J. Physiol. (1961), 159, *pp.* 339-360
With 22 *text-figures*
Printed in Great Britain

DISJUNCTIVE EYE MOVEMENTS

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(*Received* 8 *June* 1961)

Eye movements may be described in terms of two components: conjugate and disjunctive. A pure conjugate eye movement is one in which the two eyes move in a parallel fashion, while in a disjunctive movement changes occur in the orientation of one eye with respect to the other. A typical situation calling for a disjunctive movement is the change in binocular observation from a far to a near target, when the fixation lines of the two eyes have to converge.

Recordings of eye movement responses to the presentation of targets requiring convergence show the movements to be slow compared with their reaction time (Westheimer & Mitchell, 1956). In this respect they differ from the most commonly occurring conjugate eye movements, the saccadic movements. It is clear now that saccadic eye movements are not guided, in that no adjustments in response to visual clues are made during the movement (Westheimer, 1954). The time characteristics of disjunctive movements, on the other hand, would theoretically allow correction of movements during their course on the basis of visual information. That the elements for such a control system exist is evidenced by the following two facts: (1) the sensory system on which such a control system would depend is capable of making very fine discriminations—retinal disparities of less than a minute of arc can be detected—and (2) the muscular system is quite fast and capable of making fine gradations in response. The experiments reported in this paper fall into two groups. Those describing the eye movement responses to simple types of convergence stimuli are given in Part I, and those in which responses are studied to special stimulus situations designed to elucidate the properties of the control mechanism for disjunctive eye movements are contained in Part II.

PART I. DESCRIPTIVE EXPERIMENTS

METHODS

Stimulating. The subject sits in a darkened room. Each eye is presented with a target consisting of a 3 mm white spot on the face of a large cathode-ray tube 2 m from the eye.

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One of these tubes is placed directly in front of the subject and is seen by only the left eye. The other is placed to one side and is seen by only the right eye after reflexion in a front-surface mirror. This mirror also obscures the right eye's view of the left eye's target. The cathode-ray tube spots may be deflected horizontally with applied voltage signals. When equal signals are applied to both tubes, this results in a symmetrical disjunctive movement of the targets.

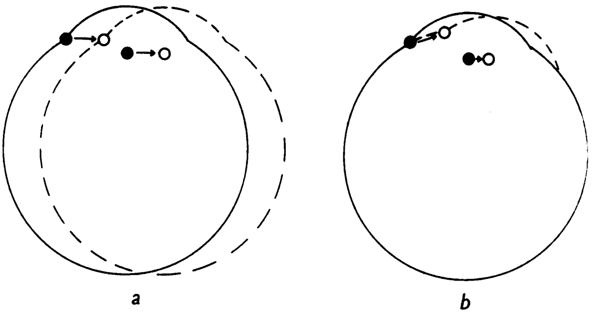

Fig. 1. Schematic diagram to illustrate relative changes in the positions of the corneal light reflex and a point on the limbus as the eye undergoes (*a*) a side-to-side translational movement and (*b*) a rotational movement.

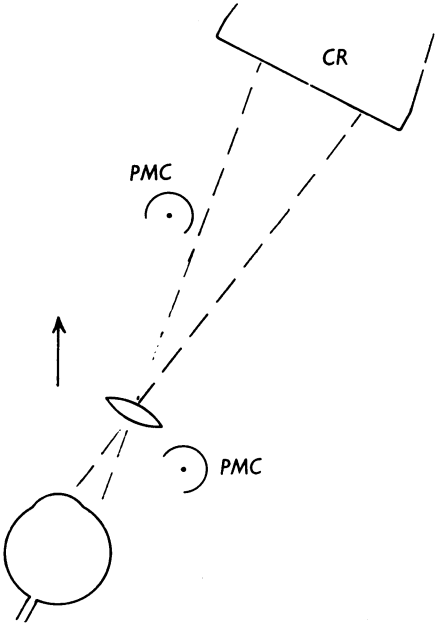

Fig. 2. Schematic plan of the experimental arrangement to record eye movements. A vertical line scans the cathode-ray tube (*CR*) horizontally and is imaged by the lens on the anterior surface of the eye. Two photomultiplier cells (*PMC*) are situated in front of the eye to register changes in the reflected light.

Recording. The movements of the eyes are recorded by a method which is designed to eliminate any artifacts which may arise from lateral displacements of the eyeballs. The method is based on the principle that, seen from one direction, the separation of two points on a rigid body remains constant during a translation but changes during a rotation around an axis normal to the plane containing the two points and the direction of observation. The two points chosen which to a first approximation have this property for horizontal eye movements are the temporal limbus and the image of a light source by specular reflexion in the anterior surface of the cornea. Seen from the front, a point in the limbus will move through the same lateral distance as the corneal reflexion of a distant light source when the eye makes side-to-side translational movement. When the eye makes a rotational movement around a vertical axis, however, these two landmarks will move through unequal lateral distances. The separation of a point on the limbus from the corneal reflexion will, therefore, be a function of rotational eye position only, unaffected by translational shifts of the eye (Fig. 1).

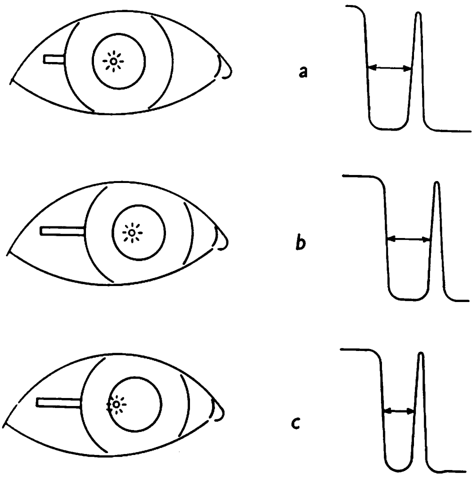

Fig. 3. Summed signals from the two photomultiplier cells in Fig. 2 (schematic). The first down turn indicates the position during the scan in which the image of the cathode-ray tube line travels across the limbus, the rise and fall show the position in which a specular reflexion from the cornea is formed at the second photomultiplier cell. When the eye makes a side-to-side translational movement (*b*) the two changes are displaced in a parallel fashion, but during an eye rotation (*c*) their separation changes. The separation, isolated electronically, is used as the signal corresponding to eye position.

