PLANNING SEQUENCES OF SACCADIES

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Abstract—Subjects used saccades to fixate a sequence of 1–5 stationary targets (separation = 90") located at the vertices of an imaginary pentagon. The latency of the first saccade in a sequence and the duration of intervals between subsequent saccades increased with sequence length at a rate of about 20 msec/target. Latency also varied with ordinal position in the sequence. These results were not due to directional differences in saccadic latency nor to latency-accuracy or to latency-precision trade-offs. Results were similar when targets were removed and saccades were directed to remembered locations. These effects may be best accounted for by models that have been proposed to account for similar effects of sequence length and ordinal position on other voluntary motor tasks, such as typing, speech and finger-tapping. In these models motor programs for a sequence of responses are planned before execution and then retrieved from memory during execution. These models are fundamentally different from the traditional saccadic models in which visual error signals evoke saccades. Instead, we propose that saccades are controlled by an organized plan for an entire sequence of saccades. Visual error signals may modify or elaborate the plans during the execution of a sequence. Our proposal is consistent with ideas developed by Laslhey [Cerebral Mechanisms in Behavior: The Hixon Symposium, Wiley, New York (1951)] in his general treatment of the central organization that determines voluntary motor performance.

Saccades Motor patterns Visual scanning

INTRODUCTION

In ordinary scanning of visual scenes observers use saccadic eye movements to look at whatever objects they choose. Despite the widespread acknowledgement of the voluntary nature of saccades, they are nevertheless typically studied as if they were reflexive eye movements (e.g. Cornsweet, 1956; Rashbass, 1961; Saslow, 1967a,b; Becker and Jurgens, 1979; Sparks and Mays, 1983). For example, in the traditional saccadic experiment a point target steps to an eccentric retinal location once or twice during a trial. The time and location of the target's steps are selected randomly based on the belief that random motions will prevent subjects from planning to look in a particular location before the target step occurs. The latency, size, and direction of saccades are analyzed as a function of the spatial and temporal properties of the target steps in an attempt to discover how the retinal position signals are processed to generate saccadic commands. The rationale for studying saccades as a function of randomly-chosen target steps is that the operation of lower-level sensorimotor processes will be accurately reflected in saccades once the tendency to plan saccades voluntarily is suppressed.

Karl Laslhey, in his deservedly famous 1951 paper entitled "The Problem of Serial Order in Behavior," showed that attempts to suppress voluntary plans cannot succeed and are based on fundamental misconceptions of how voluntary motor systems work. Laslhey pointed out that sensory input acts on a motor system "which is already actively excited and organized" (p. 112). This "background of excitation" is produced by central mechanisms which plan motor responses before sensory input is received. Central to Laslhey's argument was the thesis that what is planned is an organized pattern of motor activity. The individual component responses of the pattern are programmed with respect to the structure and purpose of the pattern as a whole—and not as reactions to local sensory stimulation. Planning an organized pattern of responses, argued Laslhey, makes it possible for the pianist to play rapid arpeggios, the centipede to coordinate the movements of its individual legs and run across the room, and the horse to switch from a trot to a gallop—2 distinct gaits that differ (accord-

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ing to Lashley) only in the way that the same component muscle contractions are organized. Lashley believed that sensory input comes into play only after the plans for the sequences are established. Lashley's argument means that we cannot understand how motor systems work based on observations of isolated, single responses. We must study responses in the context of the planned sequences in which they typically appear.

Lashley's ideas have had little impact on the study of saccades. The discussion of planning has been confined principally to the suggestion that an individual saccade may be planned in advance, based on what subjects know about the likely direction of an upcoming step (e.g. Westheimer, 1954; Wheelless et al., 1967; Norcia et al., 1979; Kowler et al., 1984). In addition, some others have suggested that general plans or patterns may guide decisions about when or where to make saccades during the inspection of stationary visual scenes (e.g. Levy-Schoen, 1981), or during maintained fixation of stationary targets (Steinman et al., 1973). But aside from these few suggestions, the role of central plans in the programming of saccades has not been considered.

In contrast to the neglect of planning in studies of saccades, a number of investigators have studied planned sequences of other voluntary motor responses. We will next briefly summarize a few of these studies because their approach to motor planning in systems other than the oculomotor provided the basis for our study of saccadic planning. Our brief description is adequate only to introduce our experiments. It does not do justice to the empirical and theoretical elegance of the prior work. Readers are encouraged to consult the cited papers.

