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Express Saccades Elicited During Visual Scan in the Monkey

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Monkeys trained to saccade to visual targets can develop separate "express" and "regular" modes in their distribution of saccadic latencies. The purpose of this study was to determine whether this occurs under more natural viewing conditions, when targets are suddenly presented in a structured visual field during visual scan. It was found that scanning saccades stopped appearing 60 msec after a target's onset, and subsequent saccades, which were directed toward the suddenly appearing target, had a bimodal distribution of latencies. Express saccades were more likely to occur as the target was presented later in a fixation. Regular mode saccades were more likely to occur with longer target durations. Scanning saccades made to stimuli of the structured visual field always had unimodal inter-saccadic interval distributions. All these effects were apparent after only 2–3 days of training. These findings, taken together with recent physiological results, suggest that the visuomotor cells of the superior colliculus mediate latency bimodality.

Rhesus monkey   Saccidic eye movements   Express saccades   Visual scan   Superior colliculus

INTRODUCTION

When a primate's task is to make a saccadic eye movement toward a novel visual stimulus, saccadic latencies can form a bimodal distribution (Fischer & Boch, 1983). In the monkey, for example, saccades can be initiated either about 80 msec or after 120 msec following target onset, forming "express" and "regular" latency modes, respectively, but few saccadic latencies occur around 100 msec.

In previous studies, the procedure for evoking express saccades has required a subject to fixate a point in the center of his visual field before presenting a saccade target in the featureless periphery. A temporal "gap" has been introduced by removing the fixation point a short time (typically 100 or 200 msec) prior to target onset in almost every experiment (a short list includes Fischer & Boch, 1983; Boch, Fischer & Ramsperger, 1984; Boch & Fischer, 1986; Smit & Van Gisbergen, 1989; Weber & Fischer, 1990; Jüttner & Wolf, 1992; Weber, Latanov & Fischer, 1993; Nothdurft & Parlitz, 1993). This traditional paradigm, however, does not represent everyday conditions encountered by primates. Natural visual scenes are generally structured, and thus any sudden visual change that might elicit a saccade usually occurs amidst other background, non-target stimuli. Only two previous studies (Mayfrank, Mobashery, Kimmig & Fischer, 1986; Schiller, Sandell & Maunsell, 1987) have considered any effects of non-target visual stimuli on express saccades. Also, humans and monkeys normally scan such structured visual fields, moving their eyes at 2–5 saccades/sec with saccades ranging from 2 to 15 deg in amplitude (Bahill, Adler & Stark, 1975; Schiller, True & Conway, 1980).

Can express latency saccades occur under conditions that involve visual structure and scanning? This is important to know, in order to understand whether express saccades might be used by primates in everyday situations. Aside from a brief comment in an early paper (Fischer, Boch & Ramsperger, 1984), there have been no prior reports of attempts to determine whether express latencies occur under more natural conditions than the traditional ones described above. The present study is the first quantified effort in this direction.

In the paradigm of this report, monkeys are presented with a structured visual field. They make successive saccadic eye movements to the stimuli that comprise this field. Target stimuli are presented at random times and positions during natural fixations of the visual scan; the task is to saccade directly to the suddenly appearing target. If express latency saccades *do* occur using this paradigm, the finding would suggest that monkeys are indeed capable of foveating suddenly appearing visual stimuli with express saccades during normal visual scanning of their environment. This would be a significant step toward demonstrating that express saccades are a normal element of a monkey's oculomotor repertoire. A negative finding, that express saccades *do not* occur during this "Visual Scan" paradigm, would also be

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interesting, since determining the causes of this inability could shed more light on the mechanisms underlying express latencies.

In the course of executing the experiments described in this report, I also examined the effects of two aspects of the target's timing on elicitation of express and regular latency saccades: the *target onset lag* (i.e. the asynchrony between start of fixation and appearance of the target) and the *target duration*. Target onset lag effects on express saccades have never been studied before; although many investigators have varied the duration of the fixation stimulus (Fischer & Boch, 1983; Fischer & Ramsperger, 1984, 1986; Rohrer & Sparks, 1986; Boch & Fischer, 1986; Kalesnykas & Hallet, 1987; Schiller *et al.*, 1987; Smit & Van Gisbergen, 1989; Fischer, Weber & Biscaldi, 1993; Nothdurft & Parlitz, 1993), the actual durations of *foveation* of the fixation stimulus have not been reported. This study synchronizes all target onsets to the actual acquisition of the fixation stimulus and uses five randomized target onset lags to probe how length of fixation affects saccadic latency. Also, during early testing sessions it was noticed that very short target durations markedly reduced the animals' ability to perform the tasks. This decrement in the frequency of correct trials as target duration decreased was due solely to a loss of longer latency saccades. Since an earlier paper (Boch *et al.*, 1984) had reported no effect of target duration on bimodal saccadic latency distributions, the target duration effects observed in the present study were thoroughly investigated.

METHODS

Subjects

Two rhesus monkeys (*Macaca mulatta*) were the subjects for these experiments. Each animal underwent surgery for the implantation of a head post and scleral search coil (Robinson, 1963; Fuchs & Robinson, 1966). Surgery was performed in sterile conditions, with animals under sodium pentobarbitol anesthesia. Animals received analgesics and antibiotics for several days following the surgery, and training on oculomotor tasks began 2 weeks after recovery. Monkeys were deprived of water in their home cage but were rewarded with apple juice during testing and allowed to drink until satiated after testing. All animal use followed NIH guidelines.

One subject, monkey C, had never been used in any experiment before this study. Monkey D was initially naïve to this study's paradigm, and had not been trained previously to produce express saccades.

Computers and equipment

Each monkey sat in a primate chair 65 cm from a 60 Hz interlaced color monitor. A PDP-11 computer drove the graphics, ran the real-time stimulus presentation programs, and collected the data. Eye position samples and task event information were stored every 5 msec. The controlling program waited for vertical retrace of the monitor before drawing a target, to ensure accurate presentation.

Timing of all trials

A fixation spot appeared to start an experimental trial and was continuously lit until the trial ended (Fig. 1). If an animal did not foveate the fixation stimulus within 10 sec, the trial was aborted and a new trial began after the inter-trial interval of 1500 msec. If the subject's eye position did enter a computer-defined "window" near the fixation spot, and if it remained there for a minimum time, collection of eye position samples commenced. The program did not present a target immediately but continued to wait during a "target onset lag" period. The trial was aborted if the eye position left the fixation window during the target onset lag. If the trial was not aborted, a target would then be flashed for a certain duration. The length of time from target onset to initiation of a correct saccadic eye movement was the saccadic latency (determined off-line). A direct saccade that terminated in a window around the target would be rewarded with a drop of juice. Randomly, one out of three incorrect responses were rewarded to keep the animal from quitting during difficult tasks. Note that all trials were the "overlap" type, i.e. fixation stimuli remained on throughout target presentation.

Target windows measured 2.8 × 2.8 deg, i.e. 4 deg diagonally. The fixation window sizes were chosen to balance two considerations: the window had to be big enough that most foveations of the fixation stimulus occurred within it, but it had to be small enough that most saccades passing through the window would not remain within it long enough to be erroneously judged a fixation. Fixation windows for monkey D were 2.8 × 2.8 deg, and the minimum fixation time (Fig. 1) for this animal was 30 msec. To achieve shorter target onset lags for monkey C (see Task parameter selection, below), the minimum fixation time was set to 10 msec and the fixation windows were set to 2.0 x 2.0 deg. All window

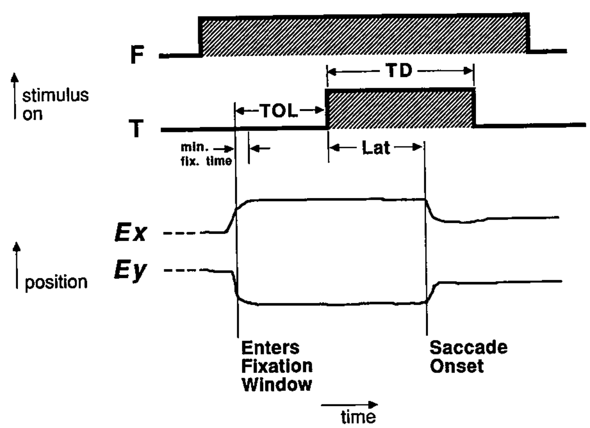


FIGURE 1. Timing diagram for all trials of the paradigm. A fixation spot (F) appears to begin the trial. The eye position (components *Ex*, horizontal, and *Ey*, vertical) enters a fixation window and remains for a minimum length of time (min. fix. time). After a target onset lag (TOL) period, the target (T) is illuminated for a target duration (TD). The time that elapses after target onset until the monkey initiates a saccade to the target is the latency (Lat).