We use a vertical line (produced by 60 kc/s vertical scanning of the spot) on a short-persistence cathode-ray tube and image it by means of a lens on the anterior surface of the eye. The line is made to scan the tube face horizontally in a saw-tooth manner at the rate of 300 c/s. The image is about 1 mm high and moves nasally from the sclera across the cornea at the level of the widest horizontal diameter of the cornea. The light reflected from the anterior surface of the eye is measured by two suitably placed photomultiplier cells (Fig. 2). During a single scan the output of the one cell undergoes a change when the image crosses from the sclera to the cornea, and that of the other detects the instant a specular reflexion of the image from the cornea is formed at this particular cell. In the summed output of the two cells the time interval of the two changes is a measure of the rotational eye position (Fig. 3). The time interval is isolated electronically and a signal proportional to eye position is available. The apparatus is duplicated before the other eye, and records can be obtained of the horizontal movement of each eye separately or, by electronic differencing, of convergence.

The gain of the recording system was so adjusted that the voltage output of each eye's channel was equal to the voltage required to drive each stimulus spot on its cathode-ray tube through a distance corresponding to the movement of the eye. Linearity was demonstrated by the maintenance of this correspondence over the range of eye movements used by us, up to 8°. Translational movements are about five times less effective than if the limbus position alone had been recorded (Rashbass, 1960) and about ten times less than if the corneal reflexion method had been used. The noise level remains under 5 minutes of arc. The frequency response of the recording system is estimated to be good from zero to at least 30 c/s.

Procedure. The subject is placed before the experimental apparatus with his head held firmly in place by means of a bite-bar and a head clamp. The mirror in front of the right eye is adjusted so that when each spot is in the centre of its viewing tube face, the subject sees a single spot in binocular view somewhere near the middle of the angular range within which he can maintain single vision (fusional range). Near the edge of this range quite different responses might be found; we have not analysed these nor have we attempted to analyse phenomena close to the noise level of the recording apparatus. Preliminary tests showed that such factors as size, brightness and sharpness of the viewing spots do not materially influence the characteristics of the responses.

Nomenclature. We shall use the term 'target vergence' to denote the angle between the lines joining the centre of rotation of each eye with the apparent target for that eye. 'Eye vergence' will be used for the angle between the fixation lines of the two eyes. 'Disparity' is the difference between target vergence and eye vergence.

RESULTS

Records of disjunctive eye movements in response to horizontal target vergence stimuli were obtained in eight young adult subjects, none of whom showed any evidence of oculomotor imbalance, as determined by tests for heterophoria and fusional range. The results described below are typical of the records obtained on all subjects. Variation between subjects, except where mentioned, appeared negligible. Except where noted, movements in the direction of convergence and divergence had similar characteristics. The targets remained at the same physical distance throughout, so that any additional effects that a real near target might introduce, such as 'cross-talk' from accommodation, were avoided.

It is clear now that the response mechanisms mediating conjugate and disjunctive eye movements operate separately (Westheimer & Mitchell, 1956; Yarbus, 1957; Rashbass & Westheimer, 1961). This means that the method of display adopted here, in which only the disjunctive component of the binocular eye movement is shown, is a sufficient measure of the phenomena studied. In any case, when the target vergence is introduced symmetrically before the two eyes, as was done throughout, the conjugate components of the eye movements are small.

Step stimuli

Figure 4 shows a representative eye vergence response when a 2° target vergence change is suddenly introduced. The reaction time is typically about 160 msec. A constant velocity of eye vergence is soon developed and maintained for nearly 200 msec, after which the velocity falls off. The final level of eye vergence is reached in about 800 msec, so that in total about 1 sec elapses between the onset of the stimulus and the stabilization of the response at the new level of eye vergence. These time characteristics of step vergence responses are similar to those of accommodation (Campbell & Westheimer, 1960).

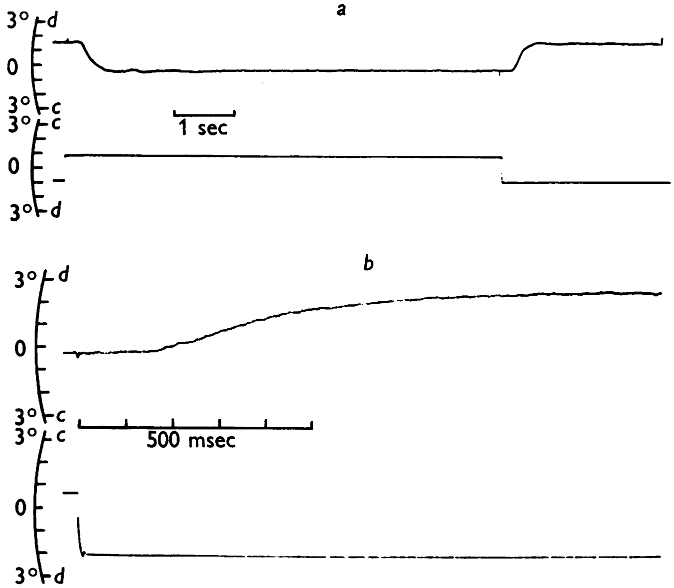

Fig. 4. (*a*) Eye-vergence response (upper trace) to a step change in target vergence of 2°. Allowance should be made for the arc of the pen. The direction of convergence is marked *c*, and of divergence, *d*. (*b*) Same, but at a higher recording speed.

Figure 5 shows responses to step stimuli of various amplitudes with the gain of the recording system changed to compensate. Characteristic changes occur as the amplitude of the step target vergence stimuli is decreased. The larger movements are slowed relatively earlier in their course and reach their final level asymptotically. The 20′ movement, on the other hand, has an overshoot in one direction.

The amplitudes of the eye vergence movements match the target vergence changes very well. It appears that if there is any maintained disparity it certainly does not exceed a few minutes of arc, a fact that has also been demonstrated in recent experiments with the contact-lens method of recording eye movements (Riggs & Niehl, 1960).

Figure 6 shows a 3° movement recorded from subject E.F.M. This particular subject shows oscillations for movements in one direction not only around the final position but also during the movement. We shall see similar oscillations in another subject when ramp stimuli are illustrated below.

