Vision Research Vol. 21, pp. 347 to 354
Pergamon Press Ltd 1981. Printed in Great Britain

0042-6989 81 030347-08$02.00 0

SPATIAL AND TEMPORAL FACTORS IN THE PREDICTIVE GENERATION OF SACCADIC EYE MOVEMENTS

JOHN M. FINDLAY
Department of Psychology, University of Durham, South Road, Durham, DH1 3LE, England

(*Received* 2 *March* 1980)

Abstract—Horizontal saccadic eye movements were recorded when a spot target moves in a sequence of steps, designed to manipulate the variables of spatial and temporal predictability. This allowed a comparison of anticipatory saccades with saccades elicited by visual stimulation, and evidence is presented which suggests that these categories are discrete and exclusive. Anticipatory saccades were produced both when the target position was predetermined and when it was not, but only in the former case was there also a systematic effect of temporal predictability. Spatial predictability and temporal predictability both reduced latencies for visually elicited saccades, and no interaction was found. The results are interpreted in terms of a model where the timing of a saccade is controlled by a separate mechanism from that controlling the amplitude.

INTRODUCTION

The human oculomotor system is well adapted for following targets. The smooth pursuit sub-system allows the eye to match target movements over a wide range and the saccadic sub-system operates to correct positional errors (Robinson, 1968). If a target makes step movements, following saccades will also occur. For unpredictable movements, the latency of the saccade is typically 170–350 msec. However in the case of a target making a predictable movement, this latency can be reduced and saccades may occur which are synchronous with or even in advance of the target movement. This is seen clearly in the situation where a target moves between two positions in regular steps. After a few cycles of this sequence, the saccade no longer lags behind the stimulus (Stark *et al.*, 1962; Horrocks and Stark, 1964).

The predictive saccades seen in this condition are one manifestation of a general property of the human saccadic system; it can operate either under the control of visual signals or under the control of internally generated signals (an internal programme). The analysis presented in this paper attempts to discover at what point these two control pathways merge.

For successful predictive saccades to be made, the observer must have knowledge both of the location of the new target position in space, and also of the instant at which the movement will occur. In a study of saccade latencies, Michard *et al.* (1974) have shown that providing an observer with knowledge about the exact point in time of a target movement resulted in considerably lower saccadic latencies (ca 100 msec faster). They also show that information about possible future positions where the target could move also reduced latencies (by *ca.* 20 msec), but the two effects appear to be independent. Other work has failed to find any effect of the number of possible target positions on saccade latencies (Saslow, 1967). This discrepancy may be attributable to the different range of saccade sizes and directions used in the different studies (Heywood and Churcher, 1980). These experiments were all concerned with saccades whose latencies suggest that visual guidance was involved. The present study manipulates spatial and temporal uncertainty in a situation in which some predictive saccades are produced.

METHOD

Subjects

Four laboratory workers aged between 20 and 40. All but one (HC) had some previous experience in eye movement experiments.

Apparatus

The subject viewed an oscilloscope screen (Tektronix 602; P31 phosphor) from a distance of 1 m. He was seated and his chin and forehead restrained in a headrest. The subject was asked to follow, as automatically as possible, a point on the oscilloscope screen which moved in the manner described below. Following a 40 sec practice block to familiarise the subject with the stimulus, the subject was given four experimental sessions lasting 80 sec, containing approximately 160 target movements. At the beginning and end of each block a calibration was carried out for the eye movement record. The whole procedure was under computer control, experimenter intervention occurring only to initiate the calibration procedures.

Stimuli

The stimulus "spot" consisted of a square array of nine points. The square had sides of less than 1 min arc and the points could not be resolved by the subject. The stimulus spot moved in a series of steps in the sequence (centre)—(left/right)—centre—(left/right)—(centre), etc. between three positions. The movements away from the centre were to right or to left with a probability of 0.5 for each. Each step (both towards and away from the centre position) followed the preceding one with an interval (the foreperiod) selected from the set 350, 400, 450, 500, 550, 600 and 650 msec with equal probability. Thus the average station time was 500 msec, an interval that produces optimum prediction with regular signals (Stark *et al.*, 1962). For each subject approximately 40 centre directed saccades and 40 peripherally directed saccades were recorded for each of the seven foreperiods giving a total of about 600 saccades per subject. For subject MJM, one block was unsatisfactory; consequently his results are based on about 450 saccades. The stimulus movement was 1.90° except for one subject (AS) where a typing error when introducing the parameters led to a distance of 2.85° being presented.