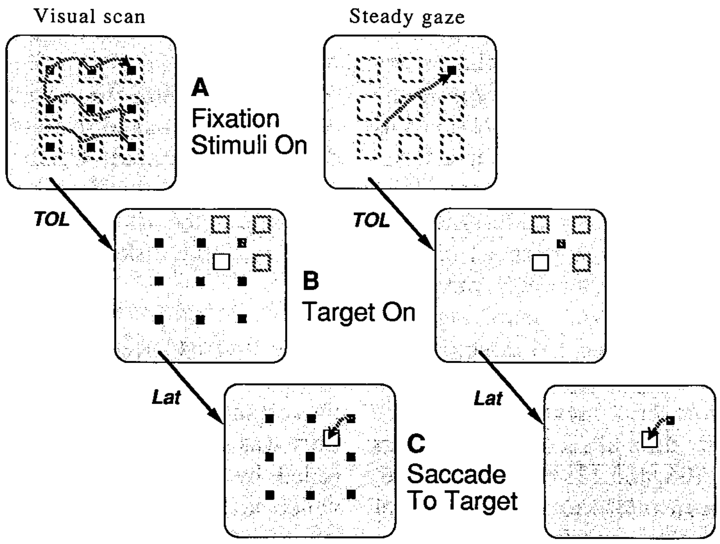


FIGURE 2. Spatial aspects of each task. Heavy broken curve represents eye movements, broken squares around stimuli depict windows (not seen by monkey). (A, left) In the Visual Scan task, a trial begins with the appearance of fixation stimuli at nine positions on the monitor. Monkeys scan the stimulus array with saccades. (B, left) Foveation of one of these spots triggers target onset in one of four randomized positions around the fixation position. (C, left) A direct saccade to the target results in juice reward. (A, right) In the Steady Gaze task, only one fixation stimulus appears to begin a trial. Monkeys foveate this spot immediately. (B, C, right) All subsequent trial events are identical to those of the Visual Scan task. TOL, target onset lag; Lat, saccadic latency.

sizes and minimum fixation times were established during early training of each monkey and were not changed thereafter.

Spatial aspects of trials

The fixation stimuli were 0.3 × 0.3 deg black squares, the target stimulus was a 0.6 × 0.6 deg white (71 cd/m^2) square, and the background was gray (9 cd/m^2). Dim ambient light in the testing room allowed objects such as the monitor, monitor stand, and walls to be seen; hence, the black squares on the monitor provided a local structure within a larger unchanging visual scene. The fixation spot array (Fig. 2, left) over which visual scan occurred was drawn so that the center stimulus was directly ahead of the monkey. This 3 × 3 array measured 16.0 deg diagonally. All targets were presented 4.0 deg eccentric to the foveated fixation stimulus, obliquely at either 45, 135, 225, or 315 deg meridian from horizontal. A target presented within the array would be centered between four fixation stimuli [e.g. Fig. 2(B, C) left].

Visual Scan task

At the start of a Visual Scan trial, an array of fixation point stimuli appeared on the monitor [Fig. 2(A), left]. Although the fixation stimuli were all identical in appearance, the computer program randomly pre-selected one of these stimuli to be the "trigger" for target onset. Monkeys responded to presentation of the array by performing a rapid visual scan over the array. Note that an animal was free to foveate any of the fixation stimuli, in any order, and for any length of time; the only time constraint was the previously mentioned 10 sec trial limit. Once the pre-selected trigger fixation stimulus was foveated, a target onset lag ensued and the target was presented [Fig. 2(B, C), left]. A typical eye movement trace generated by a monkey successfully performing a Visual Scan task trial is shown in Fig. 3(A).

Steady Gaze task

Since it was not known *a priori* whether express saccades would occur during the Visual Scan task, a negative finding could have meant either that (1) the Visual Scan task itself inhibited express saccades, or that (2) the monkeys just were not capable of making express saccades or were not sufficiently trained. Therefore, control trials were used to determine whether the monkeys could even make express saccades in the more traditional task. These trials were termed "Steady Gaze" because no scanning was involved. The computer program implemented this task by running a Visual Scan trial with *only* the pre-selected "trigger" fixation stimulus drawn [Fig. 2(A), right]. An animal would saccade directly to this fixation stimulus and trigger target onset [Fig. 2(A, B, C), right]. Figure 3(B) shows a typical eye movement trace from a Steady Gaze trial.

Inter-saccadic intervals measurements

Eye position samples were usually not recorded during the saccades of visual scan that occurred before the trigger fixation stimulus was foveated. In order to estimate the durations of the pauses between scanning saccades, the program recorded, on-line, every time a subject's eye position entered or left each fixation window. The amount of time spent in each fixation window could then be calculated from these data, resulting in estimates of the inter-saccadic intervals.

Task parameter selection

Stimulus parameters were randomized in time and space to minimize anticipatory responses. Location of a trial's pre-selected trigger fixation stimulus was pseudo-randomized, as was target position, such that every fixation/target position combination would occur in one "block". Thus each block of testing consisted of 36 trials (9 trigger fixation positions × 4 target positions). Independent of these spatial randomizations, for each trial one of five target onset lags was pseudo-randomly selected. These target onset lag values were set in early training to probe comparable periods in each monkey's mean inter-saccadic interval. Target onset lags for monkey D were 57, 76, 101, 126, and 151 msec (i.e. 29, 39, 52, 64, and 77% of its mean inter-saccadic interval of 196 msec). Due to a more brief mean inter-saccadic interval of monkey C, this animal's target onset lags were shorter, at 36, 56, 81, 106, and 131 msec (i.e. 23, 36, 52, 68, and 84% of its mean inter-saccadic interval of 156 msec). The 36 spatial × 5 temporal parameters provided a total of 180-fold spatio-temporal randomization, by trial.

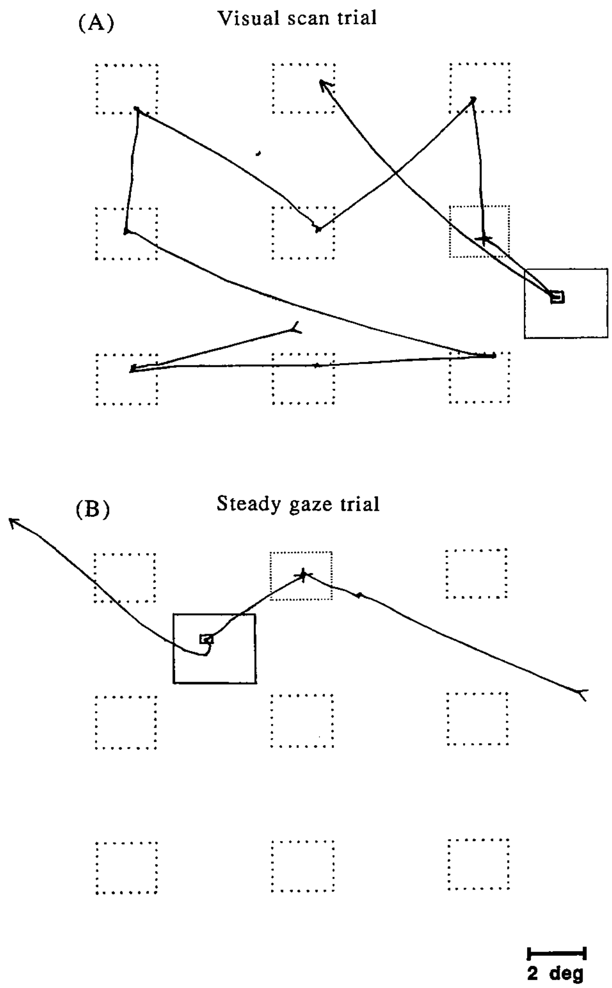


FIGURE 3. Typical eye movement traces of monkey "C", during the (A) Visual Scan and (B) Steady Gaze tasks. Eye position samples have been connected with straight lines for clarity. Arrowheads show start and end of trace, as well as direction of movement. Windows around each fixation spot location are drawn with dotted lines, and the trigger fixation spot's window is depicted with a finer grain. Largest square represents window around the target; for juice reward, the monkey had to saccade directly into the target window. A small cross and small square mark the initial and final positions, respectively, of the first eye movement that occurred after entering the trigger fixation window. Spatial scale is shown at lower right.

