



Express averaging saccades in monkeys

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Abstract

When monkeys are presented simultaneously with multiple stimuli, they can make one of two types of response. Either they make averaging saccades, that land at intermediate locations between the targets, or target-directed saccades, that land close to one of the targets. The two types of saccades occur at different latencies and are thought to reflect different processes; fast reflexive averaging and slower target selection. We investigated the latency of averaging saccades in five monkeys, with particular emphasis on 'express' latency saccades, which are thought to be inhibited by target selection. Express averaging saccades were made prolifically by the two monkeys that made both express and regular latency saccades, but only when no specific instruction was given regarding the saccade target. When these monkeys had to choose one of the targets, on the basis of its color, they still made averaging saccades. However, the endpoints formed two distributions close to the targets as opposed to one single distribution centered between the targets, as was the case when targets were identical; also, express saccades were almost entirely absent. We conclude that express averaging saccades are a form of spatial and temporal optimization of gaze shifting. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Saccades are conjugate eye movements that re-direct the gaze in order to foveate objects of interest in the visual field. Two problems that must be solved are where and when to make saccades so as to optimize the visual information. The problem of where to make a saccade is trivial when a single stimulus suddenly appears in the periphery. In this condition, primates foveate the object directly. However, natural visual scenes often present additional challenges. Stimuli that appear suddenly may be more numerous and distributed; for example, a single bird might fly into view, but so might a flock containing any number of birds. Experiments that examine how primates generate saccades in response to multiple stimuli are crucial for understanding behavior in natural viewing situations.

If two or more stimuli appear simultaneously, there are two strategies that the oculomotor system can adopt to determine where the saccade will be directed. The first strategy is vector averaging, in which the saccade lands at an intermediate position between the targets, (e.g. Coren & Hoenig, 1972; Findlay, 1982; Ottes, Van Gisbergen & Eggermont, 1984; Deubel, Findlay, Jacobs & Brogan, 1988). The mean termination position of 'averaging saccades' is dependent on factors such as relative salience, spatial separation of the targets (Coren & Hoenig, 1972; Findlay, 1982; Findlay, Brogan & Wenban-Smith, 1993; McGowan, Kowler, Sharma & Chubb, 1998), or relative timing of target presentation (Becker & Jürgens, 1979), but it also can be biased by cognitive factors (Coëffé & O'Regan, 1987; He & Kowler, 1989). Another strategy in response to two simultaneous stimuli is to select one of the stimuli as the target, and to direct the saccade accurately to it.

The two strategies seem to take differing amounts of time to implement, with averaging occurring faster than target selection. Averaging saccades seem to occur naturally because they are made even if subjects are not

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given any specific instructions as to where to look (Ottes et al., 1984). In fact Ottes, Van Gisbergen and Eggermont (1985), found that if subjects were specifically instructed to make a saccade to one target and not the other, subjects still made averaging saccades, particularly at short latencies. In that study, only long latency saccades were accurately target-directed. Similarly, Coëffé and O'Regan (1987) showed that by delaying the onset of the saccade, subjects were able to make saccades more target-directed. Thus it would seem that there is a speed-accuracy tradeoff in the process of directing a saccade to one out of several stimuli; averaging is the initial response to the group, and extra time is required to select a specific stimulus as the target of the saccade. Even if there is a cognitive expectation or intention of selecting one stimulus, at short latencies there is insufficient time for selection to occur and the saccade is directed to the approximate center of the visual group. Thus the endpoint of a saccade made to multiple targets may be the outcome of an interaction between two processes; fast vector averaging (dependent on stimulus configuration), and slower target selection (which requires discrimination and decision) (Becker & Jürgens, 1979; Coëffé & O'Regan, 1987; He & Kowler, 1989; Kowler, Anderson, Doshier & Blaser, 1995; McGowan et al., 1998).

The studies described above used human subjects who typically exhibited saccadic latencies in the range of 160 to over 300 ms (cf. Findlay, 1982; Ottes et al., 1985; He & Kowler, 1989). However, a similar speed-accuracy tradeoff can also be observed in subjects that make extremely short latency saccades. Some subjects exhibit a bimodal latency distribution, with a first 'express' peak occurring at latencies of about 75 ms in monkey (e.g. Fischer & Boch, 1983) and 100 ms in humans (Fischer & Ramsperger, 1984). Express saccades are thought to occur within the fastest time possible for a visual stimulus to be translated into the target of a saccade (Paré & Munoz, 1996; Dorris, Paré & Munoz, 1997) and it has been proposed that they are a form of reflexive response to a visual stimulus (Fischer & Weber, 1993). As such, they cannot be made under conditions that require extra processing, such as when subjects are asked to make saccades without visual guidance (Fischer & Weber, 1992). In the scheme described above of two types of saccade (averaging and target-directed) with different time frames, it would be expected that express saccades would be averaging and that regular latency saccades would be target-directed. Indeed, it has been demonstrated that express saccades can be averaging saccades (Weber, Latanov & Fischer, 1993; Edelman & Keller, 1998). Finally, there is also some evidence suggesting that express saccades do not occur when target selection is required. In this laboratory, we have previously established that express saccades are not made when eight stimuli are presented

simultaneously and a monkey has to discriminate one odd stimulus from an array of distracters (Schiller, Sandell & Maunsell, 1987; McPeck & Schiller, 1994).

In the present study, we directly investigated the hypothesis that express saccades can only be made to a pair of targets if the spatial response is an averaging saccade, i.e. a single target is not selected. We used monkeys in this study, rather than humans, as they are more reliable subjects for investigating express saccades. Although express saccades have clearly been demonstrated in humans (e.g. Fischer & Ramsperger, 1984; Braun & Breitmeyer, 1988; Fischer, Weber, Biscaldi, Aiple, Otto & Stuhr, 1992), this remains controversial (e.g. Reuter-Lorenz, Hughes & Fendrich, 1991; Wenban-Smith & Findlay, 1991; Kingstone & Klein, 1993). Express saccades in monkey, on the other hand, have been confirmed by multiple research groups (e.g. Fischer & Boch, 1983; Lee, Rohrer & Sparks, 1988; McPeck & Schiller, 1994; Paré & Munoz, 1996). We first characterized the spatial target properties necessary to elicit averaging saccades in monkeys. In humans, averaging saccades are frequent when iso-eccentric target pairs with a 30° separation in direction or less are presented. The frequency of making averaging saccades falls off gradually as the separation is increased, with almost none made at a 90° separation (Ottes et al., 1984; Walker, Deubel, Schneider & Findlay, 1997). We show that this range of target separations has a similar effect in monkey. Having confirmed optimal conditions for eliciting averaging saccades, we investigated their latency distributions. Express saccades were more likely to be averaging than the slower regular latency saccades, but express saccades could be either averaging or target-directed. Finally, we studied whether the incidence of averaging and express saccades was influenced by task instruction. It has been shown that averaging saccades occur both when subjects are free to look at either target, or when they are explicitly instructed to look at one and not the other. We examined how such differences in instruction might affect the probability of express averaging saccade occurrence. A portion of these results has been presented in abstract form (Chou, Sommer & Schiller, 1994).

2. General methods

Five rhesus monkeys (Monkeys 1–5) with previously implanted scleral search coils (Robinson, 1963; Judge, Richmond & Chu, 1980) and head restraints were used in this experiment. All surgery was performed under sterile conditions and appropriate analgesics and antibiotics were administered pre and post-operatively. Surgical details have been described at length previously (Sommer, 1994). During each experimental session, animals were seated in a primate chair facing a computer

monitor 57 cm away, on which stimuli were presented, and they were rewarded with apple juice for correctly performing the task as described below. The animals had free access to food in the home cage, but were water deprived before performing the task. Following each day's experimental session, they were allowed to drink until they were satiated prior to being returned to the home cage. All animal use conformed to NIH and MIT animal care guidelines.

All animals had been extensively trained on visual detection and discrimination tasks, and two of the monkeys (Monkeys 4 and 5) had been shown in previous testing to generate express saccades (Monkeys 'D' and 'C', respectively, in Sommer, 1994, 1997). Six months prior to testing, Monkey 5 had undergone a procedure unrelated to this study and received a restricted V3/V4 ablation under aseptic conditions in the right hemisphere corresponding to the representation of a region of the lower left quadrant of visual space. We tested this monkey throughout his visual field, but only analyzed data from targets presented outside the areas represented by the lesion. Another monkey (Monkey 1) had received bilateral V4 aspiration lesions more than 18 months prior to testing but showed no deficits in visual detection or discrimination, or any alterations in saccade metrics or latency at the time of testing (see Schiller, 1995).

Trials were controlled by a PDP-11 computer system and stimuli were presented on a 60 Hz color monitor. All experiments were run in dim ambient light. Eye movements and task-related information were collected at 200 Hz and analyzed off line using the same algorithms as in Sommer (1994, 1997). Briefly, to be considered a saccade, an eye movement had to be greater than 0.25° in amplitude, and greater than $50^\circ/\text{s}$ in instantaneous eye velocity (see Sommer, 1994 for details). Saccadic latency was calculated as the onset time (crossing of a $30^\circ/\text{s}$ velocity threshold) of the first saccade after target presentation. Since targets drawn lower on the monitor are presented slightly later than higher ones, we took this delay into account in evaluating saccadic latency. Saccades were considered to be anticipatory and were excluded from analysis if they had a latency of less than 55 ms. These saccades made up only a very small percentage ($< 1\%$) of all saccades collected.

