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Effect of target-distractor similarity on FEF visual selection in the absence of the target

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Abstract We tested the hypothesis that frontal eye field (FEF) visual activity integrates visual information with a template of a target by examining whether a target that is not present in a search display influences the target selection in FEF. Neural activity was recorded in FEF of macaque monkeys performing visual search for a singleton target defined by color or direction of motion. The target remained constant throughout, but not across experimental sessions. Trials with distractors dissimilar to the target were interleaved with trials with distractors similar to the target. The hypothesis was tested by measuring the magnitude of activity in randomly interleaved trials with the target absent and only distractors in the display. We found that the response to the distractors was significantly greater when presented with displays consisting of distractors that resembled the absent target than when presented with displays consisting of distractors most different from the absent target. The influence of target-distractor similarity on FEF activity was also observed when the target was present, as reported previously. These data suggest that a template of the absent target can influence the selection process in FEF. This provides more direct evidence that FEF integrates visual information and knowledge of the target to determine the goal of a saccade.

Keywords Frontal eye field · Search · Saccade · Attention · Memory

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Introduction

In our daily lives, we cannot process all the information that comes onto our retina; we naturally select particular objects for regard. Usually, we shift our gaze toward stimuli of interest, but we can change our visual processing without moving our eyes through covert shifts of attention. Visual search tasks have been used extensively to investigate the mechanism of this visual selection, because this task provides an experimentally controlled analogue of the behavior of detecting and orienting to visual stimuli of interest. Psychophysical studies using search tasks have demonstrated that gaze and attention are commonly attracted to conspicuous stimuli, but that they can also be influenced by knowledge (reviewed in Wolfe 1994). One central question is how visual information and knowledge are integrated to guide attention and gaze.

The frontal eye field (FEF) is an effective locus in which to investigate these issues because it is located anatomically and functionally at the interface between processing an image and preparing an orienting response (reviewed in Schall 1997; Schall and Thompson 1999). Although the visually responsive neurons in FEF typically do not exhibit selectivity for stimulus features like color, orientation, or direction of motion (Mohler et al. 1973; Schall et al. 1995), the responses of half of them are enhanced if the stimulus is the target for a saccade (Wurtz and Mohler 1976; Goldberg and Bushnell 1981). We have investigated previously neural correlates of efficient, “pop-out” visual search in which monkeys were required to make a saccade to the target that was easily discriminated from distractors (Schall and Hanes 1993; Schall et al. 1995; Thompson et al. 1996; Sato et al. 2001). The initial activity of visually responsive neurons did not discriminate whether the target or distractors of a search array fell in the receptive field (except under very particular conditions; see Bichot et al. 1996), but the later phase of the activity of these neurons reliably differentiated the target from the distractors.

In pop-out singleton search, the conspicuous target automatically attracts attention and gaze, but orienting is more effortful and error-prone when the target is less discriminable from distractors (Treisman and Gormican 1988; Wolfe et al. 1989; Duncan and Humphreys 1989; Findlay 1997). Distractors that are similar to the target can be inadvertently selected overtly or covertly, resulting in decreased search efficiency (e.g., Duncan and Humphreys 1989; Findlay 1997; see also Bichot and Schall 1999a). The effect of similarity between target and distractors cannot be accounted for solely by local interactions between stimuli, though, because this effect persists even if the target which a distractor resembles is not present in the display (e.g., Pashler 1987). Thus, in performing a visual search task, some kind of short-term representation, or a template, of the target seems to be necessary (Duncan and Humphreys 1989; Bundesen 1990; Desimone and Duncan 1995), although the precise relationship between memory and search is not entirely clear (e.g., Chun and Jiang 1998; Horowitz and Wolfe 1998; Woodman et al. 2001). To account for the effect of target-distractor similarity on behavior, it has been suggested that the distractors similar to the template of the target attract attention and gaze (e.g., Duncan and Humphreys 1989; Wolfe 1994).

