

SACCADIC EYE MOVEMENTS TOWARDS STIMULI TRIGGERED BY PRIOR SACCADDES

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Abstract—The beginning of a saccade triggers a step in target position, and then the target is extinguished 1–300 msec later. A primary saccade follows with normal accuracy, and approximately normal latency. A corrective saccade to the invisible target is possible if the target is lit during the early part of the prior primary saccade. Clearly, important visual stimulation can occur during saccades, and the interaction of retinal and eye position information is such that saccades are goal-directed. The only finding reminiscent of perceptual “saccadic suppression” and mislocation effects is that a target which steps to a position ahead of a saccade is sometimes ignored.

INTRODUCTION

When the retinal image of the target is stepped away from the fovea, by suddenly stepping the target, a latent period lapses, and then a primary saccadic eye movement abruptly displaces the fovea to a point just short of the image. After somewhat briefer latent periods one or more smaller secondary, or corrective, saccades finally bring the fovea to the target.

An important question, for which there is no existing answer, is: Can the oculomotor pathways make an *appropriate* response to visual stimulation which occurs during a saccade? Because the retinal image is blurred (e.g. Dodge, 1905), and because perception is anomalous at the time of saccades (MacKay, 1970, 1972, 1973; Matin and Matin, 1972; Mitrani, Mateef and Yakimoff, 1970, 1971; Mitrani, Yakimoff and Mateef, 1973; Richards, 1968, 1969; Riggs, Merton and Morton, 1974; Volkman, 1962; Volkman, Schick and Riggs, 1968), the usual assumption is that the answer is no—but, with equal conviction, one can argue that there are almost certainly differences between the sensory processes leading to perception and those leading to saccadic eye movements. Some superior collicular visual units respond to high velocity images (Wurtz and Goldberg, 1972; Mandl, 1974) and other collicular units fire briefly when the eye moves through the threshold positions of their orbital mechanoreceptors at high velocity (Abrahams and Rose, 1975). One can conjecture that, under some circumstances, the oculomotor pathways routinely monitor the blurred retinal image during saccades, both to visually confirm the occurrence, direction and size of a saccade, and to control the quality of future saccades. Very conspicuous targets may be identifiable when blurred, and it is conceivable that intrasaccadic retinal stimulation can *sometimes* confirm the continued existence and approximate location of the target. It would be very surprising if such sensory operations occur under *all* conditions of everyday life: the visual scene may be too complex; or the target

may be exposed for long periods, so that there is no urgency in assessing its position; or it may be convenient to blink during a saccade in order to provide more viewing time between saccades, when the perceptual conditions are optimal.

It is important to note that the present question asks whether there is an *appropriate* response. It would not be very surprising if bright targets presented during saccades were to elicit inaccurate responses. Retinal image position codes only the angle between the target and the foveal line-of-sight. A goal-directed saccade in the present experiments is only possible if this retinal information is correlated with (non-retinal) information about the angle of the line-of-sight relative to the orbit.¹

METHODS

Methods are given in Lightstone (1973). The dark-adapted subject bites his deep dental impression in hard compound, and fixates an oscilloscope spot (very fast decay P15 blue-green phosphor) with his left eye, through an i.r. reflecting mirror and a low power microscope with a large exit pupil (2 cm). The right eye is occluded with a patch. The target is at an optical distance of 72.5 cm from the eye. The nominally 8' subtense target is previously set to 2 log above its foveal detection threshold against a large background which is at cone threshold. At the oscilloscope settings chosen there are no visible rings around the target due to electron gun optics (at much higher intensities the energy in the first ring with radius 4° is 3 times that of the target itself), nor is parasitic light from the heater filament visible to the completely dark-adapted eye, i.e. the oscilloscope screen and all surroundings are completely invisible. The oscilloscope spot intensity is stabilized, and when briefly lit for $\Delta = 1.5$ msec there is only 5–10% 60 Hz variation in energy, which should not cause any dispersion in saccade latency.

The near i.r. passband is sharply cut at 800–1100 nm (stabilized, under-run d.c. tungsten lamp, 2 Kodak 87C Wratten filters and 6 mm thickness of Corning 7-69 glass). The fully dark-adapted subject sees this with his peripheral vision as a large dim red circular source, of about 6° subtense and 1.9 log above peripheral absolute threshold (when fully visible), at 35° below the main instrument axis. During experimental trials the dim source is invisible much

¹ The sections in small print may be passed over in a first reading.

of the time (Troxler fading effect). An i.r. imaging system, separate to the illuminating system, forms an image of the eye on a very fine horizontal aperture, which is bisected vertically by a prism, and imaged by microscope objectives on small area, high impedance PIN diodes. Infrared photography shows that the pupil is black, and that the iris is of low contrast relative to the sclera. The images on the diodes are rectangular and their lengths vary reciprocally as the eye rotates. Theoretically the voltage difference between the diodes is proportional to the sine of horizontal rotation, and to the luminance of the eye, but is unaffected by vertical elevation of the eye or by change in pupil size. Experimental tests with real eyes show that linearity is satisfactory ($\pm 5\%$) over the range of $\pm 15^\circ$, and that vertical movements or large sudden changes in pupil size have little effect. Infrared television shows that the subject keeps his eyes fully open, so that eye lid movements do not affect the results, provided he is given an interesting task.

