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On the role of frontal eye field in guiding attention and saccades

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Abstract

The neural bases of shifting attention and directing gaze were investigated in macaque monkeys performing a singleton search that required a prosaccade, antisaccade, or no saccade cued by the shape of the singleton. In prosaccade trials, most neurons in frontal eye field selected the location of the singleton that was also the end point of the saccade. In antisaccade trials, most neurons selected the singleton followed by selection of the endpoint of the saccade. Other neurons selected only the endpoint of the saccade in antisaccade trials. When no saccade was produced, many of the first type of neuron still selected the singleton, and many but not all of both types of neurons later selected the stimulus opposite the singleton even though no saccade was produced. These patterns of activity are consistent with the hypotheses that covert shifts of attention can occur without saccade production and that FEF contributes to covert as well as overt orienting.

1. Introduction

We cannot respond to all of the photons that land on our retina, so we must select particular objects for regard. Usually, gaze shifts toward stimuli of interest, but visual perception can be enhanced at particular locations without an overt movement of the eyes through covert shifts of attention. While much progress has been made, debate continues over the mechanistic distinction between covert and overt orienting (e.g., Klein & Pontefract, 1994; Rizzolatti, Riggio, Dascola, & Umilta, 1987). On the one hand, visual attention can be allocated to some extent at least without moving the eyes (e.g., Posner, 1980). On the other hand several studies have shown that visual attention is allocated to the endpoint of a saccade before initiation of the movement, and that it is difficult to direct attention to a different object even if the object is close to the endpoint of the saccade (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986). Moreover, it has been shown that a shift of attention can influence the production of saccades (Kustov & Robinson, 1996; Sheliga, Riggio, & Rizzolatti, 1994, 1995).

A better understanding of the relationship between visual attention and saccade preparation can be obtained through single-unit recordings in monkeys performing a task that dissociates a shift (at least momentarily) of attention from a gaze shift. The characteristics of neural processes can constrain hypothesis about cognitive processes (Schall, 2002, 2004). Specifically, the data described in this report can be interpreted according to the logic of labeled lines—a distinction of neural processes must correspond to a distinction of functional processes. For example, distinct fibers originating in different sensory receptors and terminating in different brain centers lead to distinct sensory experiences like sight or touch. Likewise, if a neural representation of a stimulus that must be located and categorized to guide a saccade can be distinguished from a neural representation of the endpoint of a saccade, then this would be evidence for two functional kinds of selection.

The frontal eye field is an effective locus in which to investigate these issues because it is one of the areas that transforms visual information into an orienting response (reviewed in Schall, 2002; Schall & Thompson, 1999). Neural correlates of visual selection have been described during a search task in which monkeys were required to make a saccade to the singleton target (Sato, Murthy,

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Nomenclature

$SDF_{S\text{-}in}$	average spike density function from trials with the singleton in the receptive field
$SDF_{S\text{-}out}$	average spike density function from trials with the singleton at the location opposite the receptive field, corresponding to the endpoint of an antisaccade
ΔSDF_A	time-averaged difference of $SDF_{S\text{-}in}$ and $SDF_{S\text{-}out}$ for antisaccade trials
ΔSDF_N	time-averaged difference of $SDF_{S\text{-}in}$ and $SDF_{S\text{-}out}$ for no saccade trials
ΔSDF_P	time-averaged difference of $SDF_{S\text{-}in}$ and $SDF_{S\text{-}out}$ for prosaccade trials
SST_A	singleton selection time in antisaccade trials
SST_P	singleton selection time in prosaccade trials
SST_N	singleton selection time in no saccade trials
EST_A	saccade endpoint selection time in antisaccade trials
EST_N	saccade endpoint selection time in no saccade trials
SRT	stimulus-response mapping time when the direction of the saccade guided by the shape of single was first registered
SRT_{PA}	stimulus-response mapping time from prosaccade and antisaccade trials
SRT_{PN}	stimulus-response mapping time from prosaccade and no saccade trials
SRT_{AN}	stimulus-response mapping time from antisaccade and no saccade trials
ASSI	antisaccade singleton selection index, integral of ΔSDF from array presentation until EST_A divided by the baseline standard deviation of ΔSDF
NSSI	no saccade singleton selection index, integral of ΔSDF from array presentation until EST_N divided by the baseline standard deviation of ΔSDF
PSSI	prosaccade singleton selection index, integral of ΔSDF from array presentation until the median reaction time divided by the baseline standard deviation of ΔSDF

Thompson, & Schall, 2001; Murthy, Thompson, & Schall, 2001; Schall & Hanes, 1993; Schall, Hanes, Thompson, & King, 1995; Thompson, Hanes, Bichot, & Schall, 1996). The initial activity of visually responsive neurons did not discriminate whether the target or distractors of a search array fell in the receptive field, but the later phase of the activity of these neurons reliably differentiated the target from the distractors. This pattern of activity was observed even when the monkeys withheld a saccade (Sato, Watanabe, Thompson, & Schall, 2003; Thompson, Bichot, & Schall, 1997). These observations support the hypothesis that the representation of stimuli by visual activity in FEF corresponds to the allocation of attention (reviewed in Thompson, Bichot, & Schall, 2001).

The relationship between the time when visually responsive neurons in FEF select the target from distractors and the reaction time of the monkeys also supports this hypothesis. First, the time of target selection by most but not all FEF visually responsive neurons during efficient pop-out search is synchronized on stimulus presentation rather than saccade initiation (Sato et al., 2001; Thompson et al., 1996). Second, although search efficiency and response interference both affect RT, only search efficiency affects the time when neurons select the target (Sato et al., 2001). In other words, visual neurons in FEF select the target with a time course that parallels the allocation of attention. While persuasive, these findings do not completely exclude the possibility that the target selection by FEF neurons corresponds to saccade preparation. More conclusive evidence requires manipulation of stimulus-response mapping to explicitly decouple stimulus encoding and response preparation (Kornblum, Hasbroucq, & Osman, 1990).

For this study, monkeys were trained to produce a prosaccade, an antisaccade or no saccade cued by the shape of the color singleton in a visual search array (Fig. 1) (Sato & Schall, 2003). If the selection process exhibited by FEF neurons corresponds to the covert selection of the location of the singleton, then the singleton should be selected regardless of the required response, and the time of the selection should be the same across the three conditions. On the other hand, if process of selection FEF neurons corresponds only to preparation of a saccade, then only the endpoint of the saccade should be selected, and the time of the selection should be affected by the stimulus-response compatibility. Recently, evidence has been produced for both types of neurons in FEF (Sato & Schall, 2003). Here, this finding is extended by demonstrating that when no saccade is produced, many FEF neurons still exhibit selection of the singleton and later of the endpoint of the unexecuted antisaccade. This modulation for unexecuted saccades cannot be due to bottom-up visual processing and thus must be the product of an endogenous pro-

