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## What is the coordinate frame utilized for the generation of express saccades in monkeys?

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**Abstract** The latencies of saccades to suddenly appearing eccentric targets can have a bimodal distribution, with an early, express peak, and a late, regular peak (Fischer and Boch 1983, *Brain Res* 260: 21–26). Express saccades usually are a product of learning. The purpose of this study was to determine whether this learning is specific to the relative position of the target in space, the orbital position of the eye, or the vector of the saccade to be produced. Further, it was asked whether and how the frequency with which express saccades are generated is influenced by the immediately preceding saccadic vector and the familiarity of the targets. To this end, rhesus monkeys were trained to make saccadic eye movements to single targets and to two sequential targets that appeared at various positions relative to the head, relative to the initial fixation spot and relative to each other. The results show that the frequency with which express saccades are generated is determined by the saccadic vector that has to be generated and not by the relative position of a target in space, the orbital position of the eye, the immediately preceding saccadic vector, or the familiarity of the targets.

**Keywords** Eye movements · Express saccades · Target selection · Rhesus macaque

### Introduction

Saccades made to targets suddenly appearing in the visual field can have a bimodal latency distribution, with

an early peak of “express saccades” at a latency of about 90 ms and a late peak of “regular saccades” at a latency of about 150 ms in monkeys (Fischer and Boch 1983; for review, see Fischer and Weber 1993). The phenomenon of express saccades is of particular clinical interest insofar as it has been implicated in dyslexia: subjects with dyslexia make significantly more express saccades than control subjects (Fischer and Weber 1990). In normal subjects, express saccades usually only arise after training. This training is spatially specific: the frequency of express saccades can be increased when targets appear at predictable and/or trained locations, and can be reduced when they appear at unpredictable and/or untrained locations (Fischer and Boch 1983; Fischer et al. 1984; Boch and Fischer 1986; Kowler 1990; Rohrer and Sparks 1993; Paré and Munoz 1996). However, it is uncertain with respect to which coordinate frame express saccades are trained and generated: is the training specific to a particular location in space, the orbital position of the eye, or the vector of the saccade to be generated? Previous studies have yielded conflicting evidence: Paré and Munoz (1996) found that the frequency with which express saccades were generated was altered by the spatial location of the stimuli even though the saccadic vectors were kept constant. In contrast, Rohrer and Sparks (1993) showed that the probability with which express saccades are produced is unaffected by the position of the fixation spot and target as long as the saccadic vector is kept constant. Thus, the first aim of the present study was to systematically test several possibilities for the coordinate frame relevant for the generation of express saccades.

A further potential factor in the generation of express saccades is the order of stimulus presentation. It is known that eye movements and express saccades are modulated by the history of eye movements (Kowler et al. 1984; Jüttner and Wolf 1992). Carpenter (2001) has shown that express saccades in humans occur more frequently when a target appears at a different location from the location of the target on the preceding trial than when it appears at the same location. One potential

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explanation of this is that saccades are subject to inhibition of return (Abrams and Dobkin 1994a, b; Hooge and Frens 2000; Ro et al. 2000). Carpenter (2001) has also shown that when two successive saccades with the same vector are generated to two sequentially presented targets, express saccades occur with a much higher frequency than when opposite vectors are generated for the two successive eye movements. This implies that in any attempt to elucidate the coordinate frame underlying express saccade generation, the history of trials should be taken into account. Thus, the second aim of this study was to assess to what extent the generation of express saccades depends on previous eye movements.

We therefore considered the following possibilities for the coordinate frame relevant for express saccade generation: (1) A particular orbital position is coded; once learned, an eye movement to that position can be made with an express saccade irrespective of the starting position. (2) A specific location in the visual field is coded. (3) What is coded for express saccade generation is a specific saccadic vector, i.e., the direction and amplitude of the saccade to be produced, rather than the nature of the targets or their position in space. (4) The probability with which an express saccade is made depends on the saccadic vector generated for the preceding saccade. (5) Finally, we tested the possibility that express saccade generation depends on the familiarity of the target.

To assess these alternatives we carried out the following manipulations: (1) The relative locations of targets on the monitor were kept constant but orbital position of the eye was varied by placing the monitor at different positions relative to the head. (2) The location of the fixation spot was varied and the position of the objects on the monitor was kept constant. (3) The vector (amplitude and direction) of the saccade generated was kept constant and the positions of the fixation spot and targets were varied. (4) The extent to which the vector of the preceding saccade influences express saccade generation was assessed in dual-saccade paradigms. (5) Targets of different sizes, shapes and colors were presented unexpectedly at familiar locations.

