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THE RELATIONSHIP BETWEEN SACCADIC AND SMOOTH TRACKING EYE MOVEMENTS

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Dodge (1903) gave the first comprehensive description of the types of eye movement which can occur. Since that time there has been repeated confirmation that when the eyes follow moving objects they make two types of movement: jerky movements, called saccadic movements, and smooth movements in the intervals between these. Westheimer (1954*a*, *b*) has analysed the saccadic movements and shown them to be the response to simultaneous rapid changes in innervation to the eye muscles involved. The nature of the movement is determined largely by the mechanical properties of the structures in the orbit.

The smooth movements have been described by several workers. Dodge, Travis & Fox (1930) investigated the movements obtained when tracking black and white vertical bars moving horizontally across the visual field—opto-kinetic nystagmus—in man, and also the response to a 'slit' of light moving from side to side with simple harmonic motion; Rademaker & Ter Braak (1948) described opto-kinetic nystagmus in rabbits; Westheimer (1954*b*) investigated the response to the horizontal movement of a single spot of light with uniform velocity, harmonic motion, random motion, and with uniform velocity exposed intermittently.

There are three questions which have not been satisfactorily answered by these investigations on tracking movements. First, what decides whether the eyes should perform a saccadic movement or a smooth movement? Secondly, in what way are smooth movements metrically related to the movement of the target? Thirdly, are saccadic movements and smooth tracking movements different modes of action of the same neurological apparatus, or are different pathways involved?

What decides whether the eyes should perform a saccadic movement or a smooth movement? There is abundant evidence that when the target is stationary and does not lie in the line of sight, fixation is achieved by one or more saccadic movements. Smooth movements are only elicited when the image of the target moves smoothly over the retina. The association between the movement of the image over the retina and smooth tracking eye movements has led to the assertion (e.g. Walsh, 1957) that the movement of the image is the stimulus which evokes smooth tracking, although the evidence is insufficient to justify this conclusion. The evidence available is equally compatible with the view that both saccadic and smooth movements are caused by positional errors in fixation, but that smooth movements occur only when there is no discontinuity in the position of the target. Evidence will be presented here that it is indeed the movement of the image over the retina which is detected and measured, and results in a smooth tracking response.

In what way are smooth eye movements metrically related to the movement of the target? Dodge *et al.* (1930) have shown that the maximum speed of movement of the target which can be adequately tracked is about 30–40°/sec. This has been confirmed by Westheimer. However, no detailed observations have been reported which relate the way in which the final tracking speed is reached from an initial state of rest, to the speed of the target. It will be shown here that the speed of the target determines the rate at which the final tracking speed is reached. Such observations are of importance because they throw light on the way in which information about how the target moves is utilized to produce an appropriate response.

Are saccadic movements and smooth tracking movements different modes of action of the same neurological apparatus, or not? The pathways involved in fixation and tracking have not been successfully identified. It is not clear whether the cortex is necessarily involved in these movements. Stimulation and ablation experiments reported in the literature have given conflicting results, and the nature of the movements is rarely reported. The possibility exists that some information can be gleaned from the way drugs influence tracking responses. It will be shown that saccadic and smooth movements may be differentially affected by drugs.

This paper presents a re-examination of the eye-movement responses to horizontally moving targets, with particular emphasis on these three questions.

METHODS

The details of the method of recording eye movements have been reported elsewhere (Rashbass, 1960). The technique is essentially photo-electric, and has a precision of about 5′ and a time of response of 5 msec. The apparatus was calibrated by the repeated fixation of a series of five points separated by intervals of 1°.

The subject sits in a totally darkened room. The position of the head is fixed by a moulded bite-bar, a moulded forehead rest, and a firm rubber bar behind the occiput. The left eye is covered, and both the viewing and recording are carried out with the right eye. The tracking target is a sharply defined spot, 1 mm diameter, on the face of a 5″ cathode-ray tube, placed 1 or 2 m away from the subject. The phosphor is blue with negligible persistence. All movements of the target are effected silently and without warning. The experiments were performed on four young emmetropic subjects.