Evidence that sequences of responses in speech and typing are planned was obtained by Sternberg et al. (1978a). They found that both the mean latency of the first response in a sequence, and the mean time between responses in a sequence, increased as a linear function of the number of responses in the sequence. To account for these results, they proposed that a motor program is prepared and stored in a special motor program memory before the signal to begin a sequence of responses is given. The motor program is comprised of subprograms which contain information specific to each of the individual responses in the sequence. Following the signal to begin responding, a search of the memory is initiated to find the subprogram for the first response. Thus, the longer the sequence, the longer it will take to find the correct subprogram. After the search for the first response is completed, the response is executed and the search for the next response in the sequence begins. The time to initiate all the responses in the sequence was found to increase with sequence length, suggesting that all the subprograms remain in memory until the sequence is completed. Sternberg et al.'s (1978a) results and model illustrate the idea of central planning described by Lashley (1951) in that the characteristics of individual response elements are shown to depend on a pre-established motor plan for the entire sequence of responses.

Motor planning was also studied by Rosenbaum et al. (1983). They found that the time between a sequence of responses (finger-taps) depended on the ordinal position of the response in the sequence. (Effects of ordinal position have also been observed in typing and speech; Sternberg et al., 1978a,b). Rosenbaum et al. accounted for the observed timing pattern of the finger taps by proposing that the representation of the motor program for the sequence is hierarchically structured. In a hierarchical structure, information about the motor commands can be retrieved from memory in subgroups of 2 or 3 responses during the execution of a sequence.

A somewhat different approach to the study of motor planning was taken by Terzuolo and Viviani (1980) who studied the temporal patterns of typed words. They found evidence for the central organization of motor plans in their observation that the ratios of the time intervals between keystrokes could remain the same despite changes in the overall rate of typing. Viviani and Terzuolo (1980) reported finding analogous timing patterns for handwriting. (For discussion of the interpretation of timing patterns, see Gentner, 1982a,b, and Viviani and Terzuolo, 1982.)

The studies of motor performance described above demonstrated that voluntary movements are planned as whole sequences. These planned sequences exhibit certain characteristics, namely, latencies of individual responses depend on sequence length, and particular temporal patterns of responses occur within sequences.

In the present paper we ask whether saccades are also planned as whole sequences. In the experiment subjects used saccades to fixate from
1 to 5 stationary targets. This experiment is similar to Sternberg et al.'s (1978a) study of typing and speech in that subjects executed response sequences of various lengths. We used visible stationary targets, rather than the popular random step of a single target, because subjects might choose not to plan sequences or might plan inaccurate sequences, when the locations of future target positions are not known in advance. Stationary targets, unlike random target steps, allow the planning of accurate sequences of saccades.

We found that saccades, like other voluntary motor acts, have characteristics which indicate that they are planned as patterned sequences.

METHOD

Eye movement recording

Two-dimensional movements of the right eye were recorded by a Generation IV SRI Double Purkinje Image Tracker (Crane and Steele, 1978). The left eye was covered and the head was stabilized on a dental biteboard.

The voltage output of the Tracker was fed on-line through a low pass 50 Hz filter (48 dB/octave) to a 12-bit analog to digital converter (ADC). The ADC, under control of a computer (Plessey LSI 11/23) sampled eye position every 10 msec. The digitized voltages were stored for later analysis.

Tracker noise level was measured with an artificial eye after the Tracker had been adjusted so as to have the same first and fourth image reflections as the average subject's eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a standard deviation of position samples, was 0.4 min arc for horizontal and 0.7 min arc for vertical position.

Recordings were made with the Tracker's automatically movable optical stage (auto-stage) and focus-servo disabled. These procedures are necessary with Generation IV Trackers because motion of either the auto-stage or the focus-servo introduces large artifactual deviations of Tracker output. The focus-servo was used, as needed, only during intertrial intervals to maintain subject alignment. This can be done without introducing artifacts into the recordings or changing the eye position/voltage analog calibration. The autostage was permanently disabled because its operation, even during intertrial intervals, changed the eye position/voltage analog calibration.

Subjects

Two subjects were tested. One (E.K.) is an experienced eye movement subject and knew the purpose of the experiment. The other (J.W.) had never served as an eye movement subject before, and was naive as to the purpose of the experiment.

Stimuli

The stimulus was generated on a display monitor (Tektronix 608, P4 phosphor) located directly in front of the subject's right eye. The stimulus consisted of 1-5 stationary points located at the vertices of an imaginary pentagon. The length of the sides of the imaginary pentagon was 90'. The stimulus was controlled by the computer by means of digital-to-analog converters (DACs). The entire display was refreshed at a rate of 200 times per second, too rapid for the individual refreshes to be discerned, so that all the displayed points appeared to be on at the same time with no visible flicker.

The intensity of the points was set to 1.9 log units above absolute light-adapted foveal threshold for E.K. and 1.1 log units for J.W. These values were chosen according to a psychophysical criterion, which was to achieve a comfortable viewing intensity while minimizing the detectability of the faint glow of the display's phosphor produced by the beam when it was moved off the display face between refreshes.