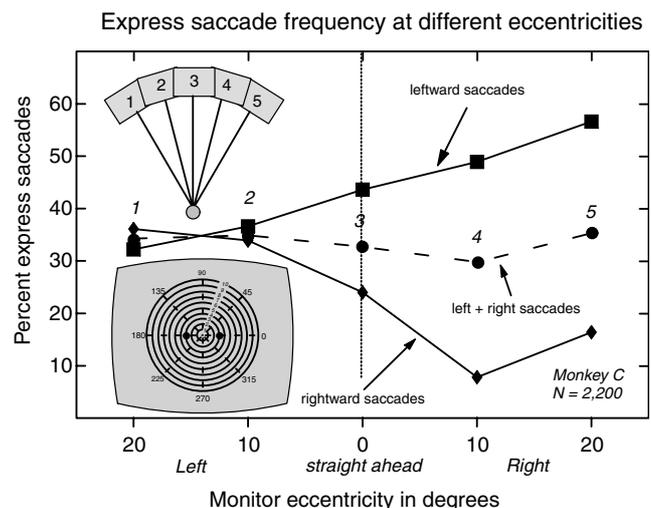
## Materials and methods

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 pre-anesthetic dose of Ketamine (10 mg/kg, IM, once) or Telazol (5 mg/kg, IM, once). They were also given atropine prior to and during surgery (0.05 mg/kg, IM, every 45–60 min). Anesthesia was induced and maintained with Pentobarbital (8 mg/kg, IV, once for induction; 4 mg/kg, IV, as needed for maintenance). Following implantation, monkeys were trained to perform several behavioral tasks as described below. During the experimental sessions monkeys sat in a primate chair with their heads secured. They faced a color

monitor placed at a distance of 57 cm. Each trial began with the appearance of a central fixation spot (a circular spot 1/5 of a degree in diameter) followed by a gap of 100 ms, and the appearance of a small circular target (0.2–0.5 degrees diameter) in one, two or four potential locations. The number of potential target locations was varied across sessions, and the particular location on each trial was chosen pseudo-randomly among the potential locations. 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. Saccades were classified as “express” if they were generated with a latency of less than 105 ms after target onset. The animals were tested on many aspects of express saccade generation, some of which have been reported in several other papers (Schiller et al. 2004a, b, c). All animal research was carried out in accordance with guidelines laid down by the NIH in the publication “Principles of laboratory animal care,” (NIH publication No. 86-23, revised 1985) and was approved by the Institutional Animal Care and Use Committee at MIT.

To answer the five questions posed in the last paragraph of the introduction, we used the following procedures, in the order below:

1. The orbital position of the eye was varied while keeping object locations constant. The animal faced a monitor at a distance of 57 cm from the eyes. The head of the animal was restrained. The monitor was placed at five different positions: straight ahead (0 degrees), 10 and 20 angular degrees to the left, and 10 and 20 degrees to the right along the horizontal meridian. This arrangement is depicted in the top inset of Fig. 1.



**Fig. 1** Plotted is the percentage of express saccades generated as a function of the location of the monitor relative to the animal’s head. Express saccades generated for leftward and rightward saccades are plotted both separately and combined. The top inset shows the monitor positions used. The bottom inset shows the coordinate scheme we use and the two target positions used in the first experiment. The rings indicate eccentricity in degrees, the radial lines indicate angular position in degrees. This convention for target position is used throughout

Monkeys C, D and J were trained on this task for several weeks.

2 and 3. The frequency of express saccade generation was assessed when the monitor was straight ahead at 0 degrees and the locations of the fixation spot and targets were systematically varied. Two to four target positions were used, which yielded different frequencies of express saccades as a result of previous training and/or the natural disposition of the animal. By placing the fixation spot at different locations it was possible to generate different saccadic vectors to the same position (2) and to generate the same saccadic vector to different target locations (3). These procedures allowed us to determine whether it is the relative target position, the absolute target position, or the saccadic vector generated that is the crucial factor in express saccade generation. The conditions used are described for each of the figures. Two monkeys, C and J, were trained on these tasks.

4. The probability with which express saccades are generated was assessed as a function of the vector of the preceding saccade, in monkeys C, D, and J. This was done by using either the standard procedure in which a single target appeared following fixation, or by using the dual-saccade task introduced by Carpenter (2001) in which two targets appeared successively. The conditions used included having the fixation spot at different locations and having two targets placed so as to generate two successive identical saccades (“away” condition) or two successive saccades with opposing vectors (“return” condition). Conditions were set up taking into account the frequency with which each animal generated express saccades to various target locations when the single-target task was used. After extensive training on the single-target task the animals became quite consistent in their performance and showed significant differences in the frequencies with which express saccades were generated to different target locations that produced different vectors. We capitalized on this natural disposition to assess performance on the dual-target task when conditions set up so as to produce saccades away or toward fixation yielded vectors that produced high and low frequencies of express saccades. These saccadic vectors were then set up for two basic “away” and “return” conditions in which the vectors normally yielding high and low frequencies of express saccades were reversed for the first and second saccade. In all cases a gap of 100 ms was placed between offset of the fixation spot and onset of the first target as well as between onset of the two targets. Fixation spot duration for this series was 250 ms with a 20% time variation, and the duration of the targets was set to 200 ms. The intertrial interval was 1,200–1,500 ms.

