Visual Neuroscience (1999), **16**, 81–89. Printed in the USA.

Saccade target selection in macaque during feature and conjunction visual search

NARCISSE P. BICHOT AND JEFFREY D. SCHALL

Vanderbilt Vision Research Center, Department of Psychology, Vanderbilt University, Nashville

(RECEIVED March 27, 1998; ACCEPTED June 16, 1998)

Abstract

To gain insight into how vision guides eye movements, monkeys were trained to make a single saccade to a specified target stimulus during feature and conjunction search with stimuli discriminated by color and shape. Monkeys performed both tasks at levels well above chance. The latencies of saccades to the target in conjunction search exhibited shallow positive slopes as a function of set size, comparable to slopes of reaction time of humans during target present/absent judgments, but significantly different than the slopes in feature search. Properties of the selection process were revealed by the occasional saccades to distractors. During feature search, errant saccades were directed more often to a distractor near the target than to a distractor at any other location. In contrast, during conjunction search, saccades to distractors were guided more by similarity than proximity to the target; monkeys were significantly more likely to shift gaze to a distractor that had one of the target features than to a distractor that had none. Overall, color and shape information were used to similar degrees in the search for the conjunction target. However, in single sessions we observed an increased tendency of saccades to a distractor that had been the target in the previous experimental session. The establishment of this tendency across sessions at least a day apart and its persistence throughout a session distinguish this phenomenon from the short-term ($<$10 trials) perceptual priming observed in this and earlier studies using feature visual search. Our findings support the hypothesis that the target in at least some conjunction visual searches can be detected efficiently based on visual similarity, most likely through parallel processing of the individual features that define the stimuli. These observations guide the interpretation of neurophysiological data and constrain the development of computational models.

Keywords: Reaction time, Eye movements, Attention, Priming, Oculomotor

Introduction

Neural correlates of visual selection and attention have been investigated in humans using neuroimaging (e.g. Corbetta et al., 1995) and event-related potentials (e.g. Luck & Hillyard, 1995). Information about neural mechanisms, though, must be obtained from invasive procedures such as single-cell recording, inactivation, or lesions. Links between human cognition and nonhuman primate physiology require employing behavioral tasks with monkeys that have a strong empirical and theoretical basis in human psychophysics (e.g. Bowman et al., 1993; Hanes & Schall, 1995).

One such task is conjunction visual search which has been pivotal in the development of theories of visual search and attention. Treisman and Gelade (1980), using conjunction search tasks, found steep slopes of reaction time as a function of set size of approximately 30 ms/item as compared to feature search with flat slopes of approximately 3 ms/item. This finding among others was interpreted as evidence that the search process was serial. However, the same results can be produced by limited-capacity parallel search mechanisms (Townsend, 1976, 1990). Moreover, subsequent experiments showed that some conjunction searches can be performed efficiently as reflected by shallow slopes (Nakayama & Silverman, 1986; McLeod et al., 1988; Wolfe et al., 1989) leading to the development of models of visual search in which selection is guided by the similarity between the target and distractors (Duncan & Humphreys, 1989), most likely through parallel processing of the individual features that define the conjunction stimuli (Cave & Wolfe, 1990; Treisman & Sato, 1990; Wolfe, 1994).

Search reaction time as a function of set size, however, provides only an indirect assessment of the mechanisms underlying visual searches. To the extent that attention and eye movements are functionally related (e.g. Sheliga et al., 1995; Kustov & Robinson, 1996), gaze provides another means of assessing the selection process. In fact, recent evidence has shown that eye movements are guided by the same selection process as attention (Kowler et al., 1995; Deubel & Schneider, 1996). A parallel feature-based selection mechanism operating during conjunction search would predict that when gaze is not directed to the target, then a distractor that shares target features would be fixated more often than one that does not.

As part of our ongoing effort to understand how the brain selects targets for saccadic eye movements (e.g. Schall et al. 1995*a*; Thompson et al., 1996; see also Bichot et al., in press; Cepeda

Correspondence and reprint requests to: Jeffrey D. Schall, Vanderbilt Vision Research Center, Department of Psychology, 301 Wilson Hall, 111 21st Avenue South, Nashville, TN 37240, USA.

et al., 1998), we examined the saccades made by monkeys to a target in a popout feature visual search and in a more complex conjunction visual search. Whereas locating the target in feature search can be achieved just by bottom-up saliency, locating the target in conjunction search requires top–down knowledge of the target properties. Little is known about how monkeys perform conjunction visual search. Preliminary studies have measured reaction time as a function of set size (Dürsteler & von der Heydt, 1992; Buračas & Albright, 1997). A study by Bolster and Pribram (1993) in which monkeys reached toward the conjunction target revealed a very steep slope of 60 ms/item, and there were more errors to distractors that shared a target property than to distractors that shared none. However, the response latencies in this study were quite long and, unfortunately, saccades were not monitored. In the present experiment, we determined whether the pattern of reaction times of monkeys performing feature and conjunction visual search corresponded to that of humans. We also examined whether the endpoint of the first saccade made by monkeys during conjunction search trials reflected the visual similarity of distractors to the target.

Methods

Subjects and surgery

Data were collected from one *Macaca mulatta* (Monkey C) and one *Macaca radiata* (Monkey F), weighing 9 and 5 kg, respectively. The animals were cared for in accordance with the National Institute of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. The surgical procedures for the subconjunctival implantation of a scleral search coil and for the attachment of a stainless-steel post to the skull to restrain the head during testing have been described previously (Schall et al., 1995*a*).

Stimuli and apparatus

The experiments were under the control of two personal computers using software developed by Reflective Computing (St. Louis, MO), which presented the stimuli, recorded the eye movements, and delivered the juice reward. Monkeys were seated in an enclosed chair within a magnetic field to monitor eye position with a scleral search coil (Robinson, 1963); eye position was sampled at 250 Hz and stored with other event times on disk for off-line analysis. Stimuli were presented on a Sony GDM-1936 video monitor (70 Hz non-interlace refresh rate, 800 × 600 resolution) viewed binocularly at a distance of 57 cm in a dark room. The background was uniform dark gray (CIE: $x = 205$, $y = 234$) with a luminance of 0.07 cd/m^2. The fixation spot was a white (30 cd/m^2) square subtending 0.1 deg, and was circumscribed within a larger, 0.2 deg square outline of the same color and luminance which remained on the screen at all times. The stimuli, spaced evenly on the circumference of an imaginary circle (7 deg eccentricity) around the fixation, were either red (CIE: $x = 621$, $y = 345$) or green (CIE: $x = 279$, $y = 615$) matched for luminance (red: 2.29 cd/m^2, green: 2.30 cd/m^2), and could be either crosses or outline circles approximately 1.5 deg across.