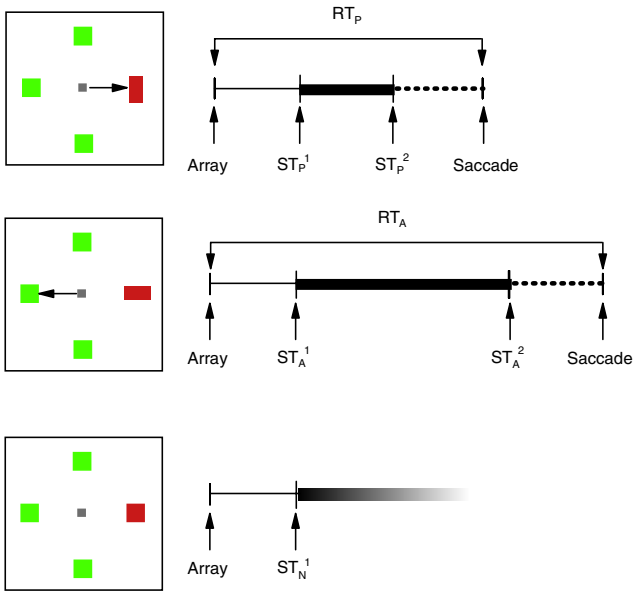

Fig. 1. Visual search with explicit stimulus-response mapping. A vertical singleton instructed a prosaccade. A square singleton required no saccade. A horizontal singleton instructed an antisaccade. RT is subdivided into an encoding stage (thin line), stimulus-response mapping stage (thick line) and response preparation stage (dotted line). This experiments investigates alternative hypotheses about how the stimulus selection time (ST) of FEF neurons and reaction time (RT) vary with stimulus-response compatibility. If the selection time is not affected by stimulus-response compatibility, then the fraction of the change in RT accounted for by the change in the selection time should be close to 0%. If the selection time corresponds to or follows the stimulus-response mapping process, then the fraction of the change in RT accounted for by the change in ST should be close to 100%.

cess that can be usefully identified with the allocation of attention coordinated with preparation of the saccade.

2. Methods

2.1. Subjects and surgery

Data were collected from three macaque monkeys (F, M, L, 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., 1995).

2.2. Behavioral training

Monkeys were trained to perform a color singleton visual search task with reward contingent on producing a prosaccade, an antisaccade or no saccade. These three conditions were cued by the shape of the singleton. After fixation of a central spot for 400–700 ms, four stimuli were presented at iso-eccentric locations equally spaced around the central fixation spot (Fig. 1). One of the four stimuli was a color singleton target, which was distinguished from iso-luminant distractors (i.e., red target among green distractors or green target among red distractors). The green was CIE $x = 284$, $y = 608$, red was CIE $x = 631$, $y = 328$ with a luminance of 11.4 cd/m^2 on a black background. The color of the singleton and distractors remained the same during each recording session and varied pseudorandomly across sessions. The four stimuli were arranged so that one of the stimuli was located in the center of the receptive field of the recorded neuron. The singleton could be a vertical or a horizontal rectangle, or a square. The vertical singleton required a prosaccade to its location within 1500 ms. The horizontal singleton required an antisaccade to the location of the distractor diametrically opposite the singleton within 1500 ms. Pro- and antisaccade trials were randomly interleaved. In both types of trials, after the correct saccade, all the stimuli but the one at the endpoint of the correct saccade disappeared. The monkeys were required to fixate the correct saccade target for 500 ms to obtain reward. In some of the recording sessions, trials were interleaved in which the singleton was square, which required monkeys to maintain fixation on the central spot for 2000 ms. Prosaccade and antisaccade trials were reported in Sato and Schall (2003). No saccade trials are the focus of this report. The distractors were always squares that scaled from 0.6° of visual angle at 6° eccentricity to 1° at 10° eccentricity. The aspect ratio of the rectangle singleton remained the same within each recording session, and was adjusted between 1.4 and 2.0 to optimize performance. The area and luminance of the rectangle was equal to that of the distractors.

Monkeys were also trained to produce memory-guided saccades to distinguish visual from saccade-related activity (Bruce & Goldberg, 1985; Hikosaka & Wurtz, 1983). A single target was flashed for 80 ms, but the monkeys were required to maintain fixation on the central spot for another interval of random duration ranging from 400 to 1000 ms. When the fixation spot disappeared, the monkeys were rewarded for shifting gaze to the remembered location of the target. Once gaze shifted, the target reappeared to provide feedback and a fixation target for the monkeys.

2.3. Data collection and analysis

Single units were recorded with tungsten electrodes (FHC). The electrode was introduced through a guide tube positioned in a 1 mm-spaced grid (Crist, Yamasaki, Komatsu, & Wurtz, 1988) and were positioned with a hydraulic drive (FHC). Action potentials were amplified, filtered and discriminated using an analog time-amplitude window discriminator (BAK). FEF

recordings were done in the rostral bank of the arcuate sulcus, which was confirmed with the magnetic resonance imaging.

Measurements of neural activity were derived from spike density functions 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, Friedlander, & Redman, 1990). The rationale for this approach, which has been described previously (Hanes & Schall, 1996; Thompson et al., 1996), was to derive physiologically plausible spike density functions.

The time at which the neuron selects the singleton or the endpoint of saccade was determined by comparing two sets of trials in a neuron–antineuron analysis (Britten, Shadlen, Newsome, & Movshon, 1992; Thompson et al., 1996). Earlier work described this in terms of the time when neurons select the target for a saccade. However, in antisaccade trials, the term target is ambiguous, for it might refer to the singleton or to the endpoint of saccade. Therefore, in this analysis more precise terminology is adopted by distinguishing singleton selection time (SST), and endpoint selection time (EST). SST is identical to the target discrimination time (TDT) described before (e.g., Thompson et al., 1996). By design, antisaccade trials permit the distinction between selecting the singleton and selecting the endpoint of the saccade. These events are designated as singleton selection time (SST_A), and endpoint selection time (EST_A) with the subscript denoting antisaccade trials.

SST and EST cannot be distinguished in prosaccade trials because the endpoint of the saccade and the location of the singleton correspond. The selection time in prosaccade trials will be designated as SST_P. The neural activity during no saccade trials happened to be similar to that in antisaccade trials, so SST_N and EST_N were determined in the same fashion.

Endpoint selection marks the conclusion of a transition. The beginning of this transition was measured. The earliest instant when neural activity distinguished the stimulus-response mapping rule based on the shape of the singleton was referred to as stimulus-response mapping time (SRT). This value is derived from a comparison across conditions (i.e., prosaccade, antisaccade and no saccade trials).

SST, EST and SRT were measured as follows. First, spike density functions were calculated for all the correct trials with the singleton in the receptive field ($SDF_{s\text{-}in}$) and for all the correct trials with the singleton diametrically opposite the receptive field ($SDF_{s\text{-}out}$). The difference between these two spike density functions was calculated:

$$\Delta SDF = SDF_{s\text{-}in} - SDF_{s\text{-}out}$$

This function describes the discrimination process of the neuron, and is highly correlated with the area of the receiver operating characteristic used in our previous work (Sato et al., 2001; Thompson et al., 1996). A baseline mean and standard deviation of the ΔSDF was calculated from 50 ms before to 50 ms after array presentation across prosaccade and antisaccade trials. The time at which the difference function crossed the mean baseline difference plus 2 standard deviations was selected as SST_P (prosaccade trials), SST_A (antisaccade trials) or SST_N (no saccade trials), only if the difference function reached the baseline plus 5 standard deviations and remained above the mean plus 2 standard deviation level for more than 15 ms.

In antisaccade trials, the singleton and the endpoint of the saccade occupied opposite location. Therefore, the trials with the singleton in the receptive field were the trials in which the endpoint of the saccade was opposite the receptive field, and the trials with the singleton opposite the receptive field were the trials in which the endpoint of the saccade was in the receptive field. Therefore, in antisaccade trials $SDF_{s\text{-}in}$ describes activity for trials in which the endpoint of the saccade was opposite the receptive field, and $SDF_{s\text{-}out}$ is the activity for trials in which the endpoint of the saccade was in the receptive field. Therefore, the time at which the neuron selected the endpoint of the antisaccade (EST_A) was defined using the same criteria as for SST_A but with the opposite sign. In no saccade trials, since the activity pattern was similar to that in antisaccade trials, the same nomenclature (SST_N and EST_N) was used and calculated with the same procedure even though no saccade was produced. The time when the selection of the stimulus opposite the singleton ended in no saccade trials was determined as the time when $\Delta SDF = SDF_{s-out} - SDF_{s-in}$ became smaller than the mean baseline difference plus 2 standard deviations.

