

Express Saccades: the Effects of Spatial and Temporal Uncertainty

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Received 10 March 1993; in revised form 26 April 1993

Once trained to make express saccades, monkeys continue to make express saccades when there is a high level of uncertainty about both the location and the time of onset of a peripheral target. Providing additional information about the location and the time of onset of a peripheral target does not increase the frequency of occurrence of short latency saccades. Furthermore, the metrics of saccades with express latencies are typical of visually-guided saccades, rather than anticipatory movements or saccades to the remembered location of a target. Finally, practice on the gap paradigm restricted to one target location always viewed from the same initial eye position does not increase the probability of producing express saccades to the same target from other initial eye positions. Instead, the practice effect is specific to targets that have the same relative location, regardless of initial eye position.

Saccades Latency Reaction time

INTRODUCTION

In most saccade reaction time experiments, subjects are asked to look as quickly as possible to an eccentric stimulus that suddenly appears when a centrally-located fixation stimulus is extinguished. Under these conditions, simple reaction times form a unimodal distribution with modal values that usually fall between 180 and 220 msec. Saslow (1967) reported that reaction times are reduced to about 150 msec if, after the offset of the fixation stimulus, the onset of the target is delayed (the "gap") by 200 msec or more. When subjects are given extensive practice with the gap paradigm, a bi- or tri-modal distribution of reaction times may be observed (Fischer & Boch, 1983; Fischer, Boch & Ramsperger, 1984). Boch and Fischer (1986) labeled the peaks of the multimodal distribution as regular long latency saccades (mode = 230 msec), regular short latency saccades (mode between 150 and 200 msec), and express saccades (modal values between 90 and 130 msec).

The extremely short reaction times of express saccades are of particular interest because when afferent delays from retina to central visual areas and efferent delays from motoneurons to extraocular muscles are subtracted, very little time remains to compute the location of the target and to program the direction and amplitude of the saccade. Since both the location of the saccade target and the time of target onset were highly predictable in most experiments in which express saccades have been observed, the direction and amplitude of express saccades could be preprogrammed and triggered

by the offset of the fixation stimulus (Kalesnykas & Hallet, 1987). The major goal of the experiments described in this paper was to see if the "gap paradigm" produced express saccades when there was a high degree of spatial uncertainty about the location of the saccade target and temporal uncertainty about the time of target onset.

The percentage of trials with express saccade latencies increases with practice and the increase in frequency of express saccades is greatest for targets used during training (Fischer *et al.*, 1984; Fischer & Ramsperger, 1986). The selectivity of the practice effect raises questions about the level of neural representation where these changes occur. Accordingly, a second goal of the experiments was to determine if express saccades are programmed in relative (retinal or motor error) or spatial (head or body) coordinates.

METHODS

Experimental subjects and recording procedures

Three adult rhesus monkeys (*Macaca mulatta*) served as subjects. A small square steel post secured to the skull by stainless steel bone screws and dental acrylic was used to fix the monkey's head in place during daily recording sessions. Eye position was recorded using the scleral search coil technique of Fuchs and Robinson (1966) as modified by Judge, Richmond and Chu (1980). The eye position signal, which had a precision of at least 0.25 deg, was digitized at 500 Hz and stored for later analysis. On-line measurement of saccade latency and construction of saccade latency frequency histograms aided in assessment of the animal's behavior during the course of the experiments.

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Behavioral tasks

In most experiments, targets consisted of light emitting diodes (LEDs) (0.2 deg dia) spaced at 2 deg intervals on a tangent screen. The array extended ± 24 deg horizontally and ± 20 deg vertically from the primary position. In some experiments, a small spot of light presented on a large screen oscilloscope with rapid decay phosphor (Hewlett-Packard 1310 or Hewlett-Packard 1321) served as the target. The phosphor in these monitors decayed to 10% in $<40 \mu\text{sec}$. Target presentations and delivery of rewards were under computer control.

After implantation of the scleral search coil, monkeys were trained to perform the following behavioral tasks.

Step task. In the step task, the monkey was required to look at a central fixation target for a variable period of time. The fixation time varied randomly from 200 to 1400 msec in increments of either 100 or 400 msec. At the end of this interval, the fixation light was extinguished, and, simultaneously, a second peripheral target was illuminated. The monkey was required to make a saccade to the new target within 500 msec in order to receive a liquid reward.

Delayed saccade task. In this task, the monkey was required to fixate a central target (duration varied as described for the step task) and maintain fixation while a second target was presented in the periphery. After 100 to 500 msec, the central fixation target was extinguished, and the monkey was rewarded for looking to the peripheral target within 500 msec.

Gap task. This was the task used by Fischer and Boch (1983) to elicit express saccades. The offset of the fixation target (duration varied as described for the step task) was followed by an interval (the "gap") in which the monkey was required to keep its eyes directed towards the position of the now absent central fixation target. At the end of this period, a target was presented in the periphery. Reward was contingent upon a saccade to the new target within 500 msec. On some gap trials (usually 10–15%) the central fixation target, rather than a peripheral target, was relit. On these "catch" trials reinforcement occurred only if the eyes remained directed at the central target. Insertion of catch trials reduced the probability of anticipatory saccades.

In preparation for extracellular recording experiments, which will be reported later, the monkeys were trained to make saccades to a briefly presented target (10–50 msec duration) in both the step and gap paradigms.

On all tasks, reward was contingent on the completion of saccades to a spatial window around the target (usually 1.5–2 deg on either side of the target) within 500 msec, which is much longer than the normal saccade

reaction time of monkeys. No additional reward was given for short latency saccades. The inter-trial interval varied randomly between 1 and 3 sec.

Data collection and analysis

Initially, monkeys were trained on the step and delayed saccade task. Once proficient in these tasks they were trained on the gap task and behavioral data were collected.

Measurement of saccade onset and offset was done by computer according to a velocity criterion (40 deg/sec). Automatic measurements were checked visually on a trial by trial basis.

RESULTS

Effects of spatial and temporal uncertainty

The monkeys learned the gap paradigm quite readily and following approx. 2 weeks of training made a high percentage of express saccades. All three monkeys made express saccades on gap trials when the location and timing of target presentation were randomized.

Figure 1 shows the results from one monkey (M334) for a single behavioral session. This monkey had run on the same set of targets on the previous 10 days (approx. 800–1000 trials per day) and had received training on gap trials for a total of 20 sessions. Within this recording session, a single block of approx. 200 step trials was followed by a block of approx. 425 gap trials. During the blocks of either step or gap trials, the target randomly appeared at one of 10 locations: either 8 or 12 deg to the right with an elevation of -8 , -4 , 0 , 4 , or 8 deg. The gap duration was randomly selected from one of the following values: 200, 250, 300, or 350 msec. No catch trials were included in this session. Saccade latency was little affected by gap duration [Fig. 4(A)] for the range of gaps used in this session. For this reason, results from trials of all gap durations were pooled and the histograms of step and gap trials compared. The saccade latencies observed on gap and step trials clearly fell into two almost non-overlapping groups. The majority of saccades made by the monkey on gap trials were in the range of express saccades (as reported by Fischer & Boch, 1983) for all 10 targets even though the time of the target onset (relative to either the start of the trial or the offset of the fixation light) and the target location were selected at random.

Data from a second monkey (M335) were collected in a manner identical to that just described. These data are presented in Fig. 2. This monkey had almost daily training in the gap paradigm for 27 sessions, but she had trained with this target set for only the last six sessions.