The coordinates we used in defining the locations of the fixation spots and the targets and the saccadic vectors generated are depicted in the bottom inset of Fig. 1.

5. The nature of the targets was varied by unexpectedly presenting objects with different shapes, colors, and sizes in place of the standard targets. Overall, such unexpected targets were presented on 24% of the trials;

each shape, color and size appeared approximately 8% of the time. The stimuli were presented at the same locations as the standard targets. Monkeys C, D, and J were trained on this task.

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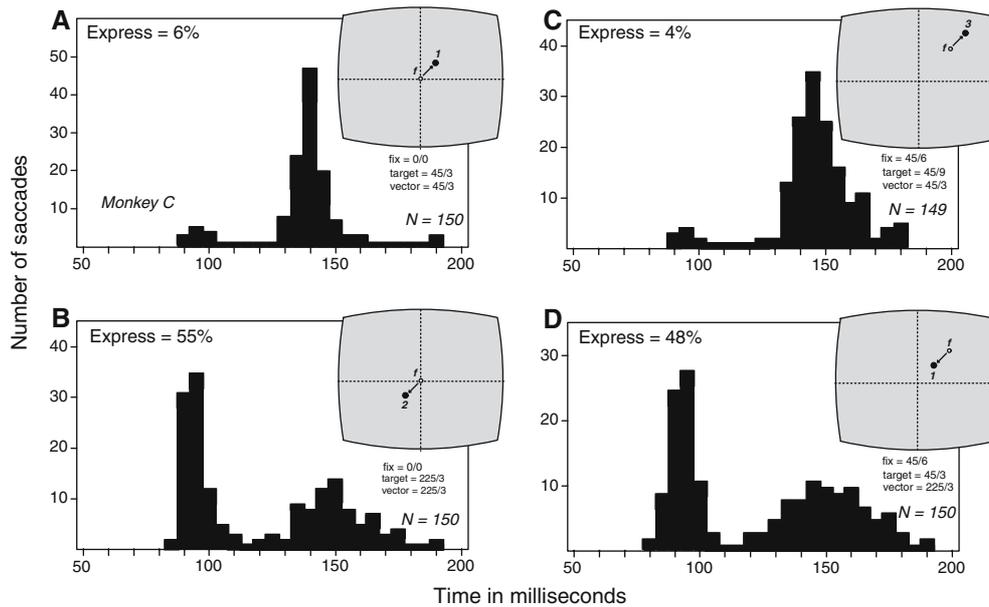
## Results

The effect of varying orbital position while keeping relative target position constant on the monitor

Figure 1 shows, for Monkey C, how express saccade generation was affected by placing the monitor at different horizontal positions with respect to the head while keeping relative target position constant. The fixation spot was kept at 0/0 (polar angle/eccentricity in degrees) on the monitor and the two target positions were 0/3 and 180/3, as indicated in the bottom inset. The coordinate system shown in the bottom inset is used also to define the saccadic vectors generated. Monitor positioning is depicted in the top inset. As the monitor was shifted progressively further to the left, the frequency with which leftward express saccades were generated showed a moderate decrease. This was accompanied by an increase in express saccades generated to the right. The inverse was the case when the monitor was shifted to the right. The total number of saccades generated was constant, as indicated by the function summing left and right saccades, suggesting that the saccadic vector generated is the primary code utilized by the animal, not the orbital position of the eye. The decrease in express saccade generation when saccades are made to increasingly eccentric orbital positions brought about by moving the monitor is most likely due to the added effort involved in making saccades to increasingly eccentric orbital positions (see Paré and Munoz 2001). The increase in express saccade generation in the opposite direction is probably due to the greater ease with which a saccade can be generated in a direction that has a less eccentric orbital position. Two other monkeys tested with this procedure using three monitor positions produced similar results.