Target duration was constant during each set of five blocks, then changed. Unless noted otherwise, six target durations were used: 33, 50, 67, 83, 100, and 150 msec. For monkey D, the Visual Scan and Steady Gaze tasks were alternated after each set of five blocks, whereas for monkey C the tasks were alternated randomly by trial.

Off-line data analysis

The first 640 msec (128 samples) of the eye position data of each trial was analyzed. Only the first eye movement of a trial was characterized for this report [this was to avoid considering saccades that were preceded by other movements, the refractory periods of which could affect saccadic latency (Carpenter, 1988)]. A change in mean eye position, computed as a running sum over six samples, that exceeded 0.25 deg was considered an eye movement. If such a movement also exceeded 50 deg/sec at peak velocity it was judged to be a *saccade*; movements with a smaller peak velocity could have involved mechanisms of the smooth pursuit system (Fuchs, 1967) and were considered non-saccadic eye movements. Saccade start and end times were determined in the velocity domain using a 30 deg/sec crossing threshold, and saccadic initial and final positions were calculated as an average of six sample positions before or after the movement.

RESULTS

The basic steady state results will be reported first. Then I will describe changes that occurred during the short-term training that led to steady state. Finally, preliminary observations of long-term training effects will be noted.

Aborted trials

The 10 sec maximum time limit for acquiring the pre-selected fixation point was hardly ever exceeded in the Visual Scan task (Table 1) and it was never exceeded in the Steady Gaze task. Trials that were aborted because the pre-selected fixation stimulus was foveated, but then the eye position left the fixation window before the full target onset lag occurred, were more common (Table 1: Visual Scan task, 18.4% of all trial initiations for monkey C, 7.4% for monkey D, Steady Gaze task, 8.6% of all trial initiations for monkey C, 1.8% for monkey D). In the Visual Scan task, these types of aborts occurred nearly always because a scanning saccade was initiated. In the Steady Gaze task, there were three reasons a trial was aborted. The most common reason was that the initial fixation landed near the edge of the electronic window and the slight inherent jitter of the eye position moved the eye trace momentarily outside the window. Secondly, a slow movement sometimes remained within a fixation window long enough to be judged a fixation but then landed just outside the window. Finally, a movement was sometimes made that brought the eye position out of the fixation window,

TABLE 1. Breakdown of the results of attempting to present a target, for each monkey in each task

Results of attempts to present target	Visual scan		Steady gaze	
	Monkey C	Monkey D	Monkey C	Monkey D
(1) Aborted, target not presented (exceeded 10 sec maximum acquisition time of fix-spot)	0.3 (10/3171)	1.7 (39/2335)	0.0 (0/2893)	0.0 (0/2197)
(2) Aborted, target not presented (left fix-spot window during target onset lag)	18.4 (582/3171)	7.4 (172/2335)	8.6 (250/2893)	1.8 (39/2197)
(3) Non-aborted, target presented	81.3 (2579/3171)	91.0 (2124/2335)	91.4 (2643/2893)	98.2 (2158/2197)

See text for details. Table entries are percentages of all trial initiations, derived from the ratios in parentheses; percentages may not sum to 100.0, due to round-off error.

toward a target location. These possibly anticipatory responses were the rarest type of abortive movement and nearly always terminated far (>3 deg) from any of the four potential target locations surrounding the fixation stimulus.

The great majority of trials of both tasks were not aborted, allowing for target presentation (Table 1). Non-aborted trials are the focus of the rest of this paper. More than 2100 target presentations during each task were tested on each monkey.

A proximity transition with latency

In Fig. 4, the proximity of the first saccade of non-aborted trials to the center of the suddenly appearing target is plotted against the saccade's latency; superimposing data from many trials results in a scatter plot. The first main result of this report is that a transition in proximity with latency is evident for the Visual Scan task [Fig. 4(A)]. Saccades that were initiated before 60 msec following sudden target onset generally land far (>3 deg) from the target location, but saccades with latencies of 60 msec or longer land very near (<2 deg) to the target location [Fig. 4(A)]. The transition zone is about 20 msec in width, from 50 to 70 msec latency. Many saccades with latencies within this transition zone appear to undergo spatial averaging, since the shift in proximity from 50 to 70 msec is gradual. This transition is also observed in the Steady Gaze task [Fig. 4(B)], but it is especially striking in the Visual Scan task because saccades are continually being elicited throughout the transition zone.

Saccades are separated into two classes for the remainder of this report, by a proximity criterion. If the first movement of a trial is a saccade that has a final proximity nearer to the target than to any of the fixation stimuli or the edge of the visible display, it is termed a "correct" saccade (crosses in Fig. 4) and the trial is a "saccade correct" trial. Otherwise, the saccade is "wrong" (circles in Fig. 4), and the trial is a "saccade wrong" trial.

Types of trial outcomes

Saccade correct trials. Table 2 shows that the first eye movement of non-aborted trials was a correct saccade at about the same frequency for both monkeys in Steady Gaze trials (59.9 and 55.4% for monkeys C and D respectively). Monkey D was more proficient at making correct saccades in the Visual Scan trials than monkey C (58.3% vs 39.4%).

The second main result of this study is that latencies of the correct saccades formed a bimodal distribution in both the Visual Scan and Steady Gaze tasks for both monkeys [Fig. 5(B, D)]: an earlier "express" mode was centered between 50 and 100 msec latency, and a later "regular" latency mode appeared after 100 msec. Correct saccade trajectories were occasionally curved in the Visual Scan task [Fig. 5(A)], but the accuracy of correct saccade final positions in the Visual Scan task was comparable to the accuracy in the Steady Gaze task [Fig. 5(C)]. For both tasks, nearly all saccades of both monkeys landed within 2 of the target's center (with most within 1 deg).

Saccade wrong trials. Wrong saccades were more than twice as common in the Visual Scan task than in the Steady Gaze task (Table 2). Figure 6 shows the trajectories and latency distributions of wrong saccades. Trajectories of wrong saccades in the Visual Scan task [Fig. 6(A)] demonstrate that most of these were scanning saccades. The latency histogram of wrong saccades from Visual Scan trials [Fig. 6(B)] reflects the effect seen in Fig. 4(A): the majority of wrong saccades in the Visual Scan task appeared from just before target onset until about 60 msec after target onset. A second, widely scattered mode of wrong saccades appeared after 200 msec latency; these typically terminated off the visible display.

In the Steady Gaze task, wrong saccades were generally corrective movements that improved on inaccurate initial fixations [Fig. 6(C)]. These occurred before 60 msec or so following target onset [Fig. 6(D)]. A small peak of wrong saccades at around 80 msec represent apparently hypometric express saccades which are also evident in Fig. 4(B). As in the Visual Scan task, saccades in the Steady Gaze task that occurred with more than 200 msec or latency generally went off the visible display.

