

Dissociation of Visual Discrimination From Saccade Programming in Macaque Frontal Eye Field

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Thompson, Kirk G., Narcisse P. Bichot, and Jeffrey D. Schall. Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *J. Neurophysiol.* 77: 1046–1050, 1997. To determine whether visual discrimination in macaque frontal eye field (FEF) is contingent on saccade planning, unit activity was recorded in two monkeys during blocked go and no-go visual search trials. The eye movements made by monkeys after correct no-go trials, in addition to an attenuation of the visual responses in no-go trials compared with go trials, indicated that covert saccade planning was effectively discouraged. During no-go search trials, the activity of the majority of neurons evolved to signal the location of the oddball stimulus. The degree and time course of the stimulus discrimination process observed in no-go trials was not different from that observed in go trials. We conclude that the discrimination of a salient visual stimulus reflected by FEF neurons is not contingent on saccade production but rather may reflect the outcome of an automatic visual selection process.

INTRODUCTION

The frontal eye field (FEF), located in the rostral bank of the arcuate sulcus, plays a key role in the generation of purposive visually guided saccades (Schall 1991). One type of neuron within FEF, termed a visuomovement neuron, begins to discharge after presentation of a visual stimulus and remains active until a saccade is made into its movement field (Bruce and Goldberg 1985; Schall 1991; Schall et al. 1995a; Thompson et al. 1996). We have shown that during a popout visual search task, the initial visually evoked activity of FEF neurons is the same regardless of whether the oddball or only distractors of the search array fall in the receptive field (Schall and Hanes 1993; Schall et al. 1995a; Thompson et al. 1996; but see Bichot et al. 1996). The activity of these neurons subsequently evolves to signal the location of the oddball target before the saccade. However, the time of target discrimination by FEF visuomovement neurons did not predict the time of saccade initiation (Thompson et al. 1996). To further investigate the dissociation of target discrimination from saccade programming, we tested the hypothesis that saccade programming does not affect the visual discrimination process evident in the activation pattern of FEF neurons.

In earlier work we reported that oddball discrimination occurred even when the monkey was rewarded for not generating a saccade to the oddball (Schall et al. 1995a). However, these data were limited in several respects. First, a limited number of cells was tested. Second, the monkey often made a saccade to the location of the oddball after the end of the trial. Third, analyses that compared the time course and magnitude of discrimination had not yet been developed. We have therefore readdressed this question by

obtaining more data from the same monkey and additional data from another monkey in a no-go visual search condition designed to discourage saccade planning.

METHODS

Data were collected from two *Macaca mulatta*. 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. Detailed descriptions of the surgical procedures and behavioral training have appeared previously (Schall et al. 1995a).

With the use of operant conditioning with positive reinforcement, the monkeys were trained to perform a series of tasks in which reward was contingent on either executing (go trials) or withholding (no-go trials) a saccade to a peripheral visual stimulus presented on a video monitor. The target for the saccade was presented alone (detection trials) or with distractors (search trials). The different task conditions were used to determine cell type, map the spatial extent of the response field, and determine the effects of saccade planning and execution on cell responses.

For this study the activation pattern of FEF neurons during go search and no-go search was compared. Each trial began when the monkey fixated a central white spot. In go search trials, after a specified interval (400–500 ms) the oddball target was presented at one of eight possible isoeccentric target locations around the fixation spot, with distractor stimuli presented at the other seven locations. Simultaneously, the central fixation spot changed color to cyan, which signaled the monkey to make a saccade to the oddball target. In no-go search trials, 500 ms before the presentation of the same search display the central fixation spot changed color to magenta, which signaled the monkey to withhold saccades and maintain fixation on the central fixation spot. The monkey was rewarded after maintaining fixation on the central spot for 600–1,000 ms after the presentation of the search array. Each trial condition was presented in separate blocks of trials so the monkey could easily predict what type of trial would be presented next. The location of the target (or oddball) stimulus was presented in pseudorandom order within each block. The oddball search stimulus was distinguished from the distractors by color (red vs. green); the stimuli were adjusted to be isoluminant. In all trial conditions the stimuli were removed at the end of the trial when the reward was given.

