An examination of the variables that affect express saccade generation

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Abstract

The frequency with which express saccades are generated under a variety of conditions in rhesus monkeys was examined. Increasing the gap time between fixation spot termination and target onset increased express saccade frequency but was progressively less effective in doing so as the number of target positions in the sample was increased. Express saccades were rarely produced when two targets were presented simultaneously and the choice of either of which was rewarded; a temporal asynchrony of only 17 ms between the targets reinstated express saccade generation. Express saccades continued to be generated when the vergence or pursuit systems was coactivated with the saccadic system.

Keywords: Eye movements, Saccades, Express saccades, Target selection, Gap

Introduction

This paper examines the conditions under which express saccades are and are not generated in rhesus monkeys with the aim of specifying the rules and coding operations involved. The fact that under certain conditions saccadic latencies form a bimodal distribution in monkeys was discovered by Fischer and Boch (1983). They termed the first mode of the distribution "express saccades" and the second mode "regular saccades." Fischer and Ramsperger (1984) reported express saccades in humans. These studies have created a great deal of interest resulting in numerous publications examining this phenomenon (for review, see Fischer & Weber, 1993). In this study, we examine three aspects of express saccade generation: first, the interaction between gap time and number of target locations; second, the role of target identity in express saccade suppression during simultaneous presentation of more than one target; and third, the generation of express saccades during coactivation of the pursuit and vergence systems.

It is now well known that during the initial phases of training express saccades are rarely made. As training progresses the frequency with which they are executed increases (Kowler, 1990; Paré & Munoz, 1996). Express saccades occur most readily when only a single target is presented after fixation; when multiple targets are presented express saccades are seldom made (McPeek & Schiller, 1994; Weber & Fischer, 1994). The introduction of a temporal "gap" between the termination of the initial fixation spot

and the appearance of the target facilitates express saccade production (Saslow, 1967; Fischer & Ramsperger, 1984; Reulen, 1984*a,b*, Reuter-Lorenz et al., 1991; Rohrer & Sparks, 1993; Paré & Munoz, 1996; Shafiq et al., 1998). Initially, it was thought that a gap is essential, but it has been shown that once monkeys have been extensively trained express saccades also can occur when there is no gap; in humans, express saccades have even been demonstrated in overlap conditions, that is, where the fixation point remains visible during target presentation (Boch & Fischer, 1986). There is, however, considerable variation among individual animals. Some monkeys, even after extensive training, hardly ever make express saccades when the gap is 0 ms whereas others may generate a third of their saccades in the express range (Schiller et al., 1987).

Another factor that has been shown to affect the frequency with which express saccades are made is the number of target locations at which a single target can appear in a given sample; the frequency of express saccades declines as the number of locations is increased (Becker, 1989; Paré & Munoz, 1996; but see Rohrer & Sparks, 1993). How this interacts with the gap time used is one of the questions we pose in this study.

When monkeys are trained to perform a discrimination on an oddities task in which a saccadic eye movement has to be made to a target that is different from a set of other stimuli presented at the same time, express saccades are practically never generated (McPeek & Schiller, 1994; Weber & Fischer, 1994). The question arises whether this is because the animal has to make a visual discrimination or because one specific saccadic vector has to be selected from several alternatives. To test this, we devised a simple task that involves the presentation of two identical targets; a

saccade made to either is rewarded thereby obviating the need to make a discrimination. By presenting the two targets with various temporal asynchronies and assessing the probability with which either target is chosen as a function of this asynchrony, one can determine whether express saccades are generated under such conditions and one can estimate the time course of the computations involved. This paired target task has been extensively used in our research addressing different questions (Schiller & Chou, 1998, 2000a,b; Schiller & Tehovnik, 2001).

The third question posed in this study is whether express saccades can be generated when in addition to the saccadic system the pursuit or vergence system is also activated. In everyday life, stimuli are often in motion and they appear at many different distances from the observer resulting in the coactivation of two or more eye-movement control systems. To determine whether coactivation of the pursuit or vergence systems with the saccadic system affects express saccade generation, monkeys were trained to track a moving fixation spot that was followed by the appearance of a single target, to make saccadic eye movements to moving targets and to make saccades to targets that appeared at different distances from the animals' eye.

Materials and methods

Four Rhesus monkeys were used. Each animal had a head post and a scleral search coil implanted. Following implantation, monkeys were trained to perform on 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 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. The procedures used have been described in previous publications (Schiller & Chou, 2000a,b). All animal research was carried out in accordance with guidelines laid down by the NIH and has been approved by the IACUC at MIT.

The three tests used in this study are as follows:

Single target test

Each trial began with the onset of the central fixation spot. After the animal shifted his gaze to it and maintained fixation for
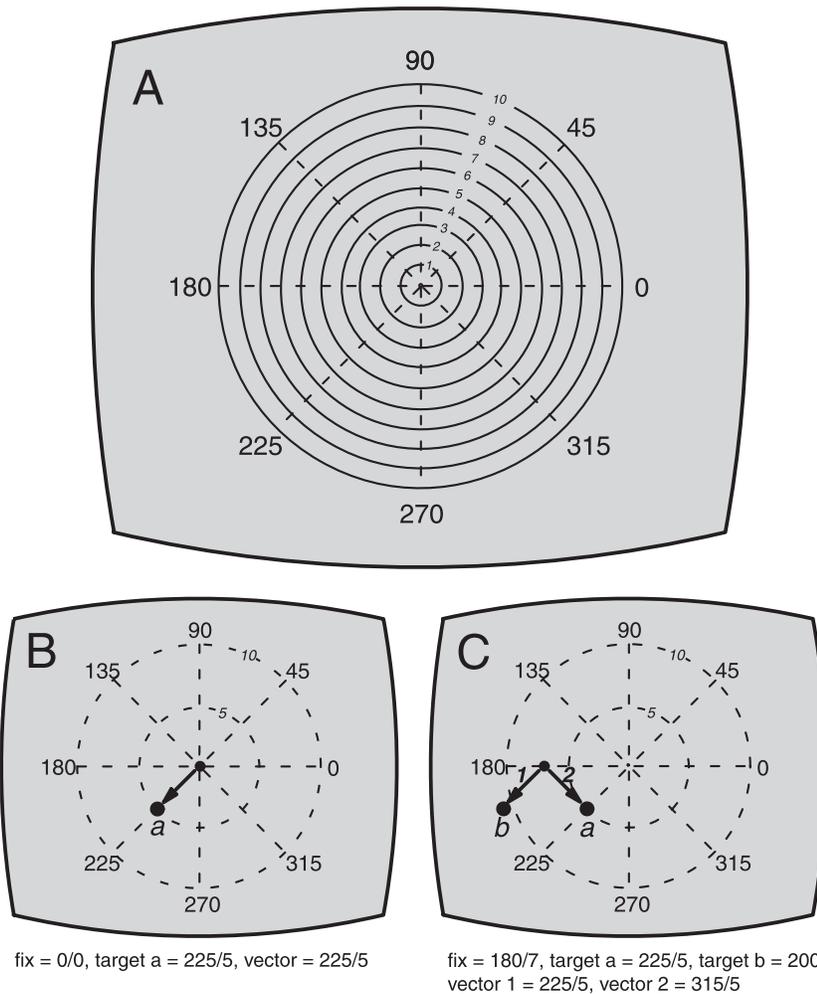