SRT is the earliest time when FEF neurons distinguished the type of trial based on the shape of the singleton. SRT_{PA} was calculated from the difference between ΔSDF for prosaccade trials and ΔSDF for antisaccade trials ($\Delta SDF_P - \Delta SDF_A$) using the same criteria used to determine SST_P, SST_A and EST_A. SRT_{PN} was calculated from prosaccade trials and no saccade trials ($\Delta SDF_P - \Delta SDF_N$). SRT_{AN} was calculated from antisaccade trials and no saccade trials ($\Delta SDF_A - \Delta SDF_N$).

To quantify the degree of singleton selection, a prosaccade singleton selection index (PSSI), an antisaccade singleton selection index (ASSI) and a no saccade singleton selection index (NSSI) were calculated for each neuron. First, ΔSDF was integrated from the time of array presentation to EST_A or EST_N or to the smaller of EST_A or the median prosaccade latency for prosaccade trials. For neurons that did not select the endpoint of the saccade at the location opposite the singleton, the

interval between the array presentation and the median RT was used for antisaccade trials, and the first 400 ms was used for no saccade trials. The integral was divided by the standard deviation of ΔSDF before the array appeared.

3. Results

3.1. Reaction time on pro- and antisaccade trials

Reaction time (RT) was influenced significantly by stimulus-response compatibility. Table 1 presents the mean RT for the three monkeys in prosaccade and antisaccade trials. RT was significantly longer in antisaccade trials than in prosaccade trials. Table 1 also presents the error rates in prosaccade and antisaccade trials. Because the error rate was higher in antisaccade trials compared to prosaccade trials, the difference in RT cannot be due to a simple speed-accuracy tradeoff. Importantly, stimulus-response compatibility did not affect the metrics or dynamics of the saccades. The average ratio of the amplitude of antisaccades to that of prosaccades for each monkey was 1.01 (L), 0.98 (M) and 0.99 (P). The average ratio of the peak velocity for antisaccades relative to prosaccades was 1.01 (L), 0.98 (M) and 1.00 (P). The normal dynamics of antisaccades in this study is attributed to the presence of the visual stimulus at the saccade endpoint.

In some of the recording sessions, no saccade trials were introduced. In these trials, the color singleton was a square, and the monkey had to maintain fixation on the central spot to earn reward. The success rates of the monkeys were lower in these trials compared to prosaccade and antisaccade trials (Table 2). Each monkey performed no saccade trials correctly on most trials, but when errant saccades were produced, they tended to be in the direction opposite the singleton corresponding to the endpoint of an antisaccade.

3.2. Overview of the physiological data

A total of 77 neurons were recorded that changed discharge rate between the presentation of the search array and the initiation of the saccade. Among these, 63 neurons were also tested during no saccade trials. The present study focused on neurons that selected the singleton in prosaccade trials. Using the criteria described above, 65 neurons discriminated the singleton from distractors in prosaccade trials; among these 52 provided sufficient data to analyze in no saccade trials.

Table 2
Performance in no saccade trials

Monkey	Percent correct (%)	Prosaccade (%)	Antisaccade errors (%)
L	69.7	3.8	23.0
M	69.7	10.0	13.8
P	71.2	3.8	15.5

3.3. Pattern of activity in prosaccade and antisaccade trials

The analysis of no saccade trials cannot be interpreted without knowing how the neurons were modulated by stimulus-response compatibility when an overt shift of gaze was required. It is crucial to note that prosaccade, antisaccade and no saccade trials were randomly interleaved. Thus, this section reviews the evidence that FEF neurons selected the singleton among distractors even when monkeys shifted gaze away from it. The next section, will describe the effect of stimulus-response compatibility on the selection time of FEF neurons. The results of these two sections have appeared elsewhere (Sato & Schall, 2003), so they will only be summarized here.

Using measurement criteria equivalent to those used for prosaccade trials, 44 neurons selected the singleton in antisaccade trials, and 21 neurons did not. The activation of a representative FEF neuron that selected the singleton in antisaccade trials is shown in Fig. 2. The presence of visually evoked activity and saccade-related activity was tested with memory-guided saccades to a stimulus flashed in the receptive field. This neuron was visually responsive with minimal activity during the delay period and little modulation associated with the memory-guided saccade. Regardless of the ultimate gaze shift, the singleton was selected around 100 ms after the array appeared. The neurons that selected the singleton in antisaccade trials will be referred to as Type I.

On prosaccade trials the singleton continued to be selected until the saccade. On antisaccade trials the

Table 1
Mean (±SD) RT (ms) in prosaccade trials and antisaccade trials with difference of means and error rates

Monkey	Prosaccade	Antisaccade	Difference of Means	Prosaccade errors (%)	Antisaccade errors (%)
L	235 ± 48 ($n = 1706$)	299 ± 81 ($n = 1707$)	64	3.6	13.4
M	198 ± 44 ($n = 2057$)	258 ± 119 ($n = 2060$)	60	5.3	9.6
P	221 ± 62 ($n = 7719$)	253 ± 75 ($n = 7721$)	32	1.8	6.1