Methods of data collection have been described (Schall et al. 1995a; Thompson et al. 1996). The data analysis methods and the motivation behind them have been described previously (Hanes et al. 1995; Schall et al. 1995a; Thompson et al. 1996). Visual response latencies were determined with the use of a Poisson spike train analysis (Hanes et al. 1995; Thompson et al. 1996). To characterize the time course and magnitude of discrimination, receiver operating characteristic (ROC) curves were calculated from the two distributions of activity obtained when the oddball and when the distractors fell in the receptive field at incrementing time intervals following the time of search array presentation (detailed

in Thompson et al. 1996). For our purposes, the area under the ROC curve provides a reliable measure of the separation of neural activity into two distributions. A best-fit cumulative Weibull function was used to describe the growth of the ROC areas with time. The best-fit Weibull curves very adequately represented the change in ROC area with time as judged by the r^2 values obtained from each cell (mean $r^2 = 0.88$, range 0.64–0.98). ROC areas ranged from ~ 0.5 to 1.0 and in this report will be referred to as the discrimination index. A discrimination index of 0.75 was the criterion level for a cell to reliably indicate whether the oddball stimulus or a distractor was in the response field.

RESULTS

Sufficient data to evaluate the hypothesis that saccade planning does not affect the visual discrimination process were collected from 22 visually responsive neurons from the FEF of two monkeys. All of these neurons had a maintained discharge until the eye movement into their response field. The histological reconstruction of recording tracks in one monkey has been described previously (Thompson et al. 1996). Physiological recordings are continuing in the other monkey.

Gaze behavior

The no-go paradigm was designed to discourage monkeys from programming saccades to the oddball stimulus in the search array. It is possible, however, that while maintaining fixation on the central spot monkeys may have covertly planned a saccade to the oddball target. To test for covert planning, we monitored the endpoint of the first saccade made in a 500-ms time window after each no-go trial was successfully completed (Fig. 1). The search array was re-

moved at the end of the trial; therefore any saccade to the target after the trial must have been to a remembered location. The 500-ms time window was selected because during go search trials, nearly all saccades were initiated within 500 ms of the trigger signal. The mean reaction time during go search trials was 198 ms. The gaze behavior observed following successful blocks of no-go trials was characterized by determining the percentages of trials that were followed by a gaze shift to the location where the oddball had been. During recording from only 2 of 22 cells, gaze shifted to the location that had been occupied by the oddball after $>15\%$ of the rewarded trials, and for no cells did gaze shift to the location that had been occupied by the oddball after $>50\%$ of the trials (see Fig. 3C).

Visual enhancement

The initial visual response of many FEF neurons to a flashed stimulus is enhanced if the stimulus is the target for a saccade (Goldberg and Bushnell 1981; Wurtz and Mohler 1976). The observation that the initial visual responses during go search trials were greater than those during no-go search trials would be further evidence that saccades were not being programmed during no-go search trials. To assess the visual response enhancement associated with saccade production, we divided the average discharge rate, based on spike count, in the initial 30 ms of response of each cell during go search trials by the same measure obtained during no-go search trials. The resulting ratio was termed the enhancement index. The cell shown in Fig. 2 had an enhancement index of 1.53. The distribution of the enhancement indexes was significantly >1.0 (1.43 ± 0.13 , mean \pm SE; binomial test, $P = 0.01$), reflecting an overall saccade-related enhancement. Thirty-eight percent of the cells had an enhancement index >1.5 . We also determined whether the initial visual response was different during go search trials compared with no-go search trials for each cell with the use of a Mann-Whitney U test. By this measure, 38% of the cells had significantly higher activity during go search and none had higher activity during no-go search. The percentage of cells in this sample that show visual enhancement is similar to that found in previous reports (Goldberg and Bushnell 1981).

