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SACCADIC AND SMOOTH PURSUIT EYE MOVEMENTS IN THE MONKEY

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SUMMARY

1. Voluntary eye movements were measured in the chronic, unanaesthetized monkey. A training technique is described which conditions the animals to follow a large variety of target trajectories.

2. The eye movements of the monkey are not qualitatively different from those of man. In response to random target motions the monkey also employs a combination of saccadic and smooth pursuit movements.

3. Monkeys execute their saccades more rapidly than humans.

4. Monkeys are capable of attaining smooth pursuit velocities which are twice as fast as those of man.

5. Most of the critical experiments showing the separate nature of the saccadic and smooth pursuit modes in man have been performed on monkeys with similar results.

6. Therefore, if one remains aware of the quantitative differences between the two primates, results of neurophysiological studies of the oculomotor system of the monkey can be expected to have considerable relevance when extrapolated to man.

INTRODUCTION

Voluntary eye movements have been recorded quantitatively in man for the last 65 years. It has been found that human eye movements are composed of two distinct components: a rapid component called a saccade which is elicited in response to a target displacement off the fovea and a slower component called a smooth pursuit movement which is elicited by target velocity. Rashbass (1961) demonstrated that the two movements are created by separate systems which possess quite different characteristics and independent neurological pathways. Some of the behaviour of the saccadic mode can be described by a discrete control system which samples every 250 msec (Young, 1963), whereas the smooth pursuit system is thought to be continuous in nature (Robinson, 1965).

In the past, the mechanisms of eye movement control have mostly been investigated by stimulating the oculomotor system from without by a target movement and noting the eye movement response. Techniques such as externally varying the intrinsic visual feedback (Fender & Nye, 1961; Young & Stark, 1963) or measuring the net isometric tension of the horizontal recti (Robinson, 1964) have also been used. The next logical step is to relate the neural activity of various oculomotor areas to specific eye movements. However, it would be difficult to study the oculomotor system of man from within since, except for certain pathological cases which usually affect diffuse areas, human material is unavailable. Therefore, in this study, the eye movements of the most convenient laboratory primate, the monkey, were investigated to show that monkey eye movements were similar to those of man and thus establish the monkey as an animal from which useful extrapolations about oculomotor organization can be made to humans.

It was found that monkeys possess both a saccadic and smooth pursuit eye movement which are qualitatively similar to those of man. In addition, these movements are subserved by different control systems which behave like those of man. These results suggest that the neurological mechanisms controlling eye movements in the monkey are similar to those in man, making the monkey an excellent animal for neurophysiological studies of the oculomotor system. Monkeys are, however, able to turn their eyes at higher velocities and so execute both shorter-duration saccades and higher-velocity smooth pursuit movements.

METHODS

Measurement of eye movements

Eye movements were measured in three unanaesthetized monkeys (7–10 lb. (3·2–4·5 kg) *Macaca Speciosa*) by the technique of a chronically implanted search coil in a magnetic field (Fuchs & Robinson, 1966). Briefly, 3 turns of fine wire are laid under the insertions of the four rectus muscles beneath the bulbar conjunctiva. The wire ends are led behind the lateral fornix and under the skin to terminate in a plug fastened to the skull. These 3 turns form a permanently implanted coil which moves with the eye. When the monkey is placed within two alternating magnetic fields in spatial and phase quadrature, a voltage is induced in the coil which when processed through electronic phase detectors gives signals proportional to the horizontal and vertical components of eye position. This technique has a sensitivity of 1·5 min of arc over a linear range of ±20° with a bandwidth of 1000 c/s.

Animal training

By having such an 'on-line' measure of eye position, the animal may be conditioned to execute specific eye movements. In order to measure eye position with respect to a fixed head, the monkey is first trained to hold his head still voluntarily.

The animal is restrained in a conventional primate chair so placed that his head projects into an open frame 2 ft. × 2 ft. × 2 ft. (61 cm × 61 cm × 61 cm) which supports the coils that create the horizontal and vertical magnetic fields. A bite bar is positioned just in front of the monkey's mouth (Fig. 1). When the monkey grasps the bar with his teeth it slides towards him a few millimetres tripping a microswitch which starts an electronic timer. If the monkey pulls continually for several seconds, he receives a liquid reward through the hollow centre of the bite bar. During early training stages the animal is required to pull for only 50 msec which amounts to just touching the bite bar. Over a period of about 2½ weeks, the time for which he must pull is gradually increased to 5 sec. Although he does not receive a liquid reward until the entire 5 sec interval has elapsed, a buzzer sounds whenever he bites the bar to provide an immediate reinforcement for the correct behaviour. Since the sound is soon followed by a squirt of orange juice, the monkey will associate it with a prospective reward, making subsequent training with additional tasks easier.

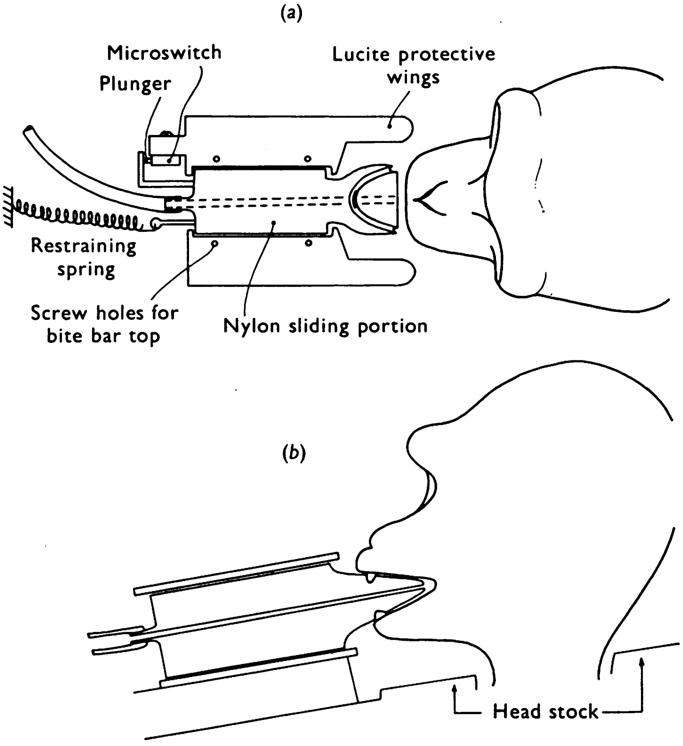

Fig. 1. (*a*) View of the bite bar with its top removed. (*b*) Mid-sagittal section of the monkey on the bite bar.

The bite bar is spring-loaded so that the monkey must maintain a constant tension to close the microswitch. Deep U-shaped grooves on an otherwise smooth nylon surface force the monkey to re-establish approximately the same head position on each pass at the bite bar. Except for studies on very small eye movements, the head may be considered as fixed whenever the monkey is pulling against the spring.

Although it is possible to observe voltage variations from the coil as the eye moves, the untrained monkey never dwells on any object in his visual field long enough to relate a specific voltage to a known direction of gaze. Lights flashing in a darkened room, a banana hung tantalizingly just out of reach or a spinning spiral which, in humans, draws the eye to its fixed centre are virtually ignored. Therefore, to establish an electrical zero and gain calibration, the monkey must be assigned a simple discrimination task.