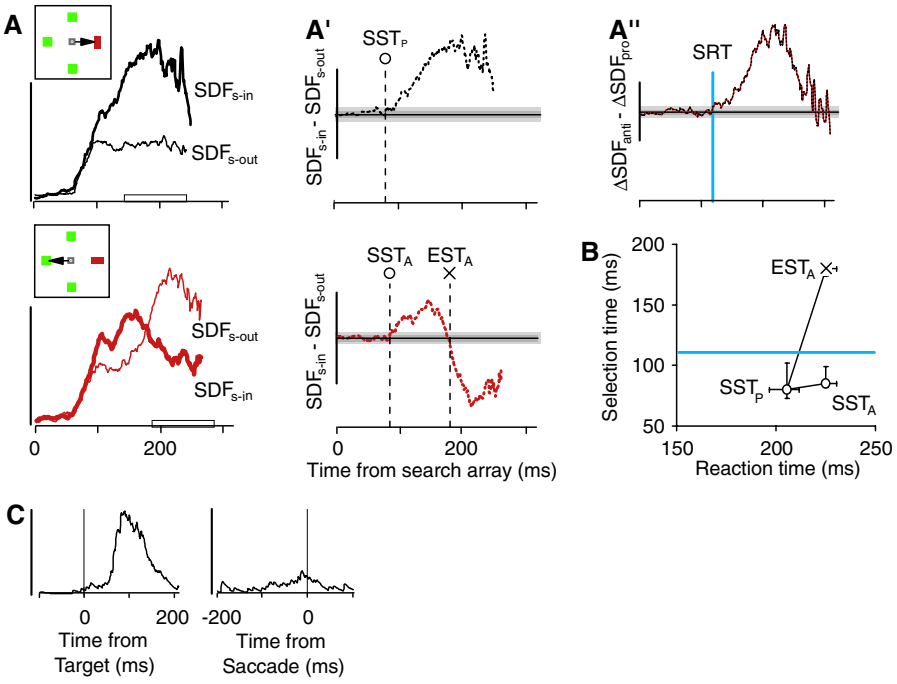

Fig. 2. Effect of stimulus-response compatibility during visual search on a Type I FEF neuron. (A) Average spike density function when the singleton fell in the neuron's receptive field ($SDF_{s\text{-}in}$, thick line) and when the singleton was located opposite the receptive field ($SDF_{s\text{-}out}$, thin line) in prosaccade (top) and antisaccade (bottom) trials. Bracket on abscissa marks range of RT. Scale bar represents 100 spikes/s. (A′) Plots of the difference between the SDF for trials with the singleton in the receptive field and that for trials with the singleton opposite the receptive field for prosaccade (top) and antisaccade (bottom) trials. The scale bar represents a difference of 100 spikes/s. The horizontal line indicates a difference of 0 spikes/s, and the gray rectangle highlights the criterion for a significant difference. Vertical dashed lines show singleton selection time in prosaccade trials (SST_P) and singleton selection time (SST_A) and endpoint selection time (EST_A) in antisaccade trials. (A″) Plot of the difference between the spike density differences from antisaccade and prosaccade trials. The blue line marks stimulus-response time (SRT), the earliest time the response is specified by the shape of the singleton. (B) Selection times as a function of median RT for prosaccade and antisaccade trials. Circles plot SST_P and SST_A and cross plots EST_A. Error bars show 95% confidence intervals derived from repeated random subsampling of the trials. Blue horizontal line marks SRT. (C) Activity during memory-guided saccades aligned on the stimulus presentation (left) and on saccade initiation (right). This neuron was visually responsive with little movement-related modulation. Scale bar represents 100 spikes/s. Modified from Sato and Schall (2003).

singleton was initially selected, but subsequently a dramatic transition occurred whereby the endpoint of the antisaccade was selected. This transition was observed in 38 of 44 neurons that selected the singleton in antisaccade trials. A few neurons in FEF selected the singleton throughout prosaccade and antisaccade trials until saccade initiation. An example is illustrated in Fig. 3.

Twenty-one neurons in FEF did not select the singleton in antisaccade trials; these will be referred to as Type II. The pattern of activation of such a neuron is shown in Fig. 4. Immediately after presentation of the array, this neuron exhibited a pre-excitatory pause (Sato & Schall, 2001). The neuron selected the endpoint of the saccade regardless of the location of the singleton. During a memory-guided saccade task, this neuron exhibited a visual response followed by elevated activity during the delay period and saccade-related modulation (Fig. 4B). Saccade-related activity was not a necessary attribute of Type II neurons. Fig. 5 illustrates the activity of a Type II neuron with only a visual response and no saccade-related modulation. Further evidence

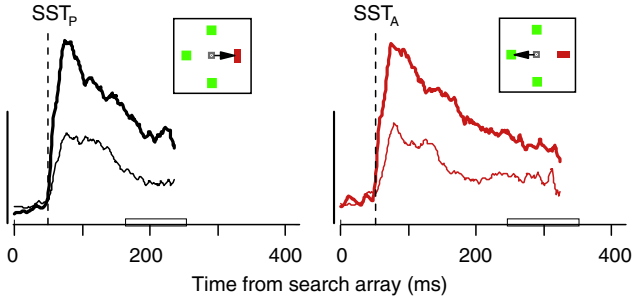

Fig. 3. Type I neuron that did not select the endpoint of saccade in antisaccade trials. Conventions as Fig. 2.

for the validity of the distinction between Type I and Type II neurons is detailed in Sato and Schall (2003).

3.4. Effect of stimulus-response compatibility on the selection times of FEF neurons

The time at which neurons selected the location of the singleton is the singleton selection time (SST_A), and the

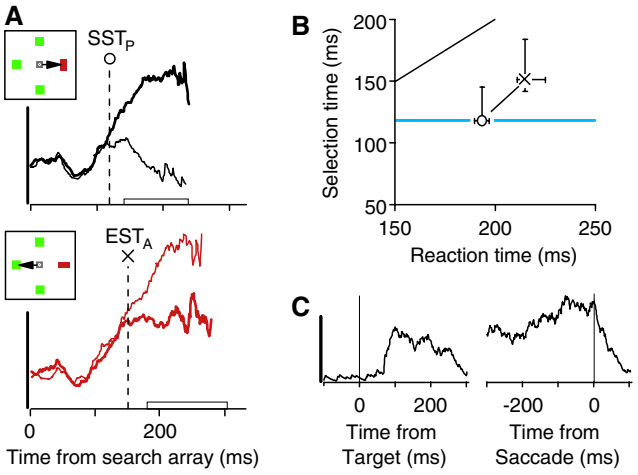

Fig. 4. Effect of stimulus-response compatibility on a Type II neuron during visual search. (A) Average spike density function when the singleton fell in the neuron's receptive field (thick line) and when the singleton was located opposite the receptive field (thin line) in prosaccade (top) and antisaccade (bottom) trials. Note that in antisaccade trials the singleton is not selected before the activity evolves to signal the location of the endpoint of the saccade. Bracket on abscissa marks range of RT. Scale bar represents 100 spikes/s. (B) Selection times as a function of median RT for prosaccade and antisaccade trials. Circle plots SST_P and cross plots EST_A. Error bars show 95% confidence intervals derived from repeated random subsampling of the trials. Blue horizontal line marks SRT. (C) Activity during memory-guided saccades aligned on the stimulus presentation (left) and on saccade initiation (right). This neuron was visually responsive with a moderate degree of presaccadic movement-related modulation. Scale bar represents 100 spikes/s. Modified from Sato and Schall (2003).

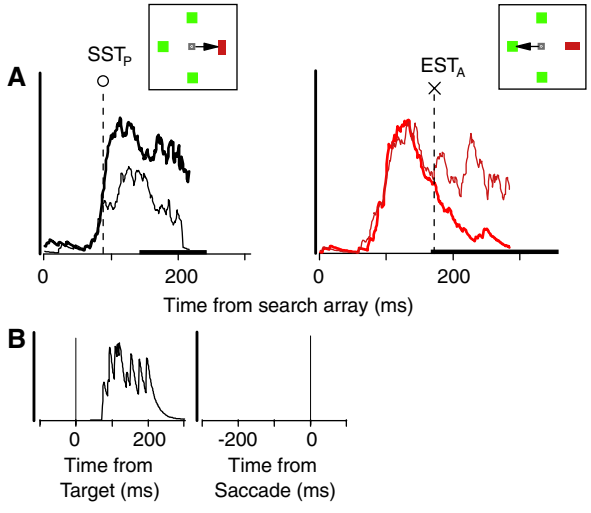

Fig. 5. Exclusively visual Type II neuron. (A) Average spike density function when the singleton fell in the neuron's receptive field (thick line) and when the singleton was located opposite the receptive field (thin line) in prosaccade (left) and antisaccade (right) trials. (B) Activity during memory-guided saccades. This neuron was visually responsive but had no presaccadic movement-related activity. Conventions as Fig. 4.

time at which the neurons selected the endpoint of the saccade is the endpoint selection time (EST_A). In prosaccade trials EST could not be distinguished from SST because the singleton and the endpoint of the saccade occupy the same location; the selection time measured in prosaccade trials is identified as SST_P. The difference of selection times in prosaccade and antisaccade trials of Type II but not Type I neurons could account for much of the effect of stimulus-response compatibility on RT.

While recording the neuron shown in Fig. 2, the median RT in prosaccade trials was 206 ms, and that in antisaccade trials was 225 ms. SST_P of this neuron was 80 ms, and SST_A was 85 ms, amounting to a difference of 5 ms. This accounted for only 26% of the difference in RT between pro- and antisaccade trials (Fig. 2B). Across the population, Type I neurons selected the singleton at a time unaffected by stimulus-response compatibility. The average percentage of the difference in RT accounted for by the difference between SST_P and SST_A was $12 \pm 15\%$, which was significantly different from 100% ($t_{43} = 5.75$, $p < 0.001$) but not from 0% ($t_{43} = 0.81$).