FIGURE 1 (*facing page*). Histograms of saccade latency for step (up histograms) and gap (down histograms) trials. Each pair of histograms shows latencies for saccades to one of 10 target locations: 8 or 12 deg to the right with an elevation of -8 , -4 , 0 , 4 , or 8 deg. These data were collected in a single session from M334. A single block of approx. 200 step trials was followed by a block of 425 gap trials. No "catch" trials were included. The gap duration was randomly selected from values of 200, 250, 300, 350 msec. Trials of all gap durations were merged for these histograms since latency was unaffected by gap duration [see Fig. 4(A)].

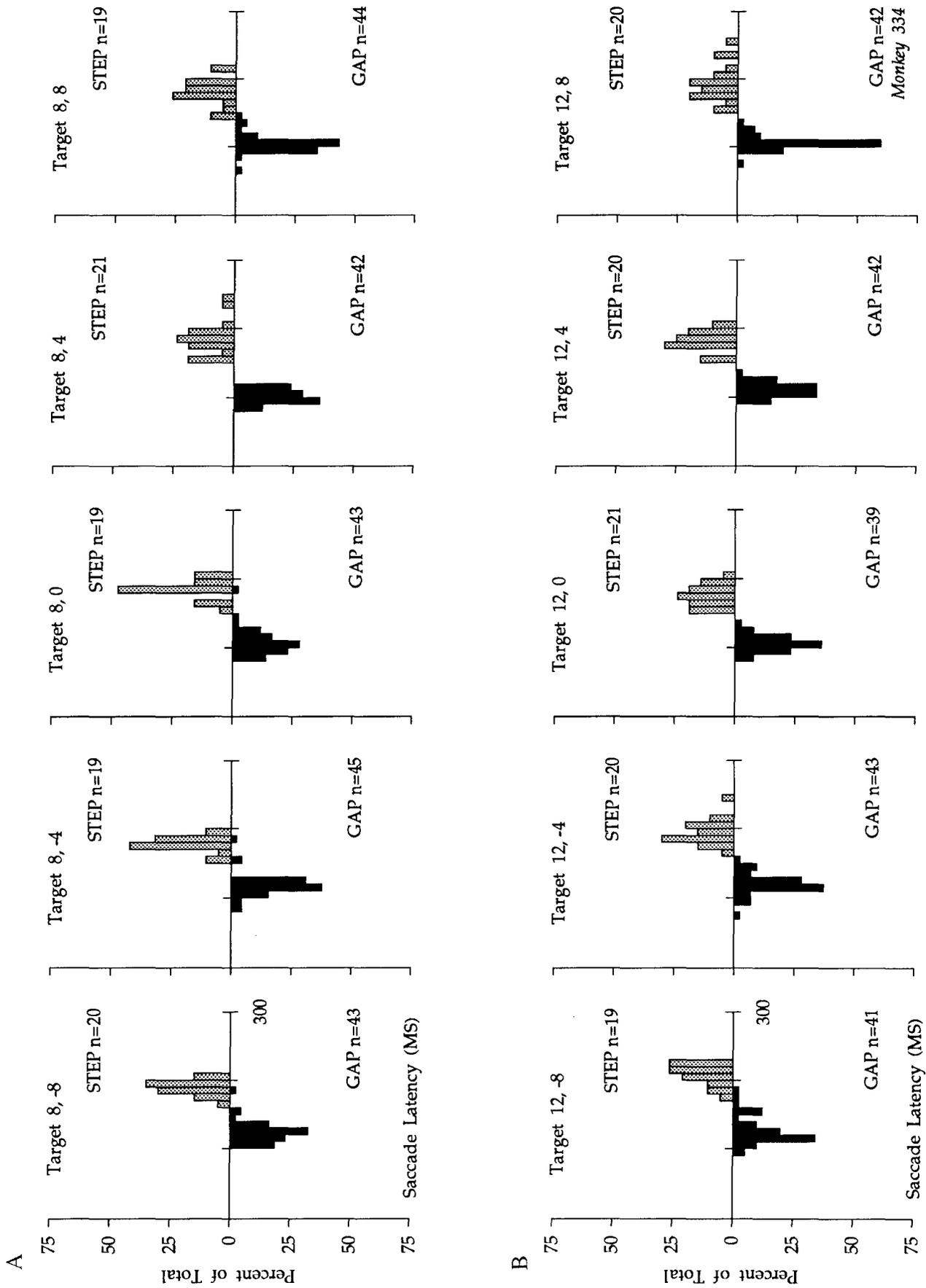


FIGURE 1

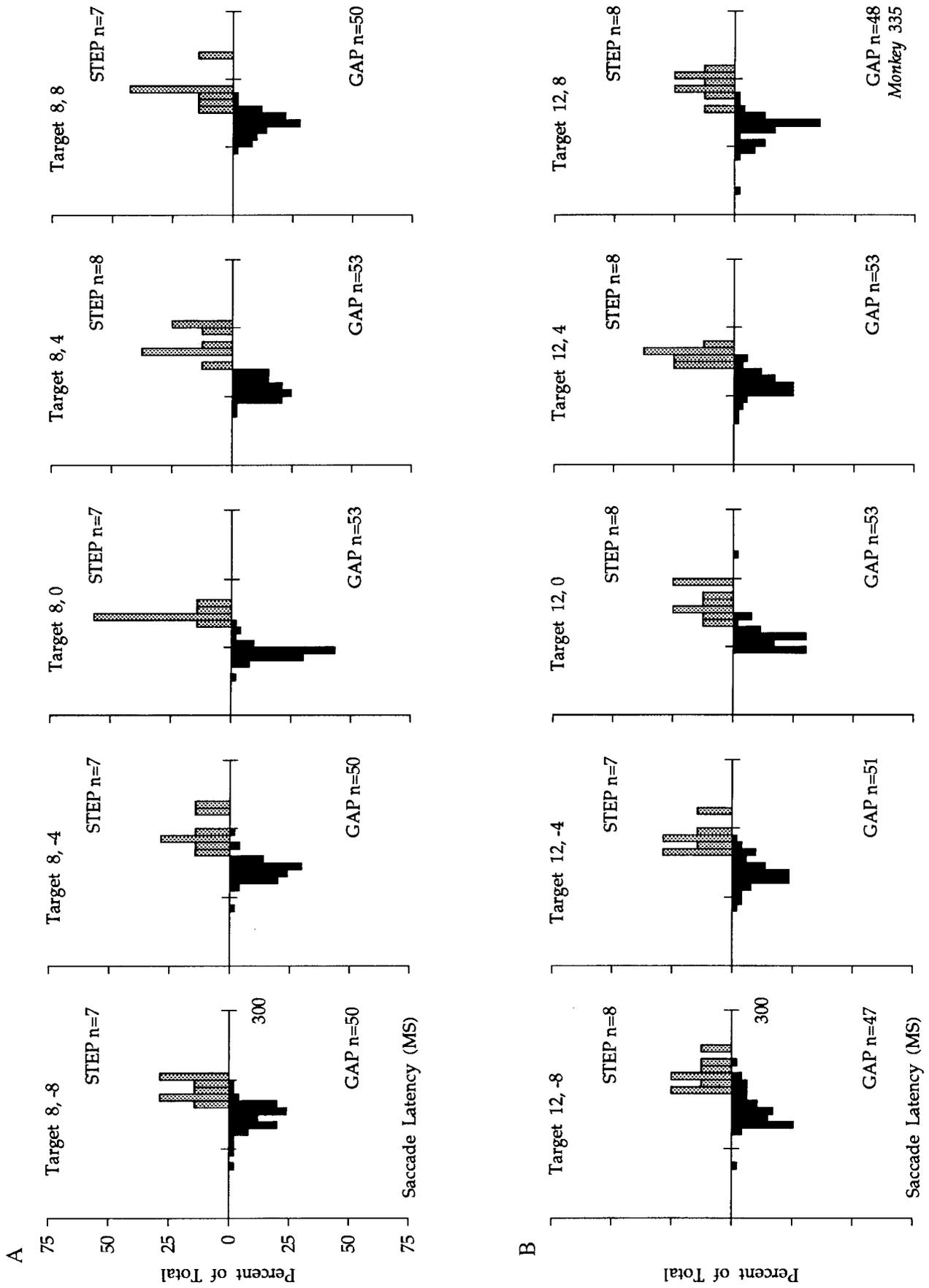


FIGURE 2

The monkey completed a block of 75 step trials followed by a block of approx. 500 gap trials. As was the case with M334, gap duration had little influence on saccade latency [Fig. 4(B)] so results for all gap intervals were pooled and the histograms of saccade latency for individual targets compared. The latencies of saccades to all targets were markedly shorter on the gap trials than on the step trials; their distributions barely overlapped for most targets. In contrast to the results from M334, however, this monkey's saccade latencies on the gap trials were longer and overlapped the distribution of latencies on step trials.

Figure 3 summarizes the saccade latency data from Figs 1 and 2. The mean saccade latency for both gap and step trials is plotted for each target location. Saccade latency was essentially independent of target location for M334 [Fig. 3(A)]. The mean saccade latency on all gap trials combined was 112 msec and for all step trials combined was 186 msec. The difference in mean saccade latency between the step and gap trials (all target locations combined) was 74 msec for M334. This difference was statistically significant ($P < 0.0001$) as shown by a *t*-test. When target locations were considered individually, the difference between the mean saccade latency on gap and step trials ranged between 61 and 88 msec (mean = 75, SD = 8.4).

Target location had a clear effect on the latency distribution in both gap and step trials for M335 which is evident in both Figs 2 and 3(B). Saccades to targets with elevation zero had shorter latencies than saccades to targets at elevations -8 , -4 or 8 regardless of trial type. This difference was not due to practice effects since M335 had equal experience with all targets. However, the mean difference in saccade latency between gap and step trials for each target location did not vary more than it did for the other monkey. The difference in the mean saccade latency for step and gap trials for individual target locations ranged from 41 to 67 msec with a mean of 53 msec (SD = 7.7). The mean saccade latency on all gap trials combined was 126 msec and for all step trials combined was 179 msec. The difference in mean saccade latency between the step and gap trials was 53 msec which is statistically significant ($P < 0.0001$) as shown by a *t*-test for unequal sample size.

The duration of the gap had little effect on saccade latency in gap trials. Figure 4 plots saccade latency as a function of the gap interval for all target locations combined. Mean saccade latency for each of the four gaps ranged between 107 and 119 msec for M334 and between 119 and 137 msec for M335. For both monkeys, the amount of variation in saccade latency on gap trials was almost constant for all gaps (range of SDs = 13–20 in M334 and 23–31 in M335) and comparable to