RESULTS

Experiment 1. The spot at which the subject was looking was moved suddenly to a new position horizontally displaced from the original position. The magnitude (0·1–5·0°) and direction of the movement were varied irregularly. The results confirm previous observations that each change in the target position is followed after a reaction time of 150–250 msec by a saccadic movement which directs the eyes towards the new position of the target. This saccadic movement generally matches the target movement to within 0·2°, but occasionally it does not, in which case it is followed after another reaction time by a further saccadic movement. In some subjects there may be three or four saccadic movements, each separated from the previous one

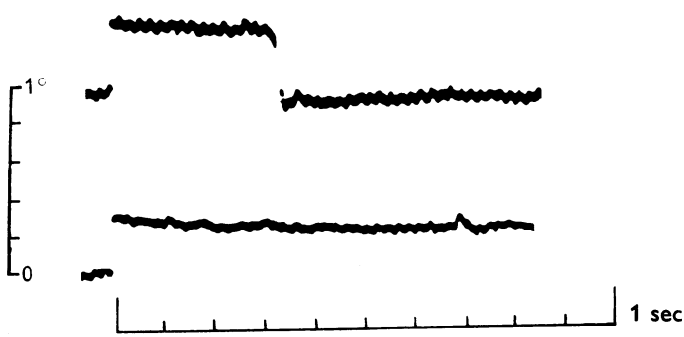

Fig. 1. Successive records of horizontal eye direction after the sudden displacement of the target near threshold. The upper record shows a saccadic response to a target movement of 0·4°; the lower record no response to a target movement of 0·3°. At the moment the target spot moves a displacement is imparted to the record equal in size to the displacement of the target. This displacement can be seen at the left-hand end of the records.

by approximately one reaction time, before the final fixation position is reached. Thereafter small saccadic movements occur around the point of fixation, but the pauses between these are usually much longer than a reaction time. Occasionally these spontaneous saccadic movements occur in trains of two or three with only a short interval (100–150 msec) between the movements.

An observation made in the course of these experiments, which has not been reported previously in the literature, is that there is a threshold target displacement. Target displacements smaller than this produce no responding saccadic movement. This threshold is about 0·25–0·5° in size. Figure 1 shows a normal saccadic response to a target movement of 0·4°, and no response to a target movement of 0·3°. This does not mean that movements smaller than 0·25° cannot occur, for such small movements frequently occur spontaneously. This suggests that the threshold is associated with the sensory aspects of the response, rather than with the motor characteristics.

Experiment 2. The spot which the subject was fixating was made to move horizontally with uniform velocity from an initially stationary position. The direction and magnitude of the velocity of the movement were varied irregularly. The movements of the eye were recorded during the first second or so of the target's movement. In general the eye movements consisted of a smooth component in the direction of the target's movement, with one or more saccadic movements also in that direction. The time of occurrence of the first saccadic movement was not constantly related to the onset of the smooth movement. Figure 2 shows records taken from one

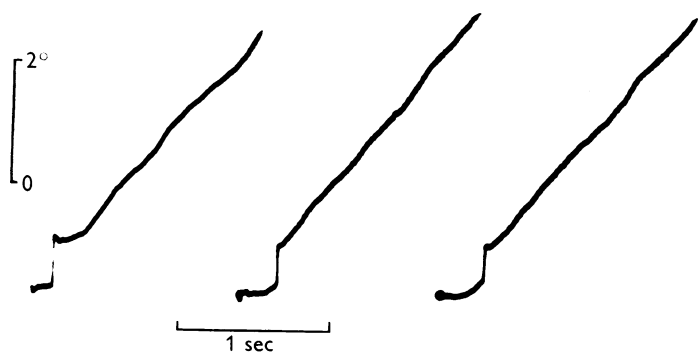

Fig. 2. Records of horizontal eye direction showing the response to the onset of the target's moving with uniform velocity. Note the independence of the saccadic movement from the onset of the smooth movement.

subject during one recording session and illustrates the saccadic movement occurring before, at, and after the beginning of the smooth movement. The appearance of these records suggests that fluctuations in reaction time can occur independently for the two types of movement.

One of the problems under investigation was the metrical relationship between the response and the movement of the target. Preliminary experiments suggested that this relationship was approximately linear; i.e. that at any time after the onset of the target's motion, the distance the eye had moved was proportional to the velocity of the target. The verification of this supposition would require the measurement and re-scaling of many records and so a modified method of recording was adopted. A multi-position switch was used to select from a range of velocities, and at the same time to alter the gain of the recording system in such a way that the product of gain and velocity was held constant. Thus, when the target spot moved slowly and the excursion of the eye was correspondingly reduced, the recording gain was increased accordingly. If the supposition that the eye movements are linearly related to the target movement is true, all the records obtained by this method will look alike. Figure 3 shows a series of records of the responses to five different velocities over a tenfold range of velocity. These records are from one subject on one occasion. The only selection that has been applied is the rejection of records with an early saccade, as it is felt that the late-occurring saccadic movements allow a clearer view of the smooth component. It can be seen that the records fall into two groups; the three faster-velocity records differ from the two slower-velocity records in that no saccadic movement occurs in the latter.