Fig. 1. A: Conventions used in placing visual stimuli on the monitor. Each position is defined relative to the center of the monitor with the first value designating the angular degrees around the clock starting at 3 o'clock (0 deg) and going counter-clockwise. The second value defines the distance from the center in degrees of eccentricity. With the monitor placed at 57 cm, 1 deg of visual angle equals 1 cm. A similar system is used in defining the saccadic vector generated. The two values specify the size and direction of the saccade without specifying the position of the eye in orbit. B: Fixation spot at 0/0, target at 225/5, saccadic vector generated is 225/5. C: Fixation spot at 180/7, targets at 225/5 and 200/11 with corresponding saccadic vectors 315/5 and 225/5.
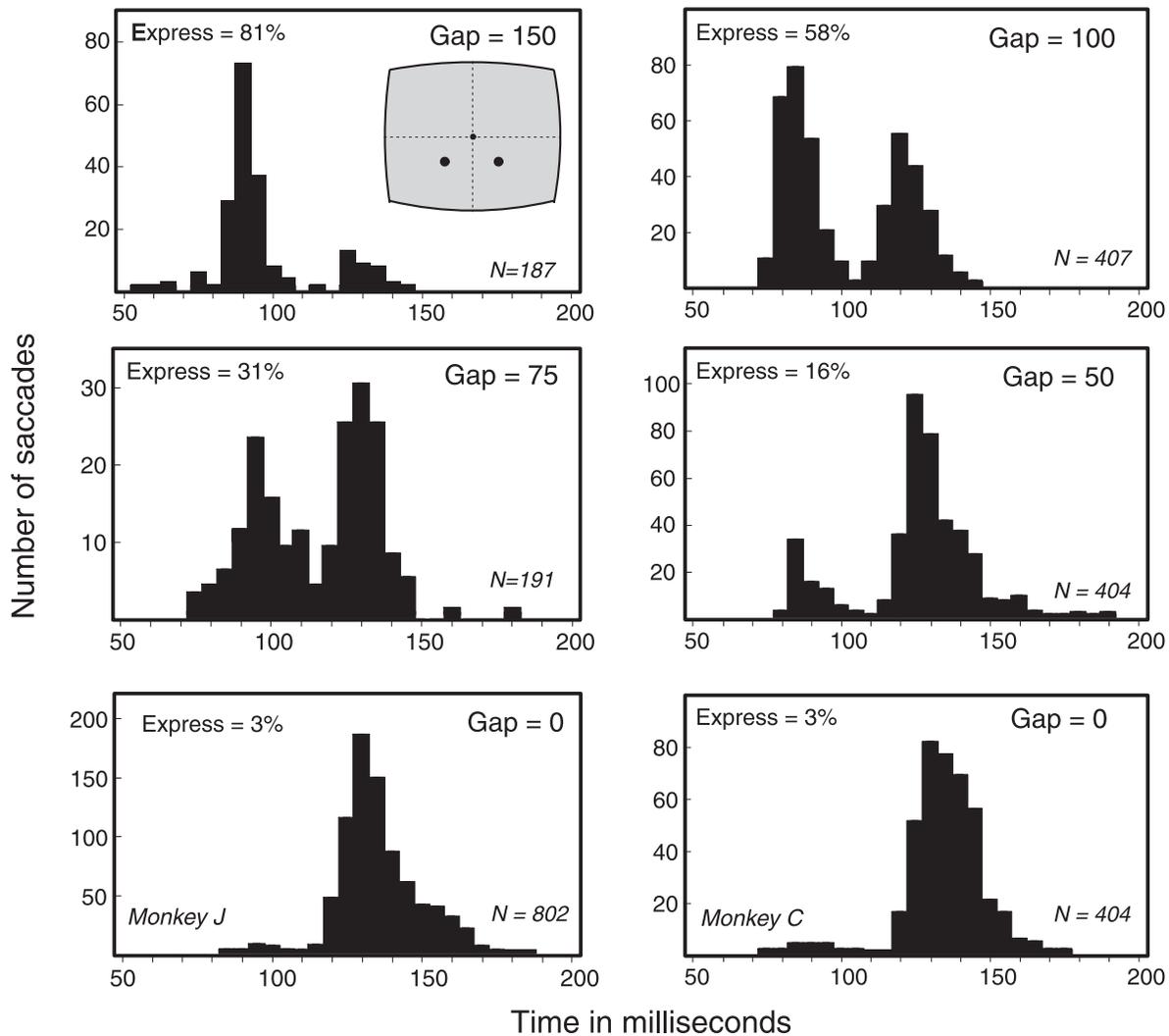
fix = 0/0, target a = 225/5, vector = 225/5

fix = 180/7, target a = 225/5, target b = 200/11, vector 1 = 225/5, vector 2 = 315/5

Fig. 2. The distribution of saccadic latencies obtained from two monkeys to single targets presented at two locations using three different gap times for each animal. The frequency of express saccades decreases with decreasing gap durations. For monkey J, the three gap times were 150, 75, and 0 ms; for monkey C, the gap times were 100, 50, and 0 ms. Shorter gap times were used for monkey C because this animal made almost all express saccades when the gap time was 150 ms.

