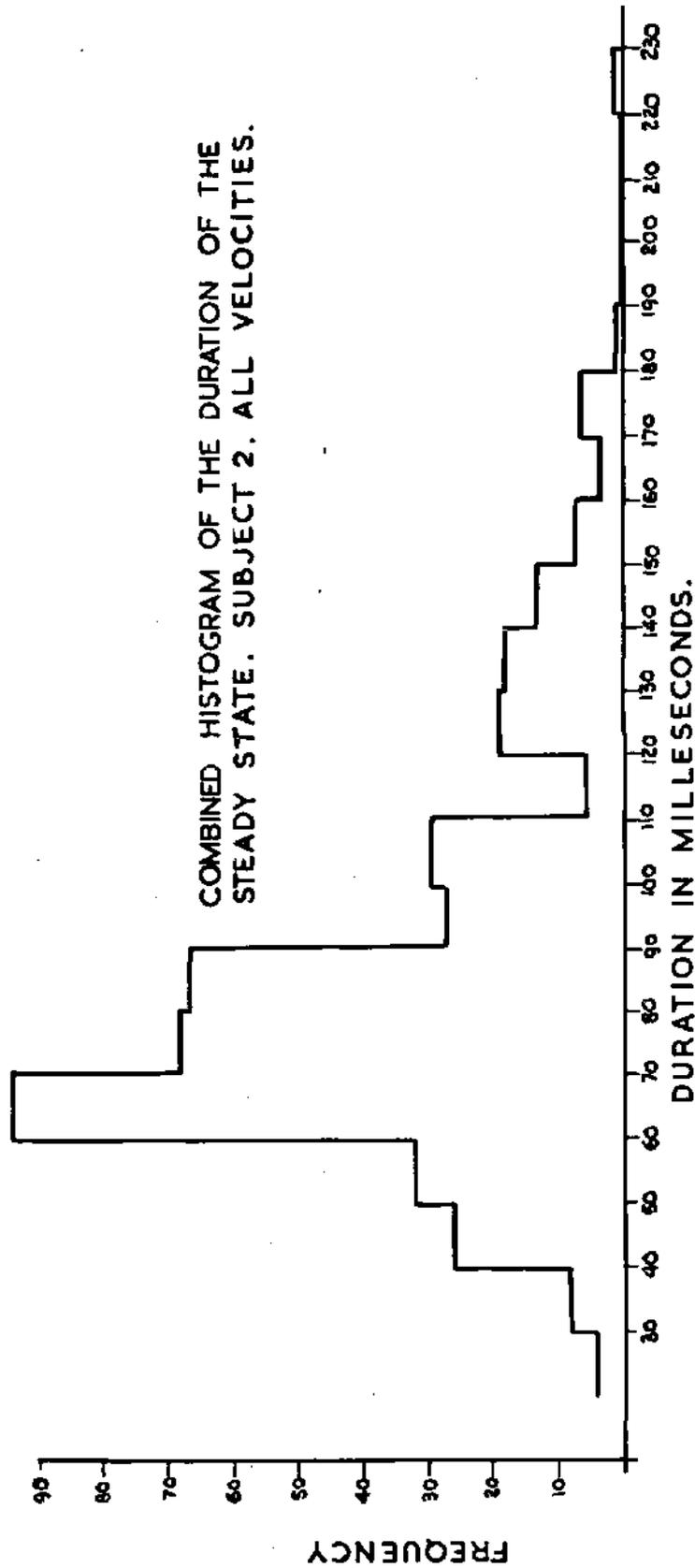
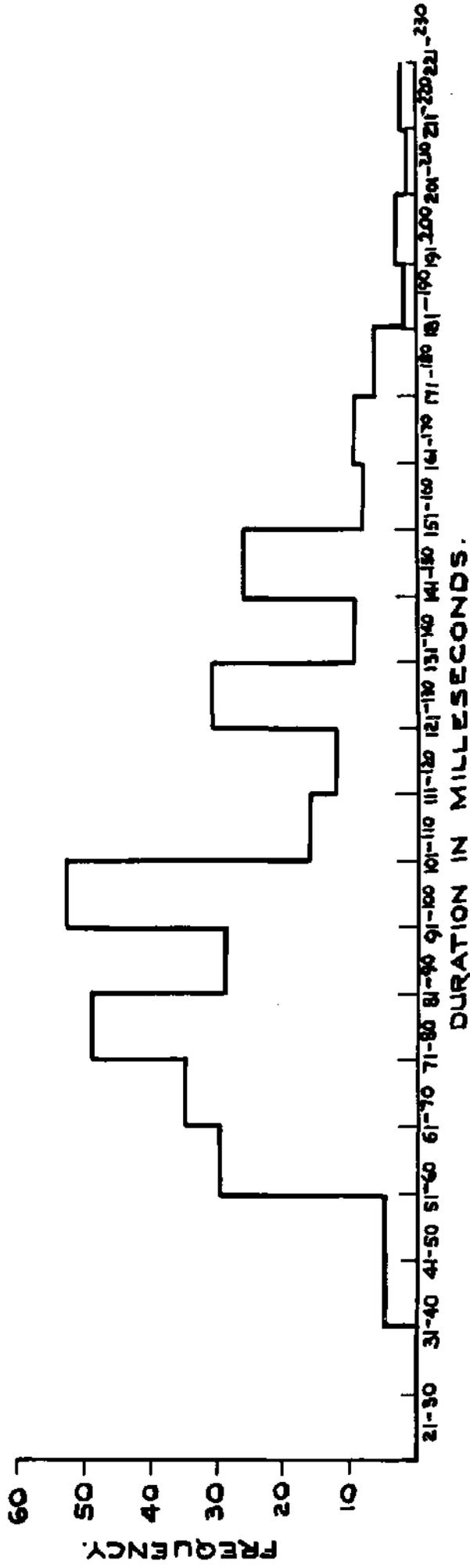
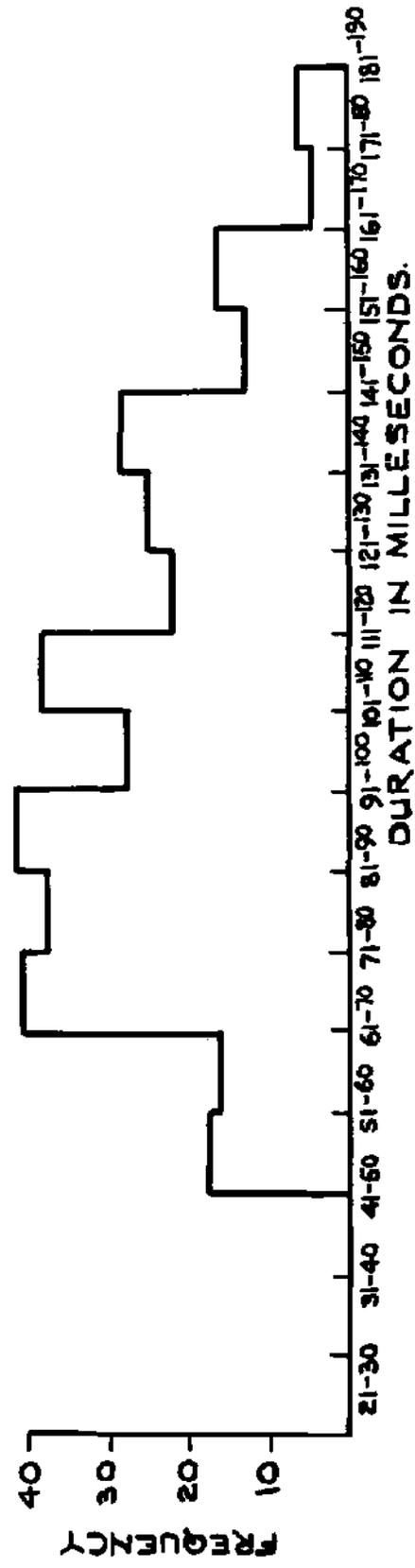


FIG. 59



COMBINED HISTOGRAM OF THE DURATION OF THE STEADY STATE.
 SUBJECT. 3. FOR TARGET VELOCITIES OF 50, 75, 100, AND 125°/SEC.



COMBINED HISTOGRAM OF THE DURATION OF THE STEADY STATE.
 SUBJECT 4. FOR TARGET VELOCITIES OF 50, 75, 100, 125°/SEC.

of eye movement in order not to move before the fixation point is reached. Such a move would possibly be considered premature and therefore liable to error.

The steady state

If the eyes on completion of the 1st saccade show a smooth pursuit movement, this steady state may continue for a long time, but if the eye position, the eye angular velocity, or both show a discrepancy with regard to target position or velocity then an error in fixation is present. When this is sufficiently great to preclude target recognition a steady state error exists and will be corrected involuntarily by the fixation reflex. It is considered that the information on which the second saccade is based must be largely obtained during the steady state, and that although some indication may doubtfully be obtained during the later part of the first saccade, position error will not be known until a steady pursuit phase has been achieved. The duration of this steady state was reduced significantly as target velocity increased. The duration varied from as short as 22 msec. to over 200 msec. It is the short durations which are of particular moment as these throw some light on the time factors involved in the fixation reflex. Individual histograms (Figs. 55-58) are shown of the durations in four of the subjects at each velocity and composite ones for each subject at all velocities (Figs. 59,60) and for

HISTOGRAM OF DISTRIBUTION OF
THE DURATION OF STEADY STATE
IN ALL SUBJECTS.

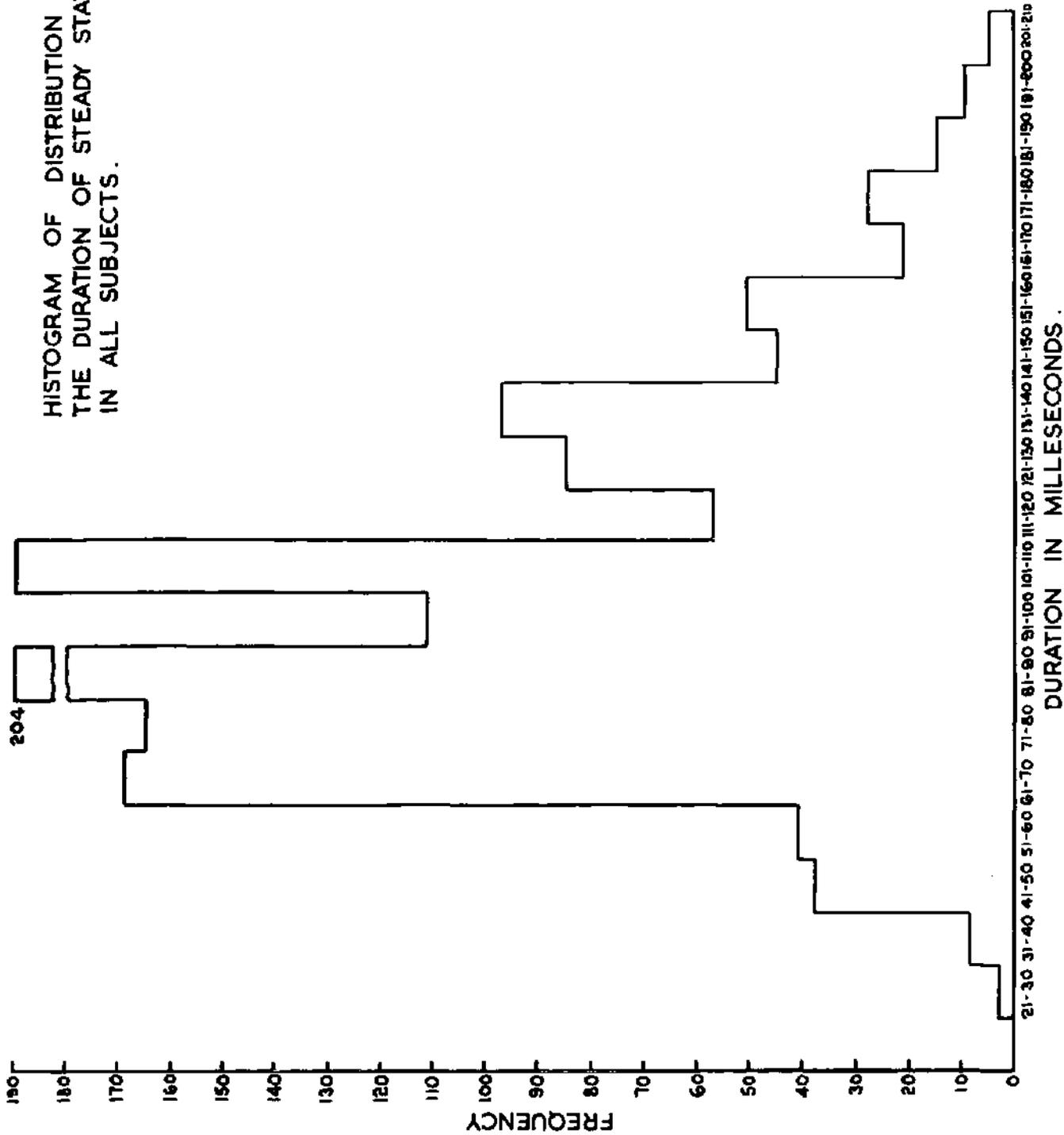


FIG. 61

all subjects at all velocities (Fig. 61).

The mean durations and significant differences of the duration are shown in Table 10.

Table 10

Mean Durations and Significant Differences of the Duration of the Steady State with Varying Target Velocities for all Subjects

Target Vel. ($^{\circ}$ /sec.)	50	75	100	125
Mean Duration (Msec.)	141.75	110.94	91.65	83.73

R.50 is greater than all others. $P = 0.001$

R.75 is greater than R.100 and R.125. $P = 0.001$

There is no significant difference between R.100 and R.125.

Standard Error 3.04. Differences required for significance:

9.79 at $P=0.05$, 13.16 at $P=0.01$, 17.36 at $P=0.001$.

Discussion of these findings in relation to the neuroanatomy and neurophysiology of the optic tract and oculomotor system is found in the final discussion in this chapter. It is at this juncture noted that the accepted elapsed time for afferent volleys from a visual stimulation to reach the visual cortex is some 30-70 msec. (Kovacs 1922, Froelich 1929, Monnier and Jeanneret 1947, Creed and Granit 1933, Monnier 1952) although Dawson (1959) and Cobb (1959) suggest that the elapsed time may be slightly shorter. There is some incompatibility in the time

100

factors found in the steady state with those of the retino-cortical pathway which leads to a hypothesis that the 2nd saccade may only involve some sub-cortical structures where there is potentially a system which could compare the obtained eye movement with the predicted eye movement and which, if the error was large, could initiate the second saccade. Such a possibility is considered to require the presence of some sense of eye position from the extra-ocular muscles. The presence or absence of such a sense has been the subject of controversy since the days of Helmholtz (1867)

The second saccade

The same features are noted in the 2nd saccade as in the first. It is a rapid overtaking movement and may be followed by a smooth pursuit phase or a subsequent third or even fourth saccade if pursuit is unsatisfactory and time of presentation of the target is sufficiently long.

In extent it varies from very minor $2-3^{\circ}$ to $10-15^{\circ}$. The mean velocities achieved appear reasonably similar to those found in the first saccade. They were not examined in detail. the occurrence of a sudden displacement of the pen of twice or more times the maximum pen deflections present on the trace during fixation of entry point was the criterion for saccadic movement occurrence.

The various factors described above are illustrated in Fig.58 in a composite display of the information obtained.

Comparison of eye movements, right to left and left to right.

The direction of movement in the previous experiments was left to right. A further series of runs were carried out with a right to left direction of target movement.

The eye movement patterns were of the same types in both directions of eye movement. There was in Subjects 2 and 3 a significant difference in the latencies. Subject 2 $P=0.01$, Subject 3 $P=0.001$. Subject 2 was faster in the left to right direction and Subject 3 in the right to left direction. Subjects 1 and 4 displayed no significant difference. The results of Subjects 2 and 3 are shown in Table 11. Each latency is a mean of 25 records.

Table 11

Comparison of Latency of Eye Movement in the Direction Right to Left and Left to Right.

Subject 2

Direction of Movement	Target Velocity °/sec.				Total
	50	75	100	125	
R - L	234.52	222.55	225.46	225.65	1732.16
	221.52	204.96	202.64	194.86	
	456.04	427.51	428.10	420.51	
L - R	201.26	199.26	191.27	189.38	1630.81
	223.64	208.20	208.52	209.28	
	424.90	407.46	399.79	398.66	
Total	880.94	834.97	827.89	819.17	3362.97

	S.S.	df	Mean Square	M.S. Ratio	Significant
Speed	569.93	3	189.98	3.81	NOT
Left or Right	641.99	1	641.99	12.88	P=0.01
Interaction	1232.6 20.71	3	410.87 6.90	8.24	P=0.01 NOT
Residual	398.80	8	49.85		
Total	2543.75 1631.43	15	—	—	—

Subject 3

Direction of Movement	Target Velocity °/sec.				Total
	50	75	100	125	
R - L	224.17	220.78	255.75	224.60	2643.36
	221.52	217.60	219.92	227.80	
	192.56	207.59	213.17	217.90	
	638.25	645.97	688.84	670.30	
L - R	244.80	248.00	257.92	261.75	2970.61
	238.59	231.85	234.19	240.69	
	239.73	259.15	259.29	254.65	
	723.12	739.00	751.40	757.09	
Total	1361.37	1384.97	1440.24	1427.39	5613.97

	S.S.	df	Mean Square	M.S. Ratio	Significant
Speed	673.14	3	224.38	1.2664	NOT
Left or Right	4462.19	1	4462.19	25.1845	P=0.001
Interaction	88.44	3	29.48	0.1664	NOT
Residual	2834.851	16	177.18		
Total	8058.621	23		1.9775	

Discussion

The movement of the eyes in the pursuit of a fast moving target was most frequently in two stages or saccades. The first occurred after a period called the latent period of eye movement and the second after a period called the intersaccadic interval. It is accepted that a fixational eye movement is programmed to ensure that the image of the object of interest is brought to the foveal area of the retina where the finest discrimination of detail within that image can take place. The eye appears to be committed to this programmed movement before eye movement actually takes place and this has been clearly demonstrated by Westheimer (1954a). He showed that when presenting a new fixation for a period somewhat shorter than the latency of eye movement, extinguishing that fixation point and reinstating the original fixation point, the eye movement would attempt to achieve fixation on a no longer existing point. After a further latent period the eyes would return to the original fixation point. The eyes do not move as a continuously tracking device when the fast movements of fixation are undertaken but demonstrate a step function, treating one fixation movement as a complete phase and following this by another equally complete phase if the image of interest is still extrafoveal. Makensen (1958) found that the pattern of horizontal eye movements was half sinusoidal and contained

a slowly starting phase, a maximum velocity phase and a slowing phase. He noted that only the intended final position of the eyes could be governed and that the movement itself was reflex and could not be altered by any voluntary control by the subject. The eye movements recorded may be considered to contain and display two reaction times, the initial latency and the inter-saccadic interval.

Any reaction time to a visual stimulus may be subdivided into 6 parts which are :-

- | | | |
|---|----------------------|---------------------|
| 1. The latent period of the retina | - Estimated duration | 20-70 msec. |
| 2. The conduction time in the optic nerve | " " | 2- 5 msec. |
| 3. The latent period of the visual cortex | " " | 10-13 msec. |
| 4. The Intra cortical integration time (opto-motor integration) | " " | 70-80 msec. |
| 5. The conduction time in the motor nerve system | " " | 2- 5 msec. |
| 6. The eye muscle contraction pattern development to achieve initial movement | " " | unknown
?7 msec. |

104+ to 173+

There is a somewhat limited knowledge of all these factors and the times involved in each. The latent period of the retina is measured from the presentation of a light stimulus to the beginning of activity in the optic nerve. Strughold

(1951) reviews the literature up to that date and notes that Froehlich (1929) assumed that retinal delay has a probable minimum of 20 msec. with a bright stimulus and increases markedly as the stimulus intensity is reduced.

During dark adaptation Kovacs (1922) found that the latent period diminishes during the initial 30 minutes and reaches a minimum comparable to the assumptions of Froelich. Adrian and Moruzzi (1940) recorded latencies of 25-50 msec. for primary responses involving cortex and 150-200 msec. for secondary responses. Noell and Chinn (1950) have recorded impulses in the optic nerve of the rabbit after 15 msec. and Monnier (1952) 28-32 msec. in man, using electroretinography (E.R.G.) as his method.

The conduction time in the optic nerve is given as about 5 msec. by Monnier and assumed to be somewhat less by Froehlich. The latent period of the visual cortex is also considered to be of small but significant magnitude. Strughold (1949 and 1951) again refers to Froehlich's assumptions and gives a possible minimum value of 13 msec. These three factors, 1, 2 and 3 above are collectively known as the latent period of perception and as such has had a small amount of interest shown in it since the days of Von Helmholtz (1851), Donders (1865), Exner (1868), Wundt (1911), Pulfrich (1922), Creed and Granit (1933) and more recently Monnier and Jeanneret (1947)

and Monnier (1952). The total duration of the combined factors is considered to be about 33 msec. and Cobb and Dawson (1959) have suggested it may be less. In rabbits Wang and Lu (1936) have rated 'off' effects* at 30 msec. in striate cortex, Van Hoff (1958) has recorded 'off'* responses at 15 msec. and 'on' responses at 40 msec. to intermittent photic stimuli. The only, but not exactly applicable, references to opto-motor integration times found are those of Monnier which he gives as 75 ± 5 msec. for the electromyographic activation (E.M.G.) of the fibres in the muscles controlling the thumb in response to visual stimuli. The 75 msec. does not include motor nerve conduction time or muscle action development.

On the conduction time through the motor system to the eye muscles and the delay in muscle contraction no definite information has been located in the literature. However, somewhat relevant are the researches of Cooper and Eccles (1930) who showed the contraction time of an extraocular muscle for an isolated twitch to be only 7 msec. which is by far the shortest contraction time of any muscle in the body. Labyrinthine stimulation has induced extraocular muscle reaction in 10 msec (Szentagothai 1952).

* Barlow (1953b) considered the trail of 'off' responses to be the information on which the frog based its fly catching ability, see Part 2, Receptor fields.

The minimum total reaction time for eye movement to commence in response to a static visual stimulation is generally that found by Diefendorf and Dodge (1908), a time of 150 msec. and Ginsborg (1953) 140 msec. For a moving target the reaction times found by Westheimer and found in these studies shows considerable variation in the general band 150-250 msec. or more. These reaction times to static and moving targets are long for so important a system but are compatible with the sum of the individual delays in the separate parts of the reaction times. The greater delay in the moving target instances may be attributable to increased opto-motor integration time.

The intersaccadic interval contains two phases, the first being that required to complete the programmed movement and the second during which it is assumed that the eye is tracking the target and obtaining data on which the corrective saccade is based.

The duration of the initial movement varied with target velocity, resulting no doubt from the greater angle through which the eye had to move to achieve fixation. The velocity of the eye movement also increased as target velocity increased and velocities of 200-500°/sec. have been estimated to occur, with targets of 50 and 125°/sec. respectively, no real estimate of the accuracy of such velocities can be given due to the

nature of the recordings.

The steady state duration varied considerably as is seen in the histograms Figs. 55-61 and Table 10. The duration diminished significantly with increasing target velocities. The hypothesis is advanced that it is only during the preceding steady state phase that the information on which the corrective eye movement is based can be obtained. The possibility has been entertained that during the final slowing of the eye movement in the terminal stage of the saccade, information may be obtained and the inclusion of this can add but few milliseconds to the steady state duration. During the fast phase when eye movement mean velocities are estimated to be 200-500°/sec. in these records and are known to be capable of exceeding such velocities, (Duke Elder 1944b), the differential velocity between moving eye and moving object may be as much as 300-400°/sec. At such velocities the object may not be seen at all.

The duration of the steady state in 90 records was less than 60 msec., the minimum being less than 30 msec., and in 600 records had a duration of less than 90 msec. If the assumption is erroneous that during the initial saccadic movement no information is obtained which is capable of being assimilated, then the total time available for organising, ordering, transmitting and developing the corrective movement increases by the

duration of the saccadic movement. The minimum recorded was 50-60 msec., there were 100 occasions when the intersaccadic periods were less than 90 msec. and 380 occasions when they were less than 120 msec. The minimum reaction time reported for an eye movement between two static points is 120 msec. and the minimum time for an intersaccadic period during eye movements between static objects and in pursuit of slowly moving targets is also 120 msec. (Ginsborg 1953, Westheimer 1954b).

The eye movements recorded have therefore shown in all subjects steady states within the intersaccadic intervals and total intersaccadic intervals which on many occasions were of shorter duration than is strictly compatible with present temporal concepts of the optic tract, cerebral representation and integration, and cortical control of motor activity.

The question arises of how such corrective movements of the eyes can be accomplished. Is it possible that in man there is a system which operates at some subcortical level either in response to photic or proprioceptive afferent impulses? Is there a combination of these two?, or are the neural pathways from the retina to eye muscles via the cortex capable of responding with greater celerity than has hitherto been demonstrated or even considered possible?

Present knowledge of neurophysiology of the tracks of the human visual system and oculomotor system has been derived from

examination of unfortunate subjects who have suffered a cranial injury or have some pathological condition during the treatment of which access became available for cerebral function investigation. The major part of our knowledge is anatomical.

In the human it is estimated that 70-80% of fibres in the optic tract end about the dorsal nucleus of the lateral geniculate body and are relayed to the striate cortex. Most of the remainder, which are concerned with light or pupillary reflexes, by-pass the lateral geniculate body and the brachium of the superior colliculus and pass to the pretectal area of the mid-brain. Lyle (1954) reports that other fibres pass to the various hypothalamic regions and that fibres have been found proceeding to the pulvinar of the thalamus and pretectal nuclei. Little is known of these fibres' function. He also reports that in some animals there are two accessory tracts, the posterior accessory tract of Gudden which passes to the mid-brain and possibly to the substantia nigra, and the anterior accessory tract of Bochenek which finds a termination in the posterior corpus subthalamus. These tracts have been found in the human embryo by Cooper (1946).

That voluntary eye movements are controlled from the frontal cortex was the opinion of Graham Brown (1922) and Holmes (1936). The latter expounding the concept that the frontal cortex "had cornered the market in eye movements". Smith (1944) added to

the knowledge of frontal cortex activity and considered that this part of the cortex imposed powers of regulation and coordination on lower order mechanisms. Injuries, loss of and lesions of the frontal cortex were reported by Holmes which left only occipital cortical control of eye movements. Such movements are usually of exaggerated fixation, difficulty in changing from one fixation point to another, and an inability to carry out any but the slow pursuit eye movements. Removal or damage to the occipital cortex usually results in complete or partial blindness. However, Bender and Pastyl Krüger (1957) reported motor defects in two cases. In one, a calcified mass in the left occipital cortex caused convulsive movements of head and eyes to the right and in the other, an atrophy of the right occipital lobe caused a nystagmus while fixating an object to the left. The authors could find no satisfactory physiological explanation for either of these events. Rademaker and Ter Brack (1948) working on dogs were convinced that the striate cortex had, in addition to sensory function, a motor one. This is in agreement with Kreiger et al (1955).

Cooper et al (1953A) has said that responses which involve cortex in man are never less than 200 msec., this is a sound average figure and corresponds well with the reaction time or latencies of eye movements which have been studied in this research. The steady states and the intersaccadic intervals

were frequently less than half that duration. The subjects are unaware of the occurrence or non-occurrence of these second saccades.

It is therefore not unreasonable to suggest that the frontal cortex is not actively involved but its action may be to free some other area from its control for the time required to continue successfully a fixation on a moving target. It may be a passive response to permit an action to take place more quickly, or with lesser restraint, an action of which the frontal cortex has approved and indeed initiated. The lack of necessity to involve intercortical pathways and structures would reduce the response time. Our present knowledge of the temporal aspects of responses involving striate cortex is as yet insufficient to indicate whether this somewhat reflex control of eye movement would be sufficiently rapid.

A second possibility is that in man this specific control of the fixation reflex is not entirely elevated to the cerebrum and that functional control may exist in the mid-brain and adjacent brainstem which is subservient to the frontal cortex, the latter having developed about the origin of the motor system.

Bishop and Clare (1955) and Bishop (1958) have attempted to correlate optic nerve fibre size with distribution areas, the large fibres relay to cortex, intermediate size to the thalamus after a relay, and small fibres to the tectum to activate the

colliculus and the pretectal area. Phylogenitically the newest systems are associated with the largest fibres, but there was also found to be fibres of all sizes in all parts of the cortex. The significance of this is unknown but he (Bishop 1958) concludes that development has consisted of a series of overlays and that nothing that the ancestors of the mammal had has been dispensed with and that the more primitive systems found in lower species still exist in mammal.

In this connection it is interesting to note the facts reported and opinions expressed by Duke Elder (1944).

"Corresponding to their unique nerve supply the extra-ocular muscles exhibit the peculiar physiological reaction of contracting under the influence of choline and nicotine in the normal condition. If an animal is injected intravenously with acetyl-choline a short sharp contraction of all the recti and obliques takes place: a slow tonic response is elicited by choline or nicotine, while the same phenomenon is seen in an isolated muscle preparation in vitro. This activity is unaffected by atropine, increased by adrenaline, and abolished by nicotine and curare. It is interesting that a precisely similar reaction is obtained from the normal striped muscle of species below mammalia, which, it will be remembered, are provided with peculiar nerve-endings resembling those found in the extra-ocular muscles. It

also occurs in the foetal muscles of mammals, but it is evident in the other voluntary muscles of fully-developed mammals only after they have been deprived of their motor nerve-supply. This reaction is analogous to the pseudo-motor contraction which occurs in skeletal muscle when the sensory supply is stimulated after degeneration of the motor fibres, a reaction which has been shown to be independent of the sympathetic, but to depend upon the activity of the small fibres which have their cell-stations in the posterior root ganglia of the spinal nerves, and which normally mediate vaso-dilatation by antidromic responses. It thus appears that the normal (non-denervated) extrinsic muscles of the eye of mammals act, so far as choline and nicotine are concerned, in a manner exactly parallel to the voluntary muscles of such species below mammalia which have been investigated, or to the other voluntary muscles of mammals before they have received their nerve supply or after they have been deprived of it. The significance of of this unique behaviour is in our present knowledge far from clear. It would seem that these muscles are able to avail themselves of an archaic and primitive mechanism which the other voluntary muscles have lost and which is analogous to that evident in the involuntary muscles; and although it is difficult to suggest any physiological reason for this

peculiarity, it is doubtless linked up with their peculiar nerve supply and their highly specialized functions."

Hines (1947) has suggested that orientation of head and eyes stems from some complex unification at thalamic level and Smith (1944) is in some agreement that movement of head or head and eyes occurs when retinal afferent impulses arrive in the mesencephalon and adjacent brainstem. They are also in agreement that these responses are regulated by activity of the frontal eye fields in the frontal cortex. In cats, Faulkner and Hyde (1958) have shown that the reticular neurons in large areas of the brainstem have access to the final motoneurons which subserve movement of the eyes, head, trunk and limbs. Barraquer-Bordas (1957) also considers the reticular activating system in the tegmental area has some governing influence on eye muscle contractions.

The third possibility is some association between the visual system and proprioceptive system in the extraocular eye muscles which exists and is active during pursuit eye movements.

Snider and Stowell (1944) and Snider (1950) have reported areas within the cerebellum of the Macaque monkey in which sensory afferents, including visual, are received with a latency of 20 msec. and consider that the responses they elicited are dependent on a pathway which probably includes the superior colliculus. The latency, however, is still some 20-50 msec.

for low intensity photic stimulation which is not greatly different from the latencies of 30-70 msec. found in striate cortex. In the frog's colliculus Andrew (1955) recorded 'off' responses at 30 msec. and 'on' responses at 50 msec.

Ruch (1951) describes visual sensory areas in the cerebellum and also areas which receive proprioceptive information from sensory endings in extraocular muscles. Granit, Holmgren and Merton (1955) showed that by cooling the anterior lobe of the cerebellum sudden reflex contraction of muscles could be re-routed to an α (faster) route instead of following the Y route (slower) which involves muscle spindle afferent and efferent fibres. Thus two systems both of which are in some way dependent on cerebellar activity can be separately brought into play, the one a fast direct system and the other a slow servo controlled system which demands muscle spindle feedback.

The presence in the cerebellum of proprioceptive responses from extraocular eye muscles and the current concept that the cerebrum decides what to do and the cerebellum how to do it may be correlated. The cerebellum may be capable of directing a movement pattern, comparing the muscle response obtained with the response demanded. It may also be in a position not only to correct a faulty muscular response but compare the degree of achievement in fixating with that actually required. A new movement pattern could conceivably result, a pattern that

achieved the desired fixation.

The only other single structures which may be of primary importance are the superior colliculi which in man were reputed to have involvement only in pupillary reflexes. Le Gros Clark (1944) states that fibres concerned in the pupillary reflexes go to the tegmentum and not the superior colliculus. The superior colliculus in lower animals appears more highly developed than in man and does subserve eye movements in response to visual stimuli. In dogs, Bechterew and Donders (cited by Kluver) demonstrated conjugate deviation of the eyes on stimulation of the optic nerve, a response which was abolished when the superior colliculus was destroyed. After destruction, eye movements could still be obtained from occipital cortex. They concluded that the superior colliculus is an optical reflex centre but not one subserving voluntary movements.

Point to point localisation between the retina, and the contralateral superior colliculus has been shown by Wang (1936) in the rabbit, by Apter (1945, 1946) in the cat, in teleosts by Buser and Dusardier (1953), and to some extent by Hamdi and Whitteridge (1954) in the goat and the rabbit. Optic nerve fibres sweep in from the direction of the lateral geniculate body, the structure in which the vast majority of optic nerve fibres find synaptic or relay stations. Cooper, Daniel and Whitteridge (1953) using penetrating microelectrodes found in addition to the known collicular surface distribution of

responses to focal visual stimuli and the deeper layers also gave similar responses. 'On' and 'off' discharges can be demonstrated when even feeble illumination of the eye in a completely dark environment is carried out. Spontaneous discharges in the dark are also to be noted. Latencies of these responses elicited were relatively short, about 25 msec. for 'on' and 40 msec. for 'off'. Other longer latencies were also found.

Cooper et al (1953b) have found in the goat's brainstem areas adjacent to one another which give visuo-sensory and extraocular eye muscle sensory responses, the latter being slowly adapting.