that seen on step trials (SD = 19 in M334 and 25 in M335).

The number of gap durations or target locations included in the session had little effect upon average saccade latency or the frequency of express saccades. Figure 5 compares saccade latencies from a block of trials in which a single gap duration and target location were presented with a block of trials in which multiple gap durations and target locations were presented. This figure includes latency data collected in the same session as the data presented in Fig. 1 for M334. Data for M335 are from two sessions: the multiple target/gap data is the same as that in Fig. 2, while the single target/gap data is from a session 6 days later. The upper histogram of saccade latency is from a block of gap trials in which only one target location and one gap interval was used. The lower histogram of saccade latency is from a block of gap trials in which ten target locations and four gap intervals (200, 250, 300, 350 msec) were used. Results for all targets and gaps are included in this lower histogram. The mean saccade latency for M334 was 104 msec for the upper histogram and 112 msec for the lower histogram. The mean saccade latency for M335 was 132 msec for the upper histogram and 126 msec for the lower histogram. Because of the large sample size and low variance, these small differences in mean reaction time were both statistically different. But note that the direction of the change in saccade latency was different for each monkey. The mean reaction time decreased for one monkey (M335) but increased for the other monkey (M334) when the number of gap durations and target locations included in a block of trials was increased. The other major point of this analysis is that increasing the uncertainty of both the onset and location of the target for a saccade did not reduce the frequency of express saccades; the histogram profiles are similar for both trial types.

Figure 6 compares the behavior of M334 on the delayed saccade and gap tasks. Both tasks provide identical warning information to the monkey regarding the time at which a saccade is to be made. The results shown in Fig. 6(A) are for blocks of trials in which both gap and delay trial types were interleaved (randomly selected). The gap durations were 100, 200, 300 msec and the delay durations were 100 and 200 msec. The upper histogram in Fig. 6(A) shows the distribution of saccade latencies on the delayed saccade task. The mean latency was 217 msec. The lower histogram shows the distribution of saccade latencies on gap trials. The mean latency was 132 msec. The distributions were almost non-overlapping and statistically different ($P < 0.0001$). Figure 6(B) compares the monkey's behavior during a block of trials in which only gap trial types were

FIGURE 2 (opposite). Histograms of saccade latency for step (up histograms) and gap (down histograms) trials. Each pair of histograms shows latencies for saccades to one of 10 target locations: 8 or 12 deg to the right with an elevation of -8 , -4 , 0 , 4 , or 8 deg. These data were collected in a single session from M335. A single block of approx. 75 step trials was followed by a block of 500 gap trials. No "catch" trials were included. The gap duration was randomly selected from values of 200, 250, 300, 350 msec. Trials of all gap durations were merged for these histograms since latency was unaffected by gap duration [see Fig. 4(B)].