Averaging saccades were defined as those made in the paired target condition that terminated between the two targets and were part of a spatial distribution that was significantly different from the distributions of saccades made to analogously located single targets. To be counted as an averaging saccade, the angular direction of a saccade had to fall outside the 95% confidence interval for the distribution of directions of saccades made to either target when presented singly.

3. Experiment 1: averaging saccades at different target separations

3.1. Methods

Monkeys 1, 2 and 3 served as subjects in this experiment. We tested saccadic reaction times and the probabilities of averaging saccade occurrence when a pair of identical targets was presented isoeccentrically with a variety of angular separations. We termed this the 'targets identical' task.

At the start of each trial, a $0.2 \times 0.2^\circ$ white square was presented in the middle of the screen (Fig. 1). After the monkey had maintained fixation of this stimulus for a pseudo-random target onset lag (TOL) (200–300 ms), either one or two targets ($1.5 \times 1.5^\circ$ white squares presented at 6° eccentricity) were flashed for 150 ms, after which all stimuli were extinguished. In two out of three trials, a single target was presented, allowing us to measure the natural variability of saccadic endpoints made to the various spatial locations. In one out of three trials, selected pseudo-randomly, two targets were presented simultaneously. Trials were run in blocks of 500 at a single target separation (30, 60 or 90° , which correspond to 3.1 , 6 and 8.5° of visual angle, respectively). Four possible target pair locations were pseudo-randomly interleaved within in each block. Therefore, on any given trial, one of 12 possible stimulus arrangements was presented: a single target at one of eight possible locations or a pair at one of four corresponding locations. Target pairs were tested in two configurations. In some blocks the centers between the targets lay on a cardinal axis (i.e. at 0 , 90 , 180 or 270°), as shown in Fig. 1. In others, the centers lay on the diagonals (i.e. at 45 , 135 , 225 or 315°).

In trials where a single target was presented, the monkeys were required to make a saccade to the target within 300 ms of target presentation. In trials where a pair of targets was presented, we did not constrain the monkeys to look at either target, but instead rewarded them for breaking fixation and making any eye movement that caused the eye to leave a $3 \times 3^\circ$ electronically-defined window around the fixation spot within 300 ms. We analyzed only the first saccade made after target presentation in either single or paired target conditions. We did not examine corrective saccades, which were very rare in any case since the target(s) were almost always extinguished by the time second saccades were initiated.

3.2. Results

Depending on the spatial separation between two simultaneously presented targets, the saccades were either directed primarily toward one of the targets or in between them. Fig. 2 shows eye traces from Monkey 3

in both the single and paired target conditions at the different target separations. The eye movements made in the single target condition are shown in the left hand column (Fig. 2, A–C). All the eye movements terminated close to the targets when they were presented singly. However, in the paired target condition (Fig. 2, D–F), some saccades were averaging, particularly at smaller separations, terminating at spatial positions

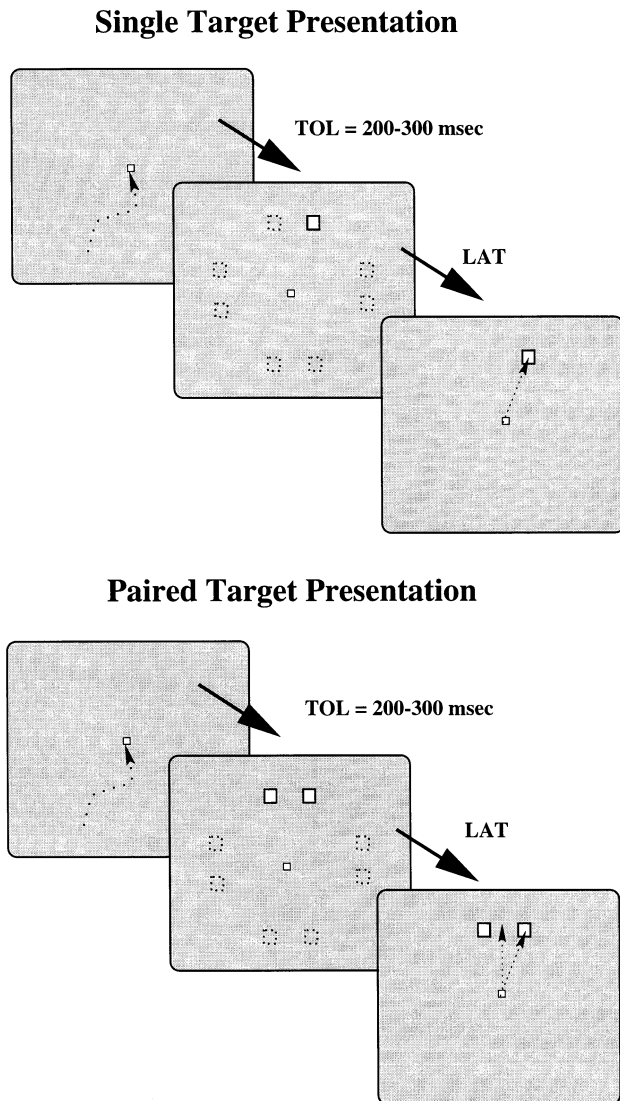


Fig. 1. Temporal and spatial arrangement of trials. Trials were initiated with the presentation of a $0.2 \times 0.2^\circ$ square fixation spot in the center of the monitor. Eye movements are depicted by the dotted arrows. The monkeys were required to maintain fixation on this spot for a randomly determined amount of time, the target onset lag (TOL), between 200 and 300 ms. Following the TOL, the target(s) were flashed, after which both fixation spot and target were cleared from the screen. The monkeys then had 300 ms in which to initiate an eye movement. In each trial, either a single target could be presented in one of eight positions, or two of the targets could be presented simultaneously, as one of four possible pairs. The saccades made to the target pairs might be made to a location between the targets or to one of the targets (bottom panel).

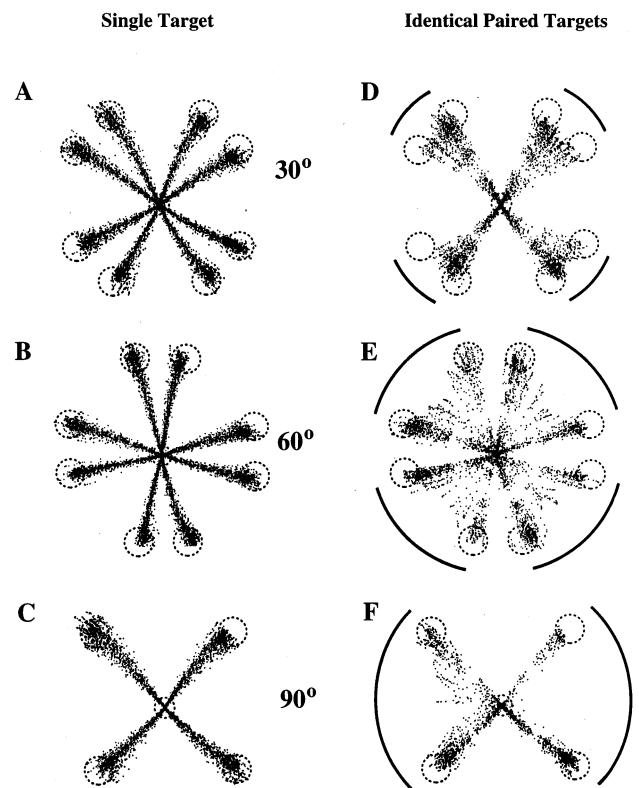


Fig. 2. Representative eye traces showing saccades made by Monkey 3 in both single and paired target conditions for three different target separations when the axes of symmetry between the targets were along the diagonal axes. The three plots on the left (A–C) show the saccades made to singly presented targets, and those in the right column (D–F) show saccades made in the corresponding paired target condition. Target pairings are indicated by the curved brackets.

intermediate between the target locations. As the target separation was increased from 30 to 90° , eye movements became more likely to terminate on or near one of the two target locations. This effect was quantified by plotting the percentage of saccades that were deemed averaging (see Section 2) against target separation (Fig. 3). As target separation increased from 30 to 90° , the percent of averaging saccades decreased for all three monkeys.

The effects of target separation on the latencies produced to paired targets are illustrated in Fig. 4. A typical result is shown for Monkey 2 in Fig. 4A: the latency distributions of saccades to paired targets shift to longer times as target separation was increased from 30 to 90° . The saccadic latency distributions for the corresponding single targets (also shown in Fig. 4), were not affected by the distance between potential locations of the targets.