The display was viewed in a dark room through a collimating lens which placed it at optical infinity. Appropriate negative lenses were placed between the eye and the collimating lens for the myopic subject (E.K.) so that the points appeared in sharp focus.

Procedure

Before a trial one of the points of the pentagon was visible. This is called the start-point. The subject fixated the start-point and pressed a button when ready. Seven hundred msec after the button press, a brief (100 msec) tone sounded and a set of either 1, 2, 3, or 4 points appeared at the onset of the tone. The points occupied successive vertices of the pentagon, proceeding in a clockwise direction from the
start-point. No vertices were skipped so that the distance between one target and the next was always 90°. These points were the targets for the saccades. The appearance of 4 target points provided both the 4-target and the 5-target stimulus. In the case of the 5-target stimulus the start-point also served as the fifth target. The subject always knew before each trial how many targets were to be fixated in sequence. Thus, although the 4- and 5-target stimuli had the same appearance, the subject knew whether to stop at the fourth target or to continue making saccades until the fifth target (the start-point) was reached.

The tone and the appearance of the targets constituted a "go" signal instructing the subject to begin making saccades as quickly as possible in a clockwise direction to look at each target in sequence. When the last target was reached, the subject was instructed to keep looking at that target until the trial was over. The end of the trial was signalled by the removal of the targets.

Trial length, defined as the time from the "go" signal to the disappearance of the targets, depended on the number of targets in the sequence. Trial length was set to 500 msec times the number of targets. Eye movement data were acquired from the occurrence of the "go" signal until the targets disappeared.

Sequence lengths of 1 to 5 targets were tested. All sequence lengths were tested with each of the 5 points of the pentagon as the start-point. We needed to test all sequence lengths using each of the start-points because there were small but reliable effects of direction on saccadic latency. Data for each sequence length and ordinal position were averaged over trials run at each of the start-points so that the differences in saccadic latency as a function of direction would not be confounded with either the effects of sequence length, or the effects of ordinal position within the sequence, on saccades.

The above procedures applied to the first experiment that will be described. A second and third experiment were also run in which the stimuli or instructions were modified. These modifications will be described and justified later, along with the results.

**Design**

There were 5 possible start-points and 5 possible sequence lengths, giving a total of 25 stimulus conditions. The order of testing the conditions was determined by a Greco-Latin square. Specifically, five stimulus conditions were tested in each session. The five conditions were selected at random with the constraint that each start-point be tested once and each sequence length be tested once. This randomization procedure meant that each of the 5 start-points and each of the 5 sequence lengths were tested once in each session. This design was used so that day-to-day variation in performance would be distributed equally among the start-points and sequence lengths.

Stimulus conditions were tested in blocks of 20 trials. An experimental session was comprised of 5 blocks (100 trials). Subjects were told which start-point and which sequence length would be tested before each block.

Ten percent of the trials were catch trials in which no "go" signal sounded. They were included to discourage subjects from making saccades to the targets before the "go" signal.

**Data analysis**

Trials in which saccades were made too early (up to 100 msec after the "go" signal) were omitted because the subject was deemed to have initiated the saccade before the "go" signal. For E.K. 4.6% and for J.W. 6.6% of the trials were omitted for this reason. Trials in which the tracker lost lock on the Purkinje image reflections were also omitted. This was done because we could not know whether saccades occurred during these lost intervals, and, therefore, could not accurately measure intersaccadic intervals in such trials; 27% of trials for E.K. and 13% for J.W. were removed because of lost lock.

Onsets and offsets of saccades were detected from the eye position records by a computer algorithm that used a velocity criterion. The criterion for each subject was determined empirically by inspection of analog records of eye position in which saccades detected by the algorithm were flagged (see Fig. 1 for representative records). Inspection of analog records showed that all saccades were detected by the algorithm.

Computer algorithms were used to compute the average size of saccades, the average latency of the first saccade of a sequence, and the average intersaccadic interval, where intersaccadic interval was defined as the time between the onset of one saccade and the offset of the previous saccade. For convenience in describing the results the latency of the first saccade and the time between subsequent saccades will both be denoted by the term "latency".
Planning sequences of saccades

Fig. 1. Representative examples of eye movements to look at 5 targets in sequence for E.K. and J.W. Targets appeared at the "go" signal. The start point and final target was the uppermost point. Top: horizontal position on the X and vertical position on the Y axis. Tic marks on each axis separate 1 deg. Bottom: same trials. Horizontal (H) and vertical (V) eye position is plotted as a function of time. Tic marks on the Y axis separate 1 deg. Tic marks on the X axis separate 1 sec. Upward deflections in the eye traces indicate movements to the right or up. The top trace (F) shows the flag indicating onset and offset of the saccade detected by the computer algorithm. Note that the duration of a saccade includes the overshoots at the end of saccades.