Target onset lag effect

The third main result of this study is that the express mode of latency distributions of correct saccades is more prominent if the target is presented later in the fixation period (Fig. 7; normalized ordinate is number of saccades divided by number of target presentations, giving

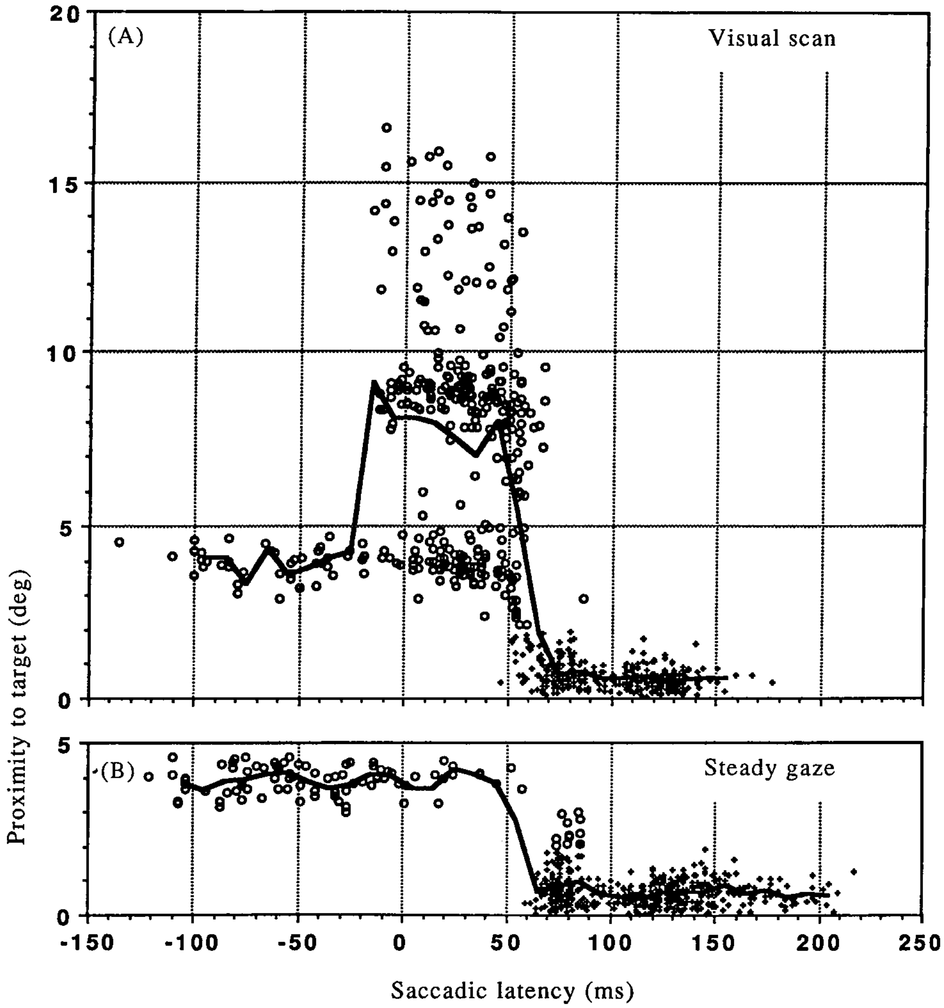


FIGURE 4. Proximity transition with latency. For saccadic first movements of non-aborted trials, each saccade's final proximity to the target is plotted against its latency (both monkeys pooled, all target onset lags pooled, target duration 150 msec). Zero on the abscissa marks the time of target onset. The heavy line is a running mean, constructed by averaging the proximities over each 10 msec latency interval and assigning that mean to the middle of the interval, then connecting these means with straight lines. Crosses represent "correct" saccades, those with closer final proximity to the target than to any fixation stimulus or edge of the visible display. Circles are all other, "wrong", saccades. (A) A sharp transition in proximity occurs about 60 msec following target onset in Visual Scan trials: the mean proximity to the target drops from around 8 deg during scanning (0–45 msec latency), to near 2 deg at 65 msec latency, stabilizing at < 1 deg by 75 msec. (B) A similar transition is seen in the Steady Gaze trials, with a drop in proximity from around 4 to ⩽ 1 deg during the interval from 45 to 65 msec latency. The few saccades that landed outside of the visible display are excluded from this figure.

overall frequency of saccade occurrence). The target onset lag effect is apparent for both the Visual Scan [Fig. 7(left)] and the Steady Gaze [Fig. 7(right)] tasks. During the Visual Scan task, the probability of evoking any correct saccade at all with a target presentation decreases as target onset lag increases, because there is a greater chance that a scanning, "wrong", saccade will occur after longer target onset lags.

The target onset lag effect is quantified in Fig. 8, to show that the ratio of express saccades to all correct saccades rises steeply for both the Visual Scan and Steady Gaze tasks, for both monkeys, from a mean of

TABLE 2. Types of the first eye movements in all non-aborted trials and the frequency of occurrence of each type, for each monkey in each task

First eye movement of non-aborted trials	Visual scan		Steady gaze	
	Monkey C	Monkey D	Monkey C	Monkey D
(1) Saccade correct	39.4 (1016/2579)	58.3 (1239/2124)	59.9 (1583/2643)	55.4 (1196/2158)
(2) Saccade wrong	56.6 (1461/2579)	40.0 (850/2124)	23.3 (617/2643)	11.9 (257/2158)
(4) Non-saccadic eye movement	1.0 (27/2579)	1.1 (23/2124)	8.5 (224/2643)	27.1 (585/2158)
(3) No eye movement detected	2.9 (75/2579)	0.6 (12/2124)	8.3 (219/2643)	5.6 (120/2158)

Table entries are percentages of non-aborted trials, derived from the ratios in parentheses; percentages may not sum to 100.0, due to round-off error.

