



# Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey

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## Abstract

In human subjects, two mechanisms for improving the efficiency of saccades in visual search have recently been described: color priming and concurrent processing of two saccades. Since the monkey provides an important model for understanding the neural underpinnings of target selection in visual search, we sought to explore the degree to which the saccadic system of monkeys uses these same mechanisms. Therefore, we recorded the eye movements of rhesus monkeys performing a simple color-odddity pop-out search task, similar to that used previously with human subjects. The monkeys were rewarded for making a saccade to the odd-colored target, which was presented with an array of three distractors. The target and distractors were randomly chosen to be red or green in each trial. Similar to what was previously observed for humans, we found that monkeys show the influence of a cumulative, short-term priming mechanism which facilitates saccades when the color of the search target happens to repeat from trial to trial. Furthermore, we found that like humans, when monkeys make an erroneous initial saccade to a distractor, they are capable of executing a second saccade to the target after a very brief inter-saccadic interval, suggesting that the two saccades have been programmed concurrently (i.e. in parallel). These results demonstrate a close similarity between human and monkey performance. We also made a new observation: we found that when monkeys make such two-saccade responses, the trajectory of the initial saccade tends to curve toward the goal of the subsequent saccade. This provides evidence that the two saccade goals are simultaneously represented on a common motor map, supporting the idea that the movements are processed concurrently. It also indicates that concurrent processing is not limited to brain areas involved in higher-level planning; rather, such parallel programming apparently occurs at a low enough level in the saccadic system that it can affect saccade trajectory. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Saccade; visual search; priming; parallel programming

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## 1. Introduction

The ability to rapidly and accurately direct gaze to objects of interest is crucial for vision. However, in many situations, there are several different objects simultaneously competing for attention. As a result, an important task for the oculomotor system is to select and orient gaze to one object from among the many possibilities present in the visual scene.

Although several studies of gaze-shifting behavior in more natural situations have recently been reported (Ballard, Hayhoe, Li, & Whitehead, 1992; Land & Lee, 1994; Land & Furneaux, 1997), much of the work on

saccade target selection has used visual search tasks, because they provide a simplified paradigm for studying this important process. The allocation of gaze shifts during visual search has been studied extensively in human subjects (e.g. Williams, 1966; Gould & Dill, 1969; Viviani & Swenson, 1982; Epelboim et al., 1995; Hooge & Erkelens, 1996; Zelinsky, 1996; Findlay, 1997; Williams, Reingold, Moscovitch, & Behrmann, 1997; Eckstein, Beutter, & Stone, 1998; Hooge & Erkelens, 1998; Scialfa & Joffe, 1998; Greene, 1999; Gilchrist, Heywood, & Findlay, 1999; McPeck, Maljkovic, & Nakayama, 1999), but it has only recently begun to be studied in detail in the monkey (e.g. Motter & Belky, 1998a,b; Bichot & Schall, 1999). Since much of our knowledge of the neural mechanisms responsible for eye movements has been derived from experiments with

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rhesus monkeys, it is important to determine the extent to which the search performance of monkeys is similar to that of humans.

The aim of the present study is to characterize the oculomotor performance of monkeys in a simple color-odddity search task. In human subjects, two mechanisms have recently been described for improving the efficiency with which subjects can direct gaze to a visual target in a search array. First, it has been found that human attentional shifts (Maljkovic & Nakayama, 1994, 1996, 2000) and eye movements (McPeck et al., 1999) are affected by an unconscious, automatic, short-term memory system, which has been called ‘priming of pop-out.’ This priming facilitates orienting toward targets which have visual features (such as color or shape) in common with recently-attended visual targets. It has been shown that subjects typically refixate the same set of objects repeatedly when performing routine visuo-motor tasks (Ballard et al., 1992; Hayhoe, Bensinger, & Ballard, 1998), suggesting that this priming could improve the efficiency of the eye movement system in such situations (McPeck et al., 1999; Maljkovic & Nakayama, 2000). In this study, we will examine the extent to which saccades in the monkey are affected by color priming.

Second, several studies have suggested that humans are capable of programming two saccades to different goals in a temporally overlapping manner (see Fig. 1), such that processing of a second saccade goal begins even before an initial saccade has been executed (Becker & Jürgens, 1979; Viviani & Swensson, 1982; Morrison, 1984; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Mokler & Fischer, 1999; McPeck, Skavenski, & Nakayama, 2000). This ‘concurrent processing’ of saccades can result in a sequence of two saccades separated by a very brief inter-saccadic interval. In the

present study, we will explore evidence for the ability of monkeys to program two saccades to different targets concurrently. Comparisons with human performance will be facilitated by the fact that human behavior has recently been studied under very similar task conditions (McPeck et al., 1999, 2000). Such comparative studies provide essential evidence to link oculomotor neurophysiology, which is largely studied in the monkey, to human eye movement behavior. Carefully establishing this link is especially important for more complex tasks such as search, which can involve higher-level mechanisms like priming and concurrent processing. Indeed, this study can be viewed as forming the basis of our own forthcoming neurophysiological studies of these phenomena in search (e.g. McPeck & Keller, 1999, 2000).

### 1.1. Short-term color priming

The task we use is a color-odddity search, requiring subjects to make a saccade to an odd-colored target along with three distractors which are all of the same color. The color of the target is randomly selected to be either red or green on a trial-by-trial basis and the distractors are always of the opposite color. Prior results with humans (McPeck et al., 1999) showed that under similar conditions, when the color of the target remains the same from trial to trial, saccade latencies are shorter and subjects are more likely to make a saccade to the correct target, rather than to a distractor. On the other hand, when the color of the target is different from its color in previous trials, saccade latencies are longer and humans are more likely to make a saccade to a distractor.

This color priming effect for saccades is similar to a priming effect for focal attention, which has been studied extensively by Maljkovic and Nakayama (1994,

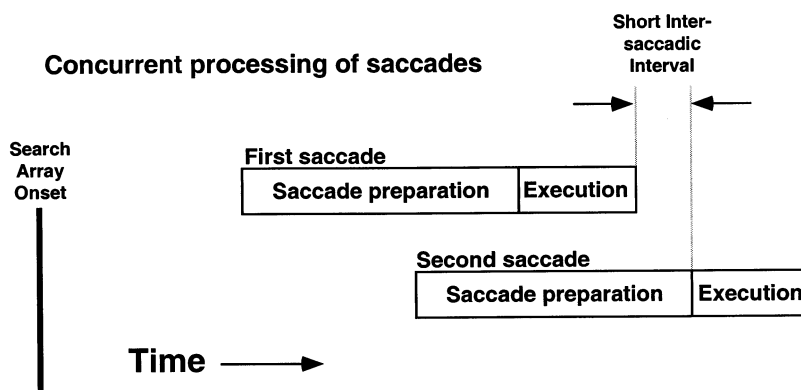


Fig. 1. Schematic diagram showing the temporal sequence of events underlying the hypothesized concurrent processing of two saccades. First, the search array is presented and, perhaps due to priming from previous trials, a distractor is initially selected as the saccade target. During the latent period of this saccade, further visual processing indicates the position of the correct target. This triggers programming of a second saccade to the correct target, which proceeds in parallel with programming of the first saccade to the distractor. As a result, the second saccade can be executed shortly after the end of the first saccade.

1996, 2000). These investigators used a color-oddy search task in which subjects were required to focus attention on the target without making eye movements, and found that focal attention could be shifted to the target more quickly when the color of the target repeated from trial to trial than when it switched. It was shown that this memory accumulates over several trials, and is not affected by subjects' awareness or volition. Thus, it can be described as a form of short-term priming used for the deployment of focal attention.

McPeck et al. showed that the duration and magnitude of this priming effect for the human saccadic system is similar to the priming effect for focal attention. This congruence supports the idea, which has been put forward by several recent studies (e.g. Hoffman & Subramanian, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Deubel & Schneider, 1996; McPeck et al., 1999), that a focusing of attention on the target is a prerequisite for the generation of a saccade. One aim of the present study is to ascertain whether these same relationships between the history of target colors, and saccade latency and accuracy, hold for monkeys. If so, this would suggest that in monkeys, as in humans, saccades require a focusing of attention on the target.