The diodes are connected to preamplifiers, with capacitive feedback, then via remote operational amplifiers for offset and scaling adjustment, to a differential amplifier and Brush 240 pen recorder. Most recordings are with low pass, linear phase, filtering at 20 Hz corner frequency. The subject maintains, and is able to reproduce, his head position with high fidelity, as shown by using the tracker to monitor a black stripe attached to a spectacle frames worn by the subject. System noise over the period of a trial has S.D. = 3'. The chart paper is read to $\pm 10'$ and ± 4 msec. Target motions and lighting are determined by a PDP8 computer with a clock that is triggered from the eye velocity channel. Subject PEH was 35 yr old and 0.25 D myopic in his left eye and AMR was 24 yr old and 0.75 hypermetropic. Both subjects had normal acuity, fundi, fields and movements by routine ophthalmological testing.

With respect to the experiment of Fig. 2 cue periods of $\Delta = 1, 50, 100, 200$ and 300 msec are used for subject PEH and $\Delta = 2, 5, 20, 50, 100, 200$ and 300 for AMR. In some experiments the blanking period ω is randomly selected from values of 250, 350, 370, 400 and 500 msec. The original records (e.g. Lightstone, 1973) include velocity, expanded velocity and expanded position traces. The expanded velocity trace is used to define the beginnings and ends of saccades.

RESULTS

A typical trial

The otherwise fully dark-adapted subject fixates the 2 log supra-foveal threshold, 8' subtense, blue-green target as soon as it is switched on at the beginning of a trial. After a random delay the target makes virtually instantaneous horizontal steps, some triggered by clocks, others by saccades, to randomly chosen positions in the visual field, eventually returning to its origin on the instrument axis. The subject is ignorant as to the specific nature of the experimental session, which overlaps with other sessions on other aspects of eye movements, and is not specially trained. He is simply instructed to follow the target. Introspection is difficult because of the extensive randomization and the brevity of the trials. At the end of an experimental session both subjects give poor descriptions of target motion, and can only say that the target makes a few steps before returning to the instrument axis. They are uncertain as to whether the target remains continuously lit, and make poor guesses about possible apparatus arrangements or eye movement patterns.

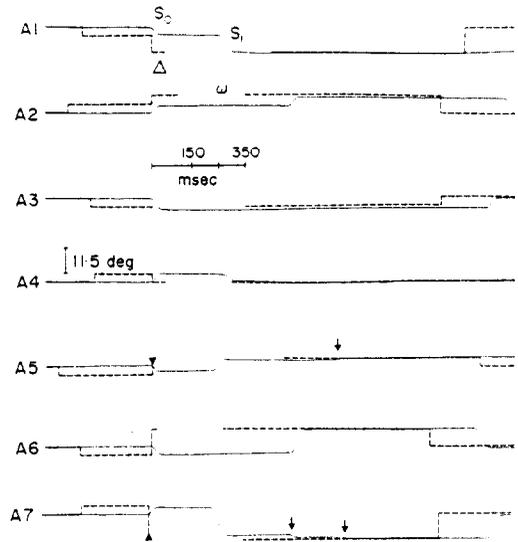


Fig. 1. Examples of the seven main patterns of target position, excluding mirror image varieties. Saccade S_0 triggers the second step to a randomly chosen position and then, after a randomly chosen period Δ , the target is blanked out before re-illumination. When Δ is brief it is represented by a triangle, the base of which is actual target position. The trials are aligned on the trigger point. Time marks of 150, 250 and 350 msec (lower limit, mean, upper limit of reaction time) are shown. For A1–A7 $\Delta = 50, 100, 5, 50, 1, 20$ and 5 msec. Trials are for observer PEH, except A3, 6 and 7, which are for AMR. Her responses are of greater amplitude than PEH's and are sometimes later. The arrows indicate corrective saccades delayed until after blanking.

Figure 1 illustrates the seven main patterns of target position most extensively studied, but only a few of the variations in lighting. After an initial random delay the target jumps at random, left or right, to initiate the triggering saccade S_0 . When the velocity of this saccade reaches about $37^\circ \text{ sec}^{-1}$, after about 8–12 msec and 6–10' (approx 1 target dia) into the saccade, the target is triggered to jump to a second randomly chosen position in the range $\pm 11.5^\circ$ with respect to the instrument axis. As the target steps in multiples of 3.83° there are seven main varieties of position pattern (Fig. 1), counting left-ward and right-ward mirror image pairs as being one main variety. The target is exposed after the second step for a cue period Δ , of random duration (1–300 msec), and is then blanked off for a period $\omega = 250$ –350 msec. The target remains stationary during the blanking period and is finally re-illuminated for 750 msec, before stepping back to the instrument axis at the end of the trial.