RESULTS

(I) Saccades to Visible Targets

Subjects used saccades to look at the targets in sequence

A representative trial showing saccades made to fixate a sequence of 5 consecutive targets is reproduced for each subject in Fig. 1. The same saccadic pattern is represented as a two-dimensional scan pattern, and as horizontal and vertical eye position as a function of time. These saccadic patterns represent typical performance in that they show subjects making the correct number of saccades required for a given sequence length. E.K. made the correct number of saccades on 288 of her 307 trials, J.W. on 262 of his 349 trials. The proportion of J.W.'s trials containing the correct number of saccades decreased from 1.0 to about 0.6 with increasing sequence length. The proportion of E.K.'s trials containing the correct number of saccades remained above 0.9 for all sequence lengths.

The few trials in which E.K. did not make the correct number of saccades were divided almost equally between trials in which targets were skipped (0.53) and trials in which too many saccades were made (0.47). When J.W. did not make the correct number of saccades he usually (0.79) skipped targets.

In the next section performance will be described as a function of the number of targets in the sequence, not as a function of the number of saccades that were actually made. Later, we will justify this procedure and discuss its implications by analyzing J.W.'s performance as a function of the actual number of saccades he made in a sequence.

The latency of the first saccade of the sequence increased with sequence length

The purpose of the experiment was to determine whether saccades are planned as sequences. One way to do this is to examine the latency of the first saccade in the sequence. If saccades are planned individually, as responses to visual error signals, then the latency of the first saccade should be the same, regardless of how many targets have to be scanned after the first. On the other hand, if saccades are planned as sequences, then one might expect the latency of the first saccade to increase with sequence length because the longer the sequence the more time would be required to plan, or to retrieve plans, for the saccades.

Figure 2 shows that the mean latency of the first saccade did increase as the number of targets in the sequence increased for both E.K. and J.W. This result supports the hypothesis that saccades are planned as sequences. We computed the slope of the best fitting straight line by a least squares method to summarize the increase in latency with sequence length. Slopes

Fig. 2. Mean latency of the first saccade of a sequence as a function of the number of targets in the sequence. Each datum point is based on 48-67 trials for E.K. and 49-82 for J.W. Vertical bars represent 1 SE.
were 11 msec/target for E.K. and 15 msec/target for J.W., both significantly greater than zero (P < 0.0005).

The slopes of the latency functions were similar to those observed in Sternberg et al.'s (1978a) study of typing and speech. Sternberg et al. concluded that straight-line fits to their latency functions were appropriate because deviations from linearity were not statistically significant. The latency functions we observed for saccades (Fig. 2) appeared to deviate somewhat from linearity, so a test for "lack-of-fit" was used to determine whether some nonlinear model would provide a significantly better fit (Kleinbaum and Kupper, 1978). The "lack-of-fit" test showed that the linear model could not be rejected (P > 0.25).

The increase in latency with sequence length could have been caused by the greater number of targets that must be visually analyzed in longer sequences. But visual analysis, by itself, did not account for the increase in mean latency as a function of sequence length because the mean latency of the first saccade was longer for the 5-target sequence than for the 4-target sequence for both subjects (see Fig. 2). The visual stimulus for both of these sequences was identical. The 4- and 5-target sequences differed only in the number of saccades that had to be made, not in the number of targets displayed.

The increase in the latency of the first saccade in a sequence as a function of sequence length had also been observed for two other subjects who were tested previously with stimuli very similar to those described here (Kowler, 1982). Also, a recent paper by Inhoff (1986) reported increases in saccadic latency as the number of targets to be scanned increased from 1 to 3.

The latency of saccades, after the first, increased with sequence length

The effect of sequence length on the latency of the second through the fourth saccade in a sequence is shown in the upper graphs of Fig. 3. (The latency of the first saccade, replotted from Fig. 2, is included to facilitate comparison.) The latency of E.K.'s second saccades increased by 19 msec/target and third saccades by 13 msec/target. Both of these values were significantly greater than zero (P < 0.0005 for second saccades and P < 0.025 for third saccades). The latency of E.K.'s fourth saccades did not increase when sequence length increased from 4 to 5 targets.

J.W. showed an effect of sequence length on latencies of third (slope = 57 msec/target, P < 0.0005) and fourth saccades (slope = 13 msec/target, not significantly different from zero, P > 0.5). Latencies of his second saccades were about the same for all sequence lengths (see Fig. 3). The effect of sequence length on saccadic latency is summarized by the lower graphs of Fig. 3. In these graphs the mean latency of all saccades for a given sequence length, regardless of ordinal position, is shown as a function of sequence length. E.K.'s latencies increased at a rate of 22 msec/target and J.W.'s at a rate of 20 msec/target. Both values were significantly greater than zero (P < 0.0005)*.