Eye movement recording

Horizontal eye movements were recorded using a modification of the procedure described by Findlay (1974) in which a fibre optic Y guide is used both to illuminate the iris-sclera boundary and to detect reflected light. In the version used in this experiment chopped infra-red light was used as a light source and phase sensitive detection methods were used in the photocell amplifier. Short term resolution (noise limited) was 5 min arc or better. Long term stability was assessed from the calibration records. Before and after each 30 sec session, a calibration record was taken with the subject fixating points spaced by 2°. For three of the four subjects, the maximum sensitivity change noted during the course of a block was 20 min arc over 2°. The average sensitivity change was about half this value. Some of the changes may represent genuine changes in fixation position (Boyce, 1967).

Data analysis

During the experimental session, a digitised record was obtained on magnetic disc of the subject's horizontal eye position (digitising rate 100/sec; digitising interval ca 0.5 min arc), together with an indication of the stimulus sequence. At some later point a further programme was used to analyse this record. The object of this programme was to pick out the saccades and measure their amplitudes. The criterion for detection of a saccade was that two successive 10 msec intervals should register position changes in the same direction greater than a criterion (fixed in computer units but corresponding to about 5 min arc). This is roughly equivalent to a velocity criterion of 10 deg/sec. Saccade amplitude was then measured as the difference between presaccade signal (the average of the records from 60–10 msec before saccade detection) and post-saccade signal (the average of the records from 60–110 msec after the detection of the saccade. Saccade maximum velocity was also measured as the maximum change in signal in any 10 msec interval during the saccade. Thus it can be seen that the duration of the saccade was defined for measurement purposes as 60 msec. (A series of preliminary checks had shown this procedure to operate satisfactorily.) After detection of a saccade, the saccade search procedure was disabled until 60 msec following this point. The programme produced a print-out of all saccades occurring in the interval between 250 msec before and 400 msec following each stimulus. This was checked and cases where the velocity appeared inappropriate to the saccade size were examined on the original record (displayed on a screen). This allowed easy elimination of blinks and also the occasional case in which a second saccade was registered because the first saccade and following drift were not quiescent at the end of the 60 msec period. The procedure registered all saccades with amplitudes above about 0.2 degrees, but microsaccades were not recorded. For each stimulus step, the *primary* saccade was identified as follows. The saccade designated as primary was the first saccade in the 250 pre to 400 msec post period, except that in the period 250 msec pre stimulus to stimulus onset, saccades were only so designated if (i) they were not the primary saccade of the preceding stimulus (ii) no subsequent saccade more than twice the size occurred in the post stimulus period. This procedure was introduced to cope with the possible misclassification of delayed primary and corrective saccades to the preceding stimulus step. It is probably somewhat conservative in that some genuine small anticipatory saccades may have been eliminated.

RESULTS

Distribution of saccade latencies

One of the conclusions that will be drawn from the results is that anticipatory saccades and visually controlled saccades are distinct. This was suggested by Horrocks and Stark (1964) who measured saccade latencies in a task where an observer followed a spot moving in regular steps between two positions. Thus each movement had, objectively, complete spatial and temporal predictability. They report a bimodal distribution of saccade latencies with one peak occurring in which the saccade precedes the target by 50–300 msec and a second where the saccade follows the stimulus by 100–200 msec. Relatively few saccades occur with latencies in between these peaks, particularly in the 0–100 msec region. Horrocks and Stark attribute this to a fast acting inhibitory effect of the visual stimulus which blocks any anticipatory saccades in the process of generation.