Behavioral training and tasks

Using operant conditioning with positive reinforcement, the monkeys were trained to perform a variety of visual tasks in which a juice reward was contingent on accurately executing a saccade to a target presented alone (detection trials) or with distractors (feature and conjunction search trials). Each experimental session started with a block of approximately 100 detection trials that instructed monkeys what the target would be in feature and conjunction search trials during the daily session. The target stimulus could be a combination of either of two colors (e.g. red or green) and shapes (e.g. cross or circle); it was chosen pseudorandomly across experimental sessions with the requirement that the same color/shape combination was not used in two consecutive sessions. The detection trials began when the monkeys fixated a central fixation spot. After a 500-ms fixation period, the fixation spot disappeared and simultaneously the target stimulus was presented at a position chosen randomly from among the 12 possible. The monkey was rewarded for making a single saccade to the target and maintaining gaze at its position for 500 ms. If the monkeys broke fixation before stimulus presentation, made a saccade to a location other than the target, made a saccade to the target but failed to fixate it for the prescribed period, or did not initiate a saccade within 2 s of target presentation, the trial was immediately aborted and the monkeys failed to receive the liquid reward. All stimuli were removed from the screen approximately 40 ms after a trial abort. This undermined an analysis of subsequent saccades but encouraged monkeys to find the target on the first saccade.

The block of detection trials was followed by a block of feature search trials. The procedure for these trials was essentially the same as for the detection trials except that the target was presented along with distractors that differed from it in either color or shape; the two resulting feature search types were alternated every 20 trials. To measure the variation of reaction time as a function of set size, the number of distractor items varied randomly across trials such that displays contained either 4, 6, or 12 stimuli, but never the same number of stimuli on two consecutive trials. In the twelve-stimulus configuration, each stimulus was either on the horizontal or vertical meridian, or 30 deg off the meridian. To avoid potential effects associated with presenting stimuli at different locations across display configurations, the positions of the stimuli in displays containing four and six stimuli were rotated randomly across trials such that the target would appear on average at the same locations as it would in the twelve-stimulus configuration. After a few practice trials in each feature search condition to make sure that monkeys were doing the task properly, each monkey ran at least 500 feature search trials per session.

Following a short break, the experimental session was continued with a block of conjunction search trials. The procedure and display configurations for the conjunction search were the same as in the feature search condition except for the properties of the distractor stimuli. The four-stimulus display contained, in addition to the target, one distractor that had the target color but not the target shape (hereafter referred to as the *same-color* distractor), another distractor that had the target shape but not the target color (hereafter referred to as the *same-shape* distractor), and finally one that had neither the target color nor the target shape (hereafter referred to as the *opposite* distractor). In the six-stimulus display, there was an additional same-color distractor and an additional same-shape distractor. In the twelve-stimulus display, there were four of each of the same-color and same-shape distractor, two opposite distractors, and the last distractor was chosen randomly across trials to be either a same-color or a same-shape one. With these choices of distractors, the four- and six-stimulus displays were balanced for the number of stimuli containing any given shape or color, whereas the twelve-stimulus display contained one

more item with the target color than items with the target shape, or *vice versa*. Following practice trials that were not included in the data analyses, each monkey ran at least 500 or more conjunction search trials for that block in that session.

Following a 15–30 min break, another block of detection trials was collected to re-familiarize the monkeys with the target; these data also indicated whether the saccadic latencies of the monkeys became longer as compared to the first block of detection trials, an index of possible fatigue as the session progressed. We then usually ran a second and occasionally a third block of approximately 500 conjunction trials to investigate the constancy of the search strategy used by the monkeys.

Results

Overall performance

Each monkey ran 24 sessions, with six sessions for each of the four color-shape target combinations, yielding more than 80,000 trials overall. For each monkey and each target type, the target attributes in consecutive sessions changed twice in color only, twice in shape only, and twice in both color and shape. Monkey C ran 49 blocks of conjunction search and, monkey F, 46. As shown in Table 1, the overall performance of the two monkeys in the various tasks was quite similar. The monkeys performed all the visual tasks at levels well beyond those predicted by chance performance although, not surprisingly, the conjunction search task proved more difficult than the feature search task. Furthermore, the performance of both monkeys clearly improves in feature searches with increasing set size, whereas the opposite is true in conjunction search. Also, performance appears to be somewhat better in color feature search than in shape feature search.

To investigate the effect on accuracy of alternating the search dimension every 20 trials during blocks of feature search, we calculated the percentage of correct saccades in four successive groups of five trials of search within a given feature dimension. The results of this analysis are shown in Fig. 1A. Both monkeys made more errors in the first five trials following the switch of the search dimension, and their performance stabilized within the next five trials.

Saccade latency

The first part of our analysis compared the pattern of reaction times of the monkeys to previous findings in human subjects. A comparison of saccade latencies during feature and conjunction searches is shown in Fig. 2. In general, saccade latencies of monkey C were shorter than those of monkey F. Both monkeys exhibited much shorter latencies during detection trials (181 ms for monkey C and 166 ms for monkey F) than they did during feature or conjunction search trials. Also, for both monkeys, latencies increased in the second block of detection trials (200 and 213 ms, respectively, for monkeys C and F). Finally, both monkeys exhibited latencies about 10 ms longer to targets defined by shape than to targets defined by color in feature search.

During feature search, the slopes of saccade latency as a function of set size were significantly greater than zero for monkey C (1.5 ms/item, two-tailed *t*-test: $t_{23} = 5.9$, $P < 0.001$) and significantly less than zero for monkey F (−2.6 ms/item, $t_{23} = -8.2$, $P < 0.001$). Having found that correct performance was affected by the alternation of the feature search dimension, we investigated whether search slopes were similarly affected (Fig. 1B). Similar to the percent correct measure of performance, we found that search slopes were affected in the first five trials following the switch in search dimension, after which time they appear to asymptote reflecting stable performance. Following the search dimension switch, slopes are either more positive (monkey C) or less negative (monkey F). Average saccade latency is also similarly affected with significantly longer latencies for both monkeys in the first five trials following the switch (Fig. 1C).

In conjunction search, for both monkeys the slopes of saccade latency as a function of set size were significantly different than the slopes measured in feature search (two-tailed paired *t*-test; Monkey C: $t_{23} = 6.0$, $P < 0.001$; Monkey F: $t_{23} = 9.0$, $P < 0.001$). Monkeys C and F performed similarly to one another with positive search slopes of 3.6 and 4.3 ms/item, respectively. The average shallow slope of 3.9 ms/item is comparable to if not shallower than that obtained with human subjects in target present/absent judgments using stimuli that support efficient search; for example, Wolfe et al. (1989) report an average slope search of 7.5 ms/item for a similar color-shape conjunction search. Thus, the pattern of reaction times in macaques in feature and conjunction search correspond to what has been observed in humans under comparable conditions.