Previously, we showed that the neural selection of the target relative to distractors in FEF is weaker when the distractors resemble the target (Bichot and Schall 1999b; Bichot et al. 2001). In the present study, we examined whether the effect of target-distractor similarity on FEF visual activity persists even when the target is absent. We hypothesized that if visual information with a target template, then the effect of target-distractor similarity should remain even if the target is not present in the display. To test this hypothesis, trials were introduced in which only distractors were present. Trials were interleaved between a search array with a target that could be located efficiently (e.g., green target among red distractors), a search array that supported less efficient search (e.g., green target among yellow-green distractors), and a search array with either of the two distractors (e.g., only red distractors or only yellow-green distractors). Even during trials in which the target was not present in the display, a template of the target seems to be necessary to perform the task, be it held in working memory or some other kind of memory. We found that the activation for distractors was higher when the distractors were similar to the target compared to when the distractors were dissimilar to the target, even when the target was not present in the display. The interpretation of this finding hinges on whether the effect of target-distractor similarity occurs, so we also replicated and extended our previous finding on the effect of target-distractor similarity on FEF visual activity.

Preliminary reports of some of these data have appeared (Sato and Schall 2001).

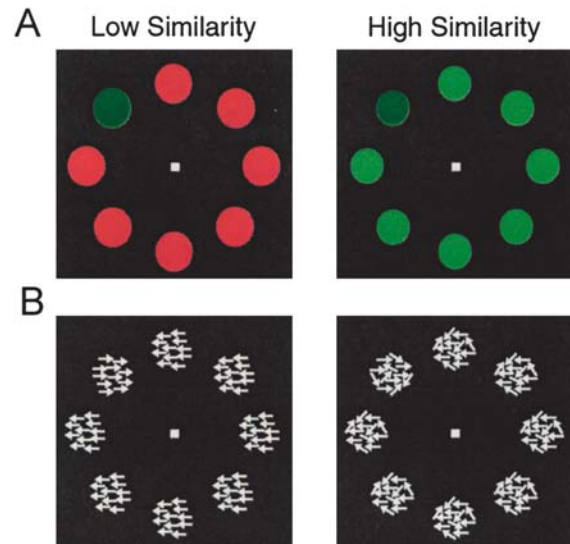


Fig. 1A, B Visual search displays. Each trial began with the presentation of a fixation point. After fixation for a variable interval an eight element circular search array appeared. **A** Color search under Low Similarity (*left*) and High Similarity (*right*). The stimuli were equiluminant, and target-distractor discriminability was manipulated by changing the chromaticity of the distractors. **B** Motion search under Low Similarity (*left*) and High Similarity (*right*). Each stimulus was a circular aperture of randomly positioned dots. The direction of motion was either left or right, with the target moving in the direction opposite to that of the distractors. Target-distractor discriminability was manipulated by changing the proportion of dots moving coherently in both the target and distractor apertures

Materials and methods

Subjects and surgery

Data were collected from four macaque monkeys (F, L, M, O), *Macaca mulatta* and *M. 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. 1995).

Behavioral training

Using operant conditioning with positive reinforcement, the monkeys were trained to perform a singleton visual search task 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 (Fig. 1A, B). The monkeys were rewarded for making a saccade to the target within 1000 ms after the search array was presented and fixating the target for at least 400 ms. For three monkeys (L, M, O), catch trials in which target was absent and only distractors were shown were randomly interleaved in 30–40% of trials. In these trials, the monkeys had to keep fixating the central spot for 1500 ms to obtain the reward. For motion search, each stimulus was a circular aperture of randomly positioned dots, a proportion of which translated coherently in a specified direction while the remaining dots were replotted at random locations every three video frames (50 ms). The stochastic motion stimulus corresponds to that used in

earlier studies (Britten et al. 1992; Kim and Shadlen 1999; Horwitz and Newsome 1999; Sato et al. 2001). The direction of motion was either left or right, and the direction of motion of the target and distractors remained the same during each recording session and varied pseudorandomly across sessions. For color search, stimuli were scaled from 0.6° of visual angle at 6° eccentricity to 1° at 10° eccentricity. For motion search, apertures were scaled from 1.5° at 6° eccentricity to 2.5° at 10° eccentricity.