All subjects tested in the present experiment made a considerable number of anticipatory saccades to target steps to the centre (i.e. with spatial predictability). Two out of the four subjects also made anticipatory saccades to target movements to the periphery;

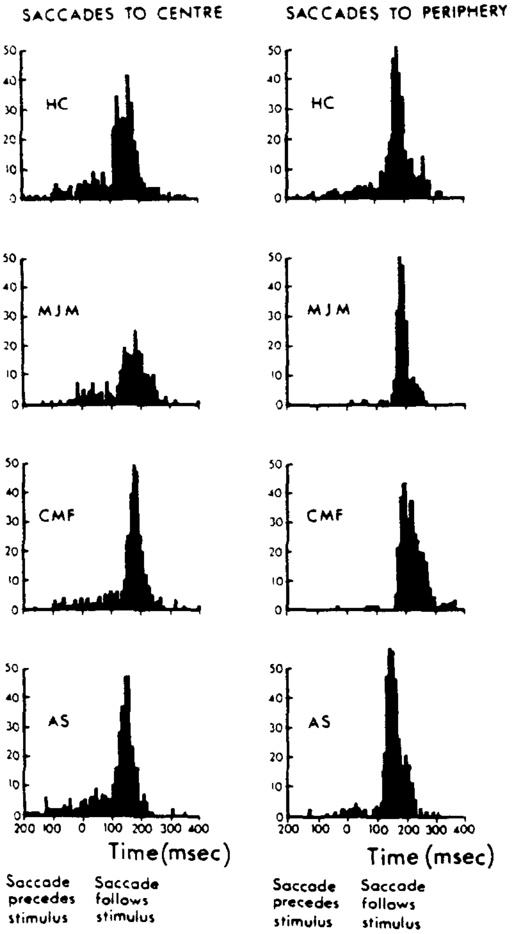

Fig. 1. Histograms showing the distributions of latencies of saccades made to a spatially predictable target (saccades to the centre position) and to a spatially unpredictable target (saccades to the peripheral positions). The sampling bin was 10 milliseconds. The graphs show some indication of a trough in the distribution just before the main peak of visually elicted saccades in the 120–200 msec region.

the other two made such movements very rarely. Figure 1 plots the distribution of saccadic responses at each latency, using a 10 msec bin size. Whilst the results are by no means as clear cut as those shown by Horrocks and Stark, there is nevertheless in each case some indication of a trough in the distribution occurring in the 20–30 msec period preceding the main peak. The most likely reason for the difference between the two sets of results is that the stimulus timing in the Horrocks and Stark study was completely regular and thus some non visual factor also contributed to the suppression (which could also explain why the suppression appears to commence before the stimulus).

Other evidence, presented in Section 7, supports the division of saccades into anticipatory and visually guided categories. For the purposes of subsequent analysis, all saccades with latencies of 100 msec or less have been classified as anticipatory and all saccades with latencies greater than 100 msec have been termed visually guided.

Velocity amplitude relationship for anticipatory and visually guided saccades

The peripheral mechanisms of the oculomotor system are now quite well understood (Robinson, 1964, 1973). To generate a saccade, a characteristic pulse-step neural signal is generated which has the effect, when transmitted to the overdamped mechanical system of the globe, of producing the characteristic saccadic jerk. Saccade size appears to be controlled by variations in the duration of the pulse. A consequence of the high degree of stereotypy in this system is that a systematic relationship exists normally between saccade duration, saccade velocity, and saccade amplitude (Zuber *et al.*, 1967). Under certain conditions, such as fatigue, alcohol, or sedatives, slower saccades at a given size are found (references in Carpenter, 1977) and it is also reported that saccades made in the dark are considerably slower (Becker and Fuchs, 1969, Riggs *et al.*, 1974).

The last result suggests that in some way the visual signal might thus provide an extra 'boost' to the oculomotor command. If this were the case differences in saccade velocities might be anticipated between anticipatory and visually controlled saccades. Figure 2 plots the saccade velocity vs. saccade size relationship