180–220 ms (time randomized), a single target appeared. The time after the fixation spot was extinguished and before the target was presented, called the gap time, was varied within a range of 0–200 ms. Gap durations were varied within blocks. The targets were either circular or square and varied between 1/3 and 3/4 deg. Background illumination was constant at 23 cd/m². The luminance of the targets ranged between 34 and 93 cd/m². The target was extinguished once the monkey had made a saccadic eye movement to it. The data collected provided percent correct performance and saccadic latencies which were calculated by determining the time between target onset and the initiation of the saccade from the fixation spot (Schiller & Chou, 2000*a,b*). Monkeys ran 1000–3000 trials during each session. The conventions used in specifying target locations on the screen are depicted in Fig. 1. Each position is defined by the distance of the target relative to the central fixation spot in deg of eccentricity and by the circular angle where 0 deg is horizontal right and 90 deg is vertical up. Thus, 0/3 defines a target location 3 deg from the fixation spot horizontally to the right or a saccadic vector generated to that location from the fixation spot.

To determine whether express saccades are generated when the pursuit and saccadic systems are coactivated, we used two procedures. In the first, upon acquisition of the fixation spot this stimulus was set in motion at 7–10 deg/s for 200–250 ms after which it was extinguished. The direction of motion was downward. This stimulus induced pursuit eye movements. A stationary target then appeared after a gap of 100 ms. In the second procedure the fixation spot remained stationary; when the target appeared it was immediately set in motion. Vertical downward movement at 10 deg/s was used most commonly. That the pursuit system was thereby activated is made evident by the fact that (1) the saccades made were to the anticipated location of the moving target, and (2) upon their acquisition pursuit eye movements were immediate. Data to this effect from our laboratory have been published (Schiller, 1998). The pursuit system in fact has a shorter activation latency than does the saccadic system (Rashbass, 1961; Miles et al., 1986; Schiller, 1998).

To coactivate the vergence and saccadic systems, the targets were placed at different distances from the animal by rotating the monitor 45 deg along its vertical axis.
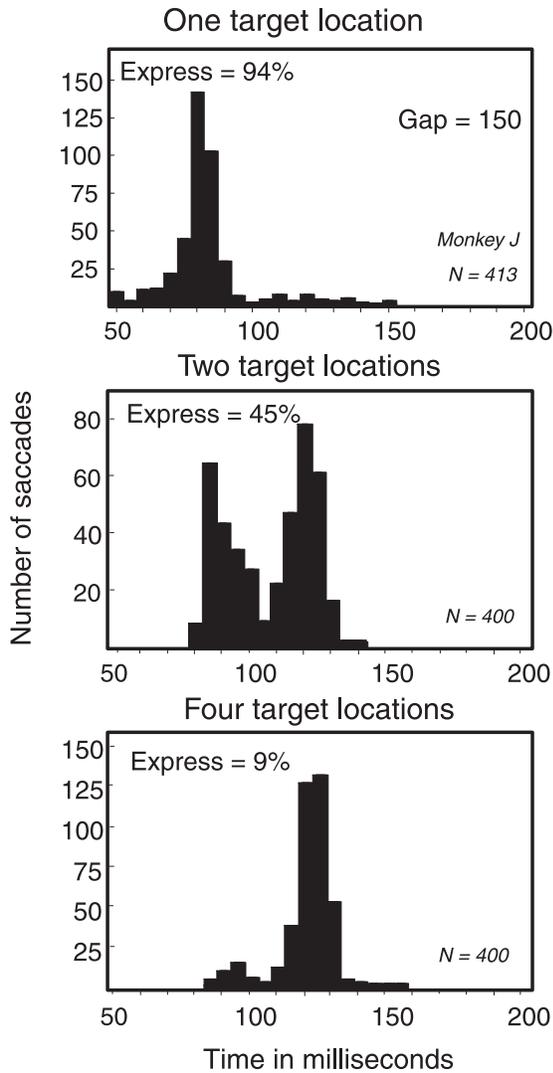
One target location

Express = 94%

Gap = 150

Monkey J
N = 413

Two target locations

Express = 45%

N = 400

Four target locations

Express = 9%

N = 400

Time in milliseconds

Number of saccades

Fig. 3. The distribution of saccadic latencies to single targets for monkey J as a function of the number of target locations used with gap time held constant at 150 ms. The frequency of express saccades declines dramatically with increasing number of target locations used in a set.

Discrimination task

Four stimuli were presented after the termination of the central fixation spot. Three of these were identical distracters; the fourth stimulus, the target, was different in size, color, or shape from the others. The animal was rewarded only if a direct saccade was made to the odd stimulus. Thus, the animal had to make a visual discrimination and also had to compute the location of the target in space for the generation of the appropriate saccadic vector.

Paired target task

Following the fixation spot two identical targets appeared, most commonly separated by 90 angular degrees. The monkey was rewarded for choosing either stimulus. The two targets were presented with various temporal asynchronies in 16.67-ms steps (frame rate) ranging between ± 50 ms. The gap used was specified by the interval between the termination of the fixation spot and the

appearance of the first target in the pair. The presentation of the stimuli with various temporal asynchronies was randomized.

Results

The interaction between gap time and number of target positions in sample

Fig. 2 shows data from two monkeys demonstrating that in these animals, as reported in earlier work in other rhesus monkeys, gap time plays a major role on the frequency with which express saccades are generated. Two target locations were used. Both monkeys made only 3% express saccades when the gap was 0 ms but made 81 and 58% express saccades at the longest gap times of 150 and 100 ms, respectively.

Fig. 3 shows the distribution of saccadic latencies for one monkey when gap time was kept constant and the number of positions used was varied. In all cases, a single target appeared after the animal fixated the central fixation spot. Trials were run in large blocks and data were collected subsequent to the animal having been exposed to the conditions used within a block for 25–50 trials to provide familiarity with the procedure. The data show that when a target repeatedly appears at the same single location (top panel), the animal makes almost exclusively express saccades (94%). On the other hand, when the target appears at one of four locations the frequency of express saccades declines dramatically (9%).

Fig. 4 shows data from two of the monkeys used in this study. A gap time of 50 ms was used for one animal and 150 ms for the other. The comparison made was between the presentation of a single target appearing at two and at four different positions in separate blocks of trials. In all cases, fewer express saccades were made under the four-position condition than under the two-target position. The magnitude of the difference, however, was greater with the larger gap time. For monkeys J and N that had gap times of 150 ms, there was a 36 and 54% drop in express saccade frequency, respectively. For monkey C, using a 50 ms gap, the drop was only 17%.

