

Properties of Saccadic Responses in Monkey When Multiple Competing Visual Stimuli Are Present

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Arai, Kuniharu, Robert M. McPeck, and Edward L. Keller. Properties of saccadic responses in monkey when multiple competing visual stimuli are present. *J Neurophysiol* 91: 890–900, 2004; 10.1152/jn.00818.2003. Important insights into the neural organization of the saccadic system have been gained when the usually stereotyped movement trajectories of saccades have been altered by experimental manipulation. In the present study we produced trajectory variability in monkeys by using a visual search task in which both the location and color of an odd-colored target were changed randomly trial by trial, and the number of distractors was varied on each trial. We wished to determine whether increasing the number of distractors also increased the movement trajectory variation, i.e., the amount of initial directional deviation, endpoint deviation (averaging), and curvature of saccades. Overall, saccade latencies and the proportion of saccades directed to distractors decreased as the number of homogenous distractors increased. We also found that saccades have much more dispersion in their initial direction when distractors are present in comparison to the case when only a single target without distractors appears. However, initial dispersion decreases systematically as the number of distractors increases. The percentage of averaging saccades produced in the search task was not consistently dependent on the number of distractors. A significant fraction of averaging saccades still occurred for much wider spatial separations of stimuli than in previous studies using two visual stimuli with no specified target. The curvature of saccade trajectories increased dramatically when distractors were present, but the amount of curvature was not systematically affected by the number of distractors. Errors present in saccade trajectory in the search task were only poorly compensated. We conclude that these variable saccade trajectories result from incomplete or inaccurate specification of the target when competing stimuli are present and that a smaller number of more widely spread distractors facilitate saccade variability, perhaps due to the greater difficulty of target selection.

INTRODUCTION

Saccades are stereotyped movements that generally follow a relatively straight trajectory and end close to single targets that appear in the visual field (Becker 1989). However, since saccades made to single targets are so stereotyped, it is often difficult to determine the parameters of movement represented by simultaneously recorded neural activity when recording from structures associated with saccade production. Is the activity related to the saccadic velocity, for example, or to the saccadic amplitude? Various methods have been utilized to vary or perturb saccade trajectories to break the usual tight correlations between saccade size, duration, and eye velocity (Edelman and Goldberg 2001; Gandhi and Keller 1999; Gossens and Van Opstal 2000; Keller and Edelman 1994; Munoz

and Wurtz 1993; Stanford and Sparks 1994). Recently, it has been reported that saccades made while scanning images of natural scenes (Burman and Segraves 1994) or while carrying out a visual search task (McPeck and Keller 2001) have much greater trajectory variability.

Most of the experimental data in studies involving stereotyped saccades have been gathered using a single visual stimulus as the target. A slightly more complex situation is generated by the simultaneous appearance of two visual stimuli at different spatial locations or by the appearance of two spatially separated stimuli in close temporal order. Both of these patterns of visual presentation can produce saccades that are directed to a location somewhere in between the stimuli (Chou et al. 1999; Findlay 1982; Ottes et al. 1984) and which may have highly curved trajectories (Minken et al. 1993). Movements that end between the locations of the two visual stimuli have been called averaging saccades (see Chou et al. 1999 for a summary of work in this area in humans and monkeys). In both monkeys and humans, averaging saccades made to double, isoecentric stimuli with 30° separation in direction are frequent, but the frequency of their occurrence falls off as the separation between visual stimuli is increased, so that, when the stimuli are separated by 90°, averaging movements become rare (Chou et al. 1999; Ottes et al. 1984). In addition, it has been reported that there is a speed–accuracy tradeoff, with longer latency saccades showing less averaging (Coëffé and O’Regan 1987).

Visual search paradigms use more complex visual presentations to study the properties of saccadic eye movements in situations that more closely approximate natural viewing. In a feature search paradigm the subject must select and saccade to the location of an odd stimulus (the target) that appears simultaneously with multiple distractors. The target may be differentiated by its odd color, shape, or other visually distinguishing feature. When monkeys or humans were tested using a color or shape oddity search task, many saccades went directly to the target with an accuracy comparable to that achieved when only a single target appeared at the same location (Bichot and Schall 1999; Findlay 1997; McPeck and Keller 2001). However, when both the location and the color (or the shape) of the odd stimulus were changed randomly from trial to trial, several alternative types of saccadic behavior not previously reported for saccades made to single targets appeared in a minority, but significant subpopulation of trials. First, a number of saccades were directed to locations between the target and a distractor (Findlay 1997; McPeck and Keller 2001). Second, some sac-

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acades in monkeys were initially pointed in a direction in between the target and a distractor, but curved during the movement to land near the target at the saccade end (McPeck and Keller 2001; McPeck et al. 2003). Finally, another sub-population of saccades was directed to the location of a distractor, but this initial error was followed after an extremely short intersaccadic interval by a second saccade made directly to the target (McPeck et al. 2000; McPeck and Keller 2001). Similar short intersaccadic intervals have been reported in other search tasks (Findlay et al. 2001; Hooge and Erkelens 1996; Theeuwes et al. 1999; Viviani and Swensson 1982).

Three of the previously cited studies show similar saccadic endpoint figures from which an impression about the frequency of averaging movements in search can be gained (Findlay 1997; McPeck et al. 2000; McPeck and Keller 2001), but each study used a different number of visual stimuli in their search pattern (3 for McPeck et al. 2000; 4 for McPeck and Keller 2001; 8 for Findlay 1997). Therefore it is not clear from these previous studies how the frequency of averaging saccades varies as a function of the number or spacing of stimuli in the search array. Also the relationship of the frequency of appearance of curved saccade trajectories to the number or spacing of distractors has not been reported in detail (McPeck and Keller 2001; Minken et al. 1993). In particular, it is not clear from these previous studies to what extent saccadic curvature can compensate for saccades initially directed in between a distractor and the target to guide the movement to end closer to the target location.

Therefore the major goal of the present study was to determine quantitatively how saccadic trajectory is altered by the number or spacing of visual stimuli in visual search paradigms. Specifically, in the present study we examined the effect of the number or spacing of the visual stimuli in the search array on the variability in the initial direction of the saccades, the saccade accuracy, the frequency of saccade curvature, and the amount of compensation for errors in saccade trajectory (redirection toward the target) produced during the time course of the saccades.

METHODS

Two male rhesus monkeys (*Macaca mulatta*) weighing between 4 and 7 kg were used in this study. All experimental protocols were approved by the Institutional Animal Care and Use Committee at the California Pacific Medical Center and complied with the guidelines of the Public Health Service policy on Humane Care and Use of Laboratory Animals.