Varying the vectors to be generated to target locations established in previous training by placing the fixation spot in different locations, and varying the position of targets in space while keeping the vectors constant

Figure 2 shows data obtained when Monkey C generated saccades to target locations that elicited two three-degree vectors, one right up 45 degrees and the other down left 45 degrees. These vectors were elicited with the fixation spot in two different locations one in the center of the screen (0,0) and the other at 45/6. The conventions used in defining the fixation spot and target locations as well as the saccadic vectors generated are laid out in the bottom panel of Fig. 1. In Panels A and B of Fig. 2 the fixation spot was central (0/0) and the target was placed either at 45/3 or 225/3 (labeled 1 and



**Fig. 2** The distribution of saccadic latencies when the position of the fixation spot is varied and the saccadic vectors generated are held constant, Monkey C. The saccadic vectors in Panels A and C are identical, 45/3. The fixation spot is at 0/0 and 45/6, respectively, and targets at 45/3 and 45/9. The frequency of express saccades generated for these two conditions is 6% and 4%. In Panels B and D the saccadic vectors generated are identical, 225/3. The fixation spot is at 0/0 and 45/6 and targets are at 225/3 and 45/3. The frequency of express saccades generated is 55% and 48%. This indicates that it is the saccadic vector, not the spatial location of the targets and the fixation spot, that determines the frequency of saccade generation

2), thereby generating opposing vector saccades. The animal made only 6% express saccades to the target at 45/3 but made 55% express saccades to position 225/3. The same two saccadic vectors were generated in Panels C and D by placing the fixation spot at 45/6 and the targets at 45/9 and 45/3, respectively (labeled 3 and 1). The target location in Panel D is the same as in Panel A, at 45/3. Due to the fixation spot location at 45/6, however, the saccadic vector generated is 225/3, which is the same vector as that generated in Panel B. Saccadic vectors of 45/3 in Panels A and C produced only 6% and 4% express saccades, respectively, whereas saccadic vectors of 225/3 in Panels B and D produced 55% and 48% express saccades. These results indicate that it is the saccadic vector that determines frequency of express saccade generation and not the relative position of targets in space. If relative target location had been the crucial factor in express saccade generation, the opposite results would have been obtained.

Figure 3 shows similar results from Monkey J, using a different set of fixation spot and target locations. Panels A and B show the distribution of saccadic latencies made to the target at 225/5 (labeled 1) and at 315/5 (labeled 2) when the fixation spot is central at 0/0. The animal made only 9% express saccades to the target

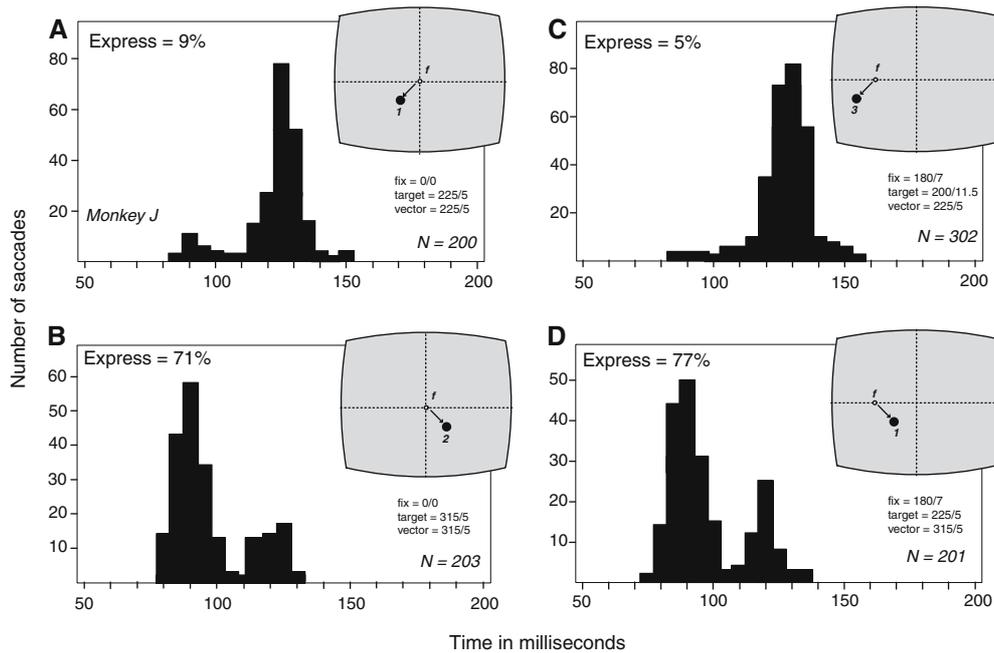
at 225/5 but made 71% express saccades to the target at 315/5. Panel C shows the distribution of saccadic latencies when the fixation spot is at 180/7 and the target at 200/11.5 (labeled 3). This condition generated the same vector saccade as in Panel A. Only 5% express saccades were made. In Panel D the target is in the same location as in Panel A (labeled 1), and the fixation spot is in the same position as in Panel C. The saccadic vector generated is the same as in Panel B. Express saccades were generated 77% of the time. These data demonstrate that the crucial dimension for this monkey is also the vector of the saccade generated, not the position of the target in space.