Latency as a function of the number of saccades in a sequence

The effect of sequence length on latency,

*The latency of saccades after the first was computed as the time between the onsets of a saccade and the offset of a prior saccade. We also examined effects of sequence length and ordinal position on the time between the onsets of successive saccades. This measure includes the duration of saccades. We found that including the duration of saccades increased the latency by a constant but did not change the pattern of variation of latency as a function of either the number of targets in a sequence or the ordinal position in a sequence.

Fig. 3. Mean latency of the first through fourth saccades in a sequence (top graphs) and mean latency averaged over ordinal position in the sequence (bottom graphs) as a function of sequence length. Each datum point in the top graphs is based on 48-67 trials for E.K. and 49-82 trials for J.W. Each datum point in the bottom graphs is based on 49-287 trials for E.K. and 66-239 for J.W. Vertical bars represent 1 SE.
not appear when latency was examined as a function of the number of saccades. Also, the rate of increase in latency with the number of saccades, regardless of their ordinal position in the sequence, was only 4 msec/target, a value not significantly greater than zero ($P > 0.10$) (see Fig. 4, bottom graph). These results suggest that the increase in saccadic latency as a function of the number of targets in a sequence (Fig. 3) represents activity at an early stage of saccadic planning, reflecting J.W.'s intention to look at all the targets, rather than later stages in which the final oculomotor commands were determined.

**Effects of sequence length on the sizes of saccades**

It was possible that the increase in latency with sequence length was not due to planning of sequences, but to an adjustment of the subjects' decision criteria. For example, perhaps subjects might have decided to shorten latency at the expense of accuracy for short sequences, and to increase latency to achieve better accuracy for longer sequences. We raise this possibility because it is known that subjects can choose to sacrifice saccadic latency to achieve better accuracy (Steinman et al., 1973; Viviani and Swensson, 1982; Ottes et al., 1985).

To find out whether latency-accuracy trade-offs explained the increase in latency with sequence length, we examined the mean saccade vector size as a function of sequence length. We also examined the standard deviation of saccade vector size as a function of sequence length to look for trade-offs of latency for precision. Consideration of precision is important because mean saccade size might be equal to the target separation (90°), but if the standard deviation of saccade size is large, then individual saccades are seldom accurate.

If a latency/accuracy trade-off accounted for the increase in latency with sequence length, then accuracy should steadily improve as sequence length increases. This is not what happened. First consider E.K.'s data. The mean vector sizes of E.K.'s saccades, shown in Fig. 5, were accurate (90°) for the 3- and 4-target sequences. Saccades in the 1- and 2-target sequences were too small and in the 5-target sequence too large. Thus, her accuracy did not improve as sequence length increased. E.K.'s latencies are also not explained by a trade-off of latency for precision. Such a trade-off would be indicated by a decrease in the standard deviation of saccade vector size with sequence length. The results of our analysis suggest that the increase in latency with sequence length is due to planning of the sequences, rather than to an adjustment of the subjects' decision criteria.
Fig. 5. Mean saccade vector size (top graphs) and the standard deviation of vector size (bottom graphs) averaged over the ordinal position of the saccade in the sequence as a function of the number of targets in the sequence. Each datum point is based on 49–287 trials for E.K. and 66–239 trials for J.W. Vertical bars in the top graphs represent 1 SE. The dotted line shows the size of the separation of the targets.

length. E.K.'s standard deviations did not decrease with sequence length, but instead were largest for the 2- and 3-target sequences (see Fig. 5).

J.W.'s saccades were less accurate and less precise than E.K.'s. Nevertheless, trade-offs of latency for accuracy or latency for precision did not account for his pattern of latencies. His saccades became less accurate as sequence length increased. Also, the standard deviation of saccade vector size increased as sequence length increased from 1 to 2 targets and remained the same thereafter (see Fig. 5).

The failure to find a consistent relationship between saccadic latency and accuracy and between saccadic latency and precision suggests that the increase of latency with increasing sequence length was not a consequence of decisions to trade latency for accuracy or latency for precision. Rather, the increase in latency may reflect the additional time required to plan the saccades in a sequence, or to retrieve the plans for the saccades in a sequence, as the number of targets to be scanned increases.

Saccadic latency and size varied with ordinal position within a sequence

Motor patterns are characterized by system-
quences in which they occurred. These properties were the length of the sequence and the ordinal position within the sequence. These results, which are similar to those observed in prior studies of other voluntary motor responses (e.g. Sternberg et al., 1978a), suggest that saccades are not determined exclusively by visual error signals, but by plans for the sequence of saccades. In the next experiment we ask whether plans are completely formed before the execution of a sequence, or whether they may be modified during sequence execution.

