

Vision Research 40 (2000) 2499-2516

www.elsevier.com/locate/visres

Research

Vision

# Concurrent processing of saccades in visual search

Robert M. McPeek<sup>a,\*</sup>, Alexander A. Skavenski<sup>b,1</sup>, Ken Nakayama<sup>a</sup>

<sup>a</sup> Department of Psychology, Vision Sciences Laboratory, Harvard University, Cambridge, MA, USA <sup>b</sup> Department of Psychology, Northeastern University, Boston, MA, USA

Received 1 July 1999; received in revised form 4 January 2000

#### Abstract

We provide evidence that the saccadic system can simultaneously program two saccades to different goals. We presented subjects with simple visual search displays in which they were required to make a saccade to an odd-colored target embedded in an array of distractors. When there was strong competition between target and distractor stimuli (due to color priming from previous trials), subjects were more likely to make a saccade to a distractor. Such error saccades were often followed, after a very short inter-saccadic interval (  $\sim 10-100$  ms), by a second saccade to the target. The brevity of these inter-saccadic intervals suggests that the programming of the two saccades (one to a distractor and one to the target) overlapped in time. Using a saccade-contingent change in the search display, we show that new visual information presented during the initial saccade does not change the goal of the second saccade. This supports the idea that, by the end of the first saccade, programming of the second saccade is already well underway. We also elicited two-saccade responses (similar to those seen in search) using a double-step task, with the first saccade directed to the initial target step and the second saccade directed to the second target step. If the two saccades are programmed in parallel and programming of each saccade is triggered by one of the two target steps, the second saccade should occur at a relatively fixed time after the onset of the second target step, regardless of the timing of the initial saccade. This prediction was confirmed, supporting the idea that the two saccades are programmed in parallel. Finally, we observed that the shortest inter-saccadic intervals typically followed hypometric initial saccades, suggesting that the initial saccade may have been interrupted by the impending second saccade. Using predictions from physiological studies of interrupted saccades, we tested this hypothesis and found that the hypometric initial saccades did not appear to be interrupted in mid-flight. We discuss the significance of our findings for models of the saccadic system. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Saccade; Visual search; Parallel processing; Parallel programming

#### 1. Introduction

Oculomotor behavior is inherently serial, yet in many scenes, several different competing regions of interest are present simultaneously. A fundamental task of the saccadic system is to select one stimulus from among many in the visual scene as the goal of an eye movement. Visual search is a simple case of this selection task, and provides a logical paradigm for studying target selection in the saccadic system. Consider the case in which one wishes to foveate a target object among distractors, perhaps in order to discriminate a

E-mail address: rmm@ski.org (R.M. McPeek).

fine detail of the target's shape. What is the quickest way to move the eyes to the target in this situation? One possible strategy would be to program a saccade to a new location only after analysis of the visual information available at the current fixation position is complete. Using this strategy, if the target were visible from the current fixation position, the eyes could be moved directly to it. Such a strategy would be optimal in the sense that it would minimize the number of saccades required to fixate the target. This would be beneficial because there are certain costs associated with each saccade: first, vision is impaired for approximately 100-120 ms around the time of saccade execution (e.g. Volkman, 1962; Zuber & Stark, 1966; Shioiri & Cavanagh, 1989; Burr, Morrone & Ross, 1994). Second, there is an appreciable latent period between the initiation of the programming of a saccade and its execution.

<sup>\*</sup> Corresponding author. Present address: The Smith-Kettlewell Eye Research Institute, 2318 Fillmore St., San Francisco, CA 94115, USA.

<sup>&</sup>lt;sup>1</sup> Deceased.

While it is difficult to determine the exact duration of the saccade preparation process, separate from the latency for sensory processing, saccades are typically spaced by 200-300 ms, and even express saccades have a latency of at least 100-120 ms in humans (Fischer & Weber, 1993).

Surprisingly, several studies of eye movements in visual search have found that a strategy of minimizing the number of saccades is not adopted by the system; rather, subjects typically make more saccades than are necessary (Hooge & Erkelens, 1996, 1998; Zelinsky, 1996). In fact, one recent study by Hooge and Erkelens (1998) has shown that even when explicitly instructed to make a saccade only after the information currently at the fovea has been analyzed, subjects have difficulty using this strategy. The fact that subjects make unnecessary saccades is puzzling, because it seems inefficient. However, it becomes more understandable if we posit that the visual and saccadic systems can operate in parallel. Parallel processing would allow visual analysis at the current fixation position to continue during the preparation of the next saccade. The situation could be improved even further if the programming of saccades were 'pipelined', such that, even as the processing of an initial saccade was still in progress, the preparation of a

subsequent saccade could begin. Overlapping the programming of two saccades in this way would greatly reduce the cost of making additional saccades by effectively shortening the latent period between them (see the upper panel of Fig. 1). Thus, if an initial saccade were already being programmed, but subsequent visual analysis (continuing in parallel with the preparation of the saccade) revealed that the goal of the saccade was incorrect, the programming of a new saccade to the revised goal location could begin immediately, rather than being delayed until after the first saccade. We will refer to such overlapping programming of saccades as 'concurrent processing'. In the following sections, we will briefly review the evidence for concurrent processing in the visuo-motor system, after which we will examine new evidence for concurrent processing of two saccades in a visual search task.

# 1.1. Continuous uptake of visual information during saccade programming

The fact that visual information processing continues, even during the programming of a saccade, was made apparent by the results of so-called 'double-step' experiments, in which a single target is presented in a



Fig. 1. Illustration of the concurrent processing hypothesis in the search task (upper figure) and in the double-step task (lower figure). In both tasks, the preparation of the two saccades overlaps in time, resulting in a brief inter-saccadic interval. In the double-step task, it is assumed that processing of the initial saccade is triggered by the first target step, while processing of the second saccade is triggered by the second target step. Thus, the prediction is that the latency of the second saccade (as measured from the onset of the second target step — labeled 'B' in the figure) should be constant and approximately equal to the latency of the initial saccade (as measured from the onset of the first target step — not labeled). The delay between the second target step and the beginning of the first saccade is labeled 'A'.

peripheral location and then, after a variable time period, abruptly jumps to a new location. It was found that the movement of the target during the latent period of a saccade could modify the endpoint of the saccade within certain spatial bounds, if the target movement occurred early enough in the latent period. This indicates that visual information processing continues during the programming of the saccade, and that the results of this processing can be used to modify a saccade in preparation, within certain limits (Komoda, Festinger, Phillips, Duckman & Young, 1973; Becker & Jürgens, 1979; Hou & Fender, 1979; Findlay & Harris, 1984; Ottes, Van Gisbergen & Eggermont, 1984; Aslin & Shea, 1987).

# 1.2. Concurrent processing of two sequentially-executed saccades

In addition to this well-known result, Becker and Jürgens (1979) also examined sequences of two saccades, made in response to the two target steps. Confirming earlier observations (e.g. Levy-Schoen & Blanc-Garin, 1974), they found that the double-step stimulus occasionally elicited two saccades with a very short inter-saccadic interval (0-100 ms). Because these inter-saccadic intervals were much shorter than usual saccadic latencies, Becker and Jürgens (1979) proposed that they resulted from the concurrent processing of two saccades. In their scheme, programming of the initial saccade was triggered by the first target step, while programming of the second saccade was triggered by the second target step (see the lower panel of Fig. 1). If this were the case, the latency of the second saccade, when measured from the onset of the second target step (labeled 'B' in the lower panel of Fig. 1), should be fairly constant and should be unaffected by the timing of the initial saccade. Becker and Jürgens confirmed this prediction, supporting the idea that two saccades can be concurrently processed.