Express saccade generation with two successively presented targets

*a. The influence of the direction of the preceding saccade on the frequency with which express saccades are generated*

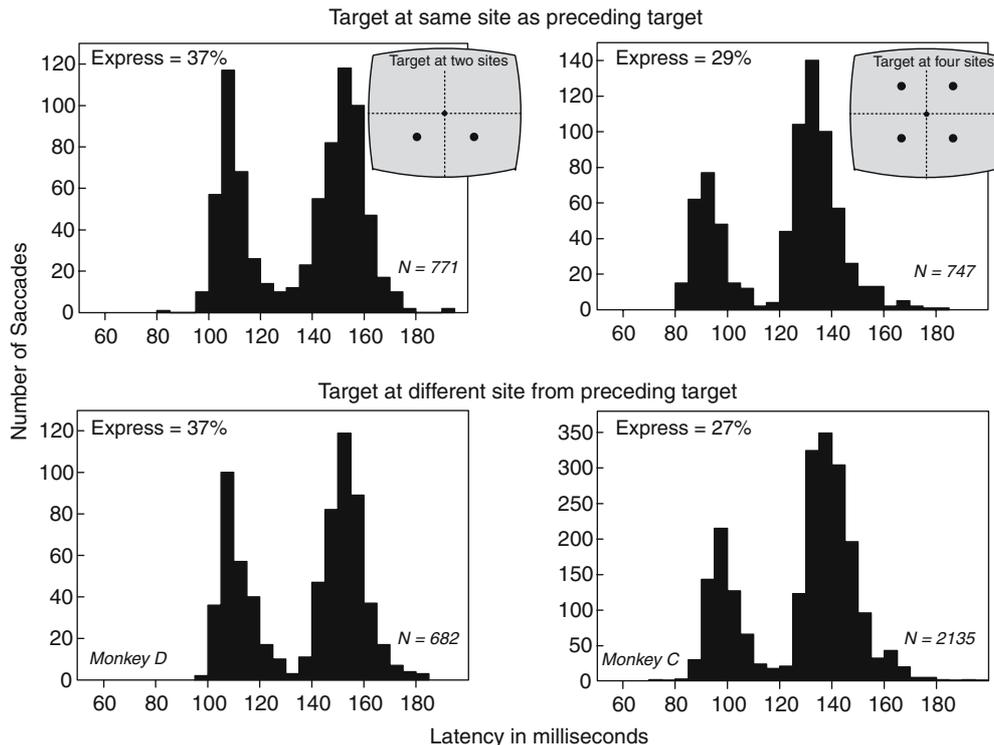
In previous work carried out in humans it has been shown that the frequency with which express saccades are generated is influenced by the location of the previous target and hence the vector of the saccade elicited (Carpenter 2001). When the vector elicited was opposite

**Fig. 4** The distribution of saccadic latencies when the target on the preceding trial is at the same site (**upper set of panels**) and at the other site(s) (**lower set of panels**). The data from Monkey D, shown in the left two panels, were collected using two target sites; the data from Monkey C, shown in the right two panels, were collected using four target sites. The frequency of express saccades was the same, suggesting that monkeys do not set up specific expectations depending on the immediately preceding history of the target locations and saccadic vectors generated



**Fig. 3** The distribution of saccadic latencies when the position of the fixation spot is varied and the saccadic vectors generated are held constant, Monkey J. The saccadic vectors in Panels **A** and **C** are identical, 225/5. Fixation spot is at 0/0 and 180/7, respectively, and targets at 225/5 and 200/11.5. The frequency of express saccades generated for these two conditions is 9% and 5%, respectively. In Panels **B** and **D** the saccadic vectors generated are identical 315/5. The fixation spot is either 0/0 or 180/7 and targets are at 315/5 and 225/5. The frequency of express saccades generated is 71% and 77%

to the one elicited on the preceding trial, fewer express saccades were produced than when the vector was the same. To determine whether this also applies to monkeys, we plotted the distribution of saccadic latencies for trials in which the previous saccade was in the opposite direction or to another location. Figure 4 shows data from two monkeys, D and C. For Monkey D (left two panels), single targets appeared randomly at either of



two locations, 225/5 and 315/5. The frequencies of express saccades were identical when the preceding trial was at the same location and when it was at the other location (left upper and lower panels). The data shown in the right two panels of Fig. 4 were obtained from Monkey C using the following four target locations: 45/3, 135/3, 225/3 and 315/3. The data are plotted separately for trials in which the target was at the same location as in the preceding trial and for trials in which the target was at a different location (right upper and lower panels). Again, the frequency of the express saccades was the same under these two situations. It appears therefore that, unlike humans, monkeys do not set up expectations depending on the position of the target on the preceding trial.