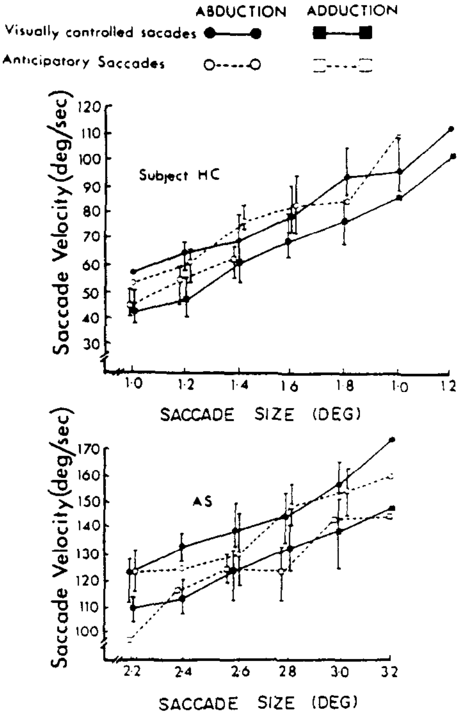

Fig. 2. Saccade velocity vs. saccade amplitude plots for two subjects, with anticipatory saccades and visually elicited saccades shown separately. Medians and interquartile ranges are plotted (the interquartile range is omitted when less than eight observations contribute to a point). Although a slight difference is present between abductive (left eye moving to the left) and adductive (left eye moving to the right) saccades, no difference is apparent between anticipatory and visually elicited saccades.

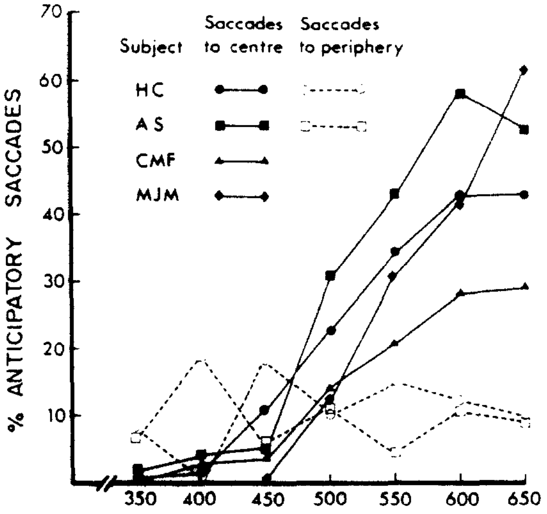

Fig. 3. The proportion of anticipatory saccades shown as a function of the foreperiod. Subjects CMF and MJM made very few anticipatory saccades to the peripheral targets. For saccades to the centre, all subjects show a regularly increasing probability of anticipation as the foreperiod increases. For three subjects the distribution levels off after about 600 msec, suggesting that they were sensitive to the statistical structure of the target movements (i.e. mean foreperiod of 500 msec). In the case of the two subjects making a substantial number of anticipatory saccades to the peripheral targets, the probability of an anticipation appears to be essentially independent of the foreperiod.

for the two observers whose saccade sizes could be measured most reliably. It is clear that no differences exist between the two conditions, although slight differences are seen between adductive and abductive saccades.

Stimulus foreperiod and anticipatory saccades

The variable interval occurring before a target movement will be termed the stimulus foreperiod for that target step. As explained in the method section, this foreperiod could take values between 350 and 650 msec. Figure 3 shows how the proportion of anticipatory saccades relates to this variable. For saccades to the centre, increasing stimulus foreperiod leads to an increasing proportion of anticipatory saccades. This suggests a signal which gradually builds up over the period in which a step might occur and which can trigger an anticipatory saccade. A similar signal has been postulated to account for the systematic decrease in manual reaction time observed when a rectangular distribution of foreperiods exists over a series of trials (Näätänen and Merisalo, 1978).

Saccades occurring before the stimulus in the case of movements towards the periphery cannot be termed anticipatory since they are as often in the wrong direction as the correct one. Nevertheless such saccades were observed and two subjects made a considerable number. The distribution of these is plotted in Fig. 3. Of the other subjects, MJM made three such anticipatory responses on trials with foreperiods of 500 msec (1) and 550 msec (2); CMF made four such responses on trials with foreperiods of 350 msec (1), 450 msec (2), and 500 msec (1). There seems no trend here for the probability of anticipatory saccades to increase with increasing foreperiod; it seems that prestimulus saccades to the periphery occur with approximately equal probability irrespective of the foreperiod. It seems necessary to conclude that these aberrant saccades in the spatial uncertainty situation are not influenced by the "expectancy" signal which controls anticipatory saccades to a spatially determinate target.