Brief inter-saccadic intervals have also been reported in free-scanning tasks (Bahill, Bahill, Clark & Stark, 1975; Skavenski & Steinman, 1995) and anti-saccade tasks (e.g. Amador, Schlag-Rey & Schlag, 1998; Mokler & Fischer, 1999), as well as in reading (Morrison, 1984; O'Regan, 1990) and in visual search tasks in which the target and distractors are difficult to distinguish (Viviani & Swensson, 1982; Hooge & Erkelens, 1996) or in which an unexpected abrupt onset is presented (Theeuwes, Kramer, Hahn & Irwin, 1998). Echoing Becker and Jürgens's proposal, it has been hypothesized that these short inter-saccadic intervals may reflect the concurrent processing of two saccades to different goals (Viviani & Swensson, 1982; Morrison, 1984; Theeuwes et al., 1998; Mokler & Fischer, 1999). In the present study, we more closely examine the characteristics of eye movement responses in which two saccades to different targets are separated by a short inter-saccadic interval. We provide evidence that such responses are, indeed, the result of concurrent processing of two saccades, and in addition, we examine the possibility that an initially executed saccade may be modified or even truncated by a concurrently-programmed second saccade. Finally, we analyze the implications of these findings for recent models of the saccadic system.

# 2. Experiment 1: spatial and temporal properties of two-saccade responses in a simple visual search task

In a previous report, we examined the linkage between focal attention and saccades in a simple visual search task (McPeek, Maljkovic & Nakayama, 1999). In this task, subjects were instructed to make a saccade to an odd-colored target, which was presented along with two distractors. When the color of the target was randomly selected on each trial to be either red or green (with the distractors being of the opposite color), we found that performance in the search task was systematically influenced by the colors of the target and distractors in prior trials. We showed that this results from a short-term priming of focal attention toward the color of the target on previous trials, and that this priming accumulates over five to seven trials (Malikovic & Nakayama, 1994; McPeek et al., 1999). In addition to its effect on saccade latencies, we also found that priming influenced saccade accuracy. Specifically, when the distractor color on the current trial was strongly primed (e.g. a red distractor in a trial which was preceded by several trials in which the target was red), subjects tended to make an initial saccade to the distractor. Such incorrect saccades were followed, often after a very brief fixation, by a second saccade to the correct target. (Fig. 3 shows some examples.)

The brevity of the inter-saccadic intervals that we observed led us to speculate that subjects may have initially programmed a saccade to a distractor (due to the fact that it was primed), but soon thereafter, determined the correct position of the target (using slower, bottom-up grouping mechanisms (Koch & Ullman, 1985; Julesz, 1986; Bravo & Nakayama, 1992)), and immediately began programming a second saccade to the correct target. The short inter-saccadic intervals could be explained if the two saccades could be 'pipelined', or processed concurrently by the system (Fig. 1, top). We will begin with an examination of the spatial and temporal characteristics of these two-saccade responses.

### 2.1. Method

The data analyzed for this experiment were taken from our previous study of the priming of saccades in



Fig. 2. Schematic illustration of the stimuli used in Experiment 1. On each trial, the target was the odd-colored diamond (either a red element among green distractors, or a green element among red distractors). The subjects' task was to make a saccade to the target.

visual search (Experiment 2 in McPeek et al., 1999). We will briefly summarize the methods used in that study.

#### 2.1.1. Stimuli

The search arrays consisted of a single odd-colored target and two distractors (see Fig. 2). On each trial, the target was randomly chosen to be red or green, and the distractors were of the opposite color. The target and distractor elements were solid, diamond-shaped figures, subtending 1.4° vertically and horizontally, with a small (15 minarc) black dot in the center. The luminance of the red diamond was 4.71 cd/m<sup>2</sup>, and the green was 5.06  $cd/m^2$ , on a background of 0.10  $cd/m^2$ . The red and green were chosen to be approximately perceptually equiluminant using heterochromatic flicker photometry. The target and distractor stimuli were positioned so as to be equidistant from each other, along the circumference of an imaginary circle with a radius of 7°, centered at the initial fixation position. There were six possible target locations, at the 1 o'clock, 3 o'clock, 5 o'clock, 7 o'clock, 9 o'clock, and 11 o'clock positions around the imaginary circle. On each trial, the target position was randomly chosen. Since the target and the distractors were always equidistant, the choice of the target position determined the distractor positions.

# 2.1.2. Procedure

Each of the three subjects was seated 50 cm from the color monitor on which the stimuli were presented. Each session of 100 trials was preceded by calibration trials in which single stimuli were presented, as well as by ten practice trials of visual search. At the beginning of each search trial, subjects fixated a central fixation point which remained illuminated throughout the trial. After a variable delay ranging from 800 to 1000 ms, the search array was presented. Subjects were instructed to make a saccade to the odd-colored target, and then to press the space bar. At this point, the search array and fixation point were removed, and after a 1.5 s pause, the fixation point re-appeared to signal the beginning of the next trial. All three subjects performed 700 trials

over a period of several days. One block of 100 trials from subject SS could not be analyzed due to a faulty calibration.

#### 2.1.3. Eye movement recording

Eye movements were recorded using the Ober2 infrared reflection system. Subjects were restrained using a rigid, deep-impression dental bite-bar and a chest support bar. Vertical and horizontal eye position was typically sampled at 240 Hz, although in some sessions, the sampling rate was 500 Hz. In Experiment 4, a 1000 Hz sampling rate was used in order to obtain more detailed velocity profiles of the saccades. The Ober2 system reliably detected saccadic movements of less than 0.3°. Within the range used in these experiments, we found the responses of the Ober2 to be approximately linear with eye position.

#### 2.1.4. Data analysis

Eye position records were analyzed offline, using an interactive computer program which detected saccades using a velocity criterion. A saccade was identified when eye velocity exceeded a threshold of approximately 30 deg/s. After identification, more precise onset and ending times for saccades were determined using lower thresholds which were individually chosen for each subject by examining a large number of records of saccades. The analysis for each trial was inspected to verify, and correct, if necessary, the marking of saccades.

For large upward movements, the records produced by the Ober2 were occasionally affected by movements of the subjects' eyelids. When it was present, this eyelid artifact resulted in an apparent decrease in velocity and increase in duration of the vertical component of movements. Since the latency of evelid movements is longer than the latency of the saccades which they accompany (Becker & Fuchs, 1988), this artifact affected only the later portion of saccades. All of the target positions used in this experiment included an appreciable horizontal component, and hence, when this artifact was present, we used the horizontal component of movements to determine the time at which the movements began and ended. Van Gisbergen, Van Opstal and Schoenmakers (1985) and Becker and Jürgens (1990) showed that for oblique saccades of the size used in these experiments, the horizontal and vertical components of movements are closely aligned in time. When it was necessary to obtain precise profiles of saccade velocity, we confined movements to the horizontal axis.

## 2.2. Results

As we reported earlier (McPeek et al., 1999), when the color of the target differs from its color on the previous trial, subjects are more likely to make a saccade to a distractor stimulus than when the color of the target remains the same. This occurs because of the priming of pop-out: the target color on previous trials becomes automatically primed, and hence, when the colors switch so that the distractors assume the color of the target on previous trials, the distractors are primed (Maljkovic & Nakayama, 1994). This can lead to erroneous saccades to a distractor.

On the trials in which the initial saccade was directed toward a distractor, an intriguing pattern of behavior immediately became obvious: subjects often executed a second, corrective, saccade toward the target after a very short latency ( $\sim 10-100$  ms). Two representative samples of this type of response are shown in Fig. 3 (left panels). As can be seen, the initial saccades are directed toward distractors, but are hypometric, ending before they reach the target. They are followed by a second saccade to the correct target location, after only a very brief fixation interval.

#### 2.3. Short inter-saccadic intervals

In order to better visualize the duration of the intersaccadic intervals, eye position traces as a function of time are shown in the right panels of Fig. 3. Each plot highlights the short inter-saccadic interval observed when the subject made an initial saccade toward a distractor, followed quickly by a second saccade to the target.