(II) Saccades to Remembered Locations

It is possible that everything about a planned sequence of saccades can be determined as soon as the visual targets appear, and that no further reference to the visual targets is needed during sequence execution. If this were true, then the saccadic pattern would not be affected by removal of the targets after the plans had been established. To find out whether targets are necessary during execution, we removed the targets immediately before execution of the sequence began. Subjects had to direct their saccades to the remembered target locations.

The procedure differed from that of the previous experiment in the following way. Instead of the start-point alone being visible at the beginning of the trial, both the start point and the targets were visible. As in the previous experiment, subjects fixated the start point and pressed a button when they were ready to start the trial. Seven hundred msec later the "go" signal sounded and the targets disappeared leaving only the start point. The subject had to make saccades as quickly as possible to each of the remembered target locations.

If the latencies and sizes of saccades were the same as they were in the previous experiment when the targets were visible, then it could be concluded that all aspects of saccades could be planned in advance and that visual targets during saccade execution were unnecessary.

Latency of saccades to remembered locations

Latencies of saccades to remembered locations, like the latencies of saccades to visible targets, generally increased with increasing sequence length. This result is shown in Fig. 7. The only exception was E.K.'s first saccades, which were largely independent of sequence length. Latencies of E.K.'s second saccades increased by 28 msec/target and third saccades by 38 msec/target (slopes significantly greater than zero, \( P < 0.0005 \)). E.K.'s latencies, averaged over ordinal positions, increased at a rate of 28 msec/target \( (P < 0.0005) \).

Latencies of J.W.'s saccades increased with sequence length at all ordinal positions. Slopes were 26 msec/target for first saccades, 76 msec/target for second saccades, and 101 msec/target for third saccades (slopes significantly greater than zero, \( P < 0.0005 \)). The rate of increase in J.W.'s latencies, averaged over ordinal position, was 41 msec/target \( (P < 0.0005) \).

Slopes of the latency functions (Fig. 7) were significantly greater when saccades were made to remembered locations than when saccades were made to visible targets (Fig. 3). The only exceptions were E.K.'s first saccades to remembered locations which, unlike the first saccades to visible targets, did not vary as a function of sequence length.

The temporal pattern of saccades to remembered locations is shown in Fig. 8 in which average latency is plotted as a function of ordinal position for each of the 5 sequence lengths. E.K.'s temporal pattern was similar to that observed when targets were visible (Fig. 6). That is, the latency of her first saccade was short, the second much longer, and the latencies
remembered locations were larger than saccades to visible targets suggests that information from available visible targets is normally used to adjust saccade size during execution of a sequence. There were, however, several similarities between the temporal and spatial patterns of saccades made to visible and to remembered locations. For example, in both cases latency increased with sequence length, although slopes were somewhat steeper with remembered locations. Also, the effect of ordinal position on E.K.'s latencies and sizes, and the effect of ordinal position on J.W.'s sizes, were much the same with visible and with remembered targets. These similarities suggest that the temporal and spatial patterns of saccades observed with visible targets were due to planning and were not due to local visual error signals. This conclusion is based on the fact that the patterns were similar when saccades were made to remembered locations and the source of the visual error signals was reduced to a single visible reference point.

(III) Saccades to Visible Targets under Instructions to Reduce Latency

In the two experiments described in the previous sections, subjects made saccades under the instructions: (1) to complete the sequence as quickly as possible, and (2) to be sure to look at each of the targets. Occasionally, average saccadic latencies were as long as 350–450 msec (e.g. the second saccades in sequences for E.K., and the third for J.W., see Fig. 6). We wondered whether subjects were actually making saccades as quickly as they could, or whether they were capable of shorter latencies without a substantial loss of accuracy. To find out we asked E.K. to try to reduce latency. E.K. was tested because her average saccadic latencies were usually shorter and her saccades more accurate than J.W.'s. It seemed, therefore, that she would be more successful than J.W. at shortening latency without a great sacrifice of accuracy. In all respects, other than the instruction to reduce latency, the procedure was the same as the first experiment in which targets appeared at the time of the "go" signal.

E.K. succeeded in shortening latencies for all saccades except the first. Latencies of the first saccades were about 30 msec longer in this experiment, in which E.K. was instructed to proceed very quickly, than they were in the first experiment. Latencies of subsequent saccades in
for the sequence had been formed before execution began. But latencies of saccades after the first did not increase with sequence length. It might have been that the large errors during execution led to the abandonment of the plans.