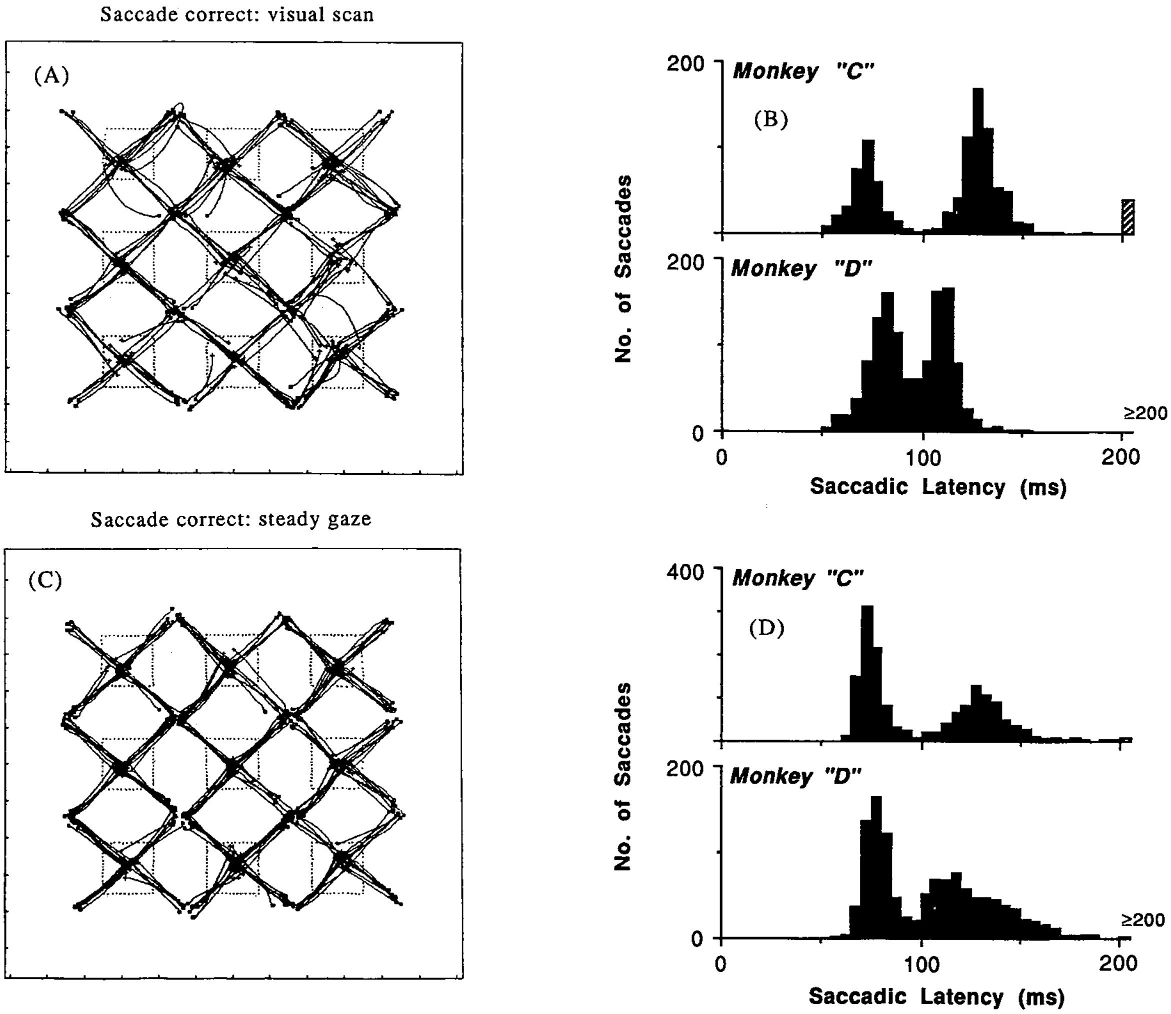


FIGURE 5. Trajectories and latencies of correct saccades. (A) Example of trajectories of correct saccades made in the Visual Scan task. A few saccades exhibit a curved trajectory, but most go directly to the target location. The saccade trace for each trial is drawn as described in Fig. 3: a small cross marks the initial position of the movement, a small square marks the final position, and the eye position samples in between are connected by straight lines. The nine large dotted squares show windows around the fixation spots. The frame around the eye movements represents the edge of the visible display, and ticks on the frame are spaced by 2 deg. (B) Latency distributions of all the correct saccades for monkey "C" (top) and monkey "D" (bottom) in the Visual Scan task. For both monkeys, the latency distributions were bimodal. (C) Trajectories of correct saccades in the Steady Gaze task. (D) Bimodal latency distributions of correct saccades for each monkey in the Steady Gaze task. Saccade traces in (A) and (C) are of monkey "D"; for clarity, only the 150 msec target duration trials are shown. Histograms in (B) and (D) pool together data from all target onset lags and target durations for each monkey.

27% at the shortest target onset lag to a mean of 68% at the longest target onset lag. This increase is highly significant (linear regression of percent express saccades against the independent variable, normalized target onset lag, gives $R^2 > 0.93$ for all four data sets).

Target duration effects

The fourth and final main result of this study is that the ability to execute a correct saccade is directly proportional to the duration of the flashed target in the Steady Gaze task, and this improvement in performance is due to modulation of the regular mode alone [Figs 9 and 10 (right column of each)]. In contrast, the probability of evoking express saccades was relatively unaffected by the target duration. This target duration effect, although consistently strong in the Steady Gaze task, was less clear in the Visual Scan task [apparent for monkey C, Fig. 10(A), but not monkey D, Fig. 9 (left) and Fig. 10(B)].

Short-term training effects

Monkey C, initially naïve, was first trained to fixate a visual stimulus for juice reward and then to saccade to a peripheral visual target. The first day that the monkey C performed this latter, saccade-to-target, task, the animal was introduced to the Visual Scan and Steady Gaze tasks and testing began. This was Day 1 for monkey C. Day 1 for monkey D, initially familiar with saccade-to-target tasks, was the first day of testing on the Visual Scan and Steady Gaze tasks.

An express mode appeared for both animals by Day 2 of training, for both the Steady Gaze and Visual Scan tasks [monkey C results are illustrated in Fig. 11(A)]. The target onset lag effect was also established on Day

2 for both animals [cf. Fig. 11(B), with Fig. 8 monkey C results]. Varying the target duration for monkey C first began on Day 2, and the target duration effect was clear on that day [cf. Fig. 11(C), with Fig. 10 monkey C results]. Examination of early training influence on the target duration effect in monkey D was not possible, because this animal performed fewer trials per day during training.

The mean and variance of each monkey's inter-saccadic intervals decreased during training [Fig. 12(A), monkey C; results of monkey D were similar]. This training effect paralleled the effects shown in Fig. 11; thus, all effects reported in this paper appeared within the first days of training and changed only gradually after that. The distributions of inter-saccadic intervals were always unimodal [a steady-state example is shown in Fig. 12(B)], even if the distribution encroached into the <100 msec or so "express" region of latencies.

Long-term training effects

Preliminary results suggest that the effects of target duration, but not of target onset lag, can be modified by extensive training. Following 4 months of daily training, monkey D now performs as well at short target durations as at long ones. Also, no effects of target duration were found in two other monkeys used in a pilot study of this experiment, both of which had been extensively trained to produce express saccades prior to exposure to this paradigm. Monkey C, however, still exhibits a strong target duration effect, even after 4 months of daily experiments. Thus, it seems that for some monkeys the response to short duration targets can improve over extensive training. In contrast, the target onset lag effects were observed in all monkeys, regardless of prior training, and they did not diminish with further extensive training.

