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Search Efficiency but Not Response Interference Affects Visual Selection in Frontal Eye Field

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Summary

Two manipulations of a visual search task were used to test the hypothesis that the discrimination of a target from distractors by visually responsive neurons in the frontal eye field (FEF) marks the outcome and conclusion of visual processing instead of saccade preparation. First, search efficiency was reduced by increasing the similarity of the distractors to the target. Second, response interference was introduced by infrequently changing the location of the target in the array. Both manipulations increased reaction time, but only the change in search efficiency affected the time needed to select the target by visually responsive neurons. This result indicates that visually responsive neurons in FEF form an explicit representation of the location of the target in the image.

Introduction

Behavioral reaction time varies unpredictably from trial to trial. A simple summation of sensory and motor transduction delays and conduction times in the nervous system cannot account for the duration and variability of reaction time. Thus, much of the delay and variability of reaction time is attributed to processes that intervene between the afferent and efferent delays (e.g., Ratcliff, 1978; Luce, 1986; Carpenter, 1991). Most explanations of reaction time make the basic assumption that presentation of a stimulus activates more or less distinct stages of processing, such as perception, memory retrieval, and response execution (Donders, 1868/1969; Meyer et al., 1988). Several studies developed means to identify these stages and manipulate them to determine how signals flow from one stage to the next (e.g., Sternberg, 1966, 1969; Pashler, 1991; Sanders, 1990; Eriksen and Schultz, 1979; McClelland, 1979; Miller, 1982, 1983). However, the lack of a direct measure of the duration of the component processes has hampered the elucidation of how the duration and the variability of reaction time derive from the duration of substituent stages.

Visual search provides the necessary elements to investigate the duration of distinct stages of processing. At least two processes take place in visual search: the analysis of the visual array and the planning of an orienting response such as a saccade (Viviani, 1990; Hooge and Erkelens, 1996). The frontal eye field (FEF) is one of the cortical areas at the interface between visual processing and motor production (reviewed in Schall, 1997). During visual search, visually responsive neurons in FEF exhibit activity related to target selection (Schall and Hanes, 1993; Schall et al., 1995a; Thompson et al., 1996, 1997; Bichot and Schall, 1999; Murthy et al., 1999; Bichot et al., 2001). The initial activity of visually responsive cells does not discriminate whether the target or distractors of a search array fall in the receptive field but the late phase of the activity of these neurons reliably differentiates the target from the distractors. The time at which these visual cells begin to discriminate the target from the distractors has been hypothesized to be a marker that partitions reaction time into pre- and postperceptual stages (Thompson et al., 1996).

In the present study, we tested this hypothesis by manipulating the search task in two different ways, one decreasing search efficiency and the other introducing response interference. These manipulations both increased the duration and variability of reaction time. Search efficiency was reduced by making the target less discriminable from the distractors (Figures 1A–1C). We investigated both color search and motion search. In color search, target discriminability was reduced by using similar colors for the target and distractors. In motion search, each stimulus was a circular aperture of randomly positioned dots, a proportion of which translated coherently in a specified direction whereas the remainder were replotted randomly (Britten et al., 1992). The direction of motion was either left or right, and the motion of the target was opposite from that of the distractors. Target discriminability was manipulated by changing the proportion of dots that moved coherently. In performing less efficient search, subjects produce more errors and longer reaction times because of the increased difficulty to locate the target (Duncan and Humphreys, 1989; Wolfe, 1994).

Response interference was introduced with the use of a task that we call search step (Murthy et al., 1999). A display supporting the most efficient color search task was used, but, in some of the trials, the target and one distractor unexpectedly swapped positions after presentation of the array (Figure 1D). When the target position changed, monkeys had to cancel the initial saccade and shift gaze to the new target position to earn reward. To adapt to the unexpected target step, monkeys increased reaction time overall. In this condition, the time to discriminate the target should not be affected, and postperceptual response preparation should contribute more to the variability in reaction time (reviewed by Coles et al., 1995).

Figure 2 illustrates how the alternative hypotheses were evaluated. If the time of target discrimination in FEF neurons marks the conclusion of perceptual processing, then the following relations should hold. First, longer target discrimination times should coincide with longer