Fig. 4 (top panels) shows summary histograms of all inter-saccadic intervals occurring between initial incorrect saccades and corrective saccades to the target. For comparison, the latencies of the initial saccades (from the onset of the stimulus until the beginning of the first saccade) are shown in the bottom panels. The latencies of the incorrect initial saccades were only slightly shorter than the latencies of the correct initial saccades (means: RM: 217 ms (correct) versus 208 (incorrect); SS: 210 ms (correct) versus 193 ms (incorrect); VM: 205 (correct) versus 194 (incorrect)), while the distribution of inter-saccadic intervals between initial and second saccades form an almost non-overlapping population. In fact, a sizable fraction of the latencies of the second saccades, when measured from the end of the initial saccades, are much shorter than the latency of express saccades (approximately 100-120 ms for humans; Fischer & Weber, 1993).

### 2.4. Spatial properties of the first and second saccades

The upper panels of Fig. 5 show a plot of the endpoints of all initial saccades (both correct and incorrect) for the three subjects. In the experiment, the target and distractors could be located at any one of six different positions around the clock, but for the purposes of this graph, the endpoints of the saccades have been normalized by a simple rotation, such that the target position is always at the right-middle (3 o'clock







Fig. 4. Summary of inter-saccadic intervals. The top three panels show, for three subjects, the inter-saccadic intervals measured between initial incorrect saccades and second saccades to the target. For comparison, the latencies of all initial saccades are shown in the lower panels. There was little difference in latency between initial correct and incorrect saccades (see text), while the latency of the initial saccades and the inter-saccadic intervals form almost non-overlapping distributions.



Fig. 5. Upper panels show plots of the endpoints of all initial saccades for each subject in the search task. The data have been normalized by a simple rotation, such that the target is always at the 3 o'clock position  $(0^\circ)$ , and the distractors are at the 7 and 11 o'clock positions (120° and 240°). Note that saccades to the target form a fairly tight cluster, while saccades toward the distractors are often hypometric. In the lower panels, the endpoints of the second saccades are shown in a similar format.

position) of the graph, and, correspondingly, the distractors are located at the 7 o'clock and the 11 o'clock positions. The center of the graph represents the position of the initial fixation point, and the amplitude of each saccade is plotted as the distance from the center. As is evident, most saccades which are not directed toward the target are directed toward one of the two distractors. Furthermore, saccades directed toward the target usually land close to the target location, forming a fairly tight cluster (depicted at a direction of  $0^{\circ}$  and an amplitude of  $7^{\circ}$ ). On the other hand, saccades toward the distractors are often hypometric, falling short of the stimulus. In the lower panels of Fig. 5, the endpoints of the second saccades are presented in a similar format. As is apparent, while the second saccades are less accurate than the initial saccades to the target, most of the second saccades land in the vicinity of the target despite the short inter-saccadic intervals between them and the initial saccades. We did not observe any correlation between the accuracy of the second saccade and the duration of the inter-saccadic interval, and Spearman correlations did not reveal any evidence for such an effect (for RM and SS, there is a non-significant trend toward more accurate second saccades following shorter inter-saccadic intervals, P >0.30 and P > 0.20, respectively. For VM, there is a non-significant trend toward less accurate second saccades following shorter inter-saccadic intervals, P >0.50).

# 2.5. Correlation between size of initial saccades and inter-saccadic intervals

Interestingly, we found that there is a strong correlation between the size of the incorrect initial saccades and the duration of the interval between the initial and second saccades (see Fig. 6): the most hypometric initial saccades are almost always followed by very short latency corrective saccades, while initial saccades with a larger amplitude tend to be followed by corrective saccades after longer time intervals. This trend was significant for all subjects (Spearman correlations: P <0.001 for each subject). As shown in Fig. 6, which plots the duration of the time interval between the first and second saccades against the size of the first saccades, there is a continuum of such responses.

#### 2.6. Discussion

These results yield several important insights. First, fixations as short as those between the initial incorrect saccades and the second saccades have rarely been studied in any detail. The fact that a second saccade can be executed so quickly after the end of an initial saccade leads us to speculate that the second saccade

may have been programmed concurrently with the first saccade (see Fig. 1; Becker & Jürgens, 1979; Theeuwes et al., 1998). In the double-step task, Becker and Jürgens (1979) supported their suggestion of concurrent processing by showing that when a second saccade was made, it occurred at a constant time after the onset of the second target step (labeled 'B' in lower panel of Fig. 1), regardless of when the first saccade occurred. The temporal overlap in the programming of the two saccades resulted in short inter-saccadic intervals. Unfortunately, in the search task, this type of analysis is impossible because there is no external event (analogous to the second target step) which triggers the change in selected stimulus. Rather, the selection of a new stimulus is an internal cognitive event, and hence its timing cannot be readily inferred. However, the concurrent processing hypothesis does provide some testable predictions for the search task, which we will consider in later sections.

Second, the fact that most saccades which do not land near the target are directed toward one of the distractors indicates that the incorrect saccades are not anticipatory or randomly-directed responses: if they were, they would be distributed with equal probability across all six possible stimulus locations, rather than directed toward one of the two distractors. Furthermore, these saccades tend to be hypometric, and this hypometricity cannot be explained by simple averaging, since the hypometric saccades are typically directed toward a distractor, rather than between a distractor and the target. This finding is not unprecedented: in double-step and double-target tasks, it has been shown that when stimuli are separated by large differences in direction, averaging is generally not seen (Ottes et al., 1984). However, this leaves open the question of why these saccades are hypometric. One view, put forward by Becker and Jürgens (1979) and Hou and Fender (1979) is that saccade preparation is a two-stage process: in the first stage, saccade direction is fixed, while in a later stage, saccade amplitude is determined. Thus, newly-arriving visual information can affect saccade amplitude but is unable to change saccade direction. This results in the well-known amplitude transition



Fig. 6. Inter-saccadic interval plotted as a function of the amplitude of the initial saccade, for three subjects. Note that hypometric initial saccades tend to be followed by brief inter-saccadic intervals.

function, relating the amplitude of an initial saccade to the time between the onset of the second target step and the beginning of the saccade. However, there is no physiological evidence for such a separation between amplitude and direction in saccade preparation (e.g. Robinson, 1972; Schiller & Stryker, 1972).

As a more physiologically-plausible alternative, we propose that the hypometric initial saccades observed here are a result of interference due to the concurrent processing of a second saccade goal during the preparation and execution of the initial saccade. Such interference could be envisaged as occurring on a common motor map, upon which both saccade goals are represented. In this scheme, the activity related to each of the two saccade goals would be mutually inhibitory. Hence, the gradual rise of neural activity related to programming of the second saccade would weaken the activity related to the initial saccade, resulting in the production of a initial hypometric saccade. This is consistent with recent physiological findings in the superior colliculus (SC), where it has been shown that activity in two distal regions of the SC is mutually inhibitory (Meredith & Ramoa, 1998; Munoz & Istvan, 1998), and that a weakening of saccade-related activity within the SC can result in the production of hypometric saccades (Paré, Crommelinck & Guitton, 1994; Stanford, Freedman & Sparks, 1996).

This proposal would predict that greater interference would occur when processing of the two saccades coincides more closely in time. This is consistent with Fig. 6, which shows that the shorter the amount of time between saccades, the more hypometric the initial saccade. Thus, we suggest that the process of programming the second saccade directly modifies or perhaps may even interrupt execution of the first saccade. We will consider the hypothesis that the initial saccade is interrupted in the final experiment.

#### 3. Concurrent processing hypothesis

The very short time intervals between the initial incorrect saccades and the second saccades suggest that the saccadic system is not operating as a serial system, but rather, is programming the second saccade concurrently with the first. We can envision this scheme as operating in the search task in the following manner: first, the process of programming an initial saccade toward a distractor (presumably due to priming of the distractor color) begins. After a certain amount of time, new information, providing the correct location of the target, reaches the system. This triggers the preparation of a second saccade directed toward the target, which proceeds in parallel with the programming and execution of the first saccade (see top panel of Fig. 1). As a result, the second movement can be initiated shortly after the end of the first saccade.