If saccades are initiated at a particular moment after the location of its endpoint is selected, then the difference in RT between antisaccade and prosaccade trials should be just the difference between SST_P and EST_A. In other words the fraction of the difference in RT accounted for by the difference of neural selection times should be 100%. EST_A of this neuron was 180 ms. The difference between EST_A and SST_P was 100 ms, which was substantially larger than the 19 ms difference in RT. The ratio of the difference between EST_A and SST_P to the difference in the median RT of antisaccades and prosaccades was 526%. Obviously, the difference between SST_P and EST_A exceeded the difference of RT between prosaccades and antisaccades. Across the population of Type I neurons the average percentage of the difference between SST_P and EST_A to the difference in RT was $337 \pm 37\%$, which was significantly different from both 0% ($t_{37} = 9.18$, $p < 0.001$) and 100% ($t_{37} = 6.46$, $p < 0.001$). Obviously, the delay of EST_A relative to SST_P overestimates the difference in RT.

The relationship between SST_P, EST_A and RT in pro- and antisaccade trials was notably different for Type II neurons. While recording the neuron shown in Fig. 4, the median RT in prosaccade trials was 192 ms and that in antisaccade trials was 215 ms. SST_P of this neuron was 118 ms, and EST_A was 151 ms. Recall, by definition Type II neurons have no SST_A. The change in RT accounted for by the difference in the EST_A and SST_P, 143%, was close to 100%. Across the population of Type II neurons, the average ratio of the difference between EST_A and SST_P to the difference in RT was $146 \pm 39\%$, which was significantly different from 0% ($t_{20} = 3.76$, $p < 0.005$) but not from 100% ($t_{20} = 1.19$).

The distributions of SST, EST and RT for prosaccade and antisaccade trials are illustrated in Fig. 8. More details about the relationship of SST, EST and RT are described in Sato and Schall (2003). To summarize, Type I neurons selected the singleton ($SST_P^I = 91 \pm 3$ ms) earlier than did Type II neurons ($SST_P^{II} = 115 \pm 6$ ms). In the population of Type I neurons the time of selection of the singleton in prosaccade and antisaccade trials did not vary with stimulus-response mapping or account for the difference in RT. However, the singleton selection time of Type II neurons in prosaccade trials was less related to array presentation and more related to the time of saccade initiation. In antisaccade trials the time of endpoint selection by Type I neurons (179 ± 4 ms) was significantly later than that of Type II neurons (159 ± 8 ms). The endpoint selection time of Type I neurons in antisaccade trials was too late to explain the increase in RT relative to prosaccade trials. In contrast, the endpoint selection time of Type II neurons in antisaccade trials, like the singleton selection time in prosaccade trials, accounted for some but not all of the delay and variability of RT.

3.5. Effect of saccade production on singleton and endpoint selection

Data from 36 Type I neurons and 16 Type II neurons were collected during no saccade trials. Of the 36 Type I neurons, 29 selected the singleton whereas the remaining 7 did not. The activity of a representative Type I neuron that initially selected the singleton and that of another Type I neuron that did not select the singleton is shown in Fig. 6. Both neurons eventually selected the location opposite the singleton that would be the endpoint of an antisaccade.

The discharge rate when the singleton was in the receptive field was lower in no saccade trials (51.1 ± 7.3 Hz) compared to prosaccade (102.0 ± 7.7 Hz, $t_{28} = 9.9$, $p < 0.001$) and antisaccade trials (62.2 ± 7.5 Hz, $t_{28} = 4.76$, $p < 0.001$).

The magnitude of selective activity was quantified with the prosaccade singleton selection index (PSSI), the antisaccade singleton selection index (ASSI) and the no saccade singleton selection index (NSSI) for 29 Type I neurons. Not surprisingly, singleton selection was greater in prosaccade trials compared to no saccade trials; PSSI (2536.4 ± 502.1) was significantly greater than NSSI (732.1 ± 161.0; $t_{28} = 4.47$, $p < 0.001$). Singleton selection in prosaccade trials was also greater than that in antisaccade trials (ASSI = 1279.3 ± 286.5, $t_{28} = 4.24$, $p < 0.001$). Finally, singleton selection was significantly greater in antisaccade trials compared to no saccade trials ($t_{28} = 3.19$, $p < 0.005$).

Surprisingly, even when monkeys made no saccade, many of the Type I neurons (24 out of 36) also selected the stimulus opposite the singleton later in the trial. This selective difference in the activity attenuated by around 400 ms after the search array onset. The selection of the

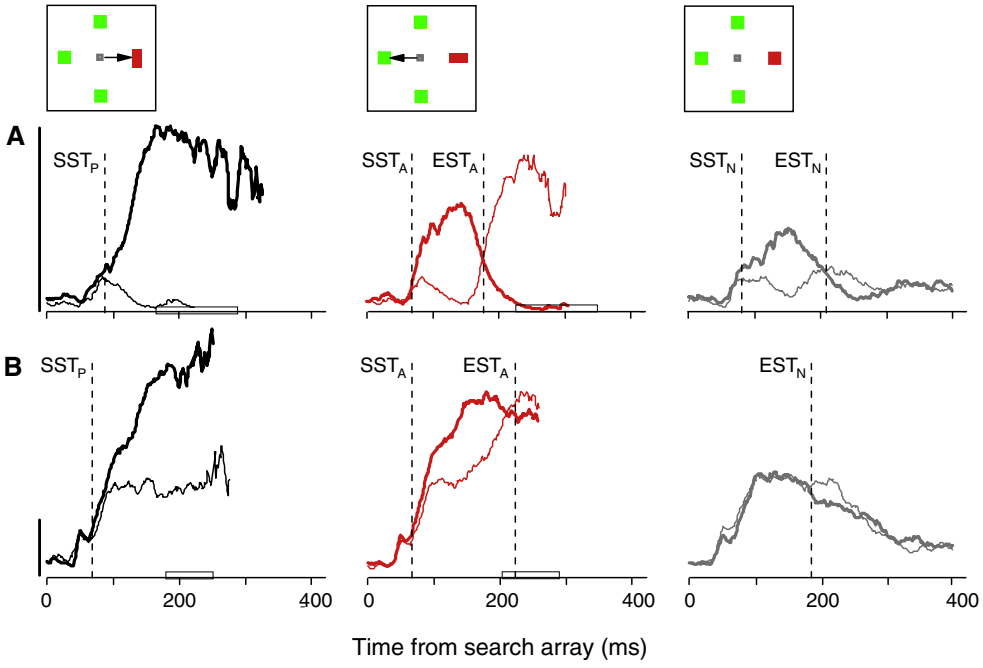

Fig. 6. Diversity of Type I neuron activity during no saccade trials. Average spike density functions when the singleton fell in the neuron's receptive field (thick line) and when the singleton was located opposite the receptive field (thin line) in prosaccade (left), antisaccade (middle) and no saccade (right) trials for two Type I neurons. (A) Type I neuron that selected the singleton and then selected the opposite location in no saccade trials. (B) Type I neuron that did not select the singleton but did select the opposite location in no saccade trials. Conventions as Fig. 2.

stimulus opposite the singleton by Type I neurons when no saccade was produced may be due to the monkeys' strategy; recall that when monkeys failed to withhold the saccade, they most often produced an antisaccade. The relationship between the selection of the location opposite the singleton and strategy was investigated by determining whether the average magnitude of endpoint selection in trials when no saccade was produced was related to the fraction of antisaccade errors occurring in that session. The antisaccade error rate was not different between sessions when Type I neurons selected the stimulus opposite the singleton ($16.8 \pm 1.3\%$) and sessions when Type I neurons did not ($17.3 \pm 2.0\%$, $t_{34} = 1.7$). This was also true for Type II neurons ($17.1 \pm 1.1\%$, $15.2 \pm 1.6\%$, $t_{14} = 0.937$, see below).