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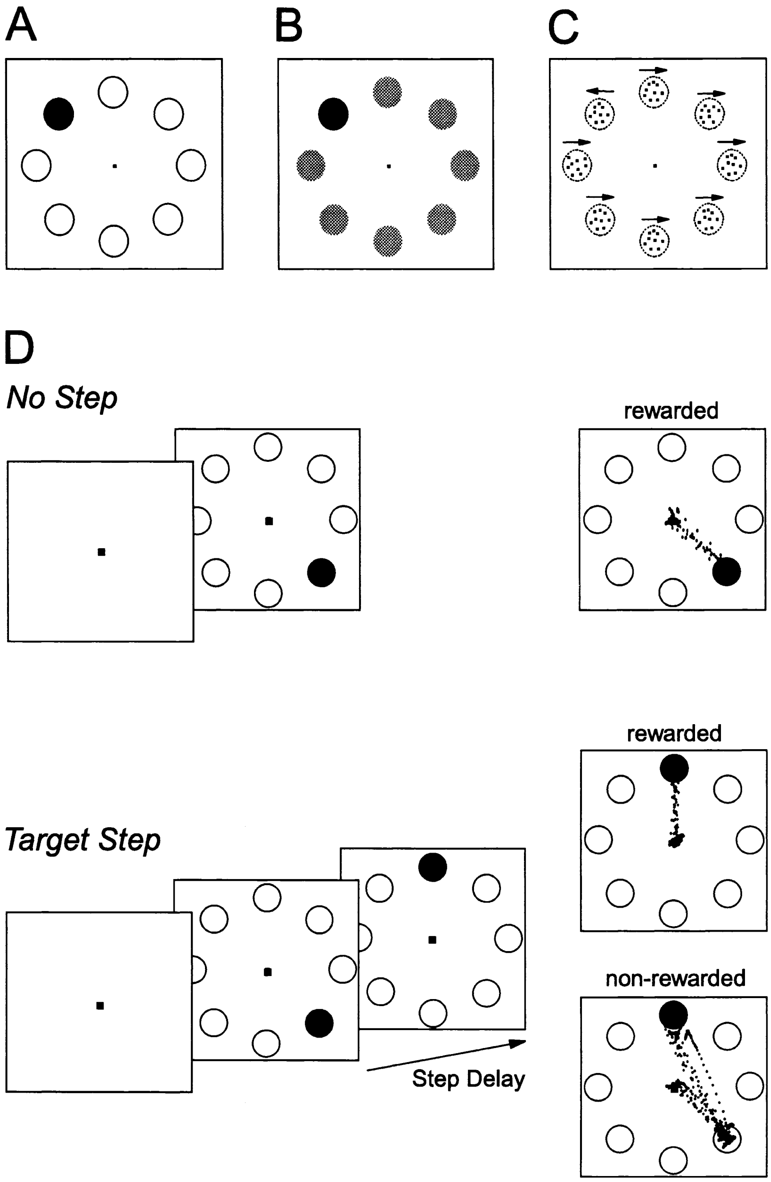

Figure 1. Visual Search Tasks

Each trial began with the presentation of a fixation point. After fixation for a variable interval the fixation point was removed and an eight-element circular search array with a single oddball target appeared.

(A) Efficient color search with green target and red distractors.

(B) Less efficient color search with green target and yellow-green distractors.

(C) Motion search. Each stimulus was a circular aperture of randomly positioned dots. The direction of motion was either left or right, that of the target being the opposite from that of distractors. Search efficiency was manipulated by changing the proportion of dots moving coherently.

(D) Search step task. On "No Step" trials, monkeys were rewarded for shifting gaze to the target. On "Target Step" trials, the target swapped positions with a distractor after a short "Step Delay," and monkeys were rewarded for shifting gaze to the new target.

reaction times for the less efficient search task because variability in the perceptual stage of processing contributes more to the variability in reaction time. In addition, target discrimination time should remain constant in the response interference task with an efficient search array because variability in response preparation contributes more to the variability in reaction time. We will present data consistent with the hypothesis that the time of target discrimination by FEF cells marks the end of perceptual processing, i.e., stimulus encoding and selection. Thus, the target discrimination time can be a useful marker to study the neural basis of mental chronometry.

Some of the findings presented in this report have appeared in abstract form (Thompson et al., 1998).

Results

Performance Data

Both the less efficient search task and the response interference task affected the reaction time of the monkeys. Monkey F was tested on the efficient color search task, the less efficient color search task, and the response interference task. For this monkey, the mean ± standard deviation of reaction time in the efficient search task was 177.6 ± 46.2 ms (12,295 trials), whereas that in the less efficient search task was 218.7 ± 81.0 ms (9013 trials), and that in the response interference task was 247.4 ± 88.7 ms (8312 trials). The reaction times in the less efficient search task and the response interference task were both significantly greater than those in the efficient search task (respectively, $t_{13273} = 43.3$, $p < 0.001$; $t_{11383} = 66.0$, $p < 0.001$; Welch's t test). Monkey M was tested on the efficient motion search task and the less efficient motion search task. The mean reaction time in the efficient search task was 209.1 ± 33.7ms (4266 trials) whereas that in the less efficient search task was 255.1 ± 76.5 ms (4365 trials), which were significantly different ($t_{6026} = 36.3$, $p < 0.001$). Monkey L was tested on the efficient search and the response interference task. The mean reaction time in the efficient search task was 206.8 ± 28.6 (1968 trials) and that in the response interference task was 235.8 ± 47.2 ms (3727