When the cue period $\Delta = 1$ or 2 msec smearing of the retinal image by saccadic eye movement is negligible. When $\Delta = 50$ msec the retinal image is a streak equal in size to the S_0 saccade. A 30-msec cue terminates about 0–10 msec after eye velocity has fallen to $0 \pm 2^\circ \text{ sec}^{-1}$ for the fastest S_0 saccades, but as saccades are variable, and their exact beginnings and ends difficult to find, it is fair to call $\Delta = 1$ –50 msec cues "intrasaccadic cues". On the other hand note that when $\Delta = 300$ msec the viewing conditions are normal, the target remains lit throughout the latent periods of most of the S_1 saccades which follow triggering saccade S_0 .

General description

The responses shown are illustrative because the timing and amplitudes of the saccades are subject to normal variation (S.D./mean = about 16% for both timing and amplitude) and because the randomization of stimulus position and timing is so extensive.

Saccade S_0 occurs with normal latency and usually undershoots its target position. It is *never* followed by the expected corrective saccade (except in the case of target pattern A3)—after a further, more or less normal, latent period the usual response is a primary saccade S_1 towards the target. This primary saccade is to be expected in the case where the cue period $\Delta = 300$ msec (Fig. 6, top), as the target is lit throughout the latent period; but, when the cue is intrasaccadic, saccade S_1 still occurs during the blanking period ω with normal accuracy and more or less normal timing, even though the target is currently invisible.

The cancellation of the corrective saccade, and the occurrence of the normal accuracy S_1 saccade in the dark, clearly indicate the effectiveness of new visual information confined to saccades—but there is further evidence. Saccade S_1 always undershoots, whatever the value of Δ , and should be followed by a smaller, short latency, corrective saccade. However, when saccade S_1 occurs in the dark (due to Δ being less than the reaction time), the subsequent error-correcting saccade is delayed until a short latent period after the target is re-lit at the end of the blanking period ω (e.g. Fig. 1, arrows). In fact, in the present experiments, the occurrence of a corrective saccade in the dark, with normal timing, is critically dependent upon the target being lit and stationary during at least the early part of the prior primary saccade.

In Fig. 1 patterns A1 and A2 (and their mirror images) will be called uncrossed patterns, the second target step advancing the target in the same direction as the first step and the triggering saccade S_0 . In the trial illustrating pattern A1 the cue is only available during the triggering saccade S_0 , yet there is an accurate saccade S_1 to the position of the currently invisible target. In the trial depicted in pattern A2, even though the cue period ($\Delta = 100$ msec) is longer than saccade S_0 , saccade S_1 is delayed until 160 msec after the end of the blanking period ω . Now a proportion of S_1 saccades will be expected to be delayed until after the end of blanking, by chance, depending upon the exact latency distribution and the sum of $\Delta + \omega$. However, in the case of the uncrossed patterns A1 and A2, there are typically more delayed responses than can be reasonably expected. Further analysis shows that many delayed saccades are due to retinal stimulation *after* the blanking period ω , the *uncrossed* Δ cue being “missed”. This is the only indication that we see of anything remotely resembling the “suppression” or “mislocation” effects that have been studied by other workers in purely perceptual experiments.

The null pattern A3 results from the triggered position being the same as that assumed in the first step. The presence of this pattern increases the general randomness of the trials. Patterns A4–A7 will be called “crossed patterns”, since the triggered target step is in the opposite direction to saccade S_0 . In the crossed patterns, the usual response to an intrasaccadic cue is a saccade S_1 of more or less normal accuracy and

timing towards the currently invisible target. The proportion of saccades delayed until after the end of blanking is somewhat greater than what would be expected on chance, but much less than in the uncrossed cases. Delays in crossed patterns can be largely attributed to the low energy of brief Δ cues, i.e. the cue is weak but not missed. Pattern A4 is particularly interesting, since the triggered step returns the target almost to the foveal centre, the eye having moved only about 1 target width at the time of triggering. The same result is obtained when the Δ cue is much briefer than illustrated. Clearly, retinal image information is not sufficient for saccade S_1 when the cue is brief: S_1 is then a response to the S_0 movement. In fact, it is generally true for all seven patterns that the oculomotor system does not act solely on the retinal position of the cue, but makes allowance also for the size and direction of the S_0 saccadic movement that occurs after the beginning of the cue. As a result of combining retinal and eye position information, saccade S_1 is always towards the true position of the target. Saccade S_1 does undershoot, but this is normal for target steps of unpredictable amplitude, and the undershoot is not related to the duration Δ of target exposure.

