Dynamic Dissociation of Visual Selection From Saccade Programming in Frontal Eye Field

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Murthy, Aditya, Kirk G. Thompson, and Jeffrey D. Schall. Dynamic dissociation of visual selection from saccade programming in frontal eye field. *J Neurophysiol* 86: 2634–2637, 2001. Previous studies of visually responsive neurons in the frontal eye fields have identified a selection process preceding saccades during visual search. The goal of this experiment was to determine whether the selection process corresponds to the selection of a conspicuous stimulus or to preparation of the next saccade. This was accomplished with the use of a novel task, called search-step, in which the target of a singleton visual search array switches location with a distracter on random trials. The target step trials created a condition in which the same stimulus yielded saccades either toward or away from the target. Visually responsive neurons in frontal eye field selected the current location of the conspicuous target even when gaze shifted to the location of a distractor. This dissociation demonstrates that the selection process manifest in visual neurons in the frontal eye field may be an explicit interpretation of the image and not an obligatory saccade command.

INTRODUCTION

Eye movements tend to direct gaze to informative elements in the image, but the location and timing of gaze shifts are only loosely related to the properties of the image (e.g., Carpenter 1981; Hooge and Erkelens 1996). This arbitrary linkage between the production of saccades in a given image can be explained by the existence of two processing stages—a visual-selection stage that identifies potential targets and a saccade-preparation stage that produces the given movement. Signals associated with both stages of processing have been identified in different classes of neurons in the frontal eye field (FEF), a critical node in the network involved in saccade production (Schall 1997). In FEF, visual neurons appear to identify targets for saccades (e.g., Bichot and Schall 1999; Thompson et al. 1996), while movement and fixation neurons generate signals sufficient to control whether and when saccades are produced (Hanes and Schall 1996; Hanes et al. 1998).

Neural correlates of visual selection has been studied recently (e.g., Bichot and Schall 1999; Gottlieb et al. 1998; Thompson et al. 1996) using search tasks that are traditionally used for studies of visual attention. Visually responsive FEF neurons manifest target selection through the evolution of greater activation when a stimulus in the neuron's receptive field is a target relative to when a stimulus is a distractor (Bichot and Schall 1999; Schall et al. 1995; Thompson and Schall 2000; Thompson et al. 1996). Furthermore, using a GO-NOGO task, Thompson et al. (1997) showed that the selection process in response to a visual search array does not depend on the production of a saccade. However, in that study, the monkeys had been trained to make saccades to the target, so it could be argued that this selection process reflects some kind of latent saccade programming. Alternatively, the selection process may correspond to automatic covert orienting to a conspicuous stimulus (e.g., Joseph et al. 1997; Kim and Cave 1995; Theeuwes 1991, 1994). The latter possibility is consistent with the emerging view that eye movements and spatial attention are guided by common selection mechanisms that can be dissociated only under special conditions (e.g., Deubel and Schneider 1996; Hoffmann and Subramaniam 1995; Kowler et al. 1995). To evaluate the hypothesis that the visual selection process observed in FEF can be dissociated from saccade production, we trained monkeys on a novel task we call search-step. The results reveal a dissociation of visual selection from saccade production in neural activity in the FEF.

METHODS

Physiological recording techniques have been described in detail elsewhere (Schall et al. 1995). Briefly, monkeys were seated within a magnetic field to monitor eye position by means of a scleral search coil. Experiments were under computer control using Tempo/Videosync software (Reflective Computing) that displayed visual stimuli (Sony Trinitron 500-PS monitor), delivered juice reward, and sampled and stored eye position (250 Hz) and unit activity (1 kHz). All experimental procedures and care of the animals conformed to guidelines established by the National Institutes of Health and approved by the Vanderbilt Animal Care and Use Committee.

The search-step task combines a standard visual search task (with equiluminant target and distractor stimuli) with the classic double-step saccade task (Fig. 1) (e.g., Aslin and Shea 1987; Becker and Jürgens 1979; Lisberger et al. 1975). On most trials (referred to as no-step trials) monkeys were rewarded for making a saccade to a color oddball target among distractors. On the remaining trials (step trials), the target and one distractor unexpectedly swapped positions after presentation of the array. When the target stepped unpredictably from its original position to a new position, monkeys were rewarded for directing gaze to the new target location (compensated trials). However, monkeys often failed to compensate for the target step and made a saccade to the original target location (noncompensated trials). This behavior was not rewarded. The target step delay was adjusted using a staircase procedure so that, on average, monkeys produced an equal