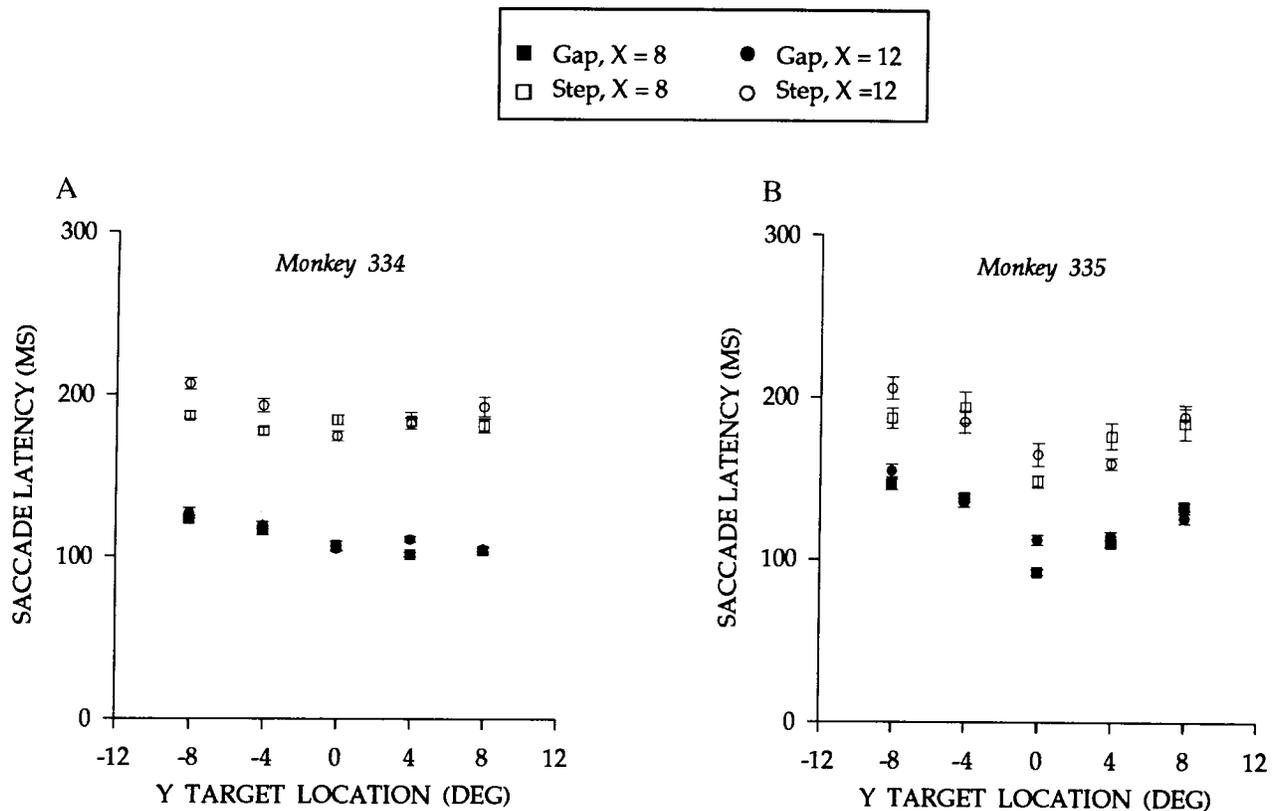


FIGURE 3. Plots of the mean and standard error of saccade latency for individual targets. The data are from the same sessions shown in Figs 1(A) and 2(B). Solid symbols represent gap trials. Open symbols represent step trials. Boxes are used for targets which appear 8 deg to the right. Circles are used for targets 12 deg to the right.

presented (upper histogram, mean = 118 msec) with the behavior on gap trials when interleaved with delayed saccade trials [lower histogram, same as Fig. 6(A)]. The distributions were similar, but the mean reaction time during a block of gap trials (118 msec) was faster ($P < 0.0001$) than the mean reaction time when gap and delayed saccade trials were interleaved (132 msec). Note, however, that the monkey was unable to use either the spatial or temporal information available to it in the delayed saccade task to reduce saccade latency. In fact, the mean latency on this task was actually higher than on step trials [217 msec vs 186 msec, compare with Figs 1 or 3(A)] as has been observed by Boch and Fischer (1986).

If express saccades result from a strategy of guessing the time of target onset based on the recent history of gap durations, then on some trials the monkey should anticipate incorrectly and move prior to the target onset. The behavior of M335 was examined on the "catch" trials in which the fixation target was re-illuminated following the gap. The monkey was rewarded only if the eyes did not move from the fixation point (no target present) during the gap. Data were taken from five sessions in which 10% of the trials were "catch" trials. Of 295 "catch" trials, the monkey aborted the trial by leaving the fixation window on only six trials (2%). This rate of failure is comparable to that seen on

step trials. The end points of saccades on the aborted trials were not close to the targets used for the gap trials.

Metrics of the express saccades

If express saccades are anticipatory movements, their accuracy should be severely compromised (Findlay, 1981; Bronstein & Kennard, 1987; Kalesnykas & Hallet, 1987) and the velocity should be reduced (Bronstein & Kennard, 1987) compared with visually-guided saccades. Figure 7 compares the velocity and accuracy of saccades on gap and step trials from the same two sessions plotted in Figs 1 and 2. Peak vectorial velocity is plotted for each target location in Fig. 7(A, C). Vectorial error is plotted for each target location in Fig. 7(B, D). The performance of M334 was nearly identical on both measures for all target locations regardless of the trial type. The difference between the two trial types is not statistically significant on either measure. Likewise, M335 showed no statistical difference between the results obtained from gap and step trial types for peak vectorial velocity. However, M335 did exhibit greater variability in peak vectorial velocity for most target locations than M334, but this may be due to the high percentage of corrective saccades generated by M335 irrespective of trial type (step = 28%; gap = 35%). For M335, average error on gap trials was significantly larger than on step trials ($t = 5.18$, $P < 0.01$), but the absolute difference was

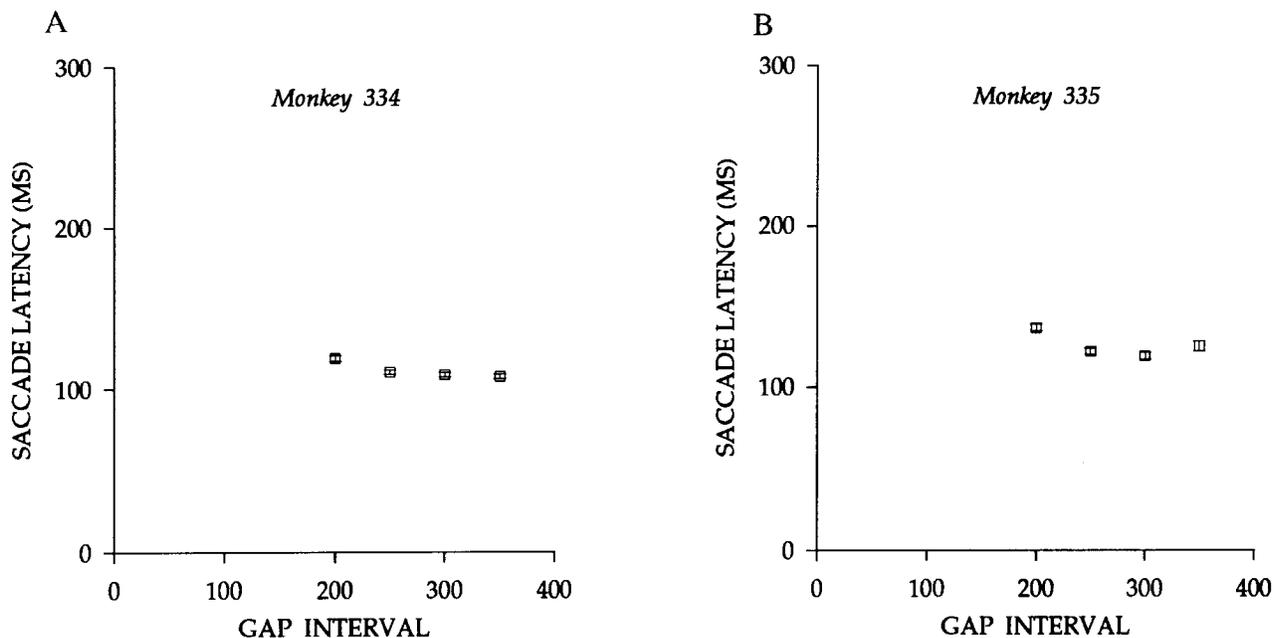


FIGURE 4. Mean and standard error of saccade latency as a function of gap interval. The data are from the same sessions shown in Figs 1(A) and 2(B). The data from all 10 target locations are included.

small (0.3 deg). Given that M335 used two saccades to acquire targets on a significant percentage of trials, the average error at the end of an express saccade was small (mean = 1.0 deg).