Of potential importance in fixation reflex understanding is their finding (Cooper et al, 1953c) that in the fibres just rostral to the central grey matter of the midbrain there are responses to visual stimuli and stretching of the ipsilateral eye muscles. Thus contralateral visual stimuli and ipsilateral external eye muscle stretch receptors were in immediate anatomical association. The cortex overlying the dorsal surface of the colliculus gave responses to visual stimuli near to areas in which muscle receptor discharges could be located. Between the colliculus and this cortical area there was a definite silent area. These responses in juxtaposition suggest that there is association between stretch receptors in extraocular eye muscles and retinal field output. Fillenz (1955) also

reports responses in the brainstem of the cat from stretch of extraocular muscles and retinal stimulation.

By a statistical process, previously described, called normalisation the presence or absence of two modes in a wide distribution of intersaccadic interval durations can be ascertained. The presence of two modes would have suggested two neural organisations, which would support the suggestion of subcortical control of the 2nd saccades. The results shown in Fig.54 do not demonstrate such a bimodal distribution. The conclusion, based only on this evidence of statistical nature, is that the neural pathways when stressed can operate more quickly than has hitherto been reported or considered possible.

Cooper, Daniel and Whitteridge (1955) strongly advocate the possibility of proprioceptors from eye muscles and their association in the brainstem and colliculus with retinal output having a part to play in eye movements and fixation, and Eason and Hyde (1957) consider fixation reflex movements to be controlled at brainstem level. Cooper et al conclude: "We have been concerned in this paper only with those stimuli arising in the ocular muscles themselves and are convinced that every eye movement, be it voluntary or reflex, tiny as in saccadic fixation movements or large as in some form of nystagmus,

120

is recorded accurately and indefatigably in the brainstem by the eye muscles. Such a recording must play an important part in maintaining or attempting to maintain the eyeballs in the optimum position for vision and in keeping them in readiness to be moved at will."

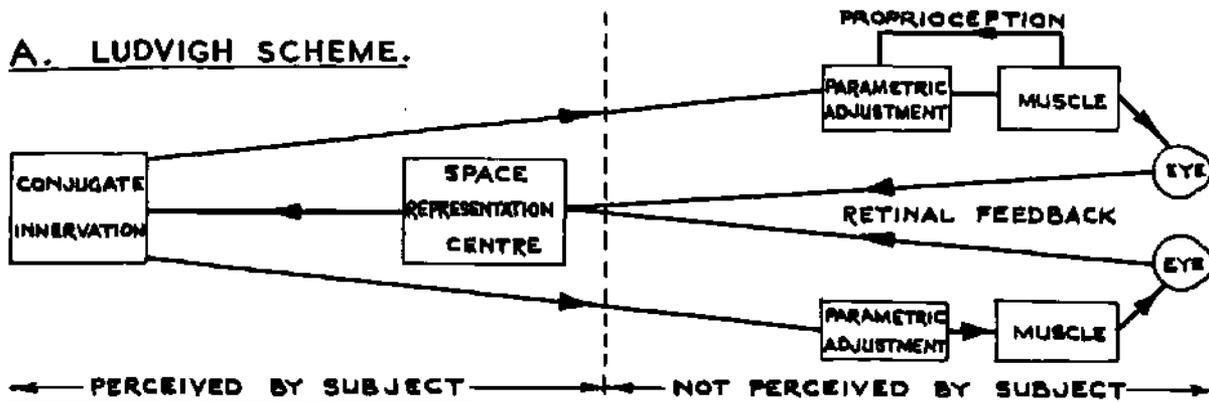
If these convictions are correct then the short corrective saccadic movements reported in this thesis may have their origin in subcortical structures which in their reflex activities are less time consuming than pathways which involve cortex.

However, despite lack of positive evidence of two separate neural organisations being involved in the control of the second saccade there is evidence of two neural pathways being within the oculomotor system. The latency of the initial movement was generally in the 150-250 msec. range, and what could be called the latent period of the 2nd. saccade movement (1st saccade + steady state) was in a range, the minimum value of which was some 60 msec., the upper limits of which was 300 msec. and the mean value about 120-160 msec.

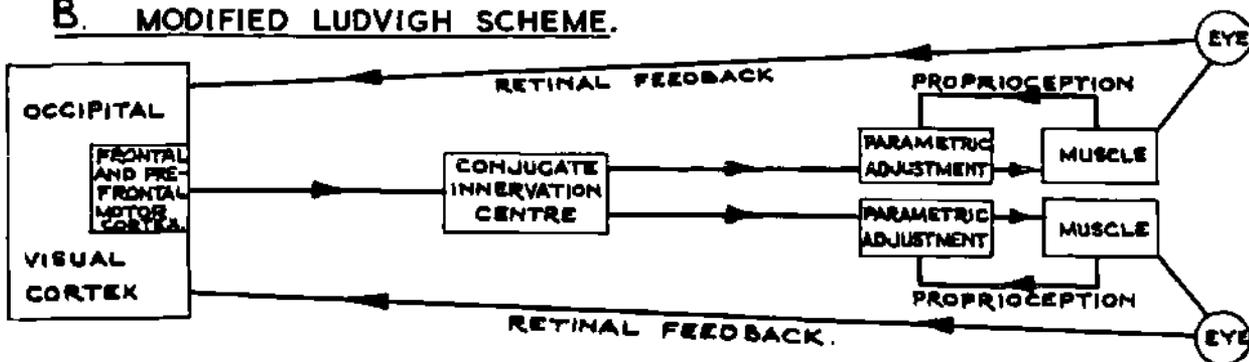
The first system is of voluntary nature and is considered to involve frontal cortex and requires considerable computation to design the original overtaking and the pursuit eye movement. The minimum period recorded was 120 msec. The second system which is involuntary or reflex could operate at much faster rates.

POTENTIAL SCHEMES OF THE OCULOMOTOR SYSTEM.

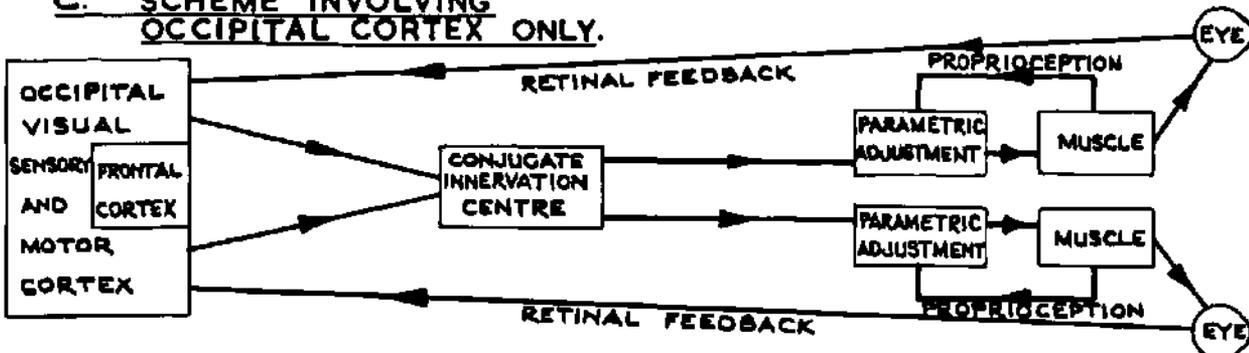
A. LUDVIGH SCHEME.



B. MODIFIED LUDVIGH SCHEME.



C. SCHEME INVOLVING OCCIPITAL CORTIX ONLY.



D. A SUBCORICAL SCHEME.

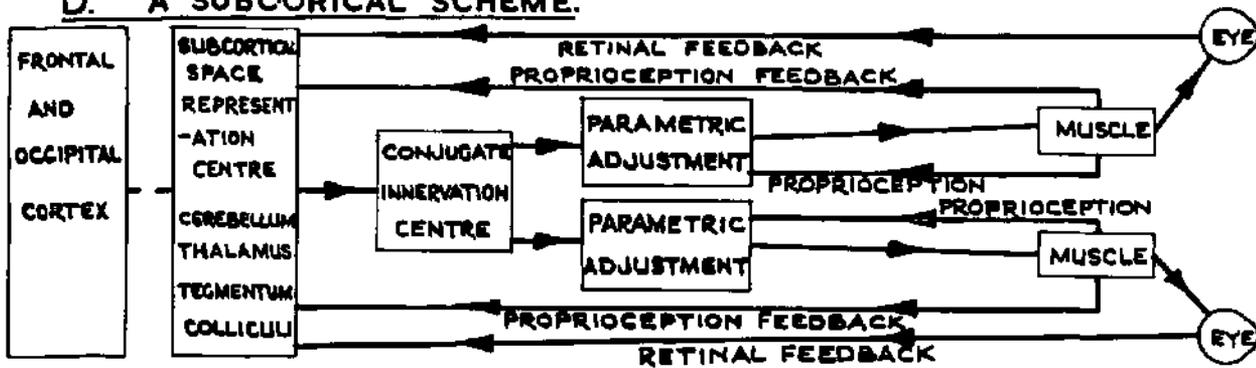


Fig. 62.

could occur repeatedly during one eye movement, and was carried out without the subject being aware of its presence. This latter system can operate in such short times that cortical involvement is somewhat doubtful but if cortical involvement does take place it would be limited to the striate cortex. The complexity of these eye movements may be considered to be of lesser degree as its function is to correct smaller errors in position and velocity than the initial eye movements.

The conclusions reached are that the eyes are controlled in pursuit movements by voluntary and involuntary or reflex systems, the latter having a capability of reacting in a time scale which suggests that control is subcortical or from striate cortex. The latter being supported by the work of Faure and Corcelle, 1955.

Potential schemes of the oculomotor system

Ludvigh has proposed the following scheme for the oculomotor system and as a result of the experiments described in this thesis alternative schemes are presented in which an attempt to depict other possibilities is undertaken. The description of Ludvigh's scheme , Fig. 62A, is his original and is quoted.

"An essential point in interpreting the subject's perception is that he is subjectively unaware of the processes occurring to the right of the dashed line. In terms of this diagram a normal eye movement of change of fixation may be described as follows. An impulse to conjugate innervation for, say

10° eye right is sent out by the conjugate innervation centre to the motor system of each eye. At the same time there is sent to the functional region designated space representation, impulses indicating the nature of the impulses sent to the motor system. The innervation sent to the motor system arrives at a parametric adjustment centre for each eye. Now, owing to the position of eyes the tonus of individual muscles, and the fixation tremor, varying proprioceptive impulses are continually being generated. The parametric centre continually adjusts to these impulses with the result that either the innervation received is modified or impulses are sent altering the response characteristics of the appropriate muscle in such a manner that, for the position of the eye and the tonus of the various extraocular muscles involved, the muscles exert the force necessary to move the eye substantially 10° right. The resultant movement of the eyes brings about a displacement of the image on the retina. Retinal feedback now occurs and nerve impulses are transmitted to the region of spatial representation. If agreement occurs between intended and accomplished movement there will be no apparent movement of the environment. There may be a $\frac{1}{2}^{\circ}$ error because of the 10° demand. After 200 msec. via the conjugate innervation centre a new set of impulses are

sent out and a 2nd movement more precise is developed."

This scheme of Ludvigh's gives a role for the proprioceptors in eye movements but one which limits the possible role to an aid to eye movement control under varying tonic conditions of the extraocular muscles. The initial eye movements in a pursuit task are well fitted to the scheme and a minor modification is suggested in Fig. 62B in which the space representation centre is shown as a striate and frontal cortex integrated system, a system with slow response characteristics which could reasonably meet the 200 msec. specification given by Ludvigh and which agrees with the initial latencies in the present experiments.

However, the corrective phase can function much more rapidly and it has been suggested that this may or may not be a cortical activity. It conceivably could be a striate cortical function or a subcortical one. In addition it has been suggested that proprioception may play more than a mere tone recording role. Figs. 62C and 62D show schemes one of which (C) reaches the striate cortex but does not involve inter-cortical integration and would therefore be less time consuming, this infers sensory and motor functions for striate cortex. The other, scheme D, depicts a subcortical mechanism and the structure potentially involved. Proprioception in D is given the additional role of providing information on eye position in addition to the

parametric function of tone control or recording. The time factors in these two systems would be more compatible with the shortness of the intersaccadic intervals so frequently recorded.

Summary

Eye movements were of two types. The one containing a second saccade which is assumed to be of corrective nature the other showing a smooth eye movement.

The latency of eye movements varied from 150-300 msec., having a mean of some 200 msec.

The incidence of 2nd saccades with target angular velocities of $50^{\circ}/\text{sec.}$ or more was 50-100%. There was some diminution in incidence at $125^{\circ}/\text{sec.}$ which indicates a commencing total failure of the oculomotor system.

The intersaccadic intervals recorded were often less than 120 msec. which is the minimum period recorded by investigators of eye movements.

The steady state period may be as short as 50-70 msec. This is the period during which a corrective eye movement is assumed to be organised and executed. This short period is not compatible with current concepts of the times involved in the oculomotor system. Some potential and alternative system schemes are discussed.

PART 6Pursuit Movements in the Vertical PlaneFailure of the system due to an illusion and apparatus limitations

The physical nature of the projection apparatus used in these experiments on the discrimination of detail in moving objects precluded presentation of the stimulus in the vertical plane. To permit pursuit eye movements in the vertical plane through the eyes the position of the subject was changed from the seated upright position to one of lying on the side with the transverse axis through the eyes vertical. It was anticipated that there might be some interaction between visual and other sensory receptors and that this would probably be seen by the subject. This anticipated interaction occurred and consisted of a false sense of the horizontal. The target which moved physically through a horizontal arc appeared to have an inclination to the horizontal. The extent of the illusion obtained was such that only limited studies on ability to discriminate the detail in the Landolt ring targets were undertaken. Miller and Ludvigh (1953) have shown that the deterioration in visual acuity found with increasing target velocity in the vertical plane is comparable to that found in the horizontal plane. The extent of the illusion was examined and the degree and direction of the inclination recorded.

Investigation of the illusion

Method. The subject lay on his side on an examination couch in a dark room with the head horizontal. This position was checked by lining up the eyes of the subject with a vertical line on a mirror. When this line passed through the centre of each eye the subject's head was considered to be horizontal. The room was then darkened. The target would now move in the vertical plane relative to the eyes and eye movements would be produced by inferior and superior rectus muscles.

The Aldis projector system was remounted to permit deviation from its horizontal traverse to one of inclination to left or right thus projecting the target with an inclined upward or downward direction with a maximum deviation from the horizontal of 25° .

The subjects were airmen of various trade groups who were unaware of potential interaction between visual and proprioceptive afferent information and were not shown the illusion at any time during the experiment. They were presented with a moving target and asked to say if its direction of travel was up, down or horizontal. On their responses adjustments were made to the direction of the target until the subjects were convinced by repeated observation that the target was moving horizontally.

Each subject carried out three estimations when lying on the left side and three lying on the right side on each of four days. The target traversed the field of view from right to left and left to right for each observation.

Results. The projected Landolt ring target travelling in the horizontal plane gave an immediate impression of climbing when the target moved from left to right (foot to head), while the subject was lying on his right side. Movement right to left (head to foot), with the subject lying on his right side gave the impression of descending. When the subjects lay on their left sides with the head horizontal the opposite effects were noted.

The occasional use of a phosphorescent rod permitted determination by the subject of the apparent vertical when the apparent horizontal had been found. The deviation in the apparent vertical was of the same order and of the same error sign as that found in the deviation from the horizontal.

The complete results are shown in Table 12. They show considerable variation in any one subject in any session or in all sessions and also show considerable variation between subjects. The errors varied from 3° to 22° of arc. There was also some variability between the opposing postures. Where this occurred is indicated by the bracketed figures in Table 12.

It was also noted that when subjects had assessed the target

movement track as being horizontal the observer could deviate the direction of the target by $\pm 1\frac{1}{2}$ - 2° without the subject noting any change in the apparent horizontal.

In the course of the 30 minute experiment some evidence is shown of increasing error (Subjects 1, 2 and 5).

As these findings were not strictly related to the general experimental programme being undertaken, no further experiments were carried out.

Eye movements

Using the corneo-retinal potential output, eye movement traces were recorded. The movement of the eyes when following the horizontal target showed no obliquity.

Discussion

The relationship existing between visual and proprioceptive functions (proprioception in this sense includes semicircular canals, otoliths, visceral, muscle tendon and skin senses) in the maintenance of orientation have been intermittently investigated since Aubert (1861) first noted that in the absence of the normal visual framework of natural or man made structures the perception of the vertical (and horizontal) can be erroneous. Aubert (1861) noted that in a dark room when the head is laterally tilted on the erect body the estimation of what is vertical has an error in the opposite direction to that of

tilt and that this error increases as tilt increases. Fielchenfeld (1903) showed that this error is reduced when the whole body is tilted and the orientation of head and body retained in a more normal relationship. This maintenance of the relationship is readily noted in people standing, walking or sitting, the head is very rarely tilted laterally but not infrequently is tilted forwards.

Lateral tilting at sea can be readily noted, a compensatory adjustment to the roll of the ship, and in aircraft this compensatory tilting in the opposite direction to that of roll can also be seen. The body makes an attempt to maintain its gravity sensitive system in the plane of normal gravitational pull. Gibson and Mowrer (1938) proposed the hypothesis "that both the visual and the postural vertical are determined by visual factors and gravitational factors acting jointly, with orientation to gravity, however, as the more decisive factor in cases of real conflict between the two types of sensory data and the primary factor genetically". They conclude that the framework of visual space is derived from and dependant upon the necessity of maintaining postural equilibrium against the pull of gravity.

Gibson and Radner (1937) and Passey and Guedrey (1949) have also noted that when tilt is maintained for some time the error in detecting the true vertical tends to increase. In an

extensive programme Mann et al (1949), Passey (1950), Mann (1951) Mann and Passey (1951) and Mann (1951, 1952) have attempted to define the relationship between visual and proprioceptive factors in the perception of the vertical. The apparatus consists of a complete conventional room which can be tilted and the subject sits in a chair, also capable of being tilted. Thus visual and proprioceptive cues can be varied separately or together. The subject is required in each experiment to return himself in his chair to the vertical plane. The errors noted are about $2-6^{\circ}$ of arc. The conclusions reached are that the determination of the vertical is a joint one of visual and proprioceptive sensory systems and that the best judgements are made when these two complement one another, and that either one alone is subject to error.

The subjects used in the experiments lay on their sides in the dark room for approximately 30 minutes, and in some subjects (1,2 and 5) there is some evidence of increase of error in the judgement of the horizontal as time of lying increased. Passey and Guedry (1949) have reported that when lying in a tilted position is continued for 60 seconds that the subject's ability to return himself to the true vertical was less accurate than under conditions of shorter exposure. This type of effect was also noted by Gibson and Radner (1937).

Conclusion

The results produced in the current experiments in which head-body orientation is maintained show not the appreciation of the vertical but the appreciation of the horizontal with moving objects. The effect is comparable and is a further indication of the interaction of the stimuli and the adoption by man of a false horizontal (or vertical) under specific conditions.

The variation in individual subject's responses on a day to day basis is somewhat large but when consideration is given to the $\pm 1\frac{1}{2}$ - 2° change which could be made without the subjects noticing, the variation is reduced to more reasonable and expected levels. The variation between subjects is marked and does suggest that the interplay between visual and proprioceptive sensory systems is not of any fixed relationship in all individuals. Some subjects may be gravity sensing sensitive and others less sensitive.

Summary

Man's inability to locate the horizontal when visual and proprioceptive cues are disparate has been demonstrated by a new method.

Subjects vary in their estimations and also show a daily variation in any one subject.

The extent of the error in locating the horizontal varied from 3 - 22° of arc.

The location of the vertical was of comparable error.

Table 12

Errors in the Determination of the Horizontal

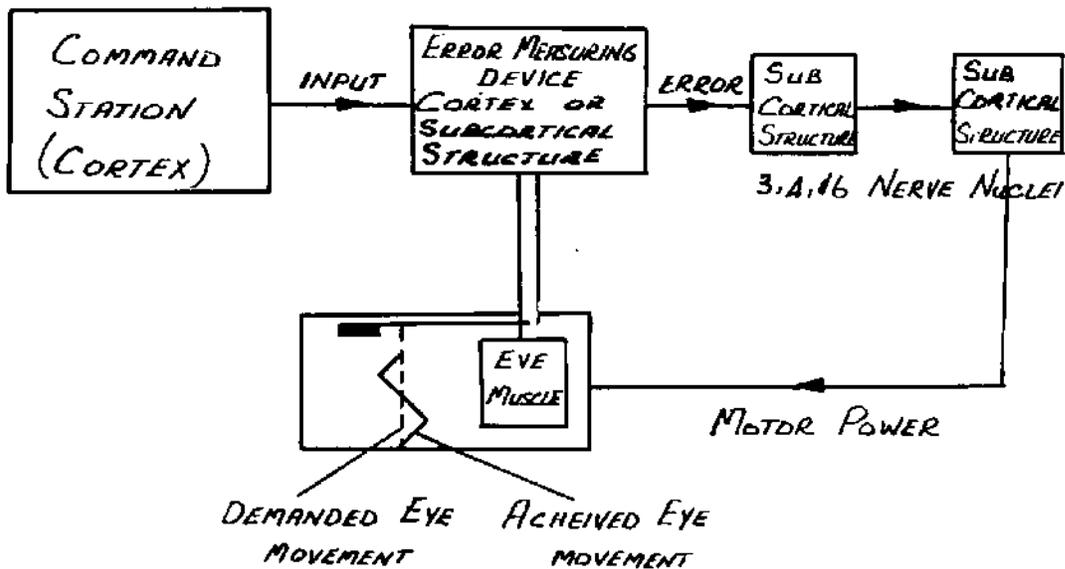
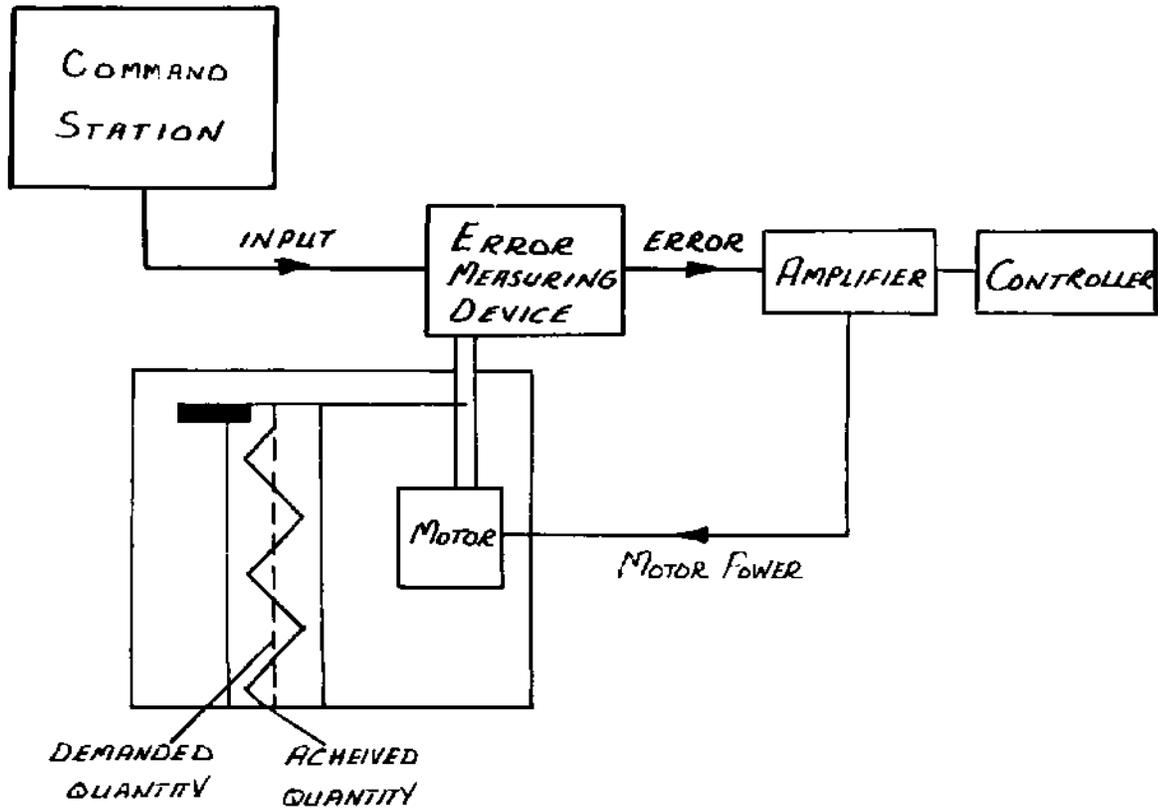
Subject	Run	Right Side Down			Mean	Left Side Down			Mean
		A	B	C		A	B	C	
1	1	11°	12°	12°		9°	12½°	14½°	
	2	11	15½	11	Mean	10	14	13½	Mean
	3	12½	11	11	12°	6½	7	7	10.5°
	4	13	11	10½		8	9½	11½	
2	1	13½	11½	14 (19½)		13½	14	12½	
	2	7	13½	14½	Mean	11½	14½	15½	Mean
	3	10	11½	9½	12.5°	8½	9½	11½	12°
	4	9	13½	14		9	10	11	
3	1	19	22	14 (15½)		15	13½	11½	
	2	19	17½	22	Mean	16	19½	19	Mean
	3				18°				15°
	4	17	18½	16½		11	13½	17½	
4	1	6½	5	5½ (8½ 6½)		4½	5½	4½	
	2	5	9	6		7	9½	11 (15½)	
	3	8	7	7½	Mean	7½	6½	7½	Mean
	4	5	6	7	7	9½	12	14	8.1°
5	1	4	9½	10		11½	12	13½	
	2	3	3	4	Mean	7½	7½	7	Mean
	3	7½	8	9	7.5°	7	10	8	10°
	4	6½	13	11½		10	11	12	
6	1	18	14	16½		9½	9½	12½	
	2	15	20	18	Mean	11	11	9½	Mean
	3	11	12	12	13.5°	4½	5	6	9°
	4	8	8	8		11½	8½	12	

Right Side Down Mean = 11° (S.D. 4.5°)

Left Side Down Mean = 10½° (S.D. 3.5°)

Overall Mean = 10.85° (S.D. 4°)

DIAGRAM OF A SIMPLE SERVO CONTROLLED SYSTEM



THE OCULO-MOTOR SYSTEM ANALOGY

Fig. 63. a & b

PART 7

The Analogy to Servomechanisms

Definition of a servomechanism

A servomechanism has been described by Brown and Cambell (1948) as a continuously error sensitive follow-up amplifying system permitting a wide range of input command remotely located from the element being controlled. A diagram by the same authors, Fig. 63A of an elementary servomechanism for temperature control is shown and the analagous physiological and anatomical functions and structures are suggested - Fig. 63B. Unfortunately the presence of a secondary system related to eye muscles and their control demand recognition of a collateral servomechanism to ensure adequate muscular response to any demand irrespective of the original eye muscle tonus. There is also evidence, Ginsborg (1953), Westheimer (1954b), that the system may respond with either a gliding movement or a saccadic movement. This mechanism is indeed complex and in addition has also to contend with simultaneous head movements.

Principal functional components of a servomechanism

1. A remotely controlled command or input station designated (a)
2. An output member or process designated (b) in the figure.
3. An error measuring means capable of measuring the difference between command and output designated as (c).

4. An amplifier or controller designated as (d) in the figure. It actuates a servomotor in accordance with some function of the error.

5. A servomotor designated as (e) in the figure. It operates the controlled member or output.

Principal functional components (shown in Fig. 63)

1. Input from the motor cortex which itself has received an input from sensory cortex which records its input from the retina designated (a)
2. Output member - retina and sensory cortex - designated (b)
3. An error measuring device which with current and accepted neuroanatomy can only be once again sensory cortex which receives its input from the retina - designated (c)
4. An amplifier or controller which may be in the motor cortex, cerebellum, tegmentum or ocular muscle nerve nuclei - designated (d)
5. A servomotor - eye muscle - designated as (e)

Present neurophysiological knowledge does not permit differentiation of location of much of (a), (b) and (c). The structures concerned in (d) also suffer from considerable lack of knowledge.

The cortical areas involved, frontal and occipital are interdependant and disease or injury to one affects the other as has been described most clearly by Holmes (1938).

The complexity of such a system may be reflected by the duration of time involved in the pursuit movements of the eyes. An initial latency of 150-250 msec. has been shown to occur, thus the servomechanism has a large delay in its initial function. Its later function of correcting errors has a somewhat smaller delay of about 90-150 msec., a delay which recurs and can be shown (Fig. 41) on occasions to occur regularly during a pursuit. Westheimer (1954a) has shown gliding movements to occur when the velocity error or position error has been small and Ginsborg (1953) has shown the same mechanisms to function when the eye moves between static targets. Thus the servomechanism is capable of responding with two types of movement but has a very marked delay in its operation, a quality indicating a mechanism higher than a first order one.

Position and velocity errors

In the visual task the input or demand is related strictly to the requirement that the target pursued should be brought on to the foveolar area of the retina and there maintained. The servomechanism function is to ensure the correction of any error which develops. The correction may be related to position error or to rate of change of position, which is a velocity error.

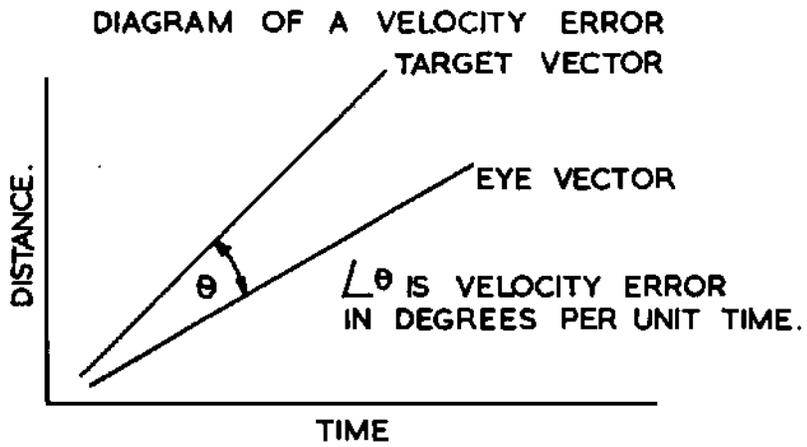


DIAGRAM OF A POSITION ERROR.

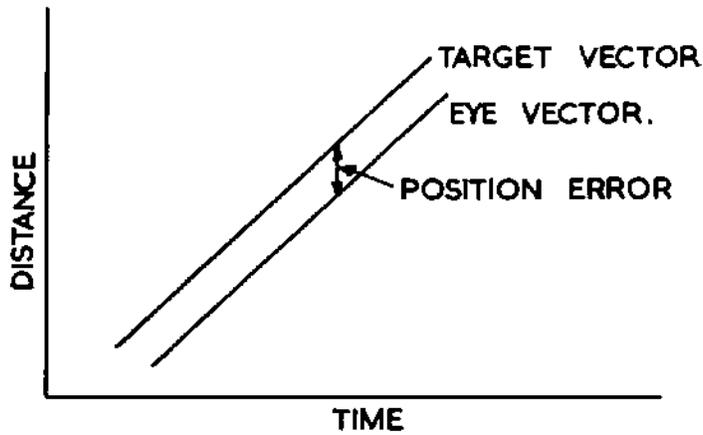


Fig. 64.

DIAGRAM OF TRANSIENT & STEADY STATE ERRORS

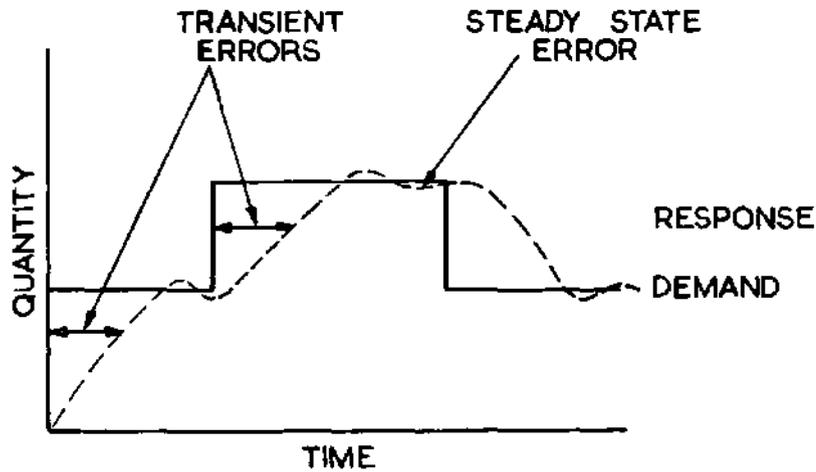


DIAGRAM SHOWING TRANSIENT ERROR & STEADY STATE ERROR BETWEEN RESPONSE & DEMAND DURING A SUDDEN CHANGE OF COMMAND.

DIAGRAM OF VARYING OSCILLATORY STABILITY

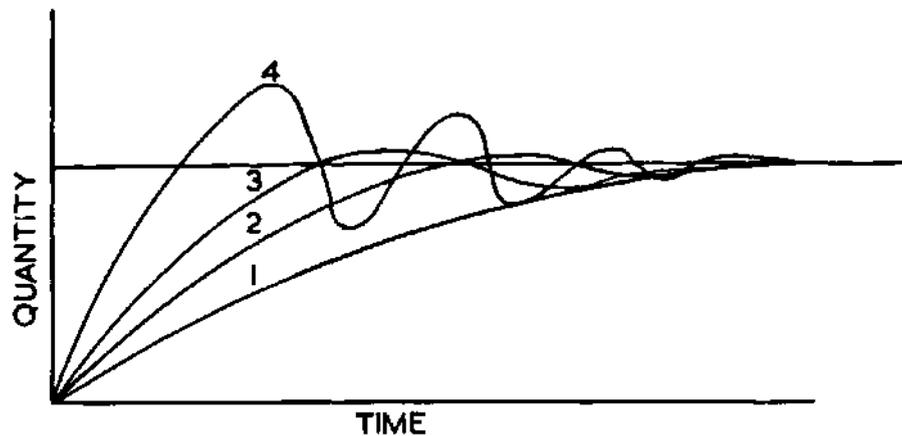


DIAGRAM ILLUSTRATING TRANSIENT STABILITY OF A SYSTEM WITH VARIOUS DEGREES OF DAMPING. CURVES 2,3, & 4 ARE PROGRESSIVELY UNDERDAMPED & SHOW INCREASING DEGREES OF OSCILLATORY INSTABILITY.

A position error Fig. 64, may be said to occur when the target is displaced from the fovea by a constant distance. A velocity error, Fig. 64, may be said to occur when the alignment of target and fovea change continuously and produce a rate of change of position error. Given time a velocity error will produce a position error. Position error can occur without velocity error.