Fig. 5 shows in detail the interaction in two monkeys between gap time and the number of target locations in the sample. A large sample of trials was collected over a period of several days with the data collected in counterbalanced blocks. The results show a significant interaction between gap time and the number of target locations used. The number of target locations used had little effect on the frequency with which express saccades were generated when the gap time was 0 ms, and had a large effect when the gap time was 100 or 150 ms.

The distribution of saccadic latencies for the paired target task and the discrimination task

Fig. 6 shows the distribution of saccadic latencies for one monkey when (1) a single target was presented at two locations, and (2) when the paired target task was used with targets presented either simultaneously or with a temporal asynchrony of 16.7 ms. Single target presentation was intermingled with the presentation of the paired targets. In all cases, a gap time of 100 ms was used where the gap in the paired target case refers to the time between the termination of the fixation spot and the appearance of the first target in the pair when presented with varied temporal asynchronies. Seven to nine conditions were randomized, two of which were single targets and the remainder paired targets with varied
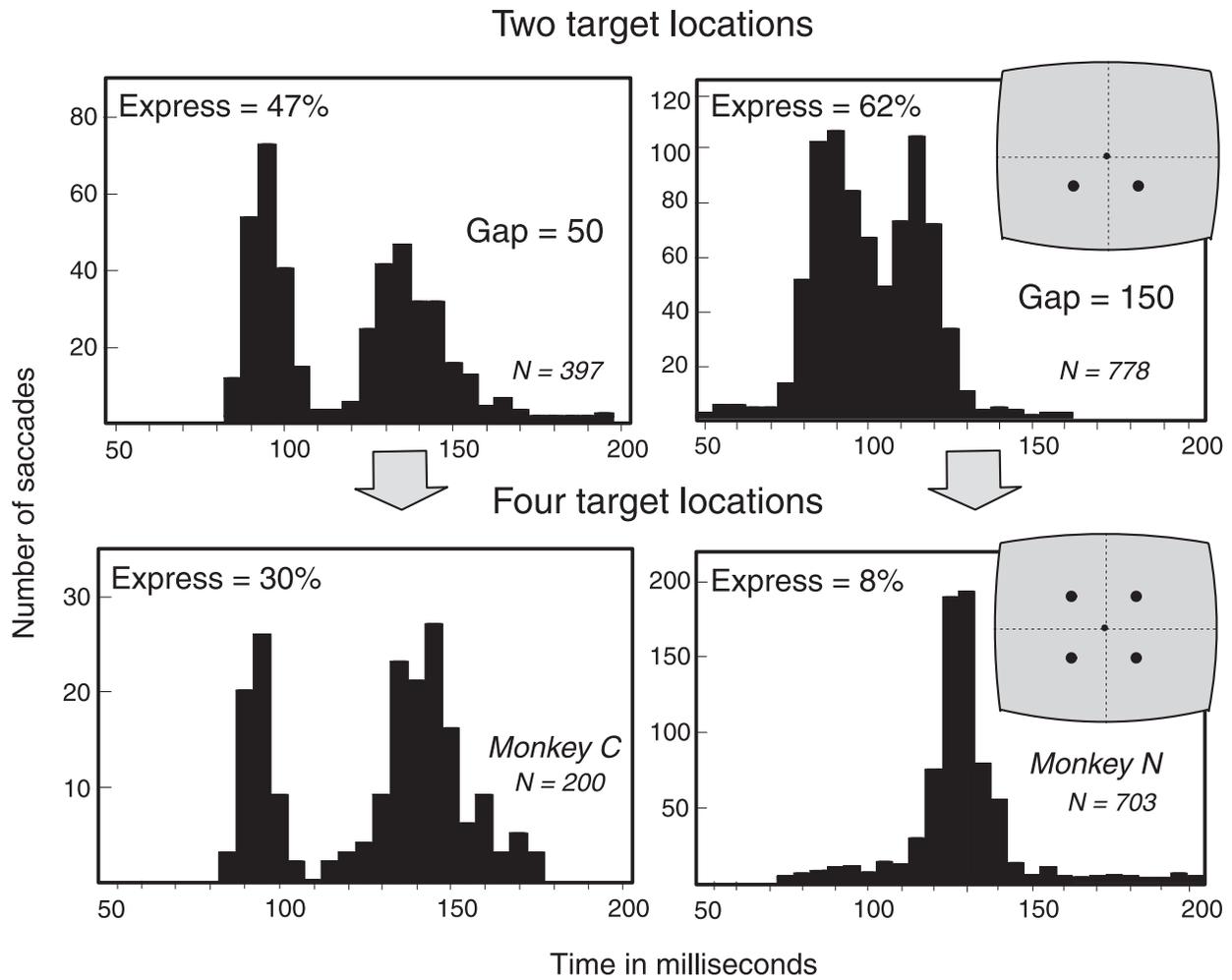
Two target locations

Four target locations

Time in milliseconds

Fig. 4. The distribution of saccadic latencies to singly presented targets for monkeys C and N when two and four target locations were used.

Express saccade frequency as a function of the number of target locations and gap duration
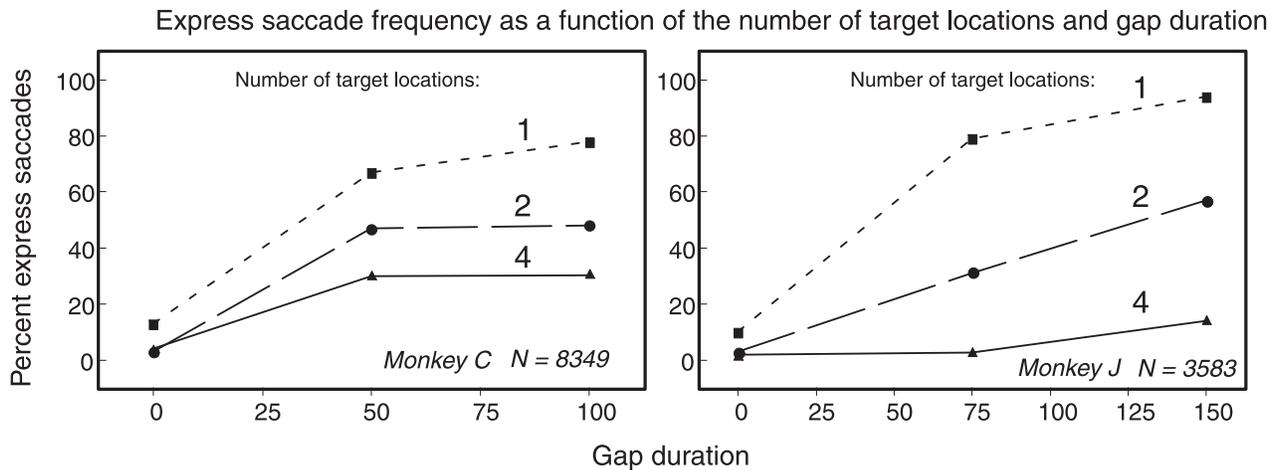