Bichot and Schall (1999) reported evidence for short-term color priming in monkeys performing visual search: across a block of 20 trials in which the colors of the target and distractors remained constant, they found that monkeys' performance was worse (longer saccade latencies and more errors) in the initial five trials than in the rest of the block. Although color priming of the sort described by Maljkovic and Nakayama may be responsible for this improvement, it could also be due to a cognitive strategy or a behavioral habit: since the color of the target changed only every 20 trials, its color in previous trials was a good predictor of its color in future trials. Consequently, in the majority of trials, the monkeys would be rewarded for choosing the same color target as in previous trials. In our task, the target color switches unpredictably from trial to trial, and thus, prior trials provide no information about the future color of the target. This allows us to better test for the presence of an automatic, dynamically-updated, short-term color priming by removing any advantage for choosing the same color target as in previous trials. This task also permits us to compare the priming to human data collected under similar conditions for saccades (McPeck et al., 1999) and focal attention (Maljkovic & Nakayama, 1994).

### 1.2. *Concurrent processing of saccades*

This priming effect can also have negative consequences for performance in the color-oddy search task. For example, suppose that the target happens to be green for several trials, and then switches to red.

Under these circumstances, attention will be primed toward the green distractors, rather than toward the red target. This results in conflicting attentional cues: color oddity information biases attention toward the target, while priming biases attention toward the distractors. As a result, saccade latencies are longer, and subjects tend to make more errors (consisting of saccades to distractors) when the color of the target changes from its color in previous trials. McPeck et al. (2000) found that when humans make error saccades to distractors, they can produce a second saccade to the correct target after only a very short inter-saccadic interval. The brevity of the pause between the initial and second saccades ( $\sim 10$ – $100$  ms) suggests that programming of the two saccades may overlap in time (see Fig. 1). Specifically, it is hypothesized that attention is initially drawn to the distractor and programming of a saccade to the distractor commences. During the latent period of the saccade, attention is shifted to the correct target, and if it is too late to cancel the initial saccade, programming of a second saccade to the target begins. Processing of the two saccades is carried out concurrently by the system, resulting in an initial saccade to the distractor, followed after a brief fixation interval by a second saccade to the target.

Several early studies using the double-step paradigm demonstrated very brief inter-saccadic intervals, suggesting that humans are capable of programming two saccades to different stimuli in such an overlapping, or concurrent, fashion (e.g. Levy-Schoen & Blanc-Garin, 1974; Becker & Jürgens, 1979). Indeed, Becker and Jürgens showed that the timing of the second saccade is directly related to the onset of the second target step, and is independent of when the first saccade occurs. This is exactly what they predicted, if the two saccades are programmed concurrently rather than serially. McPeck et al. (2000) subsequently replicated this original finding in a two-dimensional double-step task.

It has also been found that when two saccades are executed in rapid succession, the initial saccade tends to have an unusually small amplitude (Becker & Jürgens, 1979). In fact, the most hypometric initial saccades are typically followed by the shortest inter-saccadic intervals in double-step and anti-saccade tasks (Kalesnykas & Hallett, 1987), as well as in a search task (McPeck et al., 2000). One explanation for this relationship is that concurrent programming of the second saccade interferes with the initial saccade, causing it to fall short of the target stimulus. Such interactions could perhaps be due to competition between two saccade programs on a topographical motor map, such as exists in the superior colliculus or frontal eye fields.

The idea that two saccades can be programmed concurrently, first put forward in the double-step paradigm, has also been raised in several studies of saccades in more complex tasks, such as reading (Mor-

rierson, 1984), the anti-saccade task (Mokler & Fischer, 1999) and visual search with an unexpected abrupt onset (Theeuwes et al., 1998; Theeuwes, 1999). McPeck et al. (2000) provided evidence that a simple color-oddity search task can also lead to the concurrent processing of saccades.

However, the only study of concurrent programming of saccades in the rhesus monkey failed to find evidence for it (Baizer & Bender, 1989). Thus, a second aim of this study is to re-visit this issue with new paradigms developed in humans, in order to determine whether monkeys, like humans, show a pattern of performance suggesting that they are capable of concurrently processing two saccades to different goals. This, in turn, would allow the study of the neural underpinnings of this concurrent processing, which would shed light on the dynamic neural activity involved in saccade programming and target selection, particularly in situations in which there are several competing targets.

## 2. Methods

Two male rhesus monkeys (*Macaca mulatta*) weighing between 4 and 7 kg were used in this study. All experimental protocols were approved by the Institutional Animal Care and Use Committee at the California Pacific Medical Center and complied with the guidelines of the Public Health Service policy on Humane Care and Use of Laboratory Animals.

### 2.1. Preparation

The monkeys were initially trained to come out of their cages and sit comfortably in a primate chair. To allow head-fixed eye movement recordings, a scleral eye coil and a head restraint system were implanted in each monkey under isoflurane anesthesia and aseptic surgical conditions. Anesthesia was induced with an intramuscular injection of ketamine. Heart rate, blood pressure, respiratory rate, and body temperature were monitored for the duration of the surgery. A coil made of four turns of Teflon-coated stainless-steel wire was implanted under the conjunctiva of one eye using the procedure described by Fuchs and Robinson (1966), as modified by Judge, Richmond, and Chu (1980). In monkey HB, three small stainless-steel tubes embedded in dental cement were securely attached to the animal's skull using titanium orthopedic bone screws. In monkey GE, a single head-holder socket (Christ Instruments) was implanted, also using dental cement and titanium orthopedic bone screws. Both systems permitted painless immobilization of the animal's head during the experimental sessions. At the completion of the surgery, animals were returned to their home cages. Antibiotics (Cefazolin) and analgesics (Buprenex) were adminis-

tered as needed during the recovery period under the direction of a veterinarian.

### 2.2. Behavioral procedures

The monkeys were seated in a primate chair with their heads restrained for the duration of the testing sessions. They were trained to execute behavioral tasks for liquid reward, and were allowed to work to satiation. Records of each animal's weight and health status were kept, and supplemental water was given as necessary. The animals typically worked for 5 days, and were allowed free access to water on weekends.

The monkeys were trained to fixate a white spot of light subtending  $0.25^\circ$  in diameter with a luminance of  $1.24 \text{ cd m}^{-2}$  against a homogenous background of  $0.12 \text{ cd m}^{-2}$ . The monkeys were required to keep their eyes within  $1\text{--}2^\circ$  of the fixation point during a fixation interval of 450–650 msec. At the end of this randomly-varying interval, the fixation point was extinguished and a single stimulus (single-stimulus task) or a target along with three distractors (search task) was presented. The monkeys were rewarded if their initial saccade landed within  $3^\circ$  of the target stimulus. Anticipatory saccades ( $< 70 \text{ ms}$ ) and late responses ( $> 400 \text{ ms}$ ) were not rewarded and were removed from subsequent analysis. In trials in which more than one saccade was required to move the eye to within  $3^\circ$  of the target, no reward was given.