Stimulus foreperiod and visually controlled saccade latencies

The foreperiod is also found to affect the latency of visually controlled responses (i.e. saccades with latencies greater than 110 msec) as is shown in Fig. 4. Treating this data by an analysis of variance shows that the effect of stimulus foreperiod is significant (F(6, 13) = 5.22; $P = 0.003$), but the interaction between foreperiod and saccade destination (left, right, or centre) is not significant (F(12, 36) = 0.74; $P = 0.7$).

Saccade size and saccade latency: saccades to the centre target

Are the metrics of anticipatory saccades different from those of visually guided saccades? In order to approach this question, a plot has been made of saccade size against saccade latency, for each of the three subjects whose calibration allowed sufficient confidence that saccade size could be accurately assessed.

Considering first saccades to the centre position, Fig. 5 shows the data. The latency intervals were

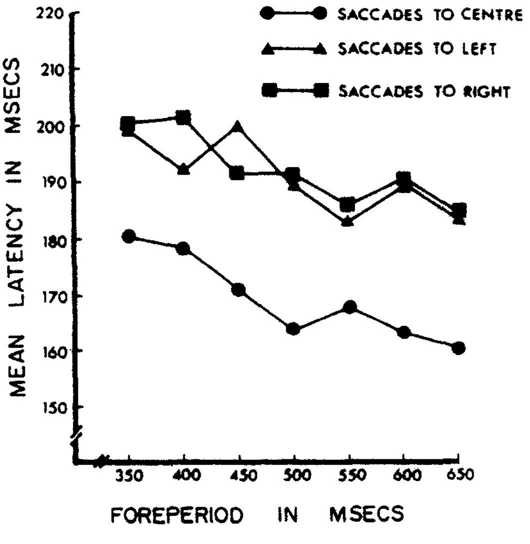

Fig. 4. Mean latency of visually elicited saccades (saccades having latencies greater than 100 msec) plotted as a function of target foreperiod for saccades to the centre and to the peripheral targets.

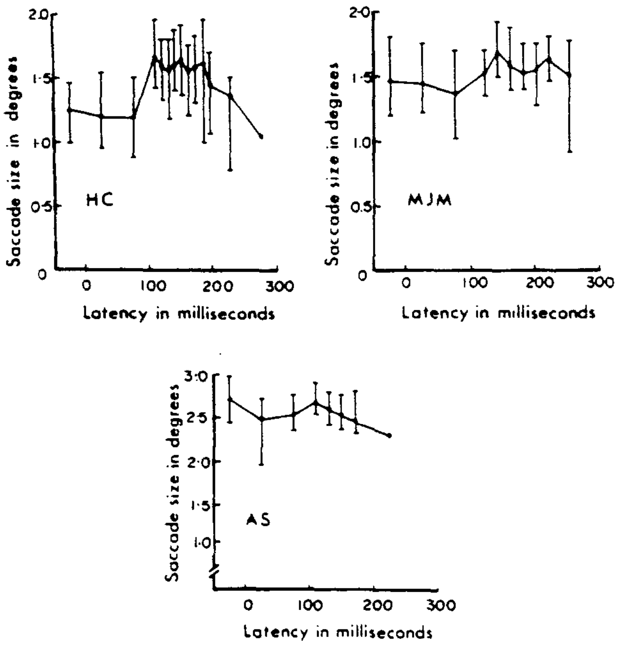

Fig. 5. Variation of saccade amplitude with saccade latency for saccades to the centre position. Results are shown for the three subjects whose calibrations allowed accurate estimation of saccade sizes. The plots are made by grouping individual saccades in intervals of 10 or 20 msec within the main peak of visually elicited saccades, and 50 msec outside this region. They show the median saccade amplitude, together with the interquartile range whenever eight or more observations are contributing.

chosen to allow a sufficiently large number of saccades at each point to be analysed (eight or more when interquartile ranges are given). The majority of the saccades made (see Section 1) are visually controlled with latencies between 100 and 200 msec. These are slightly hypometric (between 10 and 20%) and show a variance which is slightly over 10% of the saccade size. These figures are consistent with previous reports (Timberlake *et al.*, 1972) for saccades of comparable size. Saccades with latencies greater than about 200 msec may be more hypometric. This effect is seen clearly in the data from subject HC and has been observed in other situations.