Gap duration

Fig. 5. The percent of express saccades generated as a function of gap duration and the number of target locations used in different sets. Increasing the gap time between fixation spot termination and target onset increased express saccade frequency but was progressively less effective in doing so as the number of target positions used in the sample was increased.
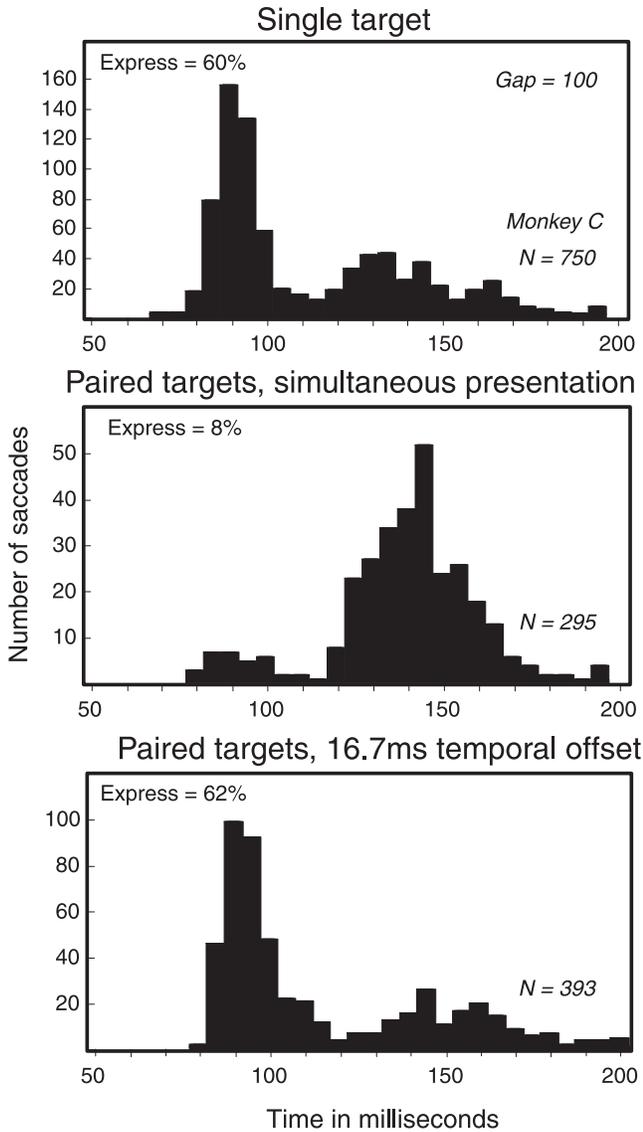
Single target

Paired targets, simultaneous presentation

Paired targets, 16.7ms temporal offset

Time in milliseconds

Fig. 6. The distribution of saccadic latencies in monkey C obtained under three conditions presented in randomized sequences: (1) Single target presentation, (2) simultaneous paired target presentation, and (3) paired target presentation with varied temporal asynchronies. The stimulus positions and target parameters were the same throughout. The animal made only 8% express saccades when the targets were presented simultaneously, but made nearly the same number of express saccades when the targets were offset by 16.7 ms (62%) as when the targets were presented singly (60%).

temporal asynchronies. Shown in Fig. 6 are the distribution of saccadic latencies to the single targets, to the paired targets presented simultaneously, and the paired targets presented with an asynchrony of 16.7 ms.

Fig. 7 plots the frequency of express saccade generation by monkey C for three different temporal asynchronies. The fact that a temporal asynchrony of just 16.7 ms can cause such a large increase in the frequency of express saccade generation compared with the simultaneous presentation condition is surprising. Increasing the gap time from 50 ms to 100 ms increased the percentage of express saccades at temporal asynchronies of 16.7 and 33.4 ms.

That the simultaneous presentation of paired targets drastically reduces express saccade production is demonstrated for another

monkey in Fig. 8. Also shown in this figure is the distribution of saccadic latencies from a discrimination task. The top left panel shows that the animal made 30% express saccades in the single target task. No express saccades were generated when the animal was required to make a visual discrimination in which four targets appeared simultaneously, one of which was different from the others (top right panel). The discrimination task greatly delays saccade execution; mean saccadic latencies are much longer, with a mean around 180 ms, than even regular saccades generated to single targets that had a mean latency around 140 ms. The bottom two panels of Fig. 8 show the distribution of saccadic latencies when two targets were presented, either simultaneously or with a 50 ms temporal offset. This animal made no express saccades when the two targets were simultaneous. For the overall sample of 450 trials, the animal chose the left target 47% of the time and the right target 53% of the time indicating that a decision was made repeatedly as to which target to look at. This is further suggested by the fact that the temporal distribution of saccadic latencies is quite different for the paired targets presented simultaneously than is the distribution of regular saccades to single targets. This difference, coupled with the lack of express saccades under the simultaneous condition, suggests that an active choice was involved in making a saccade to the two targets. By contrast, when the two targets were temporally offset, the animal chose the first target 95% of the time and made numerous express saccades. Curiously in this case the distribution is trimodal. Trimodal distributions of saccadic latencies have been reported previously (Gezeck et al., 1997; Gezeck & Timmer, 1998). Monkey C under similar conditions (Fig. 6, panel 3) did not exhibit a trimodal distribution.