Two way analysis of variance was performed to evaluate whether saccadic latency was affected by the number of targets presented (single or paired), or target configuration (30, 60 or 90° separation). For all three monkeys, the main significant effect was of task condi-

tion ($P < 0.001$); for all three monkeys there was also a significant effect of target configuration ($P < 0.001$) and a significant interaction between the two factors ($P < 0.001$). Post-hoc pairwise Bonferroni-adjusted t -tests ($P < 0.05$ criterion) revealed that for two monkeys (2 and 3) there were no significant differences in latency to single targets with different separations between potential target locations. Monkey 1 did show a significant latency difference between 60 and 90° target separation ($P < 0.001$) but not between 30 and 60° ($P = 0.34$). All three monkeys, however, showed significant changes in the latency distributions to paired targets as target separation increased. For the data from Monkey 2, for example (Fig. 4B), mean latency shifted from 124 ms at 30° separation to 136 ms at 60° separation to 140 ms at 90°, whereas single target latencies were very similar at all target separations. Thus saccadic latencies made to paired targets increased relative to those made in the corresponding single target conditions, as target separation was increased, as indicated by the significant interaction demonstrated in the ANOVA. This effect is summarized for all three monkeys in Fig. 4C. On the ordinate are the latency differences between saccades to paired targets and those made to single target controls. For all three monkeys, all differences between paired target latency at 60 and 90° target separations and their corresponding single target latencies were significant (Bonferroni-adjusted t -test, $P < 0.05$). At 30° target separation, Monkey 2 showed a significant increase in latency (9 ms) between paired and single target condition, but Monkeys 1 and 3 did not.

We then examined directly whether there was a relationship between the spatial and temporal characteristics of saccades made to paired targets. For each

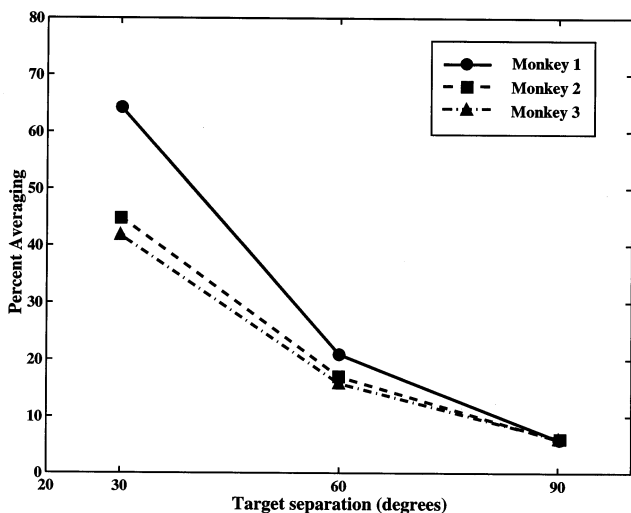


Fig. 3. Percentage of averaging saccades generated at different target separations for three monkeys. For Monkey 1, each point on the graph represents data from 1779 saccades; Monkey 2: $n = 1650$; Monkey 3: $n = 996$.

monkey, we considered the saccades made to a pair separated by 30°, a condition in which all the monkeys made many averaging saccades (see Fig. 3, left-most data points). Saccades were sorted by latency into 15 ms time bins. Since there was some variability between monkeys in the range of saccadic latencies, the minimum latency at which the first bin was placed was selected for each monkey individually such that the bins would span the range of saccadic latencies exhibited by each monkey. The percentage of averaging saccades made at each latency range was calculated (Fig. 5). Overall, the trend was that saccades with short latencies had a higher probability of being averaging whereas slower saccades were more likely to be target-directed. Combining the data from all three monkeys, we found a significant negative correlation between the frequency of averaging saccades and the latency (Pearson product moment correlation $R = -0.769$, $P < 0.01$, $n = 15$). Considering the Pearson product moment correlation for each monkey individually, there was a significant negative correlation in the data of Monkey 1 but not in that of Monkeys 2 and 3.

3.3. Discussion

To summarize, we established that averaging saccades are elicited in rhesus monkeys using similar stimulus configurations to those effective in eliciting averaging saccades in humans (Ottes et al., 1984). At 30° separation, we saw primarily averaging responses; at 60 and 90° separations, we saw primarily target-directed responses. Concurrent with the change in probability of evoking an averaging saccade was a shift in latency. At 30° target separation, saccades made to single targets had similar latencies to those made to paired targets. At 60 and 90° separations, the latencies of saccades to paired targets exceeded those to single targets by 10–20 ms. This speed-accuracy tradeoff is consistent with that observed in Walker et al. (1997). They reported that when human subjects made saccades to a target with a distracter in the field, two effects were observed: if the distracter was close to the target, saccades tended to be both short latency and inaccurate (i.e. averaging). With a greater distance between the target and distracter, saccades tended to be accurately directed to one of the targets but also had longer latencies. We show that in a paradigm where neither stimulus is identified as the target or distracter, a similar pattern of behavior is observed.

Ottes et al. (1985) hypothesized that averaging results from a fast, reflexive process that generates saccades based on poorly resolved spatial information. He and Kowler (1989) challenged the idea that the short latency process was entirely reflexive, based only on the physical properties of the stimuli; they showed that the locus of the averaging saccades could be biased by expecta-

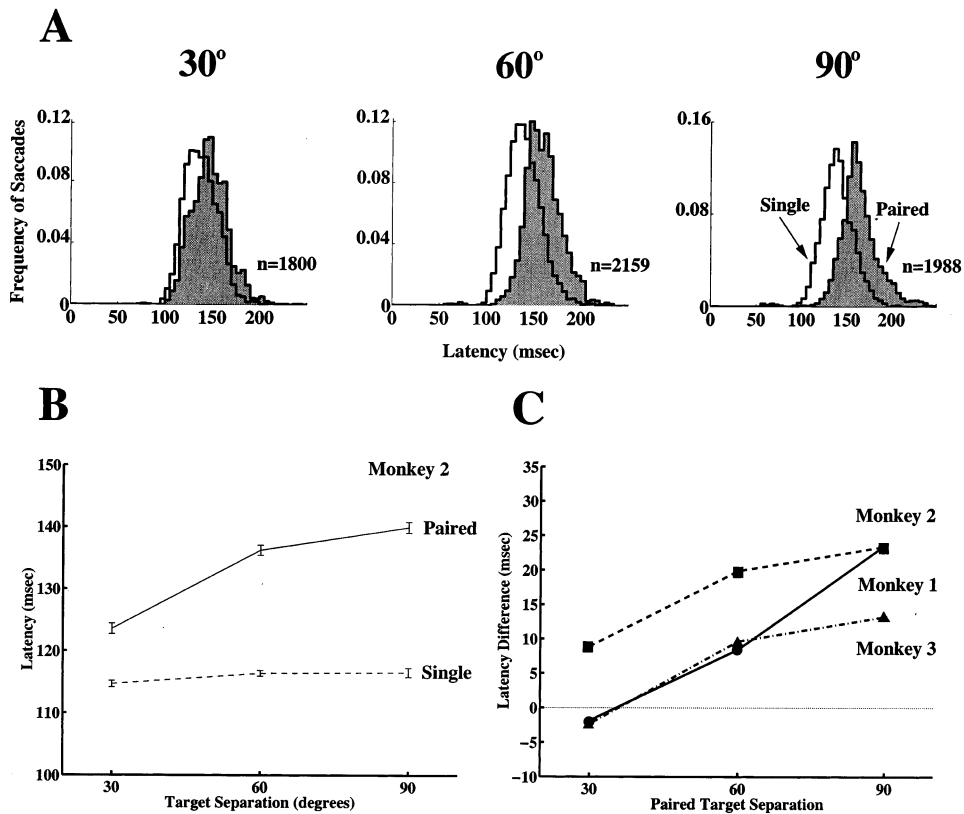


Fig. 4. Latency differences between saccades made in single and paired target conditions. (A) Latency distributions in single and paired target conditions for Monkey 2 at the different target separations. Single target trials were more common than paired target trials, but for ease of comparison in this figure, the single trial latency histograms were normalized to match the numbers of paired targets trials. (B) Mean latency versus target separation in paired and single target conditions for Monkey 2 (same data as in A). (C) Difference in mean latency at the three target separations for all monkeys. All latency differences, except for Monkeys 1 and 3 at 30° target separation are significant ($P < 0.05$ with Bonferroni adjustment).

tion of target location. However, anticipation of the potential target location alone cannot account exclusively for the occurrence of averaging saccades, as we observed many averaging saccades even though the location of the target pairs was randomized.

Express saccades are also thought to be reflexive oculomotor responses and they tend to be spatially inaccurate (Fischer et al., 1992). Their occurrence can also be manipulated by expectation of target location (Paré & Munoz, 1996). Express saccades are suppressed and only regular latency saccades are made in tasks that require either target discrimination (Schiller et al., 1987; McPeck & Schiller, 1994) or voluntary specification of saccade metrics (Fischer & Weber, 1992). We wished, therefore, to investigate how the probability of evoking express saccades might vary with the probability of evoking averaging saccades. Our hypothesis was that when two targets are presented simultaneously, only averaging saccades could be express saccades.

All three monkeys tested in Experiment 1 showed only unimodal latency distributions. Monkey 1 did make many short latency saccades, some with latencies as short as 90 ms (see Fig. 5), which could be consid-

ered as being within the 'express' range. However, the criterion for express saccades is that the saccades belong to the first population of a bimodal latency distribution, not short latency alone. Under no conditions did Monkey 1 ever show a bimodal latency distribution. Thus we considered the short latency saccades to be fast regular latency saccades, and not express saccades. To investigate the possible relationship between averaging and express saccades, we tested two monkeys that had been trained extensively to make express saccades.