Oddball discrimination

A majority (82%) of the visually responsive FEF cells we recorded exhibited activity that reliably reflected oddball discrimination during no-go trials, that is, the discrimination index exceeded 0.75. For all cells that discriminated the oddball in blocks of go or no-go visual search trials, the response when the oddball fell in the response field was greater than the response when the distractors fell in the response field. Figure 2 shows an example of the activity of such a cell during go and no-go search trials. The corresponding discrimination indexes as a function of time are also plotted. In both go and no-go search trials, the typical salient stimulus discrimination process is observed (Thompson et al. 1996). The initial visual response did not discriminate the oddball from distractors in its response field. In time, the activity evolved to discriminate the location of the

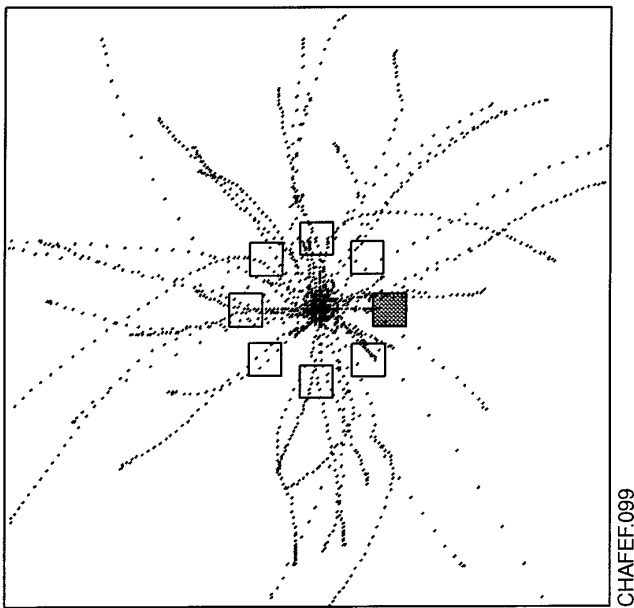


FIG. 1. Saccade behavior following rewarded no-go visual search trials. Eye position traces (250 Hz) are shown illustrating the 1st saccade after the reward during the collection of the physiological data of a frontal eye field (FEF) visuomovement cell. Eye movements were monitored in a time window of 500 ms after the end of each trial. The eccentricity of the stimuli was 7° . The oddball is shown at the right horizontal position and the eye position traces were rotated accordingly for display. Only 1 saccade of 67 was directed to location that had been occupied by the oddball.

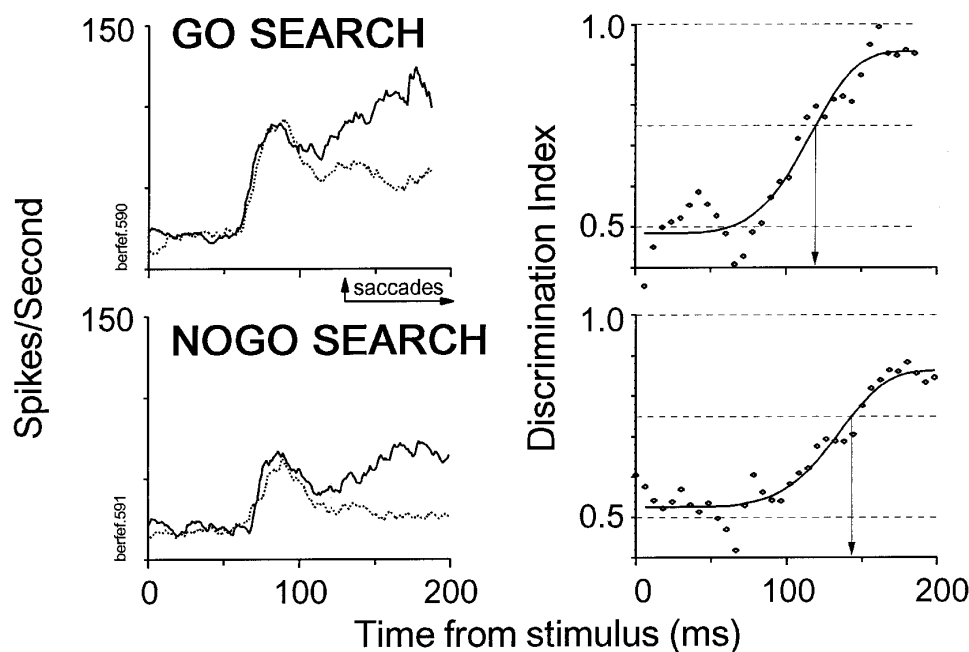


FIG. 2. Neural activity of an FEF cell that discriminated oddball location during a block of no-go visual search trials. *Left*: average spike density functions observed when the oddball fell in the cell's receptive field (—) and when only distractors fell in its receptive field (· · ·) during a block of go visual search trials (*top*) and a block of no-go visual search trials (*bottom*). *Right*: discrimination index as a function of time. The best-fit Weibull function is drawn through the points. Vertical arrows: time at which the function reached a threshold value of 0.75.

oddball. The discrimination index reached 0.75 at 120 ms during go search and at 148 ms during no-go search. The maximum level of discrimination reached was 0.93 during go search and 0.83 during no-go search.