SST_N and EST_N were measured using the procedure identical to that used in prosaccade and antisaccade trials. Across Type I neurons, the mean SST_N was 98.2 ± 14.6 ms, which was not significantly different from SST_A of these neurons (98.9 ± 5.4 ms, $t_{28} = 0.193$), but was marginally later than SST_P (90.2 ± 3.8 ms, $t_{28} = -2.29$, $p = 0.03$). The mean EST_N was 187.0 ± 4.8 ms, which was not significantly different from EST_A (181.0 ± 4.0 ms, $t_{23} = 1.08$). For most neurons the selection of the location opposite the singleton did not persist until the end of the trial. The selection of the stimulus opposite the singleton ended 293.5 ± 11.9 ms after array presentation.

Fig. 7 shows the activity of the Type II neuron illustrated in Fig. 4 during no saccade trials. As expected, most of the Type II neurons (13 out of 16) did not select the singleton in no saccade trials. However, as was the case with Type I neurons, some Type II neurons (7 of 16) selected the stimulus opposite the singleton later in the trial. The mean EST_N for these neurons was 178.6 ± 9.4 ms, which was not significantly different from EST_A of these neurons (165.0 ± 7.9 ms, $t_6 = 1.71$). Type II neurons selected the location opposite the singleton for an average duration of 292.3 ± 16.2 ms which was not different from the value for Type I neurons.

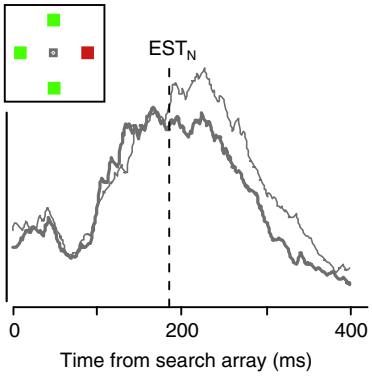

Fig. 7. Activity of a Type II neuron during no saccade trials. This neuron, which is illustrated in Fig. 4, selected the location opposite the singleton even when no saccade was produced.

3.6. Singleton shape categorization and stimulus-response mapping time

The earliest time when neural activity distinguished the shape of the singleton cuing the response is the stimulus-response mapping time (SRT). As detailed previously, this measurement requires a comparison across trial types. Formally, this was measured as the time when the difference of ΔSDF for the respective types of trials occurred. Sato and Schall (2003) report the comparison of antisaccade and prosaccade trials. The present data afford two more comparisons—antisaccade with no saccade and prosaccade with no saccade. Thus, for the particular neurons contributing no saccade data SRT was measured between prosaccade trials and antisaccade trials (SRT_{PA}) to contrast with the comparison between prosaccade trials and no saccade trials (SRT_{PN}) and the comparison between antisaccade trials and no saccade trials (SRT_{AN}). Note that while the difference between ΔSDF_P and ΔSDF_A or that between ΔSDF_P and ΔSDF_N result from ΔSDF_P becoming larger than the other two due to stronger singleton selection in prosaccade compared to the other two conditions, the difference between ΔSDF_A and ΔSDF_N could result from either ΔSDF_A becoming larger than ΔSDF_N due to stronger singleton selection in antisaccade trials or ΔSDF_A becoming smaller than ΔSDF_N due to stronger selection of the stimulus opposite the singleton in antisaccade trials. ΔSDF_{AN} was the earlier of these two.

For the Type I neurons, mean SRT_{PA} was 122.5 ± 5.1 ms ($n = 34$), while SRT_{PN} was 108.0 ± 4.4 ms ($n = 36$), and SRT_{AN} was 106.3 ± 6.6 ms ($n = 28$). For the neurons that had both SRT_{PA} and SRT_{PN}, SRT_{PA} was significantly later than SRT_{PN} ($t_{33} = 4.01$, $p < 0.0001$). Similarly, SRT_{PA} was significantly later than SRT_{AN} ($t_{25} = 5.22$, $p < 0.0001$), but SRT_{PN} and SRT_{AN} were not significantly different ($t_{27} = 0.12$). Thus, across Type I neurons, no saccade trials were first distinguished from prosaccade and antisaccade trials, and then prosaccade and antisaccade trials were distinguished. In other words, the elongation of the singleton was encoded before orientation was registered.

For Type II neurons, mean SRT_{PA} was 117.5 ± 8.5 ms ($n = 14$), and SRT_{PN} was 121.9 ± 7.7 ($n = 14$). Only two Type II neurons exhibited SRT_{AN}. The difference between SRT_{PA} and SRT_{PN} was not significant ($t_{13} = 0.79$), indicating that prosaccade trials were distinguished from antisaccade trials and no saccade trials about the same time among Type II neurons. The distributions of these SRT values are shown in Fig. 8.