4. Experiment 2: averaging express saccades

4.1. Methods

Monkeys 4 and 5, who had been previously shown to make express saccades readily to single targets (Sommer, 1994, 1997), were used in this experiment. The surgical and training protocols were the same as in Experiment 1. Stimulus presentation, data collection and the basic experimental paradigm were similar to

that described in Experiment 1. However, in this experiment we wished to observe the latencies of large numbers of averaging saccades and express saccades. To this end, we increased the chance of eliciting averaging saccades by reducing the variability of target location. Decreasing the uncertainty in target location may also facilitate the production of express saccades (Paré & Munoz, 1996, but also see Rohrer & Sparks, 1993). Within a block, a single pair of target locations was tested, so that for the whole block stimuli appeared in one of only two locations, either as a single target (80% of trials, determined pseudo-randomly) or as a target pair (20% of trials). We tested three different target separations, 30, 60 and 90°, and four different pair configurations, the center between targets lying on the cardinal axes. The stimuli were the same as those used in Experiment 1, and we discouraged anticipatory responses by randomly varying the amount of time (200–300 ms) before the target(s) were presented after fixation.

Visual inspection of latency histograms revealed that for both monkeys, when a bimodal distribution was observed, the peaks occurred consistently around the same latencies. The first was at around 70 ms, the second around 120 ms, with a trough around 100 ms. We therefore considered express saccades as being those saccades which occurred at latencies of 100 ms or less, while those that had a latency of more than 100 ms or more were classified as regular latency saccades (Fischer & Boch, 1983). Averaging saccades were defined using the same criterion as in the first experiment.

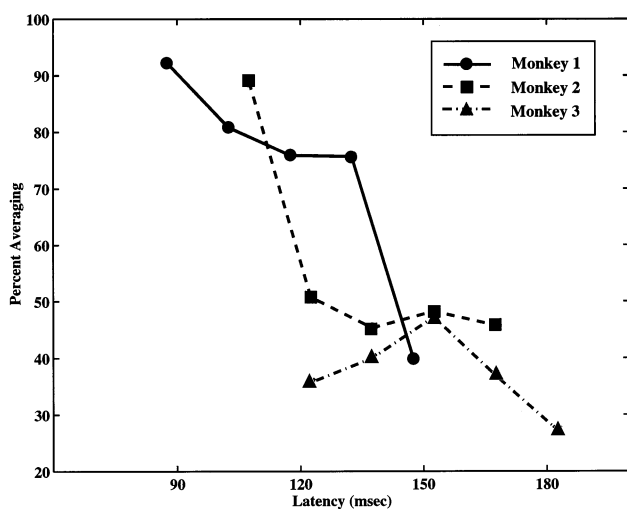


Fig. 5. Percentage of averaging saccades in relation to saccadic latency. Data are taken from saccades made to targets with a 30° separation for each monkey. Saccades in the paired target conditions were categorized by latency into 15 ms bins, centered around the location of the point on the x-axis. Approximately 30–90 saccades contributed to each bin. Total number of saccades: Monkey 1, $n = 566$; Monkey 2, $n = 467$; Monkey 3, $n = 352$.

4.2. Results

4.2.1. Accuracy and latency of saccades in single target control condition

Before examining the relationship between express and averaging saccades, we first established the occurrence of accurate express saccades in the single target condition. In almost all cases, the monkeys made accurate saccades to singly presented targets. However, due to an apparent positional habit specific to Monkey 4, arising after the experiments of Sommer (1994, 1997), many saccades made in the condition when paired targets were in the left hemifield were much less accurate, both in amplitude and direction, than those made in any other configuration. The mean peak velocity of saccades in this target configuration also was diminished and the mean latency increased. We do not know the reason for these atypical saccades, as this monkey had not received any invasive brain surgery that might have caused the positional habit. The monkey had previously been tested on a battery of visual detection and discrimination tasks (not shown) and deficits were not seen. Although the monkey did make many accurate saccades as well, we omitted all saccades made to pairs that were centered about the horizontal meridian in the left hemifield from our analysis.

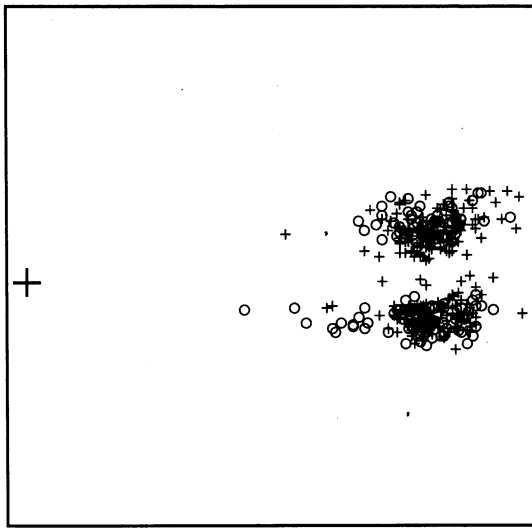
We examined the latency distributions for bimodality in the single target conditions. Monkey 4 showed a clear bimodal distribution of saccadic latencies for saccades made in all directions. As mentioned earlier, Monkey 5 had undergone a surgical ablation of a portion of V3 and V4 representing the lower left visual field, close to the vertical meridian. Since the possible effect of V3 and V4 lesions on eye movements is beyond the scope of this study, we analyzed only saccades made to target pairs located exclusively in the intact portions of the visual field. Inspection of the latency distributions confirmed that this monkey made express saccades prolifically to targets in the upper and left visual field; therefore we included only target pairs whose centers lay upwards and leftwards of the fixation point in our analysis.

4.2.2. Influence of target separation on occurrence of averaging saccades

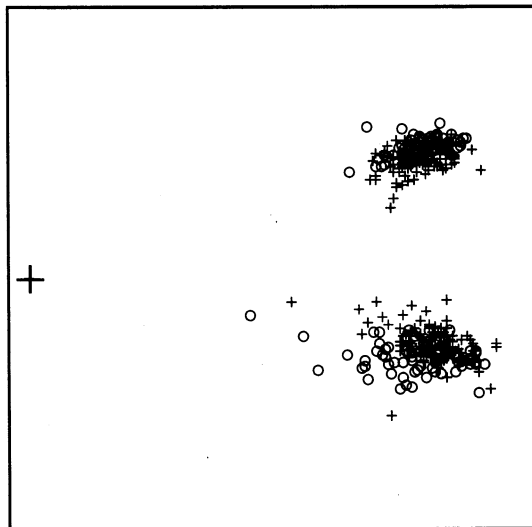
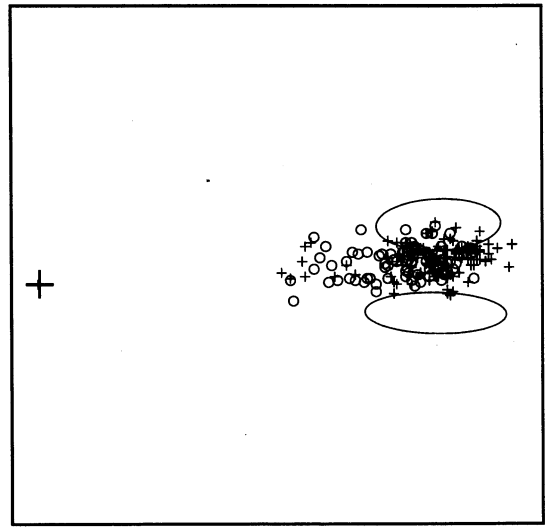
The fact that these monkeys made express saccades did not alter the basic finding from Experiment 1 that most saccades were averaging at small target separation and target-directed at larger separation in the paired target conditions. This is illustrated in Fig. 6, which shows an example of the saccadic endpoints of all saccades in the single and paired target conditions at three separations. As with the monkeys tested in the first experiment, a single cluster of saccadic endpoints was observed in between locations of paired targets that were separated by 30°; the distribution of saccade end-

SINGLE

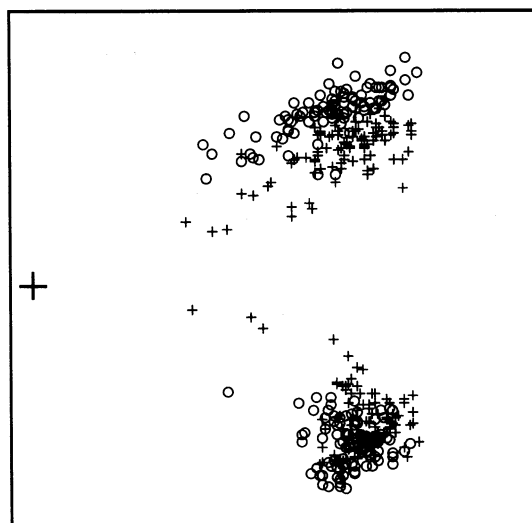
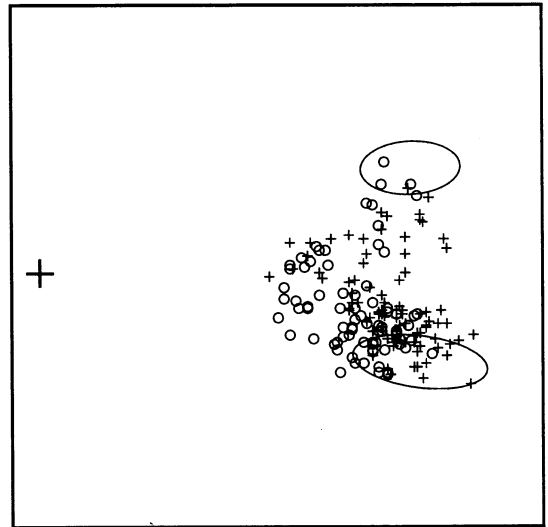
PAIRED