Some details of the time course of the responses shown here differ from those given by Westheimer & Mitchell (1956). Genuine individual differ-

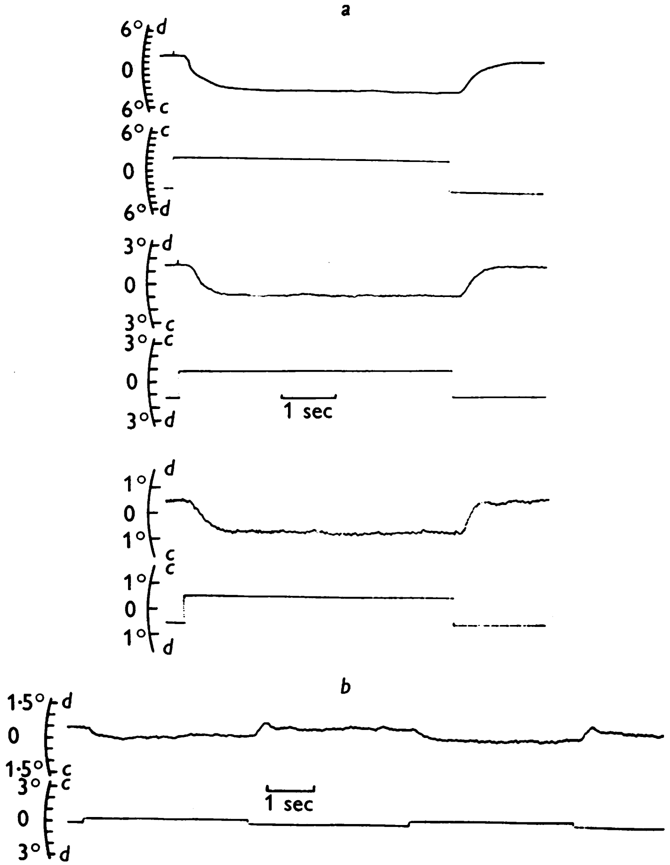

Fig. 5. Eye-vergence responses to step changes in target vergence of (*a*) 4°, 2°, 1°, and (*b*) 20′. Note changes in vertical scale.

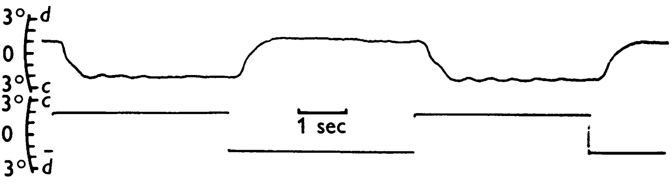

Fig. 6. Eye-vergence response to a 3° step change in target vergence from subject E.F.M.

ences might be involved, but it is more probable that the improved recording technique available for this study accounts for the discrepancies.

Are the responses shown in Figs. 4 and 5 initiated as a single event and carried through without modification as are, for example, saccadic eye movements, or are the particular response characteristics the result of changes introduced during the course of the movements? The following experiment suggests an answer to this question.

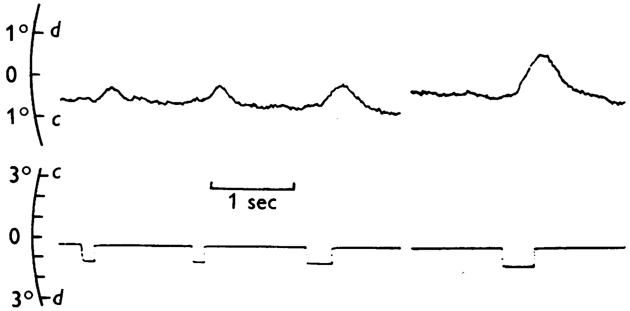

Fig. 7. Eye-vergence movements in response to 1° pulses of target vergence of various duration.

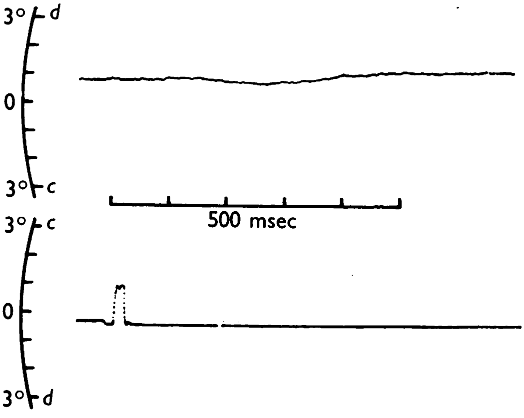

Fig. 8. Response to a 2° target-vergence pulse of 20 msec duration.

Rectangular pulse stimuli

In Fig. 7 are shown the responses to a series of sudden target vergence changes followed in each case by a return of the stimulus to the original level after a time interval increasing throughout the series. It is seen that there is an ascending and a descending limb in each response, the two separated by an interval approximately equal to the pulse-stimulus length; the response lags a reaction time behind the corresponding components of the stimulus. It is concluded that disjunctive eye movements can be modified during the course of their progress and that information concerning disparity can be assimilated during the reaction time as well as during the movement.

The initial responses to constant-amplitude target vergence pulses of various durations can all be superimposed on each other as well as on the step response to the same stimulus amplitude.

The shortest pulse we have used was 20 msec long. Figure 8 shows that there is a response.

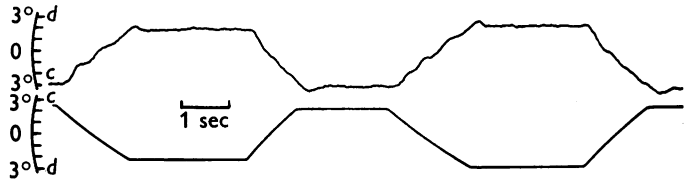

Fig. 9. Eye-vergence movements when target vergence changes at constant velocity.

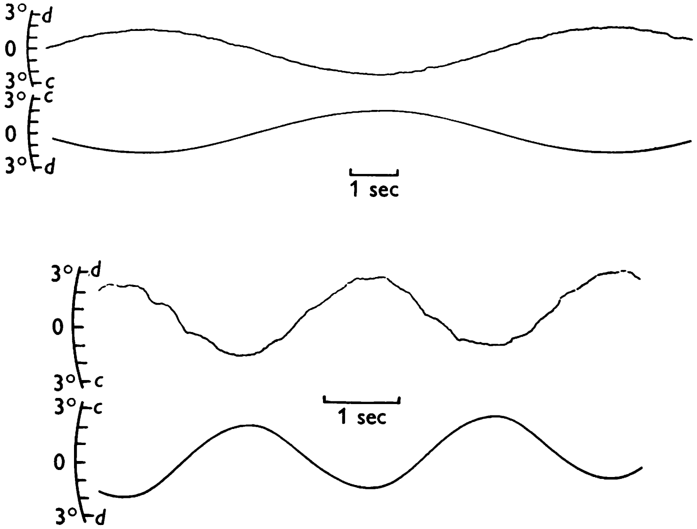

Fig. 10. Eye-vergence tracking of sinusoidal changes in target vergence at two frequencies. The records shown are from the middle of long trains of movements and do not exhibit transient changes associated with the beginnings and ends of such responses.