Although the conjunction search slopes obtained with macaques in this study are much too shallow to be consistent with a strictly serial search mechanism, the effect of set size on performance appears to be greater when error rates are also taken into account (i.e. more errors are committed by both monkeys as set size increases in conjunction search). To determine whether the

Table 1. *Overall percentage of correct initial saccades to the target in the various task conditions for each set size*

	Monkey C					Monkey F				
Set size	Detection	Color feature search	Shape feature search	Overall feature search	Conjunction search	Detection	Color feature search	Shape feature search	Overall feature search	Conjunction search
1	98.3	—	—	—	—	97.1	—	—	—	—
4	—	86.8	86.9	86.9	86.1	—	88.3	85.8	87.1	89.7
6	—	90.1	89.7	89.9	79.4	—	91.8	88.0	89.9	82.8
12	—	95.7	92.0	93.9	67.5	—	94.3	92.4	93.4	67.5

[a]Percentages of correct initial saccades based entirely on chance performance would be 25.0%, 16.7%, and 8.3% for 4-, 6-, and 12-item displays, respectively.

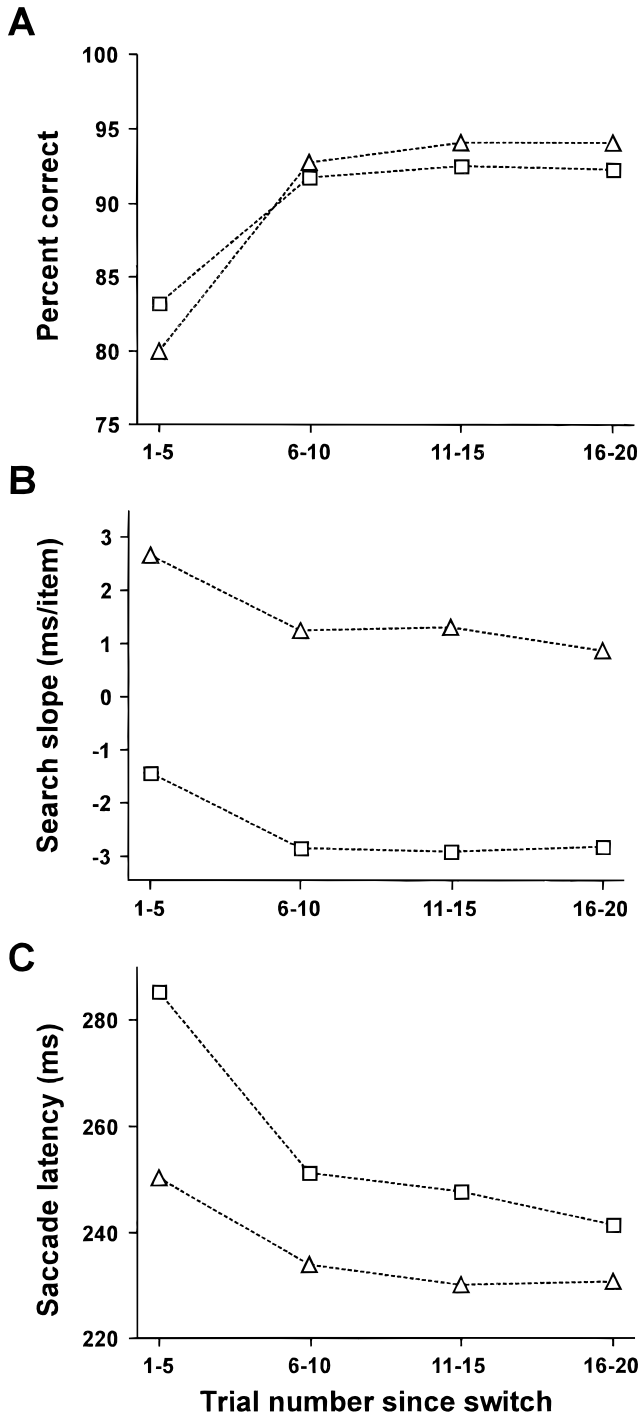

Fig. 1. Short-term perceptual priming during feature search. Measures of performance of feature search within a dimension (e.g. color or shape) were analyzed separately in four successive groups of trials from the start of the switch in the dimension of the feature search. Average percentage of correct saccades to the target (A), slopes of saccade latency as a function of set size (B), and average saccade latency (C) are plotted as a function of trial number since the dimension switch for monkey C (triangle) and monkey F (square). Data from the three set sizes were combined for the average accuracy and the average latency measures. In the first five trials following the search dimension switch, monkeys made more errors, exhibited longer saccade latencies, and performed the search with either more positive (monkey C) or less negative (monkey F) slopes. Performance asymptoted within the next five trials. The trends for the two monkeys are remarkably similar.

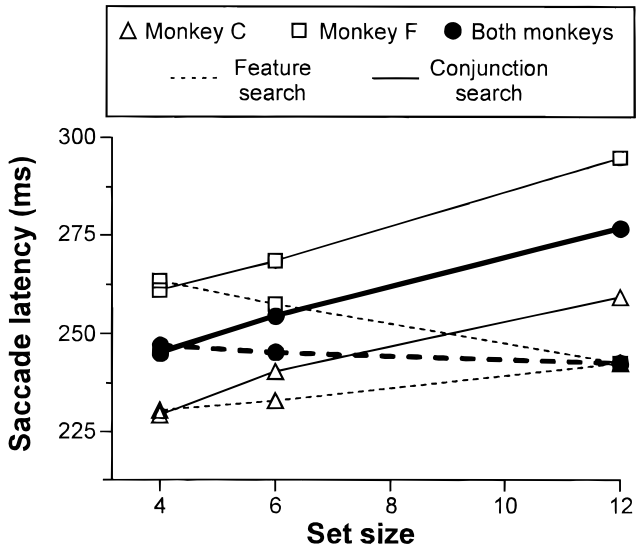

Fig. 2. Saccade latency as a function of set size during feature and conjunction visual search. Triangles plot average latencies of monkey C, squares plot average latencies of monkey F, and solid circles plot the grand average latencies of the two monkeys. Dashed lines connect average latencies measured during feature search and solid lines connect average latencies measured during conjunction search. Whereas the grand average slope of saccade latencies as a function of set size is nearly flat during feature search, the slope is positive during conjunction search.

increase in error rates is due to a speed-accuracy tradeoff, we examined whether monkeys made more errors on blocks of conjunction search trials that were accomplished with shallower slopes. The correlation between error rate and slope was not significant for either monkey (monkey C: $r^2 = 0.03$, $P > 0.05$; monkey F: $r^2 = 0.06$, $P > 0.05$), revealing that the shallow slopes we observed were not obtained by sacrificing accuracy.