Preparation

A scleral eye coil and a head-holder system were implanted under isoflurane anesthesia and aseptic surgical conditions. Anesthesia was induced with an intramuscular injection of ketamine. Heart rate, blood pressure, respiratory rate, and body temperature were monitored for the duration of the surgery. A coil made of four turns of Teflon-coated stainless steel wire was implanted under the conjunctiva of one eye using the procedure described by Fuchs and Robinson (1966), as modified by Judge et al. (1980). At the completion of the surgery, animals were returned to their home cages. Antibiotics (Cefazolin) and analgesics (Buprenex) were administered as needed during the recovery period under the direction of a veterinarian.

Behavioral procedures

Testing was performed in a dimly illuminated room. Data collection and storage were controlled by a custom real-time program running on a PC. Eye position and velocity were sampled at 1 kHz and digitally stored on disc. A Macintosh computer, which was interfaced with the PC, generated the visual displays using software constructed using the Video Toolbox library (Pelli 1997). Visual stimuli were presented on a 29-inch color cathode ray tube (Viewsonic GA29) in synchronization with the monitor's vertical refresh. The monitor had a spatial resolution of 800 by 600 pixels and a noninterlaced refresh rate of 75 Hz. The monitor was positioned 33 cm in front of the monkey and allowed stimuli to be presented in a field of view of approximately $\pm 32^\circ$ along the horizontal meridian and $\pm 30^\circ$ along the vertical meridian.

The monkeys were seated in a primate chair with their heads restrained for the duration of the testing sessions. They executed behavioral tasks for liquid reward and were allowed to work to satiation. Records of each animal's weight and health status were kept, and supplemental water was given as necessary. The animals typically worked for 5 days and were allowed controlled access to water on weekends.

Search Task

The animals were trained to perform a reaction time search task as shown schematically in Fig. 1. Initially a dim white fixation point appeared at the center of the screen. Monkeys were required to saccade to this point and hold steady fixation there (within in a window of $1.5\text{--}2^\circ$) for a random interval (450–650 ms). At the end of this interval, the fixation point disappeared and an eccentric array of visual stimuli appeared simultaneously. Each visual array consisted of a single target, presented either alone or along with a number of distractors. The target was distinguished by its odd color. The target was randomly chosen on each trial to be a red or green disc, set to be approximately equiluminant, with measured luminances of 0.90 and

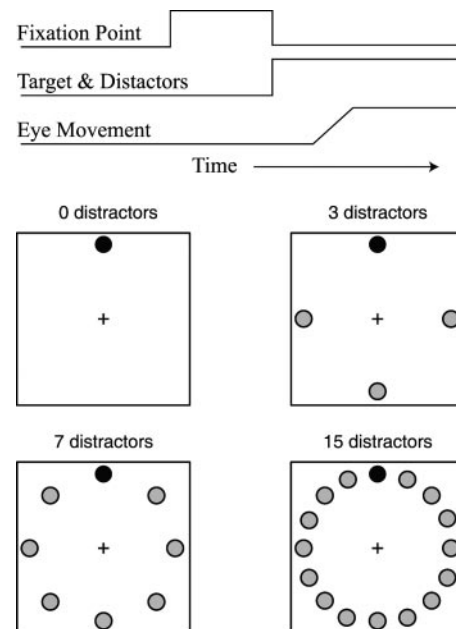


FIG. 1. Schematic representation of the visual search task. The cartoon at the top shows paradigm events in time, and the 4 panels below show the spatial arrangement of the fixation point (+), the target (dark-shaded disk), and distractors (light-shaded disks) in the 0-, 3-, 7-, and 15-distractors conditions. The target could appear at any one of 8 directions (4 cardinal and 4 oblique), but for purposes of illustration these directions are all rotated so that the target appears at the top in all panels.

0.92 cd/m², respectively. The stimuli were scaled according to the cortical magnification factor to keep their saliency constant across different eccentricities (Rovamo and Virsu 1979). At an eccentricity of 15°, the target subtended 2° of visual angle. The number of distractors (0, 3, 7, or 15) was varied pseudorandomly. In one animal (monkey M) the three-distractor condition proved to be the most difficult condition, and its appearance resulted in more errors. Therefore we included more trials of this type than would have occurred with a strict random selection process.

Figure 1 shows the spatial arrangement of these visual arrays. The target stimulus was randomly presented at one of eight possible locations. The possible target locations were all at the same eccentricity in a given session and were separated from each other by angles of 45°. The distractors were located isoeccentrically with the target and were spaced evenly around an imaginary circumference at this eccentricity. Eccentricity of the circumference was held constant at either 10, 15, or 20° within a block of trials. A block of trials consisted of about 100 trials, which, on completion, was followed by short period of rest. Several blocks of trials made up a daily session and eccentricity was kept constant for the day.

The monkeys were given a liquid reward for making a saccade to the "location of the target" without delay when the fixation point was extinguished. The "location of the target" was defined as a horizontal and vertical angular window around the target location of ± 4 , ± 4.5 , or $\pm 5^\circ$ for array eccentricities of 10, 15, or 20°, respectively. We required that a saccade with this accuracy be made within a maximum reaction time of about 300 ms in order for the monkey to receive a reward for that trial. With this time restriction both monkeys made many averaging and curved saccades, behaviors that we wanted to quantify for their potential usefulness in future studies of neurological mechanisms. Our animals might have exhibited more accurate behavior if they had been encouraged to delay the timing of the first saccade (Coëffé and O'Regan 1987). A minimum allowed reaction time (50 ms) was used to eliminate anticipatory saccades.

Data analysis

Horizontal and vertical eye movements were digitally filtered using a low-pass filter with cutoff frequency of 100 Hz. Eye velocity signals were calculated off-line with a digital differentiator. Time of saccade onset was defined as the time when radial eye velocity exceeded 50%/s, and the same threshold was used for detecting saccade endpoint. Data from each trial were visually inspected to verify the accurate identification of saccades. We analyzed only the first saccade in each trial, whether the monkey made a correct saccade to the target, an error saccade to a distractor, or a saccade in between target and distractors. Figure 2 illustrates our classification of saccades. We first examined the direction of saccade endpoint (the straight-line direction between the initial position at saccade onset and the point where the movement ended) for just the single-target trials (no-distractor case) for each of the eight possible directions and three target eccentricities. From these no-distractor data we computed the mean saccadic endpoint direction and the 95% confidence intervals of this mean for each of the eight possible target directions. The 95% confidence intervals were not noticeably different as a function of the eight possible target directions, target eccentricity, or the two animals. The mean values over both animals and all directions were $\pm 4.9^\circ$.