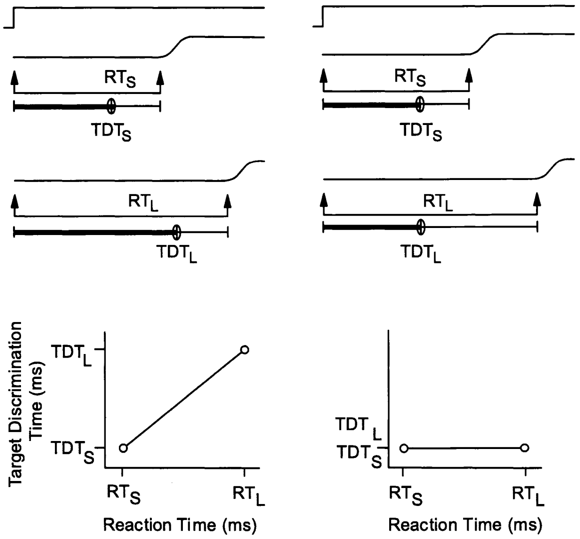

Figure 2. Alternative Hypotheses about How the Time of Target Discrimination (TDT) and Reaction Time (RT) Vary with Search Efficiency or Response Interference

Top trace shows the time of search array presentation with representative eye position traces for blocks of trials with short (RT_S) and long (RT_L) reaction times. Reaction time is subdivided into two intervals, one before TDT (thick line) and the other after TDT (thin line). Lower panels show the relation between TDT and the median reaction time for the two blocks of trials. If the increase in TDT accounts for the increase in reaction time due to the behavior manipulation, the fraction of the change in reaction time accounted for by the change in TDT (i.e., $[TDT_L - TDT_S]/[RT_L - RT_S]$) should approach 100% (left). If TDT does not change and, therefore, does not account for the increase in reaction time due to the behavior manipulation, then the fraction of the change in reaction time accounted for by the change in TDT should be close to 0% (right).

trials), which were significantly different ($t_{5595} = 28.8$, $p < 0.001$). Thus, both the less efficient search task and the response interference task increased the duration and variability of reaction time.

Neural Activity during Less Efficient Search

The purpose of this study was to test whether target discrimination time (TDT) in FEF marks the conclusion of the visual encoding and selection stage. We recorded 154 neurons from the FEF in three monkeys, 104 in the less efficient search task, and 50 in the response interference task. Of these, 82 neurons in the less efficient search task and 28 neurons in the response interference task exhibited visual activity elicited by the presentation of the stimulus and provided sufficient data to be included in this report.

The pattern of activation of a representative FEF neuron during the efficient and the less efficient search is shown in Figure 3. The presence of visually evoked activity and saccade-related modulation was tested with memory-guided saccades to a stimulus flashed in the receptive field. This neuron was visually responsive with minimal sustained activity during the delay period and no modulation associated with the memory guided saccade (Figure 3D). The forthcoming analysis is based on the premise that TDT was affected by search efficiency. To test this, an overall value of TDT was determined for each neuron. To exclude the influence of trials with extremely early or late reaction times, we determined overall TDT from the median third of the reaction time distribution collected during the most efficient and less efficient search. The mean ± standard deviation of TDT in the efficient search task was 146.0 ± 26.7 ms and in less efficient search task was 183.7 ± 29.9 ms (42 cells), which were significantly different ($t_{41} = 10.6$, $p < 0.001$; paired t test). Thus, TDT was delayed during less efficient visual search.

To examine how variability in TDT related to variability in reaction time while each neuron was recorded during less efficient visual search, trials were rank ordered by reaction time after excluding the upper and lower 5% of the distribution. Trials were then partitioned into early, intermediate, and late thirds of the reaction time distribution. The time of target discrimination and median reaction time were determined for the trials comprising each of these groups. Groups with fewer than 10 trials were excluded; most of the data included comparisons of 20–30 trials (10–15 each with target or distractors in the receptive field). In every reaction time group, the initial activity did not distinguish whether the target or distractors were in the receptive field, but the later phase of activity selected the target. From the shortest to the longest reaction time group, median reaction time increased from 206 to 290 ms, and TDT increased from 165 to 252 ms. The difference of TDT between short and long reaction time groups (87 ms) was proportional to that of reaction time (84 ms) (Figure 3C). The percentage of the change in reaction time accounted for by the change in TDT between the short latency group and the middle latency group was 165%, and that between the intermediate latency group and the longest latency group was 68%. The average of these two values was 116%.

