

# How do target predictability and precueing affect the production of express saccades in monkeys?

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*Keywords:* eye movements, Rhesus macaque, saccades, target selection

## Abstract

The extent to which target predictability and precueing affect express saccade generation was determined in Rhesus monkeys. Target predictability, as manipulated by the probability with which targets appeared at various locations, had a strong influence on express saccade generation. Pre-cueing the location of the appearance of an impending single target with an identical stimulus was effective in increasing express saccade generation when there was a gap of 50–150 ms between fixation spot termination and target onset. However, precueing was not effective when the gap time was set to 0 ms in the single target task, when several simultaneous targets appeared requiring a visual discrimination to be made using an oddity task, or when the precue was not identical to the target. These findings indicate that express saccades are facilitated by a restricted set of conditions that increase the predictability of target location and identity.

## Introduction

When primates are trained to make saccadic eye movements to single targets appearing in the visual field, a bimodal distribution of saccadic latencies is often obtained. (Fischer & Boch, 1983; Fischer & Ramspersger, 1984; Fischer & Boch, 1986; Schiller *et al.*, 1987; Kowler, 1990; Fischer & Weber, 1993; McPeck & Schiller, 1994; Paré & Munoz, 1996). Boch and Fischer termed the first mode of the distribution ‘express saccades’ and the second mode ‘regular saccades’.

It has been suggested that express saccades arise with repeated exposure to the same stimulus conditions because this increases the predictability of the target location and thus decreases saccadic reaction times (Klein, 1980; Kalesnykas & Hallett, 1987; Becker, 1989; Kowler, 1990; Paré & Munoz, 1996). We refer to this as the predictability hypothesis. An alternative hypothesis to be considered is that short-latency saccadic eye movements have emerged in the course of evolution to allow quick and expeditious responses to stimuli appearing suddenly at unexpected locations (Fischer & Weber, 1993; Ross & Ross, 1980, 1981). We refer to this as the rapid reflex hypothesis. Lastly, it has been proposed that attention or fixation disengagement triggers preparatory activity in the superior colliculus which promotes express saccade production (Fischer, 1986, 1987; Cavegn & d’Ydewalle, 1996). If predictability is central to express saccade generation, presenting targets repeatedly at specific locations should yield a higher frequency of express saccades than when targets appear at unexpected locations. The rapid reflex hypothesis makes the opposite prediction. A

pure disengagement account would not predict a modulation of express saccade frequency by target predictability.

Another way to manipulate predictability is to provide a cue as to where a target is going to appear. Several studies have been carried out using a precueing procedure in monkeys and humans. These studies show that precueing can decrease saccadic reaction times (Ross & Ross, 1981; Kimmig, 1986; Mayfrank *et al.*, 1986; Braun & Breitmeyer, 1988, 1990; Crawford & Muller, 1992; Fischer & Weber, 1993; Kingstone & Klein, 1993; Tam & Stelmach, 1993; Cavegn & d’Ydewalle, 1996; Suzuki & Hirai, 2000). However, other studies have failed to show a decrease in saccadic latencies as a result of precueing (Reuter-Lorenz *et al.*, 1991; Ro *et al.*, 2000). Furthermore, several of these studies addressed only overall reaction times and did not specifically deal with express saccade generation. In one study on Rhesus monkeys that used precueing and examined express saccade production it was found that additional information about impending target location did not increase the frequency of express saccades (Rohrer & Sparks, 1993).

The purpose of this study was to reconcile these contradictory findings by determining, in Rhesus monkeys, the role of predictability in the generation of express saccades and the effectiveness of precueing.

## Materials and methods

Three monkeys served as subjects in this study. Each animal had a head post and a scleral search coil implanted. For all surgeries, animals were first given a preanaesthetic dose of Ketamine (10 mg/kg, i.m., once) or Telazol (5 mg/kg, i.m., once). They were also given atropine prior to and during surgery (0.05 mg/kg, i.m., every 45–60 min). Anaesthesia was induced and maintained with Pentobarbital (8 mg/kg, i.v., once for induction; 4 mg/kg, i.v., as needed for maintenance).