Errors in servomechanism

Three kinds of errors are liable to occur in servomechanisms and are shown in Fig. 65, Brown and Cambell (1946). They are transient errors, steady state errors and transient oscillatory errors. If a small error induces a large change in the servomotor controlling the output the transient and steady state errors will be small. Output friction which may occur between the eyeball and the orbital tissue, and the inertia of the eyeball, would both tend to increase steady state errors and transient errors respectively. Oscillations may occur on starting or stopping an eye movement if output friction is small and is associated with a very sensitive error correcting device.

- A. Diagram showing transient error between responses (dashed line) and command (solid line) during a sudden change in command. The transient oscillatory behaviour illustrated but not labelled. Steady state error during the period of unchanging command is also indicated.
- B. Diagram illustrating transient stability of a system with varying degrees of damping. Curves 2, 3, 4 are progressively underdamped and show increasing degrees of oscillatory behaviour. Curve 1 is overdamped and shows great stability at the expense of a long response time.

A second servomechanism in eye movements

A second closed loop servomechanism is potentially present in ocular movements which takes its input from muscle spindles and other sensory receptors in the extraocular muscles - a servomechanism related to the accuracy of muscle contraction. Muscle spindles are considered by Granit to be the "private measuring instruments" of the muscle with regard to the contraction and relaxation of muscle fibres. Muscle spindles have been found in all skeletal muscle including the extraoculars, Daniel (1946) and Cooper and Daniel (1949). The afferent impulses from the latter muscles are conveyed along the nerves supplying the muscles and then according to Cooper, Daniel and Whitteridge (1953a), branch off to join the branches emanating from the mesencephalic nucleus of the 5th cranial nerve. From there it is reasonable to assume connections with the thalamus and cerebellum and thus impulses could be relayed in a modified fashion to cortex. Efferent impulses to the extraocular muscles are conveyed from higher 'centres' via unknown subcortical structures to the nuclei of the nerves, 3rd, 4th and 6th from whence direct connection is made to the extraocular muscles. Whether or not the afferent impulses subserve any position sense function is as yet undecided and has been the subject of variations of view by Helmholtz (1886), Sherrington (1918), Ludvigh (1953) and Merton, Hammond and Sutton (1956). Experi-

ments contributed in this research programme and described later suggest that there is some position sense information conveyed from extraocular muscles.

Discussion

The accuracy with which eye muscles perform the required contractions and relaxations during a pursuit movement will effect the degree of accuracy of the movement to achieve fixation. The correction of errors between demand and achievement is reflexly accomplished. Such a system must be co-ordinated with the demand from the photosensitive cells of the retina in achieving fixation and failure to achieve fixation could be the result of error in either the photoceptor (retinal) or muscular control system.

There are thus two systems in which errors could occur and both these systems may be considered as output informed, the one from retinal sensory afferents, the other from muscle spindle afferents. These are both examples of negative feedback systems in which the resulting movement is always one which reduces the error.

In dealing with the attempt to fixate a moving target the muscle contraction pattern requirement is one in which the brain must initiate a time tension pattern projected into the future. The accuracy of this pattern appears to deteriorate

as the magnitude of the contraction demanded increases as is shown by the increase in the incidence of corrective eye movements as target velocity increases. The movements of the eyes are not ordered blindly and followed up by other corrective movements until the goal is achieved. Ruch (1951) considers that the nervous system would be handicapped by such 'blind' ordering of movements. Cerebro-cerebellar circuits - reverberating circuits - could, in making use of nerve conduction time delay give a temporal patterning of the cortical discharge demanding movement of the eyes by the giving off of one or more impulses per cerebro-cerebellar circuit. Thus a pattern of acceleration, steady overtaking velocity and deceleration to the required velocity could be obtained at the right time and for the required duration. Such a system could represent not so much an error correcting device but a system which obviates or reduces the transient errors involved in correction by output informed feedback mechanisms.

The cerebellum may have a further function in view of the facts that it receives information from muscle receptors and visual information from occipital cortex. It may be that correlation of the visual input and muscle input can be compared in this structure and cerebellar-cerebro-cerebellar pathways could be utilised in the planning of movements designed to achieve fixation.

Conclusions

The analogy to servomechanisms of the functioning of eye movements in the pursuit and fixation of moving targets is not capable of being furthered in the light of present knowledge of the neural pathways and mechanisms. Such movements present evidence of complex servomechanisms to govern a system in which oscillation is undesirable, in which transient errors are large due to nerve conduction rates and neural integration time, and in which steady state errors exist. Adrian and Moruzzi (1940) have shown that transient errors are deliberately incurred by the slow and successive activation of neuronal pools. Such activation would prevent excessive and sudden overaction by muscles which rarely respond with the full power available. Such a response would produce oscillation. In addition the friction damping of eyeball movement by the fatty tissue in the orbit will tend to produce the steady state errors which have been shown to occur. Thus there remains the impression that eye movement control is rendered more acceptable or accurate by having transient and steady state errors in preference to a rapidly responding sensitive system which would demonstrate oscillatory instability.

Summary

Analogies to servomechanisms exist in the oculomotor system but are complex. The terms position and velocity error are introduced and a discussion of the limitations of the analogy presented.

PART 8The Influence of Parafoveal Visual Acuity on the Ability
to Perceive Detail in Moving Objects.

Failure to recognise detail in a moving target must result from an inadequate fixation reflex action. The inadequacy can be explained by position error of the line of sight with regard to the object, by velocity error in that a differential velocity exists between the eyes and the target, or a combination of both. The possibility exists that the tolerance to inexact foveal fixation may be greater in some subjects than others. If some subjects have a greater tolerance to inadequate fixation than others this should be shown by a typical visual acuity experiment in which the object is moved further and further into the parafoveal region and into the perifovea.

Section 1

Historical note

Wertheim (1894) produced the classical curves of visual acuity decrement in the zones of the retina from fovea to the periphery. More recent investigations have been reviewed by Low (1950). A decrease in visual acuity has been found by all investigators and the decrease continues into the far periphery at 70° from the fovea and beyond. The decrease within the foveal area is not, however, well agreed amongst the authors cited by Low. At 30 minutes of arc there is some decrement in acuity reported by most research workers. Clemenson cited by Low reported a decrease of $15^{\circ}/\circ$ at 2 min. 40 sec. of arc.

The effect of contrast has been investigated by Low (1950) and he reports that acuity is little affected until lower contrasts are used. The effect of brightness has also been investigated in photopic, transitional and scotopic conditions by Wertheim (1894) and lately by Ludvigh (1941), and Low (1943, 1946a, b, c, 1947a). The whole subject of peripheral visual acuity has been recently reviewed by Hopkins (1959).

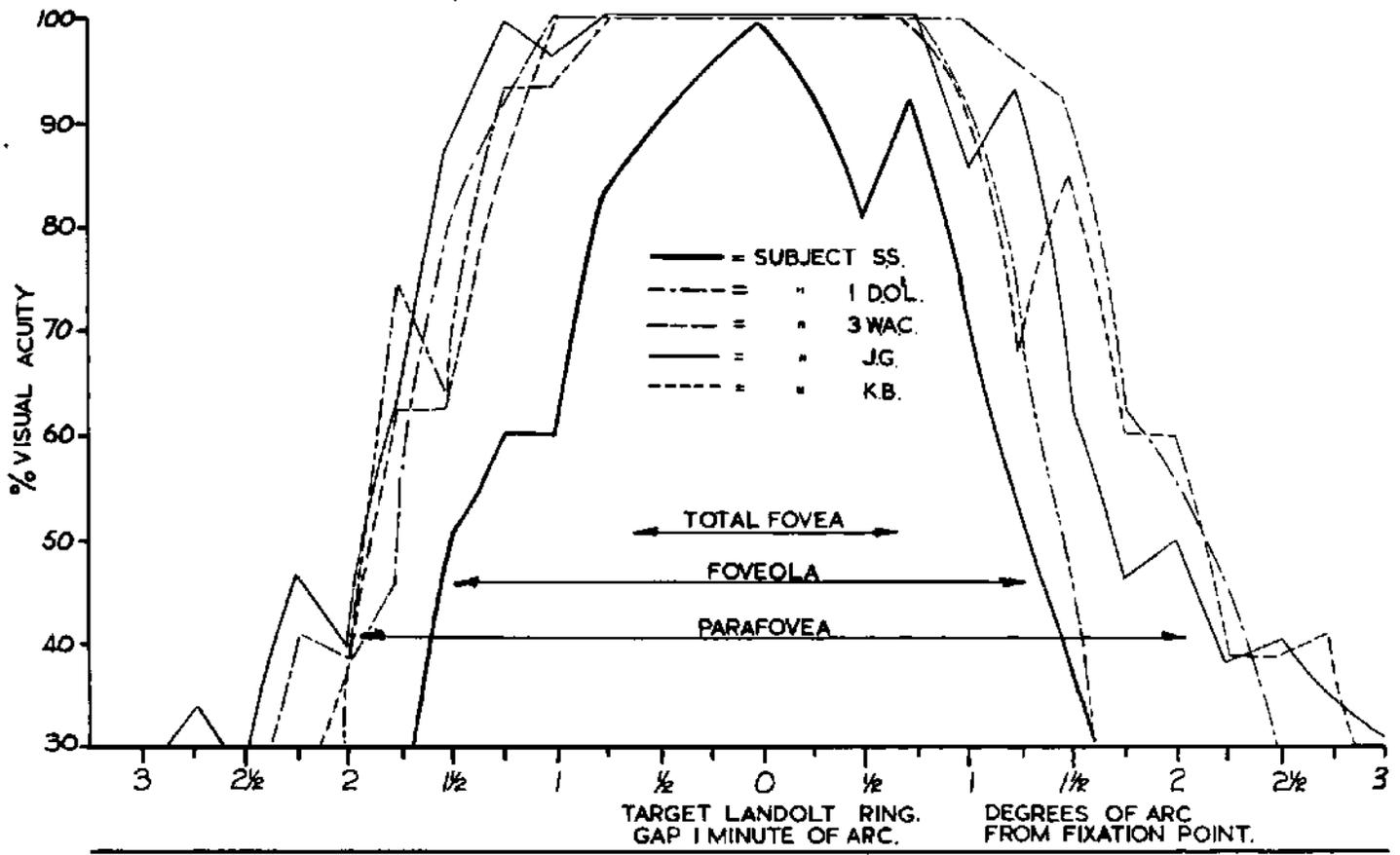
Method

The apparatus used in the exploratory experiments was again used. Six subjects regarded binocularly an illuminated Landolt

ring target which was at a distance of 70 ft. and was capable of being moved in the horizontal plane to either side of a fixation point. The gaps in the Landolt ring subtended arcs varying from 1-3 minutes, from the subject's eyes and could be rotated into any one of four cardinal positions. A fixation point was presented to the subject and the Landolt ring was moved outwards in steps of $\frac{1}{4}^{\circ}$ from this fixation point. These points were examined to left and right of the fixation point. For the one minute of arc target acuity was determined out to 3° on either side and with 2 and 3 minutes of arc targets to 4° and 6° respectively. The illumination of the target and background was 18 millilamberts and the contrast factor between the white background and the black Landolt ring was 85 per cent. The total background field subtended an area of $30^{\circ} \times 7^{\circ}$ to the subject's eyes.

Including the zero displacement of the target 25 positions, 12 to left and 12 to right, were used with each target; 32 observations were made at each point, the positions of the Landolt ring gap being selected by random methods. The target was illuminated for about one second at each observation. To complete the observation each subject attended four sessions of 20 minutes each.

VISUAL ACUITY CURVES
(POSITION ERROR TOLERANCE) 1 MIN OF ARC TARGET



VISUAL ACUITY CURVES
(POSITION ERROR TOLERANCE) 3 MIN OF ARC TARGET

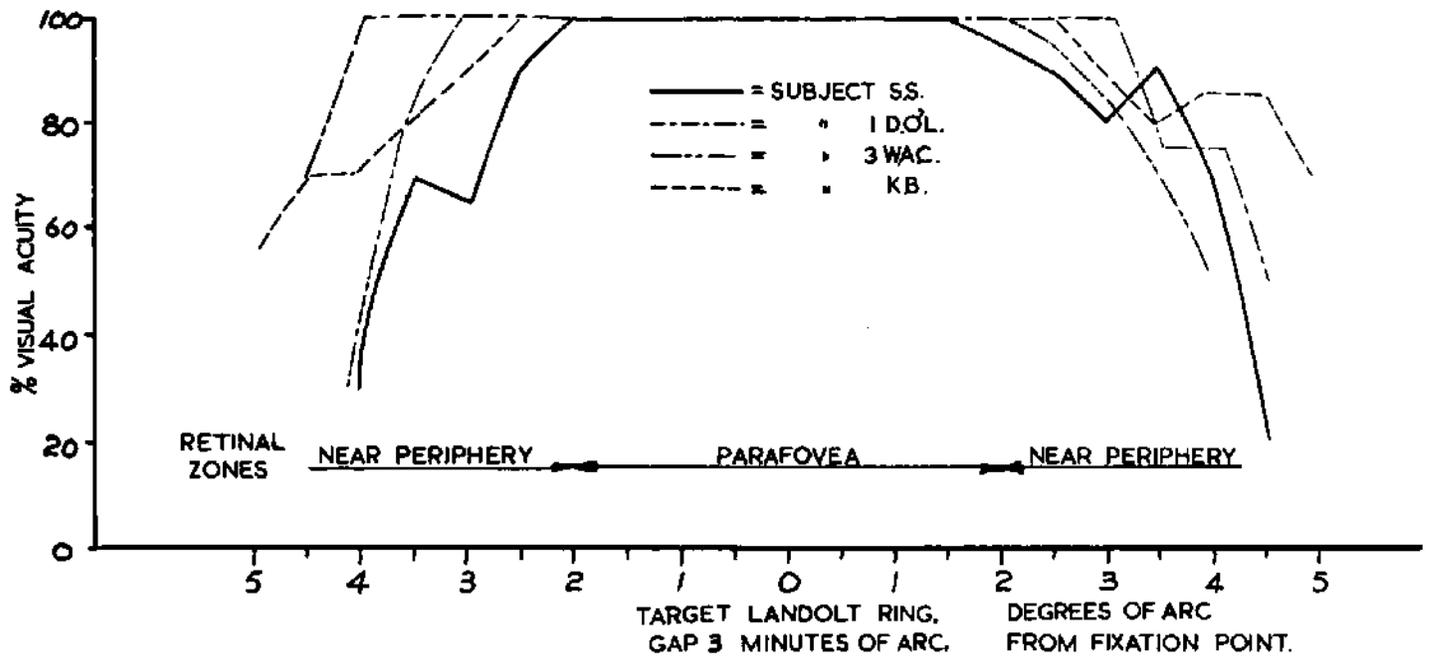


Fig. 66.

Results

The visual acuity curves showed a variation in the rate of fall off of acuity among the subjects.

These curves are shown in Fig. 66 for the 1&3 minute of arc targets and are all quite typical of the classical acuity curve of Wertheim (1894). The tolerance to 2 minutes of arc targets is intermediate to the two shown.

With increasing size of target a greater degree of inaccuracy of fixation in the position sense is tolerable without effective loss of visual acuity as measured in this system.

The variation occurs at any success rate; i.e. at 100 per cent, 75 per cent, 50 percent etc. Subjects who had previously demonstrated a high capacity for seeing detail in moving targets showed a greater extrafoveal visual acuity.

Discussion

One of the possible reasons for failing to see the presented detail in a horizontally moving Landolt ring is the inability of the fixation reflex to place accurately on the fovea the target to be viewed. It appears that for any given success rate of target recognition there will be, depending on the size of the critical detail, an acceptable or subjectively unnoticeable error in position. For 100 per cent correct recognition this permissible error of line up can be of $\frac{1}{4}$ -1° when a minute of arc target is shown, to 3° with a 3 minute of arc target.

At lower success rates tolerances of double this amount are acceptable.

Conclusions

It is suggested that the fall off in visual acuity with regard to the object used measured either in relationship to central visual acuity or in direct terms of the angle subtended at the subject's eye is one factor in the variations between individual ability to see detail in moving objects.

Section 2

The influence of a moving retinal image on the ability to perceive

Failure to recognise detail in a moving object may be caused by movement of the image of the object across the retina; the movement being the result of the eye and target having different angular velocities. A velocity error would be then present. Position error tolerance has been shown to vary with individuals and showed for all subjects a greater position error to be tolerable as target size increased. The researches of De Silva (1929) are the only data found in the literature and have been described in the general introduction.

In this experiment the differential velocity tolerance was measured.

Method

Five subjects regarded monocularly the gaps in the Landolt ring which subtended 1 and 3 minutes of arc at a distance of 70 ft., in the centrifuge chamber. The target appeared at the right hand margin of a slit in a white cardboard sheet and passed across to disappear at the left hand margin. The slit in the cardboard permitted a view of the target in a field of $\frac{1}{2}^{\circ}$ arc. The target could be rotated into any one of 8 positions and was presented in a random order of position.

The Landolt ring gap position and target velocity was controlled by the observer in the same room as the subject. This room was well illuminated and the target, target background and cardboard sheet were approximately equal in brightness, 18 ml. The targets were first presented with a high angular velocity at which no recognition took place and gradually reduced in velocity until the subject made four consecutive correct appreciations of the position of the Landolt ring. The target angular velocity was maintained at this level for a further four correct observations and then gradually speeded up until failures occurred once again at the next higher velocity. An end point was thus obtained.

Results

Five subjects gave the results shown in Table 13. There is a variation in the relative angular velocity tolerable at which no deterioration in visual acuity is demonstrable. The results are shown in Table 13 and Fig.

Table 13

Velocity Error Tolerance

Subject	1	2	3	4	5
With a 1m of arc target	3.5	3.5	3.0	3.0	1.5
With a 3m of arc target	6.5	5.5	4.9	5.0	3.7

Discussion

The discrimination of detail in targets, the retinal image of which is moving across the retina, varies with subjects. It was necessary in order to obviate any fixation reflex to expose the target for periods which were less than the time taken to initiate or even complete the reflex. The mean latencies found in previous experiments on moving targets was about 200 msec. with a general scatter from 150-250 msec. Latencies of the order of 120 msec. have been reported (Westheimer 1954b, Ginsborg 1953). To this duration of time 120 msec. there must be added time for the movement of the eye to a new position. With a $\frac{1}{2}^{\circ}$ field and a $3^{\circ}/\text{sec.}$ target velocity the duration of exposure is 166.6 msec. and at $4^{\circ}/\text{sec.}$ the duration is 125 msec. It is reasonable to suppose that eye movements to fixate the moving target are not therefore possible. At higher target angular velocities the possibility of a fixation reflex being accomplished is even more impossible.

It is of interest to note that even with experienced subjects the only method of ensuring that eye movement, or the fixation reflex, would not be effectively employed was to exhibit the target for a time less than the latent period of eye movement.

There is, as was noted with peripheral visual acuity, a variation in the relative angular velocities which can be tolerated by individual subjects.

The variation with size of target of angular velocity tolerance indicates that the larger the critical detail the greater the target velocity required to diminish visual acuity.

The examination of the relationship between decrement in visual acuity with moving targets and peripheral visual acuity yielded no information which permitted differentiating subjects whose ability varied.

Conclusion

The variation in the loss of visual acuity when the image of the target moves across the fovea (velocity error) does suggest that there is a possible correlation between ability to perceive moving objects and the ability to tolerate a moving retinal image. Subject 1, whose ability is rated highest, had also the greatest retinal movement tolerance and the smallest incidence of second saccades, Subject 2 was also rated highly, subjects 3 and 4 were average and subject 5 was poor. Experiments involving a large number of subjects would be required to substantiate the correlation. The incidence of corrective movements of the eyes during visual pursuit could be expected to be less with increasing velocity error tolerance by subjects if the error necessitating the corrective phase is one of this nature. The extent, however, of the corrective movement in the main experiments was generally such that minor variations in velocity error tolerance may be

only considered as contributing to the general variation in effectiveness of the oculomotor system.

Section 3

The influence of a moving retinal image on parafoveal visual acuity

In the previous sections the ability to perceive detail in a moving retinal image in the foveal area and the decrement in visual acuity with static targets has been described. In fixating a moving target it is also possible that retinal image movement takes place (velocity error) in the presence of inexact fixation (position error). The tolerance to simultaneous velocity and fixation error was therefore examined.

Method

The same apparatus and method used for velocity error tolerance was utilised with one modification. The white cardboard had two slits in it, the one slit static through which the moving target would be seen and the other slit through which the fixation point could be seen was moveable from $\frac{1}{2}^{\circ}$ of arc to 3° of arc from the subject's eye position. Thus as the fixation point varied relative to the viewing slit the target appeared on varying extrafoveal areas of the retina. 40 presentations were made to right and left of the fixation point and target movements were always left to right.

Results

With a 1 minute of arc target a simultaneous error of 1° /sec. and 1° of arc position error was completely intolerable by all

subjects, not one presentation was perceived.

With a 2 min. of arc target, a 1° position error and a $1^{\circ}/\text{sec.}$ velocity error accurate perception took place in less than 25% of occasions.

With a 3 min. of arc target and similar position and velocity errors only 30% of targets presented were perceived.

At higher velocity errors, 1.5, 2, 2.5, $3^{\circ}/\text{sec.}$ no recognition of targets presented took place.

Individual differences were slight with the exception of subject 4 and are shown in Table 14 for $1^{\circ}/\text{sec.}$ velocity error and 1° position error with 1, 2 and 3 minute of arc targets.

Table 14

Perception Ability with Combined Velocity and Position Errors
of 1° of arc/sec. and 1° of arc.

Target Size	Percentage Successful Perception			
	Subject 1	Subject 2	Subject 3	Subject 4
1 min of arc	0	0	0	0
2 min of arc	20	18	20	10
3 min of arc	25	24	23	16

The presence of two errors, one of velocity and one of position in a fixation on a moving target was productive of

great decrement. A decrement which is greater than that of error tolerance of position or velocity alone. Only one subject (4) demonstrated an ability poorer than the others. This is in accord with his general performance throughout the series of experiments.

Discussion

There seems little doubt that although the visual system can tolerate either position or velocity error to a small degree the simultaneous occurrence of these errors is quite intolerable. This infers that the degree of accuracy required to obtain fixation in a moving target must take account of these two parameters and demonstrates effectively the high standard of accuracy attained by eye movements during visual pursuit of an object when recognition of the moving object takes place.

Conclusions

The tolerance of a combined error of position and velocity is less than tolerance of either error occurring singly.

A Correlation between Ability, Error Tolerance and Eye
Movement Patterns

A correlation between the various factors examined which appear to be independant of one another was made. These factors are:

1. Shortness of initial latency
2. Accuracy of the initial eye movement
3. Rapidity of action of the corrective mode
4. Position error tolerance
5. Velocity error tolerance.

This is shown in Table 15.

Table 15
Correlation of Factors for Subjects 1 - 4

Factors	Subject 1	Subject 2	Subject 3	Subject 4
Discrimination Ability	1	2	3	4
Shortness of Latency	1	2	3	4
Accuracy of Initial Eye Movement (lowest incid- ence & second saccades)	1	3	2	4
Rapidity of Corrective Mode	2	1	3	4
Position Error Tolerance	1	2	3	4
Velocity Error Tolerance	1	2	3	4

The other factors measured and reported of steady state duration, mean velocity of eye movement, duration of eye movements, combined velocity and position errors, are dependent on other factors and cannot be correlated.

It is noted that the superior ability of subject 1 in discriminating detail in moving objects is reflected generally in all the factors examined above. Subject 4 whose ability is rated lowest presented an equally degraded ability in all the other factors. The correlation for Subjects 2 and 3 is not so marked but is still depicting a distinct pattern.

On this data the conclusion is reached that a superior ability is based on an overall superiority in the visual and oculomotor system.

Summary

Extrafoveal visual acuity (position error tolerance) varies with subjects.

Subjects show a variation in ability to perceive detail in a moving retinal image, (velocity error), increasing the size of the target improves ability.

A combined position and velocity error is almost intolerable.

A positive correlation of ability to perceive detail in moving objects, position error tolerance, velocity error tolerance, shortness of latency of eye movement, and the nature of corrective eye movements, is made.

HEAD AND EYE MOVEMENT RECORDING APPARATUS

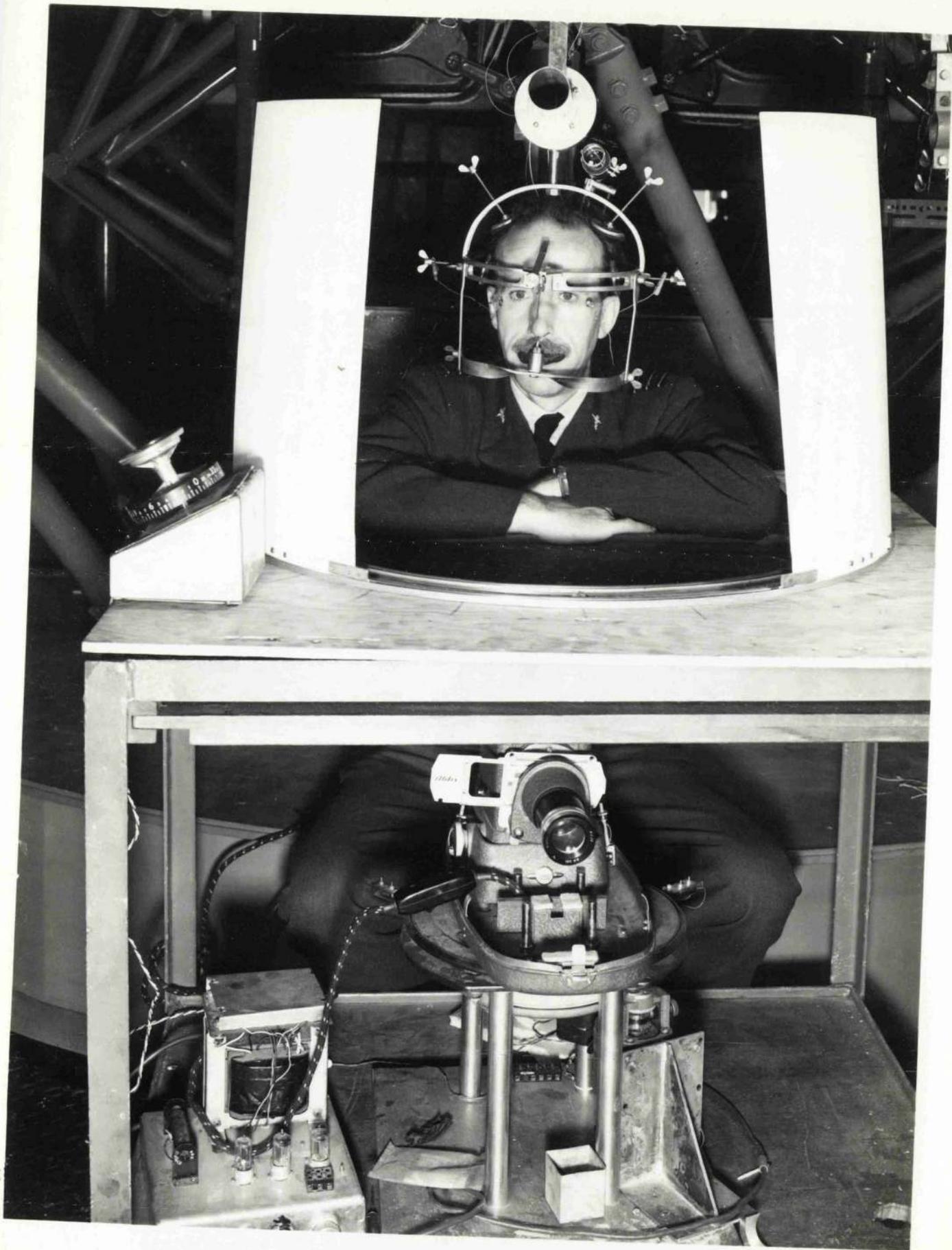


Fig. 67.

PART 9The Co-ordination of Eye and Head Movements

In Part 4 evidence was offered to show that by increasing the time of exposure to a moving target discrimination of the detail in that target is improved. Evidence was also given to the effect that further improvement in the ability to discriminate detail occurred when the head and eyes were both freely moved. This improvement occurred only when the time of exposure was at least 400 msec.

Some physiological actions underlying this improvement were investigated.

Method

The subject was seated near the centre of a 36 ft. radius circular dark room. To the subject's head was attached a light-weight headpiece, the weight of which was taken up by a mounting above the subject's head. There was thus no downward load. This headpiece, Fig. 67, the rotational inertia of which was negligible, rotated with the subject's head. It was secured to the subject's head by means of three adjustable pads in the temporal and occipital regions and also by the subject biting a wooden bar attached to the headpiece. A dental bite proved unsuitable for this purpose as the head not only rotates about the horizontal axis in large pursuit

THE HEAD MOVEMENT RECORDING SYSTEM IN THE CENTRIFUGE CHAMBER

(The two rows of photocells on the walls can be seen at A & B)

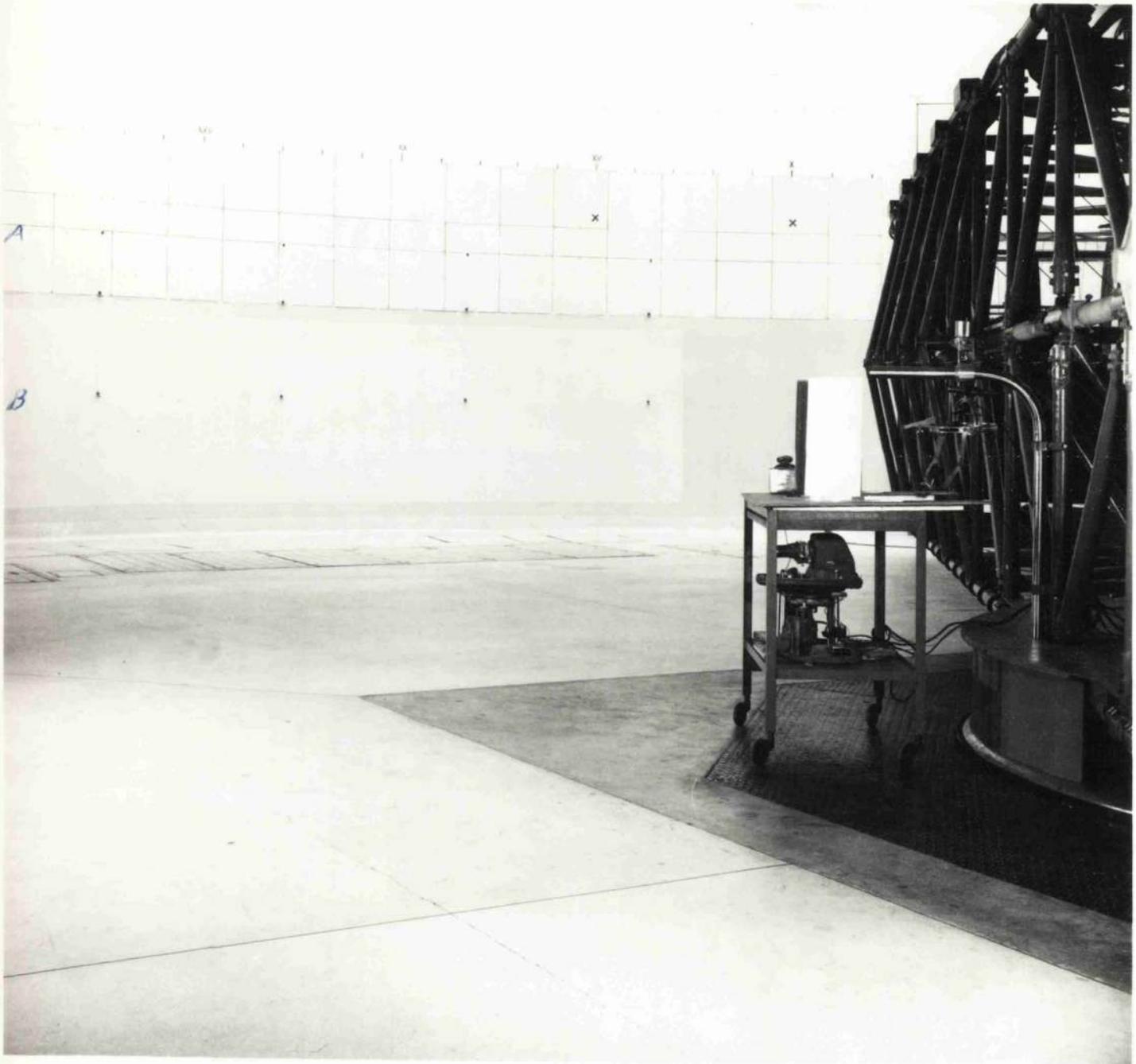


Fig. 68.

movements but inclines in the vertical plane; the apparatus only permitted horizontal movements and thus a well fitting dental bite subjected the teeth to somewhat dangerous stresses. A potentiometer in the axis of rotation of the head-piece yielded a direct coupled capacitance output to a pen-recorder system.

Rigidly attached to the headpiece was a projector which emitted a pencil beam of light. This beam was directed to the wall of the room and as the head rotated a series of photocells on the wall were activated. The photocells were arranged at 10° intervals over an arc of 160° . The central 100° only, were used in the experiments. This projected light and the photocells were not visible to the subject.

The Aldis projector system was used and the Landolt C was seen projected on to the wall of the chamber. The targets moved at selected angular velocities relative to the subject. The projected Landolt C illuminated another similarly arranged row of photocells mounted on the wall some six feet beneath the upper row and level with the subject's head. Fig. 68.