The timing of the S_1 primary saccades

An analysis of saccade latency is presented in Figs. 2–4. The major point is that, whatever the duration Δ , saccades that occur in the dark have essentially normal latencies (Fig. 2c). A more minor matter, which may be relevant to problems posed by perceptual studies, is that some S_1 saccades are late and occur after the re-lighting of the target (Fig. 1). Part of the lateness can be attributed to reduced cue energy at very short Δ . For uncrossed cues there is a strong additional factor, such that even long Δ cues may be ineffective, on occasions, as cues to target position.

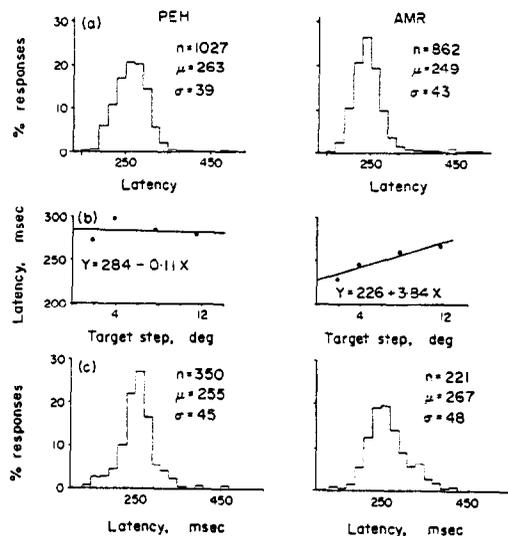


Fig. 2. Histograms of saccadic latencies to continually-lit target steps for two observers (a). Analysis of a portion of these shows that latency is not sensitive to saccade size (b). Histograms (c) of the latencies of the saccades that occur during blanking are essentially similar to those of (a), although the small differences are significant at the 99% level of confidence. (n = No. of trials, μ = mean, σ = S.D. in msec.)

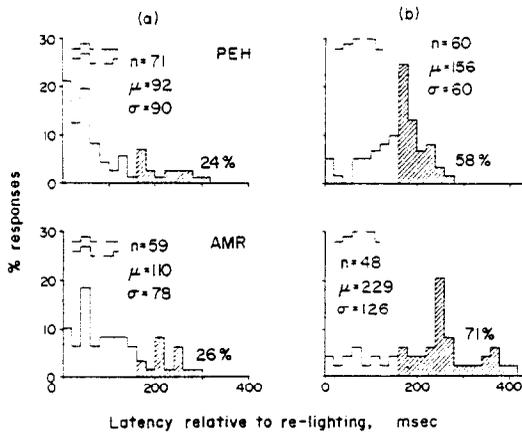


Fig. 3. Left (a): latencies of delayed saccades to crossed cues, expressed relative to the final re-lighting of the target, are rather like upper latency tails and do not suggest that many late responses are due to the cue being missed. Right (b): in the case of the delayed saccades to uncrossed cues there is better evidence for a distinct late population. The hatched areas and percentages are those latencies of greater than 160 msec, which from Fig. 2a, could be due to re-lighting, the Δ cue having been missed: μ and σ are in msec.

Late saccades to crossed cues. Such saccades are almost entirely limited (98%) to intrasaccadic cues, and are commoner for the shorter Δ values. Thirty-five per cent of S_1 saccades to crossed intrasaccadic cues are late, but only 13% should be late by chance if their latencies are distributed as in Fig. 2a. When a continually lit target is dimmed upper latency tails become more pronounced, and eventually the whole population of saccade latencies becomes more retarded and dispersed (Wheless, Cohen and Boynton, 1967). Latencies of late S_1 saccades to crossed cues are shown in Fig. 3a, as relative to re-lighting, and in Fig. 4a (shaded element) as relative to the beginning of cues. The data do seem to belong to an upper latency tail, which is slightly inflated due to the reduced luminous energy of brief cues.

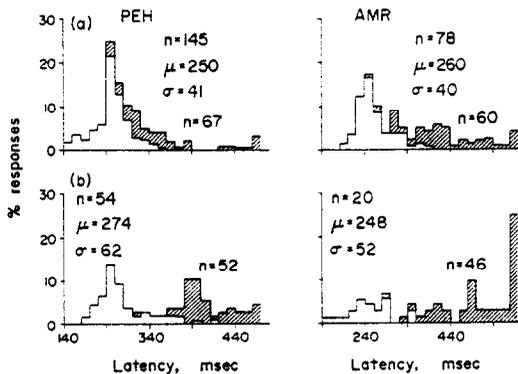


Fig. 4. Latencies for saccades where Δ = 1–50 msec, expressed relative to the beginning of the Δ cue. The unshaded areas and the averages show saccades that occur during blanking with approximately normal (cf. Fig. 2a) latency. The shaded areas are latencies of saccades that occur after the end of the blanking. In the case of crossed cues (a) the delayed saccades are in a long latency tail. In the case of uncrossed cues (b) there is definite evidence for a separate population of delayed responses which can be attributed to missed cues.