Figures 4A and 4B shows the relationship between TDT and reaction time in the inefficient search for each neuron. The line plot demonstrates that TDT covaries with reaction time. To quantify the increase of TDT relative to the increase of RT, we calculated the percentage of the increase in reaction time accounted for by the increase in TDT. The average ratio was used if the neuron discriminated the target in more than two reaction time groups. Neurons that discriminated the target in only one reaction time group did not contribute to this analysis. Table 1 gives the numbers of neurons exhibiting discriminative activity that reached the 0.75 criterion in different numbers of reaction time groups. These ratios, plotted in Figure 4B, most commonly assume values slightly less than 100%, but the values range from less than 0% to more than 100%. The ratios of the change in TDT as a function of the change in reaction time less than 0% or greater than 100% should be interpreted as natural measurement errors, so our conclusions will be based on the central tendencies of the distributions. The values of the ratio of the change in TDT divided by the change in reaction time from motion search and from color search were not different ($t_{51} = 1.04$), and so they were combined. The mean percentage of the increase in reaction time accounted for by the increase in TDT was 87 ± 8%, which was significantly different from 0% ($t_{52} = 11.4$, $p < 0.001$) but not from 100% ($t_{52} = 1.65$). Hence, the variability in TDT accounted for nearly all of the variability in reaction time in less efficient visual search.

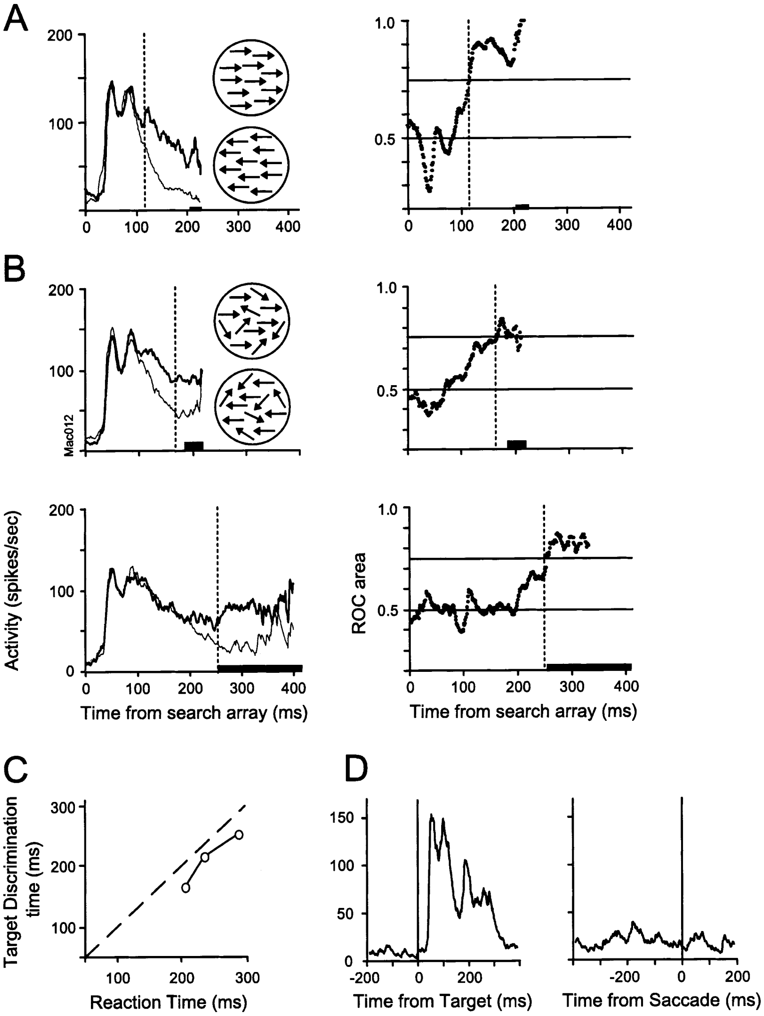

Figure 3. Effect of Search Efficiency on Target Discrimination

Time course of target discrimination by an FEF visual cell during efficient visual search (A) and during less efficient search (B) for trials with shortest (top) and longest reaction times (bottom). Left panels plot average discharge rate when the target fell in the neuron's receptive field (thick line) and when only distractors fell in the neuron's receptive field (thin line). Target and distractor features are indicated. The solid bar shown on the abscissa marks the range of reaction times. Dotted line shows the time of target discrimination (TDT). Right, ROC area as a function of time. The target discrimination time (TDT) is defined as the instant when the ROC area reaches 0.75. (C) Target discrimination time versus median reaction time for groups of trials with short, intermediate, and long reaction times. The dashed line plots the unity relation. (D) Activity during memory guided saccade trials aligned on the stimulus presentation (left) and on saccade initiation (right). The neuron was visually responsive with little sustained delay activity and no movement related modulation.