The outputs from these two rows of photocells were amplified and drove conventional pen recorders to give accurate but discontinuous information concerning the head position and target position at 10° intervals. Eye movements were recorded in the horizontal plane by measuring the variations in the

HEAD MOVEMENT RECORD
& VECTOR DIAGRAM

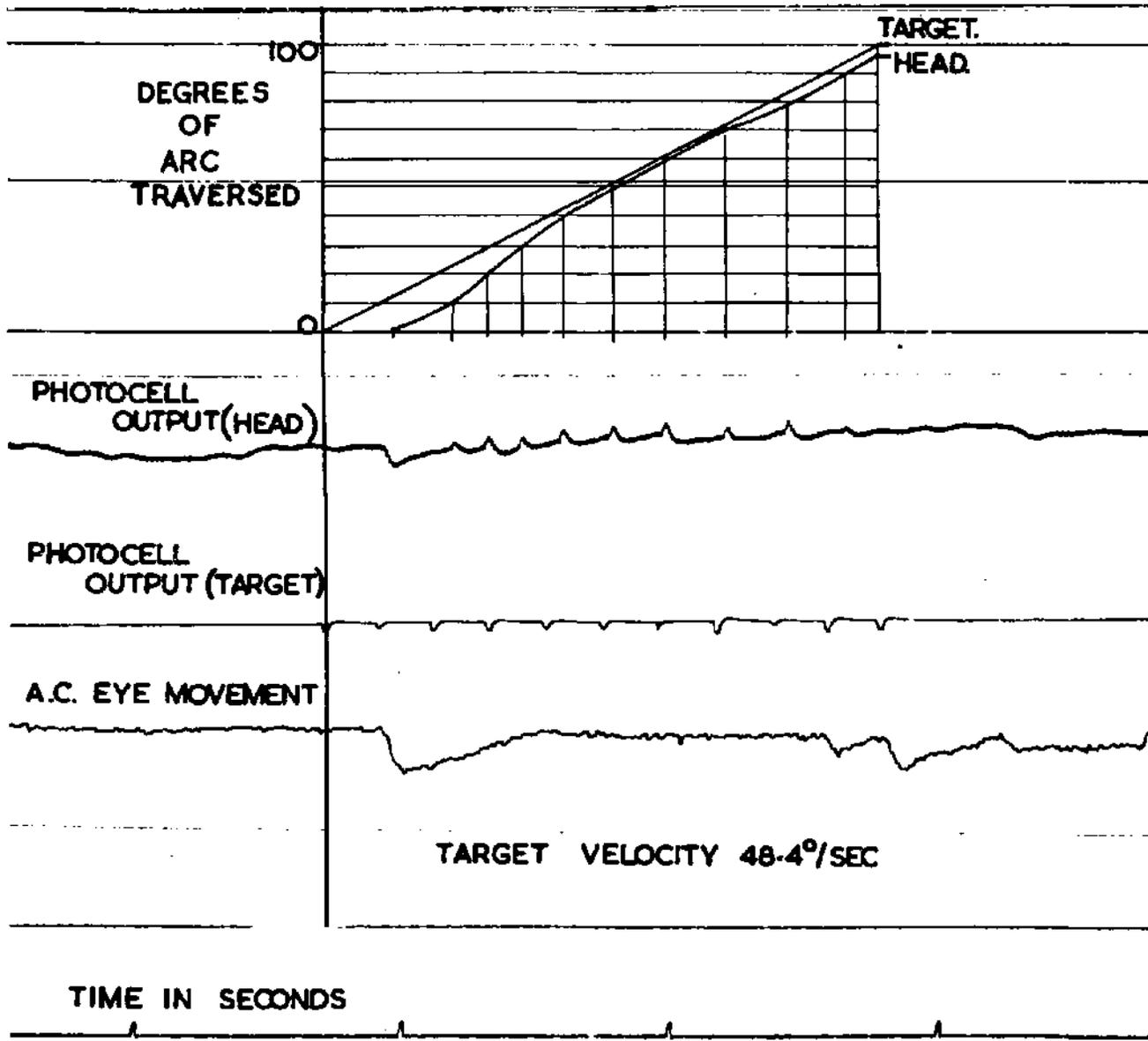


Fig. 69.

104
cornea-retinal potential as the eyes moved.

There was thus recorded (Fig.69) :-

1. Head photocell system output.
2. Target photocell system output
3. Direct coupled output from headpiece.
4. Cornea retinal potential.

The subjects (4) were neither asked to move their heads nor to refrain from moving their heads during the pursuit task. They were merely told to identify the moving target. They invariably and naturally did rotate the head. The targets had angular velocities in relation to the subject in the range $50-130^{\circ}/\text{sec}$. No attempt was made to score the results of each pursuit task although the subject responded by describing the gap in clock code, i.e. 10.30, 12 o'clock, 1.30 etc.

Results

The sequence of eye movement followed by head movement was almost invariable. The delay between the beginning of the eye movement and the beginning of the head movement varied considerably and is summarised in Table 16.

The eye movement latencies recorded are comparable to those recorded when no head freedom was allowed in previous experiments on pursuit eye movements.

Table 16

Latencies of Eye Movement and Head Movement and the Eye-Head Movement Interval (Msec.) Standard Deviations in brackets.

Subject	Eye Movement Latency	Head Movement Latency	Eye-Head Movement Interval
1	213.00(77.82)	308.85(64.82)	90.08(46.21)
2	268.10(79.10)	316.60(74.19)	70.21(48.30)
3	163.90(30.00)	249.57(42.82)	83.67(27.93)
4	177.14(30.78)	325.81(36.82)	148.67(40.78)

The photographic reproductions of typical recordings (Figs. 69 and 72) show this eye-head movement sequence. They also show the nature of the head movement which followed a pattern of acceleration to obtain a target-overtaking velocity, the maintenance of this velocity for a short period, a deceleration to a velocity comparable to that of the target and the maintenance of this velocity until discrimination had been achieved when both head and eye velocities rapidly diminished.

This pattern of events is more clearly seen in the vector diagrams of target and head movement drawn above the photocell output records. The vectors representing head movement and

POSITION ERROR OF HEAD DURING VISUAL EYE HEAD PURSUIT.

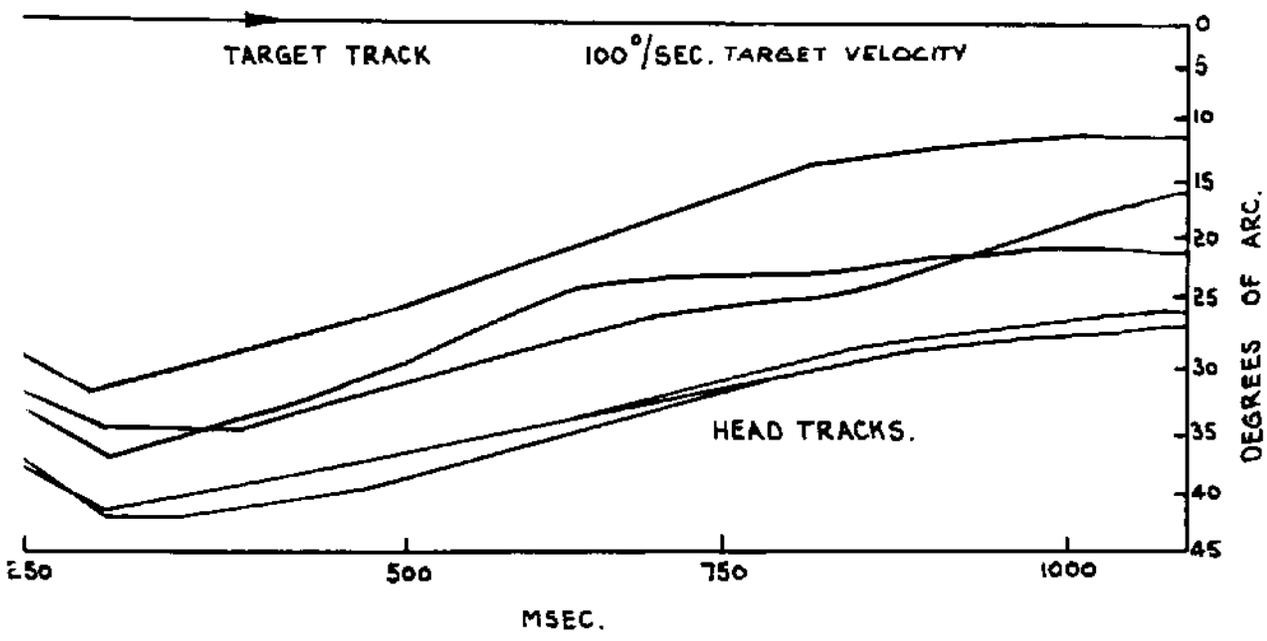
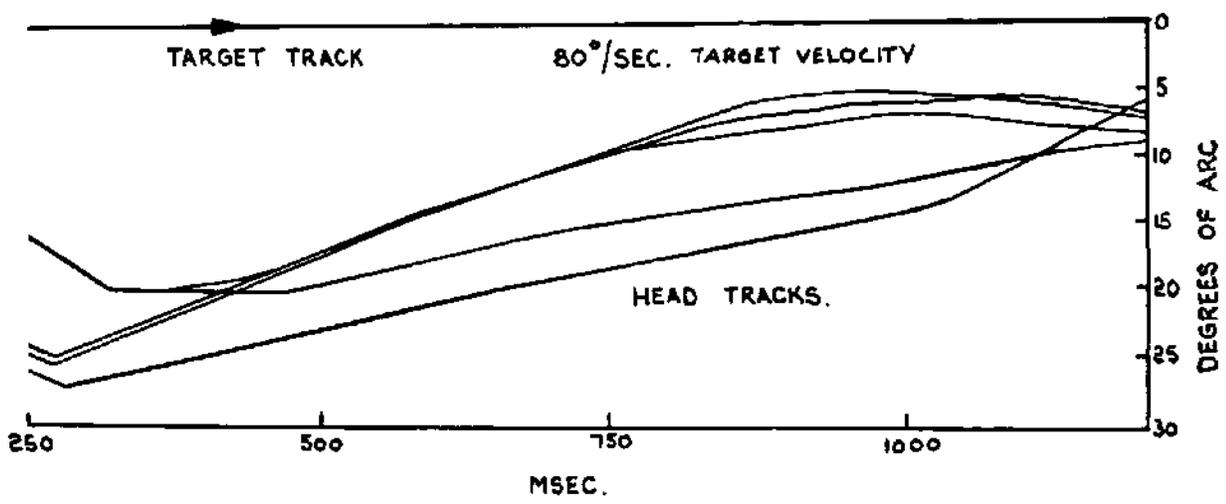
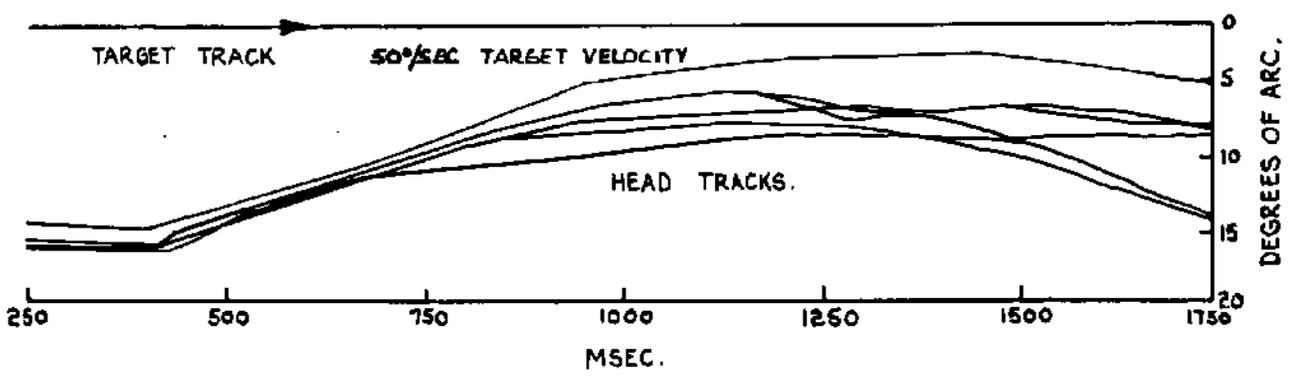


Fig. 70.

RELATIONSHIP OF HEAD MOVEMENT TO TARGET MOVEMENT
DURING VISUAL PURSUIT.

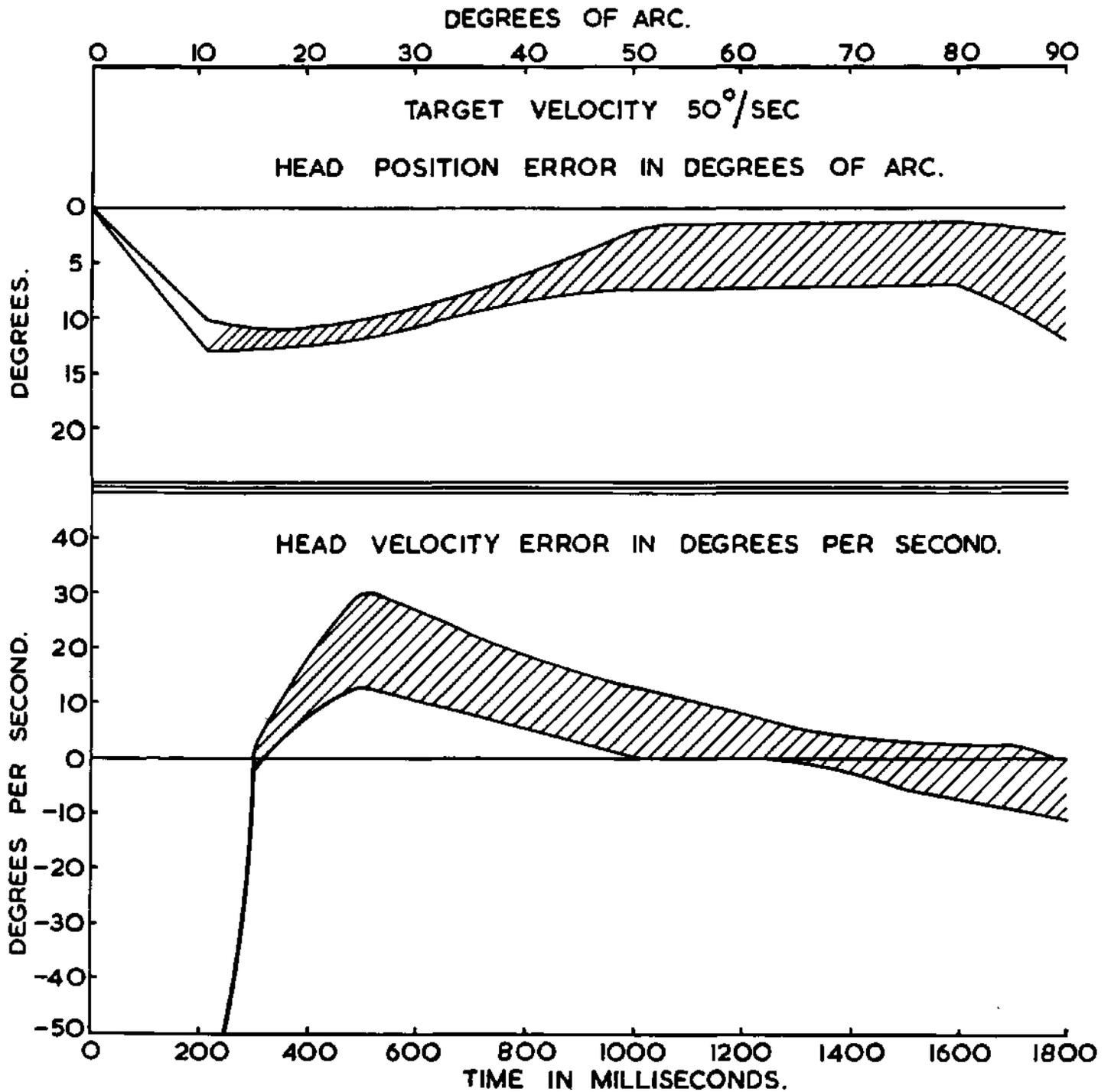


Fig. 71.

target movement are obtained by joining the points representing head position and target position at 10° intervals. The curves have been drawn smoothly along these points, the target vector being a straight line. The output from the potentiometer in the headpiece shows that there are no jerky or saccadic movements of the head. The gap between the target vector and the head vector represents the residual angular deviation required of the eyes if the target is to be fixated.

As target angular velocity increased this gap also increased. With a $50^\circ/\text{sec}$. target the gap was reduced to and maintained at $5-7^\circ$ of arc. At $100^\circ/\text{sec}$. the gap was some $15-27^\circ$ of arc. Fig. 70.

In Fig. 71 the vector diagrams of head movements relative to target movements have been integrated to show the scatter of head position error and head velocity error. The position error diagram shows the initial increase in error before the head movement commences, and reduction in the error with head movement. The velocity error shows a similar trend.

Eye movement recordings show the initial rapid horizontal rotation of the eyes and the subsequent reduction in the amount of lateral rotation as the head moves in pursuit of the target. The reduction in the eye-ball rotation required continues as the arcs traversed by the target and the head became less disparate. The record of the eye movements is the resultant

of pursuit and compensatory eye movements and the decay in the pen recording capacitance coupled system. The presence of single saccadic eye movements and multiple saccades were noted in many recordings during pursuit movements of 1-2 seconds duration.

A Spearman's rank correlation showed that eye movement latency, head movement latency and time of occurrence of the corrective eye movement if required, tended to diminish as target velocity increased.

Ranking	Eye Latency	Head Latency	2nd Eye Movement
1	2	1	1
2	3	3	3
3	1	2	2
4	4	6	4
5	5	5	5
6	6	4	6

$r = 0.714$	$r = 0.828$	$r = 0.942$
$P = \frac{0.714}{\text{NOT}}$	$P = \frac{0.828}{0.05}$	$P = \frac{0.942}{0.01}$

Discussion

The presentation of a moving object in the field of view demands attention. The stimulation is visual but this does not infer that the response should be limited to motor action by eye muscles alone. Whole body movement may be involved when required if the object noted is of interest. This varying

of response depending on restraint or lack of restraint has been described by Teuber and Bender (1951) referring to Holmes (1938) as a 'highest level function' in Jackson's terms. The end effect is a shift in the line of regard. This same wholeness of body reaction is also noted when an interesting sound is heard. There is in both cases a demand for integrated reaction of many systems to transfer attention from one source of interest to another. The limited binocular visual field of man is effectively increased by rotation of the head and body, by change in the position of the various parts and of the body position of the whole.

With specific regard to the movement of the eyes produced by extraocular muscles, movement of the head and trunk will reduce the degree of contraction required by these muscles. In their studies of the accuracy of muscular control, Hammond, Merton and Sutton (1956) have shown that the relative accuracy of muscular contractions is fairly constant and that "the sensory feedback mechanism used to carry out the task treats as of equal significance errors that are a constant fraction of a force exerted, as in Weber's Law". By reducing the amount of force required by eye muscles in the visual pursuit of an object and by having an integrated eye-head-body movement, errors in the response of eye muscles to achieve the desired visual fixation will be reduced. Fatigue of eye muscles may also be reduced and

the tremor associated with massive muscular contraction will be avoided. In experiments such as these described accuracy of eye positioning, and avoidance of extraocular muscle tremor, are essential.

This co-ordinated activity of the head and eye was first shown by Bechterew (1899) to be activated by stimulation of the caudal part of the middle convolution of the precentral gyrus of the frontal cortex. Marion Hines (1947) using the Macaque monkey and Penfold and Rasmussen (1947) in humans have confirmed and extended the knowledge of cortical sites, which, when stimulated would produce adersive (turning towards) movements involving head and eyes. More recently Bender and Pastyl-Kruger (1957) have described clonic convulsive movements to the left of head and eyes caused by a calcified mass in the right occipital lobe. There is thus ample evidence to show that cortical areas exist in the frontal (voluntary) cortex and the occipital (involuntary) cortex which are concerned directly or indirectly with eye movements and which are equally concerned with head movement.

Co-ordinated activity of the eyes in the moving head was described by Dodge (1903) and named compensatory movements. These are movements of the eyes to maintain fixation despite head movements. He (1921) noted that there was no measurable delay between head movement and eye movement in the opposing and

therefore compensatory direction. Recently (1955) Whitteridge on the pidgeon and Hodgson and Mary Lord (1954) on humans, have described this temporal compensation and Merton (1956) has shown compensatory rolling movements to be complete to 30° in man. This completeness in space and time strongly indicate the development of a system which permitted simultaneous movements of eyes and head without disturbance of fixation. In pursuit movements of head and eyes this reflex compensating mechanism is essential in order that the complicated pursuit tasks are not further complicated. Thus there is a complex system governing head and eye visual pursuit movements, a system which operates inclusive of, and despite, head movement.

Conclusions

The almost invariable sequence of eye movement followed by head movement may not necessarily indicate that this is the order of motor output from the cortical areas involved. There is no reason to assume this sequence if the concept is accepted that a moving stimulus demands a change of attention. The delay between eye movement and head movement may be the result of longer nerve pathways to the neck muscles, the greater inertia of the head and the delay inherent in the more coarse and less well innervated muscles in building up a sufficient number of muscle fibre contractions to achieve movement.

The latencies of eye movements in these co-ordinated eye and head movements were of the same order as those found in all

the numerous experiments conducted with the head partly or rigidly immobilised. There is no evidence that the more involved and more natural eye-head movement complex demanded greater cortical integration time. This finding is in accord with the responses obtained by cortical stimulation in which eye and head movements have been obtained from point stimulation.

It was therefore planned to record the activity in neck muscle involved in rotational movements of the head. This would possibly give some information on when efferent impulses reached and began activation of muscle fibres and provide further evidence of response from one cortical area.

Electromyographic responses from neck muscles during co-ordinated eye and head visual pursuit movements.

The latencies of eye and head movement, when both these structures are co-ordinated into a visual pursuit movement, have been described. The eye movement usually preceded head movement by some 80 to 100 msec. The presence in the cortex of small areas, the stimulation of which is now known to cause co-ordinated eye and head movement has also been described.

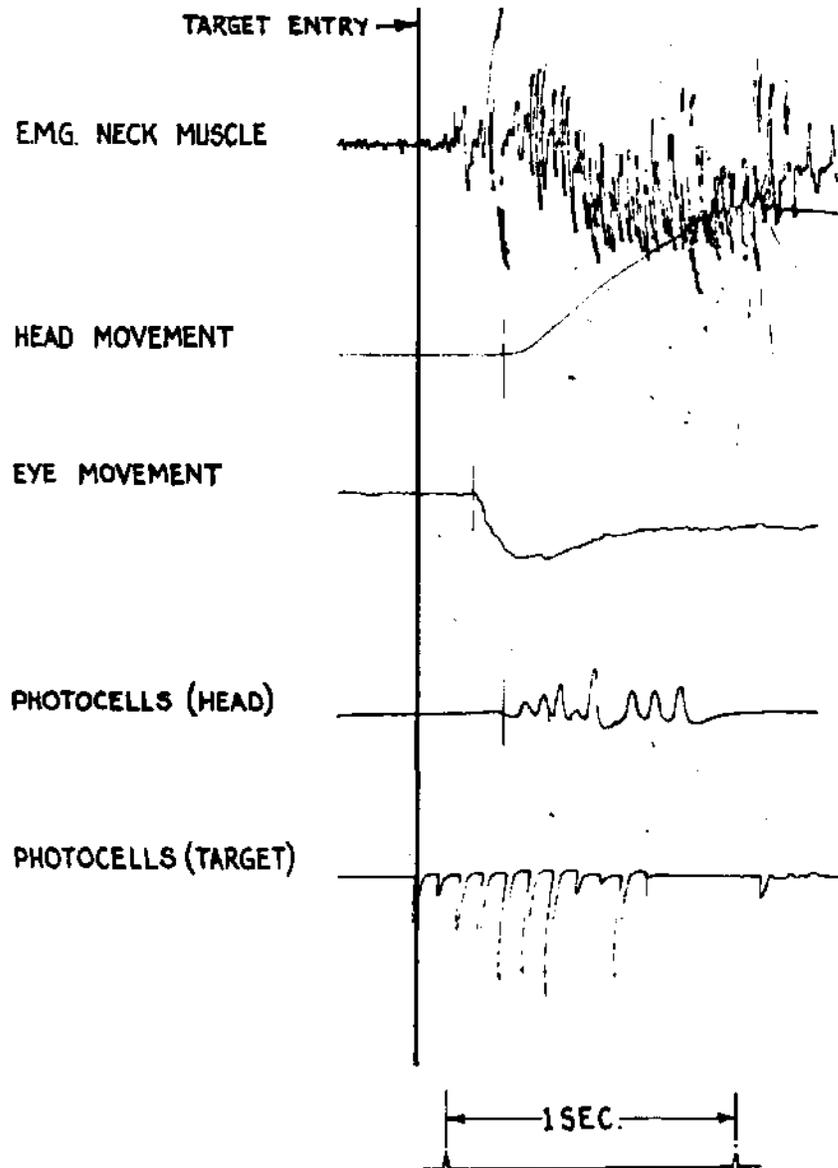
The movement of the eye and the movement of the head have been shown to consist of three phases, an acceleration phase to some predetermined velocity, maintenance of this velocity, and a deceleration phase. These phases occur in pursuit movements and also in eye movements between static objects.

Without the acceleration and deceleration phases which last a very few milliseconds in the case of the eyes the system of movements would demonstrate an oscillatory instability.

Furthermore the arborising of motor nerves to stimulate contraction in many muscle fibres in any one muscle infers that some fibres will be stimulated to contract before others. It also infers that a gradual spreading of activity occurs until the muscle contraction pattern is closely akin to the demand for such a contraction. The previously described eye movements and the head movements demonstrate the temporal factors involved from stimulus to completion of an effective mobilisation of sufficient muscle fibres to actually produce physical movement. This gives little information in the time taken from stimulus to muscle activity which would aid appreciation of the parts of the nervous system involved.

Electromyographic (EMG) recordings were obtained by surface electrodes from the sternomastoid muscle of the neck. Such surface methods cannot be used on the extraocular muscles of the eye. Penetrating needle electrodes can and have been used in the extraocular muscles of the human eye (Bjork and Kugelberg 1953, Magee 1956, Moldaver & Breinen 1956 and Momosse 1958) but not in the presence of fast pursuit type eye movements. The potential dangers of muscle damage, damage to the eyeball, haemorrhage and sepsis under the experimental procedures being

ELECTROMYOGRAPHIC ACTIVITY IN NECK MUSCLE WITH HEAD & EYE MOVEMENTS.



E.M.G. { TIME CONSTANT .03 SEC.
NO H.F. FILTER.



EYES { TIME CONSTANT 1.0 SEC.
NO H.F. FILTER.

200 μ v.

Fig. 72.

used in the experiments was considered too great by the Consultant in Ophthalmology to the Royal Air Force and was omitted from the investigation. The same apparatus that was used for the investigation of eye-head movement was used with an additional pen recording of electromyographic activity.

The latencies of eye movement, head movement and electromyographic activity were measured. From these data the eye-head interval, EMG-head and EMG-eye were obtained. A typical recording is shown in Fig. 72.

The latencies of eye movements of two subjects whose latencies were well documented were comparable with those obtained when only the eyes were moved, i.e. 150-300 msec.

The latencies of head movement were longer than those of the eyes in the large majority of pursuits. Subject KB whose eye movement latencies were much longer than the average subject, (mean 268msec. S.D. 9.10) demonstrated in 10 of 101 pursuits a head movement preceding the eye movement. Subject WAC showed the same pattern of events in 4 of 124 pursuits. The other subjects did not show this pattern in a total of 162 pursuit movements. The latencies of eye and head movements are shown in Table 17 as are also the differences between eye and head movement.

Table 17

The Latencies of Eye and Head Movements

Subject	W.A.C.	K.B.	D.O.L.
Eye Latency	213.02 (S.D. 77.82)	268.10 (S.D. 79.10)	177.14 (S.D. 30.78)
Head Latency	303.85 (S.D. 64.82)	316.60 (S.D. 74.19)	325.81 (S.D. 36.92)
Differential	90.83 (S.D. 46.21)	48.50 (S.D. 70.21)	148.67 (S.D. 40.78)

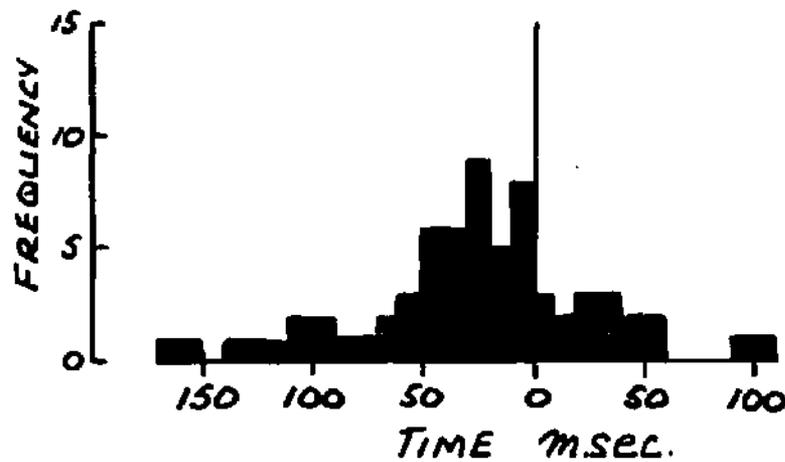
The changes in the electromyogram from a neck muscle are shown in Fig. 72.43-45. The latencies of these activities were shorter than those of the head movement and generally preceded even eye movement. These results are shown in Table 18.

Table 18

The Latencies of Eye, Head and EMG Activity.

Subject	W.A.C.	K.B.	D.O.L.
EMG Latency	183.88 (S.D. 64.96)	295.00 (S.D. 72.52)	163.24 (S.D. 39.85)
EMG Head Latency Difference	119.97 (S.D. 42.01)	44.90 (S.D. 53.63)	162.57 (S.D. 42.54)
EMG Eye Latency Difference	27.14 (S.D. 44.39)	27.00 (S.D. 60.12)	13.90 (S.D. 33.23)

HISTOGRAMS OF INITIAL ELECTROMYOGRAPHIC RESPONSES FROM STERNOMASTOID MUSCLE RELATIVE TO EYE MOVEMENT.



E.M.G PROCEEDS EYE EYE FOLLOWS E.M.G.

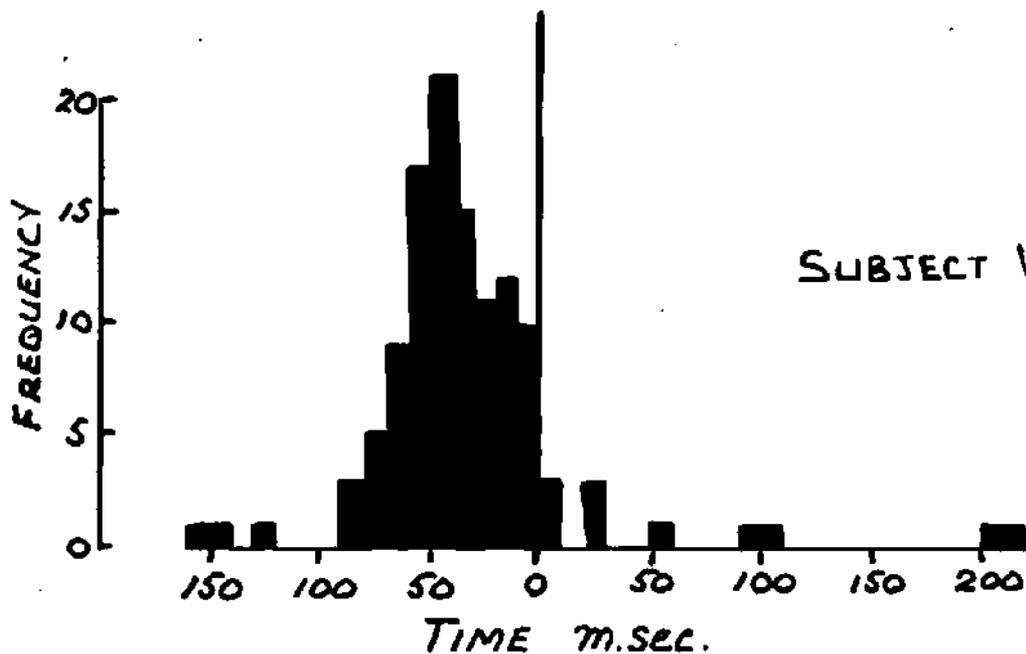


Fig. No. 73

Histograms are shown in Fig. 73 of the distribution of the time differences between the latency of eye movement and the onset of activity in the muscle as recorded by a surface electrode for all target velocities and for other velocity zones of less than $70^{\circ}/\text{sec.}$, $70-100^{\circ}/\text{sec.}$ and more than $100^{\circ}/\text{sec.}$ These indicated a decrease in latency as target velocity increased. As target velocities were varied a rank correlation by the Spearman method was carried out on eye latency, head latency and EMG latency on Subject W.A.C. This is shown in Table 19.

Table 19

Latencies of Head, Eye and EMG with Varying Velocities and Spearman Rank Correlation.

Speed	n	Head	Eye	EMG
38	15	353.73	242.93	214.73
60	27	308.07	219.81	197.70
75	16	329.25	246.88	206.88
90	17	259.41	190.00	144.24
103	10	265.20	180.90	146.30
125	16	268.38	177.31	134.38

Ranking	Head	Eye	EMG
1	1	2	1
2	3	3	3
3	2	1	2
4	6	4	5
5	5	5	4
6	4	6	6

Significance	$\tau = .420$	0.823	0.714	0.885
Significance	$P =$	0.05	NOT	0.05

Discussion

The change in muscle activity, as recorded by the EMG, occurring well in advance of any physical movement of the head indicates that efferent discharges presumably from motor cortex are arriving in muscle fibres at a time comparable with the arrival in the fibres of the extraocular muscles. The duration of the interval between EMG activity and actual head movement may be interpreted in two ways. It is possible that the whole time is taken up by the accumulation of a sufficient number of muscle fibre contractions to move the head or that a marked increase of tonus occurs in neck muscles when pursuit eye movements are about to take place. The latter is considered to be a possible explanation as the head movements are not required or even of benefit with short pursuit arcs irrespective of the stimulus velocity, they could therefore be delayed. During the delay an anticipatory state of higher general tonus could develop in preparation for a movement. This may be an example of the ascending reticular system activity and function. It is to be expected that the time interval from onset of a change in the EMG of extraocular muscles until physical movement of the eyeball occurs will be less than that of neck muscles. There are notable differences in the size of muscle fibres, the innervation, the rate and types of discharge.

Comparison of Some Qualities in Skeletal and Extraocular
Eye Muscle

	Eye Muscle	Skeletal Muscle
Type of Fibre	Fine	Coarse
Rate of Discharge	50-200/sec	5-60/sec
Action Potential Duration	0.5 - 3 msec.	3-4 msec.
Action Potential	100-600 microvolts	3-4 millivolts
Nerve Fibre Muscle Ratio	1-6	1-100gastrocnemius

Conclusions

It is tempting to suggest that the initial efferent nerve impulses would reach the eye muscles at the same time, or slightly earlier because of the shorter pathways, as the impulses to the neck muscles. The time factors involved would be significantly less than the period from stimulus to eye movement and might be of not dissimilar durations to many of the intersaccadic intervals described in Part 5

With the head held steady in a dental bite and voluntarily prevented from moving no changes occurred in the EMG during pursuit eye movements. The nature of the response is therefore considered to be associated with the voluntary motor cortex.