Becker and Jürgens (1979) suggested a similar scheme in order to account for the short inter-saccadic intervals observed in their double-step task. Theeuwes et al. (1998) also suggested that parallel processing of saccades could account for the occurrence of brief fixations in their task. They instructed subjects to make a saccade to an odd-colored target, but occasionally presented an unexpected abrupt onset, irrelevant to the search task. They found that subjects tend to make an initial reflexive saccade to the abrupt onset, followed quickly by a second saccade to the search target. In the present study, we hypothesize (as earlier suggested by Viviani & Swensson, 1982) that concurrent processing is not limited to situations in which a new stimulus suddenly appears, but rather may be seen even in a static display, when there are several competing stimuli. This would suggest that concurrent processing may be a more common part of oculomotor behavior in scenes having many different areas of potential interest.

Under the concurrent processing hypothesis, programming of both the first and second saccades begins while the eye is still fixated at the central fixation point. If this is the case, then any changes in the stimuli made during the execution of the initial saccade should not substantially affect the second saccade, since its programming would already be well underway. This prediction is tested in the following experiment.

#### 4. Experiment 2: saccade-contingent display changes

We have hypothesized that, even before the execution of an initial incorrect saccade, programming of a second corrective saccade can begin. Under this view, it takes about the same amount of time to program the second saccade as it does to program the first saccade ( $\sim 200-300$  ms). However, the inter-saccadic intervals are shorter than this due to the temporal overlap in programming the two saccades (see Fig. 1, top panel). If this concurrent processing hypothesis is incorrect, then it must be the case that the second saccade is programmed after the initial saccade (serial processing), and thus, that the second saccade is programmed during the inter-saccadic interval, a much shorter amount of time. In order to differentiate between these two alternatives, we employed a saccade-contingent search task, in which the onset of an initial incorrect saccade can trigger a change in the position of the correct target. Specifically, on 50% of the trials in which an incorrect initial saccade was made, the positions of the target and a distractor were switched, and this switch was triggered by the onset of the first saccade.

According to the serial processing hypothesis, programming of the second saccade begins after the first saccade, and hence, after the change in target position. As a result, the second saccade will be directed toward



Fig. 7. Representative response from the saccade-contingent change experiment. The subject's initial saccade is directed toward a distractor. During the course of this saccade, the locations of the target and distractor are switched (panel B). If the second saccade is programmed concurrently with the first, the subject should not be able to use information gained during the fixation between the saccades (panel C) to guide the second saccade. Accordingly, as shown in panel D, the subject's second saccade is directed to the old location of the target (now a distractor location). Finally, a third saccade to the new target location is made.

the new position of the target, assuming that the intersaccadic interval is sufficiently long to allow the switch to be visually processed before the second saccade is programmed. In order to estimate the inter-saccadic interval which would be sufficient for this, we note that the serial processing hypothesis requires that the second saccade be programmed entirely during the inter-saccadic interval. In light of the short intervals that we have observed, the time required to program the second saccade would have to be quite brief ( < 50 ms). Given this constraint, as well as the established fact that visually-guided saccades can be generated in as little as 100-120 ms in humans (Fischer & Weber, 1993), with longer inter-saccadic intervals of 120 ms or more, there should be ample time to visually process the change before the commencement of saccade programming. As a result, if the second saccade is programmed serially, it should be directed to the new target location whenever the inter-saccadic interval is more than approximately 120 ms. On the other hand, if the second saccade is programmed concurrently with the first saccade, the change in target position would always occur after programming of the second saccade was already well underway. As a result, we would not expect the second saccade to be directed to the new target location, even when the inter-saccadic interval is greater than 120 ms.

## 4.1. Method

The basic paradigm is identical to that used in Experiment 1, except the stimuli were located at an eccentricity of 12°. Furthermore, on 50% of trials in which the first saccade was directed toward a distractor, the positions of the target and one of the distractors (selected at random) were exchanged. Eye movements were sampled at 500 Hz, and an on-line algorithm detected the time of occurrence and the direction of saccades using a velocity-based criterion selected individually for each subject on the basis of an initial calibration session. Following the detection of an incorrect saccade, on 50% of the trials, the location of the target was switched. The time at which the display change became visible was recorded along with the eye movement records. We analyzed trials in which the target switch was completed either during the initial incorrect saccade, or within one video frame (13 ms) of the end of the initial saccade. Three subjects each performed 600 trials, in blocks of 100. Each block was preceded by 14 calibration trials.

### 4.2. Results

Combined, the three subjects made a total of 314 initial incorrect saccades. Of these, we recorded 109 trials in which the locations of the target and one of the distractors were switched during the initial incorrect saccade. In the majority of these cases (90%), the second saccade was directed to the old target location, rather than to its new (post-change) position. A typical response is shown in Fig. 7.

Fig. 8 shows a histogram of the inter-saccadic intervals in trials in which the target location was switched during an initial incorrect saccade. The data are combined across all three subjects. The gray bars indicate trials in which the second saccade is directed to the old location of the target and the black bars indicate trials in which it is directed to the new location of the target. As is evident, even when the fixation between the first saccade and the second saccade is longer than 120 ms, the second saccade is usually directed to the old target position. In fact, in every trial in which the inter-saccadic interval is shorter than 250 ms, the second saccade is directed toward the old target location, consistent with the idea that it was programmed concurrently with the first saccade. In contrast, in the 10% of cases in which the second saccade is correctly directed to the new target location, the inter-saccadic interval is always 250 ms or longer.

#### 4.3. Discussion

When the inter-saccadic interval is very short, we would not expect the target switch to affect the endpoint of the second saccade, because the switch would not yet have been processed by the visual system. However, for intervals longer than about 120 ms, the new visual information would presumably be processed before the onset of the second saccade, and, as discussed above, the serial and concurrent processing hypotheses would make different predictions. Specifically, the serial programming hypothesis predicts that when the inter-saccadic interval is more than about 120 ms, the second saccade will be directed toward the new target location. On the other hand, if programming of the second saccade begins much earlier, and is carried out concurrently with processing of the first saccade, we



Fig. 8. Histogram of inter-saccadic intervals for target-switch trials in which the change in target location occurred during the initial incorrect saccade. The gray bars represent trials in which the second saccade was directed toward the location of the target before the change ('old'), while the black bars represent trials in which the second saccade was directed toward the location of the target after the change ('new'). Note that when the inter-saccadic interval was less than 250 ms, the second saccade was always directed to the old target location.

would expect that the new target location information would arrive too late in the saccade preparation process to significantly change the endpoint of the saccade. Thus, if the concurrent processing hypothesis is correct, the second saccade would be expected to be directed toward the old position of the target, rather than to its new position. This latter prediction is borne out in the current experiment. In all of the cases in which the inter-saccadic interval was shorter than the normal saccadic latency of 250 ms, the second saccade was directed to the old target location, rather than to its new location.

Saccades which did reflect the change in target location were observed only when the inter-saccadic interval was greater than 250 ms. Such long intervals suggest that in these trials, subjects did not realize that they were making an incorrect initial saccade until after its execution. As a result, programming of the second saccade began after the end of the first saccade, and, hence, was able to take into account the change in target position. Thus, the results are consistent with the predictions of the concurrent processing hypothesis. In the following experiment, we test further predictions and compare our results in visual search with results in a double-step task.

#### 5. Experiment 3: comparison with the double-step task

As discussed in Section 1, Becker and Jürgens (1979) occasionally observed closely-spaced saccades to the two target jumps in their double-step task. They suggested that such responses resulted from the parallel processing of two saccades, and bolstered this argument by examining the relationship between the time of onset of the second target step and the onset of the second saccade. If the two saccades are programmed independently and in parallel, the latency of the second saccade, when measured from the onset of the second target step, should be relatively invariant (labeled 'B' in the bottom panel of Fig. 1). In particular, it should not depend on when the initial saccade is executed nor on when the initial target step occurs. This is exactly what Becker and Jürgens (1979) found in their one-dimensional double-step task, suggesting that the programming of the second saccade was triggered by the presentation of the second target step, and was programmed concurrently with the initial saccade.