**DISCUSSION**

We studied properties of saccades made to fixate up to 5 stationary targets in sequence. We found that the latency of saccades depended on the number of targets in the sequence and on the ordinal position of the saccade within the sequence. These results are not accounted for by the traditional view in which saccades are regarded as individually programmed responses to visual error signals. The results are inconsistent with this view in several respects. For example:

1. the latency of the first saccade in a sequence increased as a function of sequence length even though the visual error signal produced by the first target in a sequence was the same for all sequence lengths;
2. effects of sequence length and ordinal position on the sizes and latencies of saccades were observed when saccades were directed to

![Image of diagrams](image-url)

**Fig. 10.** Mean latency of the first through fourth saccades in a sequence (top graphs) and mean latency averaged over ordinal position in the sequence (bottom graphs) as a function of sequence length (left) and as a function of the number of saccades actually made (right) for E.K. when instructed to make saccades as quickly as possible, sacrificing accuracy if necessary. Each datum point in the top left graphs is based on 61–77 trials, in the top right on 18–96 trials, in the bottom left on 84–271 trials, and in the bottom right on 85–268 trials. Vertical bars represent 1 SE.
remembered locations, a situation in which visual error signals of the targets were absent; (3) the long saccadic latencies observed for E.K.'s second and J.W.'s third saccades in the sequence did not arise from the need to correct large position errors left behind by the previous saccade because the previous saccades (E.K.'s first and J.W.'s second) were accurate (see Fig. 6).

The results described above show that the observed dependence of saccades on the sequence was not due to properties of visual error signals. The dependence of saccades on the sequence suggests that there are pre-established, organized plans for the sequence that guide the execution of the individual saccades.

Comparison with prior studies of typing and speech

The effects of sequence length and ordinal position on the timing of saccades are similar in several respects to Sternberg et al.'s (1978a) observations of typing and speech. For example, they found, as we did, that the latency of the first response in a sequence and the time between subsequent responses increased as a linear function of sequence length. Moreover, the rate of the increase was similar to ours—about 10–20 msec/response. Also, they found, as we did, that inter-response time depended on the ordinal position of the response within the sequence. To account for these results, Sternberg et al. (1978a) proposed a model of motor planning in which the plans for a sequence of responses are stored in memory before the execution of a sequence begins. In their model, response latency and inter-response times increase with sequence length because the time taken to retrieve the plans for each response increases as a function of the number of stored plans. The similarity of the timing patterns of saccades and the timing patterns of typing and speech suggests that a memory search model might also account for the effects of sequence length on saccades.

Additional considerations are needed to account for effects of ordinal position by means of a memory search model. Ordinal position had different effects on inter-response times for typing, speech, and saccades. This was true even though inter-response times increased with sequence length for all these motor activities. The longest inter-response times generally occurred for the response preceding the final one in typing, and for the final response in speech (Sternberg et al., 1978a,b). Saccades showed still other patterns. E.K.'s longest intersaccadic intervals occurred before the second saccade, and J.W.'s before the third saccade in the sequence (see Fig. 6). J.W.'s pattern of intersaccadic intervals for saccades to remembered locations (Fig. 8) was different, bearing a strong resemblance to the timing patterns observed in typing. It is possible for a memory search model to account for these different patterns by assuming differences in the order with which the stored programs for the sequence of responses are searched (Sternberg et al., 1978a). In addition, inspection of our ordinal position results (Fig. 6) suggests other processes, namely, that programs for saccades might have been retrieved from memory in groups of 2–4 at a time. We suggest this because the latencies of J.W.'s first and third saccades to visible targets were longer than his latencies at other ordinal positions. This pattern of latencies suggests that he may have retrieved and executed plans for the first 2 saccades, and then for the last three saccades. E.K.'s latency was longest for second saccades, suggesting that she may have retrieved and executed plans for the first saccade, and then for the remaining saccades in the sequence. But, it is also possible that the effects of ordinal position on the timing of saccades might have resulted, at least in part, from idiosyncratic rhythms that subjects imposed on their saccades. Distinguishing these hypotheses will require further research specifically directed to the development and testing of models of saccadic planning. Our results show that models of planning, and not models based on visual error signals, will be required to understand saccades.

Comparison with prior studies of target-step tracking

It is worthwhile to contrast our conclusion that saccades are planned as patterned sequences with previous suggestions that, at least on the face of it, may sound similar, namely, that saccades are planned in "parallel" (Becker and Jurgens, 1979) or as a "group" (Levy-Schoen and Blanc-Garin, 1974). These proposals are actually quite different from ours. They were made to account for the unusually short intersaccadic intervals that were sometimes observed between the saccades made to track two consecutive random target steps. The gist of these proposals is that one saccade may be programmed while the programming or the execution of a prior saccade is still in progress.
These proposals, then, describe how the programming of a saccade may be independent of the programming of a prior saccade in a sequence. In contrast, the results of the present experiments demonstrate a phenomenon that was not apparent from the prior studies of target step tracking, namely, that consecutive saccades are related in that their programming depends on the characteristics of the sequence in which they occur.