The distribution of saccadic latencies when the pursuit and vergence systems are coactivated

The last question posed in this paper is whether express saccades can be generated when in addition to the saccadic system either the vergence or the pursuit system is activated at the same time. Fig. 9 shows data collected from two monkeys. Data for three conditions are shown. In the first condition, pursuit movement was induced by having the fixation spot move downward at 10 deg/s. After 250 ms of pursuit, the fixation spot was extinguished and after a gap of 100 ms a stationary target appeared at one of two locations. The data obtained appear in the top panel. In the second condition, the fixation spot was stationary and the target was set in motion immediately upon its appearance. The movement was downward at 10 deg/s. These data appear in the middle panel of Fig. 9. In the third condition, the fixation spot and the targets were stationary but they appeared at different distances from the animal by virtue of having the monitor rotated 45 deg along its vertical axis, thereby necessitating the activation of the vergence systems. To accurately place the fixation spot into each fovea at close distances, the vergence system has to be active to converge the two eyes. In all three cases express saccades were readily generated.

Discussion

This set of experiments shows that, when single targets are presented after the termination of a fixation spot, the monkeys we used in this study consistently generated bimodal distributions of saccadic latencies. The frequency with which express saccades were generated was strongly influenced by the gap and by the
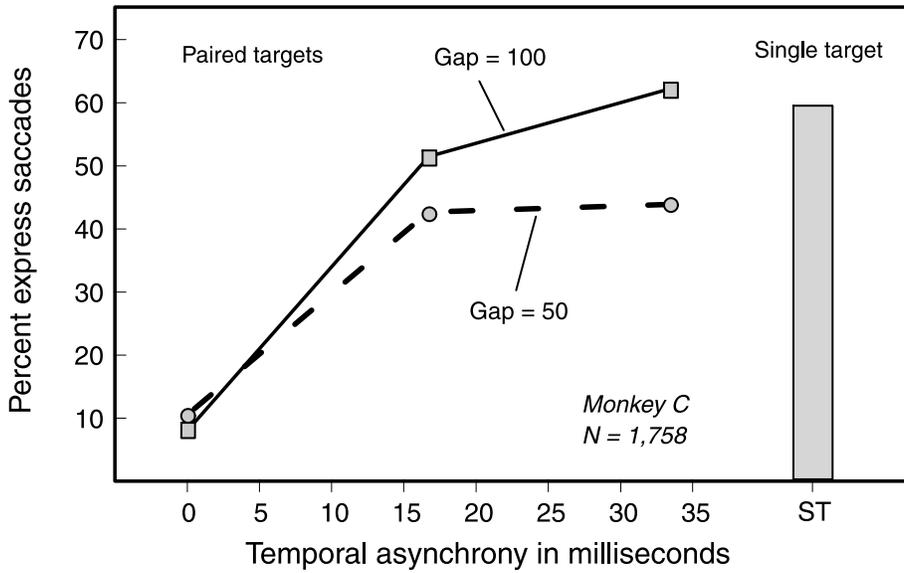
Fig. 7. The frequency of express saccade generation plotted for two gap durations using simultaneous paired targets and targets presented with 16.7- and 33.4-ms temporal asynchronies. Also shown are the frequency of express saccades generated to single targets.

number of target locations used in the sample (Fischer & Ramsperger, 1984; McPeek & Schiller, 1994). These two factors interact: increasing the gap time increases the number of express saccades but the increase is much smaller than that observed when the number of potential target locations for a single target is increased. When the gap time is set to 0 ms, few express saccades are produced no matter how many target positions (1–4) are used in a set. On the other hand, when gap time is 150 ms, there is a
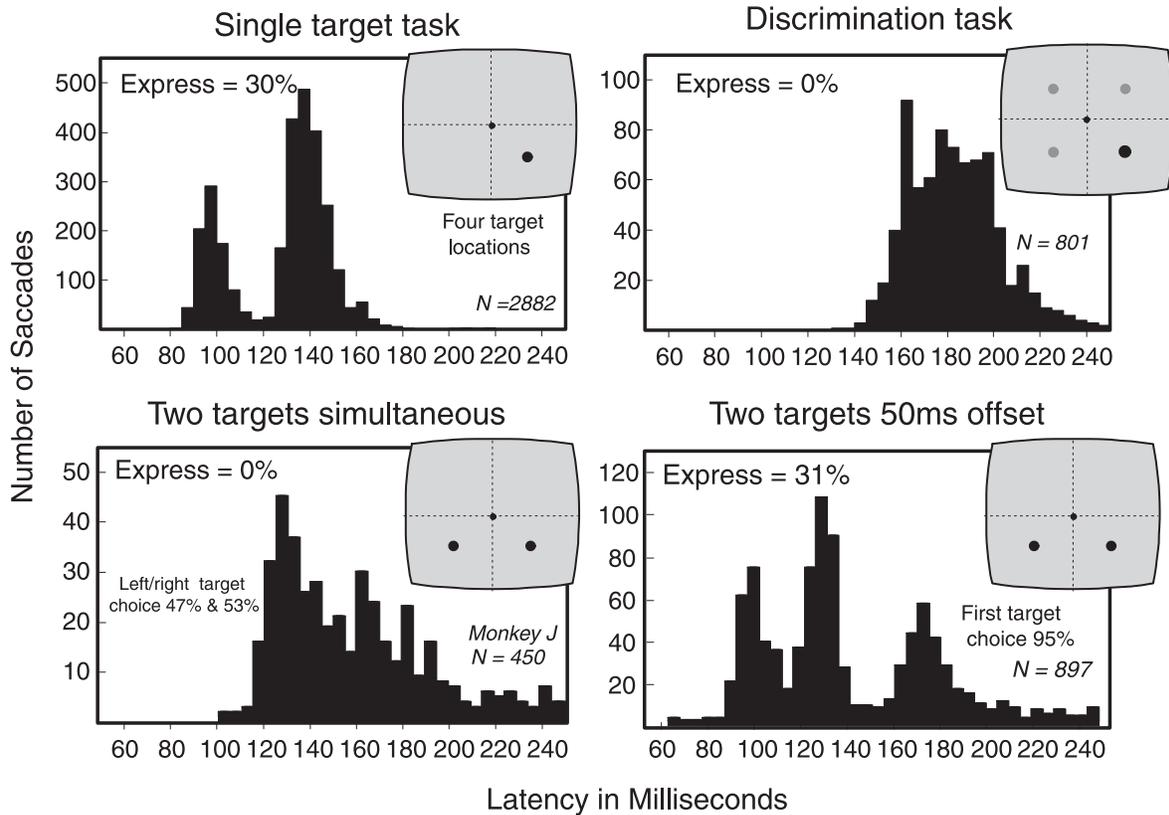