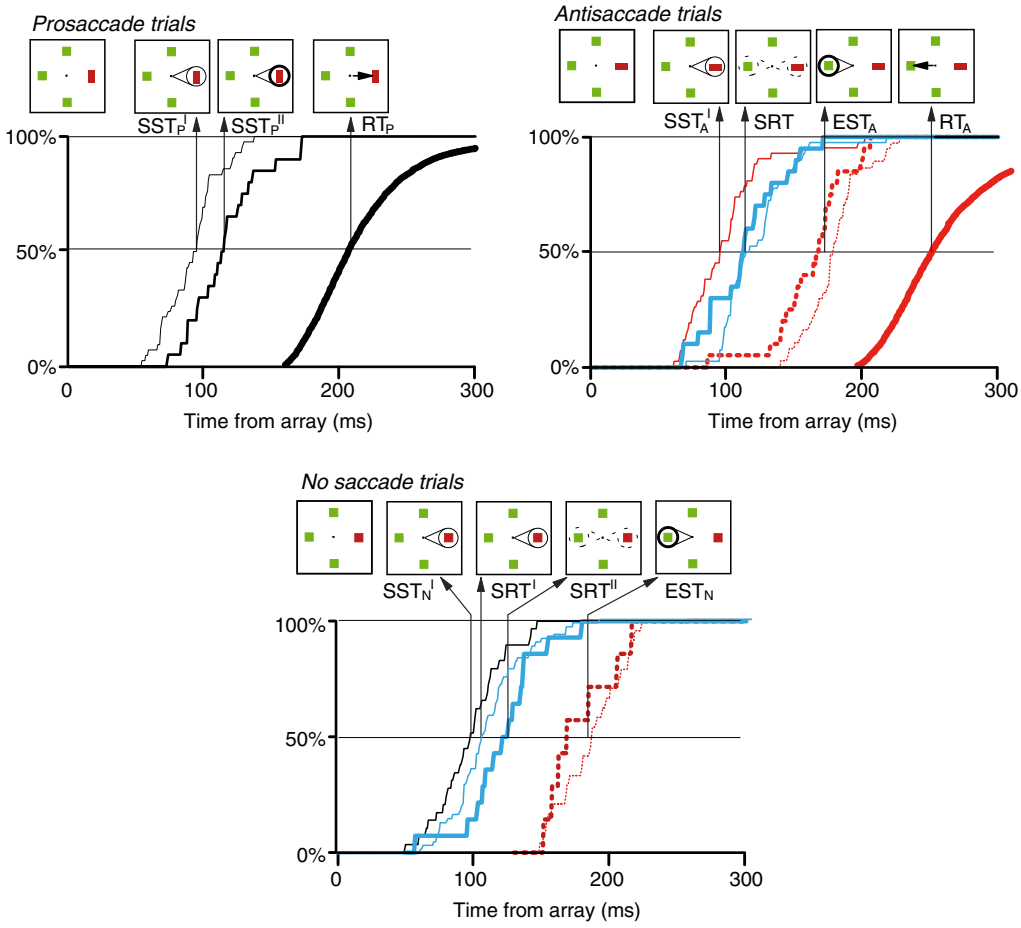

Fig. 8. Cumulative distributions of modulation times in prosaccade (top), antisaccade (middle) and no saccade (bottom) trials for Type I (thin) and Type II (thicker) neurons with corresponding RT (thickest). The inset arrays indicate hypothesized functional correlates. After presentation of the array, selection of the singleton location occurs at the SST of Type I neurons (indicated by the spotlight on the singleton); this occurs at the same time in prosaccade, antisaccade and no saccade trials and does not relate to whether or when gaze shifts. In prosaccade but not antisaccade or no saccade trials Type II neurons select the singleton at a later time which accounts for some of the variability of RT. A comparison of activation in prosaccade and antisaccade trials reveals the time at which the shape of the singleton is encoded to specify the correct saccade direction; this follows singleton selection and coincides for Type I (thin blue) and Type II (thicker blue) neurons in antisaccade trials. But in no saccade trials singleton elongation is encoded by Type I neurons before its orientation cuing the endpoint of the saccade is represented by Type II neurons. At the moment marked by SRT in antisaccade and no saccade trials the representation of the singleton decreases, and the representation of the location opposite the singleton, the endpoint of the antisaccade increases (indicated by the weaker spotlight on the singleton and growing spotlight on the saccade endpoint). At this same time in prosaccade trials the representation of the saccade endpoint is enhanced by the selection that occurs in the Type II neurons (indicated by the highlighted spotlight on the singleton). Subsequently, in antisaccade and no saccade trials the endpoint of the saccade becomes selected more than the location of the singleton by Type I (thin red, dashed) and Type II (thicker red, dashed) neurons (indicated by the highlighted spotlight on the antisaccade endpoint). The time taken to select the endpoint of the saccade predicts some of the delay and variability of RT.

4. Discussion

It is well known that visual attention and saccade preparation are closely related. The present study dissociated visual selection from saccade preparation and production by manipulating stimulus-response compatibility in a visual search task. The activity of neurons in FEF revealed a particular sequence of selection.

4.1. Distinct types of neurons in FEF

The distinction between the two types of neurons in FEF was based on the pattern of activity in antisaccade trials. About two thirds of FEF neurons selected the singleton regardless of the direction of the saccade (Type I neurons), although in antisaccade trials, nearly all of these neurons exhibited a clear transition of discharge rate such that the location of the endpoint of the saccade was selected before saccade initiation. On the other hand, about one third of neurons encountered in FEF selected only the endpoint of the saccade regardless of the position of the singleton (Type II neurons).

The relationship between the time of stimulus selection and the reaction time of the monkeys supports further the distinction between Type I and Type II neurons. The singleton selection time of Type I neurons

was not affected by stimulus-response compatibility. For Type I neurons, the difference between the endpoint selection time in antisaccade trials and singleton selection time in prosaccade trials does not correspond to the difference in RT between antisaccade and prosaccade trials. This demonstrates that the modulation of Type I neurons cannot account for the effect of stimulus-response compatibility on RT.

On the other hand, the difference between the time when Type II neurons selected the endpoint of the saccade in prosaccade trials and that in antisaccade trials corresponded better to the difference in saccade latency between these two conditions. Sato and Schall (2003) detail other lines of converging evidence that distinguishable functional classes of neurons can be observed in FEF.

It should be noted that earlier investigations of FEF have found diversity among visually-responsive neurons. For example, not every neuron in FEF exhibits the enhancement effect (Goldberg & Bushnell, 1981). Also, other studies of saccade target selection by FEF neurons have described specific differences across the population of neurons (Bichot, Schall, & Thompson, 1996; Thompson et al., 1996). Furthermore, the distinction of Type I and Type II neurons in FEF parallels observations in two recent studies of target selection in the superior colliculus. The first study, using a motion discrimination task, reported two types of prelude neurons; the first exhibited direction selectivity and were modulated by the strength of the motion stimulus, and the other showed strong saccade-related activity independent of motion strength (Horwitz & Newsome, 2001a, 2001b). The second study, using a color singleton search task reported that the time of target selection by some neurons in the superior colliculus did not vary with saccade latency, but other neurons selected the target at a time that was correlated with saccade latency (McPeek & Keller, 2002). We believe the former correspond to Type I and the latter, to Type II neurons identified in this study.

4.2. Relation to previous studies manipulating stimulus-response mapping

Neural activity associated with saccades toward a location incompatible with a stimulus has been examined in various cortical areas including the dorsolateral prefrontal cortex (Funahashi, Chafee, & Goldman-Rakic, 1993), supplementary eye field (Olson & Gettner, 2002; Schlag-Rey, Amador, Sanchez, & Schlag, 1997), FEF (Everling & Munoz, 2000), premotor cortex (Ohbayashi, Ohki, & Miyashita, 2003) and the lateral intraparietal area (Gottlieb & Goldberg, 1999; Toth & Assad, 2002; Zhang & Barash, 2000) as well as the superior colliculus (Everling, Dorris, Klein, & Munoz, 1999). Functional imaging studies have also described specific differences of activation in the frontal lobe of humans performing antisaccades as compared to prosaccades (Connolly, Goodale, Menon, & Munoz, 2002; O'Driscoll et al., 1995; Sweeney et al., 1996). Finally, a recent experiment using transcranial magnetic stimulation also provided evidence that the human FEF contributes to visual target selection distinct from saccade production (Muggleton, Juan, Cowey, & Walsh, 2003). However, none of these studies measured the time course of the evolution of the neural representations contributing to performance of the task.

The pattern of modulation of Type I neurons resembled the data in earlier studies of antisaccades with one significant difference. In the previous studies, only one stimulus was presented with no stimulus at the location to which the antisaccades were directed. In the present study, the singleton was presented with distractors, so selection of the stimulus guiding the response from distractors was required. This afforded the examination of a modulation of sensory activity rather than the mere presence of sensory activity. Moreover, the presence of a stimulus at the endpoint of the antisaccades afforded normal amplitude and velocity unlike antisaccades to a blank area (Amador, Schlag-Rey, & Schlag, 1998; Bell, Everling, & Munoz, 2000).

Neurophysiological correlates of stimulus-response compatibility have been reported in monkeys performing a variety of tasks requiring manual responses (Alexander & Crutcher, 1990; Chen & Wise, 1995; Crammond & Kalaska, 1994; Hoshi & Tanji, 2000; Mitz, Godschalk, & Wise, 1991; Ochiai, Mushiake, & Tanji, 2002; Riehle, Kornblum, & Requin, 1997; Shen & Alexander, 1997). These studies consistently showed that the early phase of the neural activity encoded the location of the stimulus whereas the late phase encoded the direction of the movement.

Although several studies have addressed the neural basis of the variability of response times (Cook & Maunsell, 2002; Dorris & Munoz, 1998; Hanes & Schall, 1996; Krauzlis & Dill, 2002; Lecas, Requin, Anger, & Vitton, 1986; Roitman & Shadlen, 2002), only one study has examined the neural correlates of stimulus-response mapping in a reaction time paradigm (Mouret & Hasbroucq, 2000). That study showed that neurons in primary motor cortex with firing rate modulated by the selected motor response were affected by stimulus-response compatibility whereas neurons with firing rate modulated by the sensory stimulus were not. This is entirely consistent with the present findings.