A circular spot of light subtending 2° at the eye is displayed on a translucent screen lowered before the monkey. For about 2 days he continues to be rewarded for the bite bar task in the presence of the circle. After this period, a square spot of the same size is occasionally substituted for the circle. Whereas pulling on the bite bar while a circle is present elicits a reward, pulling during a displayed square goes unrewarded. For at least a week, the experimenter must regulate the occurrence of circles and squares by hand since the monkey easily becomes frustrated by this new contingency.

However, at the end of this time, the behaviour pattern has been well enough established to shift the animal to an automatic schedule. An 80 slide Kodak Carousel 700 projector is remotely controlled to present a different slide every 12 sec from a random assortment of circles and squares. The projection of a circle is detected by a mechanical finger on a microswitch which senses elevations placed on the cylindrical slide tray. After the animal receives a reward, the slide is changed even though the 12 sec interval has not elapsed so that two rewards cannot be obtained for the same circle. Although nothing prevents the monkey from pulling all the time and receiving a reward with every second slide on the average, he nevertheless, falls into that behaviour pattern which yields the most rewards for the least effort. After a total of about 3 weeks of 1 hr daily sessions on the discrimination task, the attentive monkey pulls 80 % of the time at the appearance of a circle and only 20 % of the time at the appearance of a square.

When the monkey has mastered the random presentation of larger figures, their size is gradually reduced and the frequency of slide changes increased so that after 2 months from his initial introduction to the bite bar, the monkey is discriminating between figures subtending an arc of ¾° at his retina and changing at a rate of one every 8 sec. Since the monkey must pull for 5 sec during the appearance of a circle, he has only 3 sec to make an identification and must therefore keep his gaze riveted to the spot where the figures are changing. Because of the length of the training period the monkey is taught to discriminate before the search coil is implanted.

To move the target spot, a mirror mounted on a galvanometer (Model 618Y, Hewlett Packard Sanborn Division, Waltham, Mass.) is placed in the optical path from the projector to the screen. The mirror drive has a bandwidth of 30 c/s with a step response which has a 10 % overshoot and settles to its new position within 30 msec. An electrical signal to the galvanometer produces a horizontal target motion on the screen 2 ft. (61 cm) from the subject. A second mirror whose axis of rotation is at right angles to the first may also be inserted into the optical path to create vertical target motion. In this way, the target can be positioned anywhere in the monkey's visual field.

An arbitrary zero target position is established approximately along the primary direction of gaze, and the monkey is invited to perform his visual discrimination task while the zero or base line is established, i.e. the voltage from the eye coil is adjusted to equal the galvanometer voltage corresponding to zero target position. The discrimination task is then shifted 10° nasally and temporally and up and down to obtain a gain calibration. In any animal preparation, eye position can be determined only within the accuracy of the calibration. This method allows the eye's position in space to be located within about ½° of arc.

Once the zero and gain calibrations have been established, the discrimination contingency is removed, and the monkey is required to follow a moving circular target spot. Figure 2 shows the scheme to reward the monkey for accurate tracking. The voltage induced in the eye coil is led through separate a.c. amplifiers and detected against horizontal (e_x) and vertical (e_z) reference voltages to produce d.c. signals proportional to the horizontal (θ) and vertical (ϕ) components of gaze. Consider the lower path for the horizontal component. The horizontal error, e_θ, is the difference between horizontal eye position θ and a signal corresponding to the horizontal component of target position E_{T_x}. The absolute value of the error $|e_\theta|$ is derived since the monkey is rewarded for either small over $(+e_\theta)$ or under $(-e_\theta)$ estimations of the target position. If the absolute error is less than a tolerated maximum, the threshold device remains in its upper state. When the absolute error exceeds the tolerated maximum, the device drops to a new state which is sensed by the master summer Σ. The master summer also weighs the inputs from the vertical error detector (V_ϕ) whose electronics are identical to the horizontal, the projector (V_{proj}) which indicates the projection of a circle and the bite bar (V_{bb}) which indicates if the head is fixed. When all these contingencies are met, i.e. accurate tracking of a circle while pulling on the bite bar, the buzzer sounds and several seconds later as determined by the clock, a signal (V_s) is sent out releasing the solenoid valve of a liquid reservoir to give the monkey a gravity-fed 2 ml. squirt of orange juice. A dual beam oscilloscope provides a visual display of target and eye position facilitating the calibration procedures and the animal training.

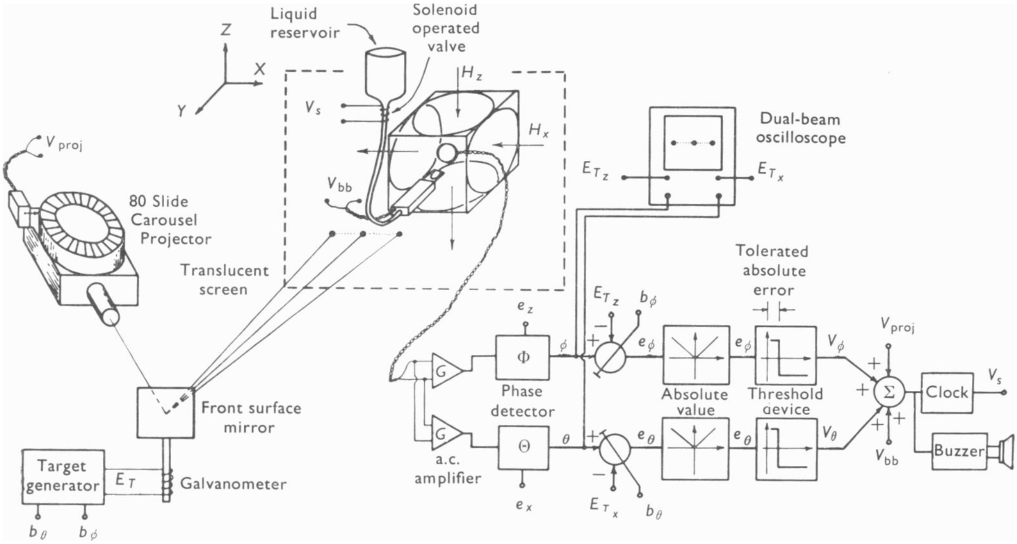

Fig. 2. Block diagram of the complete training apparatus.

It is well known that in response to random target trajectories the human eye exhibits a latency of between 200 and 250 msec before a saccadic movement. So as not to penalize the monkey for similar natural reaction times, the reward circuitry is deactivated for about 300 msec after the initiation of a target movement (e_θ and e_ϕ are forced to zero on command (b_θ and b_ϕ) from the target generator). The detailed electronics of the error detection and reward circuitry are described elsewhere (Fuchs, 1966).

The monkey's first tracking task is to look at a stationary circular spot for up to 5 sec. If the animal's gaze wanders more than the maximum tolerated distance away from the target (say ±1°), no reward is obtained. After learning to fixate the stationary target over a period of a few days, the monkey will tend to pursue a target that is moved about on the screen. The animals are broken in with rapid displacements in target position followed by constant velocity trajectories. Within a few days, the monkey can be trained to follow any complex target movement required by the experimenter.

The complete training procedure from bite bar to accurate tracking takes between 1½ and 2½ months. However, once taught a task, monkeys do not forget. On several occasions when an animal's search coil broke prematurely, he was set aside in his cage while his fellows with continuous coils were trained. After a month of inactivity, he would, within one training session, return to his previous level of competence. During the entire conditioning period, the monkey is deprived of all liquids, but in the course of a good daily session he can earn up to 200 ml. of orange juice in 2 ml. squirts. No change is made in the animal's normal solid diet.