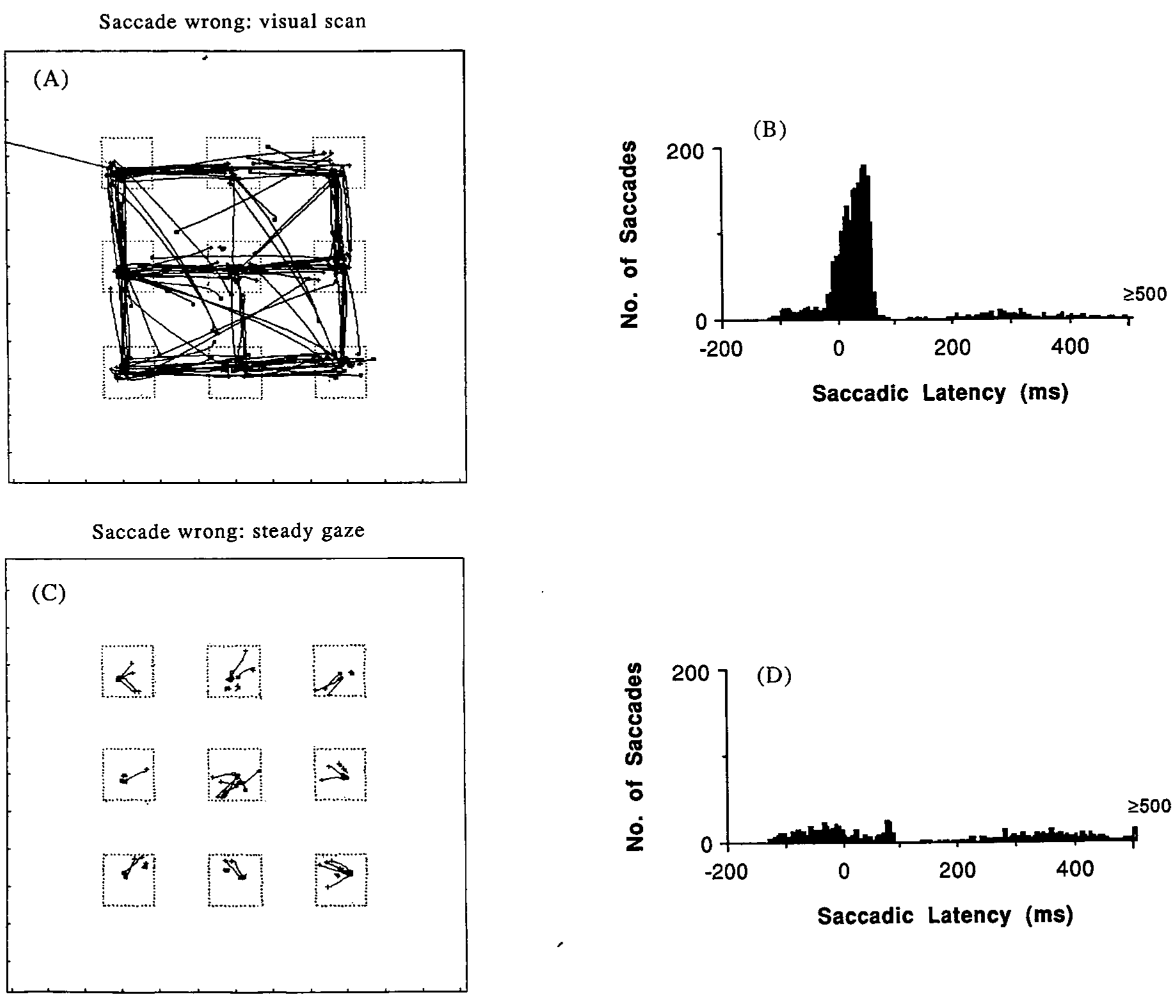


FIGURE 6. Trajectories and latencies of wrong saccades. (A) During the Visual Scan task, these movements were nearly all scanning saccades. (B) The latency histogram of these saccades shows that scanning stopped around 60 msec following target onset, as was seen in Fig. 4. Most of the saccades that resumed about 150 msec later terminated off the visible display [one such saccade is present in the upper left quadrant of (A)]. (C) In the Steady Gaze task, wrong saccades were mostly small movements that corrected for inaccurate initial fixation. (D) Latency distribution of wrong saccades in the Steady Gaze task. Saccade traces in (A) and (C) are of monkey "D", all 150 msec target duration trials. Histograms in (B) and (D) pool together data from both monkeys, all target onset lags, and all target durations.

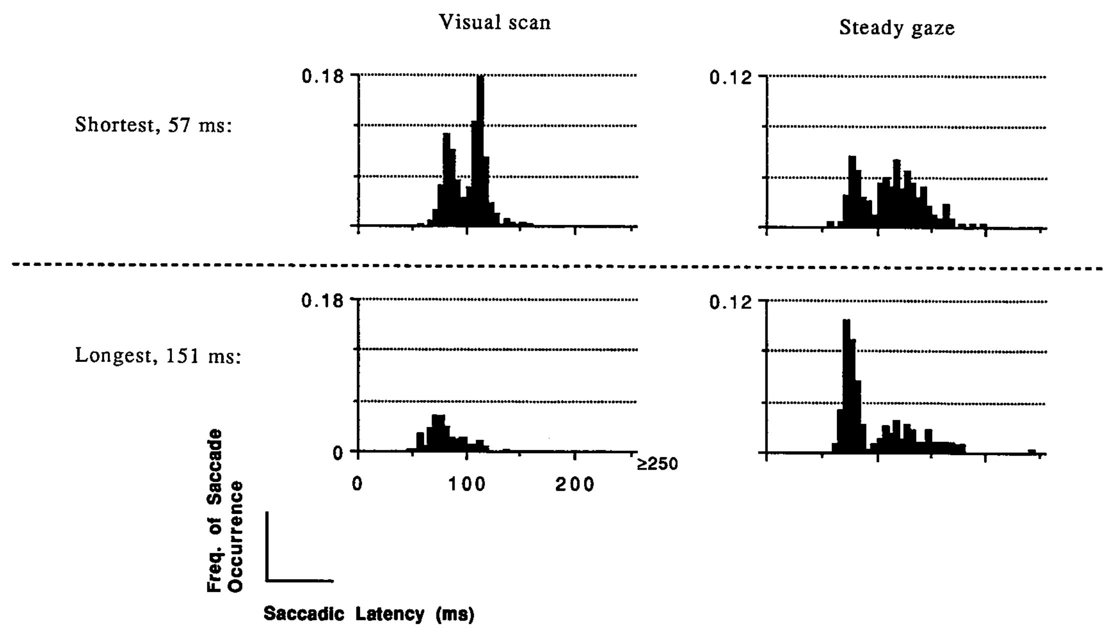


FIGURE 7. Variation in latency distributions of correct saccades with target onset lag (monkey "D", all target durations pooled). Left column, Visual Scan task; right column, Steady Gaze task. Top row, shortest target onset lag (57 msec); bottom row, longest target onset lag (151 msec). In either task, longer target onset lags favor express saccade occurrence. Ordinate of histograms is in frequency of occurrence, the number of saccades divided by the number of target presentations (300–600 target presentations per histogram).

DISCUSSION

The four main findings of this study will be discussed first, with emphasis placed on the Visual Scan task results. Drawing on these results and other recent findings, a physiological basis for express saccades will then be proposed.

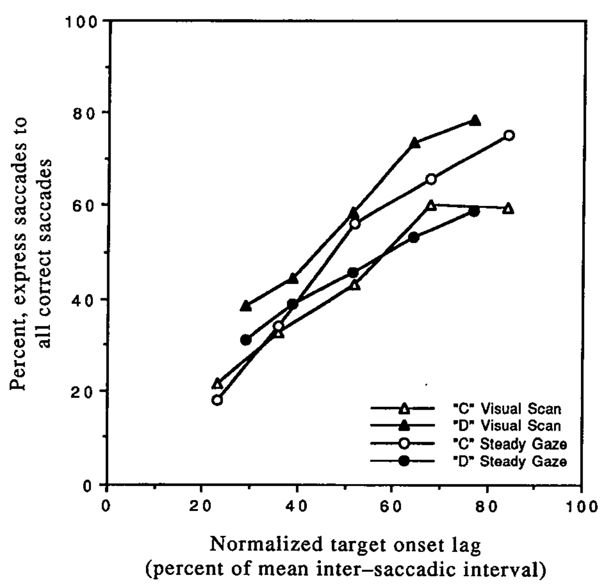


FIGURE 8. Target onset lag effect for both monkeys in the Visual Scan and Steady Gaze tasks. The percent of correct saccades that have express latency always rises with increasing target onset lag. This study's convention for calculating percentages is that latencies of <95 msec are considered express, and latencies of ⩾95 msec are regular. On abscissa, target onset lags are normalized as a percent of each monkey's mean inter-saccadic interval.

Proximity transition with latency

During a narrow transition region, the distance between saccadic endpoints and the suddenly appearing target decreased 75% in the Visual Scan task, from an average of about 8 deg proximity to the target to <2 deg proximity. Notably, the transition zone of the present study was only about 20 msec wide even though the target could randomly appear at any of five times following the start of fixation, over a total span of more than 90 msec. This strongly suggests that the proximity transition was synchronized to the onset of the suddenly appearing target, and not to any other event, such as start of fixation.

It was also quite interesting that the proximity transition from 50 to 70 msec latency was gradual in the Visual Scan task. Saccades with latencies that were within the proximity transition zone tended to exhibit spatial averaging. That is, these transition zone saccades fell closer to the suddenly appearing target than the earlier, purely scanning, saccades, but they were not as accurate as the later express and regular mode saccades (Fig. 4). Hence, averaging saccades are not only made to flashed targets separated in time (Becker & Jürgens, 1979) and to flashed targets presented simultaneously but separated in space (Findlay, 1982), but they can also be made toward a target flashed in a field that includes other, continually present, visual stimuli.