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Received 25 November 2003, revised 3 February 2004, accepted 9 February 2004

Subsequently the alert monkeys were trained to perform on several behavioural tasks as described below. During the experimental sessions monkeys sat in a primate chair with their heads secured. They faced a colour monitor placed at a distance of 57 cm. The monitor subtended 40° of visual angle horizontally and 28° vertically. The refresh rate of the monitor was 60 Hz. Each trial began with the appearance of a central fixation spot (a circular spot 1/5° in diameter) followed by one, two or four stimuli. A saccadic eye movement made to the target stimulus was rewarded with a drop of apple juice. Eye-movement data were collected at 200 Hz using a scleral search coil, as described previously (Schiller & Chou, 2000a,b). Eye movements initiated between 50 and 105 ms after target onset were classified as express saccades; saccades with latencies >105 ms were classified as regular saccades. All animal research was carried out in accordance with guidelines laid down by the NIH and had been approved by the IACUC at MIT.

Two procedures were used in this study. In the first we assessed how the probability with which single targets appeared at various locations influenced the generation of express saccades. Single targets appeared at familiar locations with varied probabilities or were presented infrequently at unexpected locations.

The second procedure to assess the role of target predictability was to provide a cue as to where an impending target would appear. To study the effects of precueing, monkeys were run repeatedly over a period of several months during which they ran tens of thousands of trials. Several cueing procedures were tried in which the composition, the time of onset and the duration of presentation of the cue stimulus was varied. Two types of cues were then selected; both types were presented concurrently with the fixation spot but were flashed on only briefly, for 16.7 or 33.4 ms. The first cueing stimulus was a circle that was presented at the location where the target subsequently appeared. Its size was larger than the target with a diameter of 1° of visual angle and was red in colour. The target fell into the centre of the region where the cue circle had appeared. The second cueing stimulus was one that was identical to the target that was presented subsequently. Gap times between 0 and 150 ms were used. Pre-cueing was also tested using a discrimination task: four stimuli were presented, one of which, the target, was different in shape from the other stimuli, the distracters. Reward was dispensed only when the animal chose the odd target by making a direct saccadic eye movement to it. The odd stimulus, the target in this series, was always the disk. It appeared either with three crosses, three squares or three triangles. The animals performed well on this task, yielding 85–100% correct performance.

## Results

### *The role of target predictability in express saccade generation*

Two experimental conditions were used to assess the role of target predictability in saccade generation. In the first, single targets were presented repeatedly at trained locations to which express saccades to singly appearing targets had been generated with high frequency in numerous preceding sessions. To manipulate predictability, the probability with which the target appeared at the various locations was varied. Figure 1 shows the distribution of saccadic latencies obtained for two sets of conditions. The gap was held constant at 100 ms for all conditions. The data were collected in repeated separate blocks of trials using four target locations. In the first set a single target appeared at the two left locations depicted in the inset of Fig. 1 89% of the time and appeared 11% of the time in the two right locations. In the second set this arrangement was reversed. The combined data are shown for saccades made to the high and low probability locations. The monkey