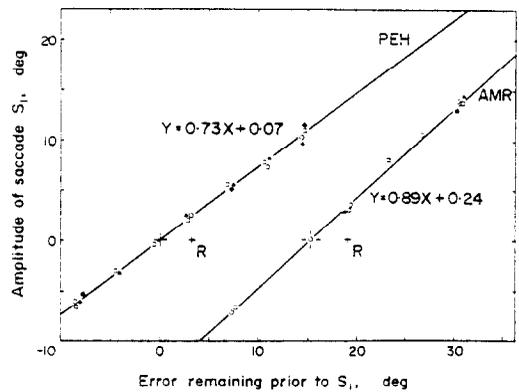


Fig. 5. Amplitude of S_1 saccade in degrees versus error that exists prior to saccade S_1 . In this convention a negative sign indicates saccades and errors in the direction of the triggering saccade S_0 , i.e. data from uncrossed trials, and the positive sign indicates crossed trials. Amplitude of saccade S_1 is calculated from the position difference between the beginnings and end of saccade S_1 . Error is calculated from target shift and the amplitude of saccade S_0 , i.e. the assumption is that on the average there is no net drift in eye position between the end of saccade S_0 and the beginning of saccade S_1 —which is justified.

The cue Δ is 1–5 (●), 50 (▲), 100 (◻) and 300 (○) msec. AMR's results displaced laterally by 15.3°. R is the origin for the (●) data when these are expressed on a retinal position basis. The scatter of points is exaggerated in this illustration—many points overlap.

Late saccades to uncrossed cues. Intrasaccadic cues account for only 83% of late S_1 saccades to uncrossed cues, and occasional saccades are late when Δ is as long as 200 msec. Since the integration time of the eye is classically 80–100 msec, or less, it is clear that low cue energy is not the important factor in the uncrossed cue case. Uncrossed intrasaccadic cues yield 55% late responses (compared to 35% for crossed cues) and only 15% should be late, given chance and the distribution of Fig. 2a. In fact, late responses comprise a distinct, abnormally late, population and are plausibly responses to re-lighting the target (Figs. 3b and 4b). Simple expectations are that such responses should (from Fig. 2a) have range 160–360 msec and mean 250–260 msec in Fig. 3b—this is not quite true—but if lateness to an uncrossed cue is due to uncertainty as to the cue's location, rather than its existence, then the cue might still act as a visual forewarning signal (e.g. Becker, 1972), and this could shorten latency to re-lighting as observed.

The accuracy of S_1 saccades

Figure 5 shows, for the various target patterns and Δ values, the mean amplitude of the S_1 saccade vs the mean error between eye position and target position that remains to be corrected when the eye is static between the S_0 and S_1 saccades. The results for different Δ values yield virtually identical regression lines through the origin. The fitted line shown runs through the origin, and through the data point for the null pattern (A3) which is close to the origin. (The regression line through the data of the individual trials is essentially similar: e.g. for PEH intercept $a = 6.8^\circ$, slope $b = 0.70$, residual S.D. = 11.5°, $n = 368$, correlation = 0.955.) Since the average proportional accuracy b of saccade S_1 is not dependent on Δ , one must conclude that the oculomotor system is not

much bothered, in the present experiments, by variations in the length or energy content of the retinal image track. In short, saccade size is related to the physical position of the target.

How would Fig. 5 look if saccade S_1 amplitude were plotted against retinal image position of the cue flash? The $\Delta = 1-5$ msec points (●) now have to be referred to the different origin marked with a + and letter R in Fig. 5. For $\Delta = 20-50$ msec the retinal image is a streak of variable brightness and indeterminate position—so these points cannot be considered. For $\Delta > 50$ msec the energy in the early parts of the retinal image streak is small compared to that deposited in the terminal point after the eye comes to rest. For these points (○□), then, both error and retinal image position scales are the same. Thus the idea, that saccades are simply proportional to retinal image distance from the fovea, can be confidently rejected: the points for Fig. 5 are more dispersed on an amplitude vs retinal position plot, and are less well fitted by a regression line which does not run through the origin.

The variability of saccade amplitude is not sensitive to the duration of visual stimulation (Lightstone, 1973). For PEH S.D./mean is 20% and is constant for $\Delta = 1-300$ msec and for continually lit targets. For AMR variability is about 14% and not systematically affected by the lighting arrangements.

The effect of blanking on corrective saccades

In simple trials in which the target steps randomly and remains lit, the present two observers respond with a primary saccade, which typically undershoots and is usually followed by a one or more shorter latency corrective saccades. Becker and Fuchs (1969) find that primary and corrective saccades occur together in the dark, when the eye makes large (40°) movement between remembered, or recently lit, fixation points. According to their "motor package" concept primary-corrective pairs are pre-programmed, and a visual sample is taken after the completion of the primary saccade, so as to allow cancellation of the corrective component if the target has moved elsewhere. This motor package concept must be modified for saccades of the present size because, in the present experiments, the occurrence of the corrective component is definitely dependent on intrasaccadic visual stimulation during the prior primary saccade.