Summary

The co-ordinated head and eye movements resulted in a less sustained deviation of the eyes from their resting position. The initial saccadic eye movement is unchanged from the 'eyes alone' situation but thereafter the head develops a velocity which markedly reduces the need for gross rotations of the eyes. The angular velocity of the head is comparable to the target velocity and lags behind the target, by some $5-20^{\circ}$ of arc, the faster the target the greater the lag in relative position.

Head movement latency is about 100 msec. greater than eye movement latency.

The head movements are smooth and show no saccades.

Electromyographic responses from neck muscles involved in eye head movement showed activity before every eye movement commenced.

PART 10

Some Observations on the Presence of Proprioceptive Information from Extraocular Eye Muscles.

Introduction

The possibility that eyeball position sense originating in the extraocular eye muscles may play a part in the control of eye movements during the visual pursuit of a moving target has been suggested. This suggestion arose as a result of the findings that the intervals between the completion of a rapid eye movement and a subsequent involuntary one could be as short as 50-60 msec. Such short temporal factors did not appear to be compatible with the present concept of the oculomotor system in which retinal delay alone amounts to 30-70 msec. Monnier (1952) has demonstrated in man retino-cortical times of 5 msec., and an optomotor integration duration of 75 msec. for a simple task.

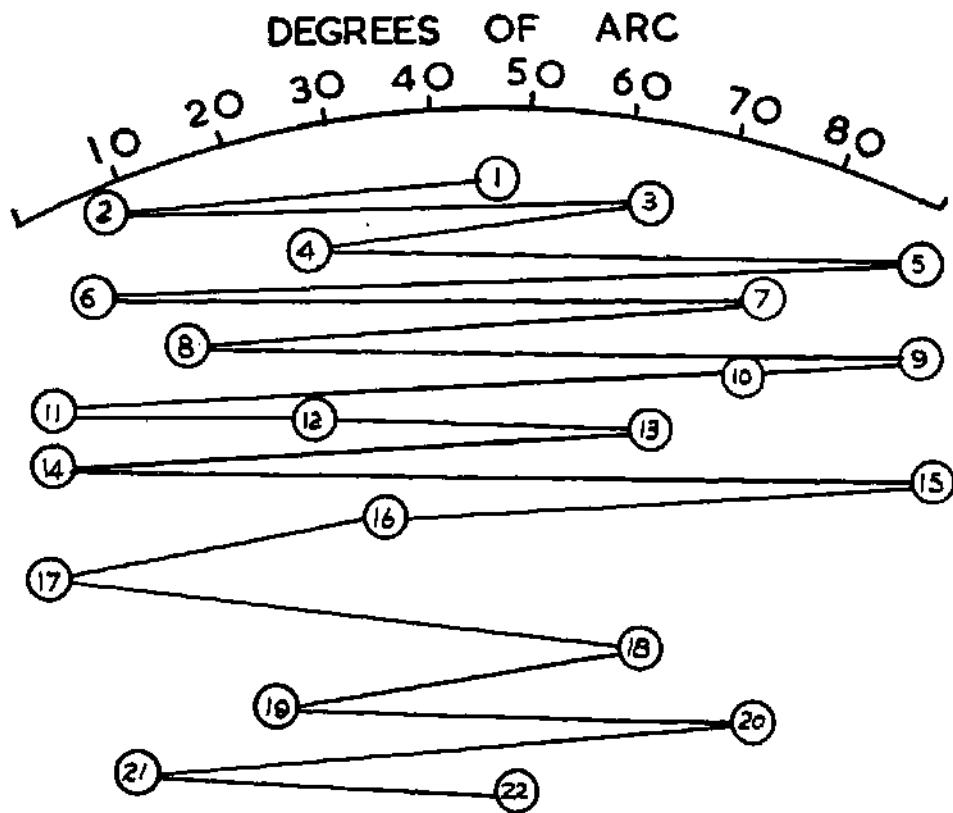
Proprioceptive efferent discharges from extraocular eye muscles have been shown to occur from stretch receptors in the eye muscles of the goat by Cooper, Daniel and Whitteridge (1953). These discharges are from the muscle spindle. Such spindles (amongst other sensory end organs) have been shown to be present in the extraocular muscles of man (Daniel, 1946). Sherrington (1894) showed that half to two-thirds of the nerve supply to a muscle is concerned with muscle sense and in 1918

was of the opinion that sensory endings in eye muscles subserved position sense. Helmholtz (1867) was of the opinion that there was no position sense in the extraocular muscles and demonstrated the lack of appreciation of passive movements of the eyeball and showed that movement of the visual field as a whole occurred when such passive movements are undertaken. This view is supported by Irving and Ludvigh (1936). Ludvigh (1952) has shown that position sense of the extraocular muscles is only present to a worthwhile degree when deviation of the eyeball from its resting location is 10° or more and that this position sense may have been obtained indirectly from the sensory receptors in the eyelids. Hammond, Merton and Sutton (1956) support the view of Helmholtz and consider that stretch receptors are only as Granit (1955) says "private measuring instruments of the muscle servomechanism".

Method

The following experiment was designed to assess the presence or absence of position sense of the eye.

The subject in a totally dark circular chamber binocularly fixated a Landolt ring projected on to the wall of the chamber which was directly in front of him at a distance of 35 ft. The subject's head was held in the rotatable head cage with a dental bite. A projecting periscope on the subject's headcage was lined up with the fixation point on the wall. This projection could not be seen by the subject.



ORDER OF PRESENTATIONS OF TARGET

Fig. 74.

The fixation point was then moved to other positions as shown in Fig. 74 and the subject was asked to move his head until he thought that it was pointing directly at the target. The angular deviation between the Landolt ring and the head projection was called the error. This error was in either direction from the Landolt ring and is called -ve when the deviation is to the right and +ve when to the left of the ring.

A control experiment was conducted in which the subject was asked to move his head through varying angles up to 40° in order to assess knowledge of head position acquired during normal life and during a short learning phase. The movements demonstrated by the subjects showed very great inaccuracies with up to 15° or more of error with mean estimated error of about 10° .

Results

The results obtained with 4 subjects are shown in Table 20. and indicate that the errors are most often less than 2° of arc but may on occasion be as much as 5° or 6° of arc. The mean errors in each group of 21 observations were between 0.5° and 1.9° of arc.

Table 20

Head Position Errors in Degrees of Arc

Arc Traversed		Subject							
From	To	1	1	2	2	3	3	4	4
50°	10°	2	3	1.5	0.5	1.5	1.5	5	1
10°	60°	-2	3	4	-1	1	2	1	2.5
60°	30°	1	0.5	-2	0	2	2	1	8
30°	80°	0	2	0.5	1	-1.5	0	1	2
80°	10°	-2	1.5	0	-0.5	1.5	0	0	0.5
10°	70°	0	4	0.5	0	3	5	1	0.5
70°	20°	2	0	0.5	0	1.5	0	2	1
20°	80°	1	-2	-2	0	1	-1	1	0.5
80°	70°	2	0	0	1	-2	-1	1	1
70°	10°	2	3.5	-1	0	2	0.5	0	2
10°	30°	0.5	-0.5	1	-0.5	0.5	1	0	1.5
30°	60°	0.5	-2	6	0	-1	-1	0.5	0.5
60°	10°	4	8	1	0.5	-2	0	1.5	0.75
10°	80°	1	-2	-1	0.5	6	1	1.5	0
80°	40°	6	1	0.5	0	4	1	5	5
40°	10°	3	2	-2	0	0	0	2.5	1.5
10°	66°	0.5	0	0.5	0.5	0.5	0.5	0.5	0.5
60°	30°	1	1	0	-0.5	2	0.5	1	0
30°	70°	-0.5	-2	-0.5	-0.5	0.5	1	0.5	0.5
70°	20°	1	-2	0	0.5	1.5	1	1.5	0.5
20°	50°	0.5	-0.5	-0.5	-1	1.5	1	0.5	3
Mean Errors		1.5	1.9	1.2	0.5	1.5	0.7	1.3	1.5

Discussion

It is considered that the information on which the head movement is based originates in the sensory afferent fibres from receptors in extraocular muscles or orbital structures. To achieve head line-up with the target, when no alignment clues of intervening structure are visible (including the subject's nose), information on the position of the eye relative to the head is required. In these experiments the resting positions of the eyeballs, the position in which antagonistic muscles would demonstrate equal activity was discerned to a degree of accuracy having a mean error of 1.5° of arc with a scatter of $0-3^{\circ}$ and occasional large errors of $4-8^{\circ}$ (8 of 168). It appears that position sense is present in the eyes at least with regard to the resting position i.e., central position.

Electromyographic studies of human extrinsic eye muscles have been conducted by Bjork and Kukelberg (1953), Glees (1953) and Magee (1956) all of whom demonstrate the very great increase in muscle activity on even slight eye movement. The fineness of the muscle fibres shown by anatomists is reflected in the rate of discharge - in excess of 150 per second (action potential durations of 0.5 to 3 msec. with an amplitude corresponding to 50 m/uV). For comparison with a relatively fine skeletal muscle, e.g. the interosseous muscle of the finger,

the above rates are some three times greater, action potential durations about four times as short and the action potential many times less, 500 microvolts compared to several millivolts.

Cooper, Daniel and Whitteridge (1951) have reported the findings of efferent impulses from the extrinsic eye muscles of the goat on stretch of these muscles. A 2 mm. stretch which corresponds to 11° of rotation in the goat yielded an increase of 90 impulses per second on the steady discharge rate. The resting discharge was 20 impulses per second with a standard deviation of the resting discharge of 6.5 impulses per second. An impulse discharge of twice this standard deviation corresponded to 1.5° of rotation. They conclude that movements of less than 1.5° are capable of being detected and suggest that as the central field of the fovea subtends 1° of arc, proprioception could play a part in the control of eye movements. Bender (1955) has postulated from clinical grounds, and pathology, the presence of an eye centring centre which is related to head movement, nystagmus and indeed all eye movements.

Thus, the nervous system controlling extraocular eye muscles demonstrates a very fine and rapid control mechanism. The similarity of Cooper, Daniel and Whitteridge's conclusions and the findings in this experiment suggests that proprioceptive

impulses not only play a part in eye movements but can in the conditions of this experiment be brought to consciousness. The head in the control experiment showed no signs of having an accurate positioning sense, innate or learned.

Conclusion

The possibility that this sense originates in some orbital structure other than eye muscles cannot be discarded. All that can be stated with certainty is that a position sense is present to a degree that is potentially useful in co-ordinated movements of the head and eyes. Much information is now available on the rapid sustained and slowly adapting discharges from muscle spindles in the extraocular muscles of goats, Cooper et al (1953a), which could form the basis of some system of comparing demanded contraction and achievement in some subcortical structure.

Summary

The presence or absence of proprioception in the control of eye movements was examined and it was found to be present in this particular test. The eyes appear to be capable of finding their resting position by orientating the head to line up with a fixation point. An awareness of eye position relative to the head appears to be present.

PART 11The Moment of Perception

In the descriptive account of eye movements and the discussion concerning the aetiology and function of the second saccades, it was assumed that these movements were corrective in function. Three further assumptions were made, firstly, that during the latent period, secondly, during the fast phase, and thirdly, during the intersaccadic interval, no perception of detail could take place. The hypothesis was formed that perception only takes place when a steady state of tracking was achieved, a steady state which was not immediately followed by a further saccade.

Method

To test the hypothesis and justify the assumptions there was attached to the Aldis projector system two devices which permitted the Landolt C to be seen for approximately 20 msec. during a pursuit movement of the eyes. One device consisted of an additional projector which cast a small (2 min. of arc) light spot on the curved screen and which was present at all times during the pursuit movement. It was this moving spot which the subject attempted to fixate. The other device consisted of a shutter which, when opened by its electro-mechanical and electronic system, permitted the light beam

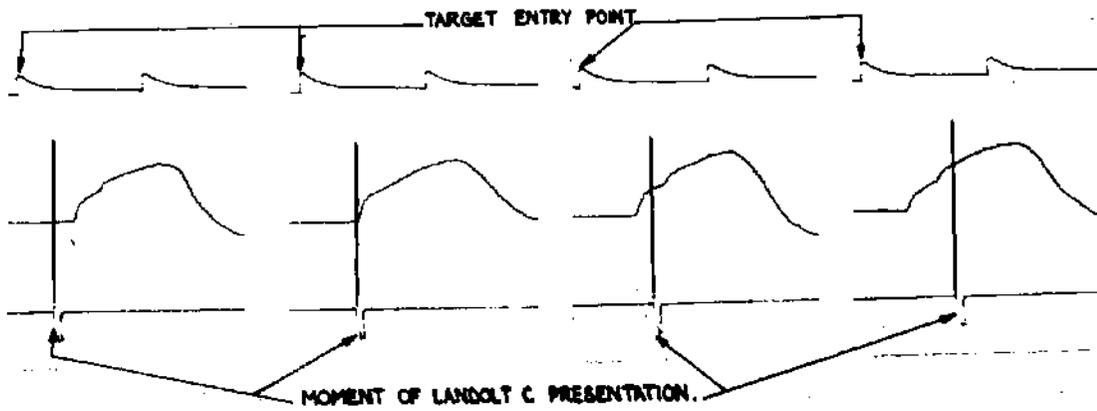
of the Aldis projector to cast the Landolt C on to the screen. During each pursuit the Landolt C was presented once at random intervals of 5 msec. between 60 and 600 msec. after the entry of the moving spot into the field of view. The Landolt C was 30 mins. of arc from the spot. The lamp in the Landolt C projector was on prior to each run and for the duration of each run. The moment of projection selected was controlled electronically to occur at any given time after the moving spot had activated a photocell at the target entry point. A static fixation point was provided, as usual, at this point for the subject. The experiments were conducted in a dark room and the brightness of the spot and Landolt ring was for each one millilambert (Holophane Lumeter). The gap in the Landolt ring was 2 minutes of arc. The target angular velocities utilised were $50^{\circ}/\text{sec.}$ and $75^{\circ}/\text{sec.}$ A full description is included in Appendix A of the electronic and mechanical systems employed.

It is quite impossible to pre-select the phases of eye movements during which the presentation should occur. This is due to two uncontrollable factors, the latency of eye movement which has been previously shown to vary from 150-300 msec., and the occurrence or non-occurrence of second saccadic movements.

Eye movements were recorded by the corneo-retinal potential method. The presentation of the Landolt C took place 20 msec.

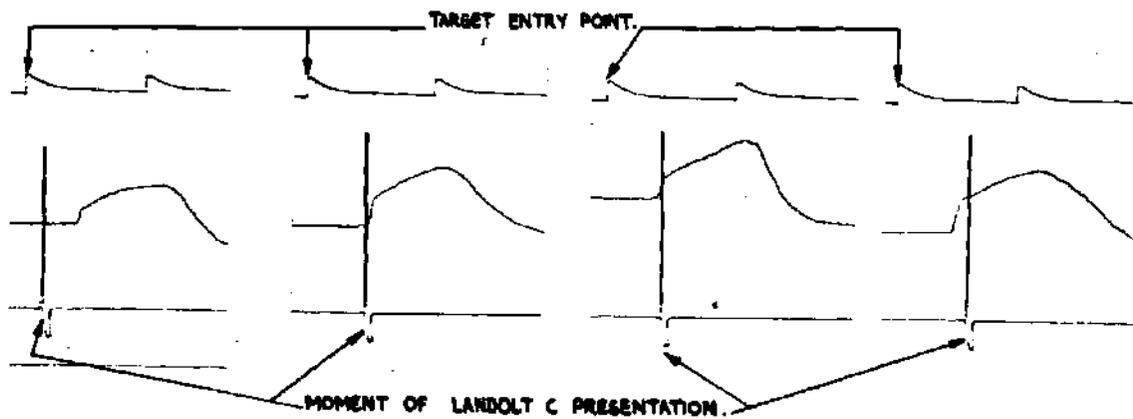
THE MOMENT OF PERCEPTION.

A. EYE MOVEMENTS WITH CORRECTIVE SACCADÉ. (CORNEA - RETINAL POTENTIAL)

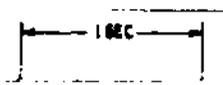


SEEN	0	SEEN	0	SEEN	11	SEEN	231
SOMETHING SEEN	227	SOMETHING SEEN	17	SOMETHING SEEN	342	SOMETHING SEEN	192
NOTHING SEEN	75	NOTHING SEEN	19	NOTHING SEEN	55	NOTHING SEEN	12

B. EYE MOVEMENTS WITHOUT CORRECTIVE SACCADÉ. (CORNEA - RETINAL POTENTIAL)



SEEN	0	SEEN	0	SEEN	3	SEEN	167
SOMETHING SEEN	150	SOMETHING SEEN	8	SOMETHING SEEN	22	SOMETHING SEEN	159
NOTHING SEEN	26	NOTHING SEEN	5	NOTHING SEEN	6	NOTHING SEEN	6




 EYES { TIME CONSTANT 1.0 SEC
 H.F. FILTER -6db 75 c.p.s.
 500V.



EYE MOVEMENT CALIBRATIONS.

THE FIGURES BELOW EACH TRACE SHOW THE INCIDENCE OF RECOGNITION, SEEN BUT NO RECOGNITION, & NOTHING SEEN, FOR ALL SUBJECTS FOR TARGETS WITH ANGULAR VELOCITIES OF 50 & 75 DEGREES PER SECOND.

FIG. 1
Fig. 45

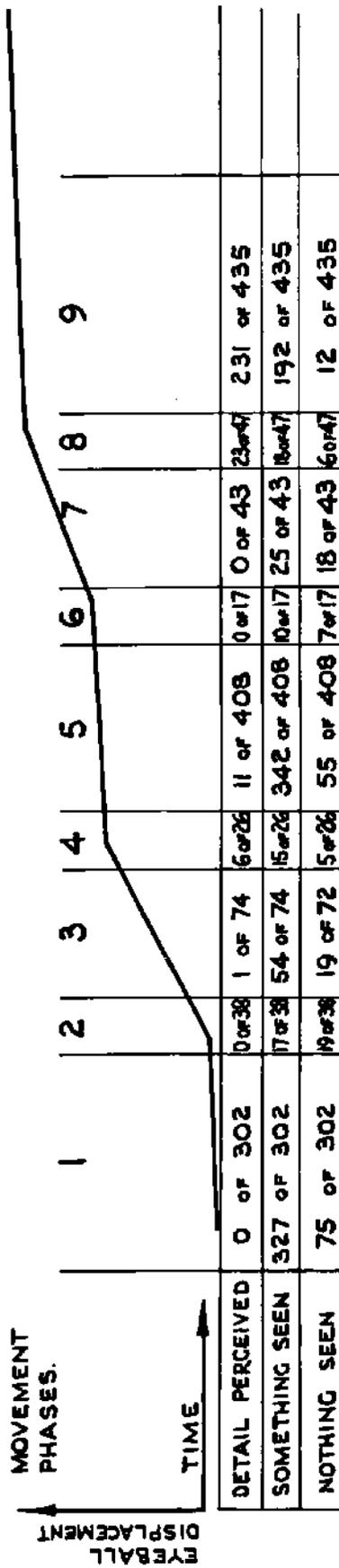
after the shutter marker on the recordings, the duration of opening and closing of the shutter being each about 10 msec. at the trigger unit speed used. Typical records are seen in Fig. 75 from some of the runs.

The subject's responses consisted of recognition of the position of the gap in the Landolt C which was scored as seen, the seeing of something but no recognition, and seeing nothing additional to the fixation spot. The orientation of the gap in the Landolt C was changed after each recognition and after each run in which the subject reported seeing sufficient detail in the Landolt ring to hazard a guess. By this method 100 pursuit eye movements per hour could be obtained. This rate of presentation would have been only 30-50 per hour had the Landolt C been moved after every pursuit movement.

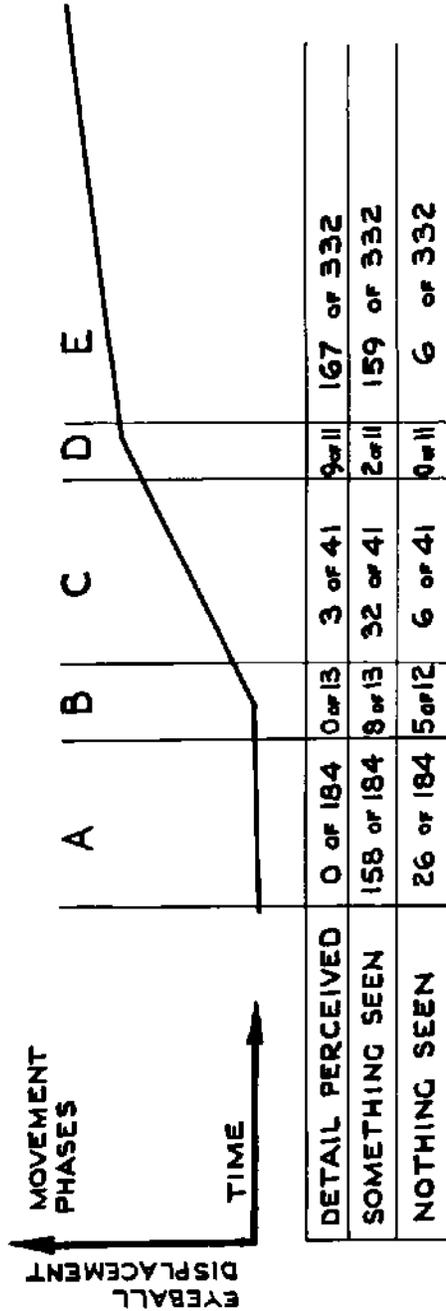
One subject (W.A.C.) carried out 1400 pursuit movements and the pattern of results obtained were confirmed by employing three other subjects for 200 runs each.

Results

All subjects showed the same trends in the localisation of the moment of perception. Subjects 2, 3 and 4 confirming the findings in the larger scale experiments on Subject 1. 99^o/_o of recognitions take place in the conditions detailed in (a) and (b) below.



(1) DIAGRAMMATIC REPRESENTATION OF AN EYE MOVEMENT WITH A SECOND SACCADE.



(2) DIAGRAMMATIC REPRESENTATION OF AN EYE MOVEMENT WITHOUT A SECOND SACCADE.

1971 RECORDS OF EYE MOVEMENT BY THE CORNEA - RETINAL POTENTIAL METHOD. CAPACITANCE COUPLED AMPLIFICATION SYSTEM.

THE INCIDENCE OF THE PERCEPTION OF DETAIL DURING THE PHASES OF PURSUIT EYE MOVEMENTS.

ALL SUBJECTS AT 50° AND 75°/SEC. TARGET ANGULAR VELOCITY.

- (a) Recognition takes place in the absence of 2nd saccades during the steady state of pursuit which succeeds the initial saccadic eye movement.
- (b) Recognition takes place in the presence of 2nd saccades during the steady state succeeding the 2nd saccadic movement.

Seeing something occurred at all phases of the two distinct types of eye movements. The reporting of nothing seen was noted at all stages in the pursuit movement but most frequently during the fast phases of eye movement.

It is inevitable with a 20 msec. exposure that some targets were presented in the phases separating latency and the 1st saccade, 1st saccade and 1st steady state, 1st steady state and 2nd saccade when it occurred, and 2nd saccade and 2nd steady state. No more precise differentiation could be carried out. The results are diagrammatically shown in Fig. 76.

A statistical evaluation of the results obtained showed that a confidence factor of 99⁰/o can be placed on the finding that during the steady state and preceding phase between saccade and steady state i.e., phases D and E, recognition takes place. A confidence factor also of 99⁰/o can be placed on recognition occurring during the steady state succeeding the second saccade and the phase immediately prior to it,

i.e. phases 8 and 9.

A confidence level of 95% can be placed on the other results.

The three recognitions which took place during fast phases where position and velocity errors of considerable magnitude must have been present can only be ascribed to guesswork.

The increased incidence of 2nd saccades was once again demonstrated between pursuit movements at the two velocities utilised, the incidence of 2nd saccades being 52% at 50°/sec. target angular velocity and 86.5% at 75°/sec. angular velocity.

Discussion

The results recorded appear to largely justify the assumptions that recognition can only take place during the steady state in any eye movement, and that the function of the second saccade is a formative, goal directed, reflex fixation eye movement.

The eye movements can be divided into 5 sections (A-E) when no second saccade occurs and 9 sections (1-9) when a second saccade does occur. Fig. 6.

During phases A and 1 (latent period) there is a velocity error between the fixated eye and the moving target of 50 or 75°/sec. It has been previously shown that velocity error

tolerance with a 2 minute of arc target varies with individuals and is about $3-5^{\circ}/\text{sec}$. Recognition should not be possible.

During phases B and 2 (end of latent period and beginning of eye movement) the eye is developing a movement which accelerates through 50 and $75^{\circ}/\text{sec}$. so that at some instant the target and eye angular velocities would be equal. There is, once again, a substantial position error present as the target at $50^{\circ}/\text{sec}$ and $75^{\circ}/\text{sec}$. has moved some 10° and 15° and peripheral visual acuity for a 2 minute of arc target is insufficient to permit recognition at these angle.

During phases C and 3 (the saccade) the eyes have moved to overtake the moving target and can conceivably, on occasion, have presented to the retinae images which have small degree errors in velocity or position. Generally the velocity difference between eye and target will be of considerable magnitude and recognition should not take place. Indeed, when the velocity error is large some 'nothing seems' should be demonstrated.

During phases D and 4 (end of saccade and beginning of steady state) the overtaking high velocity eye rotational movement is being converted to one of steady pursuit. The object image may appear relatively stationary on the retina and recognitions are to be expected. Few, if any, reports

of nothing seen can be expected.

During phases E and 5 (steady state) recognition of the object can take place or recognition of error in fixation, an error which demands reflex correction by a subsequent eye movement. Recognition can also take place during the steady state and yet an error may be developing by virtue of inequality in target and eye movement velocities which will give rise to a position error and thus a corrective saccade as the primary moving fixation point, the spot of light, is being further displaced from the foveae of the retinae.

Phases 6 and 7 (end of steady state and beginning of 2nd saccade and fast phase of 2nd saccade respectively) are considered to occur in response to an error present or developed in phase 5. They are comparable with phases B and 2, and C and 3.

During phases 8 and 9 (end of fast phase and beginning of 2nd steady state and 2nd steady state respectively) which are comparable to D and E, recognition is readily conceivable.

The seeing of something was expected during all phases except during the very fast saccadic movements when some responses of nothing seen were anticipated. It is during these phases that the angular velocities of eye movements may temporarily be greatly in excess of the target velocities; 200-400°/sec. eye velocities compared to 50 and 75°/sec.

target velocities. The seeing or not seeing is obviously dependent on more factors than are examined here. The greatest differences would be expected with variation in target brightness and size.

The origin of the not infrequently quoted statement that the eye sees nothing during fast saccadic type movements was not to be found in the literature surveyed. Gastaut et al (1957) correlate saccadic eye movements and sharp waves in the E.E.G. recorded over the occipital area and express the opinion that the mechanism of the saccadic movement tends to inhibit visual perception during such movements. When perception is taken to mean discrimination of detail then the present results would be confirmatory but if perception is to include the mere awareness of some visual stimulation then the experimental results refute the inhibition theory.

Conclusion

The second saccadic movement is corrective in function.

Perception takes place during the steady state phases of pursuit eye movements when the steady state phase is not succeeded by a further saccade.

Summary

Landolt Cs were presented for 20 msec. alongside a moving fixation point. They were introduced randomly at all points during eye movements and it was found that the second saccade was indeed corrective in function.

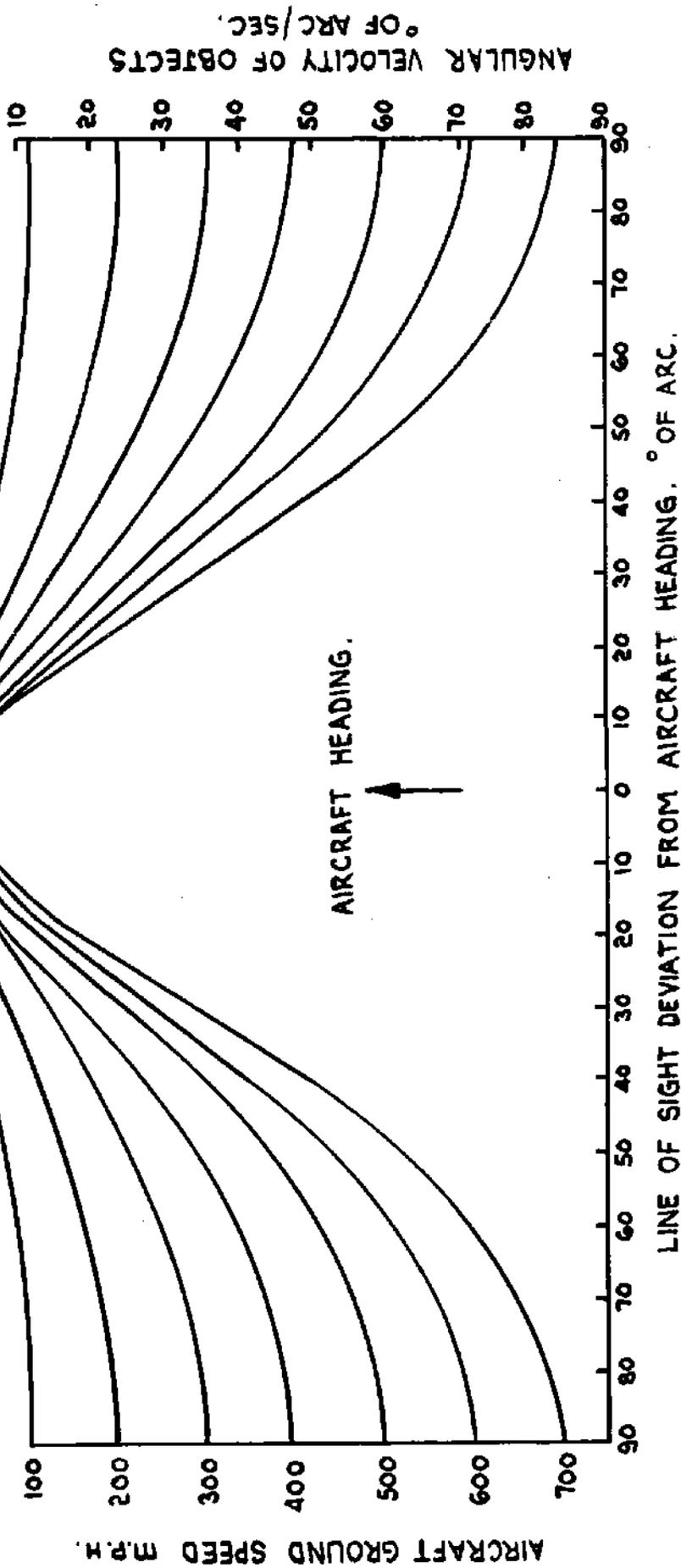
PART 12The Practical Application in Aviation.

There are three major parameters to be considered in assessing the angular velocities of objects on the ground relative to the observer in an aircraft. They are speed of the aircraft over the ground, the height of the aircraft above the ground and the distance of the object to be observed off the track of the aircraft.

The task of the observer is to obtain foveal fixation of the object viewed, and retain the image of the object on the fovea until satisfactory recognition has taken place. Decrement in visual acuity with a 1 minute of arc target may take place at an angular velocity of $30^{\circ}/\text{sec.}$, and at $50-75^{\circ}/\text{sec.}$ for a 2 minute of arc target, and at higher angular velocities as target size increases. The effects of contrast, brightness and colour are assumed to be similar to that pertaining to normal static visual acuity.

In actual flight the greatest angular velocities occur during low level flight at high speed. The objects viewed by pilots or aircrew are usually in the field of view for 1-10 seconds, they are as a rule of a size which subtends many minutes or even degrees of arc, they are most frequently on a track relative to the aircraft which is 500 feet or more to one or other side. Aircraft are frequently deliberately

ANGULAR VELOCITY OF OBJECTS SEEN FROM AN AIRCRAFT FLYING AT VARIOUS SPEEDS.



AIRCRAFT ALTITUDE 500 FT. ABOVE GROUND
TARGET 500 FT. TO LEFT AND RIGHT OF TRACK.

Fig. 77

flown to one or other side of the track required over the ground to gain a better view and longer viewing time of objects on that track. By flying immediately above track much of interest is lost to view in the 'blind' area produced by the nose of the aircraft.

The speed of the aircraft must be related to height above ground and the track of the aircraft relative to the track of the object to be viewed. The maximum angular velocity between observer and observed will occur when the aircraft passes directly over the target, this situation needs no consideration as there is no means of viewing such an object, the aircraft fusilage always cuts off this view. It is reasonable to assume that objects nearer than 500 feet from the aircraft are either hidden from view or have been seen previously at much greater distances ahead of the aircraft. Fig. 77. shows the angular velocities obtained by objects 500 feet to the side, viewed from an aircraft travelling at 100-700 m.p.h. over the ground at 500 feet above ground. It is noted that as the object viewed moves from the more or less straight ahead position, at any given aircraft ground speed, to one abreast of the aircraft, the angular velocity increases to a maximum. Speed is shown on the left, angle off, the base line and relative angular velocity on the right. The angular velocity relative to the aircraft of an object 30° off track,

aircraft speed 600 m.p.h. can easily be found by drawing a vertical line through the 30° mark, and where this intercepts the 500 m.p.h. curve a horizontal is drawn to the right hand scale. The angular velocity is then read off as $20^{\circ}/\text{sec}$.

With large targets to be observed, 1 or more seconds available for observing and freedom to use eye and head in the visual pursuit all objects presented to the crew 500 feet to right or left of track are capable of being visually discriminated. Objects subtending 1 minute of arc and 2 minutes of arc at the observer's eye may be less efficiently discriminated at $30\text{-}50^{\circ}/\text{sec}$. angular velocity, respectively.

The effect of height above ground is shown in Fig. 78 based on 700 m.p.h. as aircraft speed and the observed object once again is at 500 feet to the side of track. Height above ground makes little difference to angular velocity until the object is in the angle $60\text{-}90^{\circ}$ from aircraft heading. For a pilot to look at objects in these positions is highly dangerous at altitudes of 500 feet or less, the pilot would and must look ahead for potential obstructions. The navigator or other crewman not engaged in actual piloting would be capable of regarding objects in this contained angle of $60\text{-}90^{\circ}$ and beyond $90\text{-}120^{\circ}$ where angular velocity begins to drop in the same manner as it built up in the $60\text{-}90^{\circ}$ angle. The velocities are high and may lead to decrement in acuity. The

ANGULAR VELOCITIES OF OBJECTS SEEN AT VARYING DISTANCES OFF TRACK FROM AN AIRCRAFT.