Fig. 8. The distribution of saccadic latencies obtained in monkey J for four conditions: Single targets presented at four locations, four targets presented simultaneously in the oddities discrimination task, two targets presented simultaneously, and two targets presented with a 50-ms offset. The animal made no express saccades at all in the discrimination task and in the two-target task when they were presented simultaneously. At a 50-ms offset, however, the monkey made numerous express saccades in the two-target task.
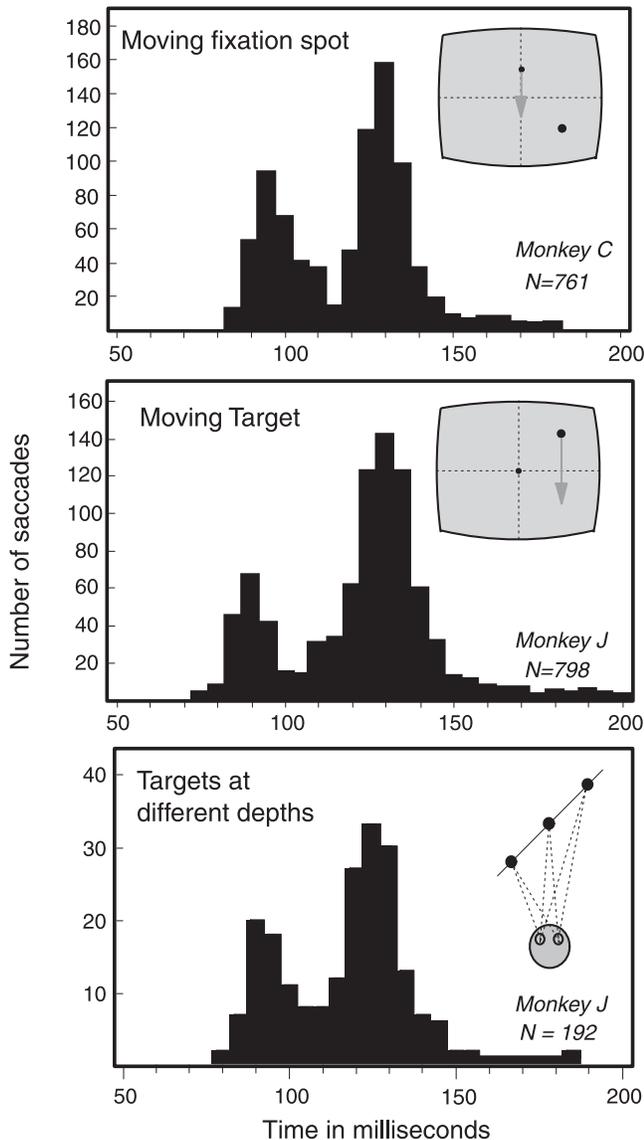
Fig. 9. The distribution of saccadic latencies for three conditions: (1) The fixation spot is set in motion when the center of gaze is shifted to it; the singly appearing targets are stationary. (2) The fixation spot is stationary and the target is set in motion immediately upon its appearance. (3) The fixation spot and targets are stationary and the singly appearing targets are presented at different distances from the animal.

large difference in the frequency of express saccade production when one, two, or four target positions are used in different sets. Similar observations had been made by Paré and Munoz (1996). Previous studies have shown that the facilitation of express saccade generation by the gap decreases as gap times exceed 250–300 ms (Weber & Fisher, 1995); thus, it is likely that the increasing effect of the number of target locations on express saccade frequency with increasing gap time would reverse with gap times longer than the ones we used.

The fact that the number of potential target locations has a major influence on the frequency with which express saccades are generated has been thought to indicate that some sort of advance preparation of motor commands or anticipatory response is involved (Kalesnykas & Hallett, 1987; Kowler, 1990; Paré & Munoz,

1996). This study shows that (1) monkeys hardly ever make saccades with latencies less than 80 ms, and (2) the width of the express saccade latency distribution is very narrow, between 15–20 ms. This is the case even though the duration of the fixation spot was randomized between 180 and 220 ms. Thus, it appears that the saccades are triggered by the visual stimulus and not by guessing.

As reported previously and verified in this study, express saccades are not generated when several targets are presented, one of which is different from the others, and the animal is required to make a saccadic eye movement to the odd target. This task requires a visual discrimination to be made in addition to computing the correct saccadic vector to shift the center of gaze to the appropriate target. It has generally been assumed that express saccades are not made because of having to make a visual discrimination that involves not only where the target is in space but also which target to choose (McPeek & Schiller, 1994; Weber & Fischer, 1994; Chou et al., 1999).

In an attempt to minimize the need to make a visual discrimination that increases saccadic reaction times, we presented two identical targets to the animal which was rewarded for making a saccadic eye movement to either target. Animals trained on this task had been run for tens of thousands of trials during which a reward was given irrespective of which target had been chosen, which meant that a visual discrimination was not central to performance. To further ease this process, the two targets were presented with varied asynchronies with equal likelihood of either target appearing first. Monkeys showed a consistent preference for selecting the first target in the series, and tended to choose the left and right targets with close-to-equal probability when they were presented simultaneously. Strikingly, even with this simple task, monkeys made few express saccades when the two targets appeared simultaneously. However, when the targets were presented with an onset asynchrony of only 16.7 ms (the frame rate of the monitor used) express saccades appeared with a frequency approximating that obtained with single target presentation. This suggests that the underlying neuronal process that forecloses express saccade generation is an extremely rapid one with a time course of a little less than 16.7 ms. The fact that express saccades are seldom made when two identical targets appear simultaneously suggests that just the decision as to where to look when there are two alternatives is sufficient to interfere with express saccade generation. Once the two targets are offset by 16.7 ms, the target appearing first has already been chosen and express saccades to it can be generated. It should be noted that the decision need not be, and given the timescale is unlikely to be, a cognitive one; rather, it is suggested that it is reflexive and the result of a competitive neuronal process at the level of the superior colliculus. In the case of asynchronous target presentation, this process is initiated earlier for the earlier target, allowing the subsequent generation of an express saccade to it. This hypothesis is consistent with the finding by Mokler and Fischer (1999) that erroneous pro-saccades in an anti-saccade task can occur in a subconscious, reflex-like manner.

