The Spatial Relationship Between Scanning Saccades and Express Saccades

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When monkeys interrupt their saccadic scanning of a visual scene to look at a suddenly appearing target, saccades to the target are made after an "express" latency or after a longer "regular" latency. The purpose of this study was to analyze the spatial patterns of scanning, express, and regular saccades. Scanning patterns were spatially biased. Express saccade patterns were biased, too, and were directly correlated with scanning patterns. Regular saccade patterns were more uniform and were not directly correlated with scanning patterns. Express saccades, but not regular saccades, seemed to be facilitated by preparation to scan. This study contributes to a general understanding of how monkeys examine scenes containing both unchanging and suddenly appearing stimuli. © 1997 Elsevier Science Ltd

Express saccades   Scanning saccades   Visual scenes   Saccadic latency   Superior colliculus
Macaca mulatta

INTRODUCTION

Natural visual scenes encountered by primates contain both unchanging and changing stimuli. Primates foveate unchanging visual stimuli with "scanning" saccadic eye movements (Yarbus, 1967; Schiller et al., 1980; Burman & Segraves, 1994). Also, primates make saccades in response to changes in the visual scene. If a stimulus suddenly appears, monkeys make a saccade to it after a varying latent period. The distribution of latencies can be bimodal, with an early mode of "express" saccades and a later mode of "regular" saccades (Fischer & Boch, 1983). Investigators typically use only unchanging stimuli (to study scanning saccades) or only suddenly appearing stimuli (to study express or regular saccades). Little is known about the saccadic behavior of monkeys when they examine scenes containing both unchanging and suddenly appearing elements.

In a previous study (Sommer, 1994), monkeys made saccades to both unchanging and suddenly appearing stimuli in a single task, the "Visual Scan" task. Monkeys scanned an array of spots on a computer monitor. Randomly, during a fixation of the scan, a target appeared at one of four isoeccentric locations. The monkey was rewarded for making a saccade directly to the target. The purpose of the study was to examine the *temporal* attributes of the saccades. Inter-saccadic intervals of

scanning formed a single, broad distribution, but the latencies of saccades made to the targets exhibited distinct express and regular saccade modes.

The purpose of the present study was to examine the *spatial* attributes of saccades made in the Visual Scan task. The task was modified so that a target appeared randomly at one of 16 locations distributed over the testing space. The patterns of scanning, express, and regular saccades were analyzed. The amount of spatial bias in each pattern was quantified, and scanning patterns were compared with the patterns of express or regular saccades.

It was of particular interest to determine if there was a relationship between scanning patterns and express saccade patterns. It has been hypothesized that express saccade generation is facilitated by the planning of metrics before target onset (Kalesnykas & Hallett, 1987; Smit & van Gisbergen, 1989; Kowler, 1990; Albano, 1993; West & Harris, 1993; Paré & Munoz, 1996). In the present study, targets for express saccades appeared randomly during fixations of visual scan, a time when scanning saccades were being prepared. Therefore, the opportunity existed for the metrical planning of scanning saccades to facilitate express saccade generation. It was expected that if such a facilitation existed, it might reveal itself through spatial correlations between express saccade patterns and scanning saccade patterns.

METHODS

Monkeys

Two monkeys (*Macaca mulatta*), designated as "C"

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Address all correspondence to: Laboratory of Sensorimotor Research, N.E.I., National Institutes of Health, Building 49, Room 2A50, 9000 Rockville Pike, Bethesda, MD 20892-4435, U.S.A [Tel (301) 496-1141; Fax (301) 402-0511; Email mas@lsr.nei.nih.gov].

A
Visual Scan
Target Trial

B
Visual Scan
Catch Trial

C
Steady Gaze
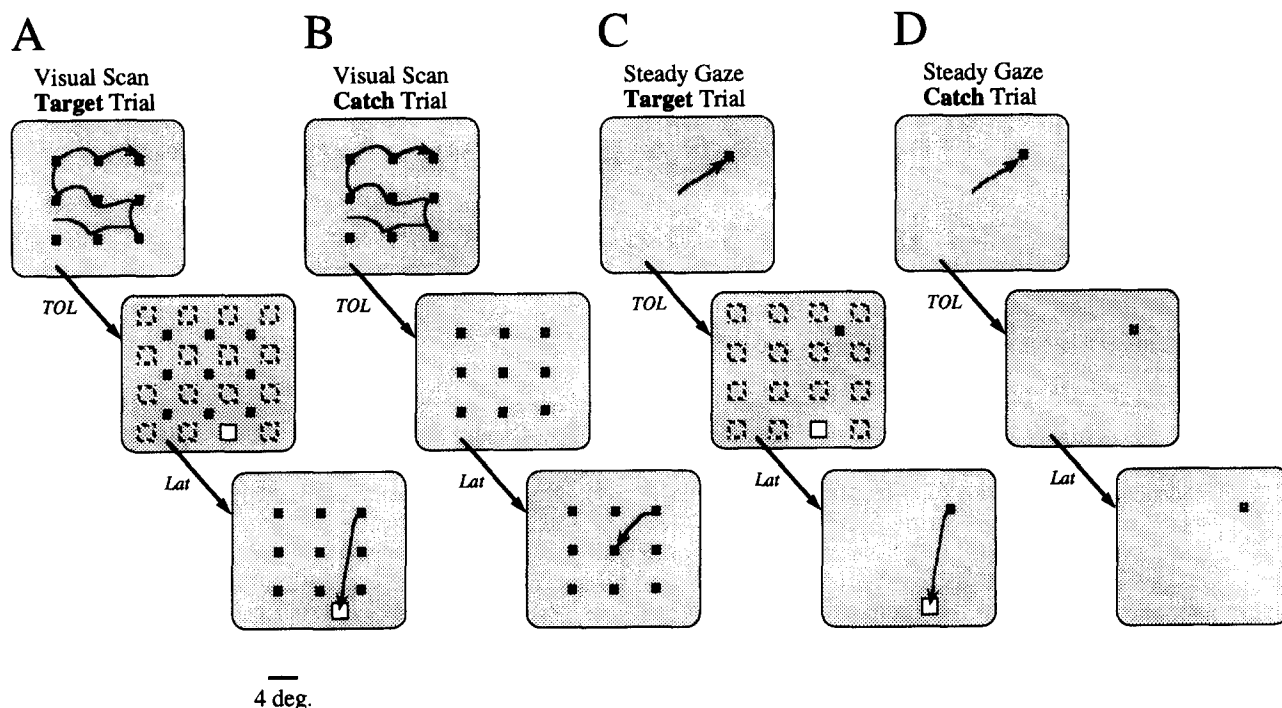### Target Trial

D
Steady Gaze
Catch Trial

4 deg.