S_0 and its corrective saccade. In 987 trials of crossed and uncrossed target patterns the S_0 triggering saccade is never followed by a corrective saccade. It is not surprising that displacement of the target at the beginning of the S_0 saccade leads to cancellation of the expected corrective saccade, when Δ is long—this is already known for continually-lit targets (Becker and Fuchs, 1969). What is interesting here, however, is that 53% of the trials are for intrasaccadic cues—yet cancellation still occurs, showing that visual stimulation during primary saccades is important for subsequent corrective saccades under the present conditions.

In the case of the null pattern (A3) the target is not displaced during the S_0 saccade and corrective saccades do occur. When $\Delta \geq 100$ msec small corrective saccades are seen in 28/47 trials, taking as a criterion the presence of a characteristic pulse in the velocity trace within 90–300 msec of the end of the primary saccade S_0 . When stimulation is restricted ($\Delta \leq 50$ msec) corrective saccades still occur, although in reduced numbers (9/43 trials).

S_1 and its corrective saccade. In 577 trials, in which S_1 is wholly in the dark, only two corrective saccades also occur in the dark—all other corrective saccades occur 1 corrective saccade latency after the target is re-lit at the

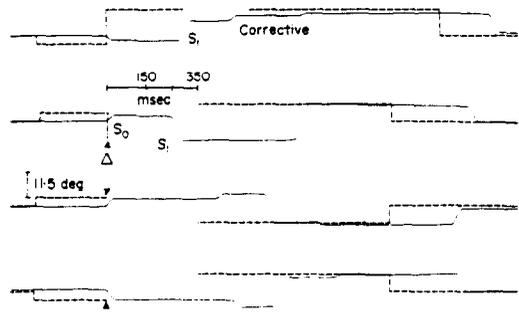


Fig. 6. The top record ($\Delta = 300$ msec) illustrates the fact that the corrective saccade to saccade S_1 can occur in the dark if the target is visible during the early part of saccade S_1 .

The lower three records ($\Delta = 5$ msec) illustrate "false cue" trials from an experiment in which the re-lighting position is independent of cue position, so that the cue is equally likely to be true or false. The S_1 saccades are still towards the extinguished cue, and being ballistic are not modified, despite being inappropriate in the lower two trials. Responses to uncrossed cues can be very late.

end of the blanking period (e.g. Fig. 1, arrows). On the other hand, if at least a portion of saccade S_1 occurs prior to blanking, there is a chance of a corrective saccade (Fig. 6, top).

One hundred and one such trials for $\Delta = 300$ msec, in which saccade S_1 begins just prior to blanking and is followed by a corrective saccade in the dark, and displayed in Fig. 7a to show the time for which visible input is available. The origin of the abscissa is the start of saccade S_1 , because the visual sample for the corrective saccade does not begin prior to the start of saccade S_1 . In some 61/101 cases (shaded in Fig. 7a) visual input is terminated before the end of saccade S_1 , yet a corrective saccade occurs. Since intrasaccadic visual input is important one must be very careful about how one expresses corrective saccade latency.

Figure 7b illustrates the timing of ordinary corrective saccades from experiments in which there is no blanking, expressed in the conventional way as relative to the end of the preceding primary saccade. In view of the present findings the true latent period includes part, or all, of the duration of the prior primary saccade. This duration depends upon saccade amplitude (Robinson, 1964; Yarbus, 1967) and ranges between 40 and 70 msec in the present experiments. Therefore the proper correction to Fig. 7b is somewhere in the range 0 to +70 msec. If the effective starting time for the latent period is distributed across this interval, in some way, then perhaps +20 to +35 msec is an appropriate average correction to the latencies of Fig. 7b. Support for a correction of this magnitude is provided by those corrective saccades which follow S_1 saccades wholly in the dark, often by quite lengthy and very variable intervals (Fig. 1, arrows). The latencies of these corrective saccades become nicely distributed (Fig. 7c), when expressed relative to re-lighting, and differ from the latencies of Fig. 7b by +18 msec on average.

Anomalous response in the absence of intrasaccadic stimulation

In a special experiment of 66 trials for PEH the patterns of Fig. 1 were presented, but the target was blanked out immediately at the beginning of the S_0 saccade ($\Delta = 0$) for a period $\omega = 370$ msec. The majority of trials are as expected—no S_1 saccades occur during blanking because there is no information about change in target position. However, in 17/66 trials the result is similar to Fig. 8. At about the end of blanking a second saccade occurs