The activity of an equal number of cells reliably discriminated whether the oddball or a distractor was in their response fields during blocks of go and no-go search trials. The activity of 14 cells reached the 0.75 level during both go and no-go search. The activity of four cells reached a discrimination index of 0.75 only during go search and the activity of an additional four cells reached this level only during no-go search. To investigate possible differences in the time course of discrimination, we compared the time that the discrimination indexes reached 0.75 for activity collected during go search trials with the time that the discrimination indexes reached 0.75 for activity collected during no-go search trials for the cells that reached this level of discrimination. A scatterplot of this comparison is shown in Fig. 3A. Except for one outlier (3.3 SD), the points were distributed around the diagonal line that represents equal times in the go and no-go conditions. The mean no-go discrimination time of 133.4 ± 8.9 (SE) ms was not significantly different from the mean go discrimination time of 134.4 ± 8.9 (SE) ms (paired t -test: $t_{26} = 0.19$). This finding is particularly noteworthy because the total interval analyzed in no-go search trials was much longer than that analyzed in go search, because the saccade latency in go search imposed a deadline for when the discrimination could be measured.

To investigate differences in the maximum level of discrimination reached during go search and no-go search, we compared the maximum value parameters of the best-fit Weibull functions obtained from the activity during the two conditions for all cells (Fig. 3B). There was no systematic tendency for cells to achieve a lower degree of discrimination in no-go trials compared with go trials. The average no-go maximum discrimination index of 0.83 ± 0.03 (SE) was not significantly different from the average go maximum discrimination index of 0.84 ± 0.02 (SE) (paired t -test:

$t_{42} = 0.53$). The lack of a relationship between saccade programming and magnitude of oddball discrimination by FEF neurons is further highlighted by a plot of the maximum discrimination index achieved during no-go search trials against the percentage of saccades made to the location of the oddball after these trials for each cell that contributed to this report (Fig. 3C). There was no relationship between behavioral evidence for saccade programming and the level of oddball discrimination.

DISCUSSION

In a previous report we have shown that the time of discrimination of a visual search target reflected by a majority of visually responsive FEF neurons does not predict the time of saccade initiation to the oddball (Thompson et al. 1996). In the current study, we further tested the dissociation between oddball discrimination in FEF and saccade execution. Central to this study was the ability to discourage saccade production and therefore saccade programming. Saccade programming was successfully inhibited as evidenced by the lack of saccades to the location of the oddball of the search array after the end of the trial. Further evidence of the lack of saccade planning was the attenuation of the initial visual responses of FEF cells during the no-go search task relative to the responses during the go search task, similar to what has been observed when single targets were presented (Goldberg and Bushnell 1981; Schall et al. 1995a; Wurtz and Mohler 1976). Even though saccades were not made to the oddball of the search array during the no-go search task, the time course and degree of oddball discrimination during the no-go and the go search tasks were not different. Thus FEF neurons signal the location of a salient stimulus even in the absence of eye movements.

Studies have shown that FEF is connected with a large number of visual cortical areas and is an important point of convergence for the dorsal and ventral visual processing streams (Schall et al. 1995b). As such, FEF does not re-