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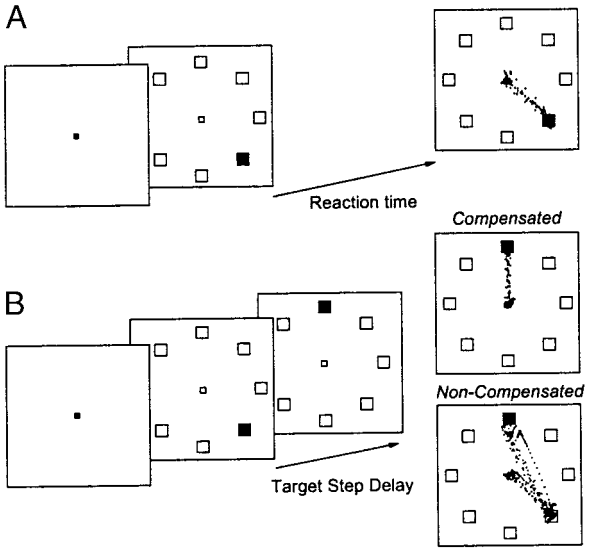

FIG. 1. Search-step task. Each trial began with the presentation of a fixation spot. After fixation for a variable interval (usually 250–750 ms) the fixation spot was removed and an 8-element circular search array with a single oddball target appeared. The target (shown in black) was distinguished from the distractors by color, usually red among green or vice versa. Right: samples of eye positions indicating the trajectory of the saccades. On no-step trials (*A*), monkeys were rewarded with juice for shifting gaze to the target. On search-step trials (*B*), the target swapped positions with a distractor after a short delay called the target-step delay, and monkeys were rewarded for shifting gaze to the new target. On search-step trials, monkeys either compensated for the target step (*top right*) or failed to compensate (*bottom right*). Noncompensated saccades were typically followed by a 2nd corrective saccade; this eye movement was not included in the present analysis.

number of compensatory and noncompensatory saccades. Noncompensated saccade trials provided data to test the dissociation of visual target selection from saccade preparation. Because these noncompensatory saccades were usually followed by corrective saccades (see Fig. 1*B*), only presaccadic spikes (i.e., before either the compensated or noncompensated saccades) were used in constructing the spike density functions. Neural activity associated with the corrective saccades will be described in a subsequent report.

RESULTS

We recorded from 55 presaccadic neurons in the FEF of two monkeys; 29 of these neurons had visual responses and formed the basis for this study. Classification was based on the pattern of activation in memory guided saccades. Visual neurons were identified as those that responded to the presentation of a flashed visual stimulus and did not exhibit a growth of activity before a saccade into their receptive field.

Figure 2 shows the responses of a typical FEF visual neuron. When tested during a memory-guided saccade task, this neuron exhibited modulation associated with presentation of the target but no modulation associated with the saccade. As shown previously (Schall et al. 1995; Thompson et al. 1996), this neuron exhibited an initial visual response that was the same when either the target or distractors fell in the receptive field. A selection process followed in which the neural representation of the distractor was reduced and the representation of the target was maintained or elevated.

To determine how this selection process relates to saccade production, we examined the activity during target-step trials when a distractor in the receptive field became the target (Fig. 2*B*). The early phase of the response during target-step trials was identical to the response elicited by a distractor during no-step trials; the early nonselective visual activity was followed by suppression. This is because the stimulus conditions were identical prior to the target step. On target-step trials in which monkeys compensated with a saccade to the final target location in the neuron's receptive field, the activation grew markedly following the target step. If the modulation was only a visual response, it should arise about 50 ms after the target step or approximately 115 ms after the search array (based on