We suggest that a similar process may be occurring when short inter-saccadic intervals are observed in our search task. However, in our task, the event which precipitates the programming of the second saccade is a change in the subject's selection of stimuli as the saccade target, rather than the presentation of a second target step. Since this change in the selected stimulus is an event which is internal to the subject, we cannot



Fig. 9. Inter-saccadic intervals for two-saccade responses in the double-step task, as a function of the amplitude of the initial saccade. Just as for the search task, the most hypometric initial saccades were followed by the shortest inter-saccadic intervals. In this task, the target was always presented at an eccentricity of 10°.

determine whether the second saccade occurs at a fixed latency after the subject's change in target selection. However, in addition to our finding of short inter-saccadic intervals in the search task, we also made two additional notable observations: first, the amplitudes of the initial saccades were smaller than normal, and second, there was a clear relationship between the amplitude reduction of the initial saccade and the brevity of the inter-saccadic interval.

One way to support the idea that the two-saccade responses in search are concurrently-processed would be to determine if a similar conjunction of results is seen in a double-step paradigm which uses the same two-dimensional configuration of target positions as used in our search task. If we find that the relationships between initial and second saccades in the double-step task are similar to those we observed in the search task. it would suggest that the responses in the two tasks are programmed using similar mechanisms. Since we are able to measure when the second saccade occurs relative to the onset of the second target step in the double-step task, it would then be possible to determine whether the second saccade occurs a fixed time interval after the second target step (see Fig. 1, bottom panel). If this were the case, it would suggest that the two saccades are programmed concurrently in this task, and by extension, in the search task.

### 5.1. Method

Following the fixation period, an initial target was randomly presented at one of six possible locations spaced equally around an imaginary circle centered at fixation. In 70% of the trials, there were no further target movements. In 30% of the trials, after a variable delay of 53-160 ms, the initial target disappeared and a new target appeared at a new location on the circle, either 120° clockwise or 120° counter-clockwise around the circle from the original position (in order to match the distractor locations used in the search task). The stimuli were presented at an eccentricity of 10°, and were achromatic and diamond-shaped ( $1.5^{\circ}$  across), with a luminance of 4.85 cd/m<sup>2</sup> on a background of 0.10 cd/m<sup>2</sup>. Subjects were seated 45 cm from the screen, and their heads were stabilized using a combination chin-rest and head-support device. Subject JI performed four blocks of 100 trials while subject RM performed seven blocks of 100 trials. Each block started with 14 calibration trials. Latencies and start- and end-points of saccades were recorded.

### 5.2. Results

The mean latency of saccades in the single-step trials for subjects RM and JI was 173 and 164 ms, respectively. As expected, the double-step stimuli occasionally elicited two saccades separated by a short inter-saccadic interval. We recorded a total of 76 of such responses for subject RM and 37 for subject JI. For these trials, the mean latency of the initial saccades was 165 ms for RM and 149 ms for JI. Previously, in the visual search task, we observed that for two-saccade responses, the initial saccade was often hypometric, and that the amplitude of the initial saccade was correlated with the inter-saccadic interval (see Fig. 6). In order to determine whether the responses recorded in the current experiment are comparable to those observed in the search experiment, we plotted inter-saccadic interval as a function of the amplitude of the initial saccade for the double-step task. The results are shown in Fig. 9. The correct amplitude was always 10°, but as evident, for two-saccade responses, the initial saccades were often hypometric. Furthermore, it is apparent that the shorter inter-saccadic intervals followed the more hypometric initial saccades. Thus, the two-saccade responses in the double-step task closely resemble those seen in the visual search task.

For each of the two-saccade responses, we computed the latency of the second saccade, as measured from the onset of the second target step (labeled in 'B' in Fig. 1). In Fig. 10, this measure is plotted as a function of the delay between the second target step and the beginning of the first saccade (labeled 'A' in Fig. 1). If the two saccades are programmed independently and in parallel, the time between the second target step and the onset of the second saccade should be independent of when the second target step occurs relative to the first saccade. As is evident, the data for both subjects conform closely to the predictions made by the concurrentprocessing hypothesis: the latency of the second saccades, as measured from the onset of the second target step, is fairly constant at a mean value of 224 ms for RM and 229 ms for JI.

We performed a linear regression to quantitatively test the prediction of the concurrent processing hypothesis. As predicted, we found that for both subjects, the slope of our measure was near zero (slope = 0.08, std. error of estimate = 0.09 for RM; slope = -0.05, std. error of estimate = 0.17 for JI), and significance testing showed that this slope did not differ significantly from zero (P = 0.37 for RM; P = 0.79 for JI).

#### 5.3. Discussion

The two-saccade responses observed in our doublestep task bear a close resemblance to those seen in the visual search task. In both cases, the shortest inter-saccadic intervals followed the most hypometric initial saccades. Thus, it is likely that the responses seen in the two tasks use common processes. The advantage of the double-step task is that it allows us to determine when the change in the saccadic goal occurs. The concurrent processing hypothesis predicts that if programming of the second saccade begins as soon as the second target

step is detected and progresses in parallel with the first saccade, the latency of the second saccade, when measured from the onset of the second target step, should be fairly constant, and should be in the latency range of normal saccades. This is exactly the result that was observed, confirming that the second saccade is indeed processed concurrently with the first. It is interesting to note that the mean latency of the second saccades, measured from the second target onset, was generally longer than the mean latency of single saccades to a single target (65 ms longer for RM and 51 ms longer for JI). This indicates that there may be a penalty associated with a concurrently-programmed second saccade, consistent with a bottleneck in processing or perhaps simply a reduction in speed of processing the second saccade.

These findings are in accord with similar results by Becker and Jürgens (1979) for horizontal saccades in a one-dimensional double-step task, and show that these earlier results can be generalized to two-dimensional movements. Interestingly, recent studies of the doublestep task in two dimensions have focused on quantifying the endpoints of initial saccades, many of which show a tendency toward averaging of the two target positions (Findlay & Harris, 1984; Aslin & Shea, 1987). Ottes et al. (1984) demonstrated that the separation between double-step targets is a critical parameter for determining whether an averaging saccade is elicited. Findlay and Harris and Aslin and Shea typically separated their targets by an angle of 30-90°, while we used an angular separation of 120° in the present experiment, to correspond to the positions of the stimuli in our search experiments. This probably accounts for the fact that we typically observed two-saccade responses, while the earlier studies primarily report averaging saccades.



Fig. 10. For two-saccade responses in the double-step task, the latency of the second saccade, as measured from the onset of the second target step, ('B' in the lower panel of Fig. 1) is plotted as a function of the time between the second target step and the first saccade ('A' in lower panel of Fig. 1). In both subjects, the second saccade occurred a relatively fixed time after the onset of the second target step, regardless of the timing of the initial saccade, in accord with the predictions of the concurrent processing hypothesis. The data have been fitted by a linear regression.

# 6. Experiment 4: test of the interrupted saccade hypothesis

This section considers the interrupted saccade hypothesis brought up in Experiment 1. In that experiment, we found that hypometric incorrect initial saccades were nearly always followed by very short-latency corrective saccades, while larger incorrect initial saccades were usually followed by longer inter-saccadic intervals. One way to explain this finding is that if a subject began preparing an incorrect saccade, but located the correct target early enough, the preparation of the second saccade might be completed during the execution of the first saccade. If this occurred, the second saccade might be able to interrupt the first saccade during its execution, halting the eye before it reaches its goal. Since preparation of the second saccade would be complete at this point, the second movement could be initiated with minimal delay. This sequence of events would result in a hypometric initial saccade to a distractor, followed, after a very short inter-saccadic interval, by a second saccade to the target.