Ramp functions

When a target vergence is introduced with a constant rate of change (Fig. 9), it is matched by a rate of change of eye vergence, but this is not achieved without some velocity overshoot and oscillations. Typically these transient effects are unequal in the two directions. A reaction time of somewhat less than 200 msec is a feature of all these records. We have recorded tracking of target-vergence changes as slow as 0·35°/sec and as fast as 5°/sec.

Sinusoidal target vergence stimuli

The targets were made to undergo vergence changes that were a sinusoidal function of time at various amplitudes and frequencies. That the vergence tracking is exceedingly accurate for stimuli with periods of a few seconds per cycle can be seen in Fig. 10, which shows records during the middle of long trains of waves. When the amplitude and frequency are such that tracking velocities of several degrees per second are demanded, the velocity oscillations—more prominent in one direction than the other—already observed in the previous section are again demonstrated. When the frequency of the sinusoidal stimuli is increased to the order of 1 c/s, the subject responds to only the first few cycles (Fig. 11); the response then fluctuates irregularly in the middle of the stimulus range. Under these conditions the subject is aware of diplopia. This phenomenon is dependent to some extent on the amplitude of the stimulus oscillations, but we have not investigated this aspect in detail.

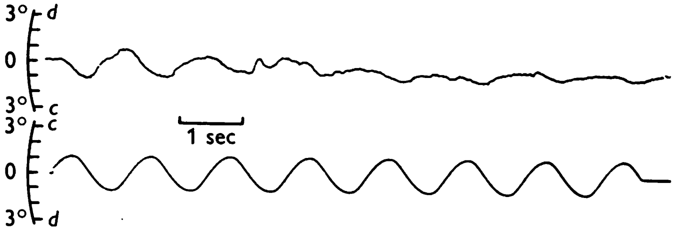

Fig. 11. Gradual deterioration of eye vergence tracking of fast (1 c/s) sinusoidal target vergence movements.

PART II. ANALYTICAL EXPERIMENTS

In the preceding part eye-vergence responses to a variety of target patterns have been described. In this part investigations are reported to determine which characteristics of the disparity determine the nature of the response, and the way they do so.

An analysis of this sort is best performed by observing the responses to disparities that are simple time functions entirely under the control of the experimenter. In the experiments described in the preceding part this is not the case. There the binocular disparity results from the combination of the movements imposed on the targets with the movements which the eyes perform. The eye movements themselves are not directly under the control of the experimenter and thus any attempt to impose a simple disparity is vitiated as soon as eye-vergence movements are made.

It is possible to surmount this difficulty by making the target spots move in a way that is predicated by the eye-vergence movements. With the apparatus described the target spots can be driven by the electrical measure of eye vergence so that any vergence movements made by the eyes are accompanied by similar movements of the targets. When this is achieved, eye vergence no longer has any effect on disparity. It is possible to introduce any desired disparity which then will remain uninfluenced by the response it evokes. This process may be termed disparity clamping and is familiar to engineers as the process of opening a feed-back loop.

METHODS

It has already been mentioned that in the course of calibration the signal from the eye-movement recording device is made equal to the signal which displaces the target so as to evoke that movement. The input to the target presentation devices is now earthed to bring both spots to their central position. When convergence on this target position is established, the DC level of the output of the eye-vergence measuring system is adjusted to earth potential. This adjustment is carried out without altering the sensitivity which has already been adjusted. It is now possible to disconnect the input to the target presentation devices and replace it by the output of the eye-vergence measuring system (which is at earth potential) without any change in position of the target spots. Should any eye-vergence movements now occur, the target spots will move so as to keep the disparity zero.

The substitution of the real earthing connexion of the target presentation devices by the output of the eye-vergence measuring device changes the stability of the system from a condition of stable to one of neutral equilibrium. After the substitution there is nothing to prevent the eye vergence from drifting, because the eye will be accompanied by the targets. With care and patience, however, it is possible to achieve a substantially drift-free base line.

It should be noticed that this procedure does not produce a stabilized retinal image. Conjugate eye movements do not appear in the output of the eye-vergence measuring system and are, therefore, not imposed on the target movements. The targets are always symmetrically disposed about the mid line.

RESULTS

Figure 12 is a typical record of the response to a convergent disparity that is suddenly imposed and subsequently maintained at a constant value. After a reaction time of 170 msec the eyes begin to converge. The movement almost instantly attains its velocity which is then sustained throughout. The movement ends either when one of the target spots goes out of sight or when the degree of convergence attained is extreme. Divergent disparities cause divergence movements which are of similar character to the convergence movements caused by convergent disparities.

Unlike the records in the previous part, those in this part show the disparity stimulus and the response at different scales. Thus it is seen that when the disparity is clamped, a small disparity evokes a movement which becomes very much greater than the disparity which causes it.

The velocity of the movement varies with the disparity. Figure 13 shows the relationship between these two quantities. Within the limits of the experimental method there is no dead zone, that is to say, disparities, however small, evoke a response. This underlines the difficulty of obtaining a drift-free base line. Within the range of ± 0·2° of disparity, the velocity of the eye vergence is linearly related to the binocular disparity that evokes it, but for higher disparities there seems to be a falling off

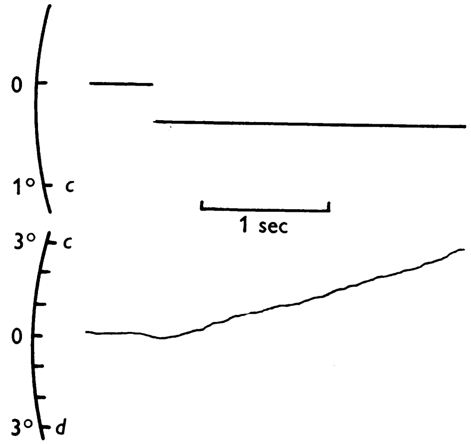

Fig. 12. Eye-vergence movement when a constant disparity is suddenly imposed and subsequently maintained. The velocity of the eye vergence is a function of the degree of disparity.