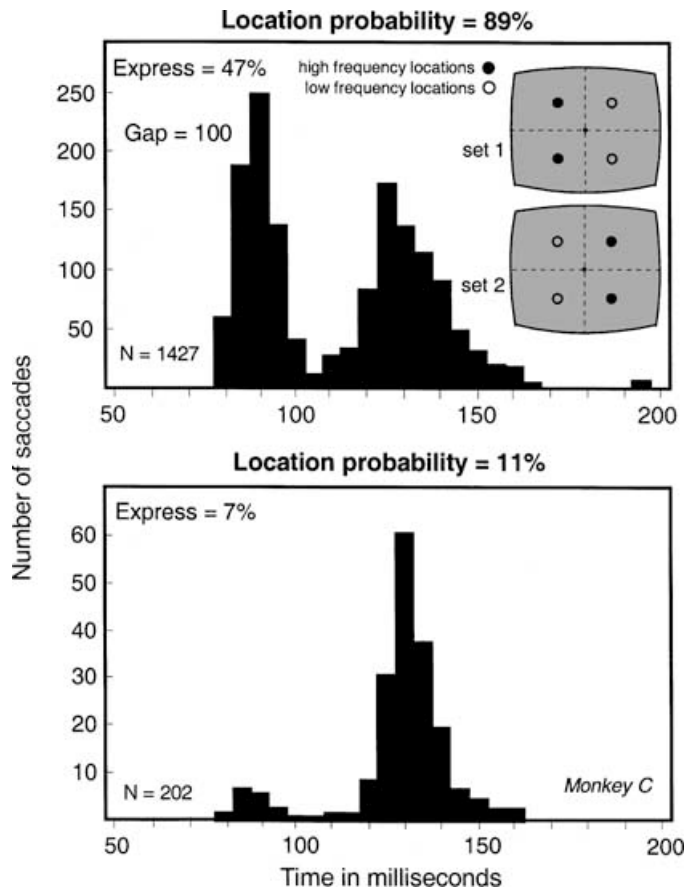


FIG. 1. The distribution of saccadic latencies obtained with targets presented with various probabilities at selected locations. The top panel shows the distribution obtained when saccadic eye movements were made to high probability locations (89%). The bottom panel shows the latency distribution obtained when saccades were made to low probability locations (11%). At high probability locations express saccades were generated 47% of the time whereas at low probability locations they were generated only 7% of the time. The high and low probability locations were reversed in separate blocks of trials.

made 47% express saccades to targets appearing at high probability locations and only 7% saccades to targets appearing at low probability locations. This difference was statistically significant ( $\chi^2 = 226.90$ , d.f. = 1,  $P < 0.001$ , Yates-corrected). This suggests that target predictability plays a central role in express saccade generation in Rhesus monkeys.

A different manipulation is shown in Fig. 2 for another animal. In this case a single target appeared at three trained locations 88% of the time. Twelve percent of the time, a target appeared at a different location to which the animal had not previously been exposed. The animal generated 62% express saccades to the trained locations and made only 7% express saccades to targets appearing at untrained locations. This difference was statistically significant ( $\chi^2 = 348.46$ , d.f. = 1,  $P < 0.001$ , Yates-corrected).

### *Pre-cueing with a circle stimulus*

Monkeys were extensively trained using the precueing paradigm. Trials were run in large, counterbalanced blocks. For each block there was either no precueing or 100% precueing. The precueing stimulus was a circle that always appeared for 16.7 ms and was presented at the same time as the fixation spot, thereby denoting the impending location of the target to which the animal had to make a saccadic

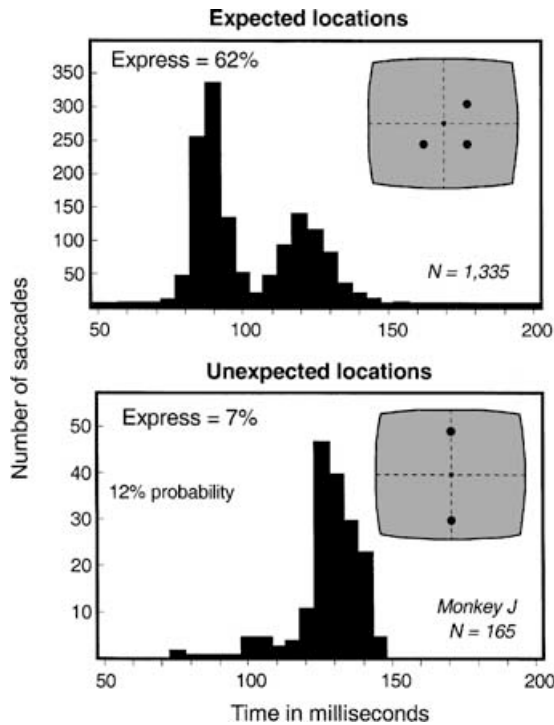


FIG. 2. The distribution of saccadic latencies to single targets presented at three trained target locations with high probability and to single target locations presented at two untrained locations with low probability (12%). The former yielded 62% express saccades and the latter 7%.

eye movement in order to be rewarded. Figure 3 shows the effects of this precueing for Monkey C after the animal had been trained on this task for several weeks. The results show that this cueing stimulus actually produced interference: the animal made fewer express saccades to the target when precued than when there was no precueing stimulus. There was an 18% decrease when two target locations were used and 10% decrease when four target locations were used. Both decreases were statistically significant (two locations:  $\chi^2 = 54.92$ , d.f. = 1,  $P < 0.001$ ; four locations:  $\chi^2 = 38.46$ , d.f. = 1,  $P < 0.001$ , Yates-corrected).