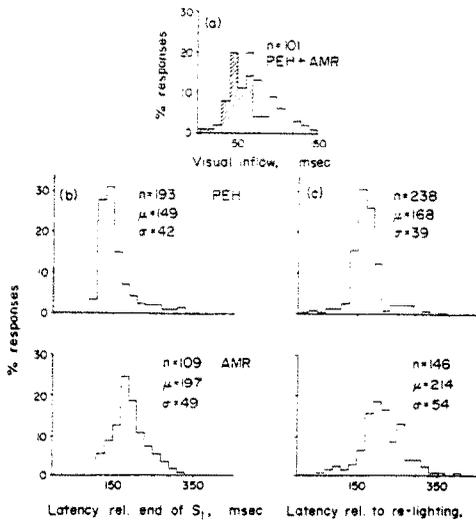


Fig. 7. (a) shows, for corrective saccades that occur during blanking, the time between the beginning of the prior S_1 primary saccade and the extinction of the target. The shaded areas represent the cases where extinction occurs during the S_1 saccade. (b) shows, for continually-lit targets, corrective saccade latency, expressed in the conventional manner as relative to the end of the prior primary saccade. But histogram (a) shows that the true time origin is intrasaccadic, so these latencies are too short. (c) shows for primary S_1 saccades that occur during blanking the latencies of their delayed corrective saccades expressed relative to the final re-lighting of the target.

in the same direction as saccade S_0 . In the case of the null and crossed patterns (A3-A7) this is quite inappropriate. The likely explanation is that for $\Delta = 0$ one has something like the classical "open-loop" situation (e.g. Robinson, 1964), in which a continually-lit, stabilized, retinal image appears to jump "with the eye", and thus elicits a sequence of futile saccades. In the $\Delta = 0$ case the target image moves by only a minute amount prior to blanking, and so we assume that the memory trace of its retinal image position is not cancelled. Consequently a second saccade sometimes occurs, because the uncanceled memory trace seems to indicate that the target has jumped with the eye. The occasional occurrence and long latency of the strange response are appropriate to the memory trace behaving like a low energy retinal stimulus.

DISCUSSION

Becker and Fuchs (1969) suspected that part of the duration of a primary saccade forms a part of the latent period of the following, short latency, corrective saccade, but rejected the idea on the grounds that perceptual inflow is seriously attenuated during saccades. Since that time so-called saccadic suppression has become more widely recognized as being a feeble effect under completely dark-adapted viewing, and the present experiments make it clear that important visual input can occur during a primary saccade.

Servomechanistic approaches (e.g. review by Robinson, 1973) correctly state that retinal image distance from the fovea is an important error signal that can cause saccadic eye movements to drive the fovea to the target. As a generalization this is not true at night, because very dim targets are viewed by the peripheral retina; nor, fortunately, is it true when the lighting is intermittent, because the eventual saccadic response

must allow for saccadic movement subsequent to the target exposure if it is to be goal-directed.

There is other satisfactory evidence (by oculomotor criteria) for the existence of eye position signals in man. Eye position in the dark can be maintained within remarkably narrow limits ($\pm 2'$) for some minutes (Skavenski and Steinman, 1970; Skavenski, 1971), even in the presence of a mechanical load (Skavenski, 1972). In complete darkness saccade size is modified for drift of the eye between successive attempts at fixating previously visible, widely separated, targets (Becker and Klein, 1973).

Certain perceptual studies (e.g. Bischof and Kramer, 1968) reveal illusions about target localization at the time of a saccade, which are possibly asymmetric about the start of the saccade or the fovea. No evidence for change in saccade size is apparent in our work: if the saccadic system does fail one must presume that it "fails safe" and there is no saccade. The inferred failure is also asymmetric, as indicated by the late responses to uncrossed cues (*vide supra*), the low frequency of responses to uncrossed cues, and the absence of a "cancellation time" when an uncrossed cue is followed by a second cue (Hallett and Lightstone, 1976). Since late responses sometimes occur for uncrossed cues as long as 200 msec, the cue is certainly visible. Perhaps uncrossed cues are poorly localized by the saccadic system? Alternatively, uncrossed cues may be well localized, but may be given low priority for some other reason.

Perceptual suppression

So-called saccadic suppression is not relevant to the present data. The magnitude and temporo-spatial course of this disturbance of visibility are not exactly known, and the disturbance seems to represent the accumulation of various retinal, oculomotor, central, perceptual and attentional difficulties. For the present viewing conditions, and intrasaccadic stimuli, threshold elevation is 0.5 log at most (Volkman, 1962; Riggs *et al.*, 1974). As visual thresholds can be raised by extraneous factors (e.g. Hallett, 1969), but not lowered without increase in the observer's fallibility (e.g. Barlow, 1957), it seems reasonable to give special weight to those experiments which show no effect (Barbara F. Brooks, personal communication; Richards, 1968, 1969;

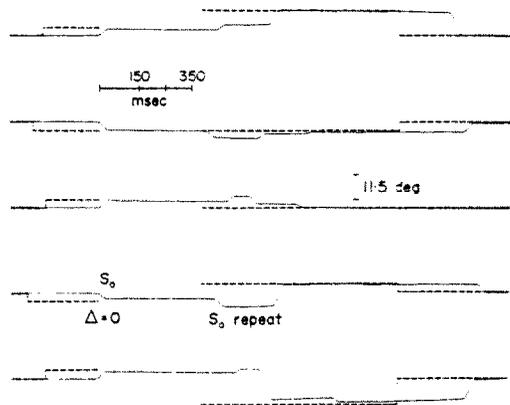


Fig. 8. In this experiment ($\Delta = 0$) the beginning of the S_0 triggering saccade extinguishes the target for 370 msec, after which it is relit at a new randomly chosen position. In a proportion of trials (illustrated here) it is as if the S_0 saccade is repeated at about the time of re-lighting.