The similarity of the distractors to the target was manipulated. The most efficient search arrays will be referred to as *Low Similarity* and the less efficient as *High Similarity*. Low Similarity and High Similarity trials were randomly interleaved. In color search, the target was green and the distractors were changed from red to yellow-green (Fig. 1A) (e.g., Nagy and Sanchez 1990; D'Zmura 1991). For one monkey (F), the green was CIE (Comission Internationale de l'Eclairage) $x=283$, $y=612$, red was CIE $x=655$, $y=327$, and yellow-green was CIE $x=363$, $y=552$, all having a luminance of 11.1 cd/m². For the other three monkeys, the green was CIE $x=281$, $y=609$, red was CIE $x=632$, $y=338$, and yellow-green was CIE $x=375$, $y=538$ with a luminance of 13.4 cd/m². 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% (Fig. 1B). Although the direction of motion of the target stayed the same, the target was not identical between the High Similarity condition and the Low Similarity condition for motion search. This was inevitable for the purpose of our experiment. The target and distractors must have the same coherence, since a motion stimulus with 50% coherence will pop-out among motion stimuli with 100% coherence or vice versa. Target-distractor similarity was adjusted so that the mean reaction time was at least 30 ms larger in the High Similarity condition.

To avoid the effects of extensive training in searching for a particular target among distractors (Bichot et al. 1996), monkeys were exposed to trials with complementary arrays sufficiently often that they shifted gaze to the singleton oddball of any search array.

Monkeys were also trained on the memory-guided saccade task to distinguish visual from movement activity for cell classification (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 fixation spot for an interval of random duration ranging from 400 to 1000 ms. When the fixation spot disappeared, the monkeys were rewarded for making a saccade to the remembered location of the target. Once gaze shifted, the target reappeared to provide feedback and a fixation target for the monkeys. Neurons with visual responses were analyzed for this study.

Four monkeys (F, L, M, O) were tested with color search task, and three monkeys (M, L, O) were tested with the motion search task.

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 win-

dow discriminator (Plexon). FEF recordings were done in the rostral bank of the arcuate sulcus, which was confirmed with the magnetic resonance imaging.

Measurements of neural activity to evaluate the hypothesis were derived from spike density functions. The spike density function was generated by convolving action potentials with a function that resembled a postsynaptic potential: $\text{Activation}(t) = (1 - \exp(-t/\tau_g))(\exp(-t/\tau_d))$. 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 rationale for this approach, which has been described previously (Hanes and Schall 1996; Thompson et al. 1996), was to derive physiologically plausible spike density functions.

The spike density functions obtained in High Similarity search trials and Low Similarity search trials were averaged over a specified interval that was determined for each neuron according to the following criteria. The measurement interval started at the instant the neuron discriminated the target from distractors in Low Similarity search trials. This time was chosen to exclude the period of the initial neural response that is the same whether the target or a distractor is in the receptive field. In other words, activity in the period before the neuron discriminated the target from distractors was not measured. The time when the neuron discriminated the target from the distractors was determined based on methods from signal detection theory. Receiver operating characteristic curves were calculated from the distributions of activity obtained when the target and when distractors fell in the receptive field at successive times following search array presentation as described previously (Thompson et al. 1996; Sato et al. 2001). 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 the immediately following 15 ms.

The end of the measurement interval depended on the latency of the saccades. Because the hypothesis was evaluated based entirely on activation before saccade initiation, spikes that occurred after saccade initiation were not included in the spike density functions that contributed to the analysis. To ensure reliable measurements of discharge rate, the average spike density function was terminated when fewer than five trials contributed. This means that the end of the analysis interval was restricted by the saccade latencies of Low Similarity rather than High Similarity search, because the reaction times of the last five trials in Low Similarity search were shorter than those in High Similarity search. In pilot testing, other intervals within this range were tested; the conclusions do not depend on the precise interval of analysis as long as it includes the period after target selection and before saccade initiation.

Results

Behavioral data

The interpretation of the electrophysiological data requires that the manipulation of target-distractor similarity affected search efficiency. The mean reaction times for the four monkeys in High Similarity search trials and Low Similarity search trials are shown in Table 1. For every

Table 1 Mean (\pm SD) reaction times (ms) in Low Similarity and High Similarity search with difference of means and results of *t*-test