#### Pre-cueing with a stimulus identical to the target

Animals were trained extensively for many weeks. The precueing stimulus was identical to the target and was flashed on for 16.7 ms when the fixation spot appeared. Extensive training on this task increased express saccade generation with precueing. Figure 4 shows this for Monkeys N and C for when two and when four target locations were used. Gap time was set at 150 ms for Monkey N and 100 ms for Monkey C. In Monkey N, precueing increased express saccade generation by 20% and in Monkey C by 14%. The increase in the percentage of express saccades generated with precueing was modest but was statistically significant for both monkeys. (Monkey N:  $\chi^2 = 213.49$ , d.f. = 1,  $P < 0.001$ ; Monkey C:  $\chi^2 = 51.24$ , d.f. = 1,  $P < 0.001$ , Yates-corrected). Repeated testing produced similar results.

Data collected in Monkey J using similar procedures appear in Fig. 5. As shown in the left two panels, precueing produced an 18% increase when two target locations were used with a gap time of 50 ms. The right panel shows the distribution of saccadic latencies when four target locations were used with a gap of 150 ms with and without precueing. Pre-cueing was highly effective in increasing the frequency of express saccades, in this case by 46%. Both sets were statistically

significant (two locations:  $\chi^2 = 124.88$ , d.f. = 1,  $P < 0.001$ ; four locations:  $\chi^2 = 549.84$ , d.f. = 1,  $P < 0.001$ , Yates-corrected).

To determine whether precueing can be effective in increasing express saccade generation under conditions that normally fail to yield express saccades, two tests were administered. In the first, single targets were presented repeatedly at one of four locations using a gap time of 0 ms. The top panel of Fig. 6 shows that precueing was ineffective in generating express saccades under these conditions. The second test involved the use of the discrimination task in which four targets appeared, one of which was different from the others. Gap time was set to 150 ms. The appropriate target location (the odd stimulus) was precued. This condition also failed to generate express saccades even after extensive training.

## Discussion

The data presented in Figs 1 and 2 establish that target predictability plays a significant role in express saccade generation. Express saccades made to single targets presented at trained locations occur much more frequently when targets at these locations are presented with a high probability than when they are presented with a low probability. When targets are presented with a low probability at untrained locations, express saccades are seldom generated. This is consistent with previous findings regarding the effect of precueing on express saccade production (Mayfrank *et al.*, 1986; Braun & Breitmeyer, 1988; Cavegn & d'Ydewalle, 1996); it is also consistent with studies showing a general decrease in saccadic latencies as a result of increased target probability (Crawford & Muller, 1992; Kingstone & Klein, 1993; Tam & Stelmach, 1993; Carpenter & Williams, 1995; Paré & Munoz, 1996), and with work showing that the increased frequency of express saccades after training is specific to the target location used during training (Fischer & Ramsperger, 1984).

These findings do not support the idea that the capacity to generate saccadic eye movements with short latencies has evolved to enable organisms to respond quickly to sudden, unexpected visual stimuli, a capacity which presumably would facilitate survival (Schiller, 1998). It appears, rather, that express saccades are a product of learning and of the predictability of target identity and location (Klein, 1980; Kalesnykas & Hallett, 1987; Becker, 1989; Kowler, 1990; Paré & Munoz, 1996). The mechanisms that underlie this facilitation are not clear. It has been proposed that it is triggered by fixation disengagement (Cavegn & d'Ydewalle, 1996) or attentional disengagement (Fischer, 1986, 1987), and it could exert its effect by providing sensory facilitation (Reulen, 1984a,b), by facilitating premotor processes (Reuter-Lorenz *et al.*, 1991), by allowing early preparation of motor programs (Kowler, 1990; Paré & Munoz, 1996), or by facilitating an early decision to make a saccade (Becker, 1989). The saccade generated is clearly stimulus-driven because there are few anticipatory saccades with latencies  $< 80$  ms and because the width of the express saccade distribution is a mere 15–20 ms wide despite a random variation in fix spot duration from 180 to 220 ms.