FIGURE 1. Spatial diagram of tasks. Arrangement of stimuli, relative timing of events, and typical eye movements are depicted. The 16 possible target locations are shown as small squares with dashed outlines. Eye movements are represented by curved lines, with arrowheads indicating direction. Stimulus sizes are not to scale, but their relative arrangements are to scale. Depicted are the four types of randomly interleaved trial: (A) Visual Scan target trial; (B) Visual Scan catch trial; (C) Steady Gaze target trial; and (D) Steady Gaze catch trial. TOL, target onset lag. Lat, saccadic latency.

and "D", were used. Both monkeys had been subjects of a previous study (Sommer, 1994). Each monkey was implanted with a subconjunctival eye coil and a head post under sterile conditions and sodium pentobarbital anesthesia (Robinson, 1963; Fuchs & Robinson, 1966). After surgery, the monkeys received antibiotics and pain-killers for several days. During testing, the monkeys did not receive water in their home cage. They received apple juice as reward during the experimental sessions, and after each session they drank water to satiation. Their care followed the guidelines of the NIH and the MIT Committee on Animal Care.

Stimulus presentation and data collection

Graphics were run on a 60 Hz interlaced monitor controlled by a PDP-11 computer. A monkey sat in dim light, 65 cm from the monitor. Each unchanging "fixation spot" was a 0.3×0.3 deg black square. A suddenly appearing "target" was a 0.6×0.6 deg white square (71 cd/m^2). The background was gray (9 cd/m^2). Eye position was sampled at 200 Hz and stored, along with the timing of task events, in a data file for off-line analysis. The computer determined on-line where the monkey was looking by checking whether the eye position was within a square window surrounding a stimulus. The target window was 2.8×2.8 deg and each fixation window was either 2.8×2.8 deg (monkey D) or 2.0×2.0 deg (monkey C) (see Sommer, 1994, for details).

Experimental sessions

Overview. Four trial types were randomly interleaved: Visual Scan target or catch trials, and Steady Gaze target or catch trials. Visual Scan trials and Steady Gaze trials occurred with equal probability. The catch trial rate was 25%. The inter-trial interval was 1500 msec. Hundreds of trials were collected in a testing session, which lasted 1–3 hr. Sessions were run a few times a week for several weeks.

Visual Scan target trials. These were the main testing trials, used to study saccades made when a scene contained both unchanging and suddenly appearing stimuli. A 3×3 array of fixation spots, 5.7 deg apart in the cardinal directions, appeared to start a trial [Fig. 1(A)]. The array was centered on the monitor. A monkey scanned the fixation spots [Fig. 1(A), top]. All the fixation spots looked alike, but one was randomly selected before each trial to be the "trigger" for target onset. Once a monkey foveated the trigger spot, and after a randomized target onset lag, a target appeared for 150 msec [Fig. 1(A), middle]. A monkey was rewarded for making a single saccade that landed in the target window [Fig. 1(A), bottom]. Target onset lags were 57, 101, or 151 msec for monkey D and 36, 81, or 131 msec for monkey C (different for each monkey because they had different mean durations of inter-saccadic intervals: ~ 200 msec for monkey D, ~ 150 msec for monkey C; Sommer, 1994). Target location varied randomly over 16 possible places (4×4 array, locations 5.7 deg apart,

centered on the monitor). If a monkey did not reach the trigger spot within 10 sec, or if a monkey reached the trigger spot but then made a saccade before target onset, the trial was aborted.

Steady Gaze target trials. These were controls, used to study saccades made to suddenly appearing targets when the fixation spot array was absent. Steady Gaze trials were exactly like Visual Scan trials, except that only one fixation spot, the trigger spot, appeared. Thus, a monkey made a saccade directly to it [Fig. 1(C), top]. After the target onset lag, the target was presented [Fig. 1(C), middle] and a monkey had to make a single saccade that landed in its window [Fig. 1(C), bottom].

Catch trials. These were additional controls, used to study saccades made when a target did not appear. Catch trials were exactly the same as target trials except that the target was gray, identical to the background, rendering it invisible. After the gray target was drawn, the monkey continued scanning, in Visual Scan trials [Fig. 1(B)], or fixating, in Steady Gaze trials [Fig. 1(D)].

Reward schedules. In target trials, monkeys were rewarded 100% of the time for correct responses and randomly 33% of the time for incorrect responses (errors were common because, in Visual Scan target trials, scanning saccades with latencies $< \sim 50$ msec cannot be suppressed, Sommer, 1994). In catch trials, all responses were randomly rewarded 33% of the time.

Training. The monkeys had been trained on Visual Scan and Steady Gaze target trials previously (see Sommer, 1994). The present study began a few months after the conclusion of the prior one. A day or two of training was provided to familiarize the monkeys with the new target locations and the insertion of catch trials, and then the formal data collection began.

Analysis

Eye movement analysis. Eye positions during the first 640 msec after target onset were studied off-line. The first eye movement made during this period was analyzed. If the first eye movement was a saccade, it was fully analyzed, otherwise the trial was discarded. Eye movements were judged to be saccades if they exceeded 0.25 deg and 50 deg/sec at peak velocity. A saccade's start and end times were found with a 30 deg/sec threshold. Saccadic latency was defined as the time from target onset until the start of a saccade. A saccade's beginning position and its final position (its "endpoint") were calculated as an average of six sample positions before or after the movement. The saccade's "proximity to target" was defined as the vectorial distance from its endpoint to the center of the target.

Collection of scanning saccades. The scanning saccades used for analysis were the ones made after the gray target was drawn in Visual Scan catch trials [Fig. 1(B), bottom]. Hence, one scanning saccade was collected during every Visual Scan catch trial. This was the best way to collect scanning saccades for comparison with saccades made to the white targets, because all the preceding events leading to the generation of the two

types of saccade, e.g. the average number of previous saccades made during a scan, were similar.

Spatial classifications of saccades. If a saccade landed closer to the target location than to any of the nine fixation locations or the edge of the visible display, the saccade was classified as "target-directed". Otherwise, it was classified as "non-target-directed."

For the purpose of pattern analysis, every saccade had to be associated with the stimulus that presumably evoked it. In target trials, because only a single target appeared, this was straightforward. In catch trials, eight non-trigger fixation spots were available to evoke each scanning saccade. A scanning saccade was judged to have been evoked by a particular fixation spot if it landed closer to that spot than to the others. The rare scanning saccades that went off the visible display were omitted from quantitative analysis.

Spatial biases of patterns. The amount of spatial bias in each saccadic pattern was derived from a standard measure of randomness, entropy. From a particular trigger spot, a monkey made either a scanning saccade to one of the 8 non-trigger fixation spot locations or a target-directed saccade to one of the 16 possible target locations. The number N_i of scanning or target-directed saccades made to location i was counted. The probability of making a saccade to a stimulus location was

$$P_i = N_i \left/ \sum_{j=1}^{S} N_j \right.,$$

with $S = 8$ for scanning saccades or 16 for target-directed saccades. The entropy was

$$\sum_{i=1}^{S} P_i \log_2(1/P_i),$$

and the number of stimulus locations targeted by saccades was $2^{entropy}$, ranging from 1 to S. Higher values of $2^{entropy}$ signified more random patterns. The non-randomness of the patterns was directly quantified as *spatial bias* $= S - 2^{entropy}$, which measured the number of the S stimulus locations avoided by saccades. Spatial bias ranged from 0 (saccades made uniformly, no bias) to $S-1$ (saccades avoided all stimuli except one, highest possible bias).