As shown in Fig. 9, top and center panels, express saccades are also generated when either the fixation spot or the target is set in motion. Both conditions yielded express saccades. It has been established that saccades generated to moving stimuli take into account the velocity and direction of stimulus movement and that subsequent to the eye movement to the stimulus pursuit is immediate; furthermore, often pursuit is initiated even before the saccade is executed (Rashbass, 1961; Miles et al., 1986; Schiller, 1998; Schiller & Chou, 2000a,b). Thus, it appears that express

saccades can readily be generated when the saccadic and pursuit systems are coactivated. Fig. 9 also shows that when the vergence system is tonically active (bottom panel) express saccades continue to be generated. Thus, it appears that the brain circuits involved in vergence eye movements do not interfere with those subserving the production of express saccades.

These findings are somewhat surprising insofar as it has recently emerged that the interactions between vergence and pursuit eye movements on the one hand and saccadic eye movements on the other hand cannot be accounted for by linear summation of the signals from two separate systems, and that the superior colliculus, which is crucial for express saccade generation, also plays a role in vergence and pursuit eye movements (Krauzlis, 2003; Walton & Mays, 2003). Thus, it remains to be determined whether the superior colliculus contains a subsystem that is specialized for express saccade generation and does not interact with the vergence and pursuit systems, or whether the paradigm used in this study was not sensitive enough to pick up such an interaction.

Acknowledgments

References

Becker, W. (1989). The neurobiology of saccadic eye movements. Metrics. *Reviews of Oculomotor Research* **3**, 13–67.

Boch, R. & Fischer, B. (1986). Further observations on the occurrence of express-saccades in the monkey. *Experimental Brain Research* **63**, 487–494.

Chou, I.H., Sommer, M.A. & Schiller, P.H. (1999). Express averaging saccades in monkeys. *Vision Research* **39**, 4200–4216.

Fischer, B. & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in the monkey. *Brain Research* **260**, 21–26.

Fischer, B. & Ramsperger, E. (1984). Human express saccades: Extremely short reaction times of goal directed eye movements. *Experimental Brain Research* **57**, 191–195.

Fischer, B. & Weber, H. (1993). Express saccades and visual attention. *The Behavioral and Brain Sciences* **16**, 553–567.

Gezeck, S. & Timmer, J. (1998). Detecting multimodality in saccadic reaction time distributions in gap and overlap tasks. *Biological Cybernetics* **78**, 293–305.

Gezeck, S., Fischer, B. & Timmer, J. (1997). Saccadic reaction times: A statistical analysis of multimodal distributions. *Vision Research* **37**, 2119–2131.

Kalesnykas, R.P. & Hallett, P.E. (1987). The differentiation of visually guided and anticipatory saccades in gap and overlap paradigms. *Experimental Brain Research* **68**, 115–121.

Kowler, E. (1990). The role of visual and cognitive processes in the control of eye movement. *Reviews of Oculomotor Research* **4**, 1–70.

Krauzlis, R.J. (2003). Neuronal activity in the rostral superior colliculus related to the initiation of pusuit and saccadic eye movements. *Journal of Neuroscience* **23**, 4333–4344.

McPeek, R.M. & Schiller, P.H. (1994). The effects of visual scene composition on the latency of saccadic eye movements of the rhesus monkey. *Vision Research* **34**, 2293–2305.

Miles, F.A., Kawano, K. & Optican, L.M. (1986). Short-latency ocular following responses of monkey. I. Dependence on temporospatial properties of visual input. *Journal of Neurophysiology* **56**, 1321–1354.

Mokler, A. & Fischer, B. (1999). The recognition and correction of involuntary prosaccades in an antisaccade task. *Experimental Brain Research* **125**, 511–516.

Paré, M. & Munoz, D.P. (1996). Saccadic reaction time in the monkey: Advanced preparation of oculomotor programs is primarily responsible for express saccade occurrence. *Journal of Neurophysiology* **76**, 3666–3681.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology* **159**, 326–338.

Reulen, J.P. (1984a). Latency of visually evoked saccadic eye movements. I. Saccadic latency and the facilitation model. *Biological Cybernetics* **50**, 251–262.

Reulen, J.P. (1984b). Latency of visually evoked saccadic eye movements. II. Temporal properties of the facilitation mechanism. *Biological Cybernetics* **50**, 263–271.

Reuter-Lorenz, P.A., Hughes, H.C. & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: An analysis of the gap effect. *Perception and Psychophysics* **49**, 167–175.

Rohrer, W.H. & Sparks, D.L. (1993). Express saccades: The effects of spatial and temporal uncertainty. *Vision Research* **33**, 2447–2460.

Saslow, M.G. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *Journal of the Optical Society of America* **57**, 1024–1029.

Schiller, P.H. (1998). The neural control of visually guided eye movements. In *Cognitive Neuroscience of Attention: A Developmental Perspective*, ed. Richards, J.E., pp. 3–50. Mahwah, New Jersey: Erlbaum.

Schiller, P.H. & Chou, I.H. (1998). The effects of frontal eye field and dorsomedial frontal cortex lesions on visually guided eye movements. *Nature Neuroscience* **1**, 248–253.

Schiller, P.H. & Chou, I. (2000a). The effects of anterior arcuate and dorsomedial frontal cortex lesions on visually guided eye movements in the rhesus monkey: 1. Single and sequential targets. *Vision Research* **40**, 1609–1626.

Schiller, P.H. & Chou, I. (2000b). The effects of anterior arcuate and dorsomedial frontal cortex lesions on visually guided eye movements: 2. Paired and multiple targets. *Vision Research* **40**, 1627–1638.

Schiller, P.H. & Tehovnik, E.J. (2001). Look and see: How the brain moves your eyes about. *Progress in Brain Research* **134**, 127–142.

Schiller, P.H., Sandell, J.H. & Maunsell, J.H. (1987). The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. *Journal of Neurophysiology* **57**, 1033–1049.

Shafiq, R., Stuart, G.W., Sandbach, J., Maruff, P. & Currie, J. (1998). The gap effect and express saccades in the auditory modality. *Experimental Brain Research* **118**, 221–229.

Walton, M.M. & Mays, L.E. (2003). Discharge of saccade-related superior colliculus neurons during saccades accompanied by vergence. *Journal of Neurophysiology* **90**, 1124–1139.

Weber, H. & Fischer, B. (1994). Differential effects of non-target stimuli on the occurrence of express saccades in man. *Vision Research* **34**, 1883–1891.

Weber, H. & Fischer, B. (1995). Gap duration and location of attention focus modulate the occurrence of left/right asymmetries in the saccadic reaction times of human subjects. *Vision Research* **35**, 987–998.