The role of visual targets during the execution of a sequence of saccades

Our conclusion that subjects plan a sequence of saccades might seem surprising because the availability of the visible targets during the execution of the sequence would seem to obviate the need for plans. Our results suggest that the visible targets were helpful in that saccades were too large without them (Fig. 8). But the role of visible targets might best be viewed as advisory: information from visible targets may have been used either to correct errors in the plans during execution, or to specify certain saccadic attributes that may not have been included in the original plans. The availability of visible targets, therefore, need not and did not substitute for the planning of the sequence of saccades before execution.

The utility of visible targets during the execution of a sequence, despite the occurrence of pre-planning, calls attention to the distinction between the retrieval of a plan and the computation of the final motor command (see Sternberg et al., 1978a, for discussion of this distinction). By computation of the final motor command, we are referring to the transformation of a retrieved plan into a representation that is suitable for immediate execution. For example, the initial representation may call for 5 saccades of equal size, but the final command may specify the size in angular units.

Our results suggest that the transformation from the initial plan to the final saccadic commands requires specification of certain parameters of saccades that may be unspecified in the initial plan. (See Rosenbaum et al., 1984, for the analogous situation in finger-tapping.) Had the initial plan been complete, then saccades to remembered locations would have been the same size as saccades to visible targets. Instead, saccades to remembered locations were 20% larger than saccades to visible targets. It is, of course, possible that the initial representation is complete, and plans are modified during execution. But if this were the case, then the latency of saccades to visible targets would have been longer than the latency of saccades to remembered locations because of the extra time needed to analyze the visual input and modify the plans. In agreement with this hypothesis, we found that the average latency of E.K.'s saccades to visible targets (290 msec, \( SD = 83, N = 883 \)) was slightly longer than the latency of her saccades to remembered locations (mean = 281 msec, \( SD = 96, N = 1009 \)). But J.W.'s average latency was longer to remembered locations (mean = 368 msec, \( SD = 213, N = 736 \)) than to visible targets (mean = 341 msec, \( SD = 104, N = 1004 \)), the opposite of what would be expected if the targets modified already established motor commands.

Our results suggest that the initial representation of the saccadic plan is incomplete, but our results do not show which information is omitted. Answering this question will require experiments in which the locations of targets are changed during the execution of a sequence so as to change the required number, direction, or size of saccades. Changes that do not cost time may be assumed to involve those aspects of saccades that are not specified until immediately before execution. Experiments such as these, to characterize the initial representation of the planned sequence, are essential for the development of models of saccades that show how neural mechanisms transform the initial representation into the final saccadic command.

What is the value of planning sequences of saccades?

The demonstration that saccades are planned as sequences seems incomplete without suggesting ways in which such planning may be useful.

First, planning sequences of saccades may be useful for visual information processing. If an entire sequence of saccades is planned at once, then execution of the sequence may proceed with relatively little effort, allowing attention to be paid to the contents of a visual scene. This possibility may be tested by experiments in which psychophysical judgments are performed during the execution of a sequence of saccades. If planning is helpful, then we would expect better visual performance when an accurate sequence of saccades is planned in advance than when accurate planning is prevented by randomly varying the target locations.
The second value of planned sequences of saccades becomes evident when saccades are considered as only one component of the voluntary behavioral repertoire. When we look around in natural situations, we do not try to direct the eye to a target while keeping the head still. Rather, we direct the eye in concert with the head and body. Movements of the limbs and fingers come into play as well once we decide to do something with an object at the same time we are looking at it. Given that voluntary movements of the head and body are planned as patterned sequences, then saccades are most likely to be planned that way as well. A single, central planner that determines all voluntary motor behaviors may be the best, if not the only, way to ensure proper integration of separate movements into a useful pattern of activity. It seems inefficient to have one scanning mechanism controlling the eye and another independent mechanism, operating under different principles, controlling all other voluntary motor activity.

An incidental observation supports this view. E.K. had considerable difficulty in the final experiment when she was asked to reduce saccadic latency and make saccades as rapidly as possible. The problem was that it became nearly impossible to keep her head on the biteboard—she had to resort to tightly clenched teeth and then try to ignore her strained neck muscles. It was clear that the intention to "look at a target quickly" really meant to "orient oneself toward the target", turning not just the eyes, but the head and eyes at the same time. This observation suggests that whatever mechanism was responsible for planning the sequences of saccades was actually a more general planning mechanism, sending commands to head and body muscles at the same time. Experiments to study the simultaneous planning of sequences of head and eye movements are underway.

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