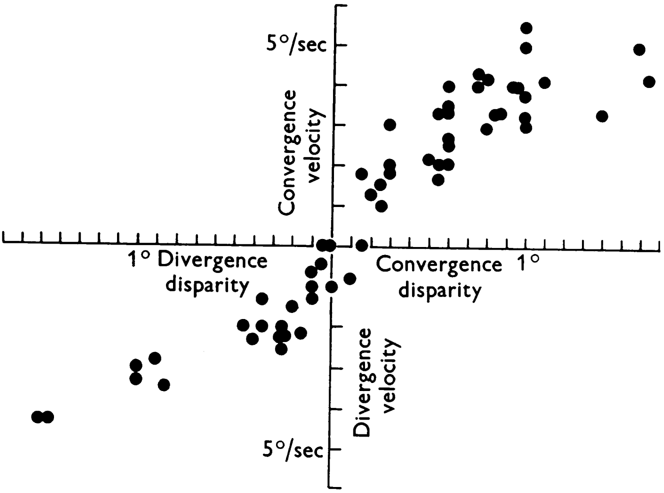

Fig. 13. Relation between the magnitude of constantly maintained disparity and velocity of eye vergence induced by it. Each point was obtained from a record such as illustrated in Fig. 12.

from linearity. In the subject on whom the results of Fig. 13 were obtained the constant of proportionality is 10°/sec per degree of disparity, this figure being obtained from the slope of the results near the origin. In another subject the constant of proportionality was 7°/sec per degree of disparity.

When the clamped disparity is alternated between the convergent and the divergent kind, the response consists of alternating convergence and divergence eye movements of uniform velocity in the form of a triangular wave delayed one reaction time with respect to the steps of disparity evoking it. This is illustrated in Fig. 14. There is no evidence that the regular repetition of changes between convergent and divergent disparities allows any anticipation of these changes. Even the later responses occur only after a reaction time has elapsed.

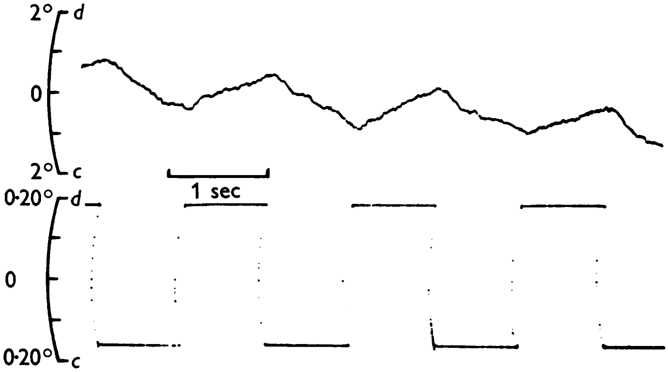

Fig. 14. Triangular wave-form of eye-vergence response to a square-wave disparity stimulus. Note the relatively large movements induced by the small amount of disparity. Drift in the upper record is practically unavoidable consequence of experimental situation required to produce disparity clamping.

At this stage it is possible to propose the following working hypothesis: the velocity of the eye-vergence movements is always proportional to what the disparity was one reaction time earlier, provided that the disparity never exceeds some prescribed bounds. The hypothesis predicts the eye-vergence movements that will occur in response to any pattern of disparity, a prediction that can be tested by observation.

Sinusoidally varying disparities provide a convenient test. The hypothesis may be expressed in the form

$$\frac{\mathrm{d}r}{\mathrm{d}t} = k\epsilon_{(t-\tau)}, \tag{1}$$

where r is the eye vergence, ϵ the disparity, τ the reaction time, and k the constant of proportionality determined above. For a sinusoidal disparity change of amplitude a and frequency ω radians/sec:

$$\epsilon = a \cos \omega t;$$

and from equation (1) it follows that

$$r = \frac{ka}{\omega} \sin \omega\, (t-\tau) = \frac{ka}{\omega} \cos\, [\omega(t-\tau) - \tfrac{1}{2}\pi], \qquad (2)$$

omitting the constant of integration which determines the mean eye vergence. The hypothesis thus predicts not only that the eye-vergence response to sinusoidally varying disparity will be a sine wave of equal frequency but also says something about the amplitude, and phase relationships between the disparity and the resulting eye vergence.

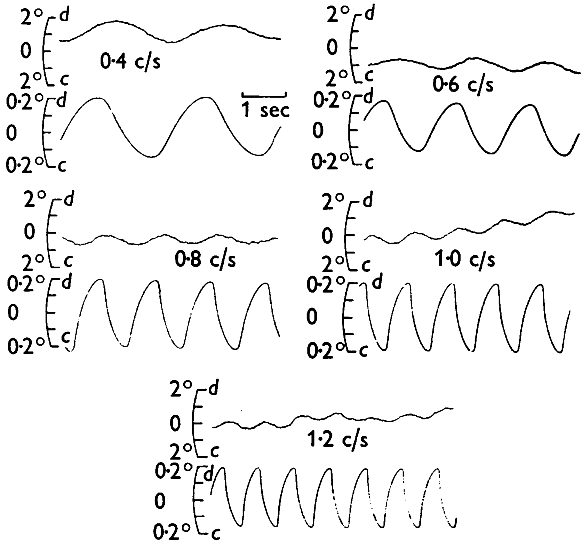

Fig. 15. Sinusoidal eye-vergence movements in response to sinusoidal disparities at various frequencies. This is an experiment in the manner of the 'open-loop' approach to servo mechanisms. Allowance should be made for the arc of the pen.

In Fig. 15 are illustrated sinusoidal disparity changes and the eye-vergence movements they evoke. It is seen that the latter are substantially sinusoidal. The records are from the middle of long wave trains. In Fig. 16 are plotted the amplitudes of the response oscillations against the amplitudes of the disparity oscillations for a single frequency. For small disparities a linear relationship exists between the two, but as the amplitude of the disparity oscillation increases there is a falling off from linearity.