Effect of initial eye position on express saccade occurrence

Monkeys make a large number of express saccades to targets located near targets to which the animal has practiced in the gap trial type (Fischer *et al.*, 1984; Boch

& Fischer, 1986). How this spatial specificity is determined is unknown. Some brain areas (e.g. the superior colliculus) encode normal latency saccades in terms of motor error, the *change* in eye position required to look to a target (Mays & Sparks, 1980; Sparks & Mays, 1983). If express saccades are a distinct class of movement their representation could be in a different frame of reference. For example, they could be coded by specifying movements that direct gaze to a

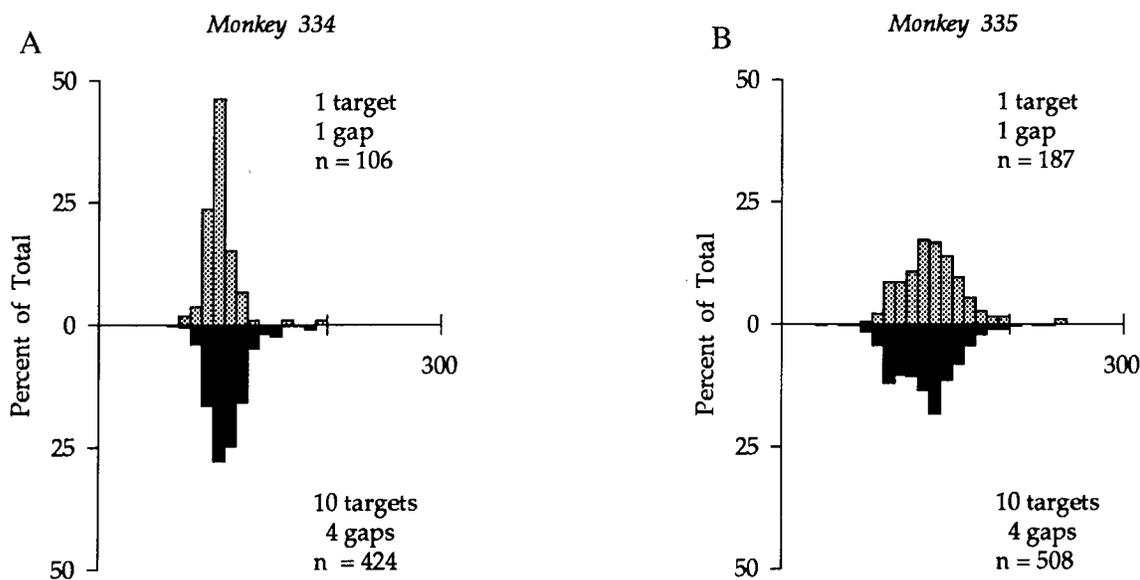


FIGURE 5. The effect of varying the number of targets and number of gap intervals upon saccade latency. Up histograms are for a block of trials with 1 target (8 deg to the right and 8 deg above the fixation point), 1 gap duration (300 msec). Down histograms are for a block of trials with 10 targets and four gap durations. Results are shown for all target locations. (A) Results from M334 in the same session illustrated in Fig. 1(B). Results from M335 were collected in two sessions.

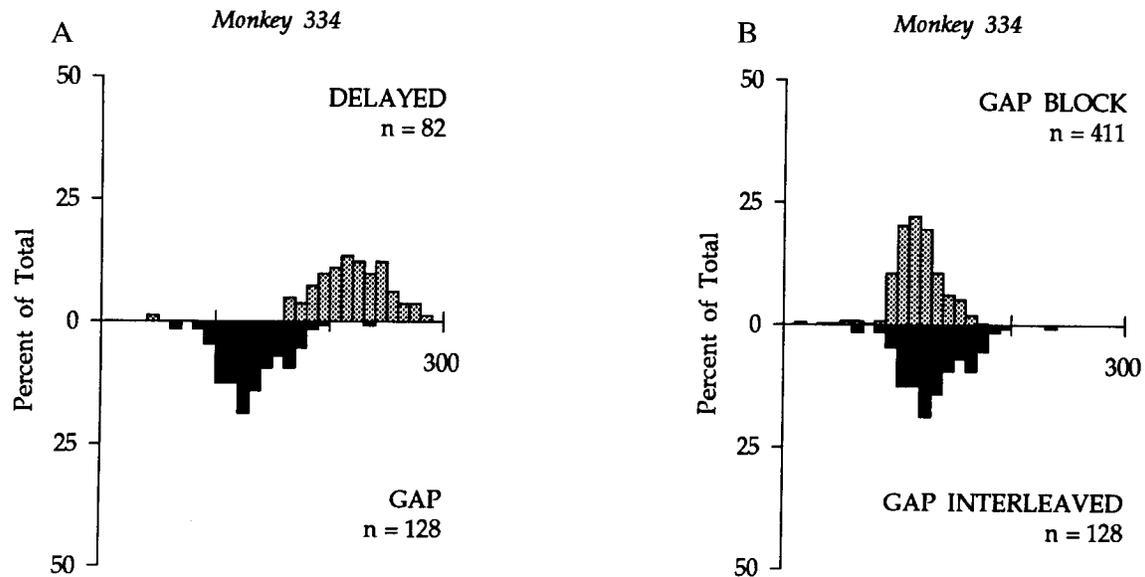


FIGURE 6. (A) Comparison of saccade latency on delayed (up histograms) and gap (down histograms) trials when both trial types are presented randomly within the same block of trials. (B) Comparison of saccade latencies on gap trials when presented in a block (up histograms) or when both gap and delayed trial types are interleaved in the same block of trials [down histograms, same as in (A)]. All plots are for a single session with M334. Results for all 10 targets were pooled.

particular location in space, rather than motor error. To distinguish these two possibilities, M334 was trained to make express saccades to two targets from a fixation point placed close to the primary position. Then experiments were conducted in which the location of the fixation point was varied but saccade amplitude and direction remained the same. If the monkey continued to make saccades with express latencies, this would be consistent with express saccades being coded in relative coordinates (changes in eye position); if she failed to make express saccades, then express saccades may be coded in an alternative fashion. The results for this experiment are presented in Fig. 8. The monkey was trained to make express saccades to target locations $-8, 8$ or $-8, -8$. Figure 8(B, E) shows histograms of saccade latency on trials in which the fixation LED was positioned near the center of the visual field (the location used during training). The monkey made saccades on gap trials with latencies distinctly shorter than on step trials. Figure 8(A, D) shows the latency histograms when the fixation point was moved to a peripheral location 8 deg to the left of the primary position. Figure 8(C, F) shows the latency histograms when the fixation point was moved to a peripheral location 16 deg to the right of the primary position. In neither case was the frequency of occurrence of express saccades diminished. These results support the notion that express saccades, like normal latency saccades, are represented in terms of changes in eye position. Performance of express saccades proceeds independently of the target location in space.

Results of another experiment which examined the same problem are shown in Fig. 9. M335 was trained to make express saccades to a target 6 deg right and

6 deg up with an initial eye position near the center of the orbit. In this session, the fixation point was moved to eight different locations around the original target location in space. The position of the target in space was fixed for all trials, but the movement required to reach the target differed depending upon initial eye position. The results clearly show that a significant number of saccades of short latency occurred only when the direction and amplitude of the required saccade was similar to those made during the training sessions. However, latency histograms for all movement vectors except Fig. 9(E, F) shows a reduction in the saccade latency on gap trials relative to that on step trials. The latency of these movements was similar to those of step trials in the experiment shown in Fig. 2. These would correspond to the regular short latency saccades of Fischer. These data suggest that the process of learning to make saccades with express latencies develops through a substrate which is organized in terms of changes in eye position rather than movements to an absolute location in space.

DISCUSSION

Express saccades occur despite uncertainty

Fischer and Boch (1983) claim that the short-latency saccades occurring on gap trials represent a separate category of saccadic eye movements. However, almost all experiments in which express saccades have been observed failed to randomize *both* target location and the time of target onset. Either timing or location was randomized, but not both (e.g. Fischer & Boch, 1983; Fischer & Ramsperger, 1984, 1986; Boch & Fischer, 1986; Jüttner & Wolf, 1992). Indeed, it has been

suggested (Kalesnykas & Hallet, 1987; Kowler, 1990) that saccades with extremely short latencies, rather than representing a separate category of saccades, occur because subjects can predict either the target location or

the time of target onset. The major purpose of these experiments was to test this hypothesis.