All of the monkey's eye movements during the daily hour session were recorded and stored on a tape recorder possessing a bandwidth of 1560 c/s between the 3 db attenuation points and a minimum signal/noise ratio of 47 db. Eye movements in response to a target trajectory were retrieved from the tape and printed by a direct writing mirror galvanometer recorder with a frequency response of 1900 c/s between the 3 db attenuation points. Both instantaneous changes in target position (step displacement trajectories) and constant velocity targets (ramp trajectories) were displayed to the monkeys. The targets were presented on a schedule drawn from a table of random numbers so that the subject never knew when, with what magnitude, or where the target would move.

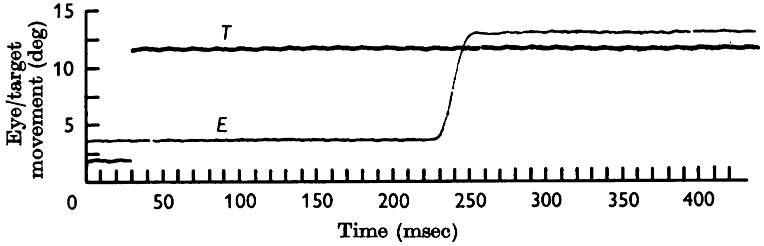

Fig. 3. A typical recording of the step response of a monkey trained for visual tracking. In this illustration and all subsequent figures containing records, the letter '*E*' will identify the horizontal eye position, the letter '*T*', the horizontal target position.

RESULTS

The step response. When a monkey is presented with an instantaneous change in target position, his response is remarkably stereotyped and typically represented by Fig. 3 for a 10° target movement. After a latency of 200 msec, the eye accelerates to a maximum slewing speed of 580 deg/sec which is reached about midway in the total trajectory. The eye then decelerates, exhibiting a time course roughly symmetrical to the acceleration phase, to bring the fovea on target with no noticeable overshoot or ringing. The duration of the movement is 28 msec. This trajectory is seen to be the monkey counterpart of the human saccade.

As the magnitude of the saccade increases above about 25°, the eye exhibits an increasing tendency to overshoot the target as can be seen from the family of typical saccades in Fig. 4. The overshoot is roughly constant at 0·5°, and the eye settles with no noticeable ringing to a steady state in 15 msec. In response to target displacements greater than 25°, the eye often falls short of the target with its initial saccade, requiring a second saccade within about 250 msec to correct the remaining error. Most of the saccades were not initiated from the primary direction of gaze, but rather their origin was offset to utilize the ± 20° linear range of the equipment. Hence, a 30° nasal saccade might start from an initial 15° temporal displacement, pass through the primary position and terminate with a 15° nasal displacement.

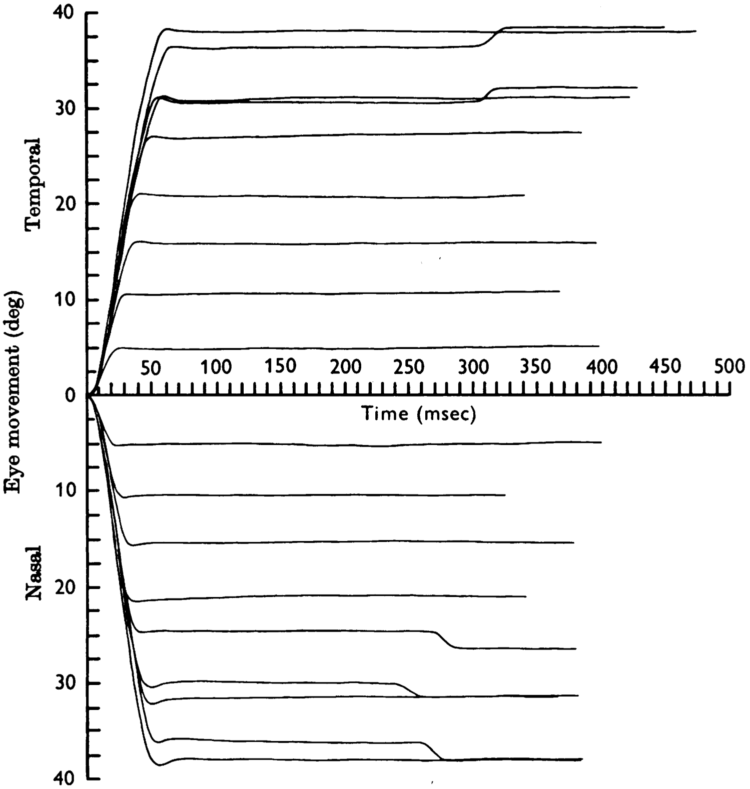

Fig. 4. Superimposed tracings of horizontal saccadic eye movements in steps between 5° and 40° selected from one monkey as representative. All the responses to a target step were averaged with regard to magnitude, duration and maximum velocity. That trajectory which best matches these averages and in addition possesses the appropriate overshoot and second saccade indicated by the majority of responses is plotted.

Figure 5 shows the variation of saccadic duration and maximum velocity with magnitude. The duration, estimated as the time from the onset of eye movement to the next velocity zero, increases approximately linearly with magnitude at a rate of 1 msec/deg. At both 5° and 10°, nasal and temporal saccades are essentially indistinguishable (a temporal movement as defined here is an abduction of the implanted eye). Above 10° temporal saccades possess a lengthening deceleration phase which causes their durations to be 4 msec longer, on the average, than the corresponding nasal saccadic durations. The maximum saccadic velocity increases at a significantly smaller rate between 20° and 30° than between 5° and 15°.

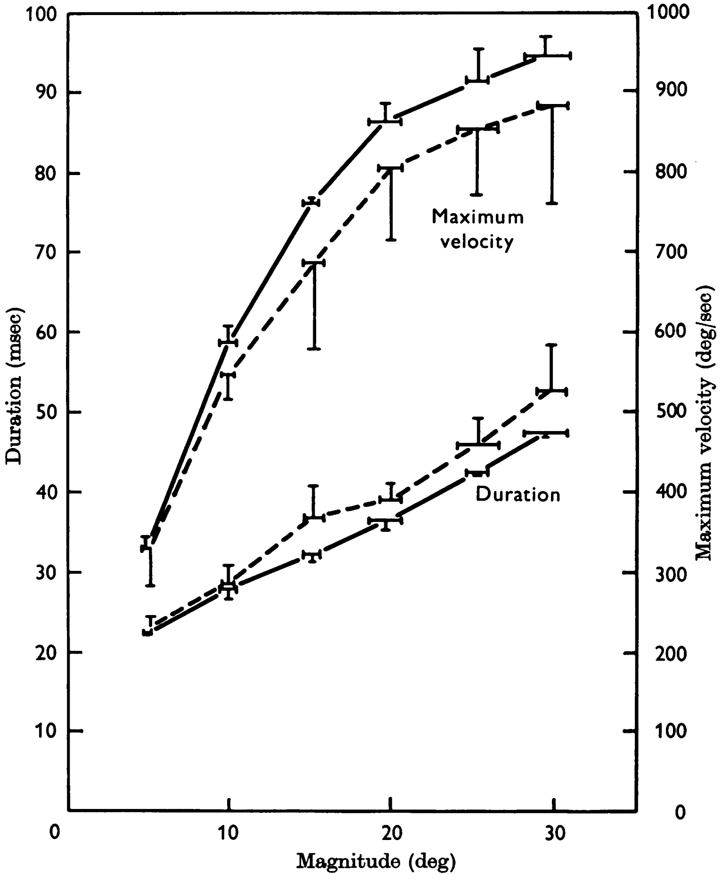

Fig. 5. Duration and maximum velocity of horizontal saccades against magnitude. Each point is the mean of at least twenty-four observations, eight from each monkey; the bars represent the standard deviations from the mean. —, Nasal; - - -, temporal.