Mitrani *et al.*, 1970, 1971, 1973). By contrast, the visibility of the $\Delta = 5$ msec cue is 2.4–3 log above static peripheral rod threshold—using data from Cabello and Stiles (1950), an integration time of 80–100 msec, and making an allowance of 0–0.3 log for pupillary constriction that can be seen on the television monitor at about the time of the saccade.

Perceptual mislocation

This effect does not seem to be closely related to the present data. The relative ineffectiveness of uncrossed cues (*vide supra*) is our only oculomotor finding reminiscent of perceptual mislocation.

Targets presented at about the time of saccades are perceptually mislocalized (Matin and Matin, 1972) and subjects point away from the target (W. B. Templeton and Tania Anstis, personal communication). The angular extent of mislocation is generally less than the saccade. The effect is believed to be a *time-dependent* disturbance of the visual world in the time span of ± 200 msec about a saccade. Variability is marked, and it may be contributed to by an uncertain memory for reference positions, or the difficulty of consistently dividing visual attention between the perceptual test target and the oculomotor task targets. Indeed, one of Monahan's (1972) subjects shows virtually no mislocation effect in the mean, only changes in the variability of his localizations. Spatial asymmetry is implied in Matin and Pearce (1965): an intrasaccadic flash is properly located with respect to the remembered fixation point at the beginning of the saccade, but the same flash is mislocalized with respect to the remembered fixation point at the goal of the saccade. In similar experiments, in the presence of persistent visual landmarks, Bischof and Kramer (1968) find that positions in the hemi-retina, which contains the saccade goal, are re-interpreted as corresponding to new physical positions too early, whereas positions in the opposite half retina are re-interpreted too late, for veridicality throughout the saccade. Their data are detailed, but MacKay (1970) argues that there may be contamination by purely sensory disturbances due to movement of the image of the scene during the saccade. Templeton and Anstis (*vide supra*) find that mislocalization is maximal at the beginning of a saccade, but is temporarily zero two-thirds of the way through the saccade. They do not find spatial asymmetry, and mislocalization persists in the presence of a landmark (a 2-sec duration saccade target). In contrast to perception, oculomotor performance is constant for targets briefly exposed, before, during and after saccades (Hallett and Lightstone, 1975).

Other work

The contact lens technique, for continually-lit target steps of 2° and 3°, yields 0.54–0.76 for the slope *b* of saccade size on step size, with 15–25% for the S.D. mean of saccade size—in good agreement with the present data for flashed and continually-lit targets (Timberlake, Wyman, Skavenski and Steinman, 1972), and with later data (Hallett and Lightstone, 1976).

Pernier, Jeannerod and Gerin (1969) step the fixation point to 10 deg eccentricity and then extinguish it for a period. In the continuously-lit (control) condition there is a single saccade (EOG technique), and the same is true for three subjects in the experimental condition. For four other subjects the saccade is delayed, is correspondingly reduced in size, and is followed by a second (corrective) saccade after re-lighting. Responses return to normal if target exposure is sufficiently protracted. The implication is that some subjects may perform worse than PEH and AMR in the present paradigm.

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Résumé—Le début d'une saccade déclenche un déplacement en échelon de la cible, et puis on éclipse la cible après 1-300ms. Une saccade première suit avec une précision et une approximative délai normale. Une saccade secondaire de correction à la cible invisible arrive si la cible s'illumine pendant la première partie de la saccade première et antérieure. Evidemment, une stimulation visuelle d'importance est possible pendant une saccade, et la corrélation de la position de l'image rétinienne et de la position de l'oeil est précise. La seule observation suggestive de la suppression perceptive et les erreurs de localisation est qu'on ignore quelquefois la cible qui traverse à une position au-delà d'une saccade.

Zusammenfassung—Der Anfang einer Sakkade löst einen Schritt in Zielposition aus, und das Ziel ist erloscht 1-300 msec. später. Primäre Sakkaden finden statt mit normaler Genauigkeit, und ungefähr normaler Latenz. Eine sekundäre Sakkade zum unsichtbaren Ziel ist möglich wenn das Ziel während des früheren Teils des vorgehenden primären Sakkaden beleuchtet ist. Es ist klar das bedeutende visuelle Reizung während Sakkaden stattfinden kann; und die Interaktion von Information vom Netzhaut und Augeposition ist so dasz Sakkaden zielorientiert sind. Die einzige Wahrnehmung die uns erinnert an wahrnehmbare Sakkadische Unterdrückung und Verschiebungseffekte, ist dasz ein Ziel dasz an eine Sakkade vorausschreitet manchmal nicht beachtet wird.