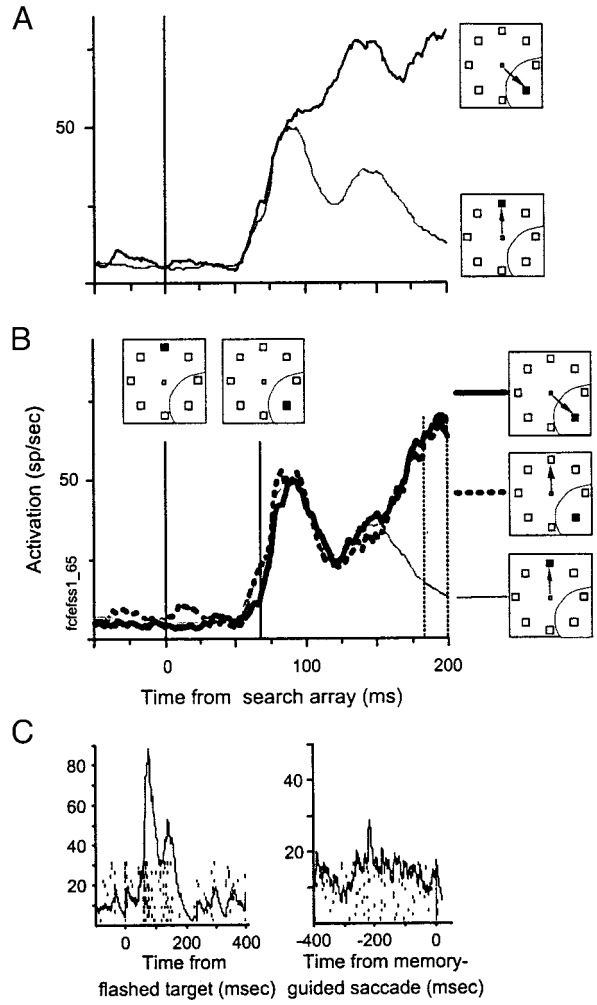

FIG. 2. Frontal eye field visual neuron. Only presaccadic spikes were used in constructing the responses. *A*: activation when the target (thick line) or distractors (thin line) fell in the receptive field (indicated by the enclosed area in the stimulus arrays). Following the initial 100 ms of activation that did not discriminate target from distractor, the activity was modulated strongly before the saccade to the target. The response to the distractor was suppressed, and the response to the target grew. *B*: averaged activity across 3 target-step delays (67 ± 17 ms) on compensated (thick solid) and noncompensated (dotted) target-step trials when the distractor in the receptive field unexpectedly became the target compared with activity on no-step trials when distractors remained in the receptive field (thin line). In both compensated and noncompensated trials, the neuron responded equally strongly to the unexpected appearance of the target in the receptive field. The fact that the activity before the mean noncompensated saccadic reaction time (the end of the plot) was indistinguishable for the search-step trials with opposing saccade directions means that the activity of this neuron could not be involved in saccade production. The quantitative analysis was performed on the activity in the interval indicated by the vertical dotted lines. *C*: activity during memory-guided saccades aligned on target flash (*left*) and saccade initiation (*right*).

the data from no-step trials in Fig. 2*A*). However, the discharge rate of the neuron became different from the distractor response around 95 ms after the target step or 160 ms after the appearance of the search array. The difference of 45 ms between the expected and observed latencies of modulation cannot be explained by visual afferent delays. Therefore the difference in activity between no-step and target-step trials shown in Fig. 2*B* is not a consequence of the stimulus in the receptive field changing color per se (i.e., a visual response) but rather is due to the stimulus achieving salience in virtue of becoming the oddball stimulus in the array.

This selection may correspond to saccade preparation, though, because the end point of the saccade coincided with the location of the target. However, on target-step trials in which monkeys failed to compensate and instead produced a saccade to the original target location outside the receptive field, the activity grew in the same manner as for compensated trials. In other words, the activity of this neuron represented accurately the new location of the target regardless of whether compensated or noncompensated saccades were produced. This is strong evidence that this selection process is distinct from immediate saccade production.

To quantify this observation across the population of visual neurons, the mean activity was measured in the 20 ms preceding the mean noncompensatory saccadic reaction time in compensated and noncompensated trials when the distractor in the receptive field became a target and in the same interval in no-step trials when the distractor remained in the receptive field. This interval was chosen to include the period of selective modulation and exclude the nonselective early visual response. The ratio of the mean activity during step trials to the mean activity during no-step trials was computed for each neuron. Only presaccadic activity from target step delays with at least three trials contributed to this analysis.

When a distractor in the receptive field became the target and monkeys compensated, the activation during the selected epoch was significantly greater than the activation when the distractors did not change (arithmetic ratio $\pm$ SE = 1.54 $\pm$ 0.09; geometric mean = 1.34, 95% confidence interval = 0.18). This difference of activation corresponds to the previously described selection process. The key result of this experiment was obtained when a distractor in the receptive field became the target but the monkeys failed to compensate and shifted gaze to the original target location. In this condition, the activation also was significantly greater than the activation when the distractors did not change (arithmetic ratio $\pm$ SE = 1.45 $\pm$ 0.09; geometric mean = 1.25, 95% confidence interval = 0.18). This indicates that a neural representation was established for the location that was not the target for the upcoming saccade.

Figure 3 plots the distribution of the magnitude of differential activity in compensated and noncompensated trials as compared with no-step trials across the population. All search-step delays are included. Indistinguishable visual activation was observed when monkeys shifted gaze to the new location of the target in compensated trials or shifted gaze to the original location of the target in noncompensated trials (paired *t*-test, $t = 1.41$, $P = 0.16$). The responses of 25 of 29 visual neurons showed the dissociation of target selection from saccade programming in at least one target-step delay.