In one animal who co-operated by executing large movements, the maximum velocity for a 40° saccade was the same as that for a 30° saccade, suggesting that a velocity saturation occurs at about 1000 deg/sec.

Figure 6 shows that the latency to the occurrence of a saccade can vary between 100 and 440 msec and is not dependent upon its magnitude. The various shadings identify the different size saccades to demonstrate that each magnitude displays approximately the same distribution as the total population. Nasal saccades possess an average latency of 226 msec (± 50 S.D.) compared to the average temporal latency of 256 msec (± 52 S.D.). However, the two populations show considerable overlap so that the mean of the above values of 241 msec can be used as the typical saccadic latency independent of magnitude or direction.

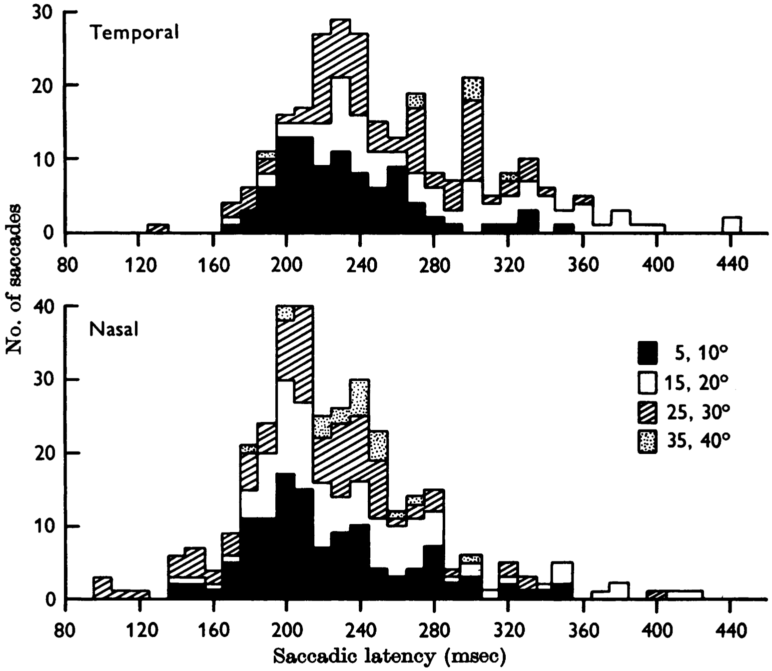

Fig. 6. Histogram of the number of saccades occurring at each latency.

Vertical saccadic responses are qualitatively similar to the horizontal. An upward saccade is preceded by an average latency of 244 msec (± 32 S.D.) and a downward saccade by an average latency of 223 msec (± 41 S.D.). 90 % of the vertical responses were either critically damped or overdamped with upward saccades less heavily damped and consequently shorter than downward saccades. As with horizontal saccades, the vertical saccadic duration increases linearly with magnitude, but at a greater rate (about 1·2 msec/deg for upward and 1·5 msec/deg for downward movements). Therefore, since the durations of 5° horizontal and vertical movements are about the same, the vertical saccadic duration becomes larger than the horizontal at a rate of $\frac{1}{4}$ msec/deg.

The ramp response. Contrary to the relatively stereotyped saccadic response to a step displacement in target position, Fig. 7 shows the variety of trajectories that are observed in response to a ramp target movement. The response consists of a smooth component and a saccadic component which may occur before, during or after the completion of the smooth portion. In response (*a*), the initial movement is a saccade. In both responses (*b*) and (*c*), the eye first undergoes a smooth correction in an apparent attempt to match the target velocity. In trajectory (*c*), the eye actually attains target velocity before being interrupted by the saccade. These trajectories are qualitatively similar to those recorded by Rashbass (1961) on human beings.

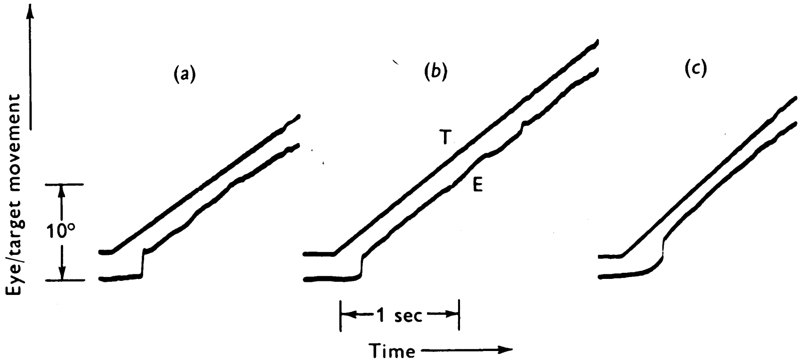

Fig. 7. Records of monkey responses to a target moving at 10°/sec.

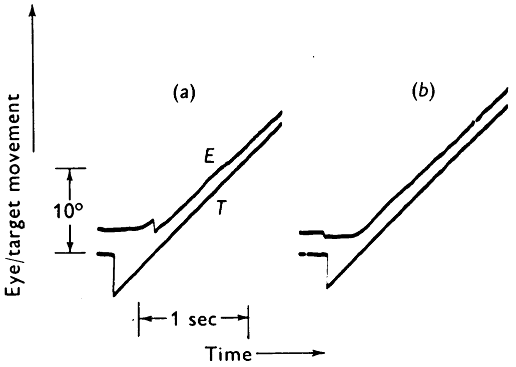

Fig. 8. Eye movements in response to a step-ramp target trajectory with a velocity of 13°/sec.

To demonstrate that the smooth component of the ramp response is elicited by the target velocity and not target displacement like the saccade, the monkey was presented with the Rashbass step-ramp target trajectory.

Figure 8*a* shows that the target first steps in one direction before commencing a constant velocity in the opposite direction. After a delay, the response exhibits a smooth component which moves the eye away from the target but in the direction of target motion. A saccade in the opposite direction is then necessary to bring the eye back on target. The fact that smooth pursuit responses are elicited by target velocity accounts for the paradoxical observation that the initial response takes the eye further from the target than if no response at all had occurred.

If the step offset in the trajectory of Fig. 8*a* is adjusted so that the target recrosses its zero position in about one saccadic reaction time, a smooth pursuit movement only without the attendant saccades will result (Fig. 8*b*). The latency of the smooth response has increased from 150 to 200 msec, indicating that the initial step has not gone unnoticed. From at least ten such responses each at 9, 13 and 18 deg/sec, it was found that the mean durations of the smooth pursuit accelerations from zero to maximum velocity were 131 msec (± 25 S.D.), 137 msec (± 28 S.D.), 153 msec (± 61 S.D.) respectively, indicating that large velocity changes take more time than small velocity changes. However, the percentage variation in smooth pursuit duration is small (17 % increase from 9 to 18 deg/sec compared to 36 % increase in saccadic duration from 10 to 20°); furthermore, the large standard deviation at 18 deg/sec leads to additional ambiguity between the three smooth pursuit durations. Therefore, the mean of the above values of 140 msec is a good figure for the time required by the eye to change from one velocity to another. This figure agrees closely with the one published by Robinson (1965) for man.