For the remainder of the trials (with distractors present), we counted a movement as "on-target" if it landed within the 95% confidence limits at each position as determined by the behavior for single-target presentations. An example of the on-target region for one target position is shown by the dark-shaded sector in Fig. 2. Saccades that landed in either of the adjacent light-shaded sectors on either side of the on-target sector were counted as "averaging" saccades. Each sector of averaging saccades extended from a border of the on-target sector to the inner border of the 95% confidence interval for the adjacent stimulus position. Note that the confidence limits placed

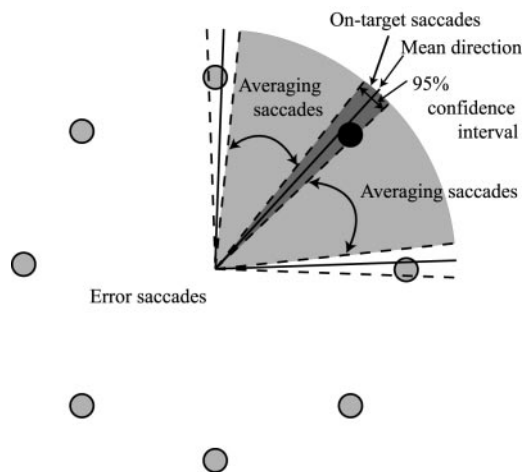


FIG. 2. Schematic drawing showing how "on-target," "averaging," and "error saccades" were defined. In the illustration, only the situation where the target (dark-shaded disk) appears at 45° up in the right visual field is shown. Locations of the distractors (light-shaded disks) are shown for the 7-distractor case where the array stimuli are separated by 45°. The mean direction of saccades made to the target (in the 0-distractor case) when it was located in the upright direction is shown by the solid central line. Similarly the mean directions of saccades when the single target appeared in the pure up or pure right directions are shown by the upward and rightward solid lines. Note that the mean saccade directions for the single-target case are usually not exactly in the direction of the target at any location. The 95% confidence limits about these means are shown with dashed lines. An on-target saccade is defined as a saccade whose direction falls within the 95% confidence intervals for the mean saccade direction to the target when no distractors were present (dark-shaded central sector). An averaging saccade was defined as a saccade that landed in either of the light-shaded sectors on either side of the central on-target region just defined. Averaging saccades fall outside the 95% confidence intervals for the target and outside the confidence intervals for the target when it was located in the up or right directions. All other saccades were regarded as error saccades (the remaining large unshaded sector).

around the adjacent stimulus locations in Fig. 2 were obtained from the calculations for single-stimulus trials when the single targets were located at these particular locations. All other saccades were classified as "error saccades" (the unshaded hypersector in Fig. 2). In the present study we concentrated our analysis on saccades of the on-target and averaging classes. Error saccades occurred on 13% of the total trials with distractors present in one animal and on 28% in the other. A majority of the errors were made to adjacent distractors in both animals.

Our classification of each saccade as on-target or averaging could only be made off-line when the data on single-target behavior at each position were made available. Nevertheless, our criteria for rewarding the monkey's behavior (see above) were very close to the on-target classification. For example, for the 20° array eccentricity, the animals were rewarded for making a saccade within an angular window of $\pm 5^\circ$, while on-target saccades were defined as being within about $\pm 4.9^\circ$ of the mean single-target behavior.

In this paper, circular distributions such as mean angle, angular deviation, and confidence interval were calculated based on circular statistics (Zar 1984). Unless otherwise noted, significance tests were performed using the Mann-Whitney *U* test. For significance testing, we used a criterion level of $P < 0.05$ unless otherwise noted.

The summary analyses presented below were obtained from the following calculations. First, we computed instantaneous saccade direction from saccade onset to saccade end as a function of the number of distractors. The instantaneous direction (ID) of saccade trajectory was obtained by computing the tangent of radial eye velocity at each time point

$$ID = \arctan \left(\frac{Vel_v}{Vel_h} \right) \quad (1)$$

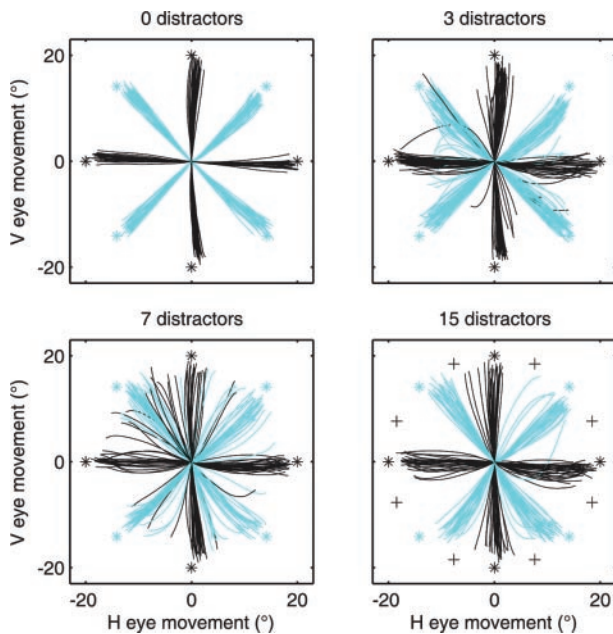


FIG. 3. Saccade trajectories from one recording session in monkey M using the visual search task. The possible locations of the target are shown in each panel (*). The upper left panel shows saccadic eye movements when the target was presented without distractors. The remaining panels show the eye movements when distractors appeared simultaneously with the target. Target and distractors were separated from each other by 90, 45, and 22.5°, respectively, in the 3-, 7-, and 15-distractors conditions. The locations of the distractors (+) are shown in the panel for the 15-distractor condition only for clarity. All data for each movement are plotted from saccade onset to saccade end. Alternating color coding is used to differentiate sets of saccades made to different target locations. In our directional convention the 0 direction is right, horizontal, 90° is up, etc.

where Vel_h and Vel_v are horizontal and vertical velocities, respectively. A similar definition for instantaneous direction was used by Aizawa and Wurtz (1998). To quantify the amount of curvature present in saccades we measured the maximum deviation of each saccade trajectory perpendicular from a straight-line path between the fixation location to the saccade endpoint and normalized the deviation by the radial magnitude of the saccade. Separate measures of mean curvature were computed for each of the eight target directions and for each number of distractors. This method is similar to that used by Smit and Van Gisbergen (1990) to quantify the trajectory curvature of saccadic eye movements.

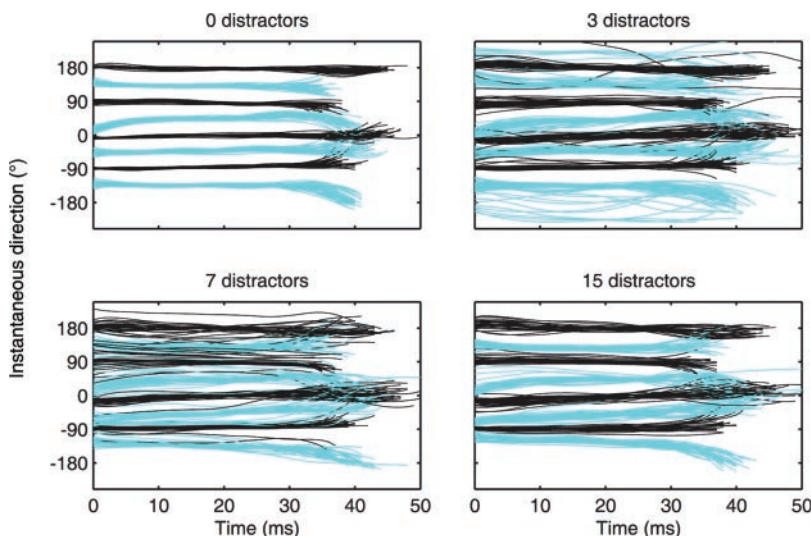


FIG. 4. Instantaneous direction of saccadic eye movements in the visual search task. Same recording session as that illustrated in Fig. 3. In each panel the instantaneous direction of each saccade is shown from saccade onset to saccade end. The arrangement of results and color coding in the panels are the same as that shown for the 4 panels in Fig. 3.