Neural Activity during Response Interference Task

If TDT is related simply to saccade production, then TDT should increase whenever saccadic reaction time increases. To test this, we analyzed data from the search step task in which reaction time to an efficient search array was elevated because of interference with response preparation. Activity of a representative neuron is shown in Figure 5. The initial visual response of this neuron to the search array (Figure 5A) was attenuated relative to the response to the target presented alone (Figure 5C) as we have reported previously (Schall et al., 1995a; see also Basso and Wurtz, 1998). Note that only data from trials with no target step contributed to this analysis; the neural activity associated with target step trials is the subject of another report (Murthy et al., 1999). The relationship of TDT to reaction time observed during the response interference task was different from that observed during the less efficient search. TDT did not change across short, intermediate or long reaction time groups. Although the reaction time increased 118 ms from the short latency group to the long latency group, TDT increased only 15 ms. The percentage of the change in reaction time accounted for by the change in TDT between the short latency group and the middle latency group was 22%, and that between the intermediate latency group and the longest latency group was 9%. The average of these two values was 15%.

Figures 4C and 4D shows the relationship between TDT and reaction time for each cell recorded in the no-step trials in the search step task. The percentage of the increase of reaction time accounted for by the increase of TDT was 23 ± 12%, which was significantly different from 100% ($t_{17} = 6.35$, $p < 0.001$) but not different from 0% ($t_{17} = 1.88$). Furthermore, the percentage of the increase in reaction time accounted for by the increase in TDT during the less efficient search was significantly greater than that observed during the response interference task ($t_{69} = 4.32$, $p < 0.001$). Thus, the variability in reaction time during less efficient visual search derives mainly from the duration before explicit target discrimination, whereas the variability in reaction time in the response interference task derives mainly from processes after target discrimination.

Discussion

It is well known that perceptual load or response interference increases reaction time. The results of the present study demonstrate that the duration of target selection

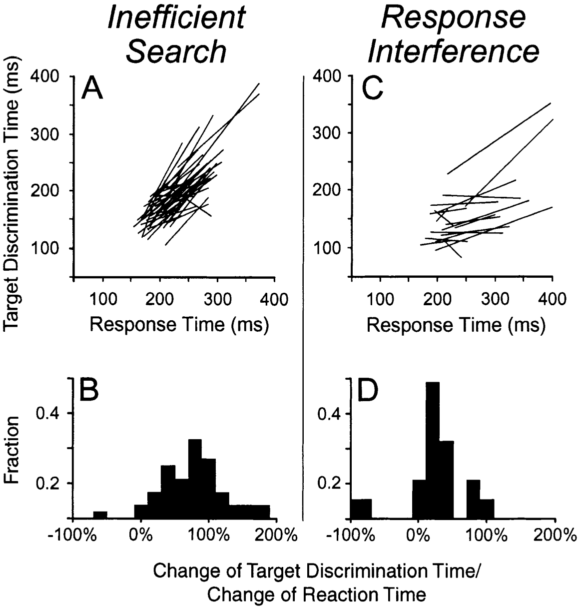

Figure 4. Effect of Search Efficiency and Response Interference on Target Discrimination Time

Relation between the time of target discrimination and reaction time in the less efficient search task (A and B) and the search step response interference task (C and D).

(A) and (C) Each line connects values of TDT as a function of the median reaction time for the most extreme reaction time groups in which the neural activity discriminated the target from the distractors.

(B) and (D) Distribution of the percentage of the change in reaction time accounted for by the change of the time of target discrimination for single FEF neurons.

by FEF neurons during visual search was influenced by manipulating target-distractor similarity but not by manipulating response preparation. This finding indicates that the time of target discrimination in FEF marks the conclusion of the encoding and selection stage of processing.

Neural Correlates of Search for Motion

In earlier work, we have shown target selection in FEF based on color and form (e.g., Schall et al., 1995a; Bichot and Schall, 1999). We now report that neurons in FEF select the target in a visual search array based on motion. In fact, we have observed search target selection based on either color or motion for a small sample of FEF neurons (unpublished observation). While not entirely surprising, the implications of this observation should not be overlooked. The anatomical basis for target selection based on a range of visual features is likely due to the extensive innervation FEF receives from a variety of extrastriate visual areas including areas MT and MST as well as V4 and TEO (Huerta et al., 1987; Stanton et al., 1995; Schall et al., 1995b). These observations support the hypothesis that the representation instantiated by visually responsive neurons in FEF is a salience map (reviewed by Thompson et al., 2001).