The monkeys were presented with many ramps from 5 to 45 deg/sec. Figure 7 shows it would be difficult to plot a family of typical responses because the component smooth and saccadic responses show a variety of temporal relations. In response to a 5 deg/sec target motion, the three monkeys exhibited eight different saccadic–smooth pursuit combinations, including one trajectory using a smooth pursuit movement only. Between 10 and 20 deg/sec, however, certain responses are common to all the animals and represent about 50 % of the trajectories of the entire monkey population. The trajectories of Fig. 9 are the means of these most frequent responses which have been reconstructed from averages in time, position and velocity at various salient points in the trajectory (i.e. the onset and conclusion of each smooth pursuit and saccadic component). Mean latencies to the initiation of smooth movement are 174 msec (± 34 S.D.), 157 msec (± 23 S.D.) and 144 msec (± 23 S.D.) respectively, demonstrating a decrease in latency with stimulus velocity. By the end of the smooth pursuit phase, the eye has reached about 60 % of target velocity [6·9 deg/sec (± 1·5 S.D.), 9·4 deg/sec (± 2·7 S.D.), 11·7 deg/sec (± 3·5 S.D.) respectively],

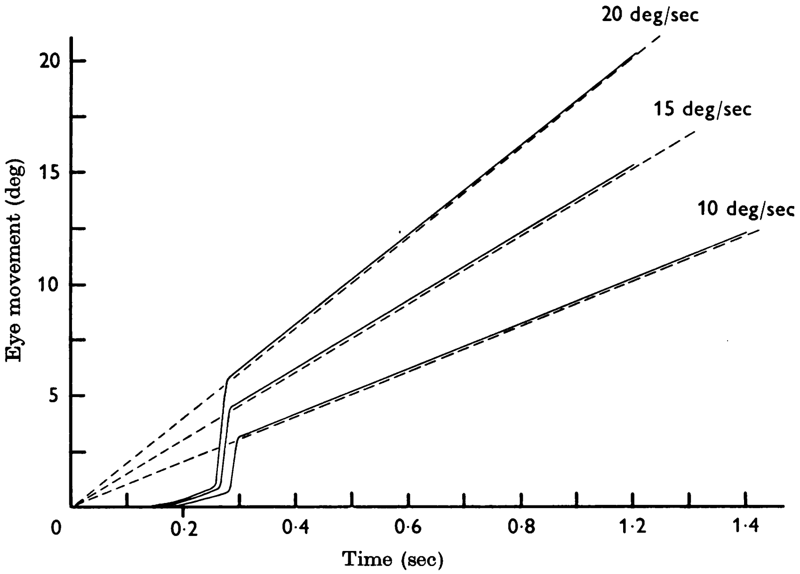

Fig. 9. Eye movement responses to 10, 15 and 20°/sec target ramps. Each trajectory is the segmental mean of at least 20 of the responses most common to the monkey population. Targets are shown by interrupted lines.

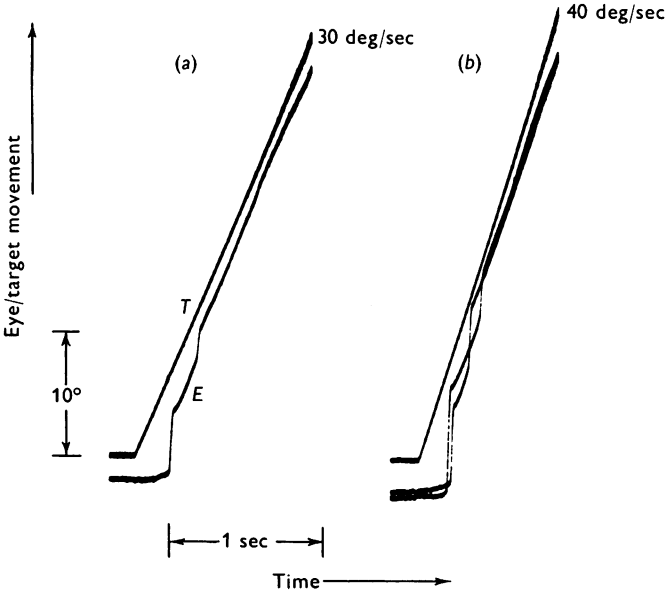

Fig. 10. Selected recordings of responses to 30 and 40°/sec target ramps.

while closing less than $\frac{1}{3}$ of the position error [0·7° (±0·3 S.D.), 0·9° (±0·4 S.D.), 1·0° (±0·5 S.D.)]. The magnitude of the saccade increases with ramp velocity [2·6° (±0·6 S.D.), 3·6° (±0·6 S.D.), 4·7° (±0·6 S.D.)] and is always sufficient to get the eye on target at the correct velocity.

In response to ramps between 25 and 45 deg/sec, the monkey again displays many combinations of saccade and smooth pursuit movements and no one trajectory can be considered as typical. Whereas the eye can catch a 15 deg/sec target within three movements (the smooth, saccadic and smooth components of Fig. 9), at higher velocities Fig. 10 shows that more preliminary manoeuvres are necessary. The initial saccade now usually falls short leaving a small position error which elicits a second saccade either after a relatively brief interval (range 40–160 msec) or after about one reaction time (Fig. 10*b*). A saccade following the shorter interval generally carries the eye past the target, and a smooth component then brings the eye on target at the correct velocity. However, by waiting the normal reaction time, the eye jumps precisely on to the target. Since the longer saccadic delay is followed by a more accurate saccade, the oculomotor system may use the additional time to form a better estimate of the retinal disparity. The notion that error processing occurs between saccades in monkeys requires a modification of the simple sampled data model for humans proposed by Young (1963).

The 'panic response', composed of the rapid double saccade pair followed by a smooth pursuit movement on to the target, allows the time required by the eye to catch faster targets to be only 30% longer than for slower targets. Average elapsed times from the onset of target movement until the eye is accurately tracking are 648 msec (±247 S.D.), 328 msec (±42 S.D.), 301 msec (±38 S.D.), 351 msec (±17 S.D.), 447 msec (±95 S.D.), 455 msec (±71 S.D.), 483 msec (±32 S.D.) and 442 msec (±22 S.D.) respectively for all responses in 5 deg/sec intervals between 5 and 40 deg/sec.

All monkeys were able to overtake and track ramps moving up to 40 deg/sec. Higher velocities could not be studied, since at 50 deg/sec the target moves between 20 and 30° before the eye can overtake it; hence we are constrained by the ±20° system linearity. However, responses to sine wave targets showed that the maximum smooth pursuit velocity for the average monkey is between 40 and 45 deg/sec.

Separation of the saccadic and smooth pursuit modes. The above results suggest that the saccadic and smooth pursuit responses are the products of separate systems. The two components have been shown to occur with complete temporal independence. Saccades are elicited by displacement of the target, whereas smooth movements are responses to target velocity. Latencies before a saccade are, on the average, 80 msec longer than before a smooth pursuit movement. Finally, the saccade is a rapid movement of short duration (28 msec for 10°) compared to the slower, long duration smooth pursuit movement (131 msec to change from 0 to 9 deg/sec).