RESULTS

We collected data on saccadic behavior in the search task in the two animals using separate sessions in which the eccentricity of the stimuli was fixed at 10, 15, or 20°. Figure 3 shows the patterns of saccade trajectories obtained in one monkey for all on-target and averaging saccades in a typical block of trials. The stimuli in the search array were located at an eccentricity of 20° in this block of trials. Results in the other animal were similar. From the data shown in this figure it is easily seen that the presence of distractors greatly increases the spatial spread and variability of saccade trajectories over that exhibited by the saccadic system when only a single target is present. However, it's not immediately clear from these raw data whether the presence of increasing numbers of distractors causes an increase in the spatial spread or curvature of the trajectories as a function of the number of distractors. We therefore analyzed the trajectories in quantitative detail.

Initial saccade direction

Figure 4 shows instantaneous saccade direction from saccade onset to saccade end for the same session of trials used to illustrate Fig. 3. The directional results shown in the four plots of Fig. 4 support the impression gained from the trajectory plots shown in Fig. 3 that saccades have more spread in direction when distractors are present. In addition, this figure shows that much of this directional spread or dispersion is present even at the time of saccade initiation. The directional dispersion was defined as the angular SD of instantaneous saccade direction. Initial dispersion is defined as the value of directional dispersion present at the epoch of saccade onset. We initially examined the results for each of the eight possible target directions separately, but found no systematic difference in the quantitative analyses that follow for any particular direction (e.g., cardinal directions and oblique directions) in either monkey. Therefore in the following detailed analyses we have collapsed all the data for different target directions into single analyses that include all target directions. Table 1 gives individual data for each animal and for separate sessions, each with a fixed array eccentricity. The entries in each row in this table show mean values computed for each session. The two sets of data for 20° amplitudes (monkey M) came from differ-

TABLE 1. Individual data for each animal and for separate sessions

Monkey Amplitude, °	Dispersion of Initial Direction, °				Percentage Averaging, %			Curvature				
	No. of distractors				No. of distractors			No. of distractors				
	0	3	7	15	3	7	15	0	3	7	15	
M												
20	4.3	18.9	15.0	10.0	36.8	37.9	54.0	0.022	0.042	0.044	0.044	
20	6.4	23.8	20.2	11.3	33.5	41.7	62.5	0.023	0.039	0.048	0.039	
15	4.4	15.1	16.1	13.6	34.6	45.6	61.3	0.023	0.041	0.056	0.055	
10	4.4	24.1	16.1	11.0	47.3	46.3	42.0	0.026	0.079	0.056	0.044	
Overall mean	4.9	20.5	16.9	11.5	37.7	42.0	54.8	0.023	0.048	0.049	0.044	
C												
20	4.4	19.5	13.4	7.7	38.9	46.7	50.5	0.030	0.041	0.058	0.041	
15	4.2	19.3	13.2	9.3	23.8	35.0	31.3	0.031	0.048	0.051	0.039	
10	4.6	18.6	15.7	12.8	31.1	43.1	28.4	0.034	0.044	0.062	0.052	
Overall mean	4.4	19.1	14.1	9.9	31.0	41.4	37.3	0.031	0.044	0.057	0.043	

ent sessions on 2 separate days. We conducted a two-way, unbalanced ANOVA on the data from each animal with saccade amplitude and number of distractors as factors. The case with zero distractors was not included in the ANOVA and was treated as a separate condition in subsequent analyses. The main effect of the number of distractors was significant in both monkeys ($P < 0.01$). The main effect of amplitude was not significant in either animal ($P = 0.56$ and 0.65 for M and C, respectively). Furthermore, there was no significant interaction between amplitude and numbers of distractors in either animal ($P = 0.16$ and 0.9 for M and C, respectively). We averaged initial directional dispersion in each animal across eccentricity and obtained the means as a function of number of distractors plotted in Fig. 5. A separate ANOVA on the effect of distractors present and the no-distractor condition showed that these conditions were significantly different in both animals ($P < 0.01$).

The overall mean results for each animal shown in Fig. 5 quantifies the impressions gained from an inspection of the raw plots in Figs. 3 and 4 for initial directional dispersion. The mean values of initial directional dispersion are much smaller when no distractors are present. In both monkeys the mean dispersion is greatest in the three-distractor case, but then declines for larger number of distractors (7 and 15). This trend for less initial dispersion as the number of distractors increased was significant in both animals (linear contrasts, $P < 0.01$ in both animals).

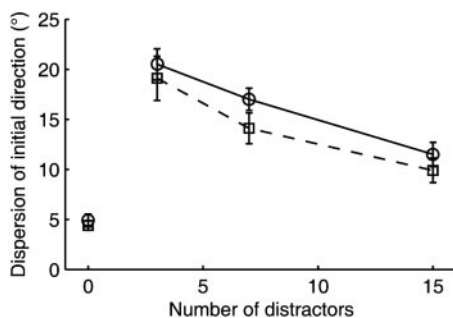


FIG. 5. Dispersion of initial instantaneous saccade direction as a function of the number of distractors for monkey M (open circles and solid lines) and for monkey C (open squares and dashed lines). The mean values of the SDs of the initial instantaneous direction are plotted as a function of the number of distractors. ○, the animal whose raw data were used to construct Figs. 3 and 4 (monkey M). Data averaged across sessions with different array eccentricities. SE are indicated by the vertical bars in this and all subsequent figures.