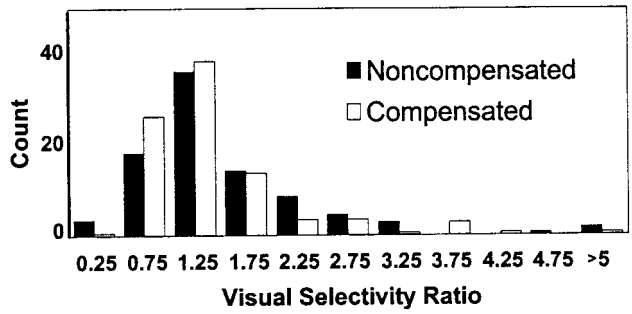

FIG. 3. The distribution of the magnitude of differential activity in compensated and noncompensated trials as compared with no-step trials across the population of visual cells.

DISCUSSION

The role of FEF in overt orienting by directing gaze is undisputed (Bruce and Goldberg 1985; Hanes et al. 1998), but the role of FEF in selecting targets for covert orienting is less agreed on. Previous single-unit studies have reported that visual responses in FEF are not enhanced when monkeys respond to an eccentric stimulus without shifting gaze (Goldberg and Bushnell 1981). This has been regarded as evidence that FEF is responsible for overt but not covert orienting. However, the manner and extent to which attention was allocated in the Goldberg and Bushnell study is not entirely clear especially given the costs associated with dissociating gaze and attention (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Kowler et al. 1995). In the Goldberg and Bushnell study, a significant fraction of interleaved trials required a response to a visual change at the fixation spot instead of the eccentric stimulus. Therefore it seems unlikely that monkeys would allocate attention exclusively to the eccentric stimulus. Moreover, the original report did not disprove that the change of the eccentric stimulus could be detected without allocating attention. Finally, the enhanced visual response occurred most commonly several hundred milliseconds before the stimulus change to which monkeys responded. Therefore it seems neither necessary that nor clear how the magnitude of the visual response could relate directly to the attentional allocation required to respond to the eccentric stimulus. Also, no explicit test or comparable human data on the allocation of attention in this condition has been presented. Early studies of the superior colliculus using the same methods drew the conclusion that it was not involved in covert orienting (Goldberg and Wurtz 1972). But subsequent studies have produced evidence for a role for the superior colliculus in covert orienting (e.g., Kustov and Robinson 1996). Therefore the detection of a change of a single eccentric stimulus in an otherwise blank display may not be a reliable diagnostic for a neural correlate of attention.

Several lines of evidence are consistent with the hypothesis that FEF contributes to covert orienting or at least representing visual salience in parallel with related brain structures such as the parietal lobe (Gottlieb et al. 1998; Steinmetz and Constantinidis 1995) and the superior colliculus (Findlay and Walker 1999) because the representation of salient stimuli guides the allocation of attention. First, previous studies of FEF have shown a dissociation between target selection and saccade generation during a pop-out search task (Thompson et al. 1996, 1997). The selection observed in visually responsive FEF neurons is consistent with the findings in the psychological

literature indicating that attention is automatically drawn to the singleton in a visual search array (Joseph et al. 1997; Kim and Cave 1995; Theeuwes 1991, 1994). Second, in conjunction visual search experiments (Bichot and Schall 1999), the strength of selection was found to vary in proportion to the number of features a distractor shared with the target. This pattern of activation of FEF neurons corresponded to the pattern of gaze shifts (Bichot and Schall 1999) and the allocation of attention by humans in such arrays (Kim and Cave 1995). Third, recent functional imaging studies have shown that the human homologue of FEF is involved in both overt and covert shifts of attention (e.g., Corbetta et al. 1998; Nobre et al. 1997). Finally, we now show that visual neurons in FEF selected conspicuous stimuli that were not the target for the immediately following saccade.

What does the selective FEF visual activity do? If, as shown by the present results, it does not dictate the end point of first saccade to the search array, all that is left is to represent the location of the new location of the salient target. The fact that monkeys commonly made a corrective saccade after a noncompensated initial saccade is clear evidence that the new target location received preferential processing on step trials. But if visual neurons in FEF could select the new target location, why did noncompensated trials happen in the first place? According to the race model that accounts for the performance (Becker and Jürgens 1979), saccades to the original target location are premature responses. The occurrence of such premature responses is further evidence for distinct sensory and response stages, and in other work, we have reported that the movement-related activity in FEF accounts for saccade production in this task (Murthy et al. 1999). The fact the monkeys commonly made a corrective saccade after the noncompensated saccade to the distractor at the old target location raises the possibility that the selection we observed could be related more to the production of the corrective saccade. The results of this study cannot refute an interpretation of the neural selection in FEF as responsible for planning the corrective saccade, but we prefer the interpretation that the activation of the visually responsive neurons in FEF corresponds to the preferential processing of the visually salient location, which corresponds to the allocation of attention, that can subsequently produce the corrective saccade.

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