The results of precueing shown in Figs 3–5 establish the fact that, when monkeys are extensively trained and the precueing conditions are optimized, the frequency of express saccades can be significantly increased by precueing. Curiously, precueing was effective only when the precue was identical to the target. It is unclear why this is the case. One possibility is that the facilitatory effect of precueing with identical cues results from activation of the same sets of neurons by the precue and the target in eye movement centres such as the superior colliculus. This could trigger preparatory activity in saccade-related neurons in the superior colliculus, which has been shown to correlate with the increased express saccade frequency on gap trials (Dorris *et al.*, 1997).

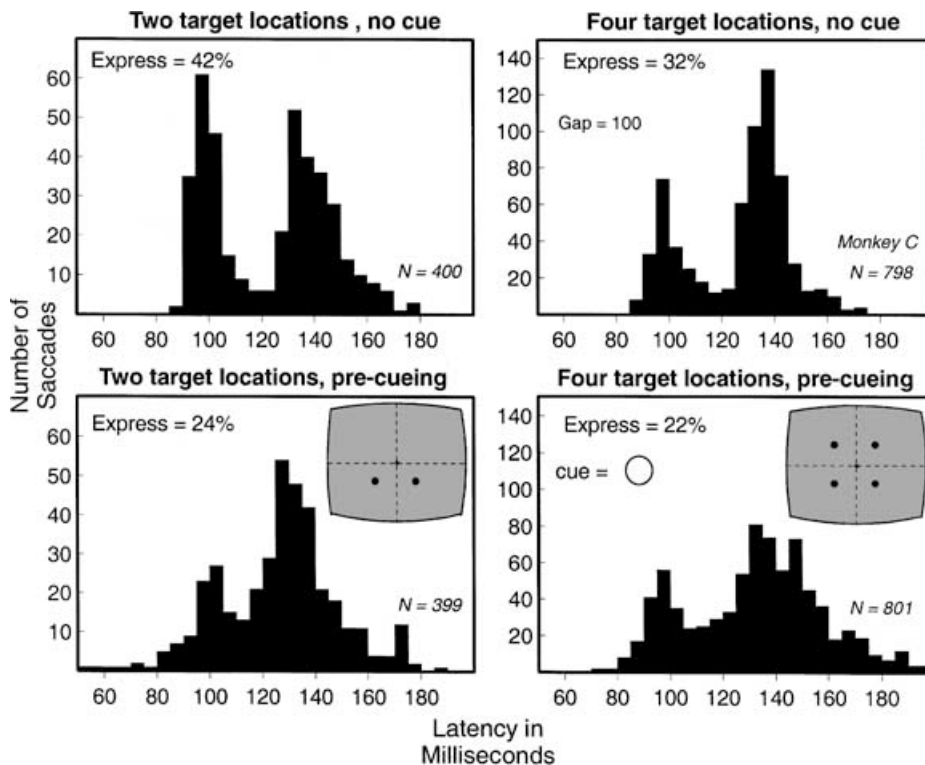


FIG. 3. The effect of precueing using a circle stimulus to denote the location of the impending target. Data are shown for two and four targets. Pre-cueing with this stimulus actually reduced the frequency of express saccades.

Furthermore, the effect is limited to situations in which single targets are presented and a gap of 50–150 ms is used. Pre-cueing is ineffective when a gap of 0 ms is used in conjunction with a single-target task, and it is also ineffective when the monkey performs on a discrimination task. Thus even though the impending location of the correct stimulus in the discrimination task is clearly and consistently indicated, the

animal is incapable of utilizing this information for the generation of express saccades. The latencies with which the eye movements are initiated in this situation are the same as those generated when there is no cue, indicating that a visual discrimination is made in the usual fashion although it would seem not to be necessary to do so. This finding is consistent with previous work showing that the simultaneous