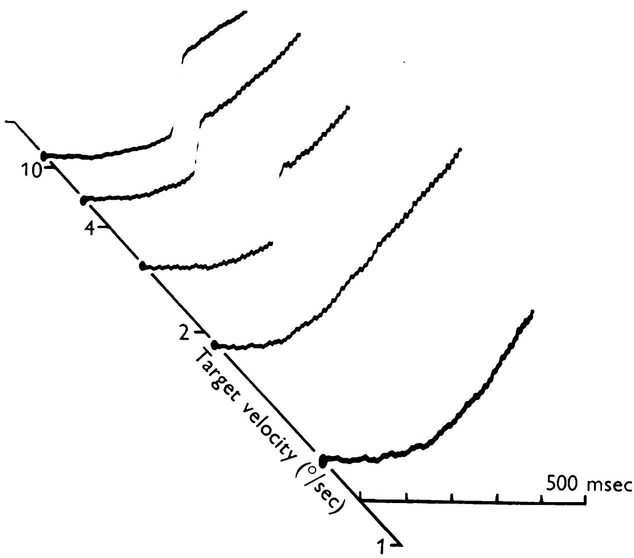

Fig. 3. Records of a series of responses to the onset of a uniform velocity movement of the target. The target was moved at various velocities. Time is displayed horizontally, eye position vertically, and target velocity along a third axis at 45°. The gain of the recording system is made inversely proportional to the target velocity.

The saccadic movements in the three faster records are similar deflexions. Because of the dependence of gain on target velocity, the actual magnitude of the saccadic movements is smaller the slower the target velocity. The saccade in the response to the 3°/sec target velocity is 0·6°. If there were a similarly-appearing saccade in the next slower record it would represent a movement of somewhat less than 0·4°. Its absence is therefore compatible with the threshold for saccadic movements which has been noted earlier.

The smooth movement in all five records appears substantially the same. There is some flattening of the smooth movement in the fastest record (12·5°/sec) and this tendency is more striking in records taken at even greater velocities. However, within the range from 10°/sec down to the slowest velocities which produce significant eye movements within 250 msec of the target moving, about 0·8°/sec, the smooth movement appears linearly related to the target movement.

The smooth movements begin after a reaction time of about 150 msec, and do not reach the same speed as the target until about 400 msec has elapsed since the target began moving. The smooth movement alone must therefore inevitably leave the point of fixation of the eye trailing behind the target even when the eye and the target are both moving at the same

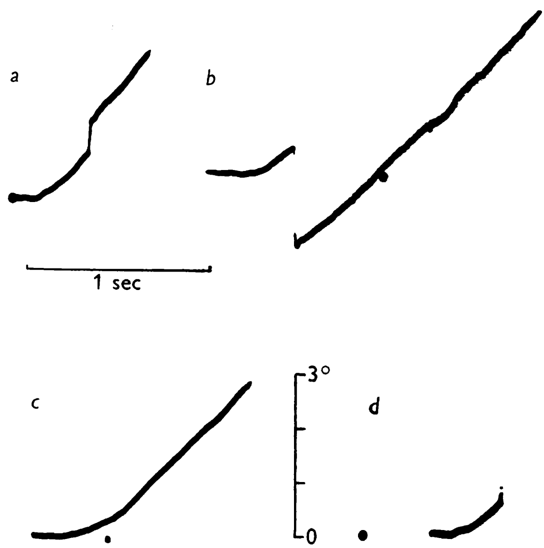

Fig. 4. Tracking responses to a target moving with uniform velocity preceded by a variety of displacements. (*a*) no displacement; (*b*) 3° displacement in a direction opposite to the velocity; (*c*) 1° displacement in a direction opposite to the velocity; (*d*) 1° displacement in the same direction as the velocity. Note the similarity of the smooth component in all cases.

speed. This lag is corrected by saccadic movements in much the same way as an error in fixation of a stationary target.