A comparison of anitipatory and visually controlled saccades shows clear differences in two out of the three subjects. HC and MJM produce anticipatory saccades whose amplitudes are, respectively 75 and 90% of the visually controlled saccade amplitudes (the differences are significant at the 5% level in both cases). No obvious difference is apparent in the case of subject AS; this might be an inter-subject difference or represent a consequence of the greater target distance used with this subject.

Saccade size and saccade latency: saccades to the peripheral targets

The plots of saccade size versus saccade latency for movement to the peripheral targets is presented in Fig. 6. Subject MJM made only three anticipatory saccades but subjects HC and AS shows considerably more. In all cases it is evident that the anticipatory saccades are hypometric. Visually controlled saccades to peripheral targets are slightly larger than the visually controlled saccades to the centre and size appears as an increasing function of latency. This can be attributed at least in part to the scoring procedure used. The rising trend is produced by saccades which are large and also have a long latency. Examination of these showed that in some cases a small anticipatory saccade, in the opposite direction to the target, occurred, but was not classified at the primary saccade by the criteria used.

Separation of anticipatory saccades from visually controlled saccades

In Section 1 of the results, the frequency histograms of saccade latencies were held to support a dichotomous distribution of saccades into anticipatory and visually guided classes. Several other analyses confirm the validity of this distinction and these are now given.

(a) For the two subjects who make significant numbers of anticipatory saccades to the peripheral locations, no wrong direction saccades occur with latencies greater than 100 msec. Examining all saccades occurring with latencies of 90 and 100 msec, subject AS makes 8 saccades only one of which is in the wrong direction (and is also very hypometric). Subject HC makes 6 saccades in this latency interval again with only one hypometric wrong direction saccade. For latencies of 80 msec and below, the proportion of wrong direction saccades appears to equal that of correct direction saccades.

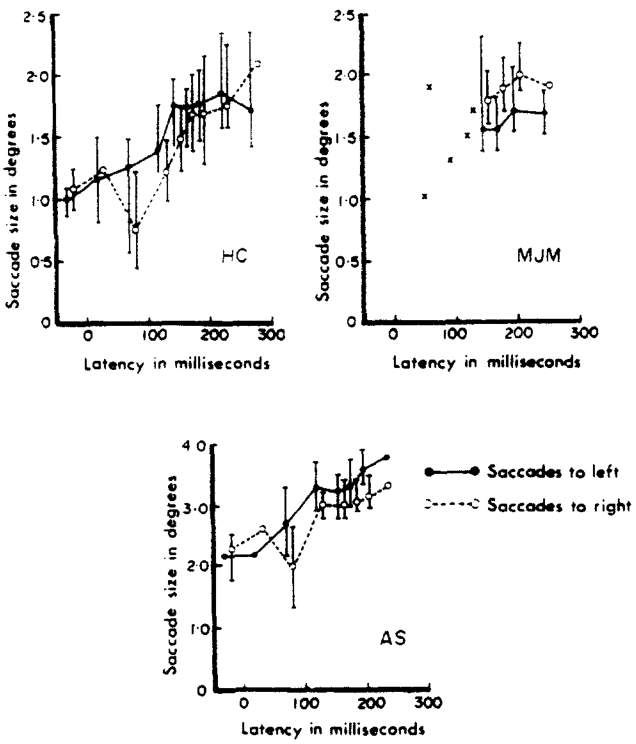

Fig. 6. Variation of saccade amplitude with saccade latency for saccades to the peripheral targets. Results plotted as in Fig. 5. Subject MJM only made five saccades to the periphery with latencies lower than 150 msec: these are plotted individually. The results show clearly that anticipatory saccades are hypometric and suggest that long latency visually elicited saccades are hypermetric.

(b) If saccades with latencies greater than 100 msec actually contained a proportion of those which were in fact directed by an anticipatory route, this proportion would vary with the foreperiod since on a substantial number of short foreperiod trials anticipatory saccades would have occurred had the foreperiod been longer (see Fig. 3). Thus one would expect to find differences dependent upon foreperiod for both latency and also amplitude for the subjects showing hypometric anticipatory saccades. Figure 4 shows that latency differences dependent upon foreperiod do indeed occur, but these are identical for saccades to the centre, where the proportion of anticipations is high and those to the periphery where the proportion is much lower.