Therefore, this result demonstrates how the monkey saccadic eye movement system reacts to the sudden appearance of a behaviorally significant visual stimulus during a saccadic scan of visual structure. Scanning saccades are halted shortly after the onset of the flashed stimulus. During a 20 msec transition period, saccades land in averaged positions between the structural stimuli

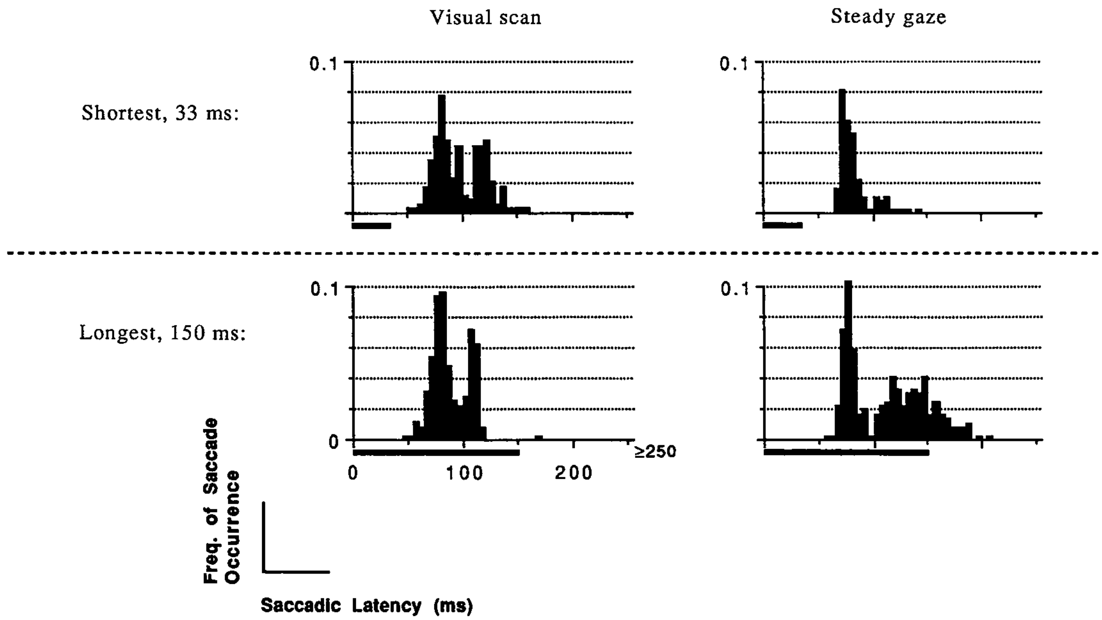


FIGURE 9. Variation in latency distributions of correct saccades with target duration (monkey "D", all target onset lags pooled). Top row, shortest target duration (33 msec); bottom row, longest target duration (150 msec). Longer target durations increase regular mode occurrence in the Steady Gaze task (right), without affecting the express mode. Target duration had little effect on Visual Scan task distributions (left) for this monkey. Target duration is represented by a bar below the abscissa of each histogram.

and the suddenly appearing target. Saccades that appear after this transition land at the suddenly appearing target location with high accuracy. Since the cessation of scanning occurs at around 60 msec latency, the latency at which express saccades appear in the monkey, this effect might be termed "express" scanning suppression.

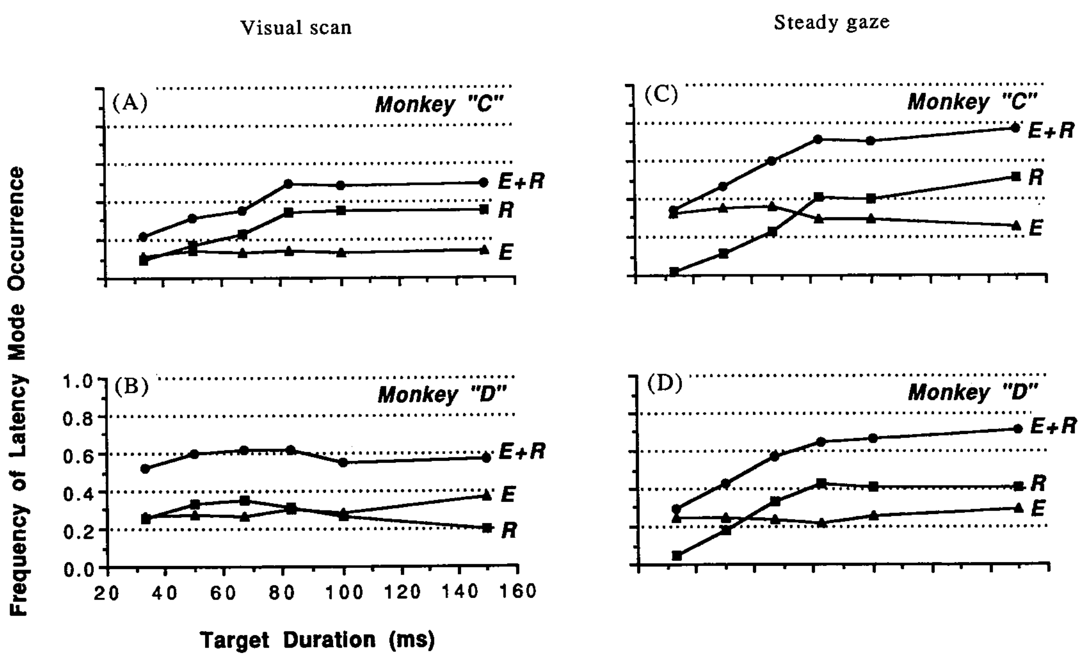


FIGURE 10. Quantitative summary of the target duration effect. Each datum is the frequency of occurrence of an express (triangles) or regular (squares) saccade, obtained by integrating under the express mode (by convention, from 0 to 95 msec) and regular mode (≥95 msec) of histograms such as those in Fig. 9. The data are connected to form E and R curves vs target duration. E + R curve (circles) is the sum of the express and regular mode curves, which gives the overall frequency of correct saccades. In the Steady Gaze task (right), saccades of the regular mode (R curve) become increasingly frequent as target duration is increased, for both monkeys (C, D); this causes a doubling in the probability of evoking correct saccades in general (E + R curve), from a frequency between 0.3 and 0.4 at 33 msec target duration to a frequency between 0.7 and 0.8 at 150 msec target duration. The frequency of express saccades always remains relatively unchanged with target duration. During the Visual Scan task (left), monkey "C"(A) shows an increase in regular saccades from 33 to 83 msec, but this is not seen with monkey "D" (B).