Saccade endpoint

The main goal of our analysis was to determine how visual selection guided gaze. To accomplish this, we determined whether the endpoint of the saccades made by the monkeys in conjunction search reflected differences in the visual similarity of the various distractors to the target. To determine whether a saccade was made to a distractor's location, we used a more conservative method than that used in other studies which have assigned the saccade to the stimulus nearest its endpoint. Using only trials in which monkeys made a correct saccade to the target, we first determined the polar coordinates of the average saccade to each of the 12 potential stimulus locations. Whenever a saccade was not made to the target, we determined the potential stimulus location with a polar angle closest to the direction of the saccade made, and if that position was occupied by a distractor, a saccade was considered made to that distractor only if the amplitude of the saccade was within $\pm 25\%$ of the average saccade amplitude for that stimulus position. Of all trials in which the initial saccade was not made to the target, 88% (monkey C) and 94% (monkey F) were accounted for by saccades to one of the distractors. The latencies of saccades made to distractors were longer than the latencies of saccades made to the target (an average difference of 6 ms for monkey C and 24 ms

for monkey F). This saccade latency difference shows that saccades to distractors were not the result of speed-accuracy tradeoff.

We determined the incidence of saccades to same-color, same-shape, and opposite distractors. Because the relative number of these different distractors varied within and across the three set sizes, a normalization procedure was employed. We first computed the percentage of saccades made to each distractor type in trials in which an initial saccade was made to a distractor. Then, to account for differences in these rates due to different numbers of each distractor type in the displays which would be expected if monkeys shifted gaze to distractors randomly, we divided the obtained percentages for each distractor type by the number of distractors of that type in the display. Finally, to allow comparison across the three set sizes, we normalized the last percentages so that the sum of the percentages for the three distractor types would equal 100%, regardless of set size. The value resulting from this normalization will be referred to as the *incidence* of saccades to the different distractor types.

The distribution of the incidence of saccades to the different distractor types is shown Fig. 3A. The mean values of the distributions for each distractor type, as well as the values for each monkey, are shown in Table 2. For both monkeys and for all three set sizes, the incidence of saccades to a distractor with one of the target properties was significantly different from the incidence of saccades to a distractor with neither target property (Friedman two-way ANOVA lowest $\chi^2 = 56.1$, $d.f. = 2$, $P < 0.001$) (Siegel & Castellan, 1988). Subsequent group comparisons demonstrated that the incidence of saccades to both same-shape and same-color distractors was significantly greater than the incidence of saccades to the opposite distractor (smallest mean rank difference was 1.12 for monkey C compared to the adjusted $z_\alpha = 0.05$ criterion level of 0.48 and was 1.22 for monkey F compared to a criterion level of 0.50). Also, the incidence of saccades to same-shape and same-color distractors was not significantly different (largest mean rank difference was 0.37 for monkey C and was 0.24 for monkey F). Also, note that the distributions of gaze incidence to same-color and same-shape distractors shown in Fig. 3A do not exhibit any clear bimodality, suggesting that, across trials, both color and shape information were used equally.

On closer inspection of the data, we also made the unexpected finding that saccade target selection was affected by the history of target properties across sessions. This effect, possibly reflecting a form of long-term priming, revealed itself as a significantly increased incidence of saccades to a distractor that was the target during the previous session (Fig. 3B, Table 2). Having collected data from two blocks of conjunction search trials in most sessions, we determined that this priming effect was not limited to the first few trials of conjunction search (besides the practice trials that made sure that the monkeys were performing the task properly and that were not included in the analysis). During the first block of conjunction trials the average incidence of saccade to a distractor was 49.0% when it was primed, and 25.5% when it was not. Although this difference was somewhat smaller during the second block (44.8% when primed and 27.6% when not), it was still highly significant (Mann-Whitney U test: $z = -3.7$, $P < 0.001$).

We also investigated the persistence of this target trace between sessions. Overall, 26 sessions were run 1 day apart, 14 were run 2 days apart, two were run 3 days apart, and six were run a week or more apart. The ratio of saccade incidence to a distractor when it was primed and when it was not primed was 1.9 for sessions 1 day apart, 1.5 for sessions 2 or 3 days apart, and 1.2 for sessions more than a week apart. Thus, although diminishing with increasing delay between sessions, this priming effect appears to last around a week.

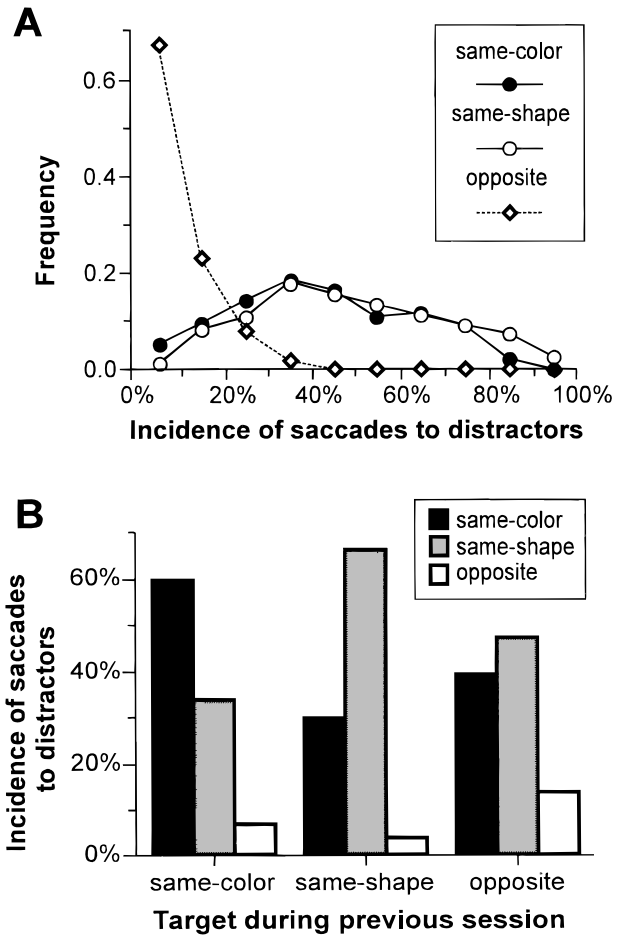

Fig. 3. Analysis of endpoint of saccades directed to distractors during conjunction search. (A) Distribution of saccade incidence to same-color (filled circles, solid line), same-shape (open circles, solid line), and opposite distractors (diamonds, dashed line). Saccade incidences were calculated separately for each set size in each block of conjunction search trials. Thus, the total number of values of saccade incidence to each distractor type was the product of the total number of conjunction blocks (49 blocks for monkey C plus 46 blocks for monkey F) times the number of set sizes (3). These values are plotted with a binwidth of 10%. The average value of the distribution for each of the distractor types is shown in the lower right corner of Table 2 (bold values). Monkeys shifted gaze to same-color and same-shape distractors significantly more frequently than to opposite distractors. (B) Effect of target history across consecutive sessions on gaze behavior. Incidence of saccades to same-color (black), same-shape (gray), and opposite (unfilled) distractors are shown as a function of the target properties in the previous session. Monkeys exhibited a tendency to shift gaze to distractors that had been the target during the previous session.