The stimuli consisted of red or green discs, which were chosen to be approximately equiluminant, with measured luminances of 0.90 and  $0.92 \text{ cd m}^{-2}$ , respectively. In the search task, all three distractor stimuli were of the same color (either red or green), and the target was delineated by being of the opposite color. The stimuli were presented at an eccentricity of 15, and subtended  $2^\circ$  of visual angle. The position of the target was randomly chosen in each trial from among eight possibilities consisting of the four cardinal directions ( $0, 90, 180,$  and  $270^\circ$ ) and four oblique directions ( $45, 135, 225,$  and  $315^\circ$ ). In each trial, the target was equally likely to be red or green. Each experimental block consisted of 40–80 trials. In the majority of experimental blocks, we presented the target along with three distractor stimuli, presented at the same eccentricity as the target, but separated in direction by  $90^\circ$  intervals (see Fig. 3). However, in single-stimulus blocks, we presented only the target stimulus (randomly selected to be red or green in each trial), without distractors. Finally, in intermixed blocks, we randomly intermixed single-stimulus trials, which were presented with 20% probability, with trials in which the target was presented along with distractors, which were presented with 80% probability. Following several weeks of training in the search task, we collected 660 trials from Monkey HB in the search task and 361 trials in

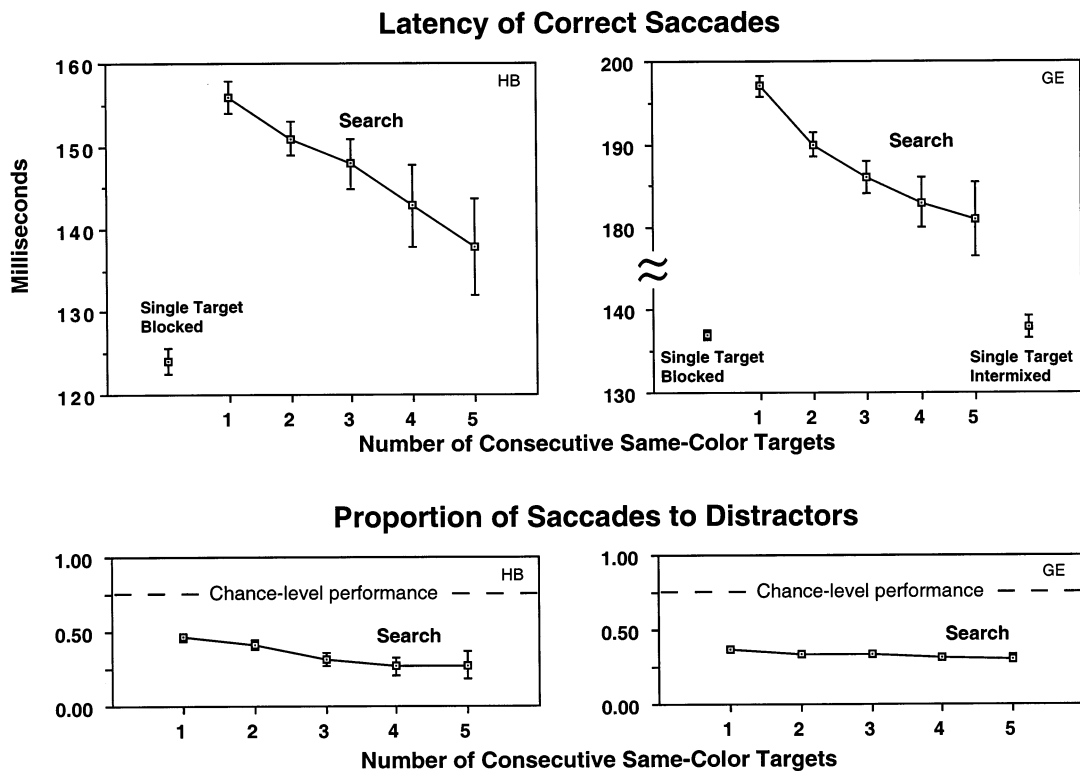


Fig. 2. The effects of color priming on the latency of saccades to the target and on the proportion of mis-directed saccades. The upper panels show, for the two monkeys, the latency of correct saccades to the target as a function of the number of consecutive same-color trials. The lower panels show the proportion of saccades directed toward one of the distractors as a function of the number of consecutive same-color trials. As is evident, both the latency of correct saccades and the proportion of mis-directed saccades (to distractors) decrease as the number of consecutive same-color trials increases, indicating that color priming influences saccades in the monkey. For comparison, the latency of saccades to single stimuli (presented without distractors) is shown at the extreme left of the upper panels. For Monkey GE, at the extreme right of the plot, the latency of saccades made to single stimuli interleaved with search trials is shown.

the single-stimulus task, while monkey GE performed 814 trials in the search task, 448 trials in the single-stimulus task, and 234 trials in which the search and single-stimulus task were randomly intermixed.

Data collection and storage was controlled by a real-time program running on a PC. Horizontal and vertical eye position and velocity were sampled at 1 kHz and digitally stored on disc. A Macintosh computer, which was interfaced with the PC, generated the visual displays using software constructed with the Video Toolbox library (Pelli, 1997). Visual stimuli were presented on a 29 inch color CRT (Viewsonic GA29), in synchronization with the monitor's vertical refresh. The monitor had a spatial resolution of 800 by 600 pixels and a non-interlaced refresh rate of 75 Hz. The monitor was positioned 57 cm in front of the monkey and allowed stimuli to be presented in a field of view of approximately  $\pm 25^\circ$  along the horizontal meridian and  $\pm 20^\circ$  along the vertical meridian. Off-line analysis of the eye movement data was performed by algorithms using velocity and acceleration criteria to detect the beginning and end of saccades. The algorithm's identification of saccades was inspected to verify its accuracy.

### 3. Results

#### 3.1. Color priming

Initially, we analyzed blocks of trials in which the target was always presented along with three distractors, and the colors of the target and distractors could vary randomly from trial to trial. Previous work with humans showed that when the color of the target happens to remain the same across several trials, saccade latencies are shorter and fewer saccades to distractors are made (McPeck et al., 1999). Fig. 2 shows saccade latency and the rate of saccades to distractors for two monkeys as a function of the number of consecutive same-color targets. Thus, a value of one on the ordinate denotes trials in which the color of the target differed from its color in the previous trial. Two on the ordinate denotes trials in which the color of the target was the same as in the previous trial, but differed from its color two trials ago, and so on. It is clear that as the number of consecutive same-color trials increases, saccade latency decreases. Linear contrasts verified that the decreases are significant ( $P < 0.05$  for HB and  $P < 0.01$  for GE).

The lower two panels show the proportion of initial saccades directed toward a distractor (errors) as a function of the number of consecutive same-color targets. Monkey HB made more errors overall and the proportion of errors decreases as the number of previous same-color targets increases. Linear contrasts show that this trend is significant ( $P < 0.05$ ). Monkey GE was trained more extensively before testing, and thus was more accurate overall. While monkey GE shows a slight decrease in error rate as the number of consecutive same-color targets increases, this decrease is not significant. The humans subjects tested by McPeck et al. (1999) showed similar individual differences in accuracy, and the overall error rates for the human and monkey subjects are comparable.

### 3.2. Latency of saccades in search vs. saccades to single targets

We also analyzed the latency of saccades made in blocks of trials in which only a single stimulus was presented, without distractors. These data are shown at the extreme left of the upper graphs. As can be seen, Monkey HB shows consistently shorter latencies than Monkey GE, even in the single-stimulus condition. Furthermore, saccades made by both monkeys in the single-stimulus condition had much shorter latencies than saccades made in the presence of distractors, as has previously been described by Schiller, Sandell, and Manusell (1987).

Is this difference in latency between saccades made to a single target and saccades made in search due to the adoption of different top-down strategies in the two cases (i.e. to go quickly in blocks of single stimulus trials vs. to delay the execution of the saccade in blocks of search) or is it due to the presence or absence of competing distractor stimuli in the visual scene? To address this question, we analyzed the latency of saccades made in single-stimulus trials which were randomly interleaved (with 20% probability of occurrence) within a series of search trials. This data was collected for monkey GE only, so our conclusions are limited. However, the results in this monkey were quite clear: we found that the latency of saccades in single-stimulus trials was virtually the same regardless of whether the trials were embedded in a block of all single-stimulus trials or in a block in which 80% of the trials were search trials. The mean latency of saccades in single-stimulus trials which were interleaved with search trials is plotted at the extreme right of the upper right panel of Fig. 2, and did not significantly differ from the mean latency of single-stimulus trials presented in a block ( $t$ -test:  $P > 0.20$ ). Correspondingly, there was also no significant difference in mean saccadic latency for search trials intermixed with single-stimulus trials and search trials presented in a block ( $t$ -test:  $P > 0.30$ ).