Comparisons between patterns. Scanning saccade patterns were compared with target-directed saccade patterns using Spearman rank correlation and the Chi-square test. Target locations were labelled 1–16 and fixation spots were labelled "a"–"i" [Fig. 2(A)]. In Fig. 2(B), the method of measuring saccadic endpoint distributions is shown for the case in which the trigger spot (T) was at fixation spot "c". Eight regions of space were defined, each of which included one non-trigger fixation spot and the four target locations 4 deg away from it. For example, region 1 [Fig. 2(B)] included fixation spot "a" and target locations 1, 2, 5, and 6. Other regions are depicted in Fig. 2(C). Numbers of scanning saccades, NS_r, and target-directed saccades, NT_r, landing
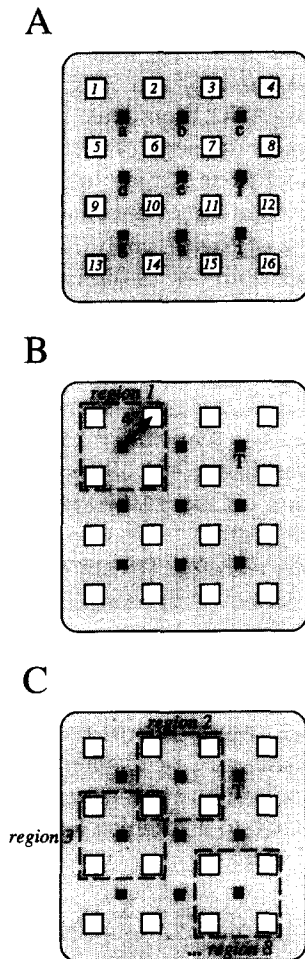
A

B

C

FIGURE 2. Method for quantifying the distributions of saccadic endpoints. Scale shown in (B). (A) The 16 target locations, labeled 1 to 16, are shown as white squares. The nine fixation spot locations, labeled "a" to "i", are shown as smaller black squares. Stimulus sizes are not to scale, but their relative arrangements are to scale. (B) Region 1, comprising fixation spot "a" and the four targets surrounding it (targets 1, 2, 5, and 6), is illustrated. The trigger spot (T) is at location "c". (C) Regions 2, 3, and 8 are depicted.

within a region r were counted. The probability that a scanning saccade landed in r was

$$PS_r = NS_r \Big/ \sum_{u=1}^{8} NS_u$$

The probability that a target-directed saccade landed in r was

$$PT_r = NT_r \Big/ \sum_{u=1}^{8} NT_u$$

The Spearman rank correlation test was used to determine if the probability of making a target-directed saccade into a region, PT_r, was correlated with the probability of making a scanning saccade into the same region, PS_r. The test was run on the pooled data from all 72 regions (9 trigger spots ×8 regions each).

The Chi-square test was used to compare the scanning patterns and target-directed saccade patterns made from

individual trigger spots. For a given trigger spot, the distribution of target-directed saccades made into each region, $(NT_1,...,NT_8)$, was compared with an expected distribution, $(X_1,...,X_8)$, based on the scanning pattern. The X_r were found according to the following hypothesis: when a target appears, the probability of making a target-directed saccade to it equals the probability of scanning to a fixation spot near the target (i.e. 4 deg from it). The latter probability could be calculated from the PS_r. When comparing $(NT_1,...,NT_8)$ and $(X_1,...,X_8)$, cases with $X_r < 5$ were omitted, because Chi-square is inaccurate for such comparisons. Hence, degrees of freedom were ≤ 7 for each test.

RESULTS

Timing and trajectories of saccades

For monkey D, 2109 Visual Scan target trials and 716 Visual Scan catch trials were fully analyzed. For monkey C, 4785 Visual Scan target trials and 1690 Visual Scan catch trials were fully analyzed. Characteristics of excluded trials (aborted or in which the first eye movement was not a saccade) were similar to those reported earlier (Sommer, 1994).

Typical results of Visual Scan trials are shown in Fig. 3. The top panel shows correct performance of a Visual Scan target trial [Fig. 3(A)]. Monkey D scanned, reached the trigger spot at the center (fixation spot "e"), and a target suddenly appeared at the far left (target location 9). The first saccade made after target onset went directly to the target. In a Visual Scan catch trial [Fig. 3(B)], the monkey scanned and reached the trigger spot, but no target appeared. The next saccade was a scanning saccade.

The latency of each saccade was compared with the place where it landed. For example, the saccade in Fig. 3(A) was initiated 85 msec after target onset and landed < 1 deg from the center of the target. In Fig. 4(A), this relationship is plotted for all of monkey D's Visual Scan target trials. Latency histograms derived from these data are shown directly below the scatter plot [Fig. 4(B)], and latency histograms from the other monkey's data are shown below that [Fig. 4(C)]. For comparison, latency histograms of saccades made in catch trials are shown in the bottom panels [Fig. 4(D, E)]. During the first 50 msec after target onset, monkeys primarily made non-target-directed saccades in both target trials [Fig. 4(A–C)] and catch trials [Fig. 4(D, E)]. These were scanning saccades. In target trials [Fig. 4(A–C)], after about 50 msec latency the monkeys made many target-directed saccades. The target-directed saccades formed two distinct latency peaks [Fig. 4(B, C)]: saccades with latencies <95 msec were considered to be express saccades, and those with latency ≥ 95 msec were considered to be regular saccades. Non-target-directed saccades, too, were made after 50 msec latency in target trials [Fig. 4(A–C)]. These seemed to be a mixture of hypometric [Fischer & Boch, 1983) and averaging express saccades (see Sommer, 1994). Because they landed at spatially ambiguous