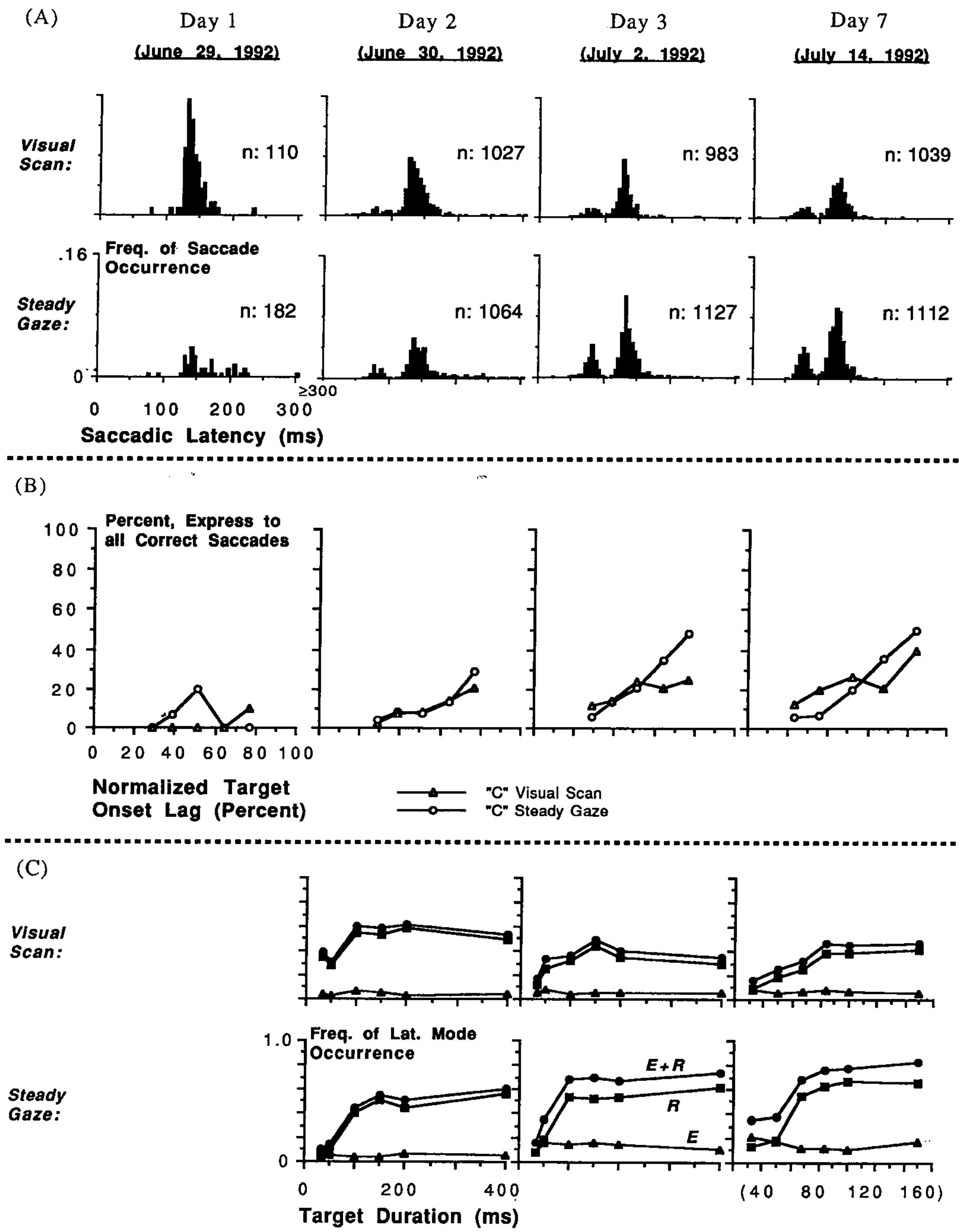


FIGURE 11. Evolution of saccadic latency bimodality, the target onset lag effect, and the target duration effect with short-term training (monkey "C"). The first three days of this animal's training are presented, and then day 7 is shown, in separate columns. (A) An express mode is seen on day 2 for both tasks, and it becomes more prominent with further training. *n*, number of trials in which the target was presented (non-aborted trials) for each task per day. (B) The target onset lag effect (see Fig. 8) is present on day 2 for both tasks. (B) The target duration effect (see Fig. 10) also was strong from day 2 onward. Variation in target duration was not tested on day 1. Target onset lags were shortened slightly from day 3 to day 7 to account for shortened mean of the inter-saccadic interval distribution that occurred during this time (see Fig. 12). A change in target durations that occurred on day 6 is indicated parenthetically on day 7.

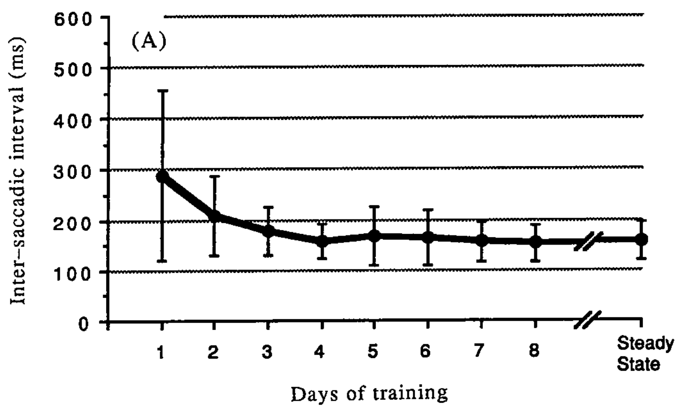
Bimodal latency distributions during the Visual Scan task

The second main finding of this paper is that the latency distribution of correct, target-directed saccades was bimodal in the Visual Scan task, forming separate express and regular modes. This was surprising, considering that two conditions inherent in visual scan should supposedly be disadvantageous for eliciting express saccades. First, visual scan conditions are "overlap", since the spot that is foveated does not disappear before target onset. Only two other studies have reported success at eliciting express saccades during overlap in the monkey (Rogal, Reible & Fischer, 1985; Boch & Fischer, 1986). This confirms those studies and also shows that express saccades can occur in the overlap condition even during extensive randomization and after very little training. Second, at the moment of target presentation there were a total of 10 stimuli present on the display (1 target + 9 fixation stimuli). It has been shown that high-contrast distractors inhibit express saccades if their onset is simultaneous with the target's onset (Schiller *et al.*, 1987; McPeek, Sommer & Schiller, 1991). The present report extends these findings to show that there are conditions in which non-target visual stimuli do not inhibit express saccades: if they are much different in appearance from the target and are present continuously, non-target stimuli have little, if any, inhibitive effect.

Target onset lag effect

The present study demonstrates that express saccades are inhibited at short target onset lags, during both Visual Scan and the more traditional Steady Gaze task, and that this effect is present as soon as express saccades appear during training. There are at least three possible explanations for this effect. First, it can be presumed that a scanning saccade is being prepared during each fixation in the Visual Scan task. If computation of its endpoint metrics is altered by the suddenly appearing target, the resulting saccade might be mistaken for an express saccade that had been prepared exclusively in response to the target. Since the likelihood of scanning saccade initiation increases as the fixation progresses, the likelihood of an express saccade, supposedly derived from the partially prepared scanning saccade signal, should also increase as fixation progresses. This explanation fails, however, because the target onset lag effect is as strong in the Steady Gaze task as in the Visual Scan task (Fig. 8). In the Steady Gaze task, the monkey does not produce, and thus presumably does not prepare, scanning saccades; rather, the monkey steadily fixates a single point. Yet express saccades occur in abundance, with the probability of their occurrence increasing with target onset lag as steeply as in the Visual Scan task.

A second possible explanation for the target onset lag effect focuses on the temporal intervals that were chosen for the five target onset lags. In the present study, five lags were chosen, spaced by 20–25 msec. The conditional probability of target appearance rises if fixation progresses and the target has not yet appeared, from 0.20 at the start of fixation to 1.0 after the fourth target onset lag has elapsed. It is possible that a subject takes advantage of this change in conditional probability, decreasing its saccadic latency through an overall increase in arousal due to expectation that a target is more likely to appear as fixation progresses. More research is



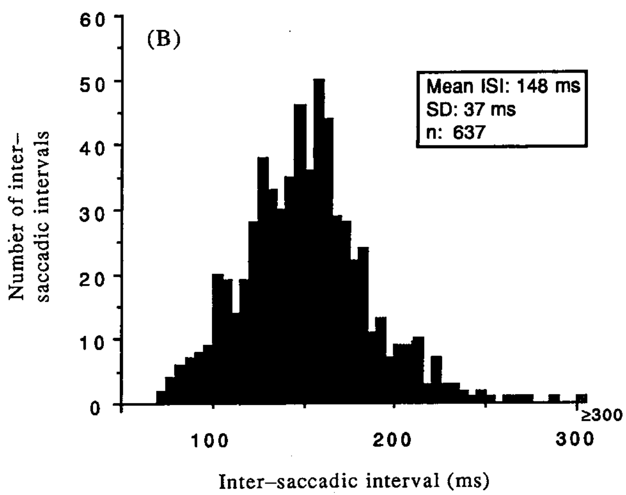


FIGURE 12. (A) Inter-saccadic intervals became shorter and less variant as training progressed (monkey "C"). (B) Typical inter-saccadic interval distribution for one session of five blocks of testing in the Visual Scan task at steady state (monkey "C", target duration 67 msec). Inter-saccadic interval (ISI) histograms were always unimodal for both monkeys, even though they often encroached into the "express" range of latencies (below 95 msec or so). SD, standard deviation; *n*, total number in histogram.