### 3.3. Short inter-saccadic intervals

McPeck et al. (2000) found that in their search task, when humans make an initial saccade to a distractor, such error saccades can be followed by a second saccade to the target after only a minimal inter-saccadic interval. When we examined eye movement behavior in rhesus monkeys, we found that after an initial error saccade to a distractor, they are also capable of making a second saccade to the target after a similarly short inter-saccadic interval, even though they were not rewarded for this behavior. The top panel of Fig. 3 shows a spatial ( $xy$ ) plot and a plot of eye position as a function of time for a typical response of this type.

We also occasionally observed responses in which the saccade was initially directed toward a distractor, but drastically changed direction in mid-flight, with no discernible inter-saccadic pause, to finally land near the target. An example of this type of response, which we termed a 're-directed saccade' is shown in the bottom panel of Fig. 3.

The upper panels of Fig. 4 show summary histograms of the inter-saccadic intervals for all two-saccade responses produced by the two monkeys. For comparison, latency histograms of all the initial saccades are shown in the lower panels. Monkey HB executed a large number of second saccades after inter-saccadic intervals of 10–100 ms. Monkey GE also made some second saccades with an inter-saccadic interval of  $< 100$  ms, but the proportion was much smaller. This is consistent with the longer overall latencies for initial saccades shown by Monkey GE, as compared with Monkey HB (see lower panels). For both monkeys, there was a small, but statistically significant difference between the latency of correct and incorrect initial saccades. However, the trends for the two monkeys were in opposite directions: Monkey GE showed slightly longer latencies for incorrect initial saccades than for correct initial saccades (196 vs. 192 ms;  $t$ -test:  $P < 0.05$ ), while Monkey HB showed slightly shorter latencies for incorrect initial saccades than for correct initial saccades (144 vs. 152 ms;  $t$ -test:  $P < 0.01$ ).

### 3.4. Saccade endpoints

Fig. 5 shows the endpoints of the initial saccades executed by each monkey. The endpoints are normalized by a simple rotation, such that the correct target location is always represented at an angle of  $0^\circ$  and an eccentricity of  $15^\circ$ . The distractors are located at  $90$ ,  $180$ , and  $270^\circ$  in direction and  $15^\circ$  in amplitude. For Monkey GE, saccades to the target form a tight cluster. Mis-directed saccades are usually directed toward one of the distractors, although they sometimes fall short of the distractor stimulus. This pattern of results closely matches those found in humans (McPeck et al., 2000).

Monkey HB also shows clusters of saccade endpoints at the target and distractor locations, as well some hypometric saccades in the direction of the distractors. However, this monkey shows a greater tendency toward averaging saccades, which land between stimuli, than did humans in a similar task (McPeck et al., 2000). This may be due to the fact that the angular separation between the stimuli was smaller in the present task than in the task used with humans ( $90^\circ$  here vs.  $120^\circ$  in humans). Earlier ‘double-target’ studies, in which two saccade targets are presented simultaneously, showed that the angular separation between stimuli is a critical factor in determining whether saccades in multi-element displays will show averaging tendencies (Ottes, Van Gisbergen, & Eggermont, 1984). Indeed, even for Monkey GE, many of the hypometric saccades to distractors show a slight endpoint bias in the direction of the target.

It is interesting to note that for both monkeys, fewer error saccades were made to the stimulus furthest from the target ( $180^\circ$  in direction) than to the stimuli neighboring the target ( $90$  and  $270^\circ$  in direction). This conforms well to similar findings in humans by Findlay (1997) and Gilchrist et al. (1999) and in monkeys by Bichot and Schall (1999), and it suggests that coarse-scale information about target location can influence even incorrect saccades.

We also examined the endpoints of the second saccades made after an initial incorrect saccade to a distractor (see bottom panels of Fig. 5). The majority of

these corrective saccades were directed toward the target (95% for GE and 82% for HB), but when the second saccade was not directed to the target, it was usually directed fairly accurately toward a distractor. We failed to find any systematic relationship between the accuracy of the second saccade and the duration of the inter-saccadic interval: linear regressions showed slight non-significant trends for more accurate second saccades following shorter inter-saccadic intervals ( $P = 0.18$  for HB and  $P = 0.25$  for GE).

### 3.5. Inter-saccadic interval and saccade amplitude relationship

In humans, it has been shown that when two saccades are made in rapid succession, the shorter the inter-saccadic interval between the two saccades, the more likely the initial saccade is to be hypometric (McPeck et al., 2000; Kalesnykas & Hallett, 1987). This raises the possibility that concurrent processing of the second saccade may disrupt or modify the initial saccade. Fig. 6 shows, for two-saccade responses in monkeys HB and GE, the relationship between the amplitude of the initial saccade and the duration of the inter-saccadic interval. It should be noted that many of the hypometric saccades plotted here also showed some averaging tendencies. Nonetheless, for both monkeys, the shortest inter-saccadic intervals usually followed the most hypometric initial saccades. In fact, the great majority of hypometric initial saccades are followed by

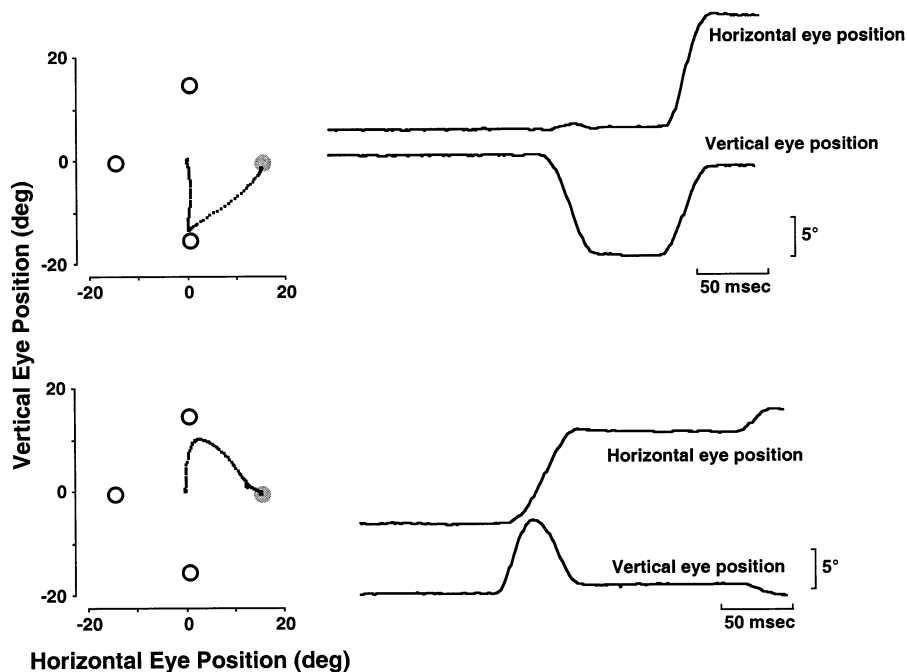


Fig. 3. The upper plots show a spatial ( $xy$ ) plot and plots of eye position as a function of time for a sequence of two saccades separated by a short inter-saccadic interval (44 ms) in the search task. Shown below are corresponding plots for a ‘re-directed’ saccade, which is initially directed toward a distractor, but which changes direction (apparently without an intervening fixation) and lands near the target.