Relation to Previous Studies of Target Selection

Neurons that carry signals appropriate for target selection have been identified in various brain areas, including the superior colliculus (Glimcher and Sparks, 1992; Horwitz and Newsome, 1999); extrastriate areas including V2, V4, and TEO (Chelazzi et al., 1993; Motter, 1993, 1994; Luck et al., 1997); area LIP (Shadlen and Newsome, 1996; Gottlieb et al. 1999); and prefrontal cortex (Chen and Wise, 1995; Rainer et al., 1998; Kim and Shadlen, 1999, Gold and Shadlen, 2000). As mentioned, FEF is interconnected heavily with extrastriate visual cortex, prefrontal cortex, and the superior colliculus (Huerta et al., 1986, 1987; Stanton et al., 1995; Schall et al., 1995b), but how the target selection process in one area relates to that in the other areas is not clear. One possibility is that selection of the target occurs concurrently throughout the network. Another possibility is that certain areas (e.g., visual cortex) achieve an explicit representation of target location and identity that is conveyed subsequently to other areas (e.g., frontal lobe). To understand whether target selection is localized temporally and anatomically, it is necessary to collect data across multiple brain areas simultaneously. The tasks and analyses employed in this report may provide the leverage necessary to determine whether target selection occurs sequentially or concurrently.

Relation to Mental Chronometry

Cognitive psychologists seek to understand human information processing in terms of component processes that perform distinct functions requiring a certain amount of time. Behavioral measures represent the total duration and final output of successive processing stages, so they do not offer more than an indirect look at the component processes. Thus, a procedure for measuring directly the duration of a component process is needed to understand the architecture of cognition.

Markers of the beginning or end of distinct stages of processing have been sought with event related potentials. For example, the P300 seems to mark the end of the stimulus evaluation process (e.g., Duncan-Johnson and Donchin, 1982, Coles et al., 1985), and the lateralized readiness potential coincides with motor preparation (e.g., Coles et al., 1988; Miller and Hackley, 1992; Osman et al., 1992). When stimulus discriminability was manipulated, both the P300 and reaction time were delayed; but when stimulus-response compatibility was

Table 1. Number of Neurons that Discriminated the Target from Distractors in Short, Intermediate, and Long Reaction Time Groups and in One, Two, Three, or None of the Three Reaction Time Groups

	Reaction Time Group			Number of Groups				
	Short	Intermediate	Long	One	Two	Three	None	Total
Less Efficient Search	50	51	55	19	22	31	10	82
Response Interference	18	21	19	8	4	14	2	28

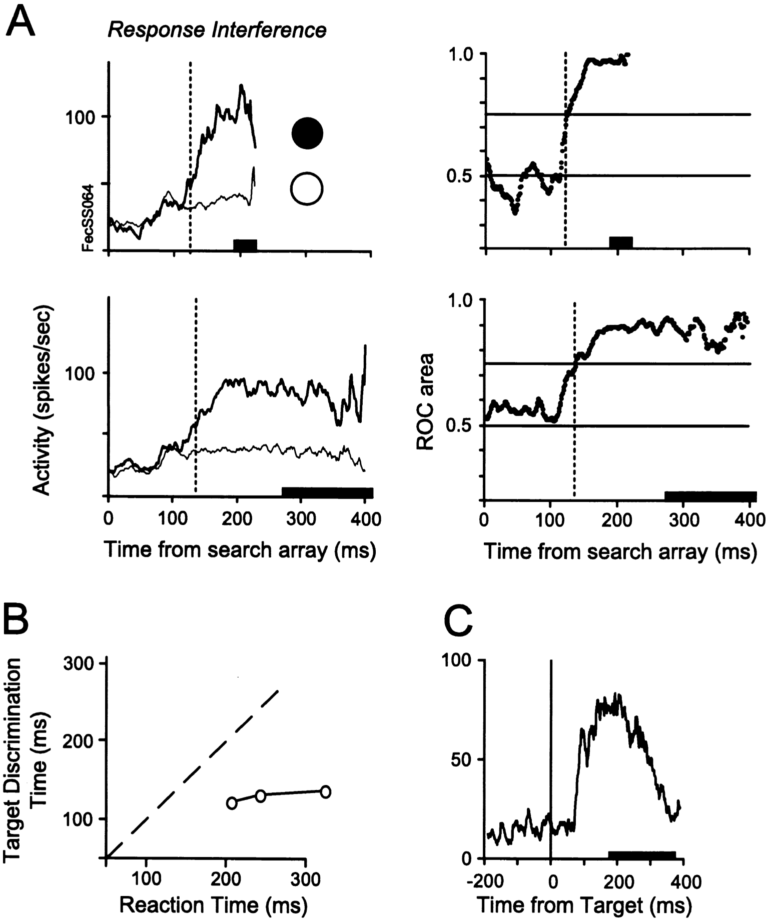

Figure 5. Time Course of Target Discrimination of an FEF Visual Cell in the Response Interference Task