It is important to note that this priming effect does not undermine the original observation that gaze lands more frequently on distractors that resemble the conjunction target than on those that do not. This conclusion is due to the fact that the properties of the targets on two consecutive sessions were counterbalanced, and the fact that the delay between two consecutive sessions was the same regardless of the correspondence of target properties between them (Kruskal-Wallis one-way ANOVA; $\chi^2 = 4.7$, $d.f. = 2$). In fact, inspection of Table 2 shows that when a given distractor that

Table 2. *Incidence (in percent) of initial saccades to the different distractor types during conjunction search for each set size and previous session history*

		Monkey C				Monkey F				Both monkeys			
		Set size				Set size				Set size			
Target during previous session	Distractor type	4	6	12	Mean	4	6	12	Mean	4	6	12	Mean
Opposite	Same-color	36.2	28.2	35.4	33.3	44.4	44.8	46.5	45.2	40.3	36.5	40.9	39.2
	Same-shape	48.6	57.5	48.5	51.6	47.7	43.0	37.8	42.8	48.1	50.2	43.2	47.2
	Opposite	15.3	14.3	16.0	15.2	7.9	12.3	15.7	12.0	11.6	13.3	15.9	13.6
Same-color	Same-color	57.0	57.9	62.1	59.0	58.1	61.2	61.7	60.3	57.6	59.5	61.9	59.7
	Same-shape	37.7	34.7	30.5	34.3	34.8	34.0	30.0	32.9	36.2	34.3	30.3	33.6
	Opposite	5.4	7.5	7.4	6.7	7.1	4.8	8.3	6.7	6.2	6.1	7.8	6.7
Same-shape	Same-color	25.0	23.5	29.8	26.1	29.5	36.0	35.1	33.5	27.2	29.8	32.5	29.8
	Same-shape	71.3	72.8	66.5	70.2	67.6	61.0	58.2	62.3	69.5	66.9	62.3	66.2
	Opposite	3.8	3.7	3.7	3.7	2.9	3.0	6.7	4.2	3.3	3.4	5.2	4.0
Mean	Same-color	39.4	36.5	42.5	39.5	44.0	47.3	47.8	46.4	41.7	41.9	45.1	**42.9**
	Same-shape	52.5	55.0	48.5	52.0	50.0	46.0	42.0	46.0	51.3	50.5	45.3	**49.0**
	Opposite	8.1	8.5	9.0	8.5	6.0	6.7	10.2	7.6	7.0	7.6	9.6	**8.1**

shared a target feature (i.e. same-color or same-shape) was the target during the previous session, then the other distractor that shared a target feature (i.e. same-shape or same-color) but was not affected by this priming effect still attracted gaze significantly more often than did the distractor that shared neither target property. Furthermore, when there was a priming advantage for the opposite distractor, same-color and same-shape distractors both still attracted gaze significantly more often.

Finally, we investigated whether saccades made to distractors showed any spatial relationship to the location of the target. In other words, we determined whether monkeys were more likely to make a saccade to a distractor near the target than to a distractor far from the target. Comparing the average saccade rate to distractors adjacent to the target to the average saccade rate to all other distractors, we found more frequent saccades to distractors near the target during feature search than during conjunction search. The ratios of the average number of saccades to distractors adjacent to the target to the average number of saccades to the other distractors for Monkey C was 2.6 (4-item display), 2.6 (6-item display), and 4.9 (12-item display). The corresponding values for Monkey F were 1.8 (4-item display), 2.0 (6-item display), and 3.3 (12-item display). In contrast, this spatial relationship was much weaker for conjunction search (Monkey C: 1.2, 1.3, and 1.0; Monkey F: 1.5, 1.5, and 1.2). This observation demonstrates that saccades to distractors in conjunction search are guided more by their similarity to the target than by their proximity to the target.

Discussion

In performing feature search monkeys, like humans, showed a tendency to shift gaze to distractors near the pop-out target and exhibited a short-term (<10 trial) priming effect when the feature search dimension switched. In conjunction search monkeys, like humans, exhibited very shallow slopes of reaction time as a function of set size. Also, when in error, monkeys selected a distractor that resembled the target more often than a distractor that did not and were less likely to select a distractor near the target than in feature search. We also made the interesting observation that distractors that resembled the target of the previous session were selected significantly more often than were the other distractors.

Relation to previous human performance studies

During feature search, the monkeys' rates of correct initial saccades to the target increased with increasing set size. This finding is consistent with the operation of pop-out, or saliency detection mechanisms in feature search. As the number of distractors decreases substantially, thereby decreasing the density of the elements, the relative saliency of the target decreases making its detection less efficient. The increasing likelihood of making a saccade to a distractor adjacent to the target as compared to other distractors with increasing display size is also consistent with strong saliency effects during feature search leading to automatic capture of attention by singletons (e.g. Theeuwes, 1991; see also Findlay, 1997). The increasing efficiency in detecting the target with increasing set size is also reflected in the negative slopes of reaction time as a function of set size seen with monkey F. Negative slopes in pop-out searches with set sizes ranging from 3 to 12 have also been observed in human subjects (Bravo & Nakayama, 1992). Monkey C, in contrast, exhibited positive search slopes perhaps due to a relatively greater reliance on top–down factors than monkey F (for additional evidence of top–down influence on pop-out search with monkeys see Bichot et al., 1996). In spite of this curious difference in search reaction time slopes, because both monkeys' performance was the same on all the other measures our interpretation is that they were using similar strategies in detecting the target.