A Visual Scan Target Trial

B Visual Scan Catch Trial
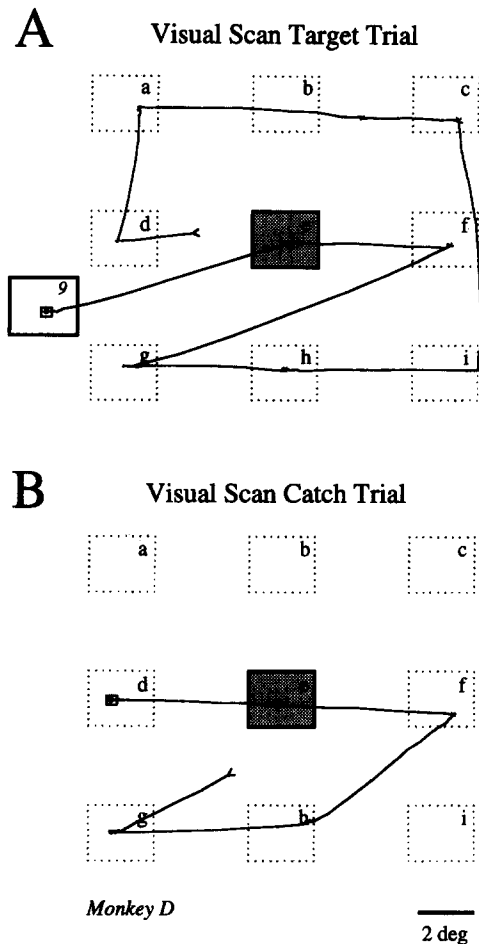

Monkey D

2 deg

FIGURE 3. Eye traces from two Visual Scan trials of monkey D. Dotted squares are the electronic windows around the fixation spots, each of which is labelled as in Fig. 2(A). The trigger spot, at fixation spot "e", is surrounded by a shaded, solid-outlined window. Eye movements are shown as the continuous solid line, created for clarity by connecting the sampled eye positions with straight line segments; an arrowhead shows the beginning and direction of the sequence of eye movements. A small cross marks the starting position of the first saccade made after target onset, and a small square marks this saccade's endpoint. (A) Typical Visual Scan target trial is shown. Large white square depicts window around the target, which appeared at location 9 [see Fig. 2(A)]. Target onset lag was 101 msec. (B) Typical Visual Scan catch trial is shown. No target appeared, so the monkey continued scanning.
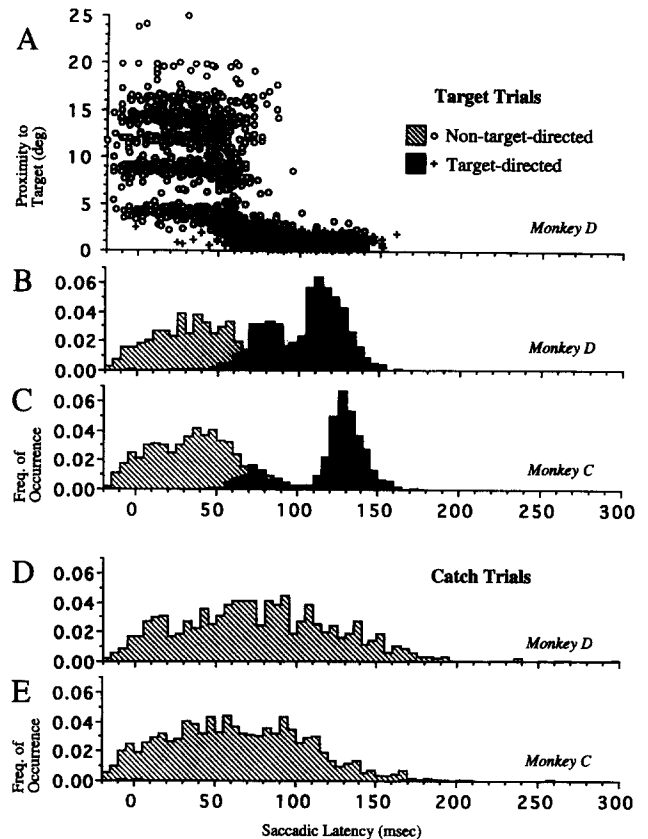

FIGURE 4. Proximity and latency distributions of saccades from Visual Scan trials. Ordinate of the latency histograms is normalized as "frequency of occurrence", the number of saccades in a bin divided by the total number of target presentations. (A) The relationship between a saccadic endpoint's proximity to the target and the saccade's latency is shown for all saccades evoked in target trials, for monkey D. (B) Saccadic latency histograms derived from the data in (A) are shown. There were 2135 white target presentations. (C) Saccadic latency histograms from target trials for monkey C are shown (5249 white target presentations). (D) Saccadic latency histograms from catch trials for monkey D are shown (724 gray target presentations). (E) Saccadic latency histograms from catch trials for monkey C are shown (1819 gray target presentations).

locations, they were omitted from further analysis. In catch trials [Fig. 4(D, E)], monkeys kept making scanning saccades until about 200 msec after target onset.

Example trajectories of saccades are shown for monkey C in Fig. 5. All saccades began at the trigger spot at the upper right (fixation spot "c"). Scanning saccades [Fig. 5(A)], made in catch trials, usually went to fixation spots. Express saccades [Fig. 5(B)] and regular saccades [Fig. 5(C)] made in target trials, landed near target locations (cf. Figure 2(A)]. Trajectories of express and regular saccades were nearly always straight, going directly to targets, except for rare saccades that seemed to start as a scanning saccade and then change trajectory in midflight (e.g., in Fig. 5(C)]. Only 0.4% of the express or regular saccades exhibited such trajectory changes. The total numbers of scanning, express, and regular saccades

made from each trigger spot location, for each monkey, are shown in Table 1.

Scanning saccade biases

From a particular trigger spot, monkeys tended to scan to some fixation spots but not to others. For example, the scanning saccades in Fig. 5(A) usually went to non-trigger fixation spots "a", "b", and "f". In that example, the spatial bias was 5.3, reflecting the fact that the monkey avoided scanning to approx. five of the available eight non-trigger fixation spots. Scanning patterns made from other trigger spot locations, for both monkeys, exhibited comparable biases [Fig. 6(A)]. The mean spatial bias of scanning was 3.2 (SD 1.5) for monkey D and 3.9 (SD 1.6) for monkey C.

The biased scanning patterns of each monkey were idiosyncratic. For example, from a trigger spot at the center, monkey C usually made scanning saccades up or down, but rarely leftward, whereas monkey D often made

A   Scanning Saccades

B   Express Saccades

C   Regular Saccades

Monkey C
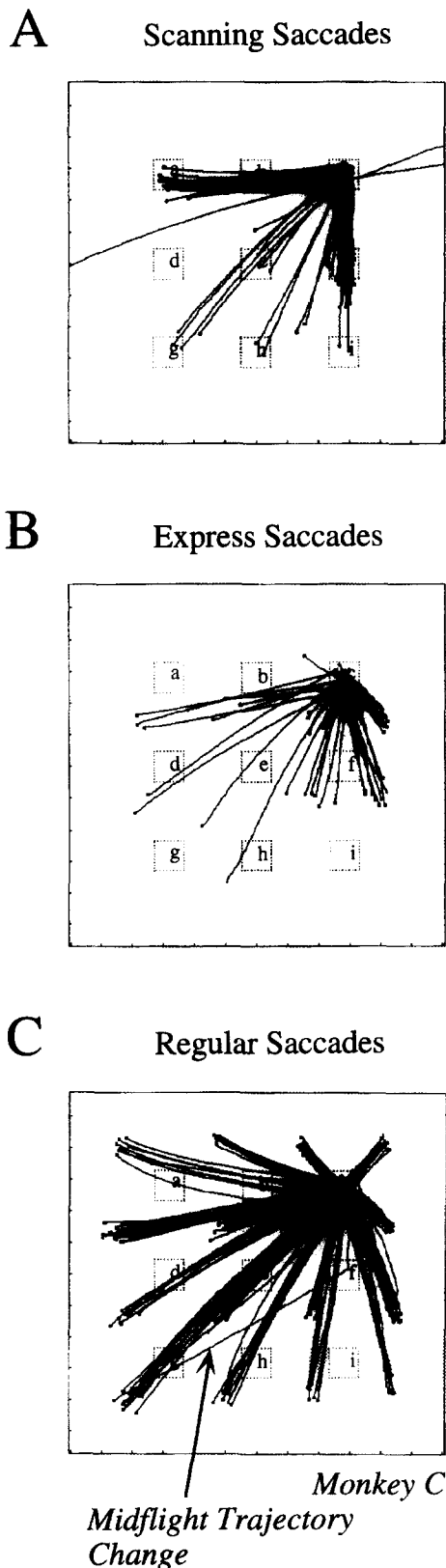*Midflight Trajectory*
Change

FIGURE 5. Examples of saccades made during Visual Scan trials by monkey C when the trigger spot was at the upper right (at fixation spot "c"). Saccades from many trials are superimposed. (A) Scanning saccades collected during Visual Scan catch trials are shown. (B) Express and (C) regular saccades collected during Visual Scan target trials are shown. Small dotted squares show windows around the fixation spots. Frame depicts the edge of the lit portion of the monitor. Tics on the frame are separated by 2 deg. As in Fig. 3, the saccadic trajectories were constructed by connecting the eye position samples by line segments, and the endpoint of each saccade is represented by a tiny square.

scanning saccades leftward, but rarely up or down (not shown). It was noticed during testing that a monkey's scanning patterns changed little from day to day. This is reflected by the fact that strong biases were detectable despite a period of data collection that lasted several weeks.