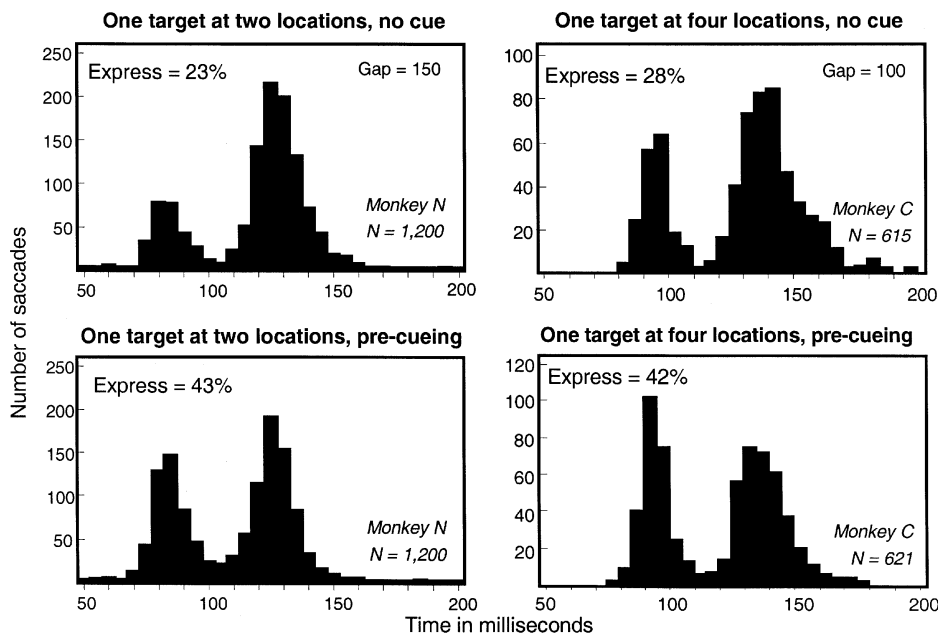


FIG. 4. The effect of precueing when presenting a cue identical to the target for 16.7 ms with onset time equal to fix spot onset. The data are shown for Monkeys N and C using gap times of 150 and 100 ms and two and four target locations, respectively. The frequency of express saccades was significantly increased when there was a precueing stimulus.

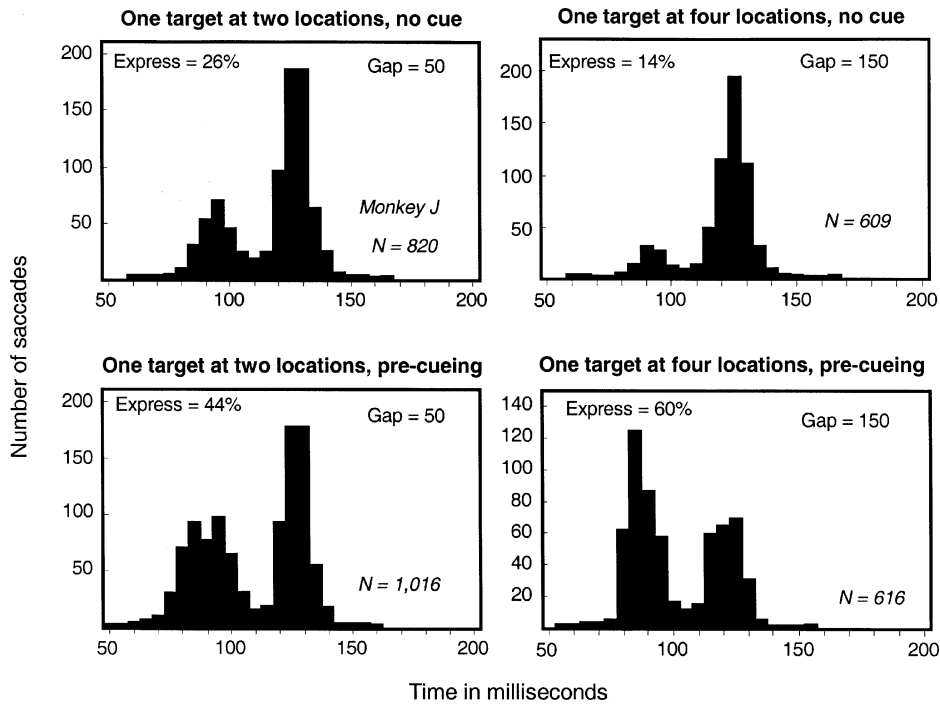


FIG. 5. The effect of precueing in Monkey J using the same cueing conditions as in Fig. 4. Single targets appear at either two or four locations using gaps of 50 and 150 ms. Pre-cueing results in a highly significant increase in the frequency of express saccades.