The effects on accuracy, saccade latencies, and search slopes of alternating the feature search dimension show that extraretinal factors also play a role in feature searches. Nakayama and colleagues have shown that repetition of the target and distractor properties or the target location across trials during a pop-out search improves performance (e.g. Maljkovic & Nakayama, 1994, 1996). This effect, called perceptual priming, had a cumulative influence with a time span of 5–8 trials or approximately 30 s. Our results show remarkable quantitative similarity to those of Nakayama and col-

leagues, despite the fact that in our study distractor properties changed across feature dimensions, whereas in those experiments target or distractor properties varied within a feature dimension (e.g. red among green *vs.* green among red or red among blue or blue among green). In the first five trials following the switch in the feature search dimension, monkeys made more errors and were slower in generating a saccade to the target. They also exhibited more positive or less negative slopes, which may reflect an increased reliance on top–down knowledge of the target properties to locate it. Over the next five trials (e.g. trials 6–10), all three measures of performance reached stable values, consistent with the 5–8 trial time-span estimate of Nakayama and colleagues.

Our results during conjunction search were gratifyingly similar to what has been observed in humans using comparable stimuli; the slopes of reaction time as a function of set size were shallow, although they were significantly different from the slopes in feature searches. Such shallow slopes have been interpreted as evidence that conjunction searches are performed by parallel processing of the individual features that define the target (Wolfe et al., 1989; Treisman & Sato, 1990). Although the effect of set size appears greater when error rates are also taken into account, several pieces of evidence strongly argue against the possibility that the monkeys in our experiment performed conjunction searches in a strictly serial manner. First, shallower search slopes did not yield more errors, arguing against a speed-accuracy tradeoff. Similar increases in error rate with set size during efficient conjunction search have also been observed with humans without a correlation between error rates and search slope (Wolfe et al., 1989). Further evidence against a speed-accuracy tradeoff comes from the fact that saccade latency in our experiment was not shorter in trials when monkeys made an initial saccade to one of the distractors as compared to trials in which they made an accurate initial saccade to the target. Finally, even greater increases in error rate have been observed with humans during a search for a randomly oriented T among randomly oriented Ls that typically yields steep slopes on the order of 20–30 ms/item (Wolfe et al., 1989).

Parallel feature-based models of search predict a higher incidence of gaze shifts to distractors that share a feature with the target than to distractors that share none. Our results confirm this prediction. However, we should note that the gaze behavior of monkeys in our experiment is also consistent with a theory of visual search based on stimulus similarity (Duncan & Humphreys, 1989) that does not emphasize a distinction between serial and parallel search, or one between feature and conjunction search. According to this theory, search efficiency (as reflected by search slopes as a function of set size) forms a continuum, decreasing with increased similarity of targets to distractors or decreased similarity between distractors. This theory of visual search would also predict that distractors similar to the target (i.e. those that contain a target feature) would be gazed upon more frequently than distractors that are dissimilar (i.e. those that share no target feature). In fact, distinguishing between this account of visual search based on similarity and the aforementioned accounts of visual search based on feature-based parallel processing has been difficult (Treisman, 1991; Duncan & Humphreys, 1992; Treisman, 1992).

Similar observations about saccade target selection have been made recently in humans by Findlay (1997; see also Williams, 1967). However, in Findlay's study saccades were made much more often to distractors that shared the target shape than to those that shared the target color, whereas the monkeys in our experiment used color and shape information equally. This different pattern of results may be due to differences in the color and shape properties of stimuli in the two studies or to the fact that Findlay used more potential shapes than colors to define stimuli. In addition, in our study an extensive training period before data collection as well as running experimental sessions for many weeks allow us to conclude that this distractor- or feature-specific gaze behavior does not disappear with practice.

The fact that color and shape information was used equally in our experiment pertains to yet another account of efficient processing during conjunction search, namely the segregation hypothesis (Treisman, 1982; see also Egeth et al., 1984). According to this theory, attention can be allocated on the basis of one feature to exclude a subset of the distractors, allowing a parallel feature search within the remaining distractors. Our data show that, within blocks, monkeys used both color and shape information to find the conjunction target, making it unlikely that they were able to limit search to one feature dimension, consistent with other findings using human subjects (Treisman & Sato, 1990). It is nevertheless possible that, although both feature dimensions were used within blocks, a single feature dimension was used in individual trials. However, if this were true, it would mean that, across trials, monkeys changed the feature dimension they were using to eliminate a subset of the distractors to reduce the conjunction search to a feature search. It does not seem plausible that monkeys do this, especially considering the cost in performance of switching a feature search dimension found in this study.

A recent study by Zelinsky (1996) reports markedly different gaze behavior by human subjects reporting target presence/absence with button presses during conjunction search. Although gaze landed near the target just before the button press signaling that the target was present, saccades made during the search trial directed gaze nearly equally to distractors that were similar or dissimilar to the target. A major difference between Zelinsky's study, on one hand, and Findlay's and our study, on the other, is the role attributed to saccades. In Findlay's and our experiment, subjects were required to indicate the location of the target by fixating it. This was even more crucial in our experiment than Findlay's because monkeys had to make the initial saccade from the fixation spot to the target to receive reward. In contrast, in Zelinsky's study, the subjects were instructed to report target presence or absence with a key press; no instructions were given with regard to eye movements in the search process. Under these circumstances, eye movements may reveal less about the mechanisms underlying the search process because correct performance does not depend on accurate target fixation.

Our results are also consistent with recent findings by Kim and Cave (1995). During conjunction search, they found that letter probes appearing at locations previously occupied by distractors that resembled the target were more likely to be reported than were letter probes at locations previously occupied by distractors that did not resemble the target. Given the strong link between attention and eye movements, increased attentional allocation to the locations of distractors that share target features would lead to an increased probability of making a saccade to one such distractor over a distractor that shares no target feature.

We also made the unexpected finding that monkeys during conjunction search made more saccades to distractors that had been the target in the previous session (see Shiffrin & Schneider, 1977 for related effects in humans). In contrast to the short-term perceptual priming observed during feature search in this and other studies (e.g. Maljkovic & Nakayama, 1994), we observed a pronounced priming effect in consecutive experimental sessions at least a day apart, a clear priming influence in sessions 2 or 3 days

apart, and even a weak influence for sessions a week or more apart. We also observed that the priming observed during conjunction search was more enduring, persisting throughout the entire session. Hence, we conclude that the specific influence of experience on performance we observed may be a more enduring manifestation of the short-term priming observed in this and earlier studies.

Relation to neurophysiological studies

A number of studies have identified neural correlates of visual selection and attention (reviewed by Desimone & Duncan, 1995; Maunsell, 1995; Schall & Bichot, 1998). Some general properties of the neural selection process are emerging such as parallel processing of elements across the image and suppression of distractor representations compared to target representations. However, the present neurophysiological findings can account only partially for the present observations of conjunction search.