Monkeys shifted gaze to the target in a pop-out array that supported efficient search, but their reaction times were elevated because on some trials the target might change location. The increase in reaction time was not accompanied by an increase in target discrimination time. Conventions as in Figure 3.

manipulated (which delays response preparation), reaction time increased without a corresponding increase in P300 latency (e.g., McCarthy and Donchin, 1980). Without knowledge of the neural generators of event-related potentials, though, the conclusions drawn from these studies are limited.

The architecture of and relations between different stages of processing can be investigated with the highest resolution by recording the activity of single neurons in appropriate behavioral paradigms. The FEF is an effective locus at which to investigate these questions because it is located anatomically and functionally at the interface between processing an image and preparing an eye movement (reviewed by Schall, 1997). Several lines of evidence demonstrate that the process of target discrimination observed in visual cells in FEF can be dissociated from saccade production. First, the time at which most visual neurons in FEF discriminates the target of a search array does not necessarily predict the time of saccade initiation (Thompson et al., 1996). Second, FEF neurons select the oddball of an array even when monkeys withhold saccades (Thompson et al., 1997). Third, during conjunction visual search when saccades are directed to the target outside the receptive field, FEF neurons are activated according to the similarity of the distractors to the target (Bichot and Schall, 1999). Fourth, FEF cells select an oddball target even when monkeys shift gaze to another location (Murthy et al., 1999). Based on these converging observations, we hypothesize that the interval from presentation of the visual search array until the neural representation that distinguishes the target from distractors corresponds to the perceptual stage of processing during which sensory processing encodes stimuli and identifies the location of potential targets for saccades. A corollary of this hypothesis is that the interval from the time of neural target discrimination until saccade initiation is occupied by the motor stage during which the gaze shift is prepared and initiated. A neural correlate of this process is also manifest in FEF (Hanes and Schall, 1996) as well as in the superior colliculus (e.g., Dorris et al., 1997).

The purpose of this experiment was to evaluate this hypothesis directly by differential manipulation of the perceptual and response stages. We found clear evidence that the time of target discrimination was delayed when search efficiency was reduced, but was not affected by response interference. The strength of the conclusion depends on the reliability of the evidence, which we believe is high. For example, the TDT values for the pop-out search arrays used in this study were not substantially different from the TDT values observed in a previous study of visual selection in FEF (Thompson et al., 1996). A legitimate issue to consider is how to interpret ratios of change in TDT as a function of change in reaction time that yield values less than 0% or greater than 100%. We regard these extreme values as nothing more than outliers due to natural measurement errors. Our conclusions are based on the central tendencies of the distributions plotted in Figure 4. Furthermore, an analysis of signaling reliability of FEF neurons provides converging evidence for an increase in target discrimination time proportional to the increase in reaction time when search efficiency was decreased through singleton similarity or conjunction search array size (Bichot et al., 2001). Therefore, we conclude that the time of target selection manifest by FEF visual neurons represents the fulfillment of the encoding and selection stage of processing.

Experimental Procedures

Subjects and Surgery

Data were collected from three macaque monkeys, *Macaca mulatta* and *Macaca radiata*, weighing 4–10 kg. The animals were cared for in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. The surgical procedures have been described previously (Schall et al., 1995a).

Behavioral Training

Using operant conditioning with positive reinforcement, the monkeys were trained to perform singleton visual search tasks in which reward was contingent on shifting gaze to an oddball target. After fixation of a central spot for ~600 ms, the target was presented at one of eight iso-eccentric locations equally spaced around the fixation spot. The remaining seven locations were occupied by the distractors. The target and distractors were distinguished by either color or direction of motion (Figures 1A–1C). For motion search, each stimulus was a circular aperture of randomly positioned dots, a proportion of which translated coherently in a specified direction, whereas the remainder were replotted at random locations every three video frames. The stochastic motion stimulus corresponds to those used in earlier studies (Britten et al., 1992; Kim and Shadlen, 1999; Horwitz and Newsome, 1999). The direction of motion was either left or right, and the direction of motion of the target was the opposite from that of the distractors. For color search, stimuli were scaled from 0.6° of visual angle at 6° eccentricity to 1° at 10° eccentricity (Schall et al., 1995a). For motion search, apertures were scaled from 1.5° at 6° eccentricity to 2.5° at 10° eccentricity.