Monkey	Search	Low similarity	High similarity	Difference of means	Statistical test
F	Motion	177.6 \pm 46.2	218.7 \pm 81.0	41.1	$p < 0.001$
M	Motion	209.1 \pm 33.7	255.1 \pm 76.5	46.0	$p < 0.001$
	Color	188.2 \pm 25.15	331.8 \pm 98.8	143.6	$p < 0.001$
L	Motion	237.8 \pm 29.0	307.6 \pm 100.0	69.8	$p < 0.001$
	Color	190.0 \pm 17.4	260.4 \pm 64.9	70.4	$p < 0.001$
O	Motion	204.9 \pm 40.3	256.7 \pm 78.6	51.8	$p < 0.001$
	Color	180.2 \pm 23.7	257.9 \pm 63.6	77.7	$p < 0.001$

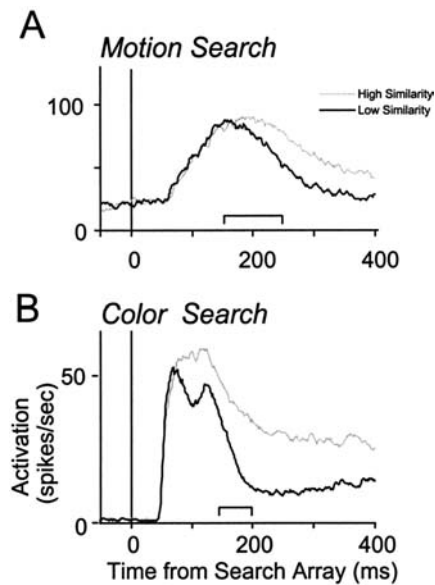


Fig. 2A, B Neural activity during interleaved trials with no target and only distractors from High Similarity search (*gray*) and from Low Similarity search (*black*). **A** Neuron recorded during motion search. Low Similarity search was for an aperture of dots moving uniformly in one direction among apertures of dots moving uniformly in the opposite direction. High Similarity search was for an aperture of dots moving in one direction embedded in randomly moving dots among apertures of dots moving in the opposite direction embedded in similarly randomly moving dots. **B** Neuron recorded during color search. Low Similarity search was for a green among red stimuli. High Similarity search was for a green among yellow-green stimuli. *Bracket* indicates the interval in which activation was measured extending from target discrimination time determined in target-present trials to the initiation time of the fifth longest saccade latency during Low Similarity search trials

monkey reaction times were significantly longer in High Similarity search trials than in Low Similarity search trials.

Neural activity when the target is absent

We recorded 117 visually responsive neurons, of which 51 were recorded with target-absent catch trials. Ninety-eight (84%) of these neurons reliably discriminated the target from distractors and were included in the present analysis (Monkey F, color 54, motion 0; Monkey M, color 8, motion 14; Monkey L, color 2, motion 7; Monkey O, color 4, motion 9). Among them, data were collected during target-absent trials for 43 neurons from three monkeys (Monkey M, color 8, motion 14; Monkey L, color 2, motion 6; Monkey O, color 4, motion 9). The results from the monkeys were indistinguishable, so the data are combined in the following analyses.

To test the hypothesis that FEF visual activity integrates visual information with a target template we determined whether target-distractor similarity influenced neural activity even if the target was not present in the display. Note that in these randomly interleaved trials the

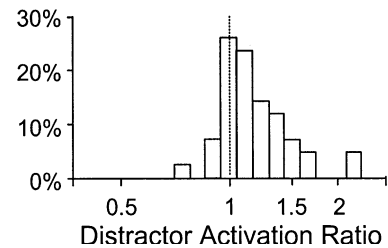


Fig. 3 Ratios of activation to High Similarity distractors as compared to Low Similarity distractors in target-absent trials for each neuron. Axes are log-scaled

monkeys were rewarded for maintaining fixation on the central spot, so the behavior was the same for High Similarity and Low Similarity trials. The pattern of activation of a visually responsive FEF neuron during motion search is shown in Fig. 2A. This neuron responded to a single flashed visual target with sustained activity during the delay period but did not show increased activity before saccade initiation; this identifies the neuron as visually responsive with no saccade-related modulation (data not shown) (Bruce and Goldberg 1985; Hanes and Schall 1996). This neuron exhibited higher activation when the distractors were similar to the target than when they were dissimilar to the target, even though the target was not present in the display. To quantify this difference, we measured the discharge rate during the interval starting at the time this neuron selected the target and ending at the time of saccade initiation in target-present trials. The identical interval of analysis was also used for the target-present trials (see below). The mean \pm SE of the activation of this neuron to the distractors was 86.1 ± 2.45 spikes/s in High Similarity search trials and 74.7 ± 2.83 spikes/s in Low Similarity search trials. The ratio of these mean values was 1.15, and the distributions were significantly different ($t_{149}=3.04$, $p<0.01$).