Express saccade biases

From a particular trigger spot, express saccades were made frequently to targets appearing at some locations but rarely to targets appearing elsewhere. For example, in Fig. 5(B), express saccades were made most often to targets appearing below the trigger spot. The spatial bias of express saccades in that example was 9.5, i.e., approx. nine target locations tended to not elicit express saccades. Regular saccades made from the same trigger spot [Fig. 5(C)] were more evenly distributed, with a spatial bias of only 1.7. The mean express and regular saccade biases for monkey D were, respectively, 5.8 (SD 1.9) and 2.5 (SD 0.8) [Fig. 6(B, C), left). For monkey C [Fig. 6(B, C), right), the mean express and regular saccade biases were, respectively, 8.8 (SD 2.3) and 2.3 (SD 0.9). Each monkey's express saccade biases were significantly greater than its regular saccade biases (Mann–Whitney rank sum test, $P < 0.001$).

Correlations between patterns

Not only were the patterns of scanning saccades and express saccades biased, but also their biases seemed correlated. For example, in Fig. 7 the endpoints from the saccades of Fig. 5 are plotted. Scanning saccades were biased strongly to fixation spot "f", just below the trigger spot, and express saccades were elicited most often by targets appearing near fixation spot "f" [Fig. 7(A)]. Elsewhere, fewer scanning saccades and fewer express saccades were made. The other monkey, too, exhibited correlations between its express saccade patterns and its scanning patterns [Fig. 8(A)]. In contrast, patterns of regular saccades did not seem to be correlated with scanning patterns [Fig. 7(B) and Fig. 8(B)].

Quantitative analysis confirmed these observations. Overall, the probability of making an express saccade into a region of space was significantly correlated with the probability of making a scanning saccade into the same region of space, for both monkeys [Fig. 9(A); Spearman rank test, $P < 0.001$). There was no correlation between the probabilities of making regular saccades and scanning saccades into regions of space, for either monkey [Fig. 9(B), $P > 0.05$).

Spatial similarities also were detected between the express saccade patterns and scanning patterns made from individual trigger spots (Table 2). For six of the nine trigger spot locations for each monkey, the Chi-square test found that the pattern of express saccades was not significantly different from the pattern predicted by scanning. In contrast, all regular saccade patterns were significantly different from patterns predicted by scanning.

TABLE 1. The numbers of scanning, express, and regular saccades made from each trigger spot, by each monkey, in the Visual Scan task

Trigger spot label	Monkey D			Monkey C		
	Scanning	Express	Regular	Scanning	Express	Regular
a	76	48	63	125	47	116
b	90	37	83	206	18	174
c	71	34	83	190	51	200
d	73	40	95	192	41	183
e	79	50	65	205	24	214
f	89	36	86	180	56	147
g	92	50	112	229	53	277
h	80	49	107	207	29	142
i	66	40	91	156	52	134
Totals	716	384	785	1690	371	1587

Steady Gaze task results

Recall that in the randomly interleaved Steady Gaze trials, the monkey was required to fixate a lone trigger spot until a target appeared. In target trials, saccades made to the target exhibited express and regular latency peaks [Fig. 10(A–C)]. Monkey C had a small peak of non-target-directed saccades, too [Fig. 10(C)]; these were

hypometric express saccades. In catch trials [Fig. 10(D, E)], monkeys tended to fixate until the trial ended, with saccades made only infrequently [and these typically were small and fixation-related, see Fig. 6(C) of Sommer, 1994].

The patterns of express saccades made in Steady Gaze trials were different from the patterns made from identical trigger spot locations in Visual Scan trials. As
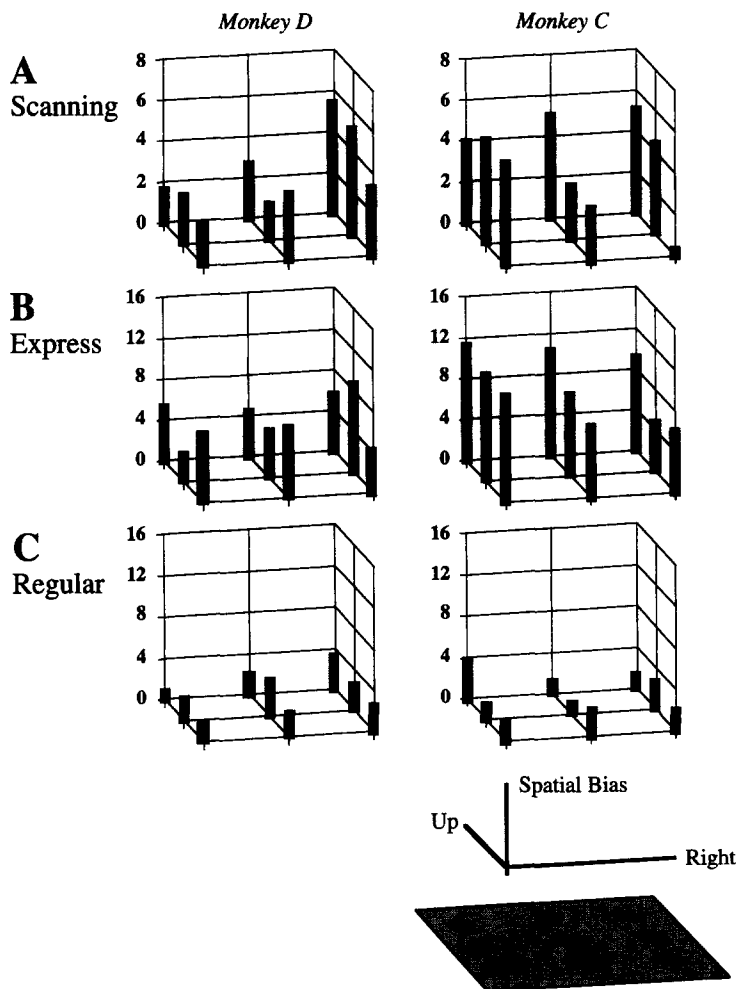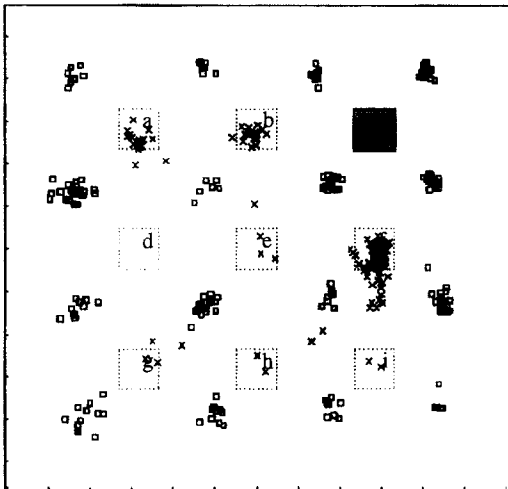

FIGURE 6. Amounts of bias in the saccadic endpoint patterns made from each trigger spot. Bottom right, the shaded space depicts the monitor and the array of nine trigger spot locations. Above that are the axes relating the array to the graphs. Monkey D data shown in left column, monkey C data in right column. The spatial biases of (A) scanning saccades; (B) express saccades; and (C) regular saccades are shown.