Neurophysiologists have shown that interrupting a saccade in mid-flight can be accomplished by stimulating sites in the omnipause region of the brainstem (OPNs: Keller, 1977) or in the rostral superior colliculus (SC: Munoz & Wurtz, 1993). We tested the interrupted saccade hypothesis by taking advantage of the stereotyped dynamics of saccades. Specifically, when the instantaneous velocity of the eye during a saccade is plotted as a function of eye position as the eve advances from its starting point to its goal (a phase-plane plot), it becomes apparent that similar size saccades have similar velocity profiles, while the velocity profiles for different size saccades diverge early in the course of the movements (Van Gisbergen, Van Opstal & Ottes, 1984). Furthermore, the peak velocity attained by a small saccade is lower than that attained by a large saccade. The plot of saccade peak velocity as a function of the amplitude of the saccade has been called the 'main sequence' for saccades (Bahill, Clark & Stark, 1975). Capitalizing on these regularities, we can predict that if a saccade begins as a large saccade, but is truncated in mid-flight, it will have an abnormally large peak velocity for a saccade of its size, both in a phase-plane plot, and in a main sequence plot. This prediction has been verified in experiments in which saccades are interrupted by stimulation of the OPNs or the rostral SC. Munoz, Waitzman and Wurtz (1996) showed that saccades interrupted by stimulation of the rostral SC have a higher peak velocity than normal saccades of the same amplitude. McPeek and Keller (unpublished observations) found that this is also true for saccades interrupted by stimulation of the OPNs. Thus, if the hypometric initial saccades are the result of an interruption during execution, these saccades should show a higher peak velocity in the phase-plane and main sequence plots.

#### 6.1. Method

In order to make precise measurements of saccade dynamics, it was necessary to confine the saccades to the horizontal axis. Thus, a search array was presented in which the odd-colored target could be located either to the left or to the right of fixation, along the horizontal axis. One distractor was located on the opposite side of fixation, at the same eccentricity as the target. A second distractor was presented above or below fixation. In order to obtain saccades of a variety of sizes, the eccentricity of the target and distractors was randomly varied from trial to trial, over a range from 0.75 to 15°. The sizes of the stimuli were M-scaled (Rovamo & Virsu, 1979), to keep their saliency constant across the different eccentricities. At an eccentricity of 1°, the stimuli were 0.26° in diameter. The colors and luminances of the stimuli and background were the same as in Experiment 1. Three subjects were tested. Subjects NF and FT each performed 600 trials, and subject RM performed 800 trials. All subjects were seated 40 cm from the video monitor, and used rigid, deep-impression bite-bars and a chest support for head stabilization. Eye movements were recorded at 1000 Hz and each block of 100 trials started and ended with the presentation of 14 calibration trials.

#### 6.2. Results

The normal, correct saccades to the target provide baseline data to which the suspected interrupted saccades can be compared. The candidates for interrupted saccades are those incorrect initial saccades which are most hypometric, and which are followed most quickly by a second saccade. We initially defined these as saccades having an amplitude of less than 70% of the correct amplitude and an inter-saccadic interval of less than 100 ms. Subsequent investigation revealed that choosing different criteria does not alter the findings.

A detailed analysis of the entire velocity profile of individual saccades was performed by comparing the phase-plane plots for potential interrupted saccades to similar plots for groups of normal saccades of the same amplitude. Fig. 11 (left panel) shows representative examples of such comparisons. As is evident, the velocity profiles of the suspected interrupted saccades (black points) do not rise above the profiles of the normal control saccades (gray points). These findings do not support the hypothesis that the saccades were interrupted. A main sequence plot (Fig. 12) summarizes the peak velocity-amplitude relationships for all suspected interrupted saccades, and allows comparison to the



Fig. 11. Phase-plane plots of potential interrupted saccades. In both panels, the black trace plots the velocity of a suspected interrupted saccade as a function of eye position during the saccade. Velocity profiles of a group of similar-amplitude normal saccades are plotted in gray. If the candidate saccades were interrupted, their velocity profiles would rise above those of the normal saccades, which they do not.



Fig. 12. Main sequence plots for potential interrupted saccades for three subjects. The peak velocity of normal saccades is plotted in gray, while suspected interrupted saccades are plotted in black. If the candidate saccades were indeed interrupted in mid-flight, their peak velocities would be higher than those of normal saccades of the same amplitude. As is evident, the candidate saccades do not have abnormally high peak velocities.

normal baseline data. We also examined other saccade parameters, such as peak acceleration, peak deceleration, acceleration duration, and deceleration duration in search of evidence for interrupted saccades, but did not find any systematic departures from normalcy for the suspected interrupted saccades. The results for all subjects indicate that the hypometric incorrect initial saccades are not interrupted in flight.

#### 6.3. Discussion

Physiologists have shown that saccades can be interrupted by stimulation of the omnipause region of the brainstem (Keller, 1977) or of the rostral superior colliculus (Munoz & Wurtz, 1993). Saccades which are initially directed to a more distant target, but which fall short of this target due to such an interruption, show a systematically higher peak velocity than normal saccades of the same movement amplitude (Munoz et al., 1996). We hypothesized that the hypometric initial saccades that we observed in the search and double-step tasks were the result of an interruption of an initial saccade, and hence, would show a similar abnormally high peak velocity. Such a finding was recently reported by Corneil, Hing, Bautista and Munoz (1999), for eye-head gaze shifts in a task in which visual and auditory stimuli were presented on opposite sides of fixation. However, in the current experiment, we were unable to find any differences between the peak velocity of suspected interrupted saccades and normal saccades of the same amplitude, nor could we find any differences in several other measures of saccade kinematics. Thus, we conclude that these naturally-occurring hypometric saccades are not the result of an interruption of a larger saccade. Similar findings and conclusions were recently reported by Goossens (1998), who examined hypometric saccades made by monkeys in a double-step task.

Thus, while it is clear from the Corneil et al. (1999) study that naturally-occurring truncated gaze shifts can be observed when conflicting visual and auditory targets are presented, based on the evidence presented here and in Goossens (1998), it appears that hypometric initial saccades are not always truncated movements. One difference between our results (as well as the Goossens results) and the Corneil et al. study is that in the latter experiments, subjects were free to move their heads, and the truncations are found in the combined eye-head gaze shifts. When the eye and head components are analyzed separately, it seems that the gazeshift truncation is most evident in the head movement, rather than the eye (in head) movement. It is also notable that in the Corneil study, evidence of truncation was largely found when targets were presented at much larger amplitudes than those used here ( $\sim 20-60^{\circ}$  vs.  $\sim 10-15^{\circ}$ ) Such large movements would offer a far greater chance for a gaze shift truncation to take place, since the duration of large-amplitude movements is considerably longer than that of smaller saccades (Becker, 1989). Thus, from the results presented here and by Goossens, we conclude that not all hypometric initial saccades can be attributed to an abrupt interruption of a larger movement.

In Experiment 1, we speculated that the hypometric initial saccades resulted from interference between two concurrently programmed saccades. One possibility is that the activity related to the second saccade results in a truncation of the initial saccade. In light of the present results, this appears unlikely. However, a second possibility remains viable, specifically, that the hypometric initial saccades observed here resulted because the activity in the superior colliculus related to the initial saccade was weakened, due to interference from concurrent processing of the second saccade. This explanation is consistent with physiological findings by Stanford et al. (1996) in the monkey and Paré et al. (1994) in the cat, who showed that when the superior colliculus is electrically microstimulated to evoke saccades, the amplitude, as well as the velocity profile, of the saccade depend critically on the duration and pulse frequency of the stimulation train. Thus, although activity of neurons at a given site in the colliculus normally produces saccades of a particular direction and amplitude (Robinson, 1972; Schiller & Stryker, 1972), when this activity is too brief, a hypometric saccade will be generated. Correspondingly, the dynamics of such a hypometric saccade would appear normal if the firing frequency of the collicular neurons was lower than normal. The supposition that concurrent processing of a second saccade could result in such a weakening of the activity related to the first saccade receives support from Munoz and Istvan (1998), who showed that activity at one site on the colliculus tends to be inhibited by activity at other distal sites. Similar inhibition could also originate from the frontal eye fields (Schlag-Rey, Schlag & Dassonville, 1992).