Averaging saccades

Examination of Fig. 3 suggests that many saccades in the search paradigm ended at a location between the locations of the target and its flanking distractors. This effect may be seen more clearly in Fig. 6, where the distributions of saccade endpoint directions (the straight-line direction between the initial position at saccade onset and the point where the movement ended) are plotted for each number of distractors for both animals for the 20° eccentricity condition. No differences in these distributions for any of the eight possible target directions were found, therefore, the data for all directions are collapsed in Fig. 6. The results for the zero-distractor condition are shown in the upper row. Mean direction for the zero-distractor case was normalized to zero and the 95% confidence limits for this mean are shown. Distributions for increasing numbers of distractors are plotted below the zero-distractor condition in separate columns for each animal. The 95% confidence limits for the zero-distractor condition (vertical lines) that were used to define averaging behavior are repeated below for each number of distractors. In these plots all saccades that ended within $\pm 100^\circ$ of the target location are included. This would include examples of all three classes of trajectories: on-target, averaging, and errors. In the conditions with distractors, there is a wider spread of the distributions and a decline in the peak of the distributions near zero error compared with the single-target condition. Many of the less accurate saccades are still clustered near the target locations with a small number scattered in between the target and the two adjacent distractor positions. In addition, small subpopulations of saccades with endpoint directions near either of the two adjacent distractors can be seen, particularly for the three-distractor case. In the results shown in the left-hand column for one animal, the local spread in the distributions (more averaging saccades) seems to increase systematically with the number of distractors, but this trend is not readily apparent in the other animal.

To quantify these initial impressions, we computed the percentage of averaging saccades after pooling the data for all eight target directions and present the results for all experimental sessions in Table 1. All values represent means computed for each session. Figure 2 shows schematically how averaging saccades were defined. We conducted a two-way, unbalanced ANOVA on the data from each animal with saccade amplitude and number of distractors as factors. The main

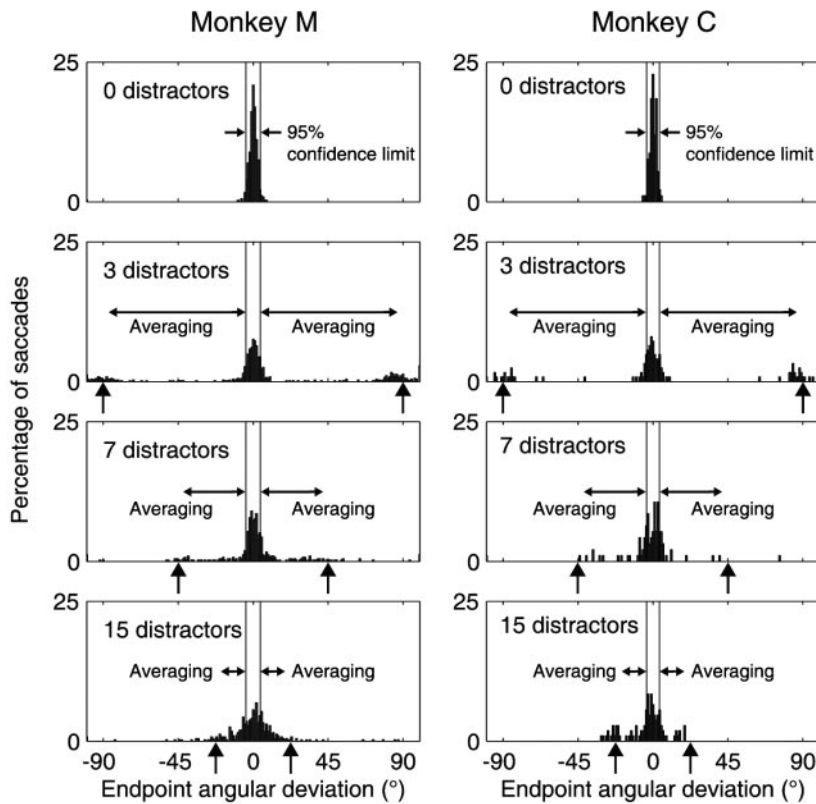


FIG. 6. Histograms illustrating the distributions of saccade endpoint variability in the visual search paradigm. The vertical axis shows the percentage of saccades for each amount of deviation from the mean single-target endpoint (binwidth is 1°) for each stimulus configuration. The column of plots on the left are for monkey M and those on the right are for monkey C. The vertical lines in each plot show the 95% confidence limits about mean saccade endpoint for single-target trials. The arrowheads along the horizontal axis in the 2nd, 3rd, and 4th rows show locations of the adjacent distractors, and the horizontal lines represent the approximate range of averaging saccades. Plots include data collapsed from all 8 target positions normalized to zero position.

effect of the number of distractors was significant in both monkeys ($P < 0.05$). The main effect of amplitude was not significant in monkey M ($P = 0.62$), but was significant in monkey C ($P < 0.05$). Furthermore, there was a significant interaction between amplitude and numbers of distractors in monkey M ($P < 0.05$), but not in monkey C ($P = 0.44$).

We plot the overall mean results in Fig. 7 for both monkeys. For the mean data obtained with the search task, the percentage of averaging saccades increased monotonically in one animal (M) with the number of distractors. This trend was significant (linear contrasts, $P < 0.01$). The other animal (C) did not show a significant trend in either direction with increasing numbers of distractors (linear contrasts, $P = 0.18$). The lack of a consistent trend in the production of averaging saccades is the same result obtained with a visual inspection of the histograms in Fig. 6.

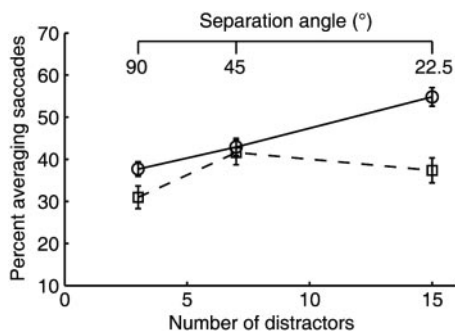


FIG. 7. Percentage of averaging saccades as a function of the number of distractors. Means values for monkey M (○). Mean values for monkey C (□). Array spacing for each number of distractors is given in the top axis.

Curved saccades

Saccade trajectories made in the single-target condition are relatively straight, but when competing stimuli for the saccade goal are present, curved saccadic trajectories have been observed (Findlay and Harris 1984; McPeck and Keller 2001; Minken et al. 1993; Port and Wurtz 2003). In the present experiments we quantified this tendency for curvature as a function of the number of distractors. The method we used to compute curvature is given under METHODS. We found no systematic difference in the results obtained at any target location, therefore, the data were collapsed across all eight target directions. The results for all experimental sessions in both monkeys are given in Table 1. All values represent means computed for each session. We conducted a two-way, unbalanced ANOVA on the data from each animal with saccade amplitude and number of distractors as factors. The case with zero distractors was not included in the ANOVA, but was treated as a separate condition. The main effect of amplitude was significant ($P < 0.05$) in one monkey (M), but not in the other (C) ($P = 0.58$). The main effect of the number of distractors was not significant in either animal ($P > 0.05$). Furthermore, there was a significant interaction between amplitude and numbers of distractors in monkey M ($P < 0.05$), but there was no significant interaction in monkey C ($P = 0.79$). A separate ANOVA on the curvature measured when distractors were present or the no-distractor condition showed that these conditions were significantly different in both animals ($P < 0.01$).