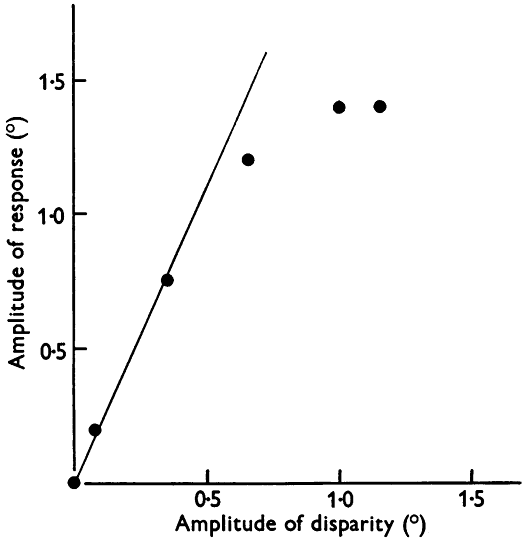

Fig. 16. Experimental data from long wave-trains of records like those in Fig. 15 showing the relationship between the magnitude of eye-vergence oscillations and that of the disparity oscillations which cause them. The slope of the straight line fitted to the data points near the origin may be called the gain of the system.

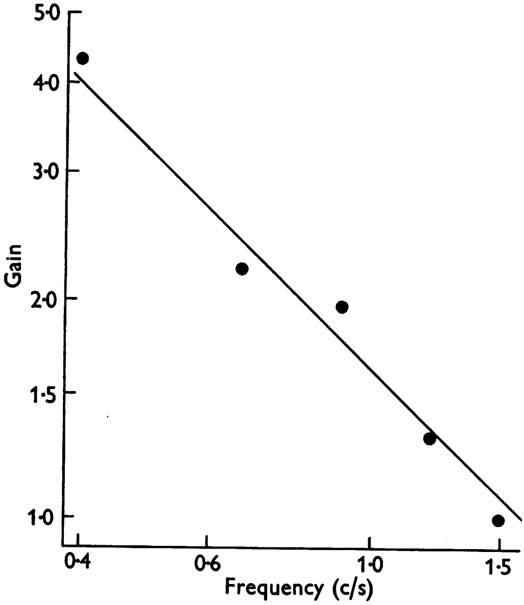

Fig. 17. Graph relating gain (ratio of eye-vergence amplitude to disparity amplitude for sinusoidal disparity changes) to frequency of the disparity changes; log. co-ordinates. Straight line has position and slope theoretically expected in a system in which disparity produces a constant velocity of eye vergence with the relationship in Fig. 13. Points are experimentally determined. Subject C.R.

The ratio of response amplitude to disparity amplitude at any frequency may be called the gain of the system at that frequency. This quantity in its linear region for small disparities has been plotted in Fig. 17 as a function of frequency on logarithmic co-ordinates for the results from subject C.R., obtained from records like those shown in Fig. 15. Superimposed is drawn the predicted line of gain, obtained by substituting in equation (2) the value of k obtained from the experiment illustrated in Fig. 13, that is 10°/sec per degree of disparity. Similar results were obtained for a second subject and are shown in Fig. 18. There is good agreement between the experimentally obtained results for gain as a function of frequency and the theoretically predicted curve.

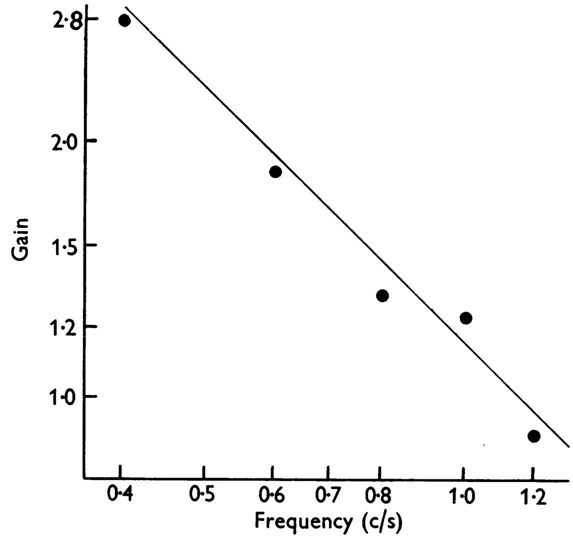

Fig. 18. Results for another subject, B.W.W., similar to those depicted in Fig. 17 for subject C.R. Log. co-ordinates.

Equation (2) also makes a prediction concerning the phase relationship between the disparity oscillations and the response oscillations. Were it not for the delay of a reaction time, the maximum velocity of the response would coincide with the maximum disparity. It is expected, therefore, that the response oscillations will follow the disparity oscillations after a delay of a quarter of cycle plus a reaction time. The straight line in Fig. 19 shows the predicted relationship between phase lag and frequency. The points represent the phase lags measured experimentally, each point being the average of about 100 measurements. It can be seen that there is no agreement between prediction and experiment; the observed phase lags

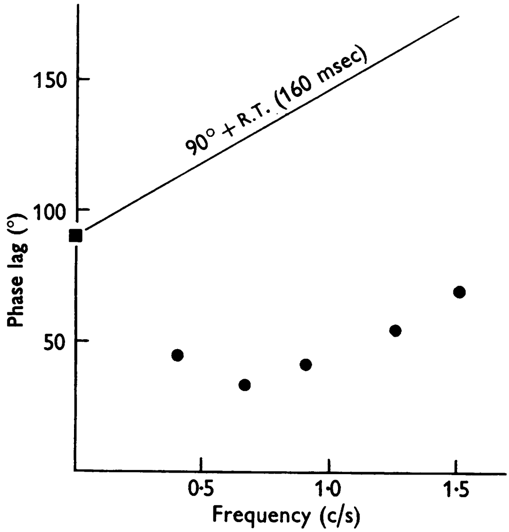

Fig. 19. Relationship between phase of sinusoidal eye-vergence movements and the sinusoidal disparity changes inducing them. Straight line is the expected behaviour of a simple system with characteristics like those in Fig. 12. Points marked ● are from records like those in Fig. 15. Point marked ■ is an expression of the fact that an integrating system (Fig. 12) has 90° phase lag at zero frequency. Measured latencies substantially shorter than expected are an indication of anticipatory behaviour of eye vergence under sinusoidal disparity stimulation. Subject C.R.