Two manipulations were used. The first manipulation influenced the visual search efficiency by making the target less discriminable from distractors. In color search, the target was green and the distractors were changed from red to yellow-green (Figures 1A and 1B). In motion search, the target and distractor were made less discriminable by reducing the proportion of coherent dots in the target and distractors from 100% to 50%–60%. Trials with easy and difficult discriminations were randomly interleaved. Search efficiency was adjusted so that the mean reaction time increased at least 30 ms.

The second manipulation influenced response preparation by introducing response interference. In this condition, the monkeys performed a task we call search step (Figure 1D) (Murthy et al., 1999). The search step task combines a standard visual search task with the classic double-step saccade task. On most trials monkeys were rewarded for making a saccade to an oddball target among distractors (no step trials). On the remaining trials the target and one distractor unexpectedly swapped positions after presentation of the array (step trials). When the target stepped unpredictably from its original position to a new position, monkeys were rewarded for directing gaze to the new target location. The probability of producing a saccade to the final target location depended on the delay of the step. The step delay was adjusted through a staircase procedure to ensure a balance between correct and error responses to the target step. Monkeys could increase the probability of producing a correct response on step trials by delaying saccade initiation. In the present report, only data from no step trials were used. Another report describes neural activity in compensated and noncompensated trials (Murthy et al., 1999).

Monkeys were also trained on the traditional memory-guided saccade task to distinguish visual from movement activity (Hikosaka and Wurtz, 1983; Bruce and Goldberg, 1985). In this task, the target was flashed alone for 80 ms, but the monkeys were required to maintain fixation on the central spot for another 400–1000 ms. When the fixation spot disappeared, the monkeys were rewarded for making a saccade to the remembered location of the target. Once the gaze was shifted, the target reappeared to provide feedback and a fixation target for the monkeys. Neurons with visual responses were analyzed for this study.

Two monkeys (F and M) were tested with the less efficient search task, and two monkeys (F and L) were tested with the response interference task. One monkey (F) participated in both.

Data Collection and Analysis

Single units were recorded with insulated tungsten electrodes (FHC). The electrodes were introduced through guide tubes positioned in a 1 mm spaced grid (Crist et al., 1988) and were positioned with a hydraulic drive (FHC). Action potentials were amplified, filtered, and discriminated using either an analog time amplitude window discriminator (BAK) or computer-based window discriminator (Plexon). FEF recordings were done in the rostral bank of the arcuate sulcus, which was confirmed with MRI.

Analysis methods have been described (Thompson et al., 1996). Briefly, the spike density function was generated by convolving action potentials with a function that resembled a postsynaptic potential:

$$\text{Activation}\ (t) = (1 - \exp[-t/\tau_g]) \times (\exp[-t/\tau_d])$$

Physiological data from excitatory synapses estimate the growth constant τ_g at ~1 ms, and the decay constant τ_d at ~20 ms (e.g., Sayer et al., 1990).

The time which neural activity discriminated the target from distractors was determined based on signal detection theory (Green and Swets, 1966). The time course and magnitude of target selection by the neuron was determined by comparing the two sets of trials in a neuron-antineuron analysis (Britten et al., 1992; Thompson et al., 1996). First, trials were sorted into those in which the target fell in the neuron's receptive field and those in which distractors fell in the receptive field. Then for each trial, the spike density function was determined. The separation of the two distributions of activity in a sliding 10 ms window (−5 ms to 5 ms) obtained from two groups was quantified by calculating the area under the receiver operating characteristic (ROC) curves derived from the two distributions. For convenience we will refer to this value as the ROC area. The ROC area was determined in a sliding 10 ms window at 1 ms intervals beginning 200 ms before target onset to the longest saccade latency. Because we were only interested in activity preceding a saccade, once a saccade was initiated activity from that trial was excluded from the analysis. The time of target discrimination was determined from the growth of the ROC area over time. Target discrimination time (TDT) was defined as the time when the ROC area reached 0.75 and stayed above 0.75 for more than 10 ms out of 15 ms immediately following. The criterion of 0.75 corresponded to that used in a previous investigation (Thompson et al., 1996). The conclusions do not depend on the precise value of the criterion.

To determine how target discrimination time (TDT) varies with reaction time, trials were grouped according to reaction time. To minimize the influence of outliers, trials in the lower and upper 5% of the reaction time distribution were excluded from further analysis. The trials were grouped into the earliest, intermediate and longest third of the remaining reaction time distribution. Then the target discrimination time and the median reaction time were calculated for each group.

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