*b. The generation of express saccades to the second of two successive targets as a function of the direction of the saccadic vectors generated*

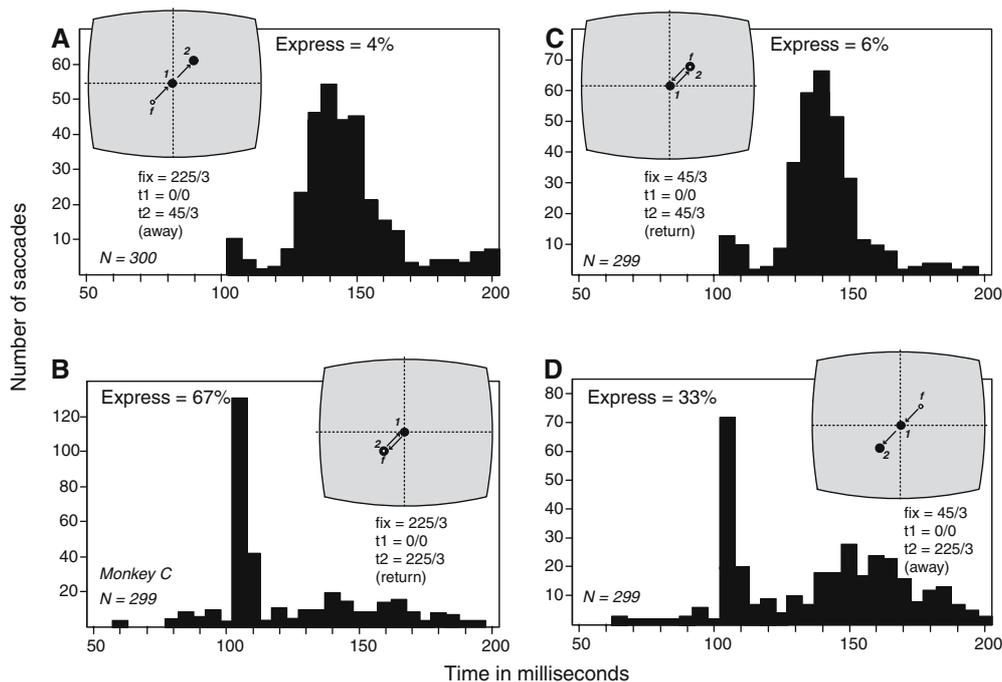
It has been shown when humans make two successive saccades to two successively presented targets, they make more express saccades when the second target is placed further away from the fixation spot (“away” condition) than the first, compared to when it is placed on the other side of the fixation spot than the first, triggering a return saccade (“return” condition) (Carpenter 2001). We examined this in monkeys, taking into account that the

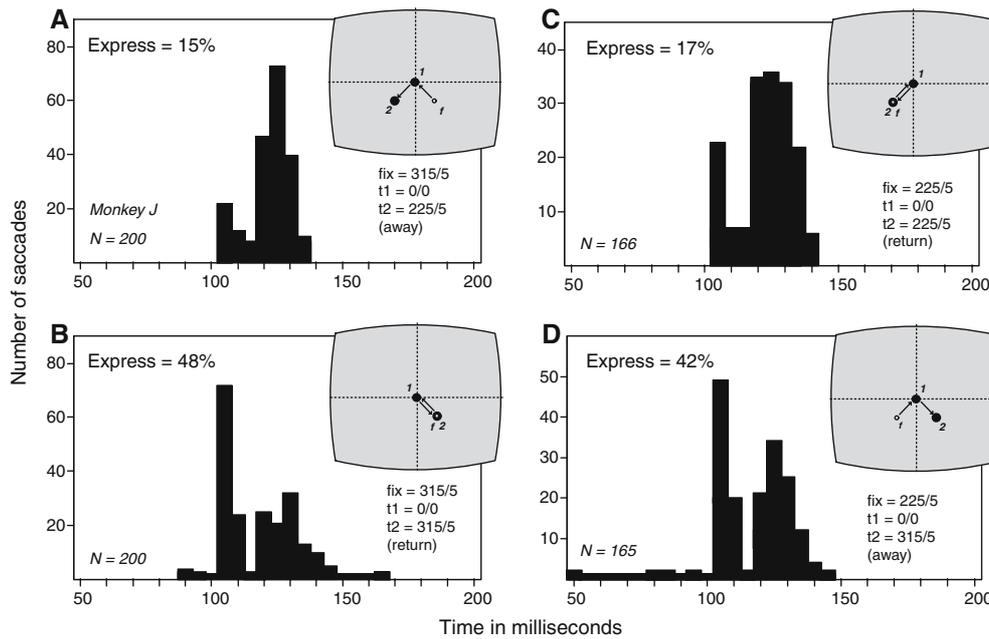
frequency of express saccade generation in these animals depends on the vectors involved. We used a method similar to the single target method shown in Figs. 2 and 3, purposefully selecting locations toward which express saccades were generated with different frequencies.