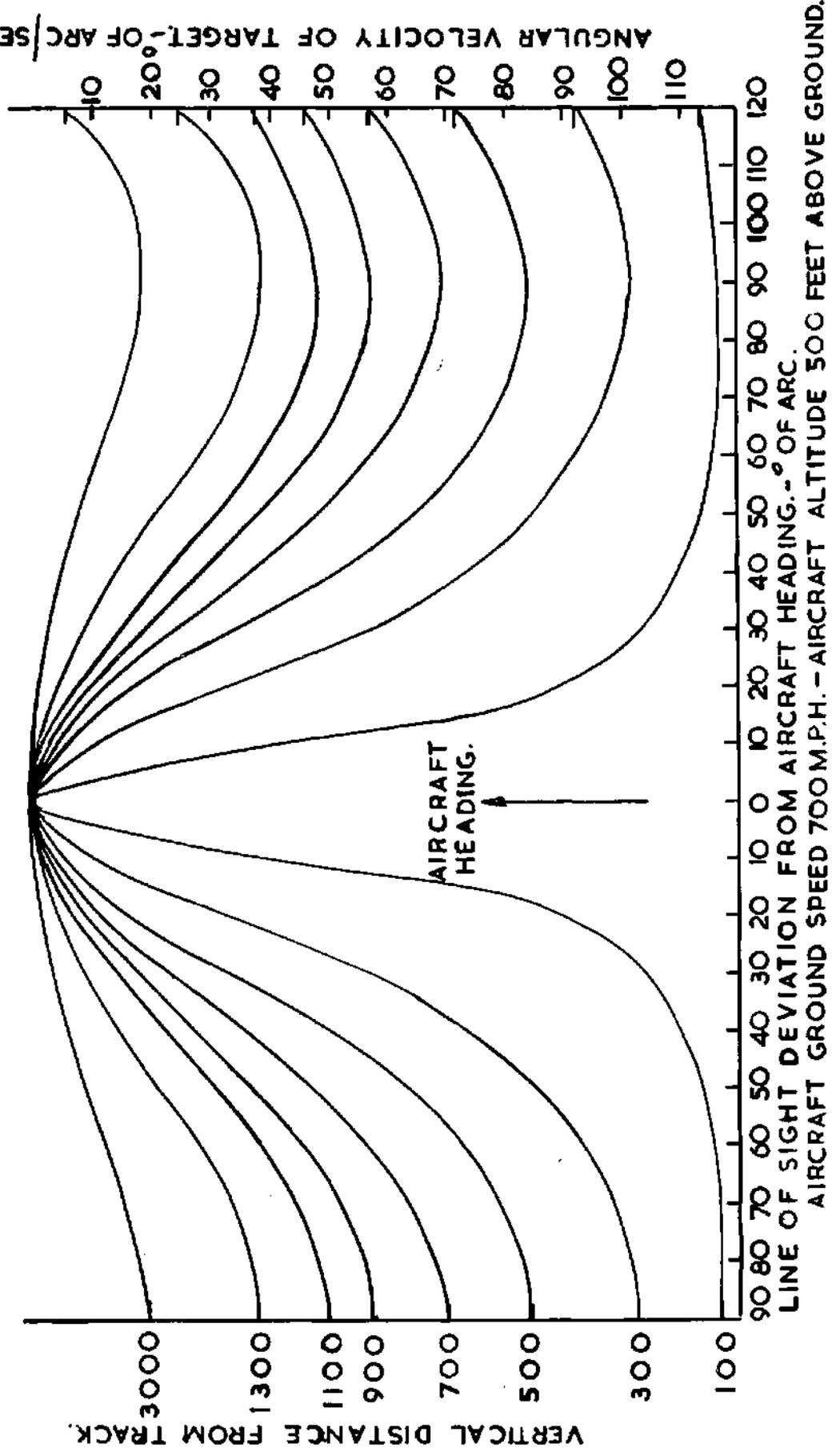


Fig. 79

effect of height can be largely counted as a secondary factor in the production of a decrement in visual acuity.

The greatest change in angular velocity occurs when the variable parameter is distance of the observed off the track from the observer. This is clearly seen in Fig. 79. At 3,000 feet ($\frac{1}{2}$ of one nautical mile) the maximum angular velocity attained by an object viewed from a 700 m.p.h. aircraft is less than $20^{\circ}/\text{sec}$.

The greatest benefit to ability to perceive detail in ground features is gained by flying parallel to track at a distance of at least $\frac{1}{2}$ mile. By this means objects of interest will be in the field of view for the maximum possible time and will not develop high angular velocities at any time.

The view directly forward from an aircraft permits objects to be seen until they disappear under the nose of the aircraft. The angular velocity of these objects will usually also be low until after cut off is established, the rate of rise of angular velocity just before cut off is high and time to view diminished. The view over the nose of an aircraft is rarely more than 15° . Thus the objects immediately ahead of an aircraft travelling at 700 m.p.h. will be hidden at a distance of 1,865 feet with an aircraft flying at 500 feet, and the angular velocity at 1,865 feet will be about $25^{\circ}/\text{sec}$. (from Fig. 79).

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At 200 feet objects will disappear at 746 feet with an angular velocity of about $60^{\circ}/\text{sec}$. It is almost inconceivable that a pilot would look in this direction at such a speed, but even if he did the object would probably be accurately perceived.

Only one other situation need be considered and that is the approach lights and runway threshold. The angular velocity between the threshold or touch down point and the pilot's eyes is maintained at zero $^{\circ}/\text{sec}$., if this is not maintained then some error in the approach path, either undershooting or overshooting is occurring. The rate of change of the angular velocity present will be small unless the approach path is grossly in error. This is unlikely to occur, errors however catastrophic their results, are small. These objects which develop a high angular velocity are rapidly approaching the abreast the aircraft position, and although they may by their movement aid the pilot in his approach are not looked at with an intention of gaining information from their detail.

It is considered that the variation in ability to discriminate detail in moving objects is of little moment except in the conditions of high speed, low level flight in which training may be of value. In normal flight the time available for viewing objects is generally long, the angular velocity low to moderate and the head is free to move. That these three factors all contribute to improvement in ability has been

demonstrated in the experimental laboratory programme.

The practical implications have been assessed in flight by actual observation at speeds up to 500 m.p.h. as the pilot of Canberra and Meteor 7 and 8 jet propelled aircraft in a low flying area. The observations on the approach to land situation are also based on considerable experience over a number of years.

PART 13Summary of Conclusions and Findings

The visual acuity of man in relation to moving objects diminishes as target velocity increases. This diminution is the result of failure of the fixational eye movements. The extent of the failure and the frequency of it is indicated by the incidence of corrective eye movements, an incidence which increases as target velocity increases.

As target velocity increases the magnitude of the initial eye movements of necessity increases not only in the angular rotation extent but in the rate of changes required.

It is considered that the primary error lies in the extra-ocular muscles, the contraction patterns of which fail to meet the demand of cortical and subcortical centres to ensure a foveally positioned image of the object of interest.

This consideration is based on

1. The improvement in ability and reduction of the incidence of corrective saccades when, by having initial peripheral retinal stimulation, the rate and magnitude of the initial eye movement is reduced.
2. The improvement in ability when the head and eyes are combined to form a pursuit movement. Such combination which is entirely normal in man reduces the magnitude of eye muscle contraction.

3. No improvement is noted when a target of known velocity is repeatedly pursued. Learning would normally take place in a series of 100 runs in human activity. The errors in fixation and acuity were present to the same extent at the beginning and end of any series. This is ascribed to variable muscle responses to an unvaried demand.

Eye movement latency varies from 150-300 msec. when the movement is one of pursuit of a fast moving target.

Eye movements are of two types. One which pursues the target and has no need of correction, the other has need of correction and displays a second saccadic movement.

This second saccadic movement is corrective in function.

The errors in pursuit eye movements may be of velocity or position, or both.

The tolerance to position and velocity errors increases with target size. This indicates that some of the improvement in ability to discriminate detail in moving objects which occurs with larger targets is due to less demanding foveal positioning of the image of the target. Eye movements of lesser accuracy can be tolerated.

Position error tolerance for a 1 minute of arc target in the experiments was about 1° of arc. For a 3 minute of arc target it was $2\frac{1}{2}$ - 3° .

Velocity error tolerance for a 1 minute of arc target is

2-3°/sec. and for a 3 minute of arc target 3-5°/sec.

Combined velocity and position errors are almost intolerable.

The normal movements in man in visual pursuit of a target is eye movement followed by head movement. The interval between eye movement and head movement is about 100 msec.

Activity of muscles in the neck associated with rotational movements occurs frequently before eye movement commences. This activity does not occur when voluntary inhibition of head movement is practised.

Proprioceptive afferent information is present in man in the circumstances of the experiment employed to detect its presence. The information reaches consciousness.

The intersaccadic intervals and the duration of the included steady state in such intervals can be so short that consideration of the locus of control in cortex or subcortical structure has been given.

These time intervals are shorter than the currently accepted times for efferent impulses from the retina to reach cortex and there organise efferent impulses to reach and affect eye muscle.

Either the visual system and oculomotor system have shorter temporal features in the stressful conditions of these experiments or only subcortical structure is involved, a subcortical structure which may have access to or is supplied with eye muscle contraction state information, proprioception from eye muscles

may play a part in the fixation reflex.

The appreciation of the true horizontal known to be inaccurate when the head is tilted in a dark environment applies to horizontally moving objects as well as to the much investigated static situation.

In all flight conditions the angular velocities at which a decrement in visual acuity occurs are rarely attained by objects which would be regarded by aircrew as being of normal interest.

The ability to discriminate detail in moving objects varies among subjects and appears to reflect an overall superiority or inferiority of the whole visual and oculomotor system.

Appendix A

This appendix describes apparatus developed during the course of the experimental investigation by the author and Mr. N.L. Andrews, an electronic technologist at the Institute of Aviation Medicine.

Practical aspects of experimental design

A white vertical screen extending from 1ft. to 5 ft. above floor level, and forming an arc of a circle of radius 16 ft. with an included angle of 90° was set up with the subject placed at the centre of the circle. Fig. 1.

A modified Aldis projector, also placed at the centre of the circle is arranged to produce two visual target images on the screen.

One of these, the 'pursuit' target, comprising a circular spot of light approx. 1cm. in diameter (i.e. subtending an angle of approx. 7 minutes of arc at the subject) is obtained by the use of a telescope rigidly mounted to the Aldis projector but adjustable in elevation and azimuth. An image of the end-on view of the filament of a 6 volt, 24 watt lamp is used to obtain the desired spot size and intensity.

A 'recognition' target, comprising a Landolt C is projected from a specially constructed slide in the Aldis projector, and is capable of being observed or projected by a rapid-action electromechanical shutter mounted in close proximity to the slide.

The Landolt C is mounted in the centre of a milled-edge disc which can be rotated continuously about the centre of the C. By a withdrawal of the slide carrier, the disc can thus be rotated by hand to change the relative angular position of the break in the Landolt C.

Projection equipment

The optical system devised for producing the pursuit target image comprises an optical bench telescope modified by the addition of lenses to produce an image of the required size (1 cm. diameter) at a distance of 16 ft. of a point source of light. To achieve maximum intensity of the image, the source is arranged to be the end-on view of a straight-wire filament type of lamp (6 volt, 24 watt). The lamp housing is constructed using a flexible metal bellows to permit alignment of the lamp filament with the axis of the telescope. It is necessary to use a matt paint inside the lamphouse and to line the inside of the telescope tubes with matt paper in order to minimise halation of the target on the screen.

The telescope projecting the pursuit target is attached at the rear end to a bracket mounted on the Aldis lamp-house casing and at the front end by means of a clamping ring to the lens tube of the projector. By means of slotted holes, the position of the telescope can be adjusted in elevation and azimuth to enable the two targets to be superimposed on the screen. In

practice, complete superimposition makes recognition of the target difficult and it is found preferable to align them to a separation of 30 minutes of arc, at which angular separation the decrement in visual acuity for 2.5 minutes of arc target is negligible.

The rotating mechanism

The complete projector assembly is securely attached to a 12 inch diameter turntable, the bearing framework of which is mounted by four pillars to a solid wooden baseboard. Fig. 67 & 68.

A thyrotron-controlled motor is used to drive the turntable carrying the projector assembly. This arrangement provides the high starting torque necessary to overcome the inertia of the moving system (which has a total weight of about 6 lbs.) and also provides an adequate constancy of speed when running.

The motor is mounted vertically below the turntable and coupled by a friction drive bearing on the inner rim of the turntable. The most satisfactory method of coupling has been found to be by using a rubber sleeve on the extension shaft of the motor, the latter being free to pivot about an eccentric vertical axis and tensioned against the turntable by means of light springs. By this means, optimum contact between the rubber sleeve and the inner rim of the turntable is obtained.

The circuit of the control unit for the motor is shown in Fig. 2. The motor used is a 20 watt Motor Generator Ref. 10KB/21.

This is fundamentally a rotary converter but is convenient for use in this type of circuit as by employing the H.T. armature winding, a current of no greater than 40 mA is required. Permanent magnet field excitation is employed. By reference to the circuit diagram, it is seen that full-wave rectified current is fed to the motor armature via two thyratrons, the conduction angles of which control the mean current. These in turn are controlled by the bias voltages applied to their grids by means of the speed control potentiometer. Feedback action is derived from the back EMF developed in the motor armature when running which is effectively injected into the grid-cathode circuit of the thyratrons. A satisfactory degree of speed stability and high torque is thereby obtained.

Reversal of the motor is effected by a change-over switch which reverses the polarity of the armature current.

A vacuum type thermal delay valve protects the thyratrons during the warming-up period of their cathodes.

The switching unit, designed to provide single sweep operation of the target projectors is shown diagrammatically in Fig. 3.

Contacts C_1 and C_2 are fitted just below the undersurface of the turntable and are operated by small ramps about $\frac{1}{4}$ " long on the turntable itself. C_1 is located in the fully anti-clockwise (homed) position of the turntable assembly, corresponding to about 45° anticlockwise of the entry point on the screen.

Contact C_2 is fitted about 135° clockwise of C_1 at a point where the target images will have left the right hand edge of the screen. At this point reversal of the turntable is required.

Control relays A and B are 500 ohm K30000 type and are fed from a separate 24 volt supply.

Assuming the turntable assembly to be in its 'homed' position, operation of the 'RUN' push-button switch will over-ride the open contact C_1 and cause relay A to operate. This relay locks-on by contact a_1 and closes the motor armature circuit by contact a_2 , causing the turntable assembly to rotate in a clockwise direction. Contact C_1 will then close and rotation continue until the reversal position is reached when contact C_2 closes. This causes relay B to operate which also locks-on through contact b_1 and at the same time reverses the polarity of the motor armature current by means of contacts b_2 and b_3 . The turntable then runs back until the 'homed' position is reached again when c_1 is opened, causing both relays to drop out, the motor to stop, and the circuit to reset ready for the next sweep. It should be noted that the 'RUN' push-button must be held depressed until contact c_1 has closed.

The projector and telescope assembly are rotatable at rates up to $225^\circ/\text{sec.}$, and were used generally at 50, 75, 100 and $125^\circ/\text{sec.}$, thus providing a means of sweeping the targets

across the screen at controlled rates.

The experimental requirements are such that the target sweeps should occur singly, each sweep being initiated by pressing a 'RUN' push-button, the sweeps being right to left or left to right. For this reason, it is not necessary for the projector assembly to rotate continuously and the apparatus is designed to produce a fully automatic sequence of forward sweep, return sweep and stop.

Two photocells mounted 50° apart on the screen in the path of the pursuit target are arranged to provide information on the rate of sweep. One of these, placed at the left hand edge of the screen, which is the normal entry point of the target, also provides an electrical impulse which, after feeding into delay and trigger circuits, is made to operate the recognition target shutter and expose the image of the Landolt C for a predetermined short interval.

Information on the movement of the eyes is obtained electrically by the corneo retinal potential method. On a normal subject, this arrangement gives a sensitivity of the order of 5-15 V/degree of eye movement. The recordings are made on a standard EEG-type Pen Recorder, using the maximum available coupling time constant (1 second) in the amplifier, no suitable d-c amplifier being available. The corneo retinal potential method is the only one which can be used to give continuous information on eye movements

over the wide pursuit angles required and utilised. Optical reflection systems, corneal lens systems and cinephotography are unsuitable.

Marker signals from the photocells are displayed on the recorder on an adjacent channel to the retinal potentials. A third channel displays a further marker signal which occurs in theory coincident in time with the exposure of the moving recognition target image on the screen, but in practice as found in calibrations preceded the exposure of the target by about 20 msec.

Typical records are shown in Fig. 74 and 4B. Fig. 1 indicates a block diagram of the general assembly of equipment.

Photocell trigger unit Fig. 5.

Photocells of the gas-filled emissive type (9oCG) are used to intercept the path of the pursuit target on the screen in order to provide information on the instant of target entry, and rate of sweep across the screen. For the purpose of the main experiment only two photocells are used; one at the point of target entry, and one at a point 50° clockwise from there, although in a preliminary phase of the experiment using the same turntable and projector assembly but with a much larger screen (30 ft. radius), up to 16 photocells have been employed, spaced at 10° intervals, in order to check the linearity of the sweep.

The sensitivity of these cells is approx. 125 A/lumen at a colour temperature of 2700°K and they have a projected cathode area of 3.0 sq.cm. The screen area of the pursuit target is of the order of 0.78 sq.cm. and in practice it has been found extremely difficult to maintain the alignment of the projector so that the target image falls centrally across the photocell cathode in each successive sweep. Hence, the order of current change in the photocell, when illuminated by the target image is of the order of 2×10^{-8} amp., producing a signal of about 20mV using a 1 megohm photocell load, but which varies considerably in amplitude from sweep to sweep.

For this reason, the voltage pulse appearing across the photocell load when the target passes over the photocell is amplified in two valve stages and then applied to the grid of a thyratron valve. The cathode of the thyratron is returned to a potential divider network across the HT line thus providing a negative bias on the valve. The leading edge of the amplified photocell pulse is sufficient to overcome this bias and allow the thyratron to conduct, the circuit being limited by the anode and cathode resistors.

The shutter and shutter trigger unit

The electromechanical shutter is designed using a K3000 type relay, to the armature of which is soldered a rod carrying a

spade shaped flag on the end. The rod is bent so that the flag intercepts the image of the ring between the slide carrier and the projector lens in the operated position of the relay, and moves clear when the relay is released. The desired exposure time which is of the order of 20 msec., has been achieved by reducing to a minimum the necessary amplitude of movement of the flag. The normal relay springset is used to obtain release of the relay armature.

There is no significance in the fact that the relay is normally operated closed and the target exposed as a result of its release. Both possible arrangements have been tried with no effective difference in exposure characteristic and the present method has been selected for electronic convenience.

Typical exposure records obtained using a photoelectric cell are shown in Fig. 6. The short-exposure record, as is used for the experiment, shows a substantially square topped exposure pulse, the 100c/s ripple content being due to the use of A.C. in the projector lamp. At longer exposure times, an approx. 10c/s mechanical oscillation of the shutter flag distorts the characteristic somewhat, and would need to be damped out if longer exposures were to be used.

Shutter trigger unit Fig. 7.

The function of this unit is to provide a suitable impulse for driving the electromagnetic shutter in the projector assembly

which controls the exposure of the recognition target as described in an earlier paragraph.

The unit is connected to the output socket of the Discriminator and Delay Unit and consists of a double triode valve cross connected as a flip-flop. In the anode of the normally conducting half of the valve is connected a 6000u K3000 type relay. Trigger action is initiated by the closure of relay contact b_2 in the Discriminator and Delay Unit which causes a positive going voltage pulse to be applied to the grid of the non-conducting half of the valve. The conducting half is then cut off and the relay released for a time depending on the setting of the Output Pulse Width Control. With the present circuit constants, this control gives an available pulse width between about 20 and 70 msec.

The duration of the pulse applied to the grid of the flip-flop valve is determined by the CR combination in the grid circuit. This is not critical but must be chosen so that the pulse is not of sufficient length to inhibit the flip flop action.

Contacts from the anode relay are taken via output sockets to be connected in series with the shutter solenoid and its D.C. supply. Both normally open and normally closed contacts are provided but in this application the former are used, the shutter solenoid being released during exposure of the target.

Taking into account the operate and release lags of the relays

concerned, the present circuit gives target exposure times variable between about 40 and 100 msec. These times include the time taken for the shutter to move both ways across the target field, the times during which the target is totally exposed being about 14 and 60 msec. respectively.

The shutter Trigger Unit is provided with a marker signal output similar to that provided on the other units to give an indication on the recorder trace when the shutter is exposed.

The unit is housed in a separate chassis but powered from an auxiliary H.T. and L.T. supply outlet on the back of the Discriminator and Delay Unit.

The inherent error in the use of this marker signal to indicate target exposure is consequent upon the release lag of the shutter solenoid and in the movement of the shutter flag. The latter has been reduced to the minimum by the mechanical design and the former has been measured by lining up the obscured recognition target image on a photocell, triggering the equipment and recording the interval between the commencement of the photocell signal and the marker signal. The error measured in this way can be as little as 5 msec.

The Discriminator and Delay Unit Fig. 8, 9 and 10.

In one phase of the experiment, it was required that the exposure of the recognition target should occur at a point on the forward target sweep determined by the characteristic of the

retinal potential wave form. The purpose of this is so that the target can be presented to the subject coincident in time with the saccades which occurred at the beginning of the pursuit eye movement. This is achieved by the use of a Discriminator and Delay Unit. This unit accepts the retinal potential and can be arranged to produce a trigger pulse at any amplitude of the retinal wave form selected by the discriminator level. It is normally arranged to operate at the commencement of eye movement, i.e. at the smallest possible increase in amplitude of the retinal wave form which is detectable above base line variations caused by irregularities in fixation. The discriminator output pulse then triggers a delay circuit which in turn produces an output pulse suitable for operating the recognition target shutter after a time delay continuously adjustable from about 30 msec. up to 200 msec. This delay is normally controlled by an observer watching the pen records who can set it to the value required to coincide target presentation with any particular saccade.

Due to the variation of the latent period of eye movement (150-300 msec.) however, this method proved rather 'hit and miss', and was abandoned as experimentally impractical though technically feasible. The discriminator was therefore made to operate at the entry point of the pursuit target (using a marker photocell to provide the stimulating signal), the time delay being set to

one of a series of statistically random values between 30 and 600 msec. The identification (or otherwise) of the recognition target was scored for 4 subjects on 2000 individual target sweeps. With this arrangement recognition target presentations occur at all stages of the eye movement pattern.

Fig. 9 indicates the timing sequences during the first phase of this experiment and Fig. 10 the circuit of the unit.

The input signal was derived from the later stages of the pen recorder amplifier where it had been A.C. preamplified using a coupling time constant of 1 second, and then passed through subsequent stages of D.C. amplification.

The amplifying stage (12AU7) employs the principle of cathode injection to convert the balanced input signal to a single-ended output voltage appearing on the anode of one half of the double triode. The polarity of the input signal is reversible by means of a changeover switch and the input circuit is capacity coupled with a time constant long enough to give a flat response down to at least 1 c/s. The response of the stage is reduced above 8-10 c/s by a shunt capacitor across the output. This band-width is adequate for dealing with the retinal potential waveform.

The response of the stage above 1 c/s is shown in Fig. 11.

The discriminator comprises a resistance network across the output anode of the amplifier valve, with a potentiometer tapping

to the trigger electrode of a cold cathode trigger valve type Z803U. This valve has a nominal striking potential of 132 volts which is stable to within $\pm 2\%$ over a long period of time.

When the voltage across the potentiometer network rises sufficiently for the trigger valve to conduct, the high speed relay in the anode circuit operates and remains closed until the valve is extinguished by opening the H.T. line by means of the RESET push button.

The discriminator bias is displayed by means of a voltmeter connected between the potentiometer tapping and earth and is adjusted to make the circuit trigger at the desired point of the rising input wave form. In the case where the unit is required to be triggered from the amplified photocell signal, the bias is set to approx. 125 volts and the rapidly rising input pulse then causes immediate firing of the trigger valve.

Operation of the high speed relay in the anode circuit of the first trigger valve opens contact a_1 in the trigger circuit of the second Z803U. This permits one of other of the switched condensers to charge up from approx. earth potential to a maximum value of 150 volts at a rate determined by the time constant of the condenser and variable resistor combination. The condenser voltage is however applied directly to the trigger electrode of the second Z803U with the result that the trigger tube fires at the instant the condenser has charged up to 132volts.

Relay B in the anode circuit then operates and remains closed until the anode circuit is broken by operation of the RESET push button.

Three switched values of delay capacitance are built in, which, together with the variable resistance, give delay ranges as follows.

- A 17 - 136 msec.
- B 27 - 312 msec.
- C 44 - 806 msec.

By the removal of a jumper plug on the rear of the unit, the internal delay control components can be switched out of circuit and an external Remote Delay Control Unit plugged in. Slightly different values of fixed condensers are used in this unit which gives ranges as follows.

- A 40 - 60 msec.
- B 80 - 290 msec.
- C 140 - 660 msec.

A control on relay B, capable of carrying 5 amps is brought out to a socket on the front panel and serves as a means of obtaining the delayed output pulse from the unit. A similar contact on the same relay produces a marker signal of approx. 70 mV amplitude for display on the pen recorder.

The Discriminator and Delay Unit is housed in a self contained chassis complete with a series-valve stabilised power unit.

Remote delay control unit Fig. 11.

This remote control unit is fitted with a calibrated dial and pointer covering three ranges of delay times. The unit has been calibrated using a dekatron driven millisecond timer unit, but a note on the significance of the calibrations is worthy of inclusion.

The calibrated time delay is the time between the receipt of an input signal large enough to strike the first Z803U trigger valve and the closure of the contacts of relay B. This is made up of the time of occurrence of three separate events :-

1. Closure of contact on relay A.
2. Charging of capacitor to striking potential of trigger valve.
3. Closure of contact on relay B.

For the calibrations to hold, (1) and (3) must be considered constant and their sum, together with the minimum value of (2), comprises the shortest delay time which can be achieved. The actual values of (1) and (3), however, depend on the immediate magnetic history of the relays. If the relays have been unenergised for some time, the values are of the order of 2-5 msec. and 5-10 msec. respectively, but if as is in the case of the actual experiment, the relays have been held energised and released (by the reset button) only a few seconds before being required to operate again, when due to remainance of the

cores, the operating times will be considerably reduced. In this particular experiment for which the equipment has been designed, the projector assembly rotates through approx. 60° between operation of the 'RUN' push button (in which is incorporated the trigger reset) and when the trigger is required to operate. At rotational speeds of 50 and 75° per second this involves a time interval of 1.2 and 0.7 seconds respectively. Care has been taken, therefore, when calibrating the dial, to ensure that the circuit is reset 1 second before a delay time measurement takes place. The calibrations are therefore likely to hold, to within the required degree of accuracy, under the experimental conditions intended to be used. It should be noted that the actual delays obtained in practice will be available for measurement on the pen records to an accuracy consistent with the resolution of the record at the paper speed employed.

Fig. 4a illustrates a typical pen record where the discriminator bias is set to initiate the delay at the commencement of the rise of the retinal potential waveform, and Fig. 4b illustrates a similar record but in this case the delay is initiated by the first photocell marker signal.

Conclusions

The equipment described, whilst having been designed to meet the detailed requirements of one specific experiment, should be

of general use in other subsequent work.

The broad specifications of the electronic units are listed below and only minor detail modifications should be necessary to adapt any unit to a particular mode of operation coming within the same general function.

- (a) Sensitive trigger unit operating from a low intensity pulse of light on a photocell. Sensitivity approx. 1.5×10^{-4} lumen. Capable of ready modification to accept a voltage input. Voltage sensitivity approx. 20 mV. Constant amplitude output pulse of 120 volts peak.
- (b) Discriminator unit capable of triggering at any point of a rising voltage at a level of about 0.5 volts to 5 volts. Minimum rate of rise of voltage approx. 12 volt/sec. Trigger causes closing of relay contact. Push button reset.
- (c) Delay Units providing operation of relay contacts at controlled time intervals (30-600 msec.) after receipt of an initiating signal (closing of contact).
- (d) Pulse unit providing variable length pulse (20-70 msec.) via relay contacts, suitable for solenoid operation etc.