Experiment 3. The next problem under investigation was whether the smooth movements are brought about by the position of the target's image on the retina, or by its movement over the retina. It is possible to perform a crucial experiment by imparting to an initially stationary target a displacement to one side, and at the same time beginning a movement of uniform velocity towards the opposite side. If smooth movements are the result of positional displacement of the target the movements will be towards the target, but if the smooth movements are brought about by the movement of the target they will be away from the target. To this end the target spot was made to move in the following manner. From an initially stationary position the target was suddenly displaced horizontally to a variable extent and in either direction irregularly. At the same time the target was made to move with a velocity of 3·5°/sec irregularly in either direction. Figure 4 shows records taken in the course of this experiment. The movement of the target supplies the time base of the records and the eye position is represented vertically. Recording was started just before the target began to move, so that a dot appears on each record and indicates the initial positions of the target and eye.

Figure 4*a* shows a record obtained in a case where there was no displacement of the target at the beginning of the movement. It is therefore a repetition of the sort of observation illustrated in Fig. 3, and shows a smooth movement supplemented by a saccade. In the case of Fig. 4*b* the target was given a displacement of 3° to one side and a velocity of 3·5°/sec towards the opposite side. Clearly, if the eye were at all times looking accurately towards the target, the record would be a straight line sloping upwards at approximately 45° through the spot marking the initial positions of the eye and target. The interpretation of the record is that after a reaction time during which the eye does not move, a smooth movement starts in the direction in which the target is moving. When this has been established, a saccadic movement occurs in the direction opposite to the smooth movement to counteract the lead which the eye has over the target. Thereafter the eye continues to move with the target, maintaining accurate fixation throughout the next 1·5 sec. This result indicates that the smooth movement is stimulated by the movement of the target irrespective of its position. The conclusion that the smooth movements are brought about by the movement of the target explains the apparently paradoxical observation that the first movement which the eye makes may take the point of fixation further from the target than if no eye movement at all were to occur.

The results of the same experiment also contain two further observations which are of interest. It has been seen that when a target moves with uniform velocity from its initial stationary position, a saccadic movement is made in the direction in which the target is travelling (Fig. 4*a*). It has also been seen that if the target is given a large (3°) displacement to one side and a simultaneous velocity towards the other side, a saccadic movement is made in the direction opposite to that in which the target is travelling (Fig. 4*b*). This suggests that an intermediate size of displacement might exist, which, when accompanied by a simultaneous velocity towards the other side, produces no saccadic movement in the response. This is the case, and it is illustrated by the recording shown in Fig. 4*c*, where the displacement is about 1°. This balance point is not difficult to achieve, because the threshold for saccadic movements (about $\pm 0 \cdot 5°$) allows plenty of leeway.

There remains one combination to be examined. This is where the displacement and velocity are both in the same direction. The eye movement corresponding to this target movement is shown in Fig. 4*d*. A normal smooth movement is followed by a large saccadic movement, only part of which is seen on the record.

The four records of Fig. 4 show the responses to a target's moving with uniform velocity accompanied by a displacement which varies in magnitude and relative direction. The responses consist of essentially the same smooth movement, on which is superimposed a saccadic movement which varies in magnitude and direction correspondingly. The inference is that the smooth movement is stimulated by the velocity of the target, and the saccadic movement is stimulated independently by the position of the target.

Experiment 4. The results of the previous experiments suggest that saccadic movements and smooth movements satisfy independent requirements and are generated independently of one another. Thus it has been seen that they have independent fluctuations in reaction time (Fig. 2), have different thresholds (Fig. 3), and may be in opposite directions (Fig. 4). Further evidence for their independence would exist if it were possible to dissociate the types of movement pharmacologically. Many drugs, e.g. alcohol and methylpentynol ('Oblivon'; British Schering), are said to cause oculomotor disturbances as side effects, the barbiturate drugs being notorious in this respect. The term 'barbiturate nystagmus' has been used for these effects, which have been described in some detail by Bergman, Nathanson & Bender (1952). Moderate doses of barbiturate drugs are said to disorganize fixation by the occurrence of random movements. Sideways deviation of the eyes whilst under their influence is characterized by a nystagmus, the slow phase of which is towards the straight forward direction. The barbiturates are therefore the drugs of choice with which to start an investigation into the possible pharmacological dissociation of the two types of eye movement. Figure 5 shows the records of the eye movements while tracking a target moving with uniform velocity before and after the intravenous administration of sodium thiopentone (Pentothal; Abbott Laboratories) 100 mgm. The drug was made up in a concentration of 1·25 g/100 ml. and administered continuously at the rate of 1 ml./min. Records of tracking a target moving at 3·5°/sec were taken at frequent intervals during the administration of the drug. The first noticeable effect was the increase in the number of saccadic movements occurring during the first second of tracking. As the amount of drug given increased, the saccadic movements increased at the expense of the smooth movement, until, after 8 min, no smooth tracking movement could be detected. Figure 5 is a record taken at this stage.