We measured the reaction time of saccades when both the location (amplitude and direction) of the targets and

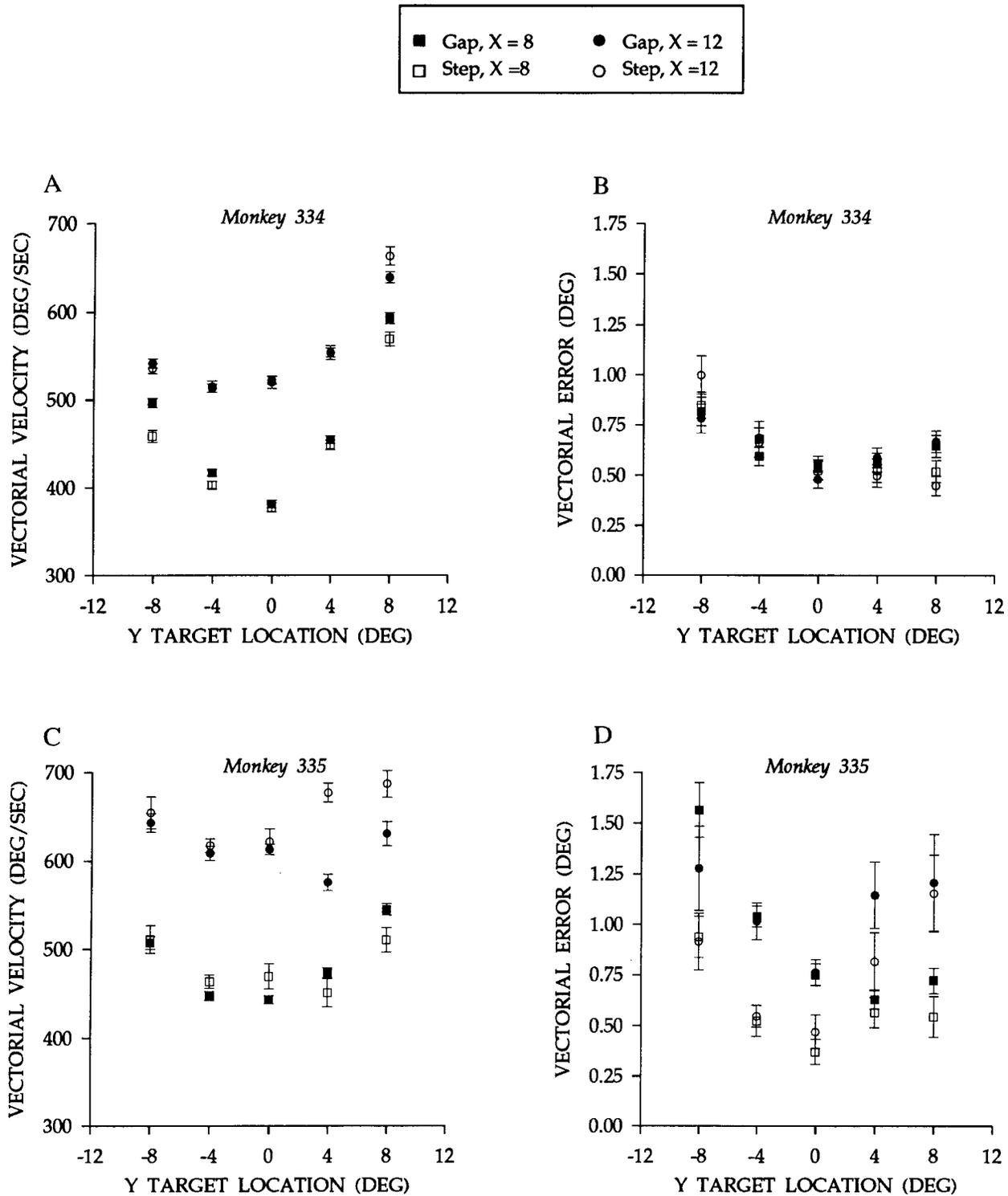


FIGURE 7. Metrics of saccades on step and gap trials. (A, C) Comparison of the mean and standard error of peak saccade velocity for step and gap trials. (B, D) Comparison of the mean saccade vector error for step and gap trials. The mean and standard error are plotted for each target. The data for M334 are shown in (A) and (B); data for M335 are shown in (C) and (D). Solid symbols represent gap trials; open symbols represent step trials. Squares represent targets appearing 8 deg to the right; circles represent targets 12 deg to the right. Data are from the same two sessions as shown in Figs 1 and 2.

the duration of all time intervals comprising a trial were randomly varied. We observed a high percentage of express saccades on gap trials, even when many target locations and gap durations were randomized within the same session. Express saccades were observed

in sessions with as many as 10 targets and four gap durations spanning 150 msec (Figs 1-3). These results indicate that saccades with express latencies are not due to anticipating the onset of a target at a known location.