If the smooth pursuit and saccadic responses are the products of separate control systems, they might be further distinguishable by their behaviours under various conditions of visual feedback. It is well known that since an eye movement in one direction causes an equal and opposite retinal image movement, a unity feedback loop exists between the input and output of the voluntary tracking system. This intrinsic feedback loop can be modified without physically disturbing the animal by controlling the target position with a signal proportional to eye position. Figure 11 shows that this external path is effectively in parallel with the internal feedback loop. The measured horizontal eye position, θ_E, is amplified by an amount α and fed back to the mirror drive where it is electrically added to the target controlling signal θ_{TC} to create the target position θ_T as

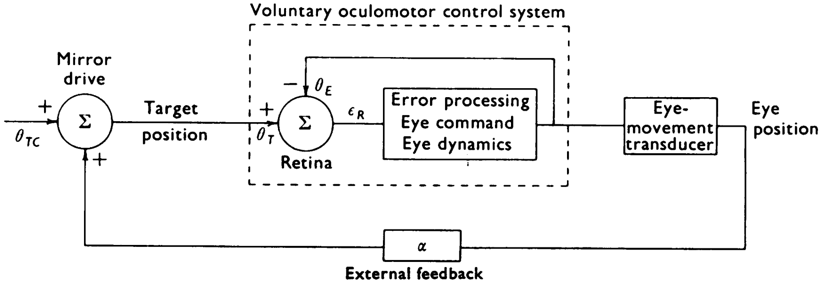

Fig. 11. Schematic illustrating the technique for externally varying the visual feedback of the oculomotor tracking system.

$$\theta_T = \theta_{TC} + \alpha\theta_E.$$

The retinal disparity ϵ_R is then seen to be

$$\epsilon_R = \theta_T - \theta_E = \theta_{TC} + (\alpha - 1)\,\theta_E = \theta_{TC} + K\theta_E,$$

where $K = \alpha - 1$ represents the total feedback around the tracking system. In normal tracking, $\alpha = 0$ ($K = -1$) so that an eye movement results in an equal but opposite retinal image movement.

For the so-called open-loop condition, the internal feedback is cancelled by external feedback ($K = 0$, $\alpha = +1$), and the retinal error is maintained constant at θ_{TC}. Therefore, every eye movement is accompanied by an equal target movement in the same direction so that the image of the target is stabilized on the retina. If we provide an initial 2° target displacement, the eye executes a corrective saccade whereupon the target simultaneously steps an equal amount ahead. Continued saccadic pursuit of the ever-receding target leads the eye down the staircase shown in

Fig. 12*a*. If the target is not given an initial displacement, the eye will exhibit spontaneous instability which manifests itself as a smooth growing time course before being interrupted by a saccade (Fig. 12*b*). This completely different behaviour under open loop conditions (actually $0 \leqslant K \leqslant +0{\cdot}1$) is interpreted as an endless pursuit mediated by the smooth pursuit system.

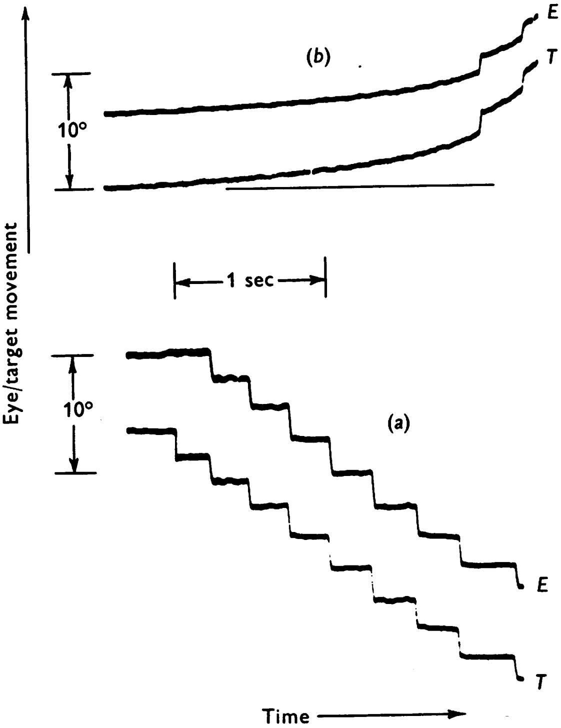

Fig. 12. Endless ocular pursuit of a target with the eye tracking system under positive feedback. (*a*) Saccadic instability after a 2° initial nasal target displacement ($K = 0$). (*b*) Spontaneous pursuit instability with no initial stimulus ($K = +0{\cdot}1$).

When the oculomotor system is subjected to sufficient negative feedback, it will break into oscillations. Consider the case for $K = -2 (\alpha = -1)$. An initial 5° target displacement elicits a saccade within one reaction time. Simultaneous with the occurrence of the saccade, the target returns to its original position. After another reaction time, the eye again attempts to saccade on to the target, but the evasive target again returns to its initial 5° displacement. If this futile pursuit continues, the machine-like saccadic oscillations of Fig. 13 result. Theory predicts that an over-all feedback of $K = -2$ should be sufficient to sustain oscillations. In monkeys, sustained oscillations occurred for $K = -2{\cdot}3$. With no initial target stimulus α must be increased to -2 ($K = -3$) before the drifts and saccades of fixation are sufficient to trigger growing oscillations.

Under negative feedback, there is no evidence of any smooth oscillations among the saccadic. Although it is possible to selectively alter the

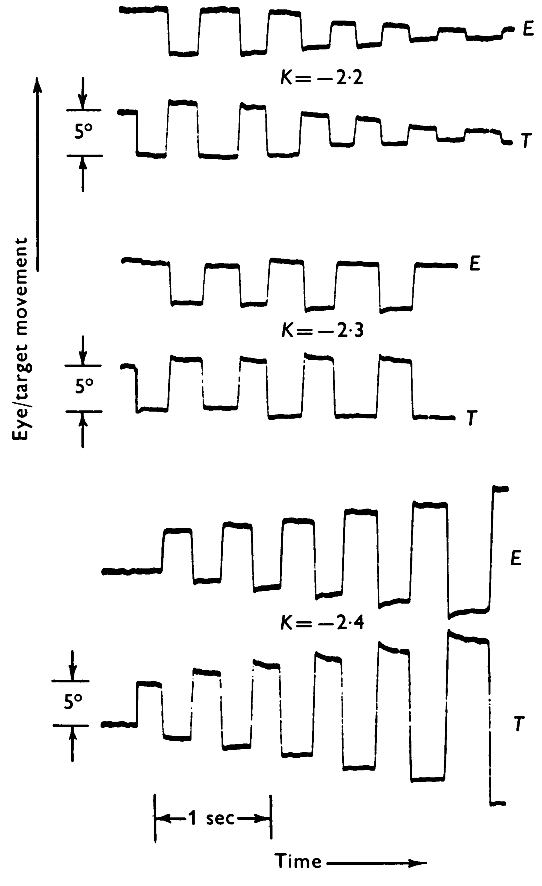

Fig. 13. Oscillatory behaviour of the saccadic mode under various conditions of negative feedback after an initial 5° target step.

feedback around the smooth pursuit system while maintaining normal saccadic feedback, such a tactic was unnecessary to demonstrate smooth pursuit oscillations in the monkey. In response to early 5–15 deg/sec target ramps, some monkeys would occasionally break into spontaneous oscillations, the largest of which is shown in Fig. 14. As the animal becomes more accustomed to these tracking tasks, the oscillations tend to disappear.