The activation of a different neuron recorded during color singleton search is also shown (Fig. 2B). For this neuron too, the activation when only High Similarity distractors were presented was significantly greater than that for Low Similarity distractors (37.7 ± 1.31 spikes/s, 16.5 ± 1.23 spikes/s respectively, ratio = 2.28, $t_{399}=11.5$, $p<0.001$).

The pattern observed in these neurons was present across the population of 43 neurons sampled. For the statistical analysis of the population data, the log of the ratios was used. However, the means and the confidence intervals were converted back so that the values could be more easily evaluated. The activation for the High Similarity distractors was significantly greater than that for Low Similarity distractors for the 29 neurons recorded during motion search (geometric mean ratio = 1.13 was significantly greater than 1, confidence interval = [1.04–1.22], $t_{28}=3.16$, $p<0.01$), for the 14 neurons recorded during color search (mean ratio = 1.26, confidence interval = [1.10–1.45], $t_{13}=3.7$, $p<0.01$), and for the combined data of 43 neurons (mean ratio = 1.17, confidence interval = [1.09–1.25], $t_{42}=4.69$, $p<0.001$).

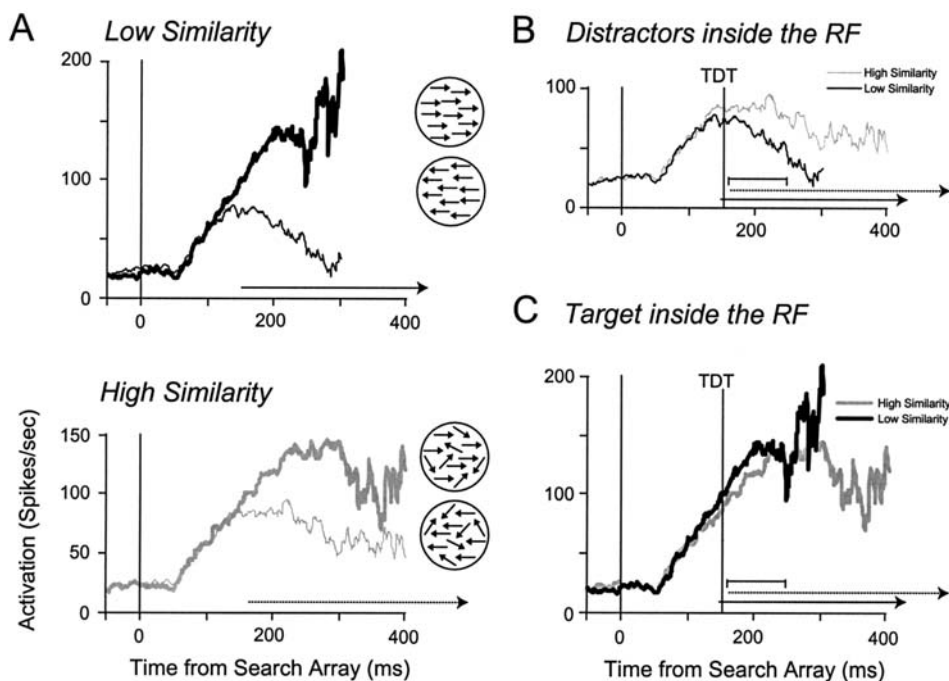


Fig. 4A–C Effect of target-distractor similarity on FEF visual activity in target-present trials. **A** Activity of an FEF visual neuron shown in Fig. 2A in target-present trials during Low Similarity motion search (*top*) and High Similarity motion search (*bottom*). Plots show the average discharge rate when the target fell in the neuron's receptive field (RF) (*thick line*) and when only distractors fell in the neuron's receptive field (*thin line*). Arrows indicate range

of saccade latencies. **B** Comparison of distractor-evoked activity in high (*gray*) and low (*black*) similarity search. *Solid arrow* indicates range of saccade latencies for Low Similarity search trials; *dashed arrow* indicates range of saccade latencies for High Similarity search trials. *Bracket* indicates the interval in which activation was measured. **C** Comparison of target-evoked activity in high (*gray*) and low (*black*) similarity search

(Fig. 3). Thus, the activation for High Similarity distractors and that for Low Similarity distractors was different even when no target was present in the display and no saccade was produced.