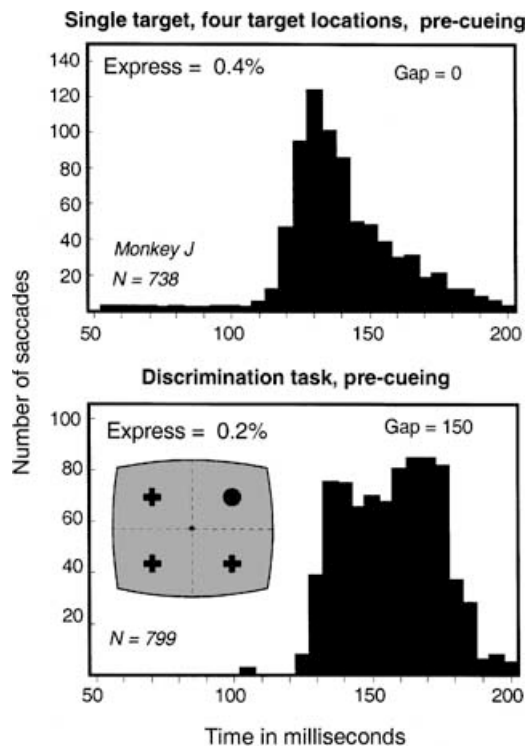


FIG. 6. The distribution of saccadic latencies when precueing was applied in conjunction with the presentation of single targets at (top) four locations with a gap of 0 ms and (bottom) in the oddities discrimination task using a gap time of 150 ms. Pre-cueing was ineffective for both conditions.

onset of a target and a field of distracters completely suppressed express saccades (Weber & Fischer, 1994).

Several human studies have shown that precueing by various kinds of cues can decrease saccadic reaction times (Ross & Ross, 1981; Kimmig, 1986; Mayfrank *et al.*, 1986; Braun & Breitmeyer, 1988, 1990; Crawford & Muller, 1992; Fischer & Weber, 1993; Kingstone & Klein, 1993; Tam & Stelmach, 1993; Cavegn & d'Ydewalle, 1996; Suzuki & Hirai, 2000). Our findings confirm these earlier studies and therefore suggest that the Rhesus Macaque monkey is a useful model for studying the effects of precueing on express saccade generation. Also, we show that the decrease in times found in these studies, most of which provide only the mean of reaction times, is probably due to a decrease in the frequency of regular saccades and an increase in the frequency of express saccades rather than merely an overall reduction in reaction times, as has been discussed by Fischer & Weber (1993).

From previous human studies it also emerges that precueing may be temporally limited; Weber *et al.* (1998) and Fischer & Weber (1998) showed that the generation of express saccades is reduced in a pro-cued antisaccade task or in an anticued pro-saccade task under conditions where the cue lead time (CLT) is <200 ms, while the interference by the cue ceases at longer CLTs. In these studies pro-cued refers to a cue that appears at the same location as the visual target and anticued refers to the cue appearing at the location opposite to where the visual target appears with respect to the fixation spot; saccades to be made to the location of the visual target are called pro-saccades, whereas saccades to be made to the opposite location from the target are called antisaccades. In accordance with these findings, we show a facilitation of express saccade generation by a pro-cued pro-saccade task at short CLTs, and it is likely that this effect is restricted to short CLTs. Whether it can also be observed at long CLTs is a subject for further study.

In summary, predictability of target location and identity plays an important role in express saccade generation in Rhesus monkeys and precueing can increase express saccade generation, but only when single targets presented with a gap between fixation spot termination and target onset are used, and only when the precue is identical to the target.

## Acknowledgements

This research was supported by EY08502. The authors thank Warren Slocum and Christina Carvey for their help.

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