30°



60°



90°

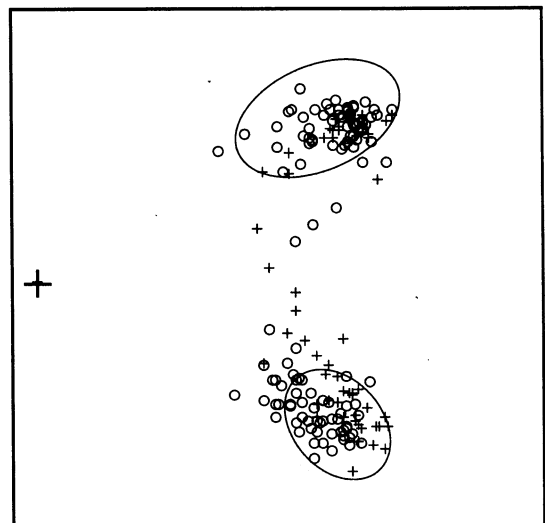


Fig. 6. (caption overleaf)

points became more bimodal and target-directed with increasing separation (Fig. 6, right column). The ellipses show the 95% confidence area around clusters of saccades made to singly presented targets whose endpoints are shown in the left hand column. Note that the ellipses shown in the right hand panels are for qualitative appreciation only; saccadic direction, and not amplitude, was used to categorize saccades as being averaging or target-directed.

Fig. 7 shows quantitatively the percent of averaging saccades as a function of target separation for these two monkeys. Similar to what we observed in the monkeys that did not make express saccades (cf. Fig. 3), with a 30° target separation, both monkeys made more than 50% averaging saccades. Both monkeys showed a negative correlation between percent averaging and target separation.

4.2.3. Latency distribution of saccades in paired target presentations

Saccades made in response to paired targets had distinct bimodal latency distributions, as can be seen from the graphs in the right-hand column of Fig. 8. The size of the express peak (relative to the regular peak) varied with the distance between targets, decreasing with increasing target separation. Compared to the corresponding single target controls (left-hand column), the decrease in the relative size of the express peak was more pronounced for paired target conditions. Examination of the spatial distribution of saccadic endpoints in the paired target condition (Fig. 6), it was obvious that both averaging saccades and target-directed saccades could be of either express latency (Fig. 6, crosses) or regular latency (Fig. 6, circles).

As in Experiment 1, we used a two-way ANOVA to evaluate the effects of task condition (single versus paired) and the separation between targets or potential target locations (30, 60 or 90°) on saccadic latency. For both monkeys, the main significant effect was of task condition ($P < 0.001$) but both monkeys also showed significant effects of target configuration ($P < 0.001$), as well as a significant interaction between target number and separation ($P < 0.001$). Post-hoc multiple pairwise comparisons (Mann–Whitney U , Bonferroni adjusted $P < 0.05$ criterion) revealed that saccades made to paired targets had longer latencies than those made to single targets. Also, in the paired target condition, mean latency increased with increasing target separation. These effects were consistent with those observed in Experiment 1. In this experiment, however, both

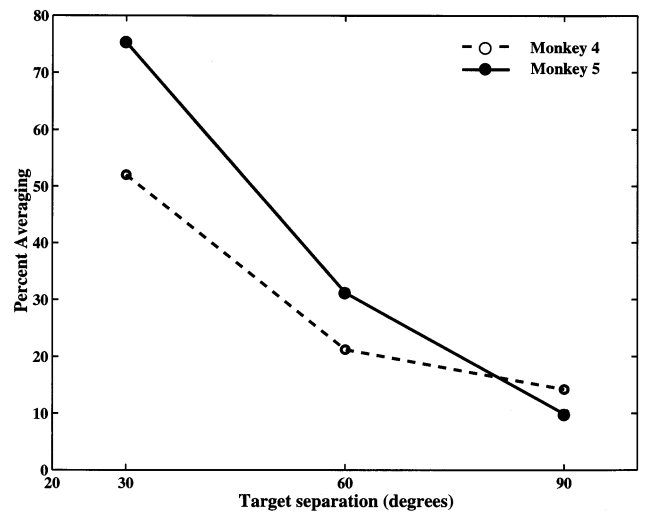


Fig. 7. Probability of averaging saccades shown as a function of target separation for monkeys that made express saccades. For each monkey, the mean percentage of averaging saccades across all target configurations in which accurate express saccades were observed (centers up down and right for Monkey 4; centers up and left for Monkey 5) is plotted for each target separation. For Monkey 4, each data point represents data derived from 3564 saccades, Monkey 5, $n = 730$.

monkeys also showed a small, but significant effect on saccadic latency of separation between potential target locations in the single target presentations. Mean latency increased significantly with the separation between potential target locations (e.g. see Fig. 8, left column). This may have been due to planning before target onset (Paré & Munoz, 1996; Sommer, 1997), as the general location where the singly presented target would occur was predictable in blocks of 30° separation trials, but less so in blocks of 60 or 90° separation trials.

In summary, the differences in saccadic latency between single and paired target conditions, and at different target separations were consistent with those observed in monkeys that did not make express saccades (see Fig. 4). However, in Monkeys 4 and 5, the latency differences were primarily due to changes in the relative proportions of express and regular saccades. A decrease in the size of the express peak with increasing target separation can be seen in Fig. 8, right hand column.

We also separately examined the latencies of averaging and target-directed saccades in the paired target condition. The mean latency of averaging saccades was significantly shorter (Mann–Whitney U , $P < 0.01$) than that of target-directed saccades at all target separations,

Fig. 6. Saccadic endpoints in single and paired target condition made by Monkey 4. Three different target separations are shown, with target pairs centered about an axis rightward from the fixation point (large cross). Express saccades are plotted as small crosses, regular saccades as circles. For comparison, the location of saccadic endpoints to single targets are shown as ellipses which represent the 95% confidence interval of endpoint distribution, derived from data in left hand column.

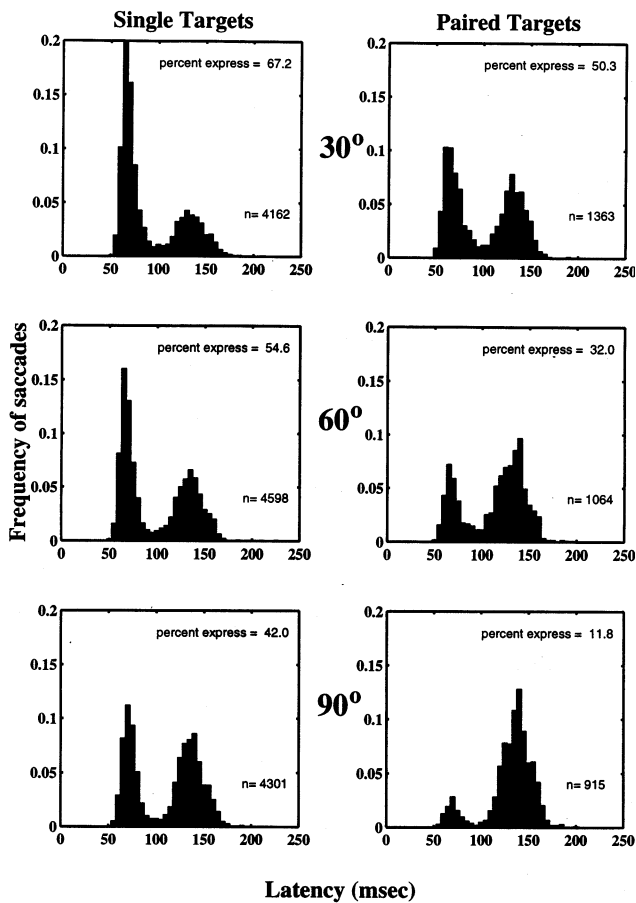


Fig. 8. Saccadic latency histograms for Monkey 4 in single and paired target conditions for the three different target separations tested. Saccadic latencies from all single target presentations at one target separation are collapsed into single plots shown in the left hand column. The latency histograms for the corresponding paired target presentations are shown in the right hand column.

for both monkeys. Plotting the latency histograms for averaging and target-directed saccades separately (Fig. 9) revealed explicitly that averaging saccades did exhibit a distinct bimodal latency distribution. Moreover, the relative size of the express peak compared to the regular saccade peak was larger for averaging than for target-directed saccades at all target separations.