While no explanation is advanced for this phenomenon, it allows the smooth pursuit mode to be investigated under 'natural' oscillatory conditions. Possessing a peak velocity excursion of about 3 deg/sec about the steady state velocity, the oscillations appear roughly sinusoidal, waxing and waning at frequencies between 2·5 and 3·3 c/s. These smooth oscillations appear in sharp contrast to the square saccadic oscillations which occur at frequencies between 1·8 and 2·3 c/s.

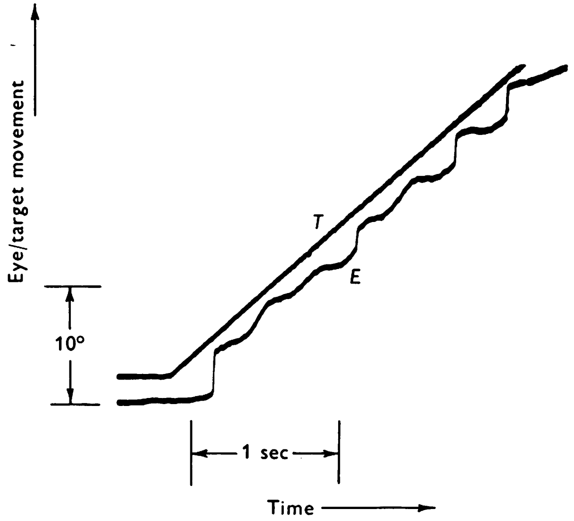

Fig. 14. Spontaneous smooth pursuit oscillations to an early 10°/sec ramp.

DISCUSSION

The behaviour of the monkey saccadic system under both open loop and negative feedback conditions is symptomatic of either a discrete control system whose errors are sampled and corrected about every 250 msec or a system possessing a pure delay of 250 msec. An experiment by Westheimer (1954*a*) on humans indicated to Young (1963) that the former was correct. If the target steps, say 10°, to one side and returns after 100 msec, he showed that the eyes respond with a 10° saccade after 200 msec despite the fact that the target has already returned to its initial position. Then instead of returning to its initial position within 100 msec as would the response of a system with a pure delay, the eye waits 200 msec before coming back. Recently, however, Wheeless, Boynton & Cohen (1966) have disputed this result by demonstrating that the eye has a 32 % chance of altering its response if the target change occurs 85 msec before the saccade. The eye has better than a 50–50 chance if the target changes position before ½ reaction time. Clearly, the saccadic response cannot be accounted for by a simple 250 msec sampler. Suppose, however, that the sample was taken over half a reaction time, a position correction decided on the basis of all this continuous information, and this correction effected without change half a reaction time later. Such a system would display both the Wheeless results and the variable feedback behaviour. For cataloguing purposes, such a system could be called semi-discrete to distinguish it from the smooth pursuit mode. Although similar experiments were not tried on monkey reaction times, all the rest of their saccadic behaviour closely paralleled that of humans and pointed to the existence of a similar saccadic control system.

TABLE 1. Comparison of the saccadic and smooth pursuit modes in the monkey

Property	Saccadic	Smooth pursuit
1. Temporal dependence	None	None
2. Stimulus necessary to elicit a response	Target displacement	Target motion
3. Latency (msec)	241 msec	174 msec
4. Duration (msec)	28 msec	131 msec
5. Maximum response	Undetermined	45°/sec
6. Type of control system	Semi-discrete	Continuous
7. Behaviour under positive feedback	Staircase walk away	Smooth run away
8. Amount of negative feedback to insure forced oscillations	$K = -2\cdot3$	Undetermined
9. Frequency of oscillations	1·8–2·3 c/s	2·5–3·3 c/s

The smooth open loop instability and the sinusoidal oscillations during smooth tracking indicate that the smooth pursuit system is continuous. During ramp responses the eye was seen to undergo smooth changes in velocity. Discrete velocity changes were only observed in conjunction with a saccade.

Table 1 is a summary of the differences between the horizontal saccadic and smooth pursuit systems of the monkey. The target stimuli for items 3 and 4 were a 10° position displacement and a 10 deg/sec ramp respectively.

All of the foregoing eye movement recordings demonstrate that, in response to random target trajectories, monkeys employ combinations of saccadic and smooth pursuit responses which are qualitatively similar to those of humans. Monkeys are, however, able to execute their horizontal saccades more quickly than humans as can be seen from a comparison of their durations in Fig. 15. Each point on the lowest curve is the average of the temporal and nasal means of Fig. 5. The shading indicates the temporal and nasal standard deviations from those means. Human saccadic data show generally good agreement despite a variety of recording techniques. Dodge & Cline (1901) measured eye movements by exposing a photographic plate, constrained to fall at constant vertical velocity, to a corneal highlight. Robinson (1964) employed a scleral search coil in a magnetic field while Cook (1965) used a photo-electric technique to detect differences in infra-red light scattered by the sclera during an eye movement.

Since neither Cook (1965) nor Dodge & Cline (1901) specified how they determined duration (an important point since an overshooting monkey saccade requires an additional 15 msec to settle to its final position), the measurement technique of Robinson (1964) (who considers saccadic duration as the time from the onset of movement to the next velocity zero) was employed to establish a basis for direct comparison. A 5° human saccade takes 30 msec, whereas a 5° monkey saccade lasts just 23 msec. As the movements become larger, man must allow an additional 2·2 msec/deg on the average although the monkey requires only 1·1 msec/deg. Hence, as the two characteristics of Fig. 15 diverge, the difference in durations becomes more noticeable with 30° monkey saccades requiring just over half the time necessary for a similar human movement.

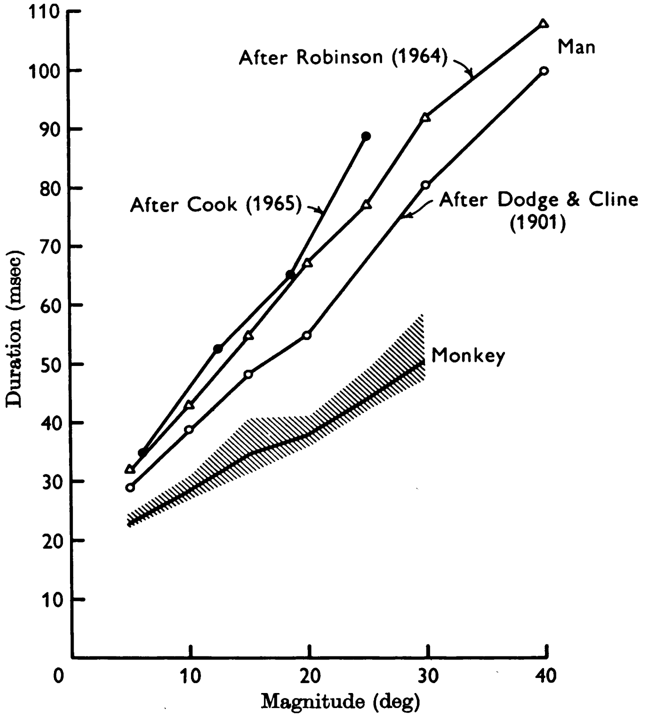

Fig. 15. Monkey and human horizontal saccadic duration against magnitude.