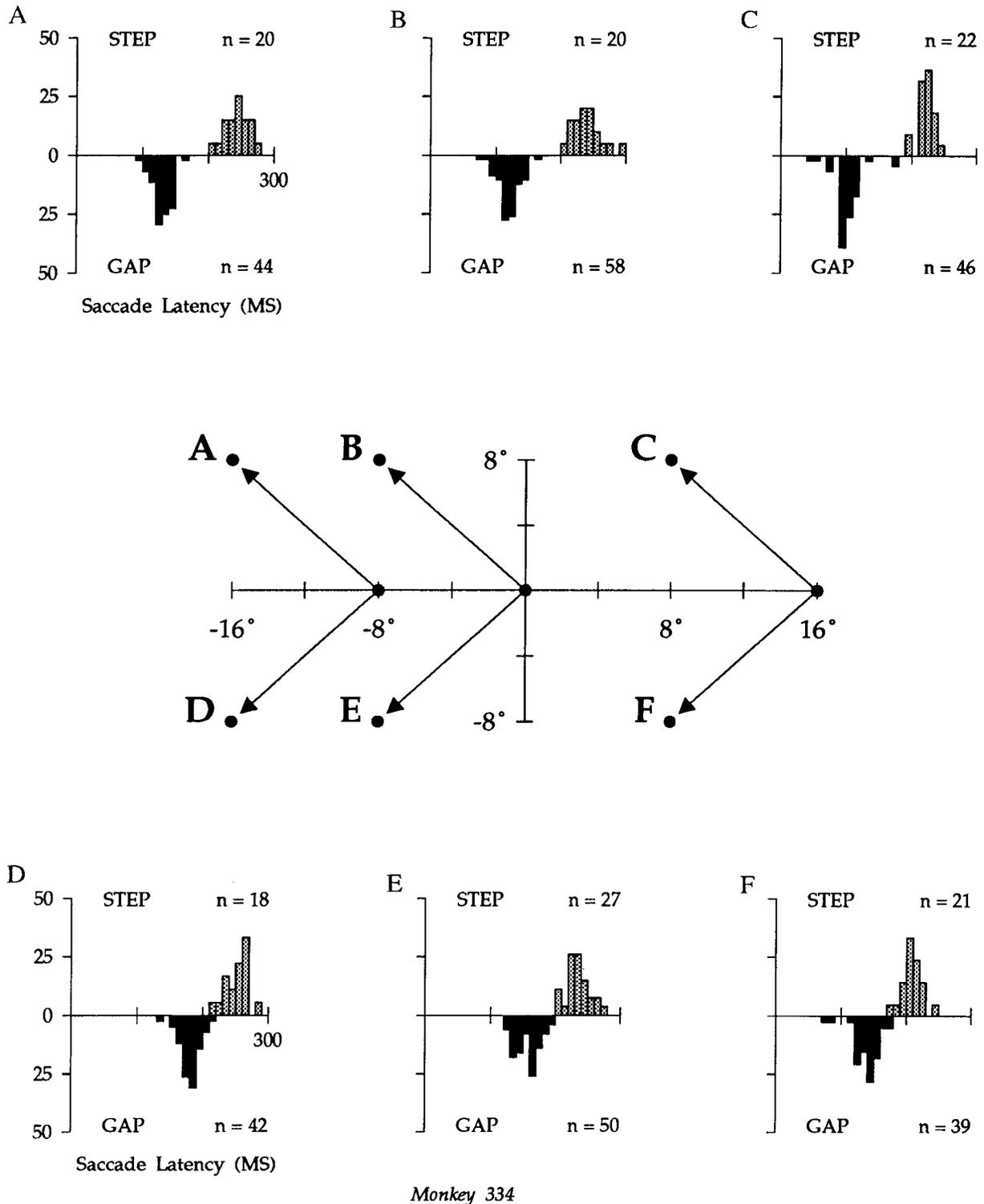


FIGURE 8. Effect of initial eye position on the occurrence of express saccades. The center figure shows the start and end points of the movements tested. The latency histograms across the top and bottom go with the correspondingly labeled movement. The monkey had been trained in the gap paradigm for movements (B) and (E) initiated from the primary position. Movements (A), (D), (C), and (F) were initiated from the eccentric positions shown. Results are for M334 and were collected in a single recording session. Step and gap trials were randomly interleaved.

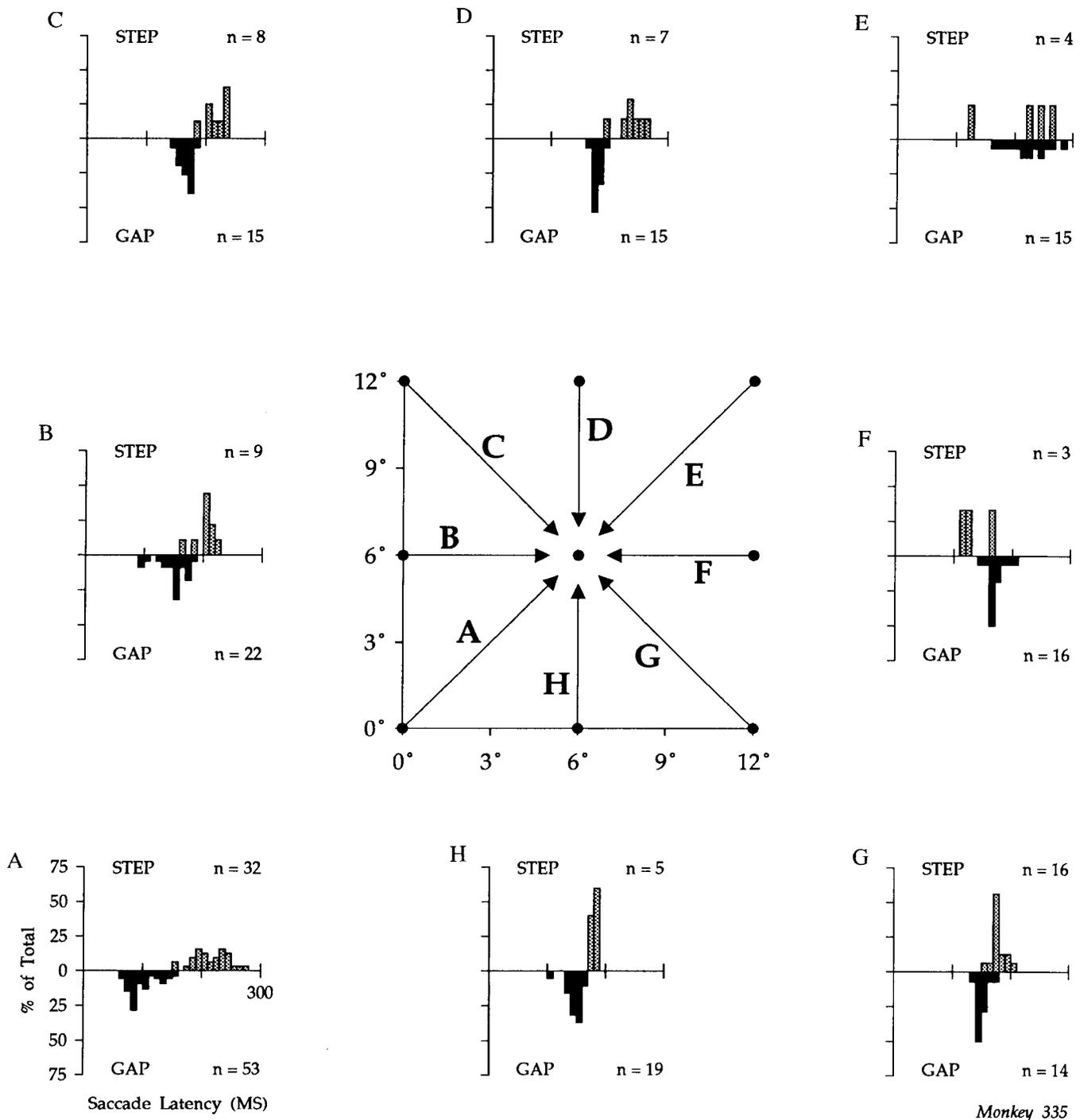


FIGURE 9. Saccade latencies on trials in which the target location in space remained constant, but the trajectory of the movement required to reach the target was altered by varying the initial fixation position. The monkey had received extensive training on the gap paradigm with a single central fixation position (0,0) and a single eccentric target located 6 deg to the right and elevated by 6 deg. Step and gap trial types were interleaved (30% step; 70% gap). Results are shown for gap 300. Results are for M335 and were collected in a single recording session.

The frequency of express saccades does not increase under predictable conditions

If the short latency of express saccades is based on knowledge of the target locations and gap durations obtained from previous trials, then performance should be improved by reducing the variability of target location and time of onset. We tested the monkey's

performance under two conditions in which the predictability of the stimulus onset was reduced relative to the first experiment.

First, we compared the performance in blocks of trials in which there was only one target and one gap with blocks of trials in which there were ten targets and four gaps. Reducing uncertainty about the location and time of target onset did not reduce the latency of saccades on gap trials for either monkey (see Fig. 5). Reaction time

Monkey 335

distributions were virtually the same under the two conditions.

Second, we compared performance on gap and delay trials. If express saccades occur on gap trials because of information about target location and onset gained from previous trials, then express saccades should also occur on delayed saccade trials. In the delayed saccade task, the target is presented for a variable period (delay duration) before the fixation light disappears. The same information about the time at which to initiate the saccade is available on both delayed and gap trials. The delay duration (delay task) and gap duration (gap task) each could act as a warning signal. Furthermore, in the delayed saccade task, information about the exact target location is available prior to the offset of the fixation light; this eliminates the spatial uncertainty which exists in the gap task. A clear dichotomy in performance was observed: saccades with express latencies occurred on gap trials, but not on delayed trials (see Fig. 6). Thus, neither the warning period nor prior knowledge of target location are sufficient to produce express saccades on delayed trials. These findings confirm an earlier observation of Boch and Fischer (1986) when they used a delayed saccade task as a control condition and failed to observe express saccades.