As in the first experiment, we examined the percentage of averaging saccades made at different latencies. Fig. 10 shows the relationship between probability of averaging and saccadic latency at the 30° target separation (at which the most averaging and express saccades were evoked). Express saccades, which are represented to the left of the 100 ms cutoff, were more likely to be averaging than regular latency saccades (Monkey 4 percentage of averaging saccades: express saccades, 54.1%; regular saccades, 42.7%; Monkey 5 percentage of averaging saccades: express saccades, 91.5%; regular saccades, 71.9%). This was consistent with the general trend for all monkeys that saccades with shorter latencies tended to be more averaging (cf. Fig. 5). However,

in the present experiment, there were no significant negative correlations from either monkeys individual data, nor from their combined data.

Besides having the tendency to be more averaging in direction, express saccades also tended to be hypometric in amplitude relative to regular latency saccades, a result that has been previously shown (Fischer & Boch, 1983; Fischer et al., 1992). Fig. 11 shows the relationship between saccadic amplitude and latency for a subset of the saccades. For both monkeys, express saccades had statistically smaller amplitudes than regular saccades. (Monkey 4: mean amplitude of express saccades 4.95°, regular saccades 5.20°, student's two-tailed t -test, $P < 0.01$, $n = 18\,079$. Monkey 5: mean amplitude of express saccades 4.43°, amplitude of regular saccades 5.71°, Student's two-tailed t -test $P < 0.01$, $n = 5052$).

4.3. Discussion

We confirmed the finding of Edelman and Keller (1998), that averaging saccades elicited by having paired targets separated in direction can indeed be

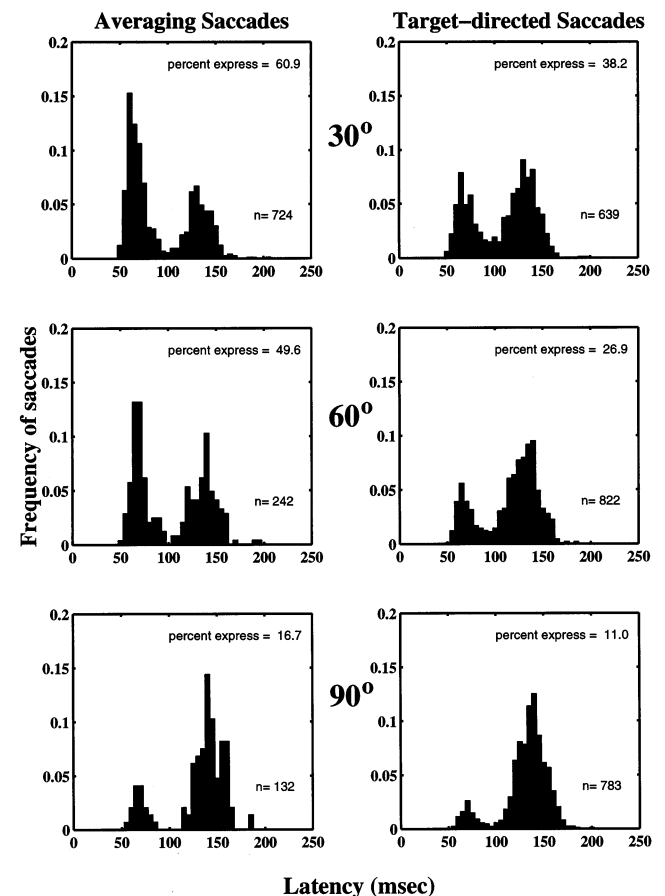


Fig. 9. Latency histograms for Monkey 4 in the paired target condition with averaging saccades (left column) and target-directed saccades (right column) plotted separately for each target separation.

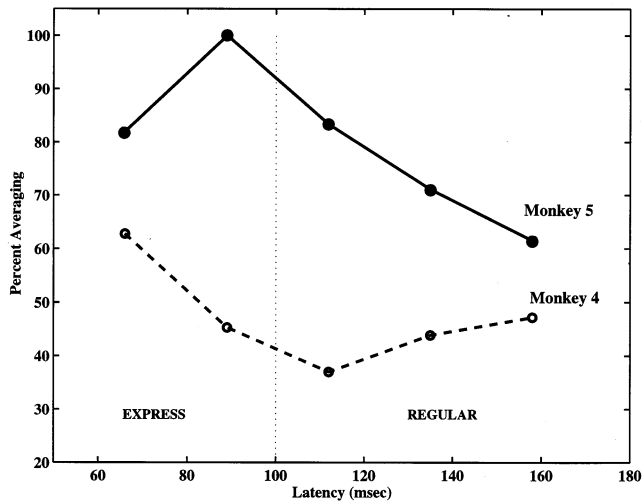


Fig. 10. Probability of averaging saccades in relation to saccadic latency for 30° target separation. Same convention as in Fig. 5, except that in this case the bins are 23 ms wide, in order to capture the wider range of latencies exhibited by these two monkeys. The dotted line is situated at 100 ms, the division between express and regular saccades. Monkey 4, $n = 1405$; Monkey 5, $n = 301$.

express saccades. In fact, averaging saccades had shorter latencies than target-directed saccades and had a higher probability of being express saccades than target-directed saccades. This would appear initially to be at odds with data that show that express saccades are suppressed when there is more than one potential

target in the visual scene (Schiller et al., 1987; McPeck & Schiller, 1994; Weber & Fischer, 1994), or when saccades are generated to blank space (Fischer & Weber, 1992). It may be that when two targets are close together, they are in fact treated as one perceptual target and the averaging saccade is made to the center of gravity of the gestalt, as has been proposed by Coren and Hoenig (1972). At large separations, there is less of a tendency for the two stimuli to be grouped, and thus the pair is 'parsed' into two potential targets, one of which has to be selected as the target of the saccade. It may be that it is the selection process that inhibits express saccades. We did indeed observe that at large separations, target-directed saccades were almost all of regular latency (see Fig. 9, bottom right). This is consistent with the notion that express saccades can be made when only one new object appears in the visual scene; at small separations, only one target (the grouped pair) is treated as the saccade target. However, some target-directed saccades could still be made at express latencies when the targets had small separations (see Fig. 9, top right).

In the present experiment, the monkeys were neither encouraged nor discouraged to make averaging or target-directed saccades, so when they made averaging saccades we did not know what they planned as the actual target of the saccade. To disambiguate the monkeys' targeting strategy, we performed the following experiment where we presented stimuli in the same spatial separations, but explicitly trained the monkeys always to make target-directed saccades, so that they were discouraged from perceptually grouping the pair.

5. Experiment 3: averaging and express saccades under conditions where the target is explicitly cued

5.1. Methods

Monkeys 4 and 5, which readily made express saccades, were again used in this study. Experimental set-up, eye movement recording and data analysis were the same as in the previous experiment. The main difference was that the monkeys were always required to make saccades to a red target, regardless of whether it occurred in isolation or in the presence of an isoluminant green distracter ('targets different' task). To distinguish this task from the previous one for the monkey, the fixation stimulus was a red square $0.5 \times 0.5^\circ$ in size. In single target trials, the target stimulus was a $1 \times 1^\circ$ square, of the same luminance and chrominance as the fixation spot. In the paired target condition, the target was presented simultaneously with a distracter (a green square of the same size). The luminance and chrominance of the stimuli were well above threshold for both detection and discrimination. When paired targets were

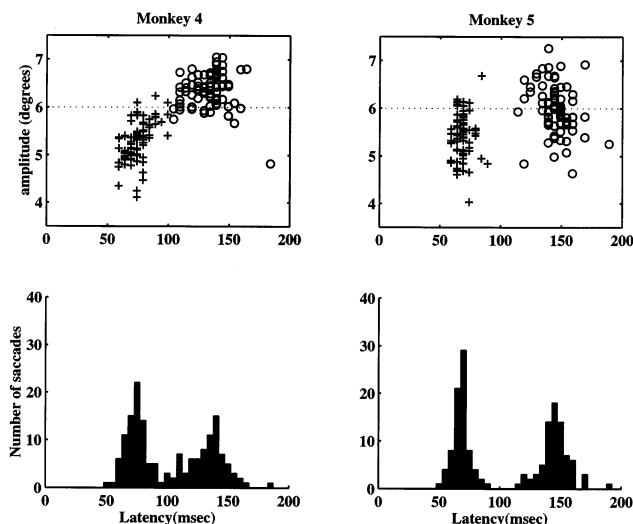


Fig. 11. Relationship between saccadic amplitude and latency. For each monkey, only a representative subset of 160 saccades is shown here for clarity. For both monkeys, saccades shown were sampled from those made to the pair of targets separated by 30°, with the center between the targets upwards above fixation. The upper graphs show the amplitude plotted against latency and the lower graphs show the corresponding latency histograms. In the upper plots, the location of the targets (at 6°) is shown as the dotted horizontal line. Express saccades are plotted as crosses, and regular saccades as circles.

presented, the monkeys were only rewarded for making accurate saccades to the red target (i.e. to within a $3 \times 3^\circ$ electronically defined window around the target). The monkeys were not rewarded for averaging saccades or incorrect choices (saccades to the green target); however, eye movements made in these trials also were analyzed. Stimuli were presented at 6° eccentricity and with angular separations of 30 and 60° . The pairs were presented symmetrically about the diagonal axes and the target could appear at either of the two target locations. In a block of trials, only one angular separation was tested, but the paired stimuli were presented in all eight spatial configurations along with the corresponding single target presentations. In Experiment 2 the monkeys were tested with predictable target locations (1 of 2 positions in any given block) in order to increase the chances of eliciting express saccades; however, this also apparently led to the emergence of position biases. To reduce these biases, we increased the uncertainty of the target position by increasing the number of possible target locations from two to eight¹. We also obtained a direct comparison between eye movements made when the target was explicitly instructed and when it remained ambiguous, as we ran the monkeys on the identical target condition in the same target configurations in Experiment 1 ('targets identical' task).