Neural activation when the target was present

Target absent data cannot be interpreted without knowing how the neurons were modulated by target-distractor similarity when the target is present. This section presents these control data, which replicate and extend previous reports (Bichot et al. 2001).

Figure 4 shows the activity of the neuron shown in Fig. 2A when the target was present. In both the High Similarity search and the Low Similarity search trials, the initial activity did not distinguish whether the target or the distractors were in the receptive field, but the later phase of activity discriminated the target from the distractors before the saccade (Fig. 4A).

This neuron exhibited clearly higher postselection activation for the distractor in interleaved High Similarity versus Low Similarity search trials (Fig. 4B). On the other hand, the activation for the target was slightly lower in High Similarity as compared to Low Similarity search trials (Fig. 4C). We measured the neural activation during the interval after target selection (TDT) and before saccade initiation, the same interval that was used for

target-absent trials. The activation of this neuron to the distractors was 85.2 ± 4.26 spikes/s in High Similarity search trials and 63.9 ± 2.87 spikes/s in Low Similarity search trials. The ratio of these mean values was 1.33 and the distributions were significantly different ($t_{111}=3.40$, $p<0.001$). The activation of this neuron when the target fell in the receptive field was 120.7 ± 4.09 spikes/s in High Similarity search trials and 129.4 ± 5.46 spikes/s in Low Similarity search trials. The activation was slightly lower in High Similarity search trials, with a ratio of the mean values of 0.93, although the distributions of activation were not significantly different ($t_{111}=0.82$, $p>0.05$).

The pattern of modulation observed in this neuron was consistent across the population of 98 neurons. The distractor activation was significantly higher in High Similarity than in Low Similarity search (data from motion search—mean ratio = 1.26, confidence interval = [1.15–1.38], $t_{29}=5.04$, $p<0.001$, data from color search—mean ratio = 1.43, confidence interval = [1.31–1.56], $t_{67}=8.21$, $p<0.001$; combined data—mean ratio = 1.37, confidence interval = [1.28–1.47], $t_{97}=9.45$, $p<0.001$). In contrast, the activation for the target during High Similarity search was significantly less than that during Low Similarity search (data from motion search—mean ratio = 0.87, confidence interval = [0.82–0.93], $t_{29}=4.67$, $p<0.001$; data from color search—mean ratio = 0.73, confidence interval = [0.68–0.78], $t_{67}=9.44$, $p<0.001$; combined data—mean ratio = 0.77, confidence interval =

[0.73–0.81], $t_{97}=10$, $p<0.001$). Thus, across the population of neurons in this sample, the neural response to distractors after target selection was larger and that to the target was smaller if the distractors were similar to the target.

Discussion

The effect of target-distractor similarity on search efficiency has been demonstrated many times (Treisman and Gormican 1988; Wolfe et al. 1989; Duncan and Humphreys 1989; Findlay 1997). It has also been shown that the effect of target-distractor similarity does not require the presence of the target in the display (Pashler 1987). Previously, we reported that the neural selection of the target relative to distractors is weaker when the distractors resemble the target (Bichot and Schall 1999b; Bichot et al. 2001). The finding was replicated with additional information that this occurs because the neural activation for the distractor is greater and that for the target is lesser in High as compared to Low Similarity search.

The goal of the present study was to determine for the first time whether the effect of target-distractor similarity on visual selection in FEF requires the presence of the target in the display. We found that the effect of target-distractor similarity on the neural activity for the distractors persisted even in trials in which no target but only distractors were presented. An influence of target-distractor similarity when no target is visible is consistent with the hypothesis that a template of the target influenced the neural selection process in FEF.