We averaged curvature across eccentricities and obtained the pooled means for each animal as a function of number of distractors. These averages are plotted in Fig. 8. Curvature increased dramatically when distractors were present in comparison to the situation when only the target appeared. The

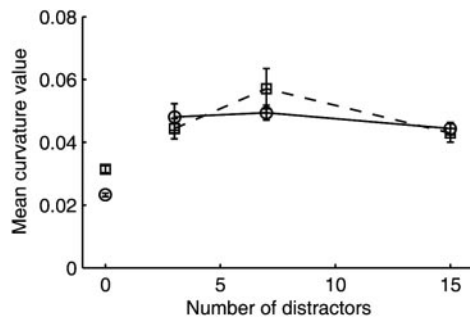


FIG. 8. Mean curvature values as a function of number of distractors. The mean curvature values of saccade trajectories for the search task (0, 3, 7, and 15 distractors) are shown with the same symbol notation as in Fig. 7.

amount of curvature decreased somewhat as the number of distractors increased, but this trend was not significant in either animal (linear contrasts, $P = 0.26$, monkey M and $P = 0.92$, monkey C).

Compensation

The analyses presented so far show that saccadic trajectories are considerably more variable when distractors are present that compete with the target as the goal of an upcoming saccade. The data plotted in Fig. 5 suggest that this variability is present right from the onset of saccades when distractors are present. In addition, saccades are also more curved when distractors are present as shown by the data plotted in Fig. 8. It is possible that this curvature acts to direct initially deviated movements back toward the target by the end of the saccade. We were therefore interested in the amount of compensation that was produced during saccades with or without distractors present. We used a similar metric to that introduced recently by Quaia et al. (2000) to quantify compensation. These authors computed the percentage compensation for saccades made to single targets, a condition in which the absolute directional errors between saccade trajectory and target location were very small. These authors reported the surprising result that movements once deviated from the direction of the target showed unexpectedly small amounts of compensation by movement end. We computed the percentage compensation in trajectory during the search paradigm by measuring the deviation of each individual saccade trajectory from the mean saccadic trajectory for the single-stimulus (zero distractor) case in each direction. The percent compensation (C) is defined by

$$C = 100 \times \frac{(m - f)}{m} \quad (2)$$

where m is the maximum perpendicular deviation from the mean saccadic trajectory, and f is the perpendicular deviation from the mean trajectory at the end of a saccade. For both m and f , deviations in the counterclockwise direction from the mean single-target trajectory were assigned positive values. Deviations in the opposite direction were assigned negative values. Values for compensation were computed separately for each of the eight possible target directions and then were pooled.

The distribution of compensations for each search array condition was computed separately. These distributions did not differ for either the number of distractors or the spatial eccen-

tricity of the array. Therefore Fig. 9 shows the distribution of compensations for each animal for only the no-distractor and the seven-distractor cases. Compensation values of 100% indicate that any deviation during a saccade from the mean saccadic trajectory for the no-distractor case was fully compensated by saccade end, i.e., the saccade ended at the same point as the mean saccade endpoint measured for no-distractor presentations. Null compensation values (0%) indicate that errors present during the saccade either increased or remained constant as the movement progressed. Values of compensation larger than 100% indicate that a directional error present during the movement was overcompensated so that by saccade end the trajectory had crossed over the mean saccade trajectory for the no-distractor case. The modal values of the distributions for all array configurations for both animals were located in the lowermost, 0 to 10% compensation bin, which suggests only modest compensation occurred. In monkey M the median value of compensation was only 10% for the no-distractor case and was about the same (13%) in the monkey C. Compensation did not vary systematically when distractors were present in either animal. Results for the seven-distractor case are shown as an example in Fig. 9 (*bottom*). Most often when compensation did occur, the trajectory correction overshoot the mean no-distractor, end-saccade direction. This fact can be seen by comparing the larger numbers of cases in the rightmost bin in each distribution (values $> 120\%$) with the small number of cases with close to 100% compensation.

Cursory inspection of the raw trajectory data in Fig. 3 suggests that some saccades with large initial errors appear to produce the most compensation (the highly curved trajectories that arc toward the target by movement end). We wondered whether there was a correlation between the size of the initial directional error and the amount of compensation that occurred in individual movements. We computed the correlation between percentage compensation and the absolute value of initial directional error separately for each animal and for each number of distractors and never found a significant correlation between these two variables ($P > 0.1$). In fact the largest values of initial error tended to produce very low values of compensation ($< 5\%$).

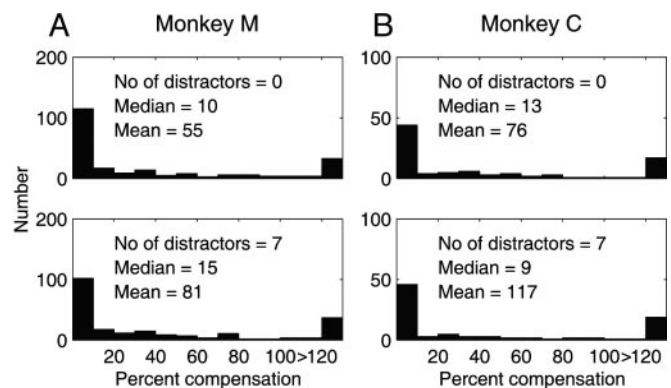


FIG. 9. Examples of the distribution of percentage compensation for saccade direction. See text for a definition of how compensation was computed. Sample distributions for the no- and 7-distractor conditions are given in the top and bottom sets of panels, respectively. A: monkey M. B: monkey C.

TABLE 2. Latency data for both animals across all sessions

Amplitude, °	No. of Saccades	Mean Latency, ms				Overall Mean 3, 7, and 15 distractors
		0	3	7	15	
M						
20	1489	142	205	191	189	197
20	981	147	195	193	186	192
15	582	140	194	178	172	184
10	876	136	182	156	163	168
Overall mean		142	197	182	181	
C						
20	420	144	208	179	168	185
15	446	135	205	177	167	183
10	609	151	255	229	212	235
Overall mean		143	224	196	180	

Saccade latency

It has been reported that saccade latency increases when distractors are present in comparison to the single-stimulus case, even when the single-stimulus presentations are randomly interleaved with trials containing distractors (McPeck and Keller 2001; Walker et al. 1997). In addition there is evidence of a speed-accuracy trade-off in saccade production (Chou et al. 1999; Coëffé and O'Regan 1987). In the Walker et al. (1997) report, only single distractors with no behavioral significance were used. In the McPeck and Keller (2001) report a visual search task was used with four equally spaced stimuli (three-distractor case). In the present experiments we measured latency in blocks of trials with intermixed conditions of no distractors and variable numbers of distractors. Table 2 shows the latency data for the two animals across all sessions. Sessions with equal eccentricities of stimuli in the search array make up the rows and the number of distractors makes up the columns. After log transform (Glantz and Slinker 2001), an unbalanced two-way ANOVA was performed separately for each animal using stimulus amplitude and number of distractors as factors. The case with zero distractors was not included in the ANOVA, but was treated as a separate condition. The main effect of the number of distractors was significant in each animal ($P < 0.01$). In addition, the main effect of amplitude was also significant ($P < 0.01$) in each animal, but in monkey M latency increased with array eccentricity while latency was actually longer for the 10° eccentricity than for the larger amplitudes of movement in monkey C. Latency has previously been shown to increase slightly with larger amplitude saccades (for the single-target case) over the range of amplitudes that we studied (Becker 1989; Kalesnykas and Hallett 1994). We have no explanation for the opposite effect observed in monkey C, but since we were mainly interested in the effect of the number of distractors on latency, we will not consider the effect of array eccentricity further. There was also a significant interaction between amplitude and number of distractors ($P < 0.01$) in monkey M, but no significant interaction in monkey C ($P = 0.70$). A separate ANOVA on the effect on saccade latency for the cases when distractors were present and when no distractors were present showed that these conditions were significantly different in both monkeys ($P < 0.01$).