A Scanning (x) vs. Express (□) Endpoints

A Scanning (x) vs. Express (□) Endpoints

B Scanning (x) vs. Regular (□) Endpoints
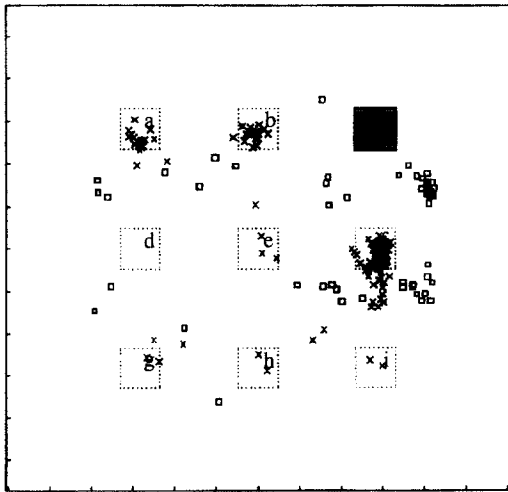
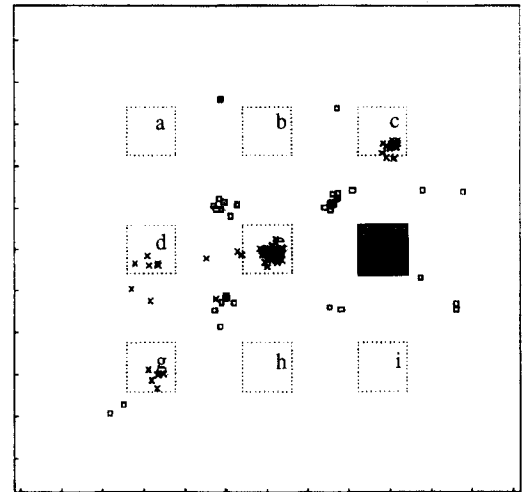*Monkey C*

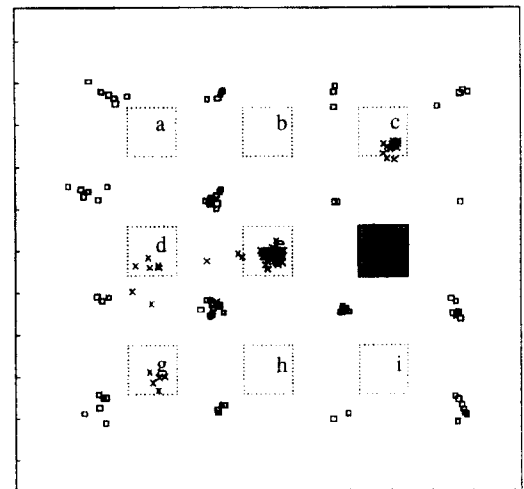**B** Scanning (x) vs. Regular (□) Endpoints

Monkey D

FIGURE 7. Comparison of scanning saccade endpoints with (A) express saccade; or (B) regular saccade endpoints. Same data as in Fig. 5. Trigger spot window is shaded with solid outline, at fixation spot "c".

FIGURE 8. Example of saccadic endpoint patterns from monkey D. In this case, trigger spot is at fixation spot "f". Comparison of scanning saccade endpoints with (A) express saccade; or (B) regular saccade endpoints.

an example, consider the case when monkey C initially fixated at the lower left (fixation spot "g"; Fig. 11). In Visual Scan trials, the monkey generally made scanning saccades up or to the right [Fig. 11(A)]. Similarly, the targets most likely to elicit express saccades were those appearing at the upper left or the lower right [Fig. 11(B)]. In the Steady Gaze task, the pattern of express saccades made from the same trigger spot was different [Fig. 11(C)]. Targets appearing at the upper left rarely evoked express saccades, but targets appearing near the center frequently did. This biasing of express saccades toward the center was the general tendency in Steady Gaze trials.

DISCUSSION

Scanning saccade biases

Scanning saccades often were made with strong spatial biases. This was not surprising, since stereotyped scanning has been reported previously. Yarbus (1967), in humans, and Burman & Segraves (1994), in monkeys, showed that scanning is biased by visual elements of interest. Yarbus (1967) also emphasized that asymmetry in scanning is a function of the subject's task. However, the monkeys in the present study scanned with biases even though this provided no obvious task advantage and even though the unchanging elements of the scene all were identical in appearance. The reasons for this biased
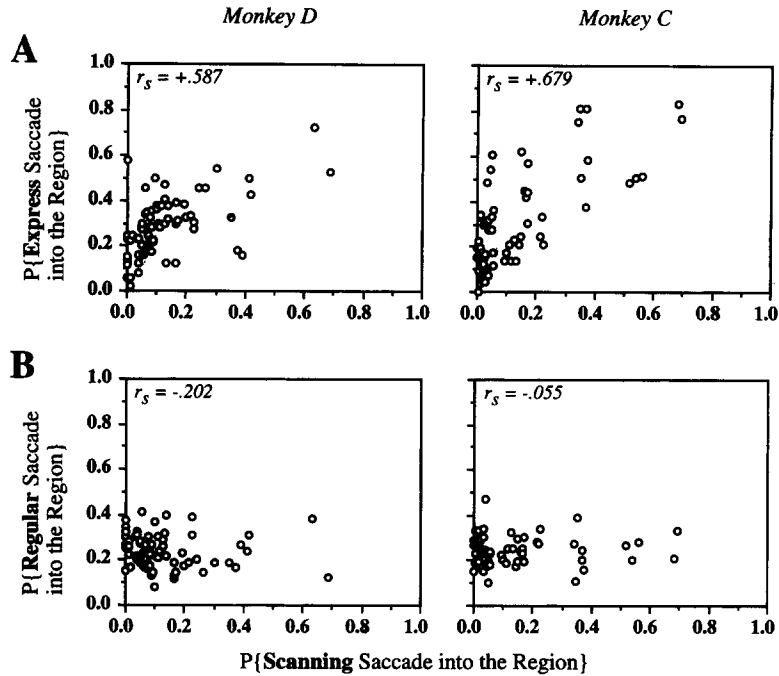
FIGURE 9. The relationships between the probability of making a scanning saccade into a region of space and the probability of making (A) an express saccade; or (B) a regular saccade into the same region of space. Left column shows data from monkey D, and right column shows data from monkey C. The Spearman rank correlation coefficient, r_S, is shown at upper left of each graph (n = 72 for each graph).

scanning are unknown, but contributing factors seemed to include an inherent tendency to make horizontal or vertical saccades rather than oblique ones, and shorter saccades rather than longer ones (e.g. see Fig. 7, Fig. 8 and Fig. 11).