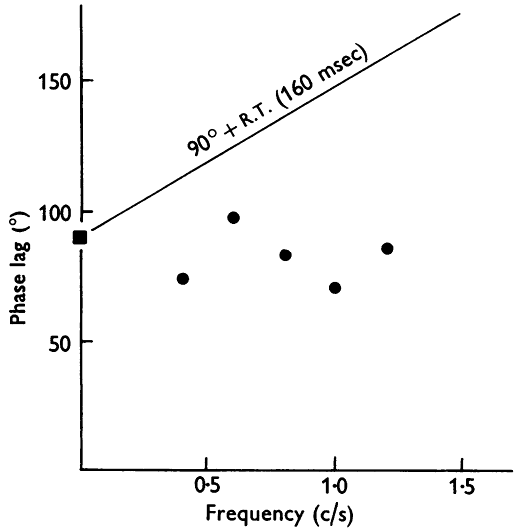

Fig. 20. Results for phase delay between sinusoidal disparity changes and eye-vergence responses for subject B.W.W. See legend for Fig. 19.

are very much smaller than those expected. A similar discrepancy is shown in the results for subject B.W.W. although not quite so markedly (Fig. 20).

There are several possible ways of considering this failure of equation (1) to account for the observed phase lags, yet no simple modification of it would yield a better concordance between obtained and predicted phase lag and at the same time account for the findings illustrated in Figs. 12, 14, 15 and 16.

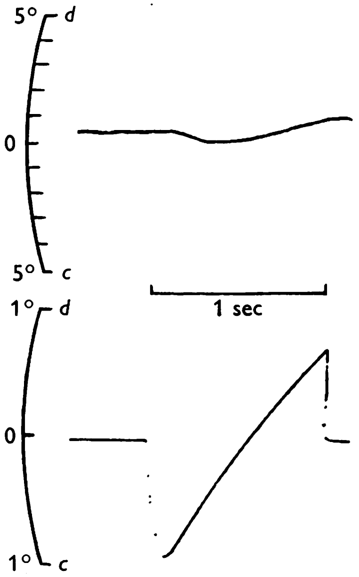

Fig. 21. An experiment to illustrate anticipatory behaviour of the disparity–eye vergence system. The disparity presented would not produce a turn-about in the response until one reaction time after it has crossed the zero level, unless anticipation had occurred.

The fact that the phase delay in the sinusoidal disparity experiment is shorter than would be expected from the hypothesis which accounts for the other findings in Part II suggests that the course of disparity is being anticipated. It might seem reasonable to account for this by the rhythmical repetitiveness of a sinusoidally varying disparity. This explanation, however, is unacceptable because regular alternation of constant convergent and divergent disparities shows no evidence of such anticipation (see Fig. 14). The anticipation of the course of the disparity which is displayed for sinusoidally varying disparities must, therefore, be accountable by some property other than its rhythmicity. The only essential difference between a sinusoidal variation in disparity and a regular alternation between convergent and divergent disparities is that the former is carried out with finite velocity, acceleration and higher time derivatives of disparity. It seems inescapable that the anticipation of the course of sinusoidally varying disparity is based on information concerning the direction in which it is changing, at what rate it is changing, and possibly, what is its acceleration.

The conclusion that it is information concerning the rate of change of disparity which permits the future course of the disparity to be anticipated can be tested by imposing a disparity which changes at a uniform rate. If a clamped disparity is imposed which declines to zero at a uniform rate and then continues to increase in the opposite sense at the same rate, and no anticipation of its course is made, then the response would reverse direction one reaction time after the disparity passes through zero. If, on the other hand, the finite rate of change of the disparity can be utilized to predict the future course, then the turn-about of the response would occur sooner than a reaction time after the disparity passes through zero. Figure 21 shows a typical result of such an experiment. It can be seen that the reversal of the response occurs even before the disparity reaches zero. Allowing for the delay involved in the reaction time, this demonstrates that considerable anticipation of the future course of the disparity has taken place.

PART III. DISCUSSION

Certain general properties of the observations in Part I can be shown to be compatible with inferences from Part II.

When a sudden change of target vergence is presented to the subject, eye vergence does not begin until a reaction time has elapsed. During the reaction time the disparity is constant and equal to the imposed change of target vergence. The initial velocity of the eye vergence would be expected, therefore, to be that velocity which we have found in Part II to be generated by that disparity. The initial velocities of the responses to sudden changes of target vergence are plotted as open circles in Fig. 22. The black dots are the sustained velocites obtained by clamping the disparity and are replotted from Fig. 13. Although there is little overlap in the ranges of disparity covered by these two sets of observations, it can be seen that the initial velocities from the Part I experiments are a compatible extension of the sustained velocities in the Part II experiments.

It has been shown in Part II that clamped disparities, however small, always generate a sustained eye-vergence movement. As the eye-vergence movement has constant velocity over its complete range, it is reasonable to assume that the velocity which a given disparity evokes is independent of the eye vergence. A stationary state of eye vergence hence cannot coexist with an added disparity. When the subject responds to a sudden change of target vergence, a state is finally reached in which eye vergence remains stationary. During that state there can, therefore, be no disparity, and this confirms the observation that ultimately the change in eye vergence is equal within the error of measurement to the imposed change in target vergence (see p. 345, also Riggs & Niehl, 1960; Westheimer & Rashbass, 1961).

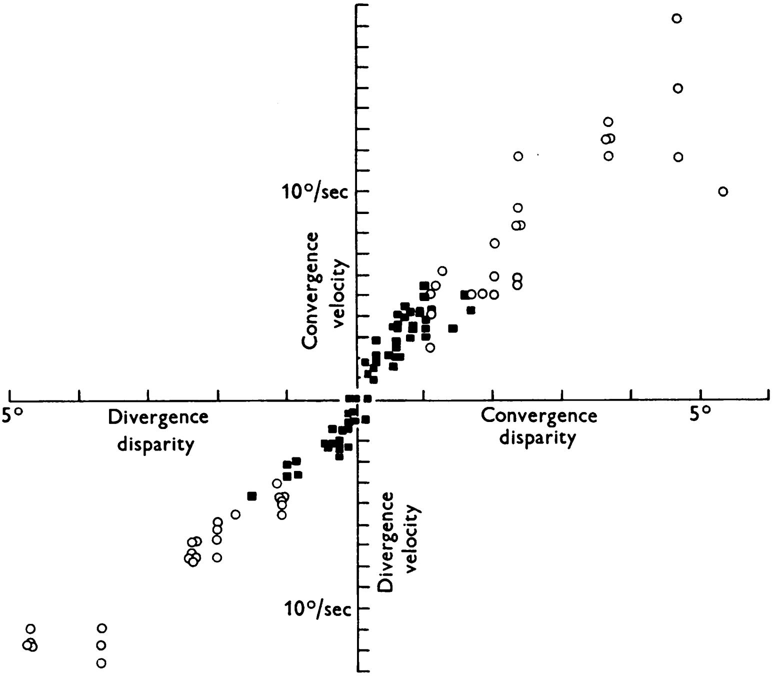

Fig. 22. Velocity of eye vergence plotted against disparity. Open circles are from early phases of eye vergence movements in response to step target vergence stimuli. Black squares are taken from Fig. 13.