Figure 10A plots the mean latency of on-target and averaging saccades after averaging over all amplitudes as a function of the number of distractors for both animals. In both monkeys

saccade latency increased from approximately 140 ms in the no-distractor trials to a much larger value for the three-distractor case and then showed a modest decline as the number of distractors was increased. This decline was significant in both animals (linear contrasts with correction for the greater number of trials with 3 distractors in monkey M; $P < 0.01$ in both monkeys). In human subjects, a similar relation has been found between the number of distractors in the search array and the latency to saccade (McPeck et al. 1999) or to shift attention (Bravo and Nakayama 1992) to the odd target. McPeck et al. (1999) found that the longest saccade latencies were induced by a two-distractor condition that we did not include. They did not investigate the interleaved, no-distractor case that showed such short latencies in the present study.

To determine whether the decrease in saccade latency with increasing numbers of distractors occurred because the monkeys

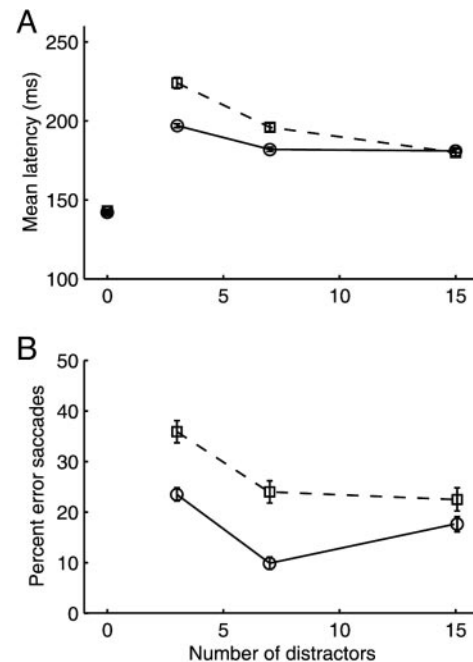


FIG. 10. A: mean latency of on-target and averaging saccades for monkey M (open circles and solid lines) and for monkey C (open squares and dashed lines) as a function of number of distractors. The mean latencies for both animals for the no-distractor condition are shown as isolated data points on the left. B: error rate as a function of the number of distractors. Same conventions as in A.

sacrificed accuracy with larger numbers of distractors, we examined the effect of the number of distractors on the proportion of error saccades (movements that are directed close to one of the distractors as defined in Fig. 2). A two-way, unbalanced ANOVA on the error rate data from each animal was conducted, using saccade amplitude and number of distractors as factors. The main effects of amplitude and number of distractors were significant in both animals, as was the interaction between the two ($P < 0.01$). We plot the percentage of error saccades as a function of the number of distractors in Fig. 10B. There was a trend for the frequency of error saccades to decrease as a function of the number of distractors and this trend was significant in both animals (linear contrasts, $P < 0.01$). Thus both saccade latency and the proportion of error saccades decrease as the number of homogeneous distractors increases. The same trend was found in humans (McPeck et al. 1999).

DISCUSSION

In the present experiments we used a color-odddity, visual search paradigm to produce variability in the normally stereotyped saccade trajectory to a target. This variability can be a useful tool in studies of the neurological organization of the saccadic system. Past efforts used to induce trajectory variability include the use of electrical microstimulation (Gandhi and Keller 1999; Keller and Edelman 1994; Munoz and Wurtz 1993), air puff stimulation (Goossens and Van Opstal 2000), or visual target manipulation (Edelman and Goldberg 2001; Stanford and Sparks 1994). The visual search task has the advantage of producing trajectory variability with visual stimulation that better approximates that in natural visual scenes. We found that each of the measures of saccade trajectory variability that we quantified was significantly increased by the presence of any number of competing distractors. Furthermore, varying the number of distractors produced significant trends for smaller values of initial directional dispersion, shorter latencies, and fewer error saccades as the number of distractors increased. However, the percentage of averaging saccades produced and the amount of curvature did not show a consistent trend as a function of the number of distractors over the two animals. We conclude that, of the configurations we tested, four-element search arrays were optimal for producing trajectory variability that could be exploited in neurophysiological experiments.

The 16-element array has a distinction that is worthy of mention. Unlike the 4- and 8-element arrays, in which distractors might appear at any of the eight possible target locations, in the 16-element array, half of the distractors appear at locations where a target will never appear. Our monkeys might have learned to ignore locations where a target never appeared. Hence, the 16-element arrays would become effectively similar to the 8-element arrays, minimizing the behavioral differences observed in the two conditions. We believe that this explanation of the similarities in the results for the later two types of arrays is unlikely in view of the extensive randomization that was present in our paradigm.

Averaging saccades

A frequent type of deviation of saccade trajectory produced in our search task was an averaging effect in which saccades

ended between the target and one of its adjacent distractors. Findlay (1997) performed a similar experiment in human observers for a fixed number of distractors ($n = 7$). He chose a fixed arc of $\pm 15^\circ$ about target positions to define "on-target" saccades. To compare our monkeys' performance to that of human observers, we reanalyzed our data on saccade endpoint accuracy using Findlay's definitions of on-target and averaging (called inaccurate saccades in his paper) for the seven-distractor case. For his six subjects he found a range of 51.6–87.5% on-target saccades, while his range for averaging saccades was 7.8–20.3%. Our two monkeys, using his definitions of performance, showed a range (when all 3 amplitudes were considered) of 53.7–86.1% on-target behavior and a range of 9.6–16.7% averaging. This very close similarity in results, at least for the seven-distractor condition, suggests that our animals were performing at about the same level as human observers.