Not only were the scanning patterns biased, but also each monkey exhibited its own patterns. Although the monkeys were not trained to make biased scanning patterns, the patterns tended to be conserved over weeks of testing. This is consistent with prior reports of idiosyncratic, repeatable, non-trained scanning routines (Yarbus, 1967, Figs 107 cf. 108; Henderson *et al.*, 1987; see also Burman & Segraves, 1994).

Express saccade biases

The patterns of express saccades in Visual Scan trials often were biased: targets that appeared at certain locations were more apt to elicit express saccades than targets that appeared elsewhere. Three aspects of the Visual Scan task might have influenced the biasing of express saccades: (1) the various initial locations of fixation; (2) the relation of the target to the fixation spot array; and (3) scanning. First, the initial location of fixation seemed to play only a minor role in the Visual Scan task. This was revealed by comparing express saccade patterns made from the same trigger spot in Visual Scan and Steady Gaze target trials. In Steady Gaze trials, express saccades tended to be biased toward the

TABLE 2. Similarities between express or regular saccade patterns and the patterns predicted by scanning, for each trigger spot, for each monkey

Trigger spot label	Monkey D		Monkey C	
	Express	Regular	Express	Regular
a	6.83 (7)*	34.83 (7)	12.94 (7)*	117.98 (7)
b	19.68 (6)	49.64 (7)	1.34 (4)*	138.12 (7)
c	7.62 (4)*	85.35 (5)	9.39 (5)*	415.59 (7)
d	3.40 (7)*	38.54 (7)	25.76 (6)	156.83 (7)
e	19.75 (7)	20.71 (7)	9.77 (5)*	84.56 (7)
f	7.42 (7)*	50.83 (7)	3.91 (5)*	253.42 (7)
g	2.68 (7)*	140.47 (7)	33.02 (6)	910.13 (7)
h	28.52 (6)	36.73 (7)	7.77 (6)*	119.99 (7)
i	6.36 (6)*	69.92 (6)	26.47 (7)	56.58 (7)

Entries are Chi-square (d.f.), followed by * if the pattern of express or regular saccades was indistinguishable from the pattern predicted from scanning (P > 0.05).
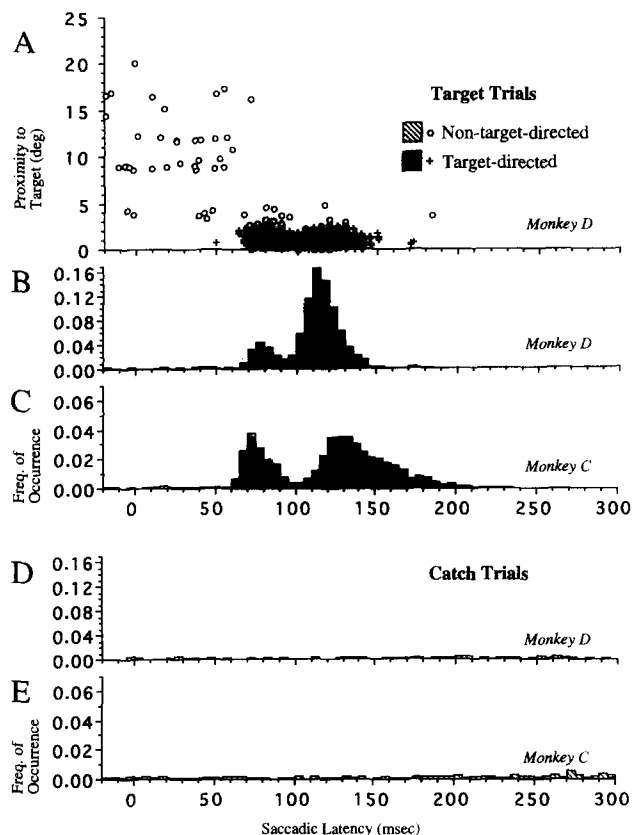
FIGURE 10. Proximity and latency distributions of saccades from Steady Gaze trials. See legend of Fig. 4 for details. (A) Scatter plot of proximity vs latency for monkey D is shown. The saccadic latency histograms from target trials are shown for (B) monkey D (2172 white target presentations); and (C) monkey C (5867 white target presentations). The saccadic latency histograms from catch trials are shown for (D) monkey D (769 gray target presentations); and (E) monkey C (2123 gray target presentations).

center, a phenomenon documented previously (Paré & Munoz, 1996). However, in Visual Scan trials, express saccades made from the same initial fixation location were biased differently and, in fact, they could avoid the center [Fig. 11(B) cf. Figure 11(C)].

Second, the target's location relative to the rest of the visual scene did not predictably influence the biasing of express saccades. Express saccades sometimes were biased to targets appearing within the fixation spot array [e.g., Fig. 8(A)], but sometimes they were biased to targets appearing outside the array [e.g. Figure 7(A) and Fig. 11(B)]. The third possible cause of express saccade biases in the Visual Scan task, scanning, is discussed next.

Correlations between scanning saccades and express saccades

Scanning seemed to have a major influence in shaping the biases of express saccades. When the express saccade patterns and the scanning saccade patterns were superimposed, it was seen that they were similar. The probabilities of making express saccades and scanning saccades into regions of space were significantly
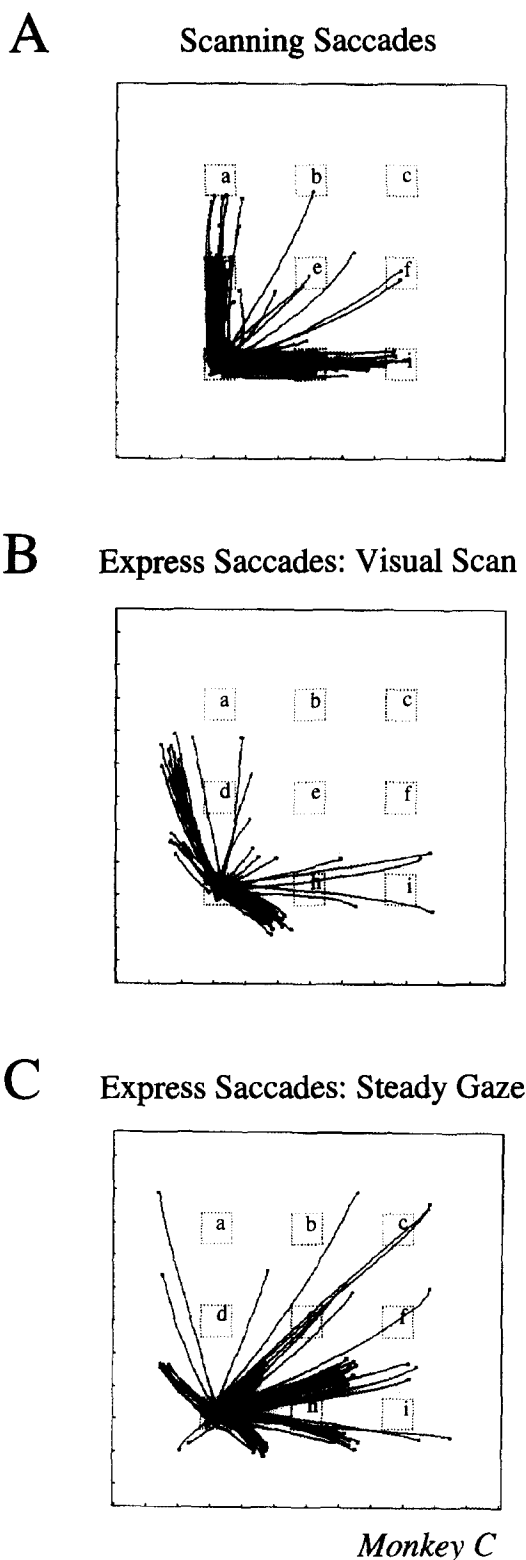