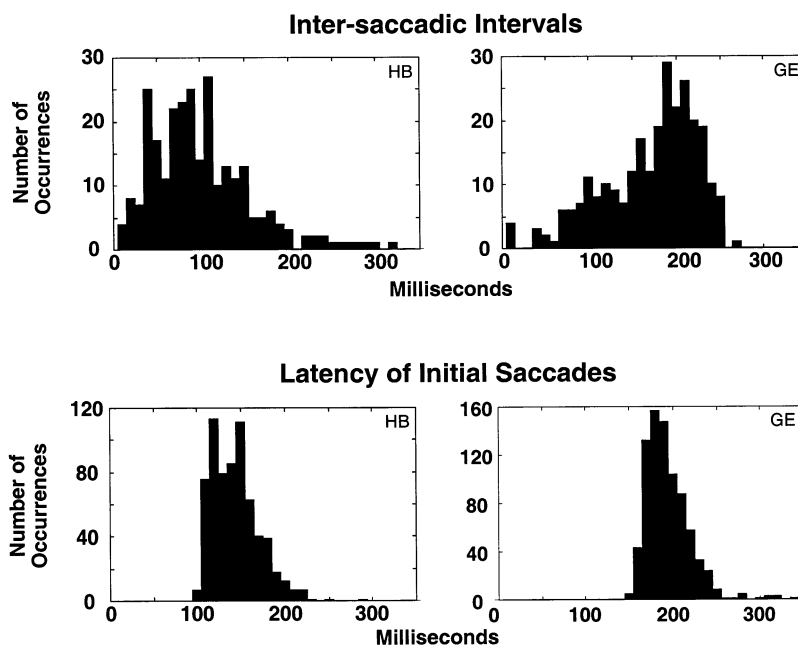


Fig. 4. The top panels show the inter-saccadic intervals observed in trials in which the monkey made two saccades directed toward different stimuli. For comparison, in the lower panels, histograms of the latency (from stimulus onset until saccade execution) of all initial saccades are shown. Monkey HB (at left) shows a large number of short inter-saccadic intervals, but the proportion is much lower. From the lower histograms, it is apparent that the latency of initial saccades for Monkey GE is also significantly longer than for Monkey HB.

inter-saccadic intervals of about 100 ms or less. This finding is very similar to the pattern seen in humans in search (McPeck et al., 1999), as well as in double-step and anti-saccade tasks (Kalesnykas & Hallett, 1987).

### 3.6. Saccade curvature

We observed that the trajectories of saccades made in search tended to be more curved than the trajectories of saccades made to single stimuli. In particular, incorrect initial saccades in search seemed to show the most curvature. We parameterized saccade curvature, using a metric described by Smit and Van Gisbergen (1990), and in Fig. 7, we plot the mean parameterized curvature (irrespective of the direction of curvature) for saccades to a single target, correct initial saccades in search, and incorrect initial saccades in search. For both monkeys, incorrect saccades are significantly more curved on the average than correct saccades in search ( $t$ -tests:  $P = 0.015$  for HB and  $P = 0.025$  for GE). For monkey HB, the curvature of correct saccades in search is also greater than the curvature of saccades to single targets ( $P = 0.022$ ). On the other hand, for monkey GE, there is no difference in curvature between correct saccades made in search and saccades to single stimuli ( $P = 0.81$ ).

We speculate that the greater curvature, particularly seen for incorrect initial saccades, may be due to competition between two populations of neurons simulta-

neously encoding two different saccade goals on a motor map. In this scheme, the neurons coding a movement to the correct target position would be activated by mechanisms processing the color-odddity information, while the neurons coding a movement to a distractor would be activated by the color priming mechanism. Even though the distractor eventually 'wins' and becomes the saccade target, the increased level of activity at the correct target location, due to concurrent processing of the second goal, may bias the initial direction of the saccade such that its trajectory curves toward the target location.

In order to test this prediction, we examined the curvature of the initial saccade of two-saccade responses to determine whether the trajectory deviates in the direction of the subsequent saccade. We excluded trials in which the target of the second saccade was in the opposite direction from the target of the initial saccade because we cannot make a prediction about the direction of saccade curvature for these trials. Fig. 8 shows spatial plots of the raw eye records for the 25% of initial saccades with the greatest curvature for one monkey. For clarity, the left panel shows only trials with stimuli in the four cardinal positions, while the right panel shows only the four oblique positions. The saccades plotted in red are followed by a second saccade to the stimulus which is in the counter-clockwise direction relative to the initial saccade goal. In contrast, saccades plotted in green are followed by a second

saccade to the stimulus which is in the clockwise direction. The trajectories of single saccades to the same locations are plotted with thick gray lines. The plots show a clear trend for curvature in the direction of the goal of the second saccade. In some cases, this curvature accompanies an averaging saccade, which lands between two stimuli, while in other cases, the initial saccade endpoint falls near one stimulus.

In Fig. 9, we examine the mean curvature of all initial saccades which were followed by a second saccade to an adjacent stimulus. In order to compare responses with similar endpoints, we eliminated all averaging saccades, which were defined as saccades landing more than  $3^\circ$  from the nearest target. We divided the initial saccades into two groups, according to whether the second saccade was directed to the stimulus clockwise or counter-clockwise from the goal of the initial saccade. Positive curvature values are defined as curvature in the counter-clockwise direction, while negative values are in the clockwise direction (Smit & Van Gisbergen, 1990). Since subjects may show some idiosyncratic curvature differences for saccades to different parts of the visual field (Thomas & O'Beirne, 1967; Viviani, Berthoz, & Tracey, 1977), for each saccade

goal we subtracted the mean curvature of saccades made to single stimuli from the curvature of the initial saccades made to the same stimulus location in search. This eliminated constant, systematic differences in curvature for the different target locations, allowing us to examine those differences which depend on the goal of the second saccade. As is evident from the figure, overall, the initial saccades showed curvature toward the goal of the second saccades, and a *t*-test verified that the curvature for the two groups was significantly different ( $P < 0.001$  for each monkey).

## 4. Discussion

### 4.1. Priming of saccades in monkeys

First we have demonstrated that the monkey shows effects of color priming on saccade latency similar to those seen in humans. Specifically, when the color of the odd target happens to repeat from trial to trial, the latency of saccades is shorter than when it changes from trial to trial. Furthermore, fewer saccades are directed toward distractor stimuli when the color of the

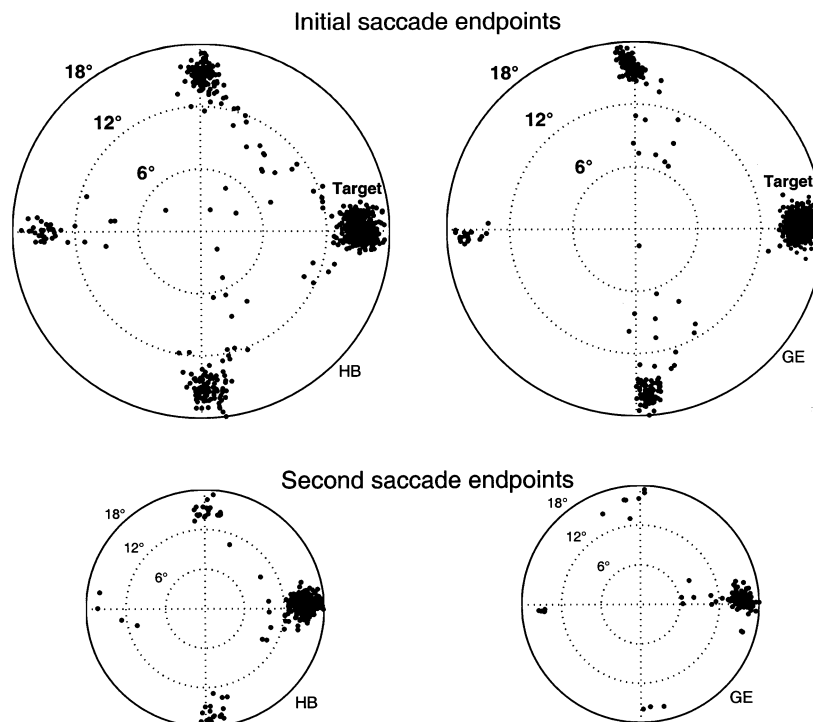


Fig. 5. The top two plots show the endpoints of all initial saccades made in search for the two monkeys. The data have been normalized by a simple rotation, such that the target is always located at a direction of  $0^\circ$  (3 o'clock position), while the distractors are always located at  $90^\circ$ ,  $180^\circ$ , and  $270^\circ$  (12, 9, and 6 o'clock positions, respectively). The stimuli were presented at an eccentricity of  $15^\circ$  from fixation. Correct saccades typically landed near the target, while some of the saccades directed toward the distractors are hypometric. The endpoints of incorrect saccades to the positions flanking the target ( $90^\circ$  and  $270^\circ$ ) also seem to have landed with a bias toward the location of the correct target. The fewest saccades were directed to the distractor located opposite the target ( $180^\circ$  position). The lower panels show the endpoints of the second saccades which followed an initial incorrect saccade. Most of these saccades were correctly directed to the target location, although the monkeys occasionally made an erroneous second saccade to a distractor.