The evidence from this and previous studies of color/shape conjunction visual search indicates that the selection process is most likely parallel. One line of physiological evidence for parallel processing is the concurrent modulation of neurons responding to all elements of a spatially extended array (e.g. Chelazzi et al., 1993; Motter, 1994; Schall et al., 1995*a*; Thompson et al., 1996; Luck et al., 1997). We infer that the similar distractor is confused for the target more often than is the dissimilar distractor because the neural representation of the similar distractor is suppressed less effectively, permitting it access to the response production (in our case saccade) system.

Conjunction visual search is a useful task precisely because although the selection process must be based on bottom–up information about the features of the elements, that information is insufficient to identify the target. Subjects must employ some form of memory to find the target with the predefined features. A hallmark property of neurons in striate and extrastriate visual areas is selectivity for the features of stimuli such as form and color (reviewed in Rockland et al., 1997), and recent evidence has also shown that some neurons in visual areas TEO and caudal TE are selective for conjunctions of elementary features such as color and shape (Tanaka et al. 1991; Komatsu & Ideura, 1993). These visual neurons provide the necessary substrate for the selection process, but top−down processing is needed to exert the influence of the memory for the target properties. In fact, physiological studies have provided evidence for modulation of visual responses in extrastriate cortex by instructions and expectations (e.g. Bushnell et al., 1981; Mountcastle et al., 1987; Chelazzi et al., 1993; Motter, 1994; Treue & Maunsell, 1996; Luck et al., 1997). To explain our results, the signals from these visual areas must access the oculomotor system to influence saccade production. One such route is through frontal cortex; visual areas V4, TEO, and caudal TE where color and shape are processed are reciprocally connected with frontal eye field (FEF) (Baizer et al., 1991; Schall et al., 1995*b*), an area that plays a central role in the production of voluntary, visually guided saccades (reviewed by Goldberg & Segraves, 1989; Bruce, 1990; Schall, 1997). In FEF, we have observed neural correlates of the visual selection of the target of an eye movement (Schall et al., 1995*a*; Thompson et al., 1996, 1997). The initial activation of visually responsive FEF neurons was the same regardless of whether the oddball target or only distractors of a pop-out search array fell in their receptive field. However, before saccade initiation, the activity of these neurons evolved to discriminate the target as reflected by an attenuation of the response evoked by distractors, regardless of the particular feature dimension used (e.g. color or spatial frequency). However, in none of these areas has a study been done using conjunction visual search. The prediction suggested by our results is that the neural representation of distractors that resemble the target will be less suppressed than will be the representation of distractors that are dissimilar to the target. The time and areas in which this pattern of modulation is expressed will be crucial to determine because it represents the flow of information and the evolution of processing across the involved areas from early to final stages of selection.

To explain the persisting influence of the previous session's target properties on visual selection entails an enduring but not permanent change in the neural representation of the target and distractor features. Luck et al. (1997) have documented a baseline shift in the activation of V4 neurons when monkey can anticipate reliably the location of the target. This may be the basis for location priming (Maljkovic & Nakayama, 1996), but to explain the bias we observed requires a change in the neural representation in feature space. In monkeys doing feature search with just one of the complementary search arrays (e.g. only red among green), we have found that around half of FEF visual responses exhibit an early, initial selectivity for the learned target which was unlike what we observed in monkeys trained to search for the target in both complementary arrays (Bichot et al., 1996). This type of change in the neural representation might account for the priming effect we observed in conjunction search.

Conclusion

An understanding of the neural basis of visual selection requires a concerted effort of performance studies, computational models, neuroimaging, and neurophysiology. Progress will be accelerated if common tasks with sound empirical and theoretical foundations are employed so that results can be compared across laboratories and experimental methods. Finding that monkeys do conjunction search, a paradigm originally developed in human cognitive studies, and that their performance can reveal interpretable properties of the selection process provides a sound basis for future neurophysiological studies across many visual and visuomotor areas of the brain.

Acknowledgments

We thank Kyle Cave, Michael Goldberg, Doug Hanes, Kirk Thompson, and two anonymous reviewers for their helpful comments on the manuscript, and Sheldon Hoffman for assistance with the TEMPO software. This work was supported by National Eye Institute Grants RO1 EY08890 to J.D. Schall, and P30 EY08126 and T32 EY07135 to the Vanderbilt Vision Research Center. J.D. Schall is a Kennedy Center Investigator.

References

Baizer, J.S., Ungerleider, L.G. & Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *Journal of Neuroscience* **11**, 168–190.

Bichot, N.P., Cave, K.R. & Pashler, H. (1999). Visual selection mediated by location: Feature-based selection of noncontiguous locations. *Perception and Psychophysics* (in press).

Bichot, N.P., Schall, J.D. & Thompson, K.G. (1996). Visual feature selectivity in frontal eye fields induced by experience in mature macaques. *Nature* **381**, 697–699.

Bolster, R.B. & Pribram, K.H. (1993). Cortical involvement in visual scan in the monkey. *Perception and Psychophysics* **53**, 505–518.

Bowman, E.M., Brown, V.J., Kertzman, C., Schwartz, U. & Robinson, D.L. (1993). Covert orienting of attention in macaques. I. Effects of behavioral context. *Journal of Neurophysiology* **70**, 431–443.

Bravo, M.J. & Nakayama, K. (1992). The role of attention in different visual-search tasks. *Perception and Psychophysics* **51**, 465–472.

Bruce, C.J. (1990). Integration of sensory and motor signals for saccadic eye movements in the primate frontal eye fields. In *Signals and Sense, Local and Global Order in Perceptual Maps*, ed. Edelman, G.M., Gall, W.E. & Cowan, W.M., pp. 261–314. New York: John Wiley and Sons.

Buračas, G.T. & Albright, T.D. (1997). Neural correlates of target selection in area MT. *Centro de Reuniones Internacionales Sobre Biologia, Workshop on Principles of Neural Integration* **70**, 54.

Bushnell, M.C., Goldberg, M.E. & Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *Journal of Neurophysiology* **46**, 755–772.

Cave, K.R. & Wolfe, J.M. (1990). Modeling the role of parallel processing in visual search. *Cognitive Psychology* **22**, 225–271.

Cepeda, N.J., Cave, K.R., Bichot, N.P. & Kim, M.-S. (1998). Spatial selection via feature-driven inhibition of distractor locations. *Perception and Psychophysics* **60**, 727–746.

Chelazzi, L., Miller, E.K., Duncan, J. & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature* **363**, 345–347.

Corbetta, M., Shulman, G.L., Miezin, F.M. & Petersen, S.E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* **270**, 802–805.