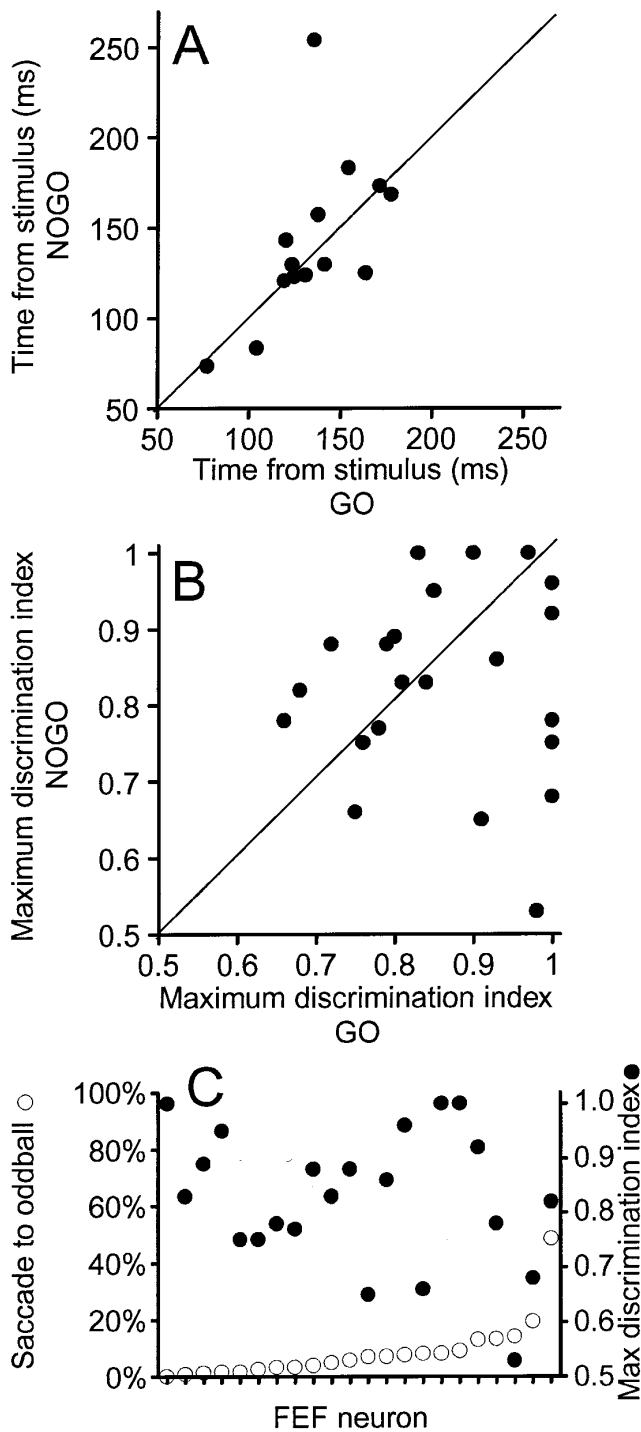


FIG. 3. Comparisons of oddball discrimination and saccade production. A: scatterplot comparing the time course of discrimination during go and no-go search trials. Each point represents the time of discrimination during no-go trials as a function of the time of discrimination during go search trials for 14 cells for which the discrimination index reached the 0.75 threshold in both conditions. B: scatterplot comparing the maximum level of discrimination reached during go and no-go visual search as determined by the asymptote of the best-fit Weibull function. Diagonal lines in A and B: 1-to-1 relationship. C: comparison of gaze behavior and the maximum level of discrimination reached in blocks of no-go visual search trials. For each cell along the abscissa, the open circles plot the percentage of trials following which gaze shifted to the location that had been occupied by the oddball after the reward was given. The cells are ordered from left to right with increasing percentages of saccades to the oddball. Black circles: maximum level of discrimination observed in no-go search trials for that cell.

spond selectively for stimulus features such as color or orientation. The discrimination process we observed in FEF may reflect the outcome of an automatic process that selects salient stimuli by combining multiple features across the visual scene. Thus one role of FEF may be that it is a visual saliency map indicating the location of possible targets for visually guided behavior. The activity of FEF visually responsive neurons likely reflects processing that occurred earlier in the visual pathways. The effects of visual salience on the activity of visually related neurons have been observed as early as V1 (Knierim and Van Essen 1992; Lamme 1995) as well as in posterior parietal cortex (Constantinidis and Steinmetz 1995).

It is important to note that in this study we trained the monkeys to discriminate and shift gaze to the oddball stimulus, in order to obtain data during blocks of go search trials. It is possible that had these monkeys not been trained in the go search task, these cells would not have discriminated the oddball. In fact, we have recently shown that experience can affect the initial visual responses of FEF cells (Bichot et al. 1996). Further work is needed to determine what effect training may have on the discrimination process.

These findings highlight the flexibility of sensorimotor integration. The identification of potential targets for saccades on the basis of salience is a clear benefit in a complex world. This ability would be a disadvantage, however, if the identification of salient stimuli automatically caused a shift of gaze.

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