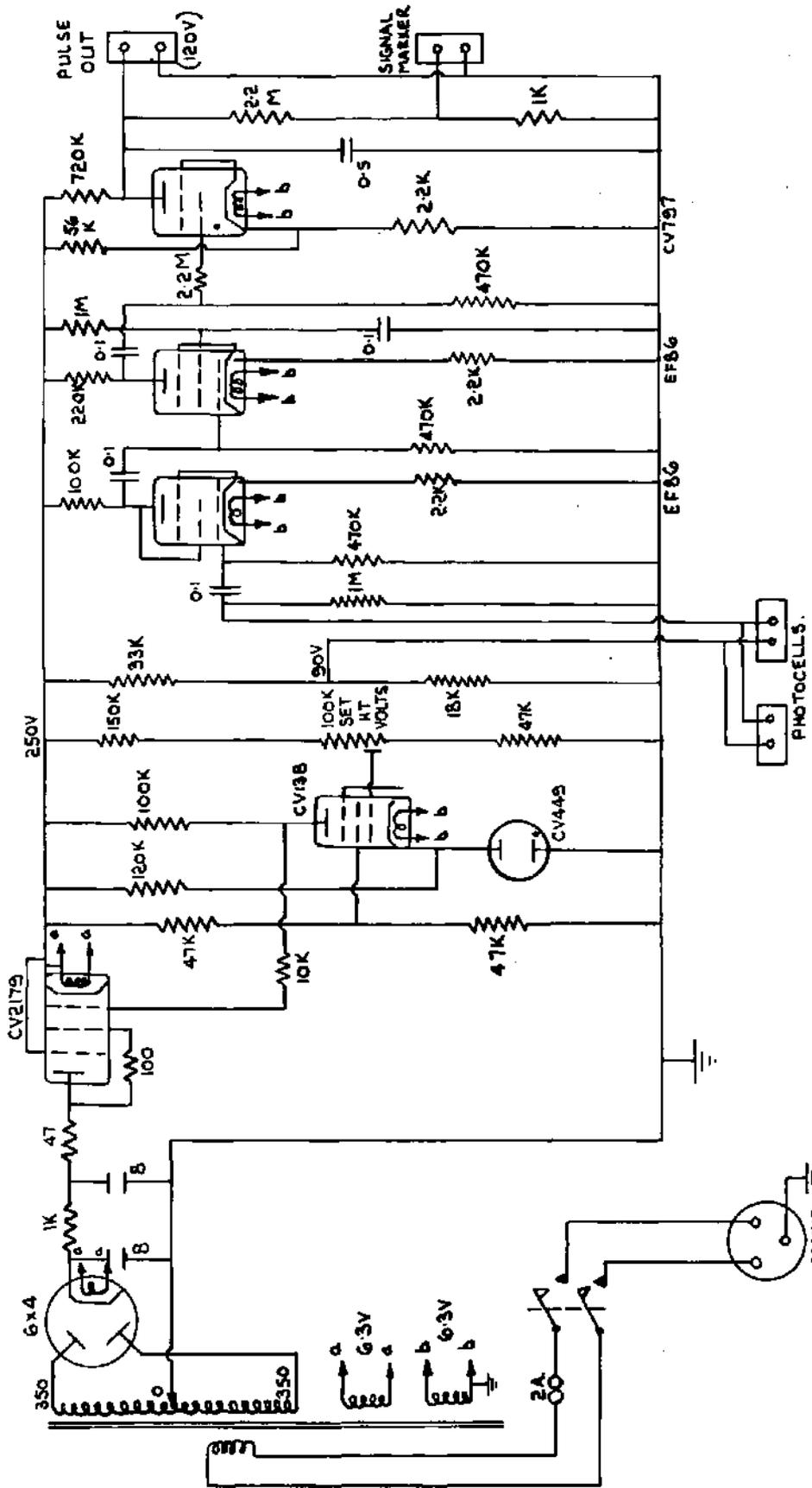


FIG. II. PHOTOCCELL TRIGGER UNIT

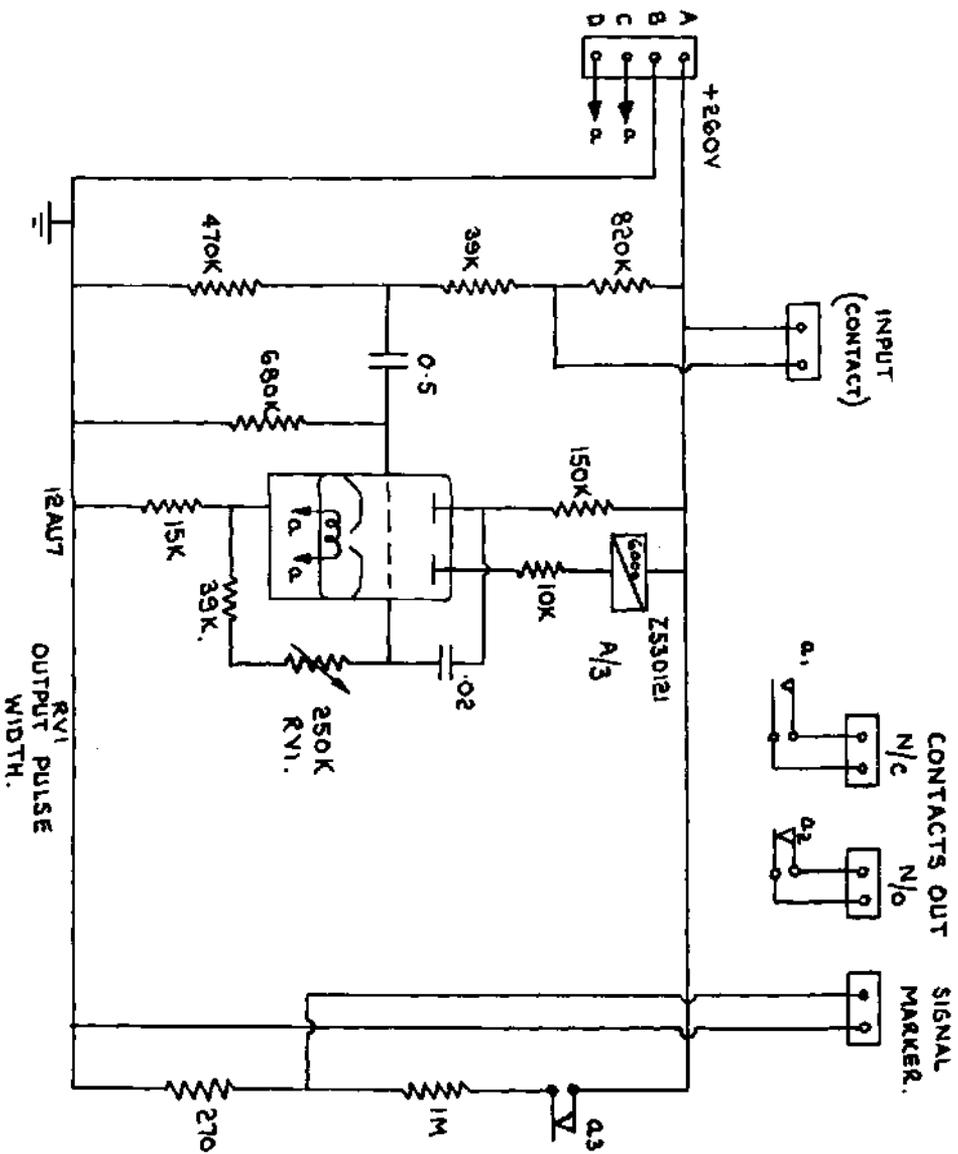
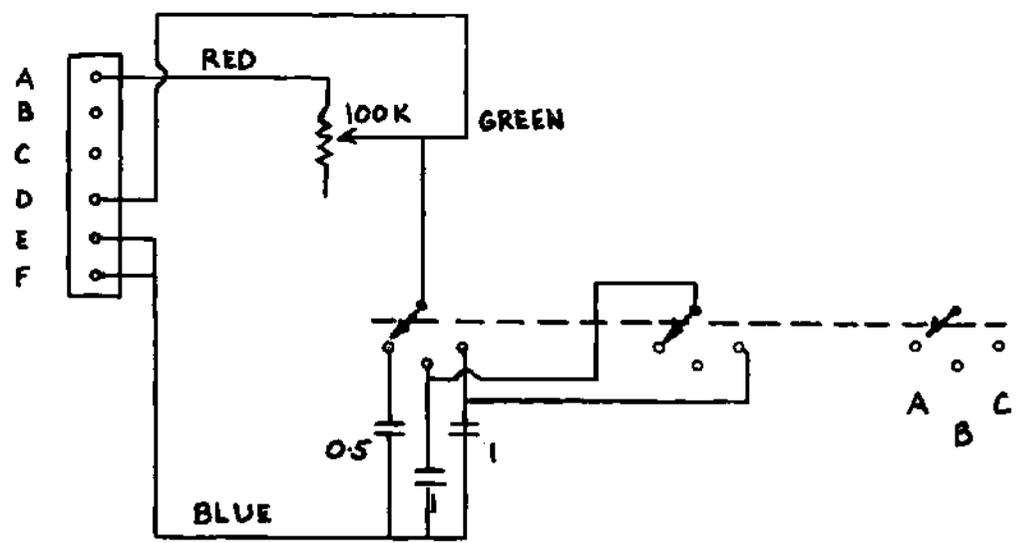
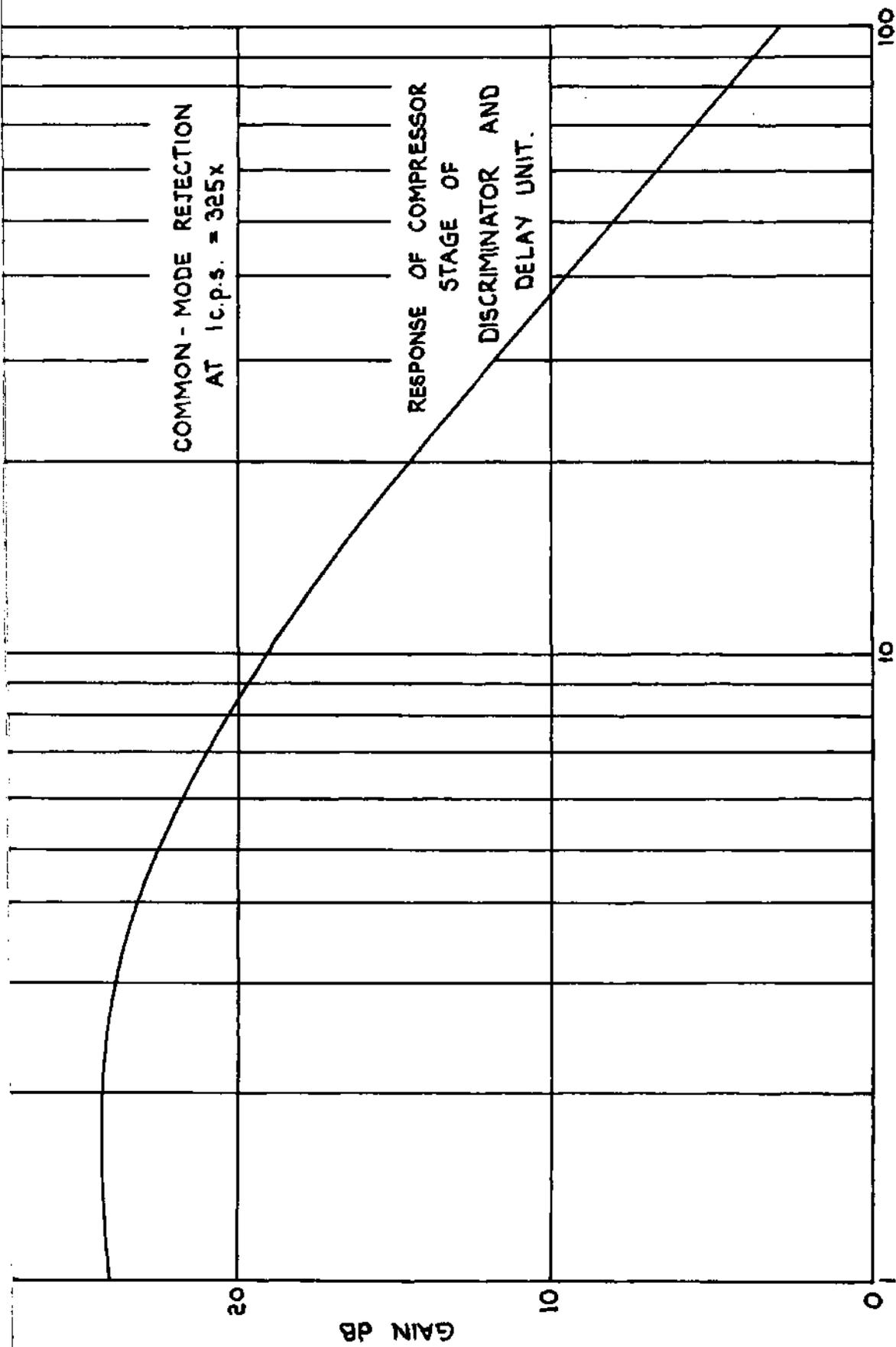


FIG. 10 SHUTTER TRIGGER UNIT.



REMOTE DELAY CONTROL UNIT

FIG 9



FREQUENCY C.P.S.

FIG. 8.

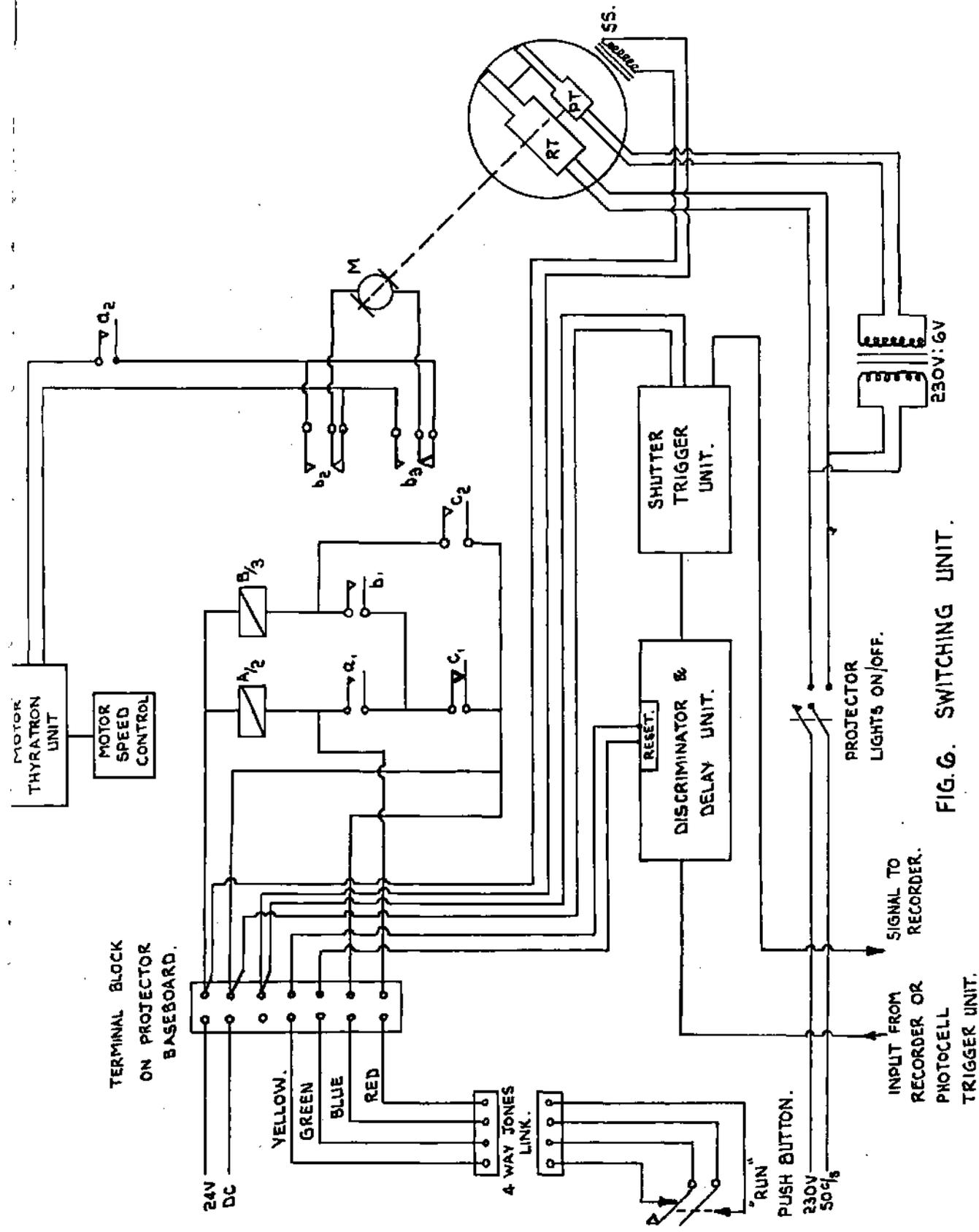


FIG. 6. SWITCHING UNIT.

MOTOR THYRATRON UNIT

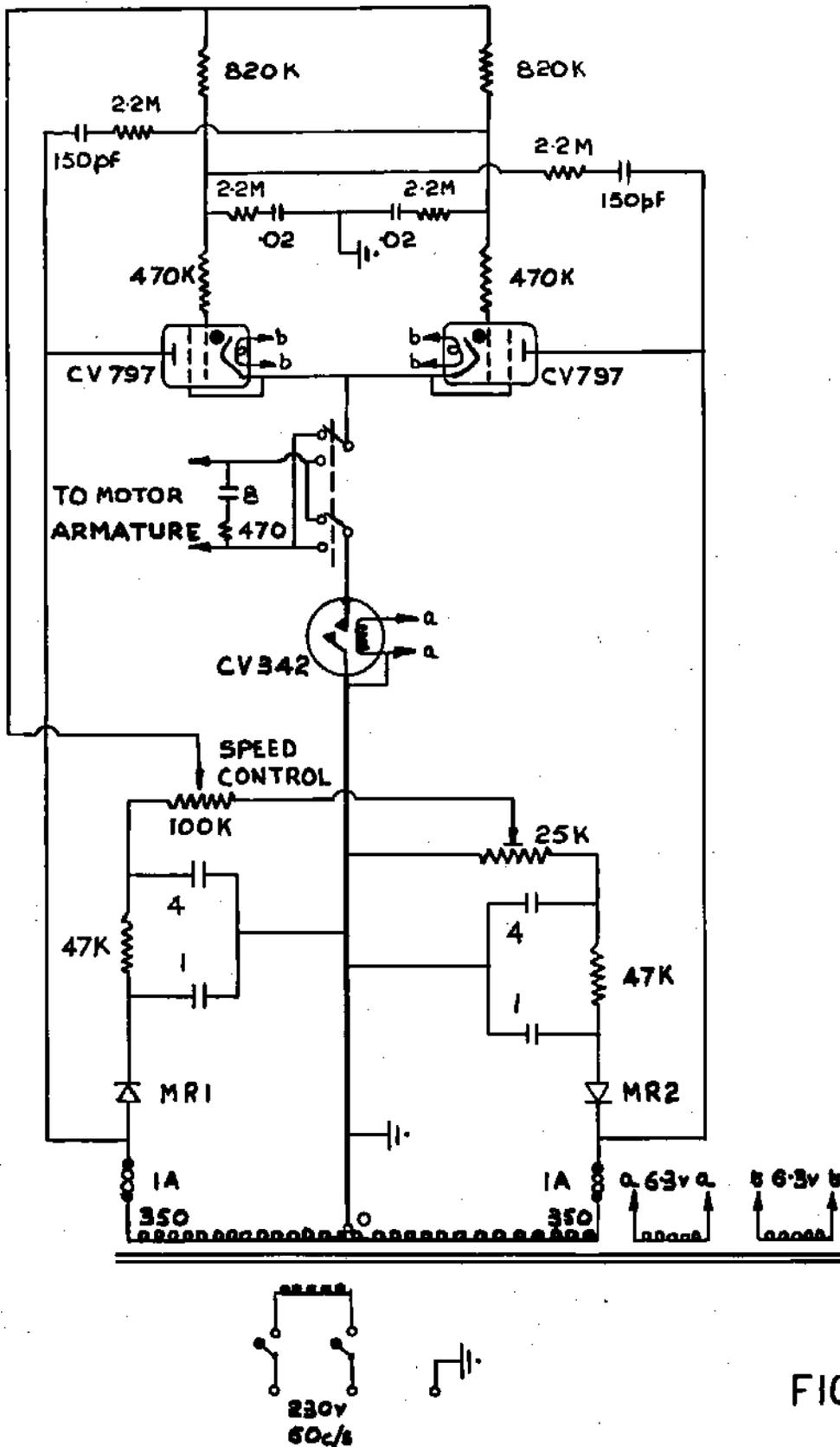
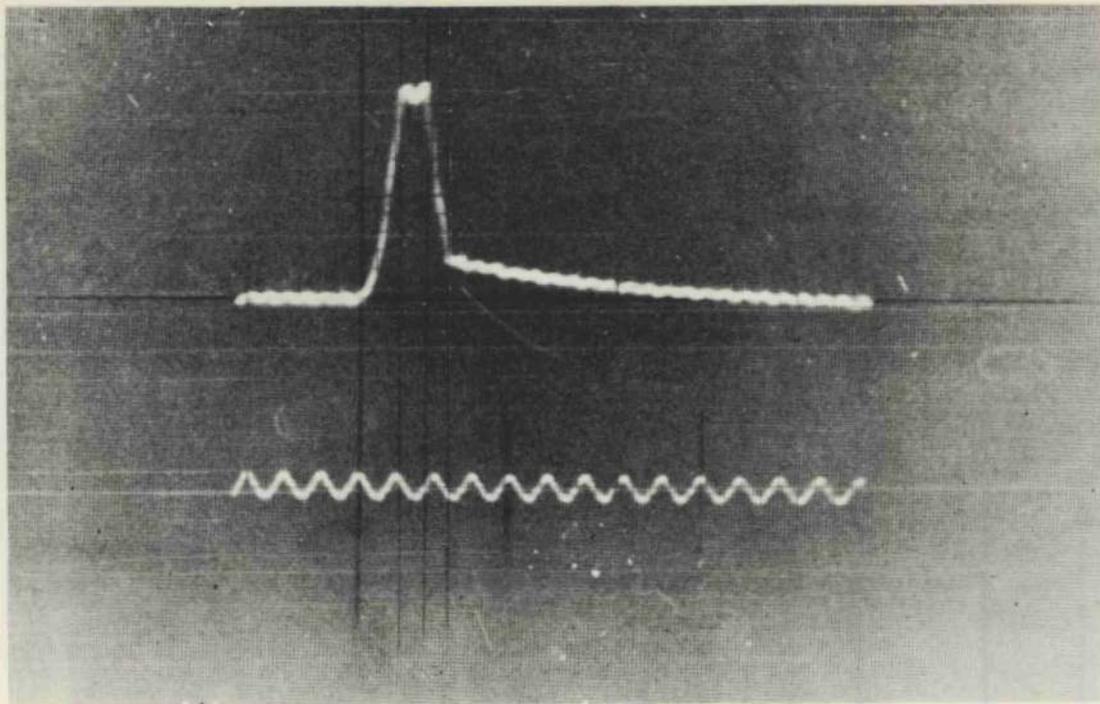
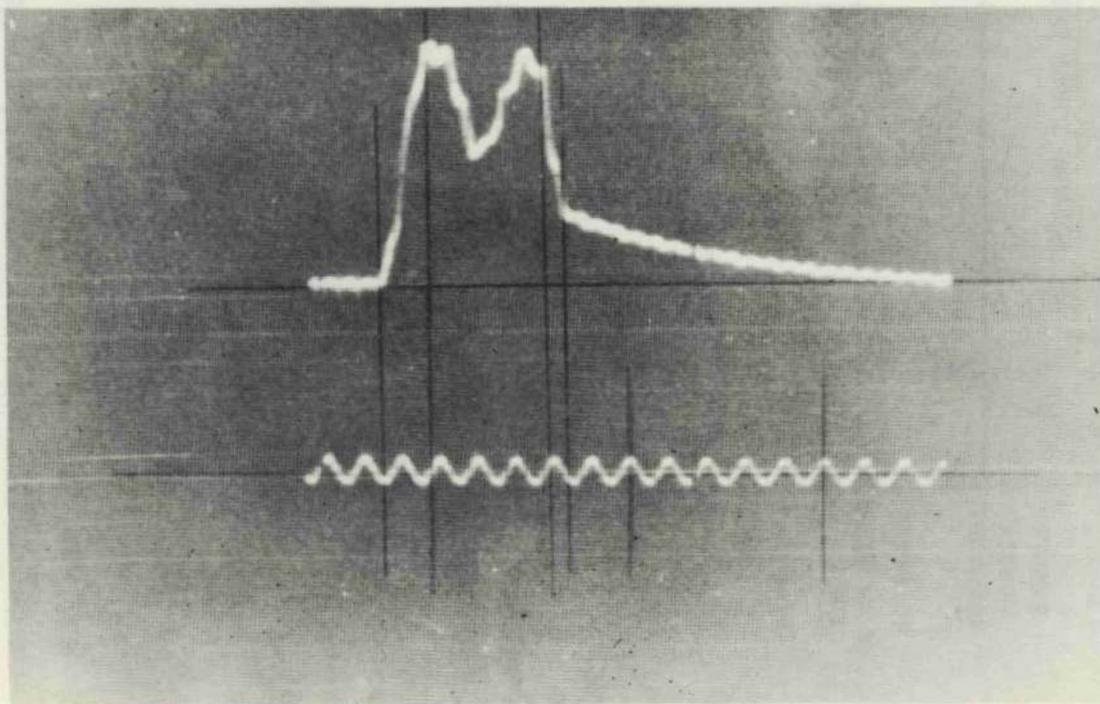


FIG. 5.



$$1\text{mm.} = \frac{100}{22} = 4.54\text{ msec.}$$

$$\begin{aligned} \text{RISE } 4.5 \times 4.54 &= 20.5 \text{ msec.} \\ \text{FULLY OPEN } 3 \times 4.54 &= 13.6 \text{ msec.} \\ \text{FALL } 2.5 \times 4.54 &= 11.4 \text{ msec.} \end{aligned}$$



$$1\text{mm} = \frac{100}{22} = 4.54 \text{ msec.}$$

$$\begin{aligned} \text{RISE } 5.5 \times 4.54 &= 25 \text{ msec.} \\ \text{FULLY OPEN } 13.5 \times 4.54 &= 62 \text{ msec.} \\ \text{FALL } 2 \times 4.54 &= 9 \text{ msec.} \end{aligned}$$

FIG. 4.

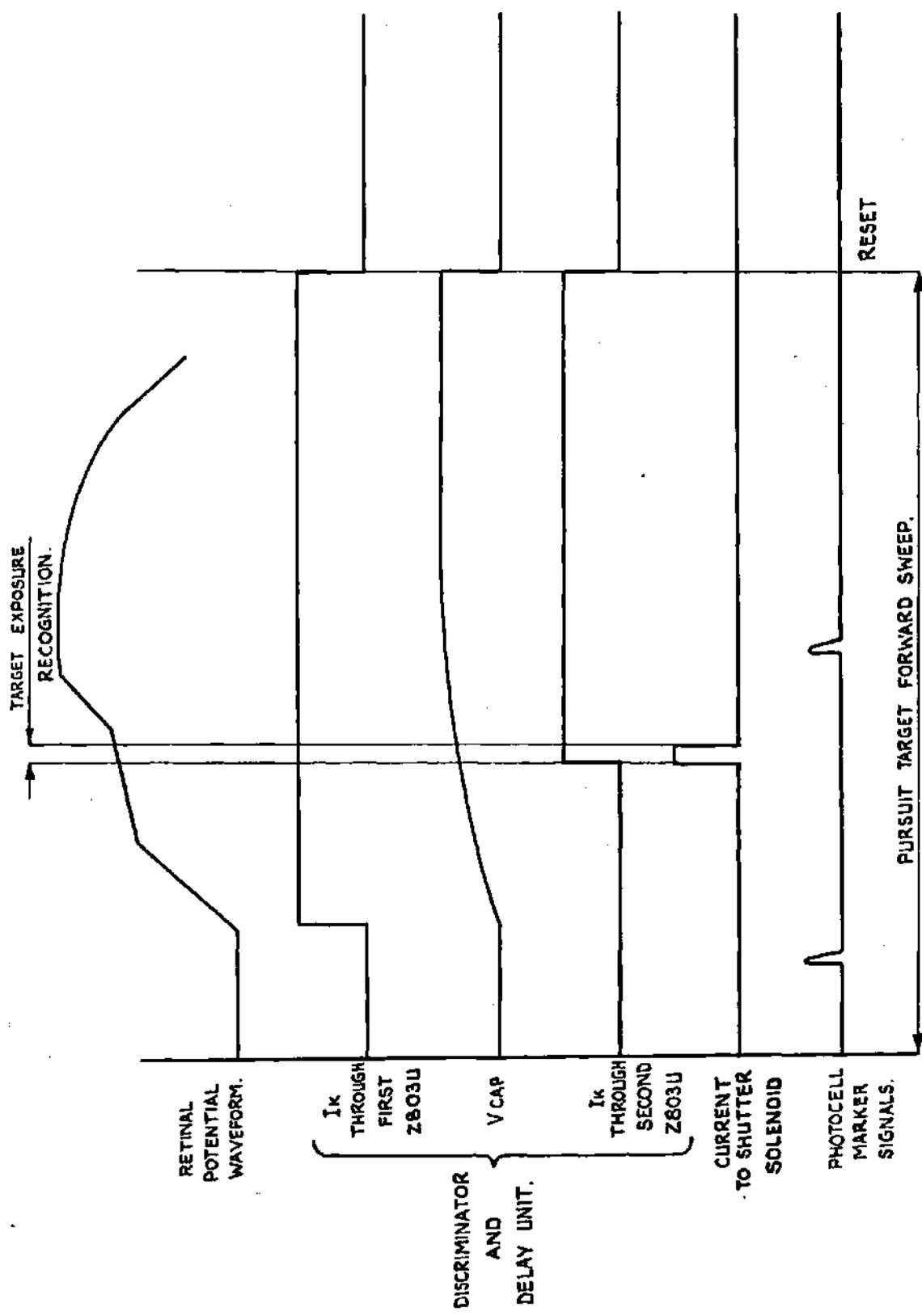


FIGURE 3.

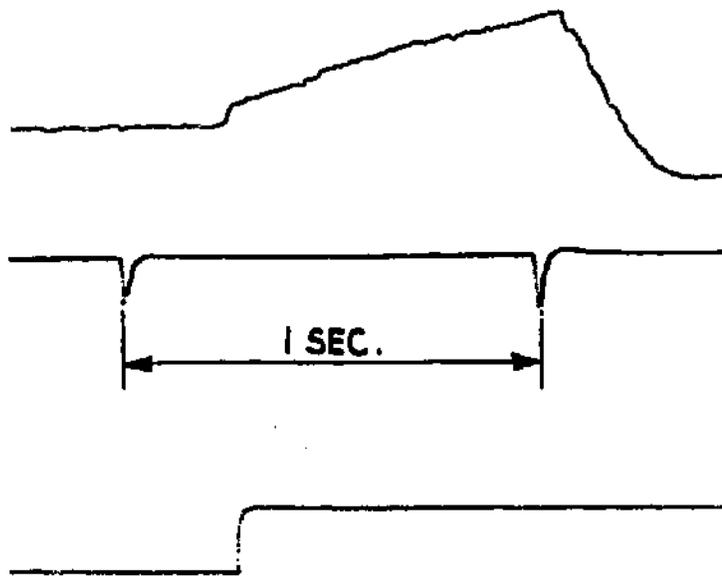


FIG. 2A.

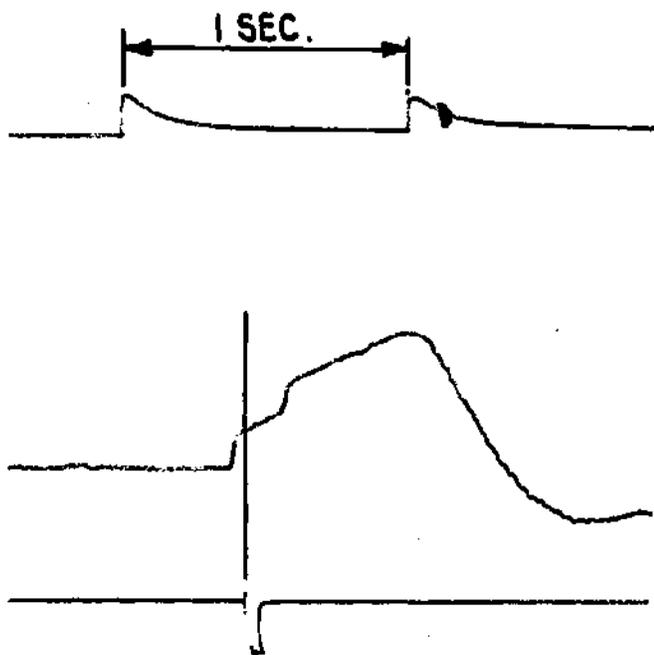
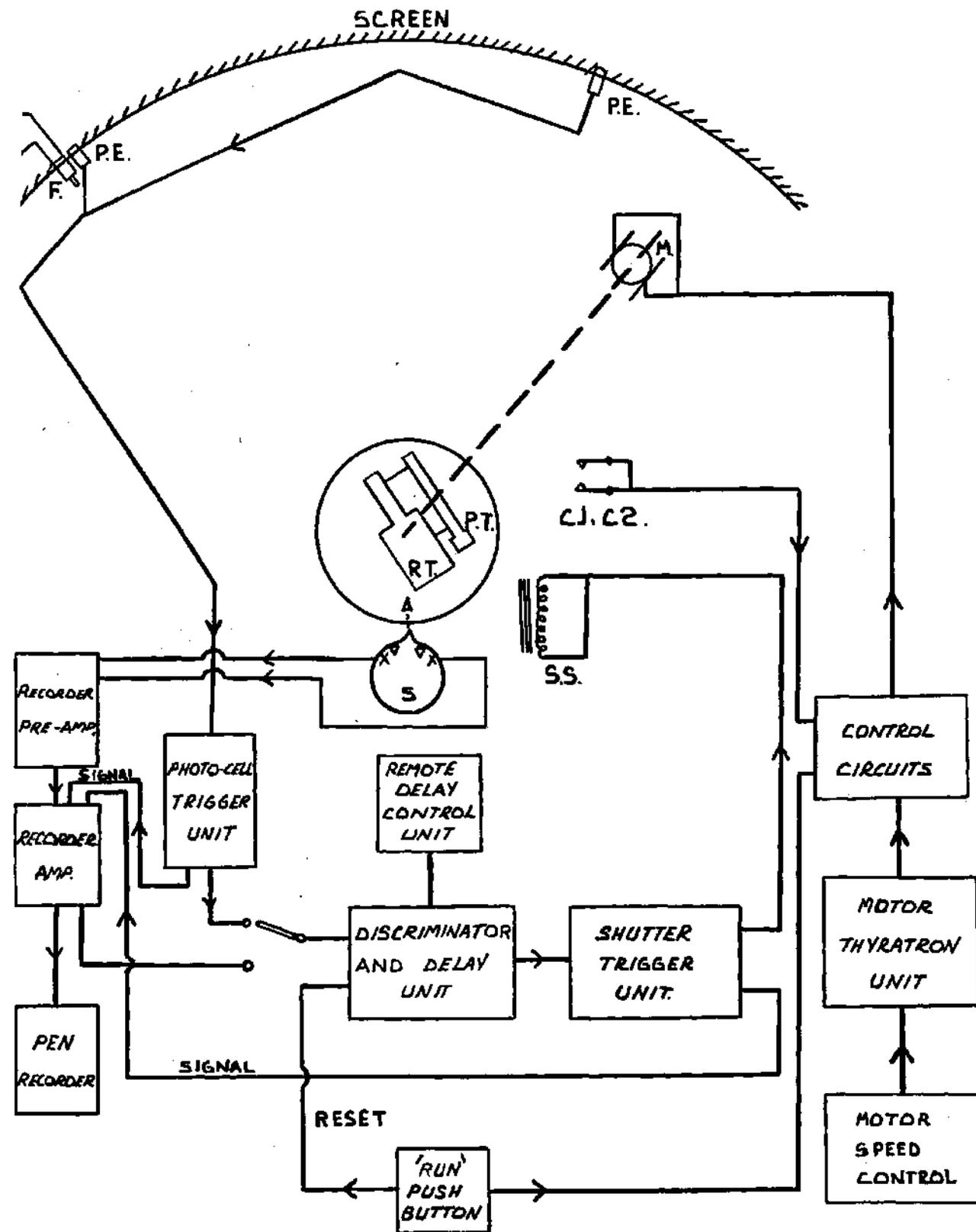


FIG. 2B.



KEY

F, FIXATION LIGHT

M, MOTOR

P E, PHOTOCCELL

PT, PURSUIT TARGET PROJECTOR

RT, RECOGNITION TARGET PROJECTOR

S, SUBJECT

SS, SHUTTER SOLENOID

FIG 1

Appendix BRecent Findings in Receptive Fields

Two recent investigations on receptive fields in the cat's retina are of interest in the fields of research described. Hubel (1959) has recorded from the striate cortex in a freely moving cat and Hubel and Wiesel (1959) in lightly anaesthetised cats, the eyes of which were immobilised by continuous intravenous injection of succinylcholine, a muscle relaxant.

Hubel noted that the great majority of cortical cells gave little or no response to a stimulus which covered most of the visual field but that small spots in a restricted region evoked a brisk response. The responses to a moving light spot often evoked greater responses than a stationary spot. He also reported that some direction effect was present, which was demonstrated by the findings that a moving spot could produce greater responses when moved in one direction than when moved in the opposite direction.

In the second paper Hubel and Wiesel reported on the size and shape of retinal fields in the cat's retina as seen from occipital cortex. The shape and symmetry reported by Barlow (1953) noted at ganglion cell level

was not maintained and fields covering an area of $1^{\circ} \times 4^{\circ}$ ($250/\mu \times 1000/\mu$ on the retina) orientated in the vertical and other planes were found. The fields were of 'on' and 'off' types, were surrounded by an area of the opposite type, and displayed mutual antagonism. Several different patterns and shapes of fields were noted with some having asymmetry of response. Other fields ranged in total size from 4° to 10° .

Patterns of response to moving spots of light were also investigated and some units were found which only responded to moving spots of light. Slit shaped spots of light were used and once again it was noted that the orientation of the slit affected the extent of the evoked response. Of particular interest is their finding of directional selectivity, a field responding strongly when the light spot moved right to left might not respond left to right.

A binocular interaction was noted in some preparations some cortical cells being driven by either eye, sometimes equally effectively, sometimes not. The usual effects of the optic chiasma on the optic nerve pathway was demonstrated. Summation of effects were noted in these preparations, were 'on' and 'off' types, and demonstrated mutual antagonism between 'on' and 'off' areas of these

summating receptor fields.

With moving light spots it was shown that opposite-type areas need not inhibit one another but may actually be mutually reinforcing; a synergism was therefore present.

The findings on receptive fields monocularly or binocularly activated would appear to be related in some way to visual acuity and in particular the superiority of binocular visual acuity as has been shown in the exploratory experiments in this thesis. The synergism of the corresponding retinal fields may also play its part in the perception of movement particularly in the extra foveal areas where visual acuity deteriorates much more rapidly than the perception of movement.

REFERENCES

- Hubel, D.H. (1959). Single unit activity in striate cortex of unrestrained cats. *J. Physiol.* 147, 226-238.
- Hubel, D.H. and Wiesel, T.N. (1959). Receptive fields of single neurones in cat's striate cortex. *J. Physiol.* 148, No.3, 574-591.

REFERENCES

- Adler, F.H. & Fliegelman, M. (1934). Influence of fixation on the visual acuity. Arch. Ophthal., N.Y. 12, 475-483.
- Adrian, E.D., Cattell, Mc.K. & Hoagland, H. (1931) Sensory discharges in single eutaeneous nerve fibres. J. Physiol. 72, 377-404.
- Adrian, E.D. & Mathews, R. (1927a). The action of light on the eye. Part 1. The discharge of impulses in the optic nerve and its relation to electric change in the retina. J. Physiol., 63, 378-414.
- Adrian, E.D. & Mathews, R. (1927b). The action of light on the eye. The processes involved in retinal excitation. J. Physiol. 63, 415.
- Adrian, E.D. & Mathews, R. (1928). The action of light on the eye. The interaction of retinal neurones. J. Physiol. 65, 273.
- Adrian, E.D. & Moruzzi, G. (1940). Impulses in the pyramidal tract. J. Physiol. 97, 153-199.
- Andrew, A.M. (1955). Action potentials from the frog colliculus. J. Physiol. 130, 25P.
- Apter, J.T. (1945). Projection of the retina on the superior collicular of cats. J. Neurophysiol. 8, 123-134.
- Apter, J.T. (1946). Eye movements following strychninisation of the superior colliculus in cats. J. Neurophysiol. 9, 73-86.
- Arden, G.B. & Weale, R.A. (1953). Variation in the latent period of vision. J. Physiol. 122, 12P.
- Arden, G.B. & Weale, R.A. (1954). Latency greater from extra foveal than foveal. Proc. Roy. Soc. (B). 142, 258-267.