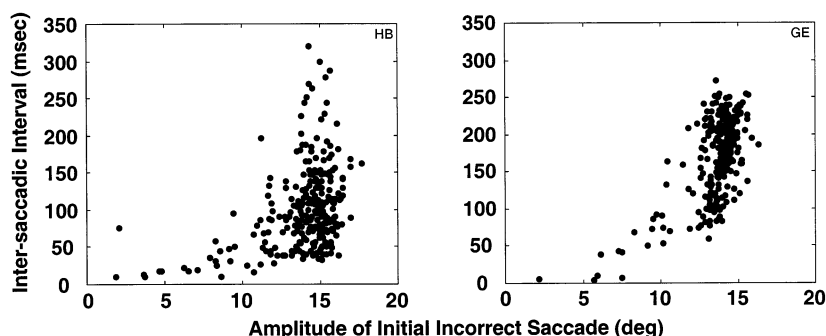


Fig. 6. Plot of the inter-saccadic interval between initial and second saccades as a function of the amplitude of the first saccade. The shortest inter-saccadic intervals often followed hypometric initial saccades, suggesting an interaction between the initial saccade and the impending second saccade.

target repeats. The task we used was almost identical to that used in experiments with humans. The magnitude of the priming, as measured by the cumulative reduction of saccade latencies was somewhat smaller on the average here than in humans, although the values fall within the observed range for individual human subjects (McPeck et al., 1999).

Bichot and Schall (1999) similarly observed that when the target and distractor colors do not change within a block, saccade latencies are longer in the first five trials of the block than in the subsequent trials. However, in their task, the target color in previous trials was a good predictor of its color in future trials. Our findings show that even when prior trials provide no information about the color of the target in future trials, monkeys, like humans, show color priming for saccades. This suggests that the priming is non-volitional. Bichot and Schall (1999) also observed a longer-term carry-over effect when monkeys were trained to search for a target consisting of the same particular conjunction of features for hundreds of trials. Under these conditions, it seems that the monkey learns to discriminate the target more quickly after extensive training, and even after the target is changed to some other conjunction of features, may continue to select stimuli having the previously-trained features. This effect can persist across days, and thus, is quite different from the short-term priming studied here, which is dynamic and adjusts quickly to changes in the relevant target feature. It has been postulated that an automatic short-term memory system such as this would be particularly advantageous for the rapid guidance of focal attention and eye movements during the performance of visuo-motor tasks in a structured environment (Maljkovic & Nakayama, 2000; McPeck et al., 1999).

Similar to the earlier report of Schiller et al. (1987), we also found that saccades made to single stimuli had consistently shorter latencies than saccades made in search. In one monkey, we collected additional data to determine whether this difference in latency arises from the adoption of different top-down strategies in the two

situations, or whether it results from the presence or absence of distractor stimuli. Specifically, we compared the latency of saccades made during blocks of single stimulus trials to saccades made when single stimulus trials were randomly interleaved in a series of search trials. We found virtually no difference in latency between the two conditions, indicating that for this monkey, the disparity in latency between saccades to single stimuli and saccades in search cannot be explained by a top-down change in strategy. Rather, the presence of distractors apparently affects saccade latency. This observation is similar to the 'remote distractor effect' examined in detail in human subjects (Walker, Kenridge & Findlay, 1995; Walker, Deubel, Schneider, & Findlay, 1997).

#### 4.2. Concurrent processing of saccades in monkeys

For both monkeys, we also observed initial incorrect saccades followed after a short inter-saccadic interval by a second saccade to the target. As previously argued for humans (Becker & Jürgens, 1979; Viviani & Swensson, 1982; Morrison, 1984; Theeuwes et al., 1998, 1999; Mokler & Fischer, 1999; McPeck et al., 2000), the brevity of these inter-saccadic intervals suggests that programming of the two saccades overlapped in time. In both search and double-step tasks, McPeck et al. found that the shortest inter-saccadic intervals were typically preceded by hypometric initial saccades. This observation was replicated for visual search in monkey in the present experiments, again showing a parallel between human and monkey performance.

We also made two new observations in the present experiments. First, we found that saccades in search tend to have greater curvature in their trajectories than saccades to single stimuli, particularly when the initial saccade is incorrect. Specifically, we found that the trajectory of an initial incorrect saccade to a distractor tends to curve toward the goal of the subsequent corrective saccade to the target. This finding supports the idea that two saccade goals can be processed concu-

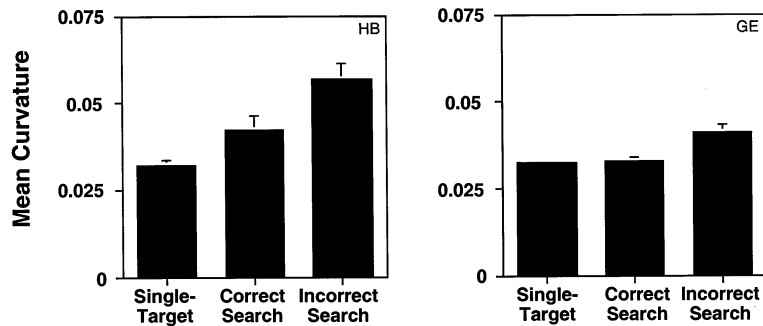


Fig. 7. Mean curvature of saccades to single stimuli, correct saccades to the target in search, and incorrect saccades to distractors in search. For both monkeys, incorrect saccades are significantly more curved than correct saccades in search. Furthermore, for Monkey HB, correct saccades in search are significantly more curved than saccades to single stimuli.

rently on a single motor map. Furthermore, it suggests that concurrent processing is not limited to brain areas involved in higher-level planning. Rather, it apparently includes areas at a low enough level in the saccadic system that saccade trajectory can be affected.

In the search task, we also observed re-directed saccades which are initially aimed toward a distractor, but which radically change direction without stopping. Similar highly curved and re-directed responses have been observed previously in humans in double-step (Van Gisbergen, Van Opstal, & Roebroek, 1987; Minken, Van Opstal, & Van Gisbergen, 1993) and visual-auditory distractor tasks (Corneil, Hing, Bautista, & Munoz, 1999).

We suggest that this collection of phenomena (hypometric initial saccades, curved saccades, and re-directed saccades) is a result of competitive interactions among groups of neurons concurrently coding the initial and second saccade goals on a common motor map, such as the ones present in the superior colliculus (SC) and in the frontal eye fields (FEF). Although it is unlikely that the SC performs the actual color discrimination involved in the search task (Ottens, Van Gisbergen, & Eggermont, 1987), it receives widespread input from cortical areas and clearly plays a key role in the development of oculomotor commands (Sparks & Hartwich-Young, 1989). Recent studies have suggested that activity in oculomotor areas such as the SC and FEF reflects the focusing of visual attention (e.g. Kustov & Robinson, 1996; Kodaka, Mikami, & Kubota, 1997) as well as the moment-by-moment development of the decision of where to move the eyes next (e.g. Gold & Shadlen, 2000; Horwitz & Newsome, 1999; Schall & Thompson, 1999). In particular, Kustov and Robinson (1996) and Gold and Shadlen (2000) showed that saccade endpoint can be deviated by shifts of attention or by a developing oculomotor decision.