# 7. General discussion

We have presented evidence for the idea that the saccadic system is capable of processing two movements concurrently. In a search task in which competing saccade targets are presented, we observed that when subjects initially make an incorrect saccade, such errors are often followed by a second saccade to the correct target, after only a very brief fixation interval. This suggests that the two saccades are programmed concurrently. We also observed that when the inter-saccadic interval is short, the initial incorrect saccades tend

to be hypometric. Using a saccade-contingent display. we found that changes in the location of the target which take place during the initial saccade do not change the goal of the subsequent saccade, except for a few cases in which the two saccades are separated by a very long fixation interval (> 240 ms). This supports the concurrent processing hypothesis: if the second saccade had been programmed serially (after the end of the initial saccade), the change in the target position should have resulted in a change in the goal of the second saccade. Using a double-step paradigm, we recorded two-saccade responses which closely resembled those seen for the search task. We showed that, regardless of when the initial saccade occurred, the second saccade of these two-saccade responses occurred at a relatively fixed time interval after the appearance of the second target step, and that this time period corresponded to the normal latency for visually-guided saccades. Again, this finding supports the idea that the programming of each saccade is triggered by the appearance of a target step, and that the two saccades are processed concurrently.

In the last experiment, we tested, and rejected, the idea that hypometric initial saccades occurred due to a mid-flight interruption resulting from processing of a second saccade. We did not find the expected systematic changes in saccade dynamics which are seen for interrupted saccades. However, it is possible that a diminution of the neural activity corresponding to the first saccade goal, due to competition from the second saccade goal, could be responsible for the reduction in amplitude of the initial saccade.

# 7.1. Implications for neural models of the saccadic system

Concurrent processing presents a difficulty for some models of the neural processing underlying saccades. Recently, it has been hypothesized that a sub-population of SC neurons (BUNs), the build-up neurons, is involved both in selecting the goal of a future movement and in controlling the trajectory of a saccade which is being executed (e.g. Wurtz & Optican, 1994; Munoz & Wurtz, 1995; Wurtz, 1996). While this scheme is plausible for serially-programmed saccades, there are obvious difficulties in extending it to concurrently-programmed saccades: in such cases, the population activity of the BUNs must simultaneously control the execution of the first saccade while signaling the target of the concurrently-programmed second saccade.

One possible solution to the problem of concurrent processing is that other areas, such as the frontal eye fields (FEF), might be able to independently signal the target of the second saccade. Indeed, it has been hypothesized that there are two parallel pathways for the generation of saccades: a posterior system involving parietal cortex, projecting to the SC, and an anterior system involving the FEF (Schiller, True & Conway, 1980; Schiller & Sandell, 1983; Schiller, 1985; Keating & Gooley, 1988; Lynch, 1992). This led Theeuwes et al. (1998) to suggest that concurrent processing of two saccades may result from the selection of different saccade goals in the posterior and anterior systems. However, preliminary evidence suggests that activity related to both saccades is simultaneously present in a single brain area: McPeek and Keller (1999) demonstrated that activity related to the second saccade target is maintained in the SC even during the execution of the initial saccade.

## 8. Conclusions

The saccadic eye movement system allows us to experience a rich and seamless visual world by rapidly and accurately moving the fovea to scan objects of interest. Given that natural scenes often contain several different areas of interest, the selection of one stimulus from among many is clearly a crucial part of programming an accurate saccade. Several recent studies have demonstrated that the saccadic system does not appear to adopt a strategy of minimizing the number of saccades (Ballard, Hayhoe, Li & Whitehead, 1992; Hooge & Erkelens, 1996, 1998; Zelinsky, 1996). Instead, subjects often initiate the programming of saccades even before visual analysis at the current fixation position has been completed (Hooge & Erkelens, 1996, 1998). However, this seemingly inefficient strategy becomes more understandable when it is realized that the system, as a whole, operates in parallel. As previous studies have shown, even after programming of a saccade has begun, visual analysis at the current fixation position continues in parallel (Komoda et al., 1973; Becker & Jürgens, 1979; Hou & Fender, 1979; Findlay & Harris, 1984; Aslin & Shea, 1987). Furthermore, the accumulation of evidence shown here and by others (Becker & Jürgens, 1979; Morrison, 1984; Theeuwes et al., 1998) indicates that the saccadic system is capable of processing two saccades in a parallel, or pipelined, fashion. These two types of parallel processing work together: even after programming of a saccade has begun, if subsequent visual analysis results in a change in the decision of where to move the eyes next, programming of a new saccade can begin immediately and can be processed in parallel with the preparation of the initial saccade. This allows the second saccade to be executed with little or no delay after the end of the first saccade.

This parallelism reduces the cost of each saccade by effectively reducing the latency, or dead-time, between movements. In fact, such a system may be more desirable than a strategy of fully analyzing the visual scene before moving, because it can allow the subject to begin

programming a saccade earlier, based on partial information about the likely position of the target, even though there is a risk that with additional time for visual processing, this information will later prove to be incorrect. If this, indeed, turns out the be the case, a corrective saccade to a more appropriate location can be made with minimal delay. In contrast, if the subject waited until the visual information was fully analyzed before programming a movement, it would be more likely that the initial saccade would be correct, but the latency of such a saccade would be longer than for the case in which a correct initial 'guess' was used. In essence, concurrent processing of two saccades can be thought of as reducing the penalty for programming movements based on preliminary or incomplete information. Thus, these results shed new light on the mechanisms of saccade programming in complex displays, and underline the fact that in order to uncover the true capabilities and limitations of the saccadic system, it is necessary to challenge the system with more demanding tasks.

### Acknowledgements

This work was supported by a grant from the McKnight Foundation and AFOSR grant F49620-92-J-0016 and to K. Nakayama, and by an NDSEG graduate fellowship to R.M. McPeek.

#### References

- Amador, N., Schlag-Rey, M., & Schlag, J. (1998). Primate antisaccades. I. Behavioral characteristics. *Journal of Neurophysiology*, 80, 1775–1786.
- Aslin, R. N., & Shea, S. L. (1987). The amplitude and angle of saccades to double-step target displacements. *Vision Research*, 27(11), 1925–1942.
- Bahill, A. T., Bahill, K. A., Clark, M. R., & Stark, L. (1975). Closely spaced saccades. *Investigative Ophthalmology*, 14(4), 317–321.
- Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence: a tool for studying human eye movements. *Mathematics and Bioscience*, 24, 191–204.
- Ballard, D., Hayhoe, M. M., Li, F., & Whitehead, S. D. (1992). Hand-eye coordination during sequential tasks. *Philosophical Transactions of the Royal Society of London*, B, 337(1281), 331–338.
- Becker, W. (1989). Metrics. In R.H. Wurtz & M.E. Goldberg, *The neurobiology of saccadic eye movements*, (pp. 13–67). New York: Elsevier.
- Becker, W., & Jürgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision Research*, 19, 967–983.
- Becker, W., & Fuchs, A. F. (1988). Lid-eye coordination during vertical gaze changes in man and monkey. *Journal of Neurophysi*ology, 60(4), 1227–1252.
- Becker, W., & Jürgens, R. (1990). Human oblique saccades: quantitative analysis of the relation between horizontal and vertical components. *Vision Research*, 30(6), 893–920.