5.2. Results

When paired targets were separated by a large (60°) angle, both monkeys performed with high accuracy in the targets different task, making accurate (i.e. within 3° of the target) saccades to the red target on over 95% of trials. When paired targets were separated in direction by 30° , the monkeys made occasional errors by making a saccade to the distracter, but they still made mostly target-directed saccades to the red stimulus. Examination of the saccadic endpoints (Fig. 12, right hand column) showed that the endpoints were spatially bimodal even at 30° separation, i.e. the saccades were predominantly directed at the red targets. However, the endpoints were shifted towards the center between the targets compared with the endpoints made in single target trials (ellipses in Fig. 12, right hand column), as if the saccade endpoints were biased by the presence of the distracter. For comparison, the saccadic endpoints made to the same target pair locations in the targets identical task (Fig. 12 left hand column) are shown. It can be seen that at both 30 and 60° target separations,

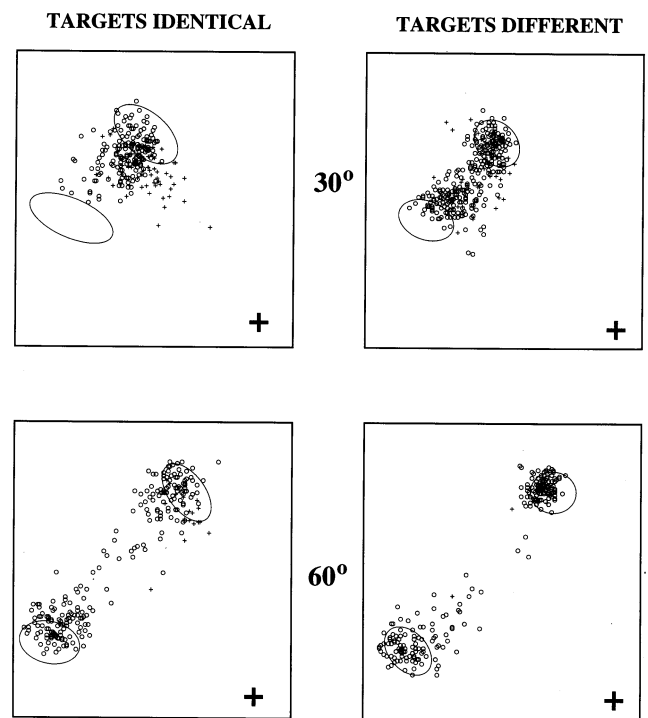


Fig. 12. Saccadic endpoints made to paired targets in targets different versus targets identical task made by Monkey 5. Convention is the same as the paired target panels of Fig. 7. In each graph the location of the majority of saccades made to single targets is represented by the 95% confidence ellipses.

there is less averaging behavior in the target different condition than in the target identical condition.

A three-way ANOVA was performed to investigate the effects of task (targets different or targets identical), target separation (30 or 60° separation between target locations) and target number (single or paired targets presented) on saccadic latency. For both monkeys, the main factor accounting for variance in latency was task ($P < 0.001$), but there were significant effects of both target number and separation as well ($P < 0.001$). For both monkeys, there were significant two-way interactions ($P < 0.05$) between each pairing of the factors. For Monkey 5 but not Monkey 4, there was a three-way interaction between all three factors. Post-hoc analysis (Bonferroni-adjusted t -tests) revealed that for both monkeys, as in the previous two experiments, saccadic latencies in the paired target conditions were significantly higher than latencies obtained in single target controls, and that latencies in the paired target condition increased with increasing target separation. However, the direction of the main effect was different for the two monkeys. For Monkey 4, latencies were slightly higher in the targets identical task than in the targets different task. For Monkey 5 however, latencies were significantly higher in the targets different than in the targets identical task (Mann–Whitney, $P < 0.01$).

¹ We reported in Experiment 2 that Monkey 5 only made express saccades in restricted portions of the visual field. Experiment 3 was performed several months later, at which time express saccades were observed in all parts of the visual field tested. Thus we included saccades to all targets in this analysis.

Examination of the saccadic latency distributions revealed that express saccades were almost entirely suppressed in the targets different task. Fig. 13 shows the latency distributions for the saccades depicted in Fig. 12. Whereas this monkey made express saccades at the 30° target separation for identical stimuli (Fig. 13A), there is almost complete suppression of express saccades for the same target locations when an accurate saccade to one particular stimulus was required (Fig. 13C).

The latency and accuracy of saccades in the targets different versus targets identical tasks are summarized for both monkeys in Fig. 14. Saccades were less averaging in the targets different task than in the targets identical task (Fig. 14A and B), and the monkeys made few express saccades in the targets different task (Fig. 14C and D). However, that the suppression of express saccades was due to the target-distracter stimulus configuration was obvious for only one of the monkeys (Fig. 14D). In the other monkey (Fig. 14C) express saccades were suppressed even in the targets identical task; we suspect this general suppression was a confound of increasing the target location unpredictability for this experiment (Paré & Munoz, 1996).

5.3. Discussion

In this last experiment we discouraged perceptual grouping of the paired stimuli by requiring the monkeys to discriminate between the two on the basis of color. We studied how the explicit target selection would affect express and averaging saccade occurrence. We observed that indeed, saccades were less averaging than in the case where the stimuli were identical and the

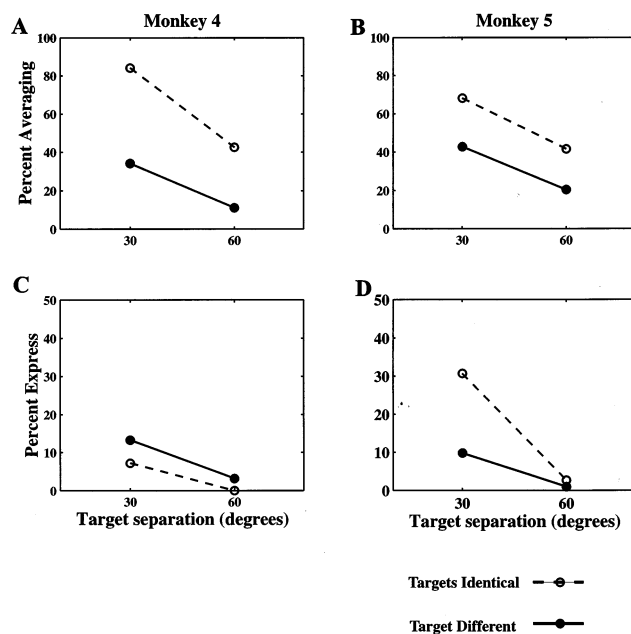


Fig. 14. Percent averaging and express saccades for each monkey in the targets different and targets identical tasks. Monkey 4, $n = 5212$; Monkey 5, $n = 10519$.

target ambiguous. Nonetheless, when the targets were close together, some degree of averaging behavior was still observed, in that the endpoints of the saccades were biased towards the direction of the distracter (Fig. 12). Thus, consistent with previous reports using human subjects (e.g. Ottes et al., 1985; He & Kowler, 1989; Walker et al., 1997), we conclude that spatial averaging is an involuntary response to multiple visual stimuli in close proximity to each other, but conscious processes such as target selection can override it to some degree.

Despite the fact that there were still some averaging saccades, express saccades were almost entirely abolished when one of the two stimuli had to be selected as a target (Fig. 14D). This lends further support to the notion that express saccades are reflexive responses: when a saccade target has to be selected from two or more possibilities, the reflex is suppressed and only regular latency saccades are made.

6. General discussion

6.1. Summary of findings

1. We have shown in this study that monkeys, like humans (Ottes et al., 1984), display two types of responses when presented with simultaneously appearing target pairs, depending on the spatial separation between the targets. Averaging saccades were made frequently to closely spaced targets. As sepa-

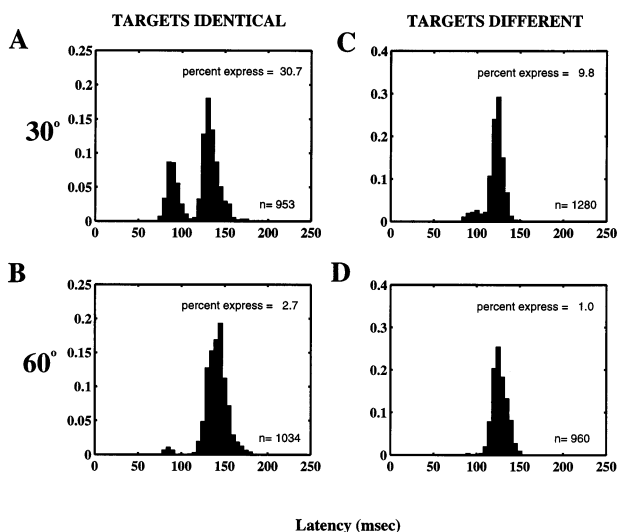


Fig. 13. Latency distributions for the saccades displayed in Fig. 13. Panels A and B show the latency distributions for saccades made to paired identical targets. Panels C and D show distributions for saccades made to stimulus pairs when the target was cued.

ration increased, the frequency of making averaging saccades decreased and more saccades were made directly to one or the other of the targets. This finding was consistent in all monkeys we tested, both in those that made express saccades and in those that did not.