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- Armstrong, H.G. (1952). Principles and Practice of Aviation Medicine, 3rd ed. Baltimore: Williams & Wilkins.
- Arner, R.S. (1957). Some visual problems in flight. Amer. J. Optom. 34, 233-240.
- Aubert, H. (1861). Eine scheinbare bedeutende Drehung von Objecten bei neigung des Kopfes nach rechts oder links. Virchows Arch. 20, 381-393.
- Aubert, H. (1887). Die Bewegungsimpfindung zweite mittheilung. A.g. Phys. 40, 459-480.
- Barlow, H.B. (1953a). Actions potentials from the frog's retina. J. Physiol. 119, 58-68.
- Barlow, H.B. (1953b). Summation and Inhibition in the frog's retina. J. Physiol. 119, 69-88.
- Barnes, B. (1905). Eye movements. Amer. J. Psychol. 16, 199-207.
- Barnes, R.W., Ingram, W.R. & Pearson, S.W. (1935). Optic corrections of the diencephalon and mid-brain of the cat. J. comp. Neurol. 62, 117.
- Barraquer-Bordas, L. (1957). Control sufranuclear de la motilidad ocular. Rev. esp. oto. Neuro. oftal. 16, 344-355, 442-462.
- Bartley, S.H. (1941). Vision - A Study of its Basis. London: Van Nostrand.
- Basler, A. (1906). Uber das Sehan van Bewegungen. Pflug. Arch. ges. Physiol. 115, 582-601.
- Bechterew, V.M. (1899). Cited by Smith, W.K. in The Precentral Motor Cortex 1944 Ed. P. Bucy. Illinois Monographs in Medical Science. Vol. IV. Univ. Illinios Press.
- Benchimal, R. & Sebas, S.R. (1952). The human eye at high speeds. Rev. med. Aeronaut. 4, 113-118.

- Bender, M.B. (1955). Eye centering system - theoretical considerations. Chicago Arch. Neurol. & Psychiat. 73, 685-699.
- Bender, M.B., Kruger, P. & Pastyl, D.M. (1957). Disorders of ocular motor functions in lesions of the occipital lobe. J. Neurol. 20, 139-143.
- Berens, C. & Sheppard, L. (1953). Abstracts on Military and Aviation Ophthalmology and Visual Sciences. Vols 1-2. Washington: The Biological Sciences Foundation.
- Bhatia, B. (1957). Eye movement patterns in response to moving light. J. Aviat. Med. 28, 309-317.
- Bishop, G.M. (1958). A second look at the sensory systems, end organs to cortex. Office of Naval Research. U.S.N. Symposium Report A.C.R.30, 77-86.
- Bishop, G.M. & Clare, M.H. (1955). Organisation and distribution of the fibres in the optic trail of the cat. J. comp. Neurol. 103, 269-304.
- Bjork, A. & Kukelberg, E. (1953). Morot unit activity in the human extraocular muscles. Electrical activity of the human eye muscles. Electrâncph. & Clin. Neurophysiol. 5, 271, 595.
- Bourdon, B. (1902). La perception visuel de l'espace. Paris Libraire-C. Reinwald.
- Breinen, G.M. (1958). Analytic studies of the electromyogram of human extraocular muscles. Amer. J. Opthal. 46, 123-142.
- Van den Brink, G. (1958). Retinal summation and the visibility of moving objects. Pub. National Council for Scientific Research. Netherlands.
- Brown, Graham, T. (1922). Reflex orientation of the optical areas and the influence upon it of the cerebral cortex. Arch. neerl. Physiol. 7, 571-578.
- Brown, J.F. (1931a). The visual perception of velocity. Psychol. Forsch. 14(3-4), 199-232.

- Brown, J.F. (1931b). The thresholds for visual movement. *Psychol. Forsch.* 14(3-4), 249-268.
- Brown, J.F. (1931 c). One time perception in visual movement fields. *Psychol Forsch.* 14(3-4), 233-248.
- Brown, J.F. (1939). The dynamics of visual speed time and space. (A reply to Cartwright, Kaekler & Wallack). *Amer. J. Psychol.* 8, 237-246.
- Brown, G.S. & Cambell (1948). Principles of Servomechanisms. New York: Wiley.
- Brown, R.H. & Conklen, J.E. (1954). The lower threshold of visible movement as a function of exposure time. *Amer. J. Psychol.* 67, 104-110.
- Brown, J.F. & Voth, A.C. (1937). The path of seen movement as a function of the vector field. *Amer. J. Psychol.* 48, 543-563.
- Buser, P. & Dusardier, M. (1953). Organisation des projections de la retine sur le lobe optique, etudiee chez quelques teleosteans. *J. Physiol. Path. gen.* 45, 57-60.
- Carmichael, L. & Dearborn, W.F. (1948). Reading and Visual Fatigue. London: Harrap.
- Clark, W.E., Le Gros. (1944). A discussion of the visual pathways. *Proc. Roy. Soc. Med.* 37, 392-394.
- Cobb, W. & Dawson, G. (1959). Personal communication on retina-cortical delay.
- Cooper, E.A.A. (1946). Accessary optic tracts in the human foetus. *Brain.* 69, 45-49.
- Cooper, S. & Daniel, P.M. (1949). Muscle spindles in human extrinsic eye muscles. *Brain* 72, 1-24.
- Cooper, Sybil, Daniel, P.M. & Whitteridge, D. (1951). Afferent impulses in the oculomotor nerve from the extrinsic eye muscles. *J. Physiol.* 113 No. 4, 463-474.

- Cooper, Sybil, Daniel, P.M. & Whitteridge, D. (1953a).
Nerve impulses in the brainstem of the goat.
Short latency responses obtained by stretching
the extrinsic eye muscles and the jaw muscles.
J. Physiol. 120, 4, 471-490.
- Cooper, Sybil, Daniel, P.M. & Whitteridge, D. (1953b).
Nerve impulses in the brainstem of the goat.
Responses with long latencies obtained by
stretching the extrinsic eye muscles.
J. Physiol. 120, 4, 491-513.
- Cooper, Sybil, Daniel, P.M. & Whitteridge, D. (1953c).
Nerve impulses in the brainstem and cortex of the
goat. Spontaneous discharges and responses to
visual and other afferent stimuli.
J. Physiol. 120, 4, 514-527.
- Cooper, Sybil, Daniel, P.M. & Whitteridge, D. (1954).
Afferent impulses from muscle spindles of extrinsic
eye muscles and their course with the brainstem.
Trans. Opthal. Soc. U.K. 74, 435-440.
- Cooper, Sybil, Daniel, P.M. & Whitteridge, D. (1955).
Muscle spindles and other sensory endings in and
extrinsic eye muscles - physiology and anatomy of
those receptors and of their connections with
the brainstem. Brain. 78, 564-583.
- Cooper, S. & Eccles, J.C. (1930). Isometric responses
of mammalian muscles. J. Physiol. 69, 377.
- Craik, K.J.W. & Vernon, M.D. (1941). The nature of dark
adaptation. J. Psychol. 32, 62-81.
- Crawford, W.A. (1958). Visual acuity, eye movements
and head-eye movement integration. J. Physiol.
145, 50-51 P.
- Crawford, B.H. & Stiles, W.S. (1933). Efficiency of
rays entering the eye pupil. Proc. Roy. Soc. B.
112, 428-450.
- Creed, R.S. & Granit, R. (1933). Observations on the
retinal action potential and special reference to
the response to intermittent stimulation.
J. Physiol. 78, 419-441.

- Daniel, P. (1946). Spiral nerve endings in the extrinsic eye muscles of man. *J. Anat. Lond.* 80, 189.
- Dawson, G. (1958). Personal communication on delay in retina and time to cortical evoked potentials from light stimulation.
- Diefendorf, A.R. & Dodge, R. (1908). An experimental study of the ocular reactions of the insane from photographic records. *Brain*, 31, 451.
- Dimmick, F.L. & Scahill, H.G. (1925). Visual perception of movement. *Amer. J. Psychol.* 36, 412-417.
- Dimmick, F.L. & Sanders, R.W. (1929). Some conditions on the perception of visible movement. *Amer. J. Psychol.* 41, 607-616.
- Ditchburn, R.W. & Ginsborg, B.L. (1953). Involuntary eye movements during fixation. *J. Physiol.* 119, 1.
- Ditchburn, R.W. & Ginsborg, B.L. (1952). Vision with a stabilized retinal image. *Nature, Lond.* 170, 4314, 36-37.
- Dodge, R. (1903). Five types of eye movement in the horizontal meridional plane of the field of regard. *Amer. J. Physiol.* 8, 307-329.
- Dodge, R. (1907). An experimental study of visual fixation. *Psychol. Monograph.* 8, 1-95.
- Dodge, R. (1921). The registration of compensatory eye movements. *Psychol. Bull. N.Y.* 8, 75.
- Dodge, R. & Eline, T.S. (1901). The angle velocity of eye movements. *Psychol. Rev.* 8, 145-157.
- Donders, F.C. (1865). *Die physiologische tyd by psychische processen.* Utrecht.
- Duke Elder, w.S. (1944). *Textbook of Ophthalmology.* Vol. 1. P. 285 Central connections of oculomotor system, p. 615 Visual field and fixation, p. 620 Velocity of voluntary eye movements, p. 1085 Perception of movement. London : Kimpton.

- Duke Elder, S., Neely, J.C. & Riddell, W.J.B. (1953).
Visual requirements in relation to modern travel.
Trans. Ophthal. Soc. U.K. 73, 237-351.
- Eason, R.E. & Hyde, J.E. (1957). A sub-cortical control
of eye movements. American Psychologist, 12, 466.
- Eurich, A.C. (1933). The reliability and validity of
photographic eye movements records. J. educ.
Psychol., 24, 118-122.
- Exner, S. (1868). Über die zur Gesichtswahrnehmung noetigi
zeit. Sitzungberichte d. Wiener Academie d.
Wissenschaften. 58. Abt. 2. 601.
- Faulkner, R.F. and Hyde, Jane E. (1958). Co-ordinated
eye and head movements evoked by brainstem stimulat-
ion in decerebrated cats. J. Neurophysiol. 21, No.
2. 171-183.
- Faure, J. & Corcelle, L. (1955). The experimental study
of certain aspects of visual perception. Ocular
movements of re-adjustment follow cortical occipital
responses. Rev. Oto. Ophthal. 27, 186.
- Ferrier, C. (1886). The Functions of the Brain.
New York : Putnams.
- Fielchenfeld, H. (1903). Zur Lageschätzung bei seitlicher
Kopfneigung. Z. Psychol. 31, 127-150.
- Fillenz, Marianne. (1955). Responses in the brainstem
of the cat to stretch of extrinsic ocular muscles.
J. Physiol. 128, 182-199.
- Fleischl, E. von. (1882). Sitz. Wien. IXXXVI, 8.
- Fritsch, G. & Hitzig, E. (1870). Über die elektrische
Erregbarkeit des Grosshirne. Arch. f. Anat.,
Physiol. Lpz. p.300.
- Froëlich, F.W. (1929). Die Empfindungszeit. Ed. 1.
Jena : Fischer.
- Gastaut, H., Alvim-Costa, C., Gastaut, Y. and Alvim-Costa
M.R. (1957). Mecanisme des potentiels occipitaux
evoque par les mouvements saccades des yeux.
Acta. Physiol. pharmacol. neerl. 6, 515-525.

- Gemelli, A. (1958a). The visual perception of movement. Arch. Psicol. Neurol. Psychiat. 14, 3-12.
- Gemelli, A. (1958b). The visual perception of movement. Amer. J. Psychol. 71, 291-297.
- Gibson, G.J. (1952). The relation between visual and postural determinants of the phenomenal vertical. Psychol. Rev. 59, 370-375.
- Gibson, J.J. (1958). Visual perception of motion and change. O.N.R. Dept. of U.S. Navy. Report A.C.R. 30, 165-175.
- Gibson, J.G. & Mowrer, O.H. (1938). Determinants of the perceived vertical and horizontal. Psychol. Rev.
- Gibson J.G. & Radner, M. (1937). Adaptation, after effects and contrast in the perception of tilted lines. I. Quantitative studies. J. Expt. Psychol. 20, 454-467.
- Ginsborg, B.L. (1953). Small voluntary movements of the eye. Brit. J. Opthal. 37, 12, 746.
- Glees, M. (1953). Eine Methode zur Elektromyographie der Augensmuskeln. Ber. dtsh.Opthal. 58, 307.
- Graham, C.H. & Hunter, W.S. (1931). Thresholds of illumination for the visual discrimination of direction of movement and for the discrimination of discreteness. J. gen. Psychol. 5, 178-190.
- Granit, R. (1955). Receptors and Sensory Perception. Yale Univ. Press.
- Granit, R., Holmgren, B. & Merton, P.A. (1955). The two routes for excitation of muscle and their subservience to the cerebellum. J. Physiol. 130, 213-224.
- Hamdi, F.A. & Whitteridge, D. (1953). The representation of the retina on the optic lobe of the pigeon and the superior colliculus of the rabbit and goat. J. Physiol. 121, Vol.2, 44p.

- Hamdi, F.A. & Whitteridge, D. (1954). The representation of the retina on the optic tectum of the pigeon. *Quart. J. exp. Physiol.* 39, 111-119.
- Hartline, J. (1940a). The receptive field of the optic nerve fibres. *Amer. J. Physiol.* 130, 690-699.
- Hartline, J. (1940c). The nerve messages in the fibres of the visual pathway. *J. opt. Soc. Amer.* 30 239-247.
- Hartridge, H. (1950). *Recent Advances in Vision Physiology*. London: Churchill.
- Hartridge, H. & Thomson, L.C. (1948). An eye movement recording system. *J. Physiol.* 107, No. 4, 25 P.
- Helmholtz, von H. (1851). *Koenigsberger Naturwiss.* Abt. 2, 169.
- Helmholtz, von H. (1867). *Handbuch der Physiologischen Optik*. Leipzig: Voss. Translation 1925 by J.P.C. Southall, Vol. 3, Sect. 29, p.242. *Opt. Soc. Amer.*
- Hines, M. (1947). The motor areas. *Fed. Proc.* 6 No. 2, 441-448.
- Hodgson, F. & Mary P. Lord. (1954). Measurement of eye movements accompanying voluntary head movements. *Nature.* 174, 75.
- van Hoff, M.W. (1958). Response of human visual cortex to intermittent photic stimulation of the retina. *Acta Physiol. pharmacol. neerl.* 7, 272-276.
- Hoffman, A.C., Wellman, B. & Carmichael, L. (1939). A quantitative comparison of the electrical and photographic techniques of eye movement recording. *J. exp. Psychol.* 24, 40-53.
- Holmes, G. (1936). Looking and seeing. *Irish J. med. Sci.* 192, 12.
- Holmes, G. (1930). Spasms of fixation. *Fr. Ophthal. Soc.* 50, 253-262.

- Holmes, G. (1938). The cerebral integration of ocular movements. *Brit. Med. J.* 2, 107-112.
- Hopkins, V.D. (1959) Peripheral vision - a review. *Brit. F.P.R.C. No.* 1078.
- Irving, S.R. & Ludvigh, E. (1936). Is ocular proprioceptive sense concerned in vision? *Arch. Opthal.* 15, 1037.
- Janes Annual Editions. (1913-58). Janes All the World's Aircraft, supplied by Samson, Low, Marston & Co. London.
- Kafka, M.M. (1955). The aviator's eye problems. *Med. Times Great Neck.* 83, 502-506.
- Kovacs, A. (1922). Über den Einfluss d. Dunkeladaption auf die Empfindungszeit und den Zeitz. Verlauf der Gesichtsempfindung. *Zeitschr. f. Sinnesphysiologie.* 54, 161.
- Kreiger, H.P., Wagner, I.H. & Bender, M.B. (1955). Eye movements obtained from subcortex of occipital cortex. *Trans. Amer. Neurol. A.* 80, 209-212.
- Kuffler, S.W. (1952). Neurons in the retina, organisation, inhibition and excitation problems. *Cold Spr. Harb. Symp. quant. Biol.* 17, 281-292.
- Kuffler, S.W. (1953). Discharge patterns and functional organisation of mammalian retina. *J. Neurophysiol.* 16, 37-68.
- Langmuir, I. (1938). The speed of the deer fly. *Science* 87, 233.
- Lashley, K.S. (1929). *Brain Mechanisms and Intelligence.* Univ. of Chicago Press.
- Lashley, K.S. (1931). Mass action in cerebral function. *Science.* 73, 245-254.
- Lashley, K.S. (1934). Studies of the cerebral function in learning. *J. comp. Neurol.* 74, 431-462.

- Low, F.N. (1943). The peripheral visual acuity of 100 subjects. Amer. J. Physiol. 140, 83-88.
- Low, F.N. (1946). The effect of training on acuity of peripheral vision. Civil Aeronautics Admin. Div. of Res. Rep. 68, 1-94.
- Low, F.N. (1946a). The peripheral visual acuity of 100 subjects under scotopic conditions. Amer. J. Physiol. 146, 21-25.
- Low, F.N. (1946b). Some characteristics of peripheral visual performance. Amer. J. Physiol. 146, 573-584.
- Low, F.N. (1946c). The development of peripheral visual acuity during the process of dark adaptation. Amer. J. Physiol. 146, 622-629.
- Low, F.N. (1947). The peripheral motion acuity of 50 subjects. Amer. J. Physiol. 148, 124-133.
- Low, F.N. (1947b). Peripheral visual acuity of 55 subjects under conditions of flash presentation. Amer. J. Physiol. 151, 319-324.
- Low, F.N. (1950). Peripheral visual acuity. O.N.R. Navy Dept. Washington.
- Ludvigh, E.J. (1941). Effect of reduced contrast on visual acuity as measured with Snellen test letters. Arch. Opthal. N.Y. 25, 469.
- Ludvigh, E.J. (1947). The visibility of the deer fly. Science, 105, 176-177.
- Ludvigh, E.J. (1948). The visibility of moving objects. Science. 108, 63-65.
- Ludvigh, E.J. (1949). Visual acuity while one is viewing a moving object. Arch. Opthal. N.Y. 42, 14-22.
- Ludvigh, E.J. (1952). Possible role of proprioception in the extraocular muscles. Arch. Opthal. N.Y. 48, 436.

Ludvigh, E.J. (1952). Control of ocular movements and visual interpretation of the environment. Arch. Ophthal., N.Y. 48, 442.

Ludvigh, E.J. (1953). Direction sense of the eye. Amer. J. Ophthal. 36, 139-143.

Ludvigh, E.J. (1953b). The influence of dynamic visual acuity on the visibility of stationary objects, viewed from an aircraft flying at constant altitude, velocity and direction. U.S.N. Sch. Av. Med. Proj. 001.075.01.0.

Ludvigh, E.J. (1955). Sumposium on physiological psychology. O.N.R. Symposium Report A.C.R. 1. March. 10. 130.

Ludvigh, E.J. (1955). Transfer of training of dynamic visual acuity. U.S. Nav. Sch. Av. Med. Joint Report No. 9, BuMed. Res. Proj. No. NM.001.075.01.09.

Ludvigh, E.J. & Miller, J.W. (1953). A study of dynamic visual acuity. U.S. Nav. Sch. Av. Med. Joint Report No. 1, BuMed Res. Proj. No. NM 001.075.01.

Ludvigh, E.J. & Miller, J.W. (1953). Dynamic visual acuity when the required pursuit movement of the eye is in a vertical plane. U.S.N. S.A.M. BuMed. Res. Proj. NM.001.075.01.02.

Ludvigh, E.J. & Miller, J.W. (1954). Some effects of training on dynamic visual acuity. U.S. Nav. Proj. No. NM.001.075.01.06.

Ludvigh, E.J. & Miller, J.W. (1954). An analysis of dynamic visual acuity in a population of 200 Naval Aviation Cadets. U.S. Nav. Sch. Av. Med., Joint Report No. 7, BuMed Res. Proj. No. NM.001.075.01.07,X.

Lyle, D.J. (1954). Neurophthalmology. Springfield, Illinois : Chas. C. Thomas.

Mc. Farland, R.A. (1953). Human Factors in Air Transportation. New York : Mc.Graw-Hill.

- Magee, A.J. (1956). The electromyogram of the lateral rectus muscle. *Amer. J. Ophthalm.* 41, No.2, 275-285.
- Makensen, G. (1958). Velocity of horizontal eye movements. *Albrecht. v Graefes Arch. Ophthalm.* 160, 47-64.
- Maldaver, J. & Breinen, G.M. (1956). Electromyography of the extra ocular muscles in man. *Trans. Amer. Neurol. Assoc.* 81st meeting, 141-144.
- Mandelbaum, J & Sloan, L.L. (1947). Peripheral visual acuity. *Amer. J. Ophthalm.* 104, 384-391.
- Mann, C.W. (1951). The effects of auditory-vestibular nerve pathology on space perception. *J. Expt. Psychol.* 42, No.6, 450-456.
- Mann, C.W. (1952). Visual factors in the perception of verticality. *J. Exp. Psychol.* 44, 460-464.
- Mann, C.W., Berry, N.H.B. & Dauterine, H.J. (1949) The perception of the vertical. 1. Visual and labyrinthine cues. *J. exp. Psychol.* 39, 538-547.
- Mann, C.W. & Passey, G.E. (1951) The perception of the vertical. V. Adjustment to the postural vertical as a function of the magnitude of postural tilt and duration of exposure. *J. exp. Psychol.* 41, No.2, 108-113.
- Marg, E. (1951). Development of electro-oculography: standing potential of the eye in registration of eye movements. *Arch. Ophthalm., N.Y.* 45, 169.
- Merton, P.A. (1956). Compensatory rolling movements of the eyes. *J. Physiol.* 132, No.2. 26P.
- Merton, P.A., Hammond, P.H. & Sutton, G.G. (1956). Nervous gradation of muscular contraction. *Brit. Med. Bull.* 12, No. 3, 214-218.
- Miller, J.W. (1956). The effect of altered illumination on visual acuity measured during ocular pursuit. U.S. Nav. Sch. Av. Med. Joint Project NM 001.110 Report No. 12.

- Miller, J.W. (1959). The effect of duration of observation upon the ability to perceive a rapidly moving target. U.S. Nav. Sch. Av. Med. Report No. 2. Project NM 17.01.11. Subtask 2.
- Miller, J.W. & Ludvigh, E.J. (1953) Dynamic visual acuity when the required pursuit movement of the eye is in a vertical plane. U.S. Nav. Sch. Av. Med. Joint Report No. 2. BuMed Res. Proj. No. NM 001.075.01.02.
- Momosse, H. (1958). Studies on the action of ocular muscles by integrated electromyography. Acta. Soc. Ophthal. jap. 62, 869-876.
- Monnier, M. (1952). Retinal cortical and motor responses to photic stimulation. J. Neurophysiol. 15, 469-486.
- Monnier, M. & Jeanneret, O. (1947). Controle objectif de la conductabilite des voies optiques centrales par l'electroretinographie et l'electroencephalographie combinees. L'Ophthalmologia Basle.
- Neff, W.S. (1936). A critical investigation of the visual apprehension of movement. Amer. J. Psychol. 48, 1-42.
- Noell, W. & Chinn, H. (1950). The effects of anoxia on the retina and optic pathways. U.S.A.F. Sch. Av. Med. Proj. 21.02.111.
- Passey, G.E. (1950a). The perception of the vertical. LV. Adjustment to the vertical with normal and tilted frames of reference. J.exp. Psychol. 40, No.6, 738-745.
- Passey, G.E. (1950b). The perception of the vertical. IX. Adjustment of the visual vertical from various magnitudes of body tilt. U.S. Sch. Av. Med. & Tulose Univ. Joint Report No. 15.
- Passey, E. & Guedry, E.G. (1949). The perception of the vertical. 11. Adaptation effects in four planes. J. exp. Psychol. 39, No. 5, 700-707.

- Penfold, W. & Raimussen, T. (1947). Further studies of the sensory and motor cortex of man. Fed. Proc. 6 No.2, 453.
- Pieron, H. (1925). Recherches experimentales sur la marge de variation du temps de latence de la sensation lumineuse. L'annee Psychol. 26, 1.
- Polyak, S. (1941). The Retina. University of Chicago Press.
- Pulfrich, C. (1922). Die Stereoskopi im dienste der isochromen und heterochromen photometric. Naturwissenschaften 10, 25.
- Rademaker, G.G. & Ter Brack, J.W.G. (1948). On the central mechanism of some optic reactions. Brain, 71, 48-75.
- Ratliff, F. Riggs, L.A., Cornsweet, Janet C. & Cornsweet, T.N. (1953). Involuntary eye movements during fixation. J. opt. Soc. Amer. 43, No.6, 495-501.
- Riggs, L.A. (1958). Visual effects of minimal eye movement. O.N.R. Dept. of U.S. Navy. Rep. A.C.R. 30.
- Riggs, L.A. & Ratliff, F. (1951). Visual acuity and the normal tremor of the eye. Science, 114, 17-18.
- Rios Sasiain, M. (1955). Problemas de oftalmologia aeronautica. Arch. Soc. Oftal. hisp-amer. 15, 1333-1346.
- Ruch, T.C. (1951). Handbook of Experimental Psychology. Ed. H.S. Langfield. London : Chapman & Hill.
- Sakiyama, A. (1953). Summation of visual acuity by binocular vision. Acta. Soc. ophthal. jap. 57, 575-577. from Ophthal.Lit. Vol. 7, No.4, 1953.
- Salaman, M. (1929). Some experiments on peripheral vision. Med. Res. Council Sh. Rep. No. 136.
- Saucer, R.T. (1954). Processes of motion perception. Science, 120, 806-807.

- Sedan, J., Joyle, G.E. & Farnarier, G. (1957).
De la superiorite de l'acuitee visuelle
binoculaire sur l'acuitee visuelle monoculaire.
Ann. Oculist (Paris) 190, 385-400.
- Sherrington, C.S. (1894). An experimental on two movements
of the eyes. J. Physiol. 17, 27-29.
- Sherrington, C.S. (1918). Observations on the sensual
role of proprioceptive nerve supply of extrinsic
ocular muscles. Brain 41, 332.
- Silver, H.R. de (1929). An analysis of the visual
perception of movement. J. Psychol. 19, 268-305.
- Slater-Hammel, A.T. (1955). Reaction time to light
stimulus in peripheral visual field.
Res. Quart. 26, 82-87.
- Smith, W.K. (1944). The Frontal Eye Fields. Vol. 4
Chpt. 12. The Precentral Motor Cortex. Ed. P.C.
Bucy. Illinois Monographs in Medical Sciences.
Univ. Illinois Press.
- Smith, W.M. & Gulick, W.L. (1956). Visual contour
and movement perception. Science 124, 316-317.
- Snider, R.S. (1950). Recent contributions to the
anatomy and physiology of the cerebellum.
Arch. Neurol. Psychiat. Chicago. 64, 196-219.
- Snider, R.S. & Stowell, A. (1942). Evidence of the
projection of the optic system to the cerebellum.
Anat. Rec. 82, 448.
- Snider, R.S. & Stowell A. (1944). Electro anatomical
studies in a tactile system in the cerebellum of
the monkey. Anat. Rec. 88, 457.
- Snider, R.S. & Stowell, A. (1944). Receiving areas
of the tactile, auditory and visual systems in
the cerebellum. J. Neurophysiol. 7, 331-358.
- Stromberg, E.L. (1942). The reliability of monocular
photography in the investigation of reading.
J. educ. Psychol. 33, 118-127.

- Strughold, H. (1949). The human time factor in flight. The latent period of optical perception. *J. Aviat. Med.* 20, 300-307.
- Strughold, H. (1951). The human time factor in flight. Unnumbered project. U.S.A.F. Sch, Aviat. Med. Jan.
- Szentahothai, J. (1952). Die Rolle der einzelnen Labryinthrezeptoren bei der Orientation von Auge und Kopf im Raume. *Kultura*, Budapest.
- Teuber, H.L. & Bender, M.B. (1951). Neuro-ophthalmology The oculomotor system. *Prog. Neurol. Psychiat.* 6, 148-178.
- Thomson, L.C. (1953). The localisation of function in the rabbit retina. *J. Physiol.* 119, 191-209.
- Walls, G.L. (1943). Factors in human visual resolution. *J. opt. Soc. Amer.* 33, 487-505.
- Wang, G.-H. & Lu, T.-W. (1936). Action potentials in visual cortex and superior colliculi induced by shadow movement across the visual field. *Chin. J. Physiol.* 10, 149-170.
- Warren, C.J. (1946). An investigation of motion acuity under scotopic conditions at various retinal positions. Dept. Psych. Columbia Univ. NRC. Rep. No. 182.
- Warren, C.J. & Brown, H.C. (1944). A preliminary investigation of form and motion acuity at low levels of illumination. *J. exp. Psychol.* 34 437-449.
- Wertheim, T.H. (1894). Uber die indireckte Schscharpe. *Zfsch. f. Psychol. u. Physiol. der Sinnesorgane* 7, 172-187.
- Westheimer, G. (1954a). Eye movement responses to horizontally moving stimuli. *Arch. Ophthal. N.Y.* 52, 932-941.
- Westheimer, G. (1954b). Mechanism of saccadic eye movements. *Arch. Ophthal. N.Y.* 52, 710-724.

- Whiteside, T.C.D. (1957). The Problems of Vision in Flight at High Altitude. London : Butterworths Scientific Publications.
- Whitteridge, D. (1955). Servo mechanisms and problems of human behaviour. Proc. Roy. Soc. 24 Part 1, 15-16.
- Wirth, A & Zetterström, B. (1954). The effect of area and intensity on size and shape of the electroretinogram. Brit. J. Ophthal. 38, 257-265.
- Wulfeck, J.W., Weisz, A. & Radin, Margaret, W. (1958). Vision in military aviation. WADC. Tech. Rep. 58-399, ASTIA Doc. No. AD 207780.
- Wundt, W. (1911). Physiol. Psychologie. 6 Aufl 3.

VISUAL ACUITY AND MOVING OBJECTS

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A Summary of a Thesis for the degree of Ph.D.

This study was undertaken to describe the ability of man to see detail in objects which have an angular velocity relative to the observer. In flight all objects viewed beyond the physical parameters of the aircraft have an angular velocity relative to the pilot or passengers. A loss of visual acuity was anticipated and has been shown to occur, and an attempt has been made to examine the functions of the oculomotor system to discern the aetiology of this loss. An appreciation of the practical significance of the loss of visual acuity to aviation was made by trials conducted as the pilot of fast low flying jet aircraft in service in the Royal Air Force.

The ability to perceive detail in moving objects can be related to the size of the object viewed, the angular velocity of the object relative to the observer, the method of observation, and the time available for observing the object. The larger the object the greater the ability, the greater the angular velocity the greater the loss in ability, co-ordinated movements of the head and eyes are more effective than eye movements alone and increasing the viewing time improves ability irrespective of the method of viewing.

Studies of eye movements during the visual pursuit revealed that the smooth following eye movements were interrupted by jerky movements known as saccades and that as the relative angular velocity of the object viewed increased so also did the occurrence of these saccades. These second saccades are considered to be evidence of the failure of the eye movement to achieve fixation and are corrective in function. The failure may be ascribed to insufficient or inaccurate retinal information, inaccurate prediction of the eye movement required, inaccurate response of the oculomotor system to the demand.

The interval between the end of the initial rapid eye movement and the beginning of the second saccade may be considered as one of reassessment of the movement required of the eyes to achieve fixation. During this interval which may be as short as 50-70 msec. a new eye movement must be made based on the error of fixation present, a new temporal pattern of muscular activity developed, and

the signs of this activity shown by a change in the recorded eye movement pattern. The estimated time for afferent volleys from the retina to reach the visual cortex is 50-70 msec. It is not unreasonable to assume that the more complex motor system from cortex to eye muscles will take at least as long. If these currently accepted estimations of the time for the impulses to pass along the nervous pathways are accurate, little, if any, time remains for integration of information from the retina into an eye movement pattern. A re-assessment of the mechanism and the temporal characteristics of the oculomotor system appears necessary.

The relationship of the free movements of the head to eye movements was investigated. The latency of head movement is 250-350 msec. which is 80-100 msec. greater than eye movement latency. The head rapidly attains a velocity reasonably comparable to that of the moving object after an overtaking phase and then trails behind the object by an arc varying from less than 5° to about 20° when the angular velocities of the target are 50° to 100° /sec. The head forms a stable moving platform and reduces the requirement for extensive extra-ocular muscular contraction and thus in theory would improve the ability to discriminate detail in moving objects by diminishing the need for massive activity of the extra-ocular eye muscles.

The electromyographic activity of neck muscles involved in head movement was recorded and showed that this activity not only preceded head movement but in the majority of recordings even preceded eye movement. This response was shown to be associated with voluntary movements only.

Owing to limitations of the apparatus it was not possible to move the target in the vertical plane. To obtain a retinal image moving in the vertical plane of the eye the subject's position was changed to one of lying on the side. The disparity between retinal and proprioceptive sensory input produced an illusion which demonstrated the inability of man to perceive the horizontal when normal visual cues are not present.

It is apparent that when visual fixation is attained some specific degree of accuracy in the positioning of the image relative to the fovea is necessary. If the target is moving the angular velocity of the eye and the target should also have some required degree of accuracy. The tolerable inaccuracies of fixation in position and velocity were relatively small but increased with increasing target size. The presentation of images which were extrafoveal and

which had simultaneous velocity errors resulted in an almost complete loss of ability to perceive detail.

The position sense of the eyes was examined and was shown to be present to a useful degree (in the particular experimental circumstances) and in addition it was noted that the position sense was consciously perceived.

An experiment was also conducted to determine when perception takes place during visual pursuit which justified the assumptions of all students of eye movement patterns that the saccades are corrective in function.

Finally the application in aviation of visual acuity of moving objects was examined and is shown to be more of academic interest than of practical importance.