Desimone, R. & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience* **18**, 193–222.

Deubel, H. & Schneider, W.X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research* **36**, 1827–1837.

Duncan, J. & Humphreys, G.W. (1989). Visual search and stimulus similarity. *Psychological Review* **96**, 433–458.

Duncan, J. & Humphreys, G.W. (1992). Beyond the search surface: visual search and attentional engagement. *Journal of Experimental Psychology: Human Perception and Performance* **18**, 578–588.

Dürsteler, M.R. & von der Heydt, R. (1992). Visual search strategies of monkey and man. *Society for Neuroscience Abstracts* **18**, 1398.

Egeth, H., Virzi, R.A. & Garbart, H. (1984). Searching for conjunctively defined targets. *Journal of Experimental Psychology: Human Perception and Performance* **10**, 32–39.

Findlay, J.M. (1997). Saccade target selection during visual search. *Vision Research* **37**, 617–631.

Goldberg, M.E. & Segraves, M.A. (1989). Visual and frontal cortices. In *The Neurobiology of Saccadic Eye Movements*, ed. Wurtz, R.H. & Goldberg, M.E., pp. 283–313. New York: Elsevier.

Hanes, D.P. & Schall, J.D. (1995). Countermanding saccades in macaque. *Visual Neuroscience* **12**, 929–937.

Kim, M.-S. & Cave, K.R. (1995). Spatial attention in visual search for features and feature conjunctions. *Psychological Science* **6**, 376–380.

Komatsu, H. & Ideura, Y. (1993). Relationships between color, shape, and pattern selectivities of neurons in the inferior temporal cortex of the monkey. *Journal of Neurophysiology* **70**, 677–694.

Kowler, E., Anderson, E., Dosher, B. & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research* **35**, 1897–1916.

Kustov, A.A. & Robinson, D.L. (1996). Shared neural control of attentional shifts and eye movements. *Nature* **384**, 74–77.

Luck, S.J. & Hillyard, S.A. (1995). The role of attention in feature detection and conjunction discrimination: An electrophysiological analysis. *International Journal of Neuroscience* **80**, 281–297.

Luck, S.J., Chelazzi, L., Hillyard, S.A. & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology* **77**, 24–42.

Maljkovic, V. & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory and Cognition* **22**, 657–672.

Maljkovic, V. & Nakayama, K. (1996). Priming of pop-out: II. Role of position. *Perception and Psychophysics* **58**, 977–991.

Maunsell, J.H.R. (1995). The brain's visual world: Representation of visual targets in cerebral cortex. *Science* **270**, 764–769.

McLeod, P., Driver, J. & Crisp, J. (1988). Visual search for conjunctions of movement and form is parallel. *Nature* **332**, 154–155.

Motter, B.C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. *Journal of Neuroscience* **14**, 2178–2189.

Mountcastle, V.B., Motter, B.C., Steinmetz, M.A., & Sestokas, A.K. (1987). Common and differential effects of attentive fixation on the excitability of parietal and prestriate (V4) cortical visual neurons in the macaque monkey. *Journal of Neuroscience* **7**, 2239–2255.

Nakayama, K. & Silverman, G.H. (1986). Serial and parallel processing of visual feature conjunctions. *Nature* **320**, 264–265.

Robinson, D.A. (1963). A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Transactions in Biomedical Engineering* **10**, 137–145.

Rockland, K.S., Kaas, J.H. & Peters, A. (1997). *Cerebral Cortex, Volume 12, Extrastriate Cortex in Primates*. New York: Plenum Press.

Schall, J.D. (1997). Visuomotor areas of the frontal lobe. In *Cerebral Cortex, Volume 12, Extrastriate Cortex of Primates*, ed. Rockland, K.S., Kaas, J.H. & Peters, A., pp. 527–638. New York: Plenum Press.

Schall, J.D. & Bichot, N.P. (1998). Neural correlates of visual and motor decision processes. *Current Opinion in Neurobiology* **8**, 211–217.

Schall, J.D., Hanes, D.P., Thompson, K.G. & King, D.J. (1995*a*). Saccade target selection in frontal eye field of macaque. I. Visual and premovement activation. *Journal of Neuroscience* **15**, 6905–6918.

Schall, J.D., Morel, A., King, D.J. & Bullier, J. (1995*b*). Topography of visual cortical afferents to frontal eye field in macaque: Functional convergence and segregation of processing streams. *Journal of Neuroscience* **15**, 4464–4487.

Sheliga, B.M., Riggio, L. & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research* **105**, 261–275.

Shiffrin, R.M. & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychological Review* **84**, 127–190.

Siegel, S. & Castellan, N.J., Jr. (1988). *Nonparametric Statistics*. New York: McGraw-Hill.

Tanaka, K., Saito, H., Fukada, Y. & Mariya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology* **66**, 170–189.

Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception and Psychophysics* **50**, 184–193.

Thompson, K.G., Hanes, D.P., Bichot, N.P. & Schall, J.D. (1996). Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *Journal of Neurophysiology* **76**, 4040–4055.

Thompson, K.G., Bichot, N.P. & Schall, J.D. (1997). Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *Journal of Neurophysiology* **77**, 1046–1050.

Townsend, J.T. (1976). Serial and within-stage independent parallel model equivalence on the minimum completion time. *Journal of Mathematical Psychology* **14**, 219–238.

Townsend, J.T. (1990). Serial vs. parallel processing: Sometimes they look like tweedledum and tweedledee but they can (and should) be distinguished. *Psychological Science* **1**, 46–54.

Treisman, A.M. & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology* **12**, 97–136.

Treisman, A. & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception and Performance* **16**, 456–478.

Treisman, A. (1991). Search, similarity, and integration of features between and within dimensions. *Journal of Experimental Psychology: Human Perception and Performance* **17**, 652–676.

Treisman, A. (1992). Spreading suppression or feature integration? A reply to Duncan and Humphreys (1992). *Journal of Experimental Psychology: Human Perception and Performance* **17**, 652–676.

Treisman, A.M. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology: Human Perception and Performance* **8**, 194–214.

Treue, S. & Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* **382**, 539–541.

Williams, L.G. (1967). The effects of target specification on objects fixated during visual search. *Acta Psychologica* (Amst) **27**, 355–360.

Wolfe, J.M. (1994). Guided search 2.0. A revised model of visual search. *Psychonomic Bulletin and Review* **1**, 202–228.

Wolfe, J.M., Cave, K.R. & Franzel, S. (1989). Guided Search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance* **15**, 419–433.

Zelinsky, G.J. (1996). Using eye saccades to assess the selectivity of search movements. *Vision Research* **36**, 2177–2187.