Along these lines, we suggest that in our task, concurrent processing of a second saccade goal may result in changes in the metrics of the initial saccade. Specifically, the relationship between the initial saccade ampli-

tude and the duration of the pause between saccades suggests that the concurrently-processed second saccade may modify or pre-empt the initial saccade. Preliminary neurophysiological evidence indicates that when two saccades in a search task are separated by a short inter-saccadic interval, processing of the second saccade is represented in the SC by low-level activity, which is maintained simultaneously with the activity related to the initial saccade (McPeck & Keller, 1999). If we assume that neurons at distant locations in the SC are mutually inhibitory (as has been demonstrated physiologically (Munoz & Istvan, 1998; Meredith & Ramoa, 1998)), the presence of activity related to the second saccade would be expected to have an inhibitory influence on the activity related to the initial saccade. Although this second saccade activity is sub-threshold for directly influencing the goal of the saccade, we hypothesize that it could, nonetheless, weaken the activity of

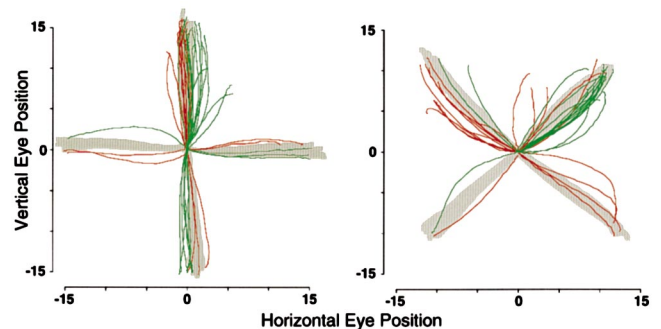


Fig. 8. Spatial plots of eye position during the 25% of incorrect initial saccades with the largest measured curvature for monkey HB. For clarity, trials in which the stimuli were presented in the four cardinal directions are plotted in the left panel and in the four oblique directions in the right panel. In green are plotted trials in which the subsequent saccade was directed to the stimulus in the clockwise direction from the goal of the initial saccade. In red are plotted trials in which the subsequent saccade was directed to the stimulus in the counter-clockwise direction from the goal of the initial saccade. For comparison, saccades to single stimuli are plotted with thickened gray lines. As is evident, the trajectory of the initial saccade tends to curve toward the goal of the subsequent saccade.

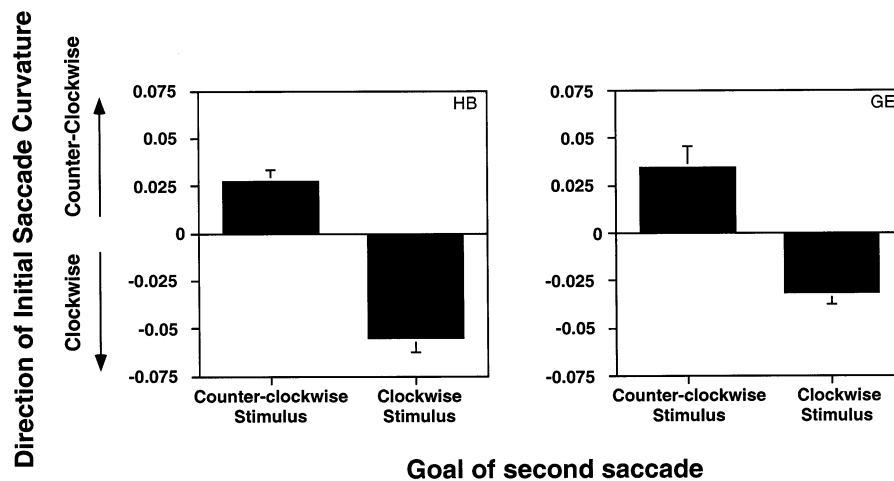


Fig. 9. Plots of the mean curvature of initial saccades as a function of the goal of the subsequent saccade. For both monkeys, the trajectory of the initial saccades was significantly curved toward the goal of the subsequent saccade. Specifically, when the second saccade goal was in the counter-clockwise direction relative to the initial saccade goal, the trajectory of the initial saccade was curved in the counter-clockwise direction, and vice-versa when the second saccade goal was in the clockwise direction.

neurons coding the first saccade to the extent that this first-saccade activity ceases before execution of the saccade has been completed. In experiments in which the SC is stimulated electrically, it has been shown that a premature cessation of stimulation can result in a hypometric saccade (Paré, Crommelinck, & Guitton, 1994; Stanford, Freedman, & Sparks, 1996). Correspondingly, in our task, a hypometric saccade could be produced if competition from neurons processing the second saccade leads to a premature cessation of activity related to the first saccade. This explanation is consistent with the finding that when the inter-saccadic interval is shorter, presumably indicating stronger activity related to the impending second saccade, the initial saccade tends to be more hypometric.

This scheme is depicted in the top panels of Fig. 10. The left-most panel shows the activity on a hypothetical motor map at saccade onset. Neurons coding each of the four search stimuli are represented by circles on the map, and the activity level of each group of neurons is indicated by its shading. Initially, the goal in the upper part of the map is supra-threshold, and results in the triggering of a saccade to the upper stimulus. A second goal is also active, but is sub-threshold. However, the maintained activity at this second location, due to concurrent processing of a second saccade goal, has an inhibitory influence on the neurons coding the upper goal. Thus, during the saccade (middle panel), this inhibition reduces the activity of the neurons coding the initial saccade to a sub-threshold level. This premature cessation of activity results in a hypometric initial saccade (pictured in the right panel).

On the other hand, curved saccades would result when the second saccade activity becomes sufficiently intense, shortly before the onset of the first saccade,

that it makes its own contribution to the calculation of the saccade goal, rather than simply weakening the activity related to the first saccade. This is schematized in the middle panels of Fig. 10. Similar to what has been observed when two different locations in the SC or FEF are electrically stimulated simultaneously (Robinson, 1972; Schiller, True, & Conway, 1979), this concurrent supra-threshold activity at two loci would result in a saccade initially directed in an averaging direction between the two specified goals (left panel). If top-down influences favored one of the saccade goals, it would eventually 'win' the competition and suppress the second locus of activity. This would allow the saccade trajectory to curve around and land near the favored goal (middle panel). On the other hand, if the competition between neurons coding the two goals were not quickly resolved, the result would be an averaging saccade which would terminate between two stimuli (not pictured). We observed such averaging saccades in this experiment, and similar averaging saccades have been reported in humans (e.g. Ottes et al., 1984 Findlay, 1982, 1997).

Finally, if the second saccade activity were initially sub-threshold, but subsequent top-down influences strengthened it during the initial saccade, it could eventually suppress the activity related to the first saccade goal and the result would be a 're-directed' saccade, which we have also occasionally observed. This scenario is pictured in the bottom panels of Fig. 10. Such saccades seem to show a change in goal without any inter-saccadic pause. Saccades resembling these have been elicited artificially in the 'colliding saccade' paradigm (e.g. Schlag-Rey, Schlag, & Shook, 1989; Schlag, Schlag-Rey, & Dassonville, 1989), in which a site in the FEF or SC is electrically microstimulated

during an ongoing saccade. The presumption is that the electrical stimulation specifies a new saccade goal and suppresses the initial goal through inhibitory interconnections. This is essentially the explanation that we are also proposing, with the difference that in our formulation, the activity related to the second goal is due to top-down input from cortex, rather than direct electrical stimulation. Indeed, Van Gisbergen et al. (1987), Minken et al. (1993) and Corneil et al. (1999) have all reported evidence that the oculomotor system is capable of changing its goal in mid-flight.