Averaging saccades seem to be a common feature of tasks that require target selection, e.g., the search paradigm (Coëffé and O'Regan 1987; Findlay 1997), and tasks that do not, e.g., the two-stimulus task with no target specified (Chou et al. 1999; Findlay 1982; Ottes et al. 1984). However, the neural mechanisms involved in producing a similar effect at the output stage might be quite different. It is instructive to compare the distributions of saccade endpoints in the Chou et al. (1999) study in monkeys (their Fig. 6 and our Fig. 7). In their study the animals were rewarded for saccading to the vicinity of the two-stimulus array. At 30° stimulus separations, saccade endpoints tended to be rather uniformly distributed between the two stimuli. At 90° separations there were few averaging saccades, but those that were present still seem uniformly distributed between the stimuli. Our search paradigm with 90° separation between stimuli still produced a large number of averaging saccades, but these are predominately located nearer the target than in the regions in between the target and adjacent distractors. One could argue that averaging produced in the no-specific-target case is driven by a noisy neural computation of the center of mass of the array configuration with limits on the spatial extent of the computation (Das et al. 1996). The averaging results obtained in the search paradigm suggest that a target selection process is involved and saccades sometimes began before target selection was finalized. Neural recordings in the superior colliculus (SC) support this hypothesis. These recordings suggest that, in our search task, a dominant locus of population activity representing the target location is present at saccade onset, but multiple loci of activity representing distractor locations are also present (McPeck and Keller 2002a; McPeck et al. 2003; Port and Wurtz 2003). The SC along with the cortical frontal eye fields have been implicated in target selection behavior in color-odddity visual search tasks (McPeck and Keller 2002b; Schall and Hanes 1993). The recording results, demonstrating multiple sites of activity in the SC, may signify an incomplete target selection process.

Initial saccade direction and error compensation

Variance in the initial direction of saccades increased dramatically when distractors were present. The increase in initial direction dispersion decreased systematically with the number of distractors. Potentially, there are two main neural mechanisms that might contribute to inaccuracy in saccade trajectory.

One type of error would result if the visual system inaccurately specifies the direction of the goal of the movement. A second type would occur if the saccadic motor system carried out inaccurate movements to an accurately specified goal. These possibilities are not mutually exclusive, but our data show the occurrence of a wide dispersion in saccade direction at movement onset when distractors are present. This observation suggests the presence of considerable noise in the visual system's estimate of saccade goal when competing visual stimuli are present. Nevertheless, these data do not rule out that transformation errors might also occur in converting an accurate goal specification into the appropriate motor program needed to direct the saccade to that goal. It is not clear why the latter type of error would be dependent on the presence of distractors while it is easy to see how goal specification by the visual system might be affected by conflicting stimuli.

Examination of Fig. 4, in which instantaneous direction during saccades is plotted, imparts the impression that the initial scatter in saccade direction that is present at movement onset remains relatively constant during the movement and may even increase by movement end in some cases. The quantitative analysis of compensation (Fig. 9) supports this view. The local feedback model of saccade control (Robinson 1975), which has served as a cornerstone for explaining the accurate generation of saccades, predicts that saccade trajectory should be corrected dynamically for errors that occur during the movement, where error is defined as deviations away from the direction of saccade goal. In a recent study using single targets Quaia et al. (2000) examined such predicted compensatory behavior during saccades in the monkey and concluded that surprisingly little compensation occurred. In cases in which their data approximately overlap ours for saccade amplitude ($10\text{--}25^\circ$), their measures of median compensation ranged from 24 to 42%. In the present study we used the same method that they used to quantify compensation. We found values of compensation that were considerably less (median values of 10 and 13%) in the no-distractor case. Furthermore, compensation did not vary systematically with the number of distractors present. With the search paradigm we were able to induce much larger directional errors when distractors were present than those produced by Quaia et al. (2000) for single-target presentations. These larger absolute errors in direction produced by competition between visual stimuli in the search task were also poorly compensated. Our values of median compensation when averaged over all conditions when distractors were present were 14.8 and 7.3% in the two animals.

Our observation of the relative lack of compensation for directional errors is consistent with the notion that the major cause of error in our experiments is a problem with target selection in an environment with strongly competing visual stimuli. If movement direction is deviated away from the target at onset, the motor system is unable to remove much of this error in direction because corrections involve a comparison between the direction of the ongoing movement and the direction of the selected goal. If the goal is specified incorrectly at onset and does not change during the movement (Robinson 1975), then there is nothing for the local feedback system to correct.

Latency effects

Previous studies have produced support for the notion that saccades directed to a visual stimulus within an array of stimuli require longer latencies than averaging saccades directed in between stimulus locations (Chou et al. 1999; Ottes et al. 1984). However, in each of these studies two visual stimuli were presented simultaneously, and subjects were not instructed to look preferentially at either stimulus, i.e., there was no uniquely defined target. Two additional studies using a visual search task have shown an increase in saccade latency when multiple competing stimuli are present in comparison to blocks of trials when only a single target without distractors appears (McPeck and Schiller 1994; Schiller et al. 1987). In these two studies a gap paradigm was used in which the fixation point was turned off before the stimulus array appeared. The presence of a gap facilitates the occurrence of express saccades, saccades with extremely short latencies (Fischer and Boch 1983). The main change noted in the two search studies cited above by Schiller and colleagues was a disappearance of the separate modal group of express saccades and a small increase in mean latency when multiple distractors were present in comparison to the no-distractor case.

In the present study, the number of distractors was manipulated randomly within a block of trials and the presence of any number of distractors produced a dramatic increase in saccade latency in both monkeys in comparison to trials in which only a single target appeared. This is perhaps not surprising, if the single-target case is viewed as a reflex response, but the ability of the saccadic system to recognize this condition within a block of predominately multistimulus search trials is worthy of notice. The magnitude of the change from the no-distractor condition to distractors present was similar to that we have previously reported for the three-distractor case alone (McPeck and Keller 2001). Walker et al. (1997) also reported an increase in latency when a single distractor was presented in the visual field contralateral to the target location in comparison to randomly embedded control trials with only the target present. However, this effect was only present when the eccentricity of the distractor was $<10^\circ$ from the fixation point. These authors hypothesized that the increased latencies were the result of an array-induced stimulation of the saccadic fixation centers, which are dominated by near foveal inputs and are hypothesized to oppose the onset of target-induced saccades. In addition, their distractor stimuli had no behavioral significance to their human subjects (i.e., they were never a potential target for a saccade). Our results suggest that, in addition to fixation center hypotheses, when competing visual stimuli for a saccade appear at similar eccentricities, the onset of the saccade is delayed until a competitive neural process involving alternative movements is able to at least partially resolve the conflict.

As the number of distractors increased, saccade latencies declined in agreement with the results of McPeck et al. (1999) in humans. This decrease in latency was accompanied by a significant decrease in the number of error saccades, indicating an overall improvement in performance with more distractors. We speculate that a greater density of homogeneous distractors makes the odd-colored target more conspicuous within the search array, leading to the improvement in performance. A greater density of homogeneous distractors has also been shown to facilitate shifts of attention (Bravo and Nakayama 1992) and

saccades (McPeck et al. 1999) to an odd-colored target in human subjects.

GRANTS

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