In Part II it has been shown that when the disparity is changing, the rate of change influences the responding eye vergence in a way which anticipates the future course of the disparity. Although the quantitative relationship between the rate of change of disparity and its effect on the response is complex and has not been worked out, certain consequences of this effect are discernible in the records shown in Part I. If the rate of change of disparity had no effect, the velocity of the response would be determined only by the magnitude of the disparity one reaction time earlier. In our subjects, with the response parameters determined in Part II, the responses to sudden target vergence changes would be expected to show a large overshoot and a prolonged period of oscillation about the final position. In fact they do not show this. The responses appear to be those of overdamped or critically damped systems. This may be explained by the effect of rate of change of disparity. As soon as eye vergence starts, the disparity begins to diminish with a finite rate of change. This rate of change will influence the response in a way which tends to reduce the rate at which the disparity is changing. The effect of this will be to reduce or prevent any oscillations about the final position.

The precise effect of the anticipation due to rate of change of disparity depends on the quantitative details of the phenomenon. If a certain degree of rate of change of disparity provokes a moderate corrective effect, the result will be as described above, i.e. a tendency to dampen oscillations that are due to a too rapid attempt to correct disparity. If a certain degree of disparity provokes a greater effect, then it is possible to generate oscillations of velocity. The record from subject E.F.M., shown in Fig. 6, illustrates such oscillations in one direction. The same effect of over-correction of rate of change of disparity is discernible in the response to target-vergence changes with uniform velocity (Fig. 9).

It is clear now that velocity as well as position information is utilized to determine the conjugate tracking oculomotor responses to the movement of images over the retina (Rashbass, 1961). We have shown here that rate of change as well as magnitude of disparity determines eye vergence responses. The estimation of rate of change of disparity might in principle be made in either of two ways: by the difference between the velocity of the movement of the images across the two retinae, or by the rate of change of the difference in the position of the images in the two eyes. The estimation of the speed at which an image is traversing the retina might be made at the retina or more centrally, but any comparison between the two eyes, be it of velocity or position, can only be made centrally. Since the operations of subtraction and differentiation are commutative, i.e. the same result is obtained independently of the sequence in which the operations are performed, this does not restrict the localization of the process of velocity measurement. Whatever the mechanism of the detection of rate of change of disparity and the precise details of its operation, its influence is to stabilize the response to step functions of a system which has appreciable time delay. This stabilization is achieved without unduly prolonging the total response time, and represents an efficient resolution of the conflict between stability and speed of response inherent in any system involving delay in the transfer of information.

SUMMARY

1. Disjunctive eye movements were recorded in normal subjects while they were presented with target spots, one for each eye, on cathode-ray tubes at a distance of 2 m.

2. Eye-vergence movements in response to suddenly introduced target-vergence changes have a reaction time of about 160 msec, begin with a constant velocity that is a function of stimulus amplitude, and then asymptotically reach their final level with a total movement time of about 800 msec.

3. Responses to momentary changes in target vergence follow each aspect of the stimulus after a reaction time. It is concluded that disjunctive eye movements can be modified during their progress and that information concerning disparity can be assimilated during the reaction time as well as during the movement.

4. Target vergences changing at uniform rate and with simple harmonic motion evoke matching eye-vergence changes after a reaction time. The tracking of higher target-vergence velocities is associated with oscillations. The tracking of high target-vergence frequencies deteriorates after only a few cycles.

5. A method was devised which permits the target vergence to be driven by the eye vergence so that any eye-vergence movements are always accompanied by similar target-vergence movements. When a disparity is now introduced which is then sustained at a constant value, the eye vergence achieves a constant velocity which is a function of the amplitude of the disparity. The constant of proportionality for small disparities is 10°/sec per degree disparity in one subject and 7°/sec per degree disparity in another.

6. The responses to a regular alternation between convergent and divergent disparities, and the shape and amplitude of the eye-vergence changes induced by sinusoidal disparity changes, conform to the pattern of a system the velocity of whose response is a linear function of the degree of disparity.

7. The phase relationship between sine-wave disparity changes and the eye-vergence changes they cause suggests that anticipation of future disparity changes takes place, and an experiment with uniform rate of change of disparity indicates that rate of change of disparity is a factor in such an anticipation.

8. There is general compatibility between the responses to simple controlled disparities and the responses to disparities modified by the movements which the eyes themselves perform.

This work was supported in part by grant MY 3034 from the National Institute of Mental Health, U.S. Public Health Service and was carried out under the auspices of the Columbus Psychiatric Institute, The Ohio State University Health Center, Columbus 10, Ohio.

REFERENCES

Campbell, F. W. & Westheimer, G. (1960). Dynamics of accommodation responses of the human eye. *J. Physiol.* **151**, 285–295.

Rashbass, C. (1960). New method for recording eye movements. *J. opt. Soc. Amer.* **50**, 642–644.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *J. Physiol.* **159**, 326–338.

Rashbass, C. & Westheimer, G. (1961). Independence of conjugate and disjunctive eye movements. *J. Physiol.* **159**, 361–364.

Riggs, L. A. & Niehl, E. W. (1960). Eye movements recorded during convergence and divergence. *J. opt. Soc. Amer.* **50**, 913–920.

Westheimer, G. (1954). The mechanism of saccadic eye movements. *Arch. Ophthal., N.Y.*, **52**, 710–724.

Westheimer, G. & Mitchell, A. M. (1956). Eye movement responses to convergence stimuli. *Arch. Ophthal., N.Y.*, **55**, 848–856.

Westheimer, G. & Rashbass, C. (1961). Stability of retinal correspondence during convergence. *J. opt. Soc. Amer.* **51**, 475.

Yarbus, A. L. (1957). Motion of the eye on interchanging fixation points at rest in space. *Biofizika*, **2**, 698–702.