Express saccades are not anticipatory

Several lines of evidence support the assertion that express saccades are made in response to the target and are not anticipatory movements to the remembered locations of targets.

The latencies of express saccades are independent of the gap duration, within the range used in our experiments (see Fig. 4). This finding corroborates the findings of earlier experiments using gaps in this range (Fischer & Ramsperger, 1984; Reulen, 1984a, b). If express saccades occur because the average of the gap durations used on earlier trials is used to predict the time of target appearance, this should be reflected in the latency distributions. Latencies of movements on trials with gap durations shorter than the average should be longer than the latencies of movements on trials with gap durations longer than the average. Such a relationship between saccade latency and gap duration was not observed for either animal (see Fig. 4). Furthermore, if such a strategy were being used, then the variation of the saccade latencies should reflect the range in the gap durations used in a recording session. This was not the case. The variation in latency observed when a single gap was used was comparable to that observed when four gaps were used (see Fig. 5).

An alternative strategy would be to initiate a saccade at the time of the shortest gap in the session. Such a strategy would result in an inverse relationship between gap duration and latency; latency would be short on trials with a long gap duration. This result was not obtained. The results indicate that the gap is not acting as a precise temporal cue although it could serve as a warning cue.

Catch trials provide additional evidence that the monkeys were not making anticipatory movements. De-

tectable saccades occurred on only two percent of the catch trials. A much higher rate of movements on catch trials would be expected if saccades with express latencies were based upon prediction of the time of target onset.

Finally, the metrics of anticipatory and visually-guided saccades are different (Kalesnykas & Hallet, 1987; Bronstein & Kennard, 1987). Compared to visually-guided movements, both the accuracy and velocity of anticipatory saccades is reduced. In our experiments, neither the accuracy nor the velocity of express saccades differed.

Prediction of the target location would necessarily require the use of memory in the calculation of the target position, even if only one target location were used. Saccades to the remembered location of a target are slower and less accurate than saccades to visual targets (Becker & Fuchs, 1969; Smit *et al.*, 1987; Gnadt, Bracewell & Andersen, 1991). We found that neither the peak velocity nor the accuracy of express saccades was lower than normal latency saccades and conclude that express saccades are not directed to the remembered location of a visual target. This conclusion is supported by an additional line of evidence. The probability of a correct guess of the target location will decline as the number of targets increases (Schiller, Sandell & Maunsell, 1987). But we found no change in the frequency of occurrence of express saccades or their accuracy when the number of targets was increased.

Effects of initial eye position

Previous experiments related to the phenomenon of express saccades have always measured the reaction time of saccades that were initiated from the same initial eye position. Because of this, it is not known if the effects of practice are specific to movements of certain directions and amplitudes (motor error coordinates), movements to stimuli activating a specific region of the retina (retinal coordinates) or movements to targets located at specific locations with respect to the head or body (spatial coordinates). We found that after practice with the gap paradigm using one initial eye position, monkeys still generate a high percentage of express saccades to targets requiring movements of similar direction and amplitude, even from different initial eye positions (Fig. 8). In a related experiment (Fig. 9), we measured reaction time when the target remained at the same location in space, but saccades to that target were initiated from eight different initial positions. A high percentage of express saccades occurred only if the direction and amplitude of the movement to the target were similar to the amplitude and direction of the practiced movement. These experiments were not designed to distinguish between retinal and motor error coordinates, but our findings do indicate that express saccades are encoded in relative rather than absolute coordinates.

Alternative explanations of express saccades

If express saccades are not based on advanced information about the location and time of appearance of a

visual target, what accounts for their extremely short latency? A number of other explanations have been proposed: sensory facilitation (Reulen, 1984a, b), facilitated premotor processes (Reuter-Lorenz, Hughes & Fendrich, 1991), attentional disengagement (Fischer, 1987; Fischer & Breitmeyer, 1987), early preparation of motor programs (Kowler, 1990), and an early decision to execute a saccade (Becker, 1989). While not designed to test these hypotheses, our results relate to some of the assumptions of certain models.

Attentional disengagement. According to Fischer *et al.* (Mayfrank, Mobashery, Kimmig & Fischer, 1986; Fischer, 1987), three sequential processing steps are required for the generation of a saccade. First, visual attention must be disengaged from its current spatial location. Following the decision to initiate a saccade (step two), the amplitude and direction of the saccade are computed in the final processing stage. Note that two of these processes, disengagement of attention and the decision to initiate a saccade, could occur before the onset of an eccentric target. Indeed, one proposed explanation for the occurrence of express saccades on gap trials is that the offset of the central fixation stimulus produces an early release of visual attention. According to this hypothesis, saccades with express latency occur because one of the three sequential stages of processing (disengagement of attention) is complete before target onset. Several lines of evidence indicate that early attentional disengagement produced by the offset of the fixation stimulus cannot be the sole explanation of saccades with express latency. First, express saccades can occur when the fixation stimulus remains present throughout the presentation of the eccentric visual target (Boch & Fischer, 1986). Second, the reduction in latency associated with gap trials does not occur if subjects are instructed to direct saccades away from the target (Reuter-Lorenz *et al.*, 1991; Fischer & Weber, 1992). This is not the expected result if disengaging attention fully accounts for the short latency. Finally, the findings that the reduction in latency following practice on gap trials is specific to the target used during the practice session (Fischer *et al.*, 1984; Boch & Fischer, 1986) and is sensitive to the initial eye position of the eye relative to the target location (Fig. 9), are not consistent with early attentional disengagement as the sole explanation of express saccades.

Early preparation of motor programs. Kowler (1990) suggested several means by which the warning signals available on the gap task could initiate preparation for a movement before the location of the target is known. In two previous studies (Schiller *et al.*, 1987; Wenban-Smith & Findlay, 1991) which observed express saccades when both the location of the targets and the duration of the gap were randomized, target *direction* was randomized, but the *amplitude* of the target displacement was fixed. Thus, Kowler argued that the amplitude of the movement could be preprogrammed before target onset and speed the computation of the saccade metrics. This could not account for the express saccades observed in our experiment because both the direction and ampli-

tude of the required saccade were randomized. Kowler (1990) also noted that experiments in which express saccades have been observed used a small number of potential targets. Thus, according to Kowler, it would be possible to store prepared motor programs in a memory buffer that is scanned for the appropriate program after a signal to initiate the movement. This type of early preparation of motor programs does not seem to account for the latency difference we observed on gap and delayed trials. The same target set was used for both trial types and subjects had extensive practice in both conditions. The prepared motor programs should be the same for both gap and delayed trials but express saccades occurred on gap trials but not on delayed trials.

Early decision for saccade execution. The results of our experiments indicate that the extremely short latencies of express saccades cannot be based solely upon prior knowledge about the location at which a target will appear or upon predictability of the time of target appearance. Our results also support earlier findings indicating that early disengagement of attention from the fixation stimulus is not the only reason for the occurrence of express saccades. These negative findings lend some support to the hypothesis (Becker, 1989) that express saccades occur because of an early decision to execute a saccade. To account for the fact that practice on gap trials increases the probability of express saccades for target locations used during the training sessions, but not for other targets, Becker (1989) hypothesized that practice on gap trials produces local changes on a topographically organized decision map. Our data indicate that any such decision map must be organized in relative, rather than absolute, coordinates.

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Acknowledgements—The authors thank Richard Scheetz for creation of the original data collection program, Kathy Pearson for further development of the collection and data analysis programs, and Isabel Ragland for technical assistance. This work was supported by NIH grants EYO1189 and P30 EY03039.