In Fig. 5 data are shown for Monkey C on the two-saccade task when two successive targets are presented. Panel A shows the “away” condition. The fixation spot is at 225/3, target 1 at 0/0 and target 2 at 45/3. Only 4% express saccades are made to the second target. In Panel B the fixation spot and the first target are arranged the same way but the second target is back at 225/3, making for the “return” condition. In this case 67% of the second saccades generated were express. To determine whether this difference is due to the “away” and “return” manipulation or to the vectors generated, the fixation spot was moved to 45/3. Panel C shows the “return” condition in this case with just 6% of the saccades generated falling into the express range. Panel D shows the “away” condition in this case with the second target placed at 225/5, which resulted in 33% express saccade generation. It appears that saccadic vectors of 45/3 generated few express saccades and vectors of 225/3 generated many express saccades irrespective of whether the net condition was “toward” or “away”.

Similar results were obtained in Monkey J as shown in Fig. 6. In this case a different set of target locations was used, again selected to provide different frequencies of express saccades. In Panel A the fixation spot was at 315/5 and the targets were at 0/0 and 225/5, yielding 15% express saccades to the second target. This we call the “away” condition. In Panel B the second target appeared where the fixation spot had been, at 315/5. This we call the “return” condition, and it yielded 48%

**Fig. 5** The distribution of saccadic latencies in Monkey C to the second target in the two-target paradigm with the second target generating the same saccadic vector as the first, the “away” condition (Panels A and D), or generating the opposite vector, the “return” condition (Panels B and C). The frequency of express saccades is determined predominantly by the vector generated, not by the “away” and “return” conditions.





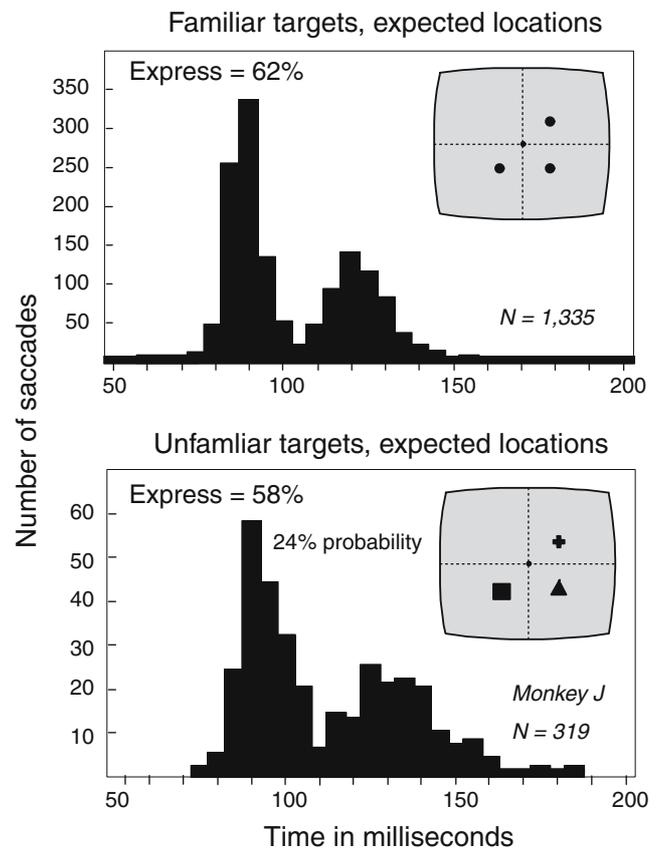
**Fig. 6** The distribution of saccadic latencies in Monkey J to the second target in the two-target paradigm when the second target generated the same saccadic vector under the “away” and “return” conditions (Panels A and C and Panels B and D). The frequency of express saccades was low for the saccadic vector 225/5 and high for 315/5 irrespective of the direction of the saccade generated relative to the fixation spot

express saccades to the second target. In Panel C the fixation spot was at 225/5 and the second target was at the same place, constituting thereby the “return” condition. Panel D shows the “away” condition with the second target at 315/5 which, for the second saccade, yielded 42% express saccades. From these data it is evident that 315/5 vectors produced numerous express saccades and 225/5 vectors yielded few express saccades irrespective of whether the conditions were away or return. Thus it is the vector that is the primary determinant of saccadic latency, not whether the saccade is toward or away from the fixation spot.