FIGURE 11. Comparison of (A) scanning saccades with express saccades made during (B) Visual Scan trials; and (C) Steady Gaze trials. Trigger spot is at lower left, fixation spot "g". See legend of Fig. 5 for plotting conventions.

correlated, for both monkeys. Express saccade patterns were indistinguishable from the patterns predicted by scanning when made from six of nine trigger spot locations, for both monkeys.

It seems likely that the target for an express saccade

usually appeared during scanning saccade preparation. During a scan, stimuli for evoking a scanning saccade (the black fixation spots) settle at their new retinal locations immediately at the start of a fixation. If a target for an express saccade (a white square) *does not* appear, a new scanning saccade begins, on average, ~150–200 msec after the start of fixation (Sommer, 1994). But if a target *does* appear, its unpredictable appearance occurs 36–151 msec after start of fixation.

These timing considerations, along with the spatial correlation results, suggest that the spatial preparation of scanning saccades facilitated the generation of express saccades. This supports prior hypotheses that express saccades are influenced by metrical planning in advance of target onset (Kalesnykas & Hallett, 1987; Smit & van Gisbergen, 1989; Kowler, 1990; Albano, 1993; West & Harris, 1993; Paré & Munoz, 1996).

The spatial region within which express saccades seemed to be facilitated by metrical planning could be estimated. When there was a high probability that a monkey planned to scan to a certain fixation spot, targets appearing nearest to that fixation spot, i.e. 4 deg away, were the ones most likely to evoke express saccades [see Figs 7(A), 8(A) and 11(B)]. Targets appearing at the next closest location, which was 8.9 deg away, rarely evoked express saccades. Therefore, the range of facilitation seemed to extend ≥4 deg but <9 deg from the location to which the monkey planned to scan.

How might scanning saccade preparation facilitate express saccades?

Scanning saccade preparation involves both visual and motor processes. Spatially restricted analysis of peripheral vision might link scanning saccade preparation and express saccade generation, but evidence regarding this is contradictory. Peripheral attention seems to be part of scanning saccade preparation (Henderson et al., 1989), but it is unclear whether peripheral attention facilitates (Cavegn, 1996) or inhibits (Mayfrank et al., 1986; Braun & Breitmeyer, 1988; Fischer & Weber, 1993; Weber & Fischer, 1995) express saccades.

A body of work suggests that the interaction between scanning saccade preparation and express saccade generation might occur nearer to the motor level. A subcortical structure, the superior colliculus (SC), is crucial for the generation of express saccades (Schiller et al., 1987). The deeper SC represents saccadic metrics on a topographic map (reviewed by Sparks & Hartwich-Young, 1989). Express saccades seem to be initiated by what has been traditionally considered the "visual" response of cells in the deeper SC (Edelman & Keller, 1996).

Some cells in the deeper SC have an extended low-frequency activity that precedes saccades (Mohler & Wurtz, 1976; Mays & Sparks, 1980; Glimcher & Sparks, 1992; Munoz & Wurtz, 1995). Such long-lead activity occurs in a broad region of the SC map that represents the upcoming saccade's metrics (Glimcher & Sparks, 1992; Munoz & Wurtz, 1995). The strength of long-lead activity seems to be correlated with the probability of making an express saccade with the metrics represented by that site (Dorris et al., 1995).

Therefore, the following scenario might explain how the preparation of a scanning saccade facilitates express saccade generation. During a fixation of visual scan, the next scanning saccade begins to be prepared, a process reflected by increased long-lead activity in a region of the SC map. If a target then appears in the part of visual space corresponding to this active region of the SC, a visual discharge occurs in the cells there (most cells with long-lead activity also have a visual response: Mays & Sparks, 1980; Munoz & Wurtz, 1995). The likelihood that the visual discharge causes an express saccade will be higher than normal because this visual discharge occurs in an SC region that is already sensitized.

The results of the present study, in the context of these physiological findings, require an addition to the visuomotor hypothesis of express saccades (Sommer, 1994). Proposals (1) and (2) of this hypothesis suggested that the separate visual and motor bursts of collicular cells are necessary for making express and regular saccades, respectively. Proposal (3) suggested that fixation-related disinhibition of the colliculus mediates the selection of whether an express or regular saccade is made. A new proposal refers to the spatial component of this selection. Like the other proposals, it is physiologically verifiable or refutable: (4) express or regular saccade selection is mediated spatially by localized sensitization in the collicular map; this sensitization can occur before a target appears.

Synthesis

A brief summary of the results of this study and the previous one (Sommer, 1994) provides an overview of how monkeys examine scenes that contain unchanging and suddenly appearing stimuli. The monkeys in this pair of studies scanned the unchanging elements of a simple scene with stereotyped patterns. Scanning saccades were separated by fixations of 150–200 msec. A target that suddenly appeared during one of these fixations elicited one of the following types of response. If the first saccade made after target onset occurred within 50 msec or so, it was another scanning saccade. If the first saccade occurred from around 50 to 100 msec after target onset, it landed either at a spatially ambiguous location or else near the target. The latter, target-directed, saccades were made prolifically and were termed "express" saccades. Express saccades were more likely to be made to targets that appeared late in fixation (Sommer, 1994) and to targets that appeared near where the monkey had been preparing to scan. Around 100 msec after target onset, few saccades of any kind were made. Finally, if the first saccade was made later than 100 msec after target onset, it nearly always was a "regular" target-directed saccade. Regular saccades were not influenced by scanning.

CONCLUSION

This study demonstrated that if a monkey is likely to

scan somewhere, a target that appears near that region of space will be especially apt to elicit an express saccade. The results suggest that metrical preparation to scan facilitates express saccade generation. More generally, this study's spatial analysis of saccades made in the Visual Scan task complements the prior temporal analysis (Sommer, 1994). This pair of studies contributes to a general description of how monkeys examine scenes composed of unchanging and changing stimuli. A full understanding of this behavior is a prerequisite to the physiological study of saccades made in natural situations.

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