(c) A similar argument can be used in the case of saccade amplitudes. For the two subjects showing clearly hypometric anticipatory saccades, a comparison was made between the amplitudes of saccades with latencies betweeen 110 msec and 190 msec in those cases where the foreperiod was short (350 or 400 msec) and in those cases where it was long (600 and 650 msec). For the subject HC, the mean amplitude after short foreperiods is 1.55° with standard deviation 0.41° (*N* = 46) and after long foreperiods the corresponding figures are mean 1.41°, standard deviation 0.33° (*N* = 32). The mean size of anticipatory saccades (latencies less than 100 msec) is 1.20°. For MJM the figures are: short foreperiods, mean 1.67° standard deviation 0.29° (*N* = 23) long foreperiods mean 1.58°, standard deviation 0.21° (*N* = 20); anticipatory saccades mean 1.46°. There is no suggestion here that short foreperiods might result in putative anticipatory saccades occurring after 110 msec since if anything the saccades are larger than those after long foreperiods.

Altogether these analyses support the distinction drawn earlier between anticipatory and visually guided saccades and give no support to the idea that an intermediate category exists, with the possible exception of saccades commencing in the period just prior to 100 msec following the stimulus. This suggests that anticipatory and visually guided saccades are dichotomous categories. It will be of interest to know whether this separation is found more generally (e.g. with a greater range of spatial and temporal uncertainties).

Secondary saccades

The study was not designed with the intention of examining secondary saccades; however since their presence might influence the interpretation of the results, they were scrutinised. The timing was designed to be such that even with the shortest foreperiod, the visually controlled primary saccade would be completed always before the next stimulus, but this would not necessarily be the case for secondary saccades. All subjects made secondary saccades extensively (50–70% of occasions) to anticipatory primaries and occasionally (2–18%) to visually controlled primaries. The latency distribution (measured from the primary saccade) showed a mean of about 200 msec for these secondaries. These figures must be subject to various qualifications. Firstly, since the majority of the corrective saccades were to anticipatory primaries, the actual target movement may have had an influence in triggering the saccade. Secondly the end of the sampling was terminated by the 400 msec sampling interval so some long latency secondaries may not have been recorded. Thirdly in some cases the subsequent target movement occurred at the time that secondary saccades are expected and may also have had some effect. It was noted that larger corrective saccades tended to have shorter latencies (cf. Becker, 1976). More importantly for the subsequent arguments, there appear to be no differences in proportions or latencies between corrective saccades at the centre and at the periphery.

DISCUSSION

The main experimental findings may be summarised as follows:

(1) Anticipatory saccades are produced frequently by all subjects when the target position is certain (i.e. movements to the centre). For all subjects the probability of such anticipatory saccades increases as the foreperiod before the target movement increases.

(2) All subjects produce quasi-anticipatory saccades when the target position is not known (movements to the periphery) although these saccades occur only rarely in two out of the four subjects. These movements do not show any systematic dependence on the foreperiod, in contrast to the anticipatory saccades to the centre.

(3) Anticipatory saccades possess the same velocity-amplitude relationship as visually controlled saccades.

(4) The latencies of visually elicited saccades, both to spatially predictable and to spatially unpredictable targets, show a systematic decrease with increasing foreperiod.

(5) Anticipatory saccades are smaller than visually controlled saccades, except in one case (AS; movements to centre) where no difference is found.

(6) The separation of anticipatory and visually controlled saccades by means of a latency criterion was justified by several analyses which showed that saccades with latencies greater than 100 msec showed different characteristics from anticipatory saccades. In the 90–100 msec region, the evidence suggests that suppressive mechanisms result from the visual stimulus information. Saccades in the incorrect direction appear particularly likely to be suppressed but there may also be a general suppressive effect.

It is well known that the final stage in the neural command pathway to the eye muscles transmits a "pulse-step" signal, which is programmed to interact with the dynamic properties of the eye to effect a step change in eye position (Robinson, 1975). This signal is produced by a pulse generator which can produce a range of output pulses corresponding to saccades of different sizes and in each case the tonic (step) change accompanying the pulse output is appropriate to maintain the eye in its new position. The fact that anticipatory and visually controlled saccades show the same velocity amplitude relationship suggests that they do not possess separate pulse generators and thus the pathways for the two types of signal join either at, or before, the input to the pulse generator.