#### The effect of presenting unexpected objects at expected locations

The last question posed in this study was whether the frequency with which saccades with specific vectors are generated is influenced by the nature of the targets presented. To examine this a fixed set of target locations was used. At these locations either a highly familiar, circular white target was presented repeatedly or a different, novel target was presented occasionally to keep it unexpected. Each of the novel targets appeared only a few times in any given set. The novel targets were squares, crosses or triangles, each presented in a variety of colors and sizes. The regular targets were presented 76% of the time. In Fig. 7 the

distribution of saccadic latencies is plotted separately for the familiar and the unfamiliar targets. The data show that the frequency of express saccades was similar



**Fig. 7** The distribution of saccadic latencies to familiar and unfamiliar targets appearing at expected locations. The frequency of express saccades is unaffected by the appearance of unexpected, novel stimuli

for the two conditions. Similar results were obtained from other monkeys. This suggests that the crucial factor in express saccade generation is the location of the targets that produce specific vectors and not the nature of the objects used.

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## Discussion

The data presented in this paper lead to the following three conclusions:

A. The primary factor determining the frequency with which express saccades are generated to singly appearing targets is the saccadic vector involved: when an animal has undergone extensive training on a particular saccadic vector, this vector will produce high frequencies of express saccades irrespective of the orbital position of the eye and the relative position of the target in space. This is consistent with previous findings showing that the probability of express saccade generation is independent of fixation spot and target position as long as the saccadic vector remains constant (Rohrer and Sparks 1993). It is inconsistent with other studies reporting the opposite effect (Paré and Munoz 1996). Relatively large deviations in orbital position do, however, influence the frequency with which express saccades are generated, as shown in Fig. 1; as the deviation of the eye in orbit is increased, the frequency of express saccades made to more extreme locations decreases, and that of express saccades made to less extreme locations increases. As might be expected, near the limits of ocular motility vector coding can become compromised (Paré and Munoz 1996).

Once a vector has been learned, it is likely that the visibility of the target is essential for express saccades to occur along this vector; it has been shown that anti-saccades rarely fall in the express range, even when they are made along learned vectors (Fischer and Weber 1992).

B. The probability with which express saccades are generated by monkeys is not significantly influenced by the saccadic eye movements generated on the preceding trial. This is the case both when single targets are used and when the animals make two successive saccades to successively appearing targets. These findings are different from those obtained by Carpenter (2001), who reported in humans that the probability with which express saccades are generated to a second target depends on the direction of the preceding saccadic vector; he found that the overall reaction times are slowest under those conditions in which the second target in the sequence necessitates a return saccade. Our findings are also different from human (Abrams and Dobkin 1994a, b; Hooge and Frens 2000; Ro et al. 2000) and monkey (Dorris et al. 1999) studies that showed that return saccades are subject to inhibition of return. These studies did not examine express saccades separately, but are at odds with our results because we find that the

overall saccadic latency in the “return” condition is either the same or *shorter* than in the “away” condition.

A potential explanation for this discrepancy in findings is the fact that our monkeys had been extensively trained over a long period of time, typically running 2000–3000 trials per session. Given the highly repetitious nature of this task, it is likely that monkeys learn to perform the task in a rather automated fashion without developing specific expectations based on immediately preceding events. In this respect, these extensively trained animals may be a better model for dyslexic express saccade makers than human subjects, who can only be trained for a few hundred trials (but see Biscaldi et al. 1996).

More generally, our results complement evidence indicating that the frequency with which express saccades are produced is influenced by the particular momentary state of the animal (Schall and Hanes 1993; Paré and Munoz 1996). It has been shown that increasing target presentation uncertainty by inserting catch trials decreases express saccade frequency, and that latencies on trials following catch trials are longer than on others (Jüttner and Wolf 1992). Furthermore, contextual factors such as gap duration, number of target locations, and randomization of the fixation foreperiod have been reported to affect the frequency of express saccades (Weber et al. 1995; Schiller et al. 2004a). Thus further work on contextual factors needs to be carried out in concert with the variables we have manipulated in this study.

C. The generation of express saccades does not seem to depend on the physical parameters of the targets used. When stimuli with different configurations (color, shape, size) appear unexpectedly at the same locations generally used, monkeys make the same number of express saccades as when the highly familiar stimuli are used. This further suggests that the critical factor in express saccade generation is the learning of specific vectors that can then be readily generated to any object placed at the appropriate location to generate the learned vectors.

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