The most likely interpretation of this record is that the drug interferes with the smooth tracking response so as to make it inoperative. However,

Fig. 5. Tracking eye movement responses to a target moving with constant velocity (*a*) before and (*b*) after the intravenous administration of sodium thiopentone (Pentothal) 100 mg.

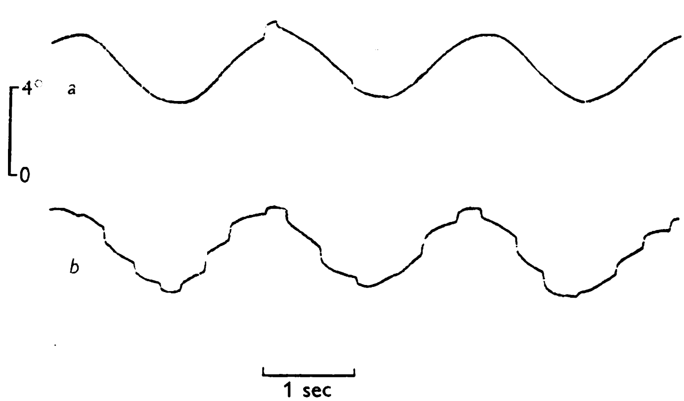

Fig. 6. Tracking eye movement responses to a target moving with simple harmonic motion (*a*) before and (*b*) 100 min after the oral administration of amylobarbitone sodium (Amytal) 300 mgm.

there is another possible interpretation which needs to be eliminated before this is established. If the barbiturate drugs acted by producing a nystagmus which happened to have the slow phase in the direction opposite to the tracking movement, and the velocity of the slow phase of the nystagmus were just equal to the velocity of the smooth tracking movement, and the nystagmus and the tracking movement combined additively, then a record something like that illustrated would result. That this is not, so was clear from the fact that the records looked the same whichever the direction of the tracking. A more convincing demonstration of this is available in Fig. 6. This shows the effect of a barbiturate drug, in this case amylobarbitone sodium (Amytal; Lilly) 270 mg taken by mouth, on the ability to track a sinusoidally moving target. The target was moving from side to side with a frequency of 0·5 c/s and an amplitude of 4°. Before the drug was taken this movement was tracked smoothly with very few saccadic movements. One hundred minutes after the drug was taken tracking was effected mainly by a succession of saccades.

DISCUSSION

The experiments reported in this paper show that the eye movements which are made in tracking consist of the superimposed movements of two independent systems. This is not an example of redundancy in the central nervous system for the mechanisms subserve different demands. The smooth movements are responses to movement of the image across the retina, and in the absence of saccadic movements could do nothing to bring the image of the target on to the fovea. On the other hand, the smooth movements do result in a stationary image being cast on the retina by a moving target, in much the same way as when a camera is slewed round to photograph a moving object.

Not only are smooth eye movements brought about by the movement of the image over the retina, but the velocity of the smooth movement is linearly related to the velocity of movement of the target. This means that the velocity of the image on the retina is not only detected but also measured with considerable precision over a fairly wide range of velocities. The measurement of velocity could be performed on the retina or more centrally. It has been argued that if the velocity of the image is the stimulus which evokes smooth tracking responses, the ultimate speed of movement of the eye must always be slightly less than the speed of movement of the target. This deficiency has never been demonstrated, except in the case of very fast moving targets, and it has been suggested that this is due to the inadequacy of recording techniques. However, it can be shown that there need be no residual movement of the image over the retina to maintain the movement of the eyes. If a movement of the image on the retina evokes an acceleration of the eyes in the direction of that movement, then the eyes will only travel with uniform velocity (i.e. without acceleration) if there is no image movement. This appears to be the way in which a precise match of eye velocity to target velocity is achieved. It is known that very slow drifts in eye position occur even during fixation of a stationary target. The error in the velocity of tracking a uniformly moving target does not exceed the velocity of these drifts.