There is still considerable uncertainty concerning the stages prior to the pulse generator, even in the case of visually evoked saccades (Robinson, 1975). One suggestion that has lately received attention is the existence of two control inputs, one concerned with the timing of the pulse (i.e. its time of onset) and the other concerned with the spatial characteristics (which affect the pulse duration). Indirect support comes from the study of saccades in reading tasks. Rayner and McConkie (1976) conclude that two different sets of factors influence fixation durations (i.e. saccade occurrence) and saccade amplitudes respectively. A more direct approach is that of Becker and Jürgens (1975, 1979). They have recorded saccadic responses to targets which moved in one direction, followed by a brief interval (50–200 msec) to a position at the opposite side of the fixation point. Saccadic latencies show a bimodal distribution—either a short latency saccade is directed at the first position or a long latency saccade at the second. Becker and Jürgens interpret this as showing a double decision mechanism responsible for the onset timing and direction of the saccade. Activity in the decision mechanism for one direction is hypothesized to suppress activity in the mechanism for the other direction.

Separation of the onset timing signals from the spatial signals would enable an explanation to be offered of the dissociation found between the effect of foreperiod on the proportion of anticipatory saccades, and the effect on the latency of visually elicited saccades. In the former case, an effect was only observed for saccades to the centre whereas in the latter case, both centrally and peripherally directed saccades were affected. Suppose the foreperiod effects are mediated through the onset timing pathway and that a saccade will only be released when there is sufficient activation in both the timing pathway *and* in a spatial pathway from either a retinal map or an anticipatory map. As the foreperiod progresses, activation in the timing pathway builds up. When there is a spatial signal from the anticipatory map, a saccade becomes progressively more likely. Likewise one could envisage that visually elicited saccades could be triggered at an earlier point as information flows from the retina if the timing pathway activation is higher.

A further feature of the Becker and Jürgens (1979) model which has some similarities with proposals made already is that activity in the onset timing decision mechanism can be suppressed; in their case the mechanism to produce saccades in one direction is suppressed by activation in the mechanism to produce saccades in the opposite direction. As discussed in Section 1 of the Results, there is some evidence that there is a general suppressive effect in the 90–100 msec period following a stimulus, with possibly a stronger effect for saccades in the "wrong" direction. A suppressive system of this nature could also solve a potential problem for the saccadic system. A visually elicited saccade must use information that is "out of date" by a time at least as long as the delay in the retina. If a previous saccade occurred during this time then the out of date information could potentially elicit a misdirected saccade. However if the visual information first suppressed the generation mechanism for a period then this situation would be prevented. It must be pointed out however that the suppression in the Becker and Jürgens study occurs at a much later point in time after the stimulus than has been found here.

Is there a separate "retinal map" and "anticipatory map" as suggested above? The calculation of saccade amplitude for a visually elicited saccade requires a conversion from spatial co-ordinates to the appropriate pulse size. It would be possible for this to proceed in a retinotopic framework. Thus a target in the visual periphery could signal place coded information about its retinal position and this be directly converted to the appropriate pulse coded oculomotor signal. This parsimonious model is given added attractiveness by the establishment of the correspondence between the retinal and oculomotor maps in the superior colliculus (Schiller and Koerner, 1971; Robinson, 1972). An account can be given of spatial attention if it is assumed that local regions of the retinal map could additionally be selectively facilitated by some central source (e.g. Wurtz and Goldberg, 1972). Furthermore if such facilitatory activity could on its own trigger saccades, appropriate anticipatory saccades might also be accounted for. More recently doubt has been cast upon this retinocentric model and an alternative put forward (Robinson, 1975) in which information about eye position is also processed to allow calculation of saccade amplitude in an egocentric frame. Mays and Sparks (1980) have suggested that this also can be supported by neurophysiological evidence. One advantage claimed for this elaboration is that centrally programmed saccades could make use of the egocentric spatial map. Neither of the models could, without further assumptions, explain the result found in the present study that anticipatory saccades have different spatial characteristics from visually elicited ones. This result suggests either that the anticipatory saccades are planned in a totally different "map" or that the eye position information used to convert egocentric to retinocentric space is systematically dysmetric.

Acknowledgement—This work was supported by MRC Grant No. G977/865/N.

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