Effect of target-distractor similarity on visual activity in FEF

The magnitude of the activation when the target fell in the receptive field varied according to target-distractor similarity, being less if the target was less discriminable from the distractors. In contrast, the level of activation associated with distractors was higher if the distractor resembled the target. The lower target activation and the higher distractor activation in High Similarity search result in lower reliability of FEF visual activity in signaling the target location (Bichot et al. 2001; see also Bichot and Schall 1999b). Studies of prefrontal cortex including FEF (Kim and Shadlen 1999; Constantinidis et al. 2001), parietal cortex (Shadlen and Newsome 2001) and superior colliculus (Horwitz and Newsome 1999) in monkeys performing discrimination tasks have reported differential activity according to the discriminability of the stimulus. Our results are consistent with these findings.

If FEF activity integrates visual processing and the knowledge of the target, the effect of target-distractor similarity should persist even when the target is not present in the display and thus no competitive stimulus

interactions between the target and distractors. To test this hypothesis, we presented randomly interleaved trials with only eight identical distractors and no target in the display. This type of manipulation has been used to distinguish stimulus interaction from attention effects in a study of inferior temporal cortex (Chelazzi et al. 1998). In these trials, monkeys were reinforced for maintaining fixation on the central spot, so the overt behavior is the same between Low Similarity and High Similarity trials. We found that the difference in distractor activation persisted even when the target was not in the display. This finding is consistent with a previous work on superior colliculus by Basso and Wurtz (1998), who demonstrated that the neural activity decreased as the target uncertainty increased, in that High Similarity distractors have 'high target uncertainty' whereas Low Similarity distractors have 'low target uncertainty'.

An effect of stimulus discriminability and the presence of the target has been reported in the studies of selective attention in extrastriate visual areas (Spitzer et al. 1988; Reynolds et al. 2000; Chelazzi et al. 1998, 2001). However, it is important to note that, unlike the neurons in these studies, neurons in FEF are typically not intrinsically selective for visual features (Mohler et al. 1973; see also Schall et al. 1995). Although some FEF visual neurons can become selective after monkeys are trained exclusively on search arrays with targets of one and distractors of another color (Bichot et al. 1996), we ensured that the monkeys used in this experiment received experience with both complements of the search stimuli. As a result, none of the monkeys exhibited a pronounced response bias for one of the search arrays. Therefore, the modulation reported here represents a different phenomenon.

It is also critical to recognize that the similarity of the distractors to the target was not intrinsic to the distractors. The visual relationship between the distractors and the target is arbitrary. If the features of the target had been different, the distractors that had been defined as High Similarity could have been Low Similarity. In other words, for example, a green target among the high noise randomly moving dot distractors would be located efficiently. Moreover, the results were not different between color search and motion search, even though in color search only the distractor changed whereas in motion search the coherence of moving dots was changed in both distractors and target. Thus, neither the nature of the display nor the overt behavior of the monkeys can explain the difference in the activation to the different kinds of distractors, so by a process of elimination it must be a consequence of some kind of endogenous process.

Implications for the role of FEF in search

The neurophysiological evidence about FEF visual activity in relation to covert as opposed to overt orienting has not been clear. The initial studies reported that visual responses in FEF are not enhanced when monkeys

respond to an eccentric stimulus without shifting gaze (Goldberg and Bushnell 1981), suggesting that the activity corresponds only to saccade preparation. In contrast, we have demonstrated that the target selection by FEF neurons can be dissociated from saccade execution (Thompson et al. 1997; Murthy et al. 2001; Sato and Schall 2003), and proposed that it corresponds to the allocation of attention (see also Kodaka et al. 1997; Moore and Fallah 2001). Our new finding does not necessarily distinguish these two possibilities. However, the present results do indicate that some kind of representation of the target that persists across trials influenced the activity of neurons in FEF during visual search, whether FEF visual activity corresponds to the allocation of attention or saccade preparation or both.

Although the precise role of target template and memory in search is not entirely clear (e.g., Chun and Jiang 1998; Horowitz and Wolfe 1998; Woodman et al. 2001), psychological studies have suggested that distractors that are similar to the target template affect search efficiency even when the target was not physically present in the display (Duncan and Humphreys 1989; Bundesen 1990; Desimone and Duncan 1995). For example, Pashler (1987) had subjects search for either of two targets (E or C). Distractors similar to one target (G, which is similar to C) slowed down detection of either that target (C) or the other target (E) to a similar degree. Taken together, our new finding may be a neural correlate of the effect of target template on behavior. This provides further evidence that FEF neurons integrate visual information and knowledge of the target to identify the location of the target.

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