Westheimer (1954*a*) has pointed out that the saccadic movement is essentially ballistic. This means that the decision concerning the magnitude of the movement is taken before the movement begins, and that the movement then follows an inevitable course. The adequacy of the movement is tested in retrospect, and any deficiencies are rectified by similar ballistic movements. The alternative to a ballistic movement is a guided one. Such a movement is under continuous control, and should the movement at any time be found to be inadequate, either because of its own inaccuracy or because of changes in the task requirement, it can be modified accordingly. The question therefore arises whether smooth tracking movements are ballistic or guided. Westheimer (1954*b*) has suggested that smooth movements are also ballistic. His reason for saying this is that he describes smooth movements as consisting of stretches of movement of uniform velocity joined by very short regions during which the velocity changes. The changes are said to last not more than 20 msec and to recur not more frequently than every 100 msec. This view is in agreement with the observation by Stroud (1950) that when tracking harmonic motions many cycles need to elapse before smooth accelerations are found in the responses. On the other hand Dodge *et al.* (1930) have described and illustrated smooth accelerations occurring within half a cycle (0·4 sec) of the onset of the oscillations, and Westheimer (1954*a*) has shown a change in velocity which occurs gradually over a period of 90 msecs. The records reproduced in the present paper suggest that it is difficult to be sure on this point. Figure 5 shows a sudden change of velocity, but the accelerations in Fig. 3 appear to occur gradually and slowly. The remaining illustrations show all graduations from very pointed to very gradual.

It is clear that the ability to distinguish sudden from gradual accelerations depends on the precision with which the eye position can be ascertained, for small deviations may make a smooth acceleration appear sudden or a sudden change of velocity appear gradual. The variance in eye position during fixation of a stationary target is about $1/10°$ (Barlow, 1952) and this may be taken as the noise level below which it is profitless to look for significant tracking movements. The distinction between sudden and gradual accelerations is equivalent to the distinction between a triangular and a sinusoidal motion, and depends on the detection of harmonic components, the largest of which is $1/9$ the amplitude of the fundamental oscillation. From these figures it can be shown that a change of velocity of $V°$/sec cannot be localized in an interval much shorter than $2/V$ sec. It would seem therefore that the question whether smooth eye movements are ballistic or guided cannot best be decided by the presence or absence of corners in the records.

The distinction between a guided system and one which makes successive approximations with a series of ballistic movements is to a certain extent arbitrary. It may be assumed that a system takes in information at discrete intervals which, in the limit, approaches continuous sampling. The response of the system to one sample of input information will extend over a certain time, which we may call the response time. If the sampling interval is large compared with the response time, then the system will be described as ballistic. Saccadic eye movements fall in this category, as do, for example, nerve action potentials. In the latter case the sampling interval is determined by the refractory period, which exceeds the response time, i.e. the duration of a spike. If, on the other hand, the response time is large compared with the sampling interval the system would be considered to be guided. Muscle contraction provides a good example of such a system. Clearly it is possible to have any degree of guidedness between the extremes, and it is doubtful whether the distinction is always worth making.

In view of the narcotic action of the barbiturate drugs it would be tempting to attribute the action which they have on tracking to a reduction in the attention which the subject gives to the task. This is not so, for a subsidiary experiment showed that nitrous oxide mixed with air in sufficient concentrations nearly to produce unconsciousness has very little effect on eye movements. So long as the subject can keep his eyes open he is able to track without impairment. The effect of barbiturates on the smooth component of tracking movements is complete with doses which do little more than induce slight drowsiness. The effect of barbiturates on tracking is, therefore, not secondary to their narcotic action, but is more direct. Together with information concerning the effect of barbiturates on other oculomotor functions (Rashbass & Russell, 1961; Westheimer & Rashbass, 1961) this helps to delimit the site of action of the drug and to distinguish the neurological pathways involved.

SUMMARY

1. Tracking eye movements were recorded in normal subjects presented with a variety of visual tracking tasks.

2. Sudden lateral displacements of the target evoke saccadic responses. Displacements smaller than about 0·25° cause no response.

3. The initial response to a target moving with uniform velocity has both saccadic and smooth components.

4. The reaction times of these two components vary independently.

5. The smooth component is linearly related to target velocity up to 10°/sec; the saccadic component has a threshold.

6. Tasks involving various combinations of displacement and velocity evoke saccadic and smooth responses; the smooth movement is determined by the task velocity, the saccadic movement by the task displacement.

7. The barbiturate drugs differentially interfere with the smooth-movement component.

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