2. Mean saccadic latencies were slower when the monkeys were presented with two targets compared to a single target. This difference in latency was more prominent when the target separations were larger. In the monkeys that did not make express saccades, this was evidenced by an overall shift in the latency histograms. In the monkeys that made express saccades, the change was due primarily to a change in the relative size of the express peak.
3. A weak relationship existed between saccadic accuracy and latency. Averaging saccades tended to have shorter latencies than target-directed saccades. Compared to the latencies of saccades made to single targets, averaging saccades had similar latencies to saccades made to single targets whereas target-directed saccades were slower on average than saccades made to single targets. In monkeys that made express saccades, there was a higher probability of express saccades being averaging than regular saccades, but express saccades could be either averaging or target-directed.
4. The occurrence of averaging saccades was greatly diminished when the subjects were explicitly instructed to make saccades to one of the stimuli, thereby discouraging perceptual grouping of the pair. However, the endpoints of the target-directed saccades were still biased towards the distracter. Express saccades were also almost entirely abolished under such experimental conditions.

6.2. *Averaging saccades optimize visual information*

One interpretation of averaging saccades is that the two targets are grouped together, and the target of the saccade is the single gestalt of the two stimuli. Evidence from humans suggests that averaging saccades are made to the perceptual ‘center of gravity’ of the targets (Coren & Hoenig, 1972; McGowan et al., 1998). If the targets are close enough together, an averaging saccade will bring both close to the fovea, and information about both targets can be processed (Kowler et al., 1995). As target separation is increased, the probability of grouping the targets together is decreased. This might account for why few averaging saccades are seen at larger separations; bringing gaze to the ‘center of gravity’ would result in neither target being near the fovea.

Another hypothesis put forth to explain averaging is that the targets are treated as being separate, but the proximity of one biases the direction of saccades di-

rected at the other. Thus even though the saccade is directed at one target, the resulting endpoint is deviated towards the other stimulus. This is consistent with the ‘near distracter’ effect of Walker et al. (1997). There is evidence from human subjects which suggests that even if the subjects are specifically instructed to make saccades to one of the two targets or even are required to attend to and identify specific features of one of the targets, the resulting saccades are still averaging, although the locus of the saccades can be biased by cognitive factors such as expectation (He & Kowler, 1989). We made a similar observation in that the endpoints of the saccades generated to the red-green target pairs were biased towards the center of the pair, even though the monkeys were constrained to make very accurate saccades. We propose that when the target selection is constrained to one particular stimulus, the signal from the distracter is voluntarily suppressed, such that the signal from the desired target leads to saccade generation. Incomplete suppression of the distracter signal would lead to partial averaging response.

We have presented two hypotheses to explain averaging: one in which the grouped figure is selected as the target of the saccade leading to complete averaging, and one in which the actual saccade target is one of the stimuli, but the saccade is deviated by the other stimulus, leading to partial averaging. We suggest that rather than being two conflicting explanations, both may be operative under different circumstances, depending on whether or not one of the two stimuli is specified as the target of the saccade.

6.3. *Relationship between averaging and express saccades*

We have found a general trend for an inverse relationship between averaging behavior and latency that was consistent with previous studies (Ottens et al., 1985; Walker et al., 1997) showing that the fast-latency saccades tend to be more averaging than later ones. We found this to be true both for monkeys that did and those that did not make express saccades. It had previously been shown that express saccades did not occur when multiple stimuli were presented (Schiller et al., 1987; McPeck & Schiller, 1994). However, the issue appears not to be the number of stimuli, but whether or not one of the stimuli is discriminated and selected as the target of the saccade. As described previously (Weber et al., 1993; Sommer, 1994; Edelman & Keller, 1998), and confirmed here under a range of conditions, express saccades can be made to in response to multiple stimuli, as long as averaging behavior is permitted. Even though more than one new target suddenly appears in the visual scene, the saccade is not made to either target per se, but to the single perceptual group.

In the trials where the monkeys made target-directed saccades, we speculate that this grouping did not occur, leading to the suppression of express saccades. When the monkeys were actively discouraged from grouping the targets, express saccades were not made.

Express saccades can be thought of as reflexive saccades in the temporal domain, because they allow the quickest possible analysis of a visual stimulus through reduced reaction time. Averaging saccades can be thought of as reflexive saccades in the spatial domain, because they allow the quickest possible analysis of multiple visual stimuli through efficient selection of the location of the saccadic termination. Discriminating between the stimuli and selecting one as the target of the saccade requires extra time, and cannot be accomplished at express latency.

6.4. *Brain structures involved in express averaging saccade generation*

We propose that there may be two different neural mechanisms for generating saccades to two targets associated with the two types of saccadic behavior (fast averaging and slower target-directed) observed psychophysically. The first is responsible for fast, averaging saccades and is probably mediated by the superior colliculus. It is known that the activity of superior colliculus neurons is essential to the generation of express saccades (Schiller et al., 1987). Single neuron recording studies have revealed different activity in some cell types in the intermediate layers before express and regular latency saccades, consistent with the idea that facilitation of the part of the collicular map associated with the upcoming saccade allows early initiation of the saccade (Edelman & Keller, 1996; Paré & Munoz, 1996; Dorris et al., 1997). Single cell recording studies have shown that averaging saccades are also represented in the superior colliculus, although it is still unclear where averaging actually occurs (Van Opstal & Van Gisbergen, 1990; Glimcher & Sparks, 1993). One possibility is that averaging saccades are a consequence of pooling the activity across two separate populations of collicular neurons (Lee et al., 1988). If two sites in the superior colliculus are electrically stimulated simultaneously, an averaging saccade does indeed occur (Robinson, 1972; Schiller & Sandell, 1983). A second possibility is that averaging occurs at a level above the superior colliculus and the resulting saccade is represented by a single population of saccade-related neurons corresponding to that saccade vector (Glimcher & Sparks, 1993). Edelman and Keller (1998) found that for express saccades, the former appears to be true. They reported that with targets separated by 45°, the activity recorded during averaging express saccades was more consistent with the response combining activity from two loci of activity. It may be that the combining

of activity from two sources within the superior colliculus yields the elevated activity that facilitates express saccades. Based on the results from the present study, and those of Walker et al. (1997), we suggest that this facilitation is spatially limited; as the targets are moved farther apart, the facilitation drops off and may even be replaced by inhibition, resulting in a decrease in express saccades.

The colliculus is under tonic inhibition from structures such as the basal ganglia (Hikosaka & Wurtz, 1983), and cells in the rostral region of the superior colliculus during fixation (Munoz & Wurtz, 1992), which is lifted prior to the generation of a saccade. This mechanism may play a role in target selection, but it is not known how focal the area of decreased inhibition is in the colliculus in response to a pause in the tonic firing of substantia nigra or rostral superior colliculus cells. It may be that a 'window' region of a fair size is released from inhibition in the colliculus such that facilitatory effects are possible within this region. Based on our study, we would hypothesize that this region would cover at least the area encoding movement direction separations of 30° or more at 6° eccentricity. This translates to a diameter of 3° but less than 6° of visual angle for this 'window region'. This range is similar to the spatial extent of express saccade facilitation observed in other experiments (Paré & Munoz, 1996; Sommer, 1997). Outside of this area of lifted inhibition, not only are the effects of facilitation negated, but also the visual responses to the two stimuli may mutually inhibit each other. In this case, a saccade is unlikely to result from the combining of activity across the two loci in the superior colliculus and another signal, possibly from an area outside the superior colliculus, is required to trigger the saccade to one of the two targets.

Such a signal may be generated in the frontal eye fields (FEF), which project to the superior colliculus and also to the basal ganglia. Thompson, Bichot and Schall (1997) recorded from frontal eye field (FEF) neurons with visual and movement-related responses during a discrimination task. FEF neurons show an initial burst of visual activity regardless of whether the target or a distracter is in the receptive field, but show a difference in firing rate approximately 100 ms after the targets are presented. This discrimination between target and distracter occurs before the saccade is initiated. The authors did not study FEF activity during express saccades, but it is known that FEF activity is not essential for the generation of express saccades (Schiller et al., 1987).

Thus we propose two different neural mechanisms for the generation of saccades to two targets that account for the two types of saccades observed psychophysically: fast averaging and slower target-directed. One mechanism is operative when targets are close together. In this case, saccadic endpoint may be spe-

cified within the superior colliculus, by averaging the activity across two loci of visual activity. This is a fast mechanism, and in the extreme, can yield express saccades triggered by the burst of visual activity alone (Edelman & Keller, 1996; Dorris et al., 1997). Because the saccade endpoint is specified by the combined activity across two sites in the superior colliculus, this mechanism has a tendency to yield averaging saccades. The second mechanism is slower, and may be mediated by structures upstream from the superior colliculus, such as the FEF. This mechanism yields saccades of longer latency, and yields accurate target-directed saccades.

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