Monkeys achieve the shorter durations by slewing their eyes at higher velocities as may be seen from Fig. 16. Once again the monkey data are the average of the nasal and temporal means of Fig. 5 with the shading representing the spread of the standard deviations. Westheimer (1954*b*) photographed the horizontal deflexion of a vertical light slit incident upon the cornea; Hyde (1959) photographed the entire eye and used the pupil as a landmark for ocular position. A fair amount of variability exists in the human data, especially between Cook (1965) who reports saccades that reach 700 deg/sec during a 25° movement and Hyde (1959) whose subjects do not reach that velocity until they are executing a 60° movement. However, monkeys attain higher velocities than the humans of either study, reaching saccadic velocities which are 150 deg/sec faster than those reported by Cook and almost twice as fast as those observed by Hyde.

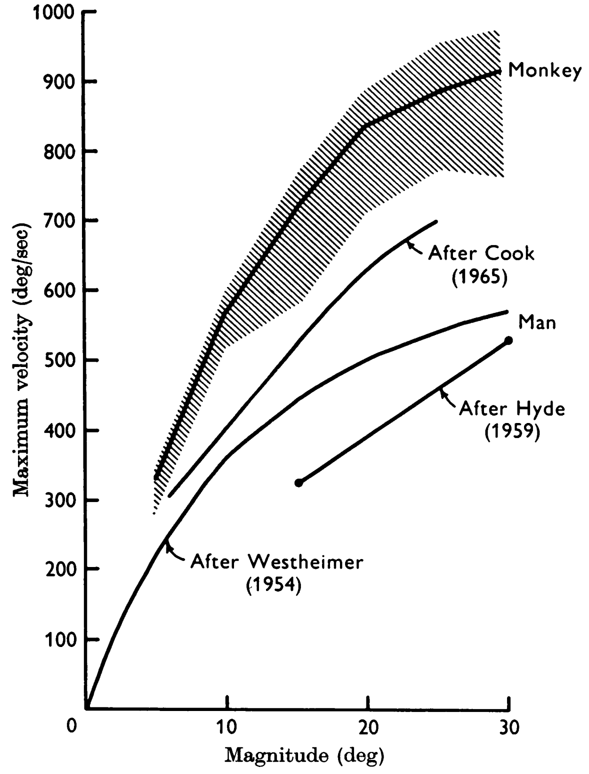

Fig. 16. Monkey and human horizontal saccadic maximum velocity against magnitude.

It is interesting to note that although monkeys are able to execute faster trajectories, the central processing latency of 241 msec before the trajectory is essentially the same as the 200–250 msec latency observed in humans. If faster saccades have developed to help the monkey survive in a hostile environment, it would have been better if evolution had shortened the reaction time which takes up 85 % of the saccadic response and not the already brief saccadic trajectory.

The behaviour of the monkey saccadic control system under conditions of variable feedback is essentially identical with that of man. Both Robinson (1965) and Young & Stark (1963) have demonstrated the human staircase walk away on 200–250 msec steps under open loop conditions. Under conditions of increased negative feedback, Young & Stark (1963) and Robinson (1965) have demonstrated the square wave oscillations of the saccadic mode. Young & Stark found, in agreement with classical control theory, that an over-all feedback of $K = -2$ was sufficient to sustain oscillations, whereas Robinson (1965) found more difficulty in maintaining an unstable oscillatory condition. Typical monkey square wave frequencies of 1·8–2·3 c/s for $K = -2{\cdot}3$ compare favourably with Young's oscillations at 2·0–2·5 c/s for $K = -2{\cdot}0$.

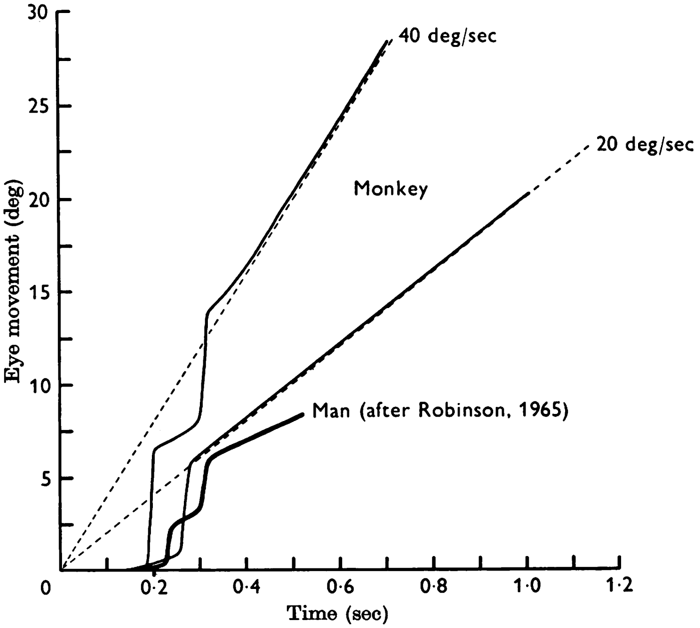

Fig. 17. Monkey and human responses to horizontal ramps of 20 and 40°/sec. Target trajectories are shown by interrupted lines.

Not only can monkeys attain higher velocities during the preprogrammed saccade (human saccadic velocity is unalterable by voluntary effort), but they also are able to wilfully turn their eyes smoothly at higher velocities in pursuit of moving targets. The upper two trajectories of Fig. 17 show typical segmental means of monkey responses to ramp targets moving at 20 and 40 deg/sec. The lower thickened curve, taken from Robinson (1965), is also a segmental mean of a human attempt to follow a 20 deg/sec ramp. After a number of corrective manoeuvres, the human reaches a velocity inadequate to match the target speed. This phenomenon of velocity saturation is most often quoted as occurring between 25 and 30 deg/sec owing to a paper by Westheimer (1954*b*) who shows no corroborative records. Monkeys, by reaching velocities of 40 deg/sec, turn their eyes twice as fast as the humans studied by Robinson (1965) and about 50 % faster than those of Westheimer (1954*b*).

When first presented with a high velocity ramp, some monkeys also have difficulty attaining target speed. The response to the first presentation of a 30 deg/sec ramp is usually composed entirely of closely spaced (116 msec average interval) saccades with no attempts to match target velocity. Only two target presentations later the monkey already tries a velocity correction although the movement is still primarily saccadic. Finally, after a total of about forty presentations, the monkey has mobilized his smooth response so as to be able to track the target for a sustained period of time. Since humans are physically capable of reaching velocities up to 40 deg/sec during the slow phase of optokinetic nystagmus (Dodge, Travis & Fox, 1930), it is possible that the velocity saturation of voluntary tracking might simply be due to insufficient practice at the higher velocities.

The monkey smooth pursuit system displays properties which closely resemble those of the human control system. In response to a 10 deg/sec target, the human latency to the onset of a smooth movement is 125 msec (± 20 S.D.) (Robinson, 1965), which is smaller than that in the monkey [174 msec (± 34 S.D.)]. Under open loop conditions, both monkey and man exhibit a smooth growing trajectory. Sinusoidal smooth pursuit oscillations occur spontaneously in the monkey at frequencies between 2·5 and 3·3 c/s which compare with the 3·3 c/s oscillations elicited by Robinson (1965) under conditions of increased negative feedback.

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