- Bravo, M. J., & Nakayama, K. (1992). The role of attention in different visual search tasks. *Perception & Psychophysics*, 51, 465–472.
- Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, 371(6497), 511–513.
- Corneil, B. D., Hing, C. A., Bautista, D. V., & Munoz, D. P. (1999). Human eye-head gaze shifts in a distractor task: I. Truncated gaze shifts. *Journal of Neurophysiology*, 82, 1390–1405.
- Findlay, J. M., & Harris, L. R. (1984). Small saccades to doublestepped targets moving in two dimensions. In A. G. Gale, & F. Johnson, *Theoretical and applied aspects of eye movement research* (pp. 71–78). Amsterdam: Elsevier.
- Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral and Brain Sciences*, 16, 553–610.
- Goossens, H. H. L. M. (1998). Sensorimotor transformations and feedback signals involved in gaze control (PhD thesis). Nijmegen, The Netherlands: Catholic University of Nijmegen.
- Hooge, I. T., & Erkelens, C. J. (1996). Control of fixation duration in a simple search task. *Perception & Psychophysics*, 58(7), 969–976.
- Hooge, I. T., & Erkelens, C. J. (1998). Adjustment of fixation duration in visual search. Vision Research, 38(9), 1295–1302.
- Hou, R. L., & Fender, D. H. (1979). Processing of direction and magnitude by the saccadic eye-movement system. *Vision Research*, 19, 1421–1426.
- Keating, E. G., & Gooley, S. G. (1988). Disconnection of parietal and occipital access to the saccadic oculomotor system. *Experimental Brain Research*, 70(2), 385–398.
- Julesz, B. (1986). Texton gradients: the texton theory revisited. Biological Cybernetics, 54, 245–251.
- Keller, E. L. (1977). Control of saccadic eye movements by midline brain stem neurons. In R. Baker, & A. Berthoz, *Control of gaze* by brain stem neurons (pp. 327–336). Amsterdam: Elsevier.
- Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Human Neurobiology*, 4, 219–227.
- Komoda, M. K., Festinger, L., Phillips, L. J., Duckman, R. H., & Young, R. A. (1973). Some observations concerning saccadic eye movements. *Vision Research*, 13, 1009–1020.
- Levy-Schoen, A., & Blanc-Garin, J. (1974). On oculomotor programming and perception. *Brain Research*, 71, 443–450.
- Lynch, J. C. (1992). Saccade initiation and latency deficits after combined lesions of the frontal and posterior eye fields in monkeys. *Journal of Neurophysiology*, 68(5), 1913–1916.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory and Cognition*, 22(6), 657–672.
- McPeek, R. M., & Keller, E. L. (1999). Superior colliculus neurons reflect concurrent programming of saccades in visual search. Third Annual Vision Research Conference: *Pre-attentive and attentive mechanisms in vision*, 156.
- McPeek, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research*, 39(8), 1555–1566.
- Meredith, M. A., & Ramoa, A. S. (1998). Intrinsic circuitry of the superior colliculus: pharmacophysiological identification of horizontally oriented inhibitory interneurons. *Journal of Neurophysiol*ogy, 79(3), 1597–1602.
- Mokler, A., & Fischer, B. (1999). The recognition and correction of involuntary prosaccades in an antisaccade task. *Experimental Brain Research*, 125, 511–516.
- Morrison, R. E. (1984). Manipulation of stimulus onset delay in reading: evidence for parallel programming of saccades. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 667–682.
- Munoz, D. P., & Wurtz, R. H. (1993). Fixation cells in monkey superior colliculus. II. Reversible activation and deactivation. *Journal of Neurophysiology*, 70, 576–589.

- Munoz, D. P., & Wurtz, R. H. (1995). Saccade-related activity in monkey superior colliculus: II. Spread of activity during saccades. *Journal of Neurophysiology*, 73(6), 2334–2348.
- Munoz, D. P., & Istvan, P. J. (1998). Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *Journal of Neurophysiology*, 79(3), 1193–1209.
- Munoz, D. P., Waitzman, D. M., & Wurtz, R. H. (1996). Activity of neurons in monkey superior colliculus during interrupted saccades. *Journal of Neurophysiology*, 75(6), 2562–2580.
- O'Regan, J. K. (1990). Eye movements and reading. In E. Kowler, Eye movements and their role in visual and cognitive processes (pp. 395-447). New York: Elsevier.
- Ottes, F. P., Van Gisbergen, J. A., & Eggermont, J. J. (1984). Metrics of saccade responses to visual double stimuli: two different modes. *Vision Research*, 24(10), 1169–1179.
- Paré, M., Crommelinck, M., & Guitton, D. (1994). Gaze shifts evoked by stimulation of the superior colliculus in the head-free cat conform to the motor map but also depend on stimulus strength and fixation activity. *Experimental Brain Research*, 101(1), 123–139.
- Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Re*search, 37, 495–510.
- Robinson, D. A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision Research*, 12, 1795–1807.
- Schiller, P. H. (1985). A model for the generation of visually guided saccadic eye movements. In D. Rose, & V. G. Dobson, *Models of* the visual cortex (pp. 62–70). New York: Wiley.
- Schiller, P. H., & Stryker, M. (1972). Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. *Journal of Neurophysiology*, 35(6), 915–924.
- Schiller, P. H., & Sandell, J. H. (1983). Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey. *Experimental Brain Research*, 49, 381–392.
- Schiller, P. H., True, S. D., & Conway, J. L. (1980). Deficits in eye movements following frontal eye-field and superior colliculus ablations. *Journal of Neurophysiology*, 44, 1175–1189.
- Schlag-Rey, M., Schlag, J., & Dassonville, P. (1992). How the frontal eye field can impose a saccade goal on superior colliculus neurons. *Journal of Neurophysiology*, 67(4), 1003–1006.
- Shioiri, S., & Cavanagh, P. (1989). Saccadic suppression of low-level motion. Vision Research, 29(8), 915–928.
- Skavenski, A. A., & Steinman, R. M. (1995). Free headed monkeys make saccades at very high frequencies in a novel laboratory environment. *Investigative Ophthalmology and Visual Science* (Supplement), 36(4), 354.
- Stanford, T. R., Freedman, E. G., & Sparks, D. L. (1996). Site and parameters of microstimulation: evidence for independent effects on the properties of saccades evoked from the primate superior colliculus. *Journal of Neurophysiology*, 76(5), 3360–3381.
- Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: capture of the eyes by new objects. *Psychological Science*, 9(5), 379–385.
- Van Gisbergen, J. A. M., Van Opstal, A. J., & Ottes, F. P. (1984). Parameterization of saccadic velocity profiles in man. In A. G. Gale, & F. Johnson, *Theoretical and applied aspects of eye movement research* (pp. 87–94). Amsterdam: Elsevier.
- Van Gisbergen, J. A. M., Van Opstal, A. J., & Schoenmakers, J. J. M. (1985). Experimental test of two models for the generation of oblique saccades. *Experimental Brain Research*, 57, 321–336.
- Viviani, P., & Swensson, R. G. (1982). Saccadic eye movements to peripherally discriminated visual targets. *Journal of Experimental Psychology: Human Perception and Performance*, 8(1), 113–126.
- Volkman, F. (1962). Vision during voluntary saccadic eye movements. Journal of the Optical Society of America, 52, 571–578.

- Wurtz, R. H. (1996). Vision for the control of movement. The 1996 Friedenwald Lecture. *Investigative Ophthalmology and Vi*sual Science, 37, 2131–2145.
- Wurtz, R. H., & Optican, L. M. (1994). Superior colliculus cell types and models of saccade generation. *Current Opinion in Neurobiology*, 4, 857–861.
- Zelinsky, G. J. (1996). Using eye saccades to assess the selectivity of search movements. *Vision Research*, 36(14), 2177– 2187.
- Zuber, B. L., & Stark, L. (1966). Saccadic suppression: elevation of visual threshold associated with saccadic eye movements. *Experimental Neurology*, 16(1), 65–79.