Interestingly, it has recently been reported that focal attention can affect saccade curvature. When subjects

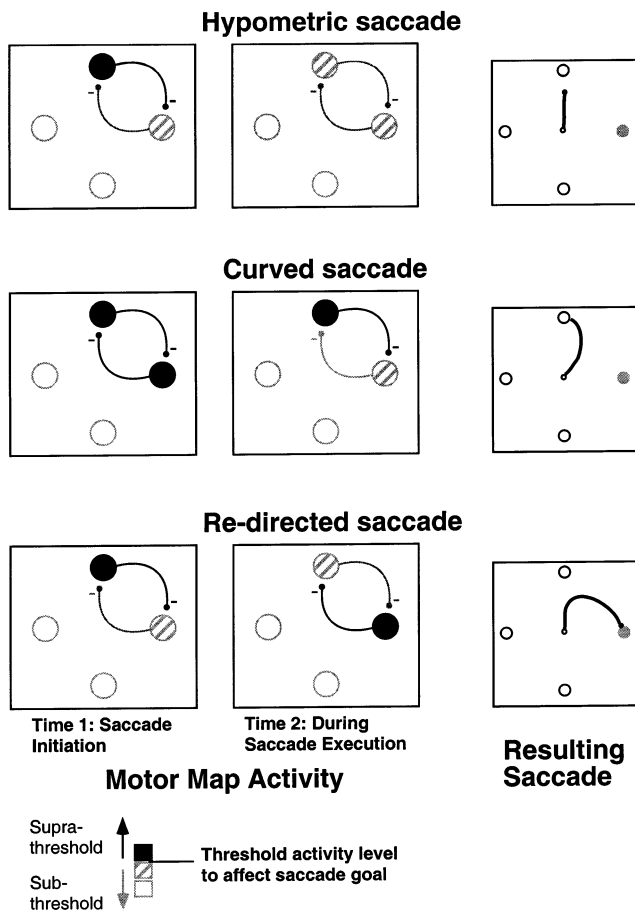


Fig. 10. Schematic of the temporal sequence of events hypothesized to occur between groups of neurons coding movements to the search stimuli. The left-most and middle panels depict a hypothetical motor map (at saccade onset and during saccade execution, respectively), upon which groups of neurons specifying the four search stimuli are shown as circles. The level of activity for each group is represented by its shading. Active groups of neurons coding different goals are mutually inhibitory, although top-down influences on the motor map (not shown) may also modulate the level of activity of the neurons coding the different goals. The right-most panels show schematic eye movements which are hypothesized to result from motor map activity. The upper panels illustrate the proposed activity for a hypometric saccade, the middle panels illustrate the activity posited to underlie a curved saccade, and the lower panels show the activity hypothesized for a re-directed saccade.

direct attention to one particular area of space and then are required to make a saccade to a target at a different location, the trajectory of the resulting saccade tends to curve away from the previously attended region of space (Sheliga, Riggio, & Rizzolatti, 1994, 1995; Sheliga, Riggio, Craighero, & Rizzolatti, 1995). One explanation of this result offered by Sheliga et al. posits that when subjects focus attention on an eccentric location, they must actively suppress the generation of a saccade to the attended location. Subsequently, when a saccade is made to a different location, suppression of the previously-attended location lingers, and results in a short-lived, localized depression of activity on the saccadic motor map. As a consequence of this imbalance of activity, the saccade is curved away from the suppressed location. Thus, this phenomenon and its explanation may be viewed as the inverse of the case presented here. In the Sheliga et al. experiments, saccade trajectory is deviated by a local decrease in activity which is related to the inhibition of a saccade. In our experiment, we argue that concurrent processing of a second saccade goal leads to a local increase in activity which causes the saccade trajectory to curve toward the second saccade goal.

We found that second saccades to the target following short inter-saccadic intervals were generally spatially accurate (see Fig. 5). This accuracy is significant for two reasons. First, if our hypothesis about concurrent processing of saccades is correct, the activity related to the second saccade must be re-mapped into new coordinates immediately after the end of the first saccade to account for the change in eye position that occurs as a result of the first movement (e.g. Mays & Sparks, 1980; Sparks & Porter, 1983; Goldberg & Bruce, 1990; Walker et al., 1995). Second, the oculomotor integrator that presumably provides the required change in eye position information must either be reset much more quickly than the approximately 45 ms time course suggested in previous studies (Nichols & Sparks, 1995; Kustov & Robinson, 1995), or it must be the case that the saccadic system does not use a resettable integrator in its local feedback loop. Similar observations have been made for closely-spaced, yet spatially accurate, saccades produced in double-step experiments (Goossens & van Opstal, 1997), in a distractor task (Corneil et al., 1999), or when saccades are momentarily interrupted by electrical microstimulation of the omnipause region of the brainstem (Keller, Gandhi, & Shieh, 1996).

Baizer and Bender (1989), using a double-step task, failed to find evidence for concurrent processing of saccades in the monkey. However, the study also failed to find evidence for concurrent processing in one of their two human subjects, while finding some degree of parallel programming in the other. One difference from

other studies which have successfully used double-step tasks to find evidence of concurrent processing (Becker & Jürgens, 1979; McPeck et al., 2000) is that the Baizer and Bender study included catch trials randomly intermixed with the single- and double-step trials. The inclusion of catch trials in a sequence of trials has been shown to affect saccade latency (Jüttner & Wolf, 1992), and thus, it is possible that their presence led subjects to adopt a strategy which discouraged concurrent processing. Becker and Jürgens (1979) have also hypothesized that concurrent processing is primarily seen when the distance between the endpoint of the initial saccade and the target of the second saccade is large. In the Baizer and Bender study, the stimuli were positioned such that this distance was typically smaller than in the other studies, suggesting that this may also have contributed to the difference in results.

#### 4.3. Differences between the monkeys

Monkey HB, which had lower overall saccade latencies, tended to correct initial error saccades quickly, with a large number of short inter-saccadic intervals (< 100 ms), similar to the human subjects tested in this task (McPeck et al., 1999). Monkey GE had higher overall saccade latencies and showed fewer short inter-saccadic intervals. One potential cause for this difference is the training regimen used. The monkeys were only rewarded when their initial saccade was to the correct target. Thus, after an initial error, there was no incentive for them to continue to search for the target and to execute a second saccade. Our informal observations of the monkeys during their training suggested that, indeed, as the training progressed, the frequency of second saccades declined. It is therefore notable that the data from monkey GE was collected after a somewhat longer training period than that collected from monkey HB. This may account, at least in part, for the smaller proportion of rapidly-executed second saccades in monkey GE.

## 5. Conclusion

The visual scene typically contains many different areas of interest, and the saccadic system must select from among these potential targets in order to direct the eyes effectively. In this study, we found evidence in the monkey for two mechanisms which have previously been hypothesized to assist the saccadic system in efficiently scanning search scenes in human subjects. First, we examined the 'priming of pop-out,' which facilitates attention shifts (Maljkovic & Nakayama, 1994) and eye movements (McPeck et al., 1999) toward targets sharing features with previously-presented targets in humans. We found that monkeys show similar priming

effects for saccade latency and for the incidence of errant saccades to distractor stimuli. Second, we examined evidence for the concurrent processing of two saccades directed to different goals. We found that monkeys, like humans, are capable of executing two saccades to different targets in very rapid succession. For such two-saccade responses, we also found that in monkeys, as in humans, the initial saccade tends to be hypometric when the fixation between the initial saccade and the second saccade is brief, suggesting an inhibitory interaction between the groups of neurons processing the two movements. Finally, we found new evidence to support the idea that two saccades can be processed concurrently. Specifically, we found that for two-saccade responses, the trajectory of the initial saccade tends to curve toward the goal of the subsequent saccade. This suggests that activity related to the two sequential saccades is simultaneously present on a single common motor map. Furthermore, it indicates that concurrent programming of two saccades is not limited to higher-level areas involved in saccade planning. Rather, it apparently occurs at a low enough level in the system that it is capable of affecting saccade trajectory. These findings demonstrate close similarities in oculomotor performance between monkeys and humans performing visual search, and provide evidence that will help to link neurophysiological findings on saccades during visual search in the monkey (e.g. Schall & Bichot, 1998; Schall & Thompson, 1999; McPeck & Keller, 1999; Hasegawa, Matsumoto, & Mikami, 2000; McPeck & Keller, 2000) with human oculomotor performance.

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