4.3. Behavior and neural selection in no saccade condition

The performance in no saccade trials was worse than that in prosaccade and antisaccade trials in all the monkeys. Interestingly, the most common type of error

was a saccade toward the stimulus opposite the singleton. This is somewhat surprising, given the fact that attention and gaze are commonly attracted to a conspicuous stimulus. This tendency must have developed through the training process because this type of error was not observed in a previous study using no saccade responses (Thompson et al., 1997).

When no saccade was produced, most of the Type I neurons selected the singleton whereas most Type II neurons did not. The singleton selection by Type I neurons exhibited three key characteristics. First, the singleton selection time of Type I neurons was not appreciably different from that in prosaccade or antisaccade trials. Second, the magnitude of activity when the singleton was in the receptive field was lower in no saccade trials compared to prosaccade and antisaccade trials. Third, the degree of singleton selection was substantially weaker in no saccade trials compared to that in prosaccade and antisaccade trials; indeed, some Type I neurons did not select the singleton at all if no saccade was made.

We have reported singleton selection in monkeys making no saccades previously (Thompson et al., 1997). The first two characteristics were observed before. The unchanging selection time indicates that the process of singleton selection by Type I neurons is an automatic process that is not affected by the nature of the behavioral response. The reduced discharge rate on no saccade trials may be explained as an absence of enhancement on these trials (Goldberg & Bushnell, 1981). The reduced degree of selection of the singleton observed in this experiment contradicts our previous report. Two explanations that are not mutually exclusive are possible. First, the singleton in prosaccade and antisaccade trials is distinguished from distractors in two dimensions (shape and color) whereas that in no saccade trials is distinguished in only one dimension (color). It seems reasonable that a singleton in two dimensions can be selected more easily because it is more distinct than a singleton in one dimension. Second, because this task could be solved by attending only to the shape of the stimulus, monkeys might have ignored the color. Psychological studies have shown that a singleton in a particular dimension can be ignored under certain conditions (Bacon & Egeth, 1994), and physiological studies showed that neurons in prefrontal cortex exhibits enhanced activity toward stimuli of behaviorally relevant dimension (Everling, Tinsley, Gaffan, & Duncan, 2002; Rainer, Asaad, & Miller, 1998; Sakagami & Niki, 1994; Sakagami & Tsutsui, 1999). Interestingly, the analysis of stimulus-response time demonstrated that Type I neurons discriminated no saccade trials cued by singleton elongation before encoding the difference between prosaccade and antisaccade mapping cued by singleton orientation. In contrast, Type II neurons discriminated prosaccade trials from antisaccade and no saccade trials at about the same time.

A significant number of both Type I and Type II neurons selected the location opposite the singleton around 200 ms after the array appeared, although the difference was attenuated beyond 400 ms in most of these neurons. This pattern of activity was not observed in a previous study with no saccades (Thompson et al., 1997). The unnecessary selection of the location opposite the singleton cannot be a stimulus-driven process, so we believe it must therefore be a consequence of the training to produce antisaccades and the tendency in no saccade trials for errors to be saccades toward the stimulus opposite the saccade. This surprising finding indicates that the monkeys initially attended to the singleton, and later shifted attention unnecessarily toward the stimulus opposite the singleton.

4.4. Neural and mental chronometry

Human cognition can be described in terms of different processes performing distinct functions requiring a certain amount of time (reviewed by Meyer, Osman, Irwin, & Yantis, 1988; Sternberg, 2001). This description has been challenged, though, by the difficulty obtaining measurements of the durations of constituent processes. Event-related scalp potentials have provided useful information (e.g., Smulders, Kok, Kenemans, & Bashore, 1995), but the activity of single neurons provides greater spatial and functional resolution. We believe that the present data in conjunction with earlier work affords an especially informative description of the processes that occur in performing this task. The sequence and timing of these neural events provides useful constraints on models of visual attention, categorization and response generation.

For reasons detailed previously, it has been argued that the time when most visually responsive neurons in FEF distinguish the target from distractors marks the end of the process of stimulus localization, encoding and selection (Sato et al., 2001; Sato & Schall, 2003; Thompson et al., 1996). The present data provides further evidence for this by dissociating the time of selection of the singleton location (SST) from the time of encoding the stimulus-response mapping rule (SRT) and the time of selection of the endpoint of the saccade (EST). Moreover, the presence and timing of these different kinds of selection distinguished Type I and Type II neurons. The new data in this report provide additional information about covert selection when no saccade is produced. These results suggest certain plausible relationships between these selection times and the covert processes that are presumed to occur during this task (Fig. 8).

The SST of Type I neurons was not much different across the three conditions. This is consistent with the hypothesis that the SST of Type I neurons corresponds

to the time the singleton was located. SRT consistently followed SST. In other words, the singleton was localized before its properties were encoded. This sequential timing provides useful constraints on theories of the architecture of attention and categorization (e.g., Logan, 2002). Surprisingly, the SRT of Type I neurons measured in no saccade trials cued by a square singleton was earlier than the SRT measured in prosaccade and antisaccade trials. This indicates that the elongation was registered before the specific orientation of the singleton.

At the EST of Type I neurons, the neural representation of the endpoint of the saccade first exceeded that of the singleton location. We could measure EST for two thirds of Type I neurons even when no saccade was produced. This suggests that the location opposite the singleton received preferential processing later in no saccade trials even though unnecessary.

The timing of endpoint selection by Type II neurons was consistent with the hypothesis that the time at which Type II neurons select a stimulus corresponds to the time when the endpoint of the saccade was selected. The difference between the time when Type II neurons selected the endpoint of the saccade in prosaccade trials and that in antisaccade trials corresponded to the difference in RT between these two conditions. In prosaccade trials the time of singleton selection of Type II neurons varied with saccade latency. This is also consistent with the hypothesis that these neurons are concerned more with the time of selection of the saccade than with the selection of the stimulus. In addition, a significant number of Type II neurons selected the stimulus opposite the singleton in no saccade trials around the same time as in antisaccade trials. For Type II neurons, SRT in antisaccade compared to prosaccade or in comparison with no saccade trials was not distinguishable. This is further evidence that the location opposite the singleton was treated unnecessarily as a potential target for a saccade. However, the fact that some neurons did not select the singleton in no saccade trials and those that did exhibited weaker selection of the singleton in no saccade trials as compared to antisaccade and prosaccade indicates that this selection represents less of a commitment of resources. Still, if the square singleton was encoded correctly by Type I neurons, then why should any of the neurons select the opposite location at all?

4.5. Linking attention, neurons and behavior

While everybody may know what attention is, the description of attention in the neuroscience literature is rather confused with statements that are mutually incompatible or commit category errors. Attention is commonly regarded as a mechanism by which a specific aspect of the environment is selected for scrutiny. It is also said that attention can be directed to different locations or attributes. The basic observation made by many laboratories is that the activity of (certain) neurons in (diverse but not all parts of) the brain is modulated when monkeys (in which the neurons reside) are (said to be) attending. Many authors argue about attention residing in some but not other parts of the visual pathway. But how can attention be both in the visual pathway and directed to an object at a particular location? Also, many authors refer to the effects of attention; thus, for attention to have any effects, it must be causal. In fact, it is not uncommon to read about attention influencing the activity of neurons. However, this clearly cannot be the case, only neurons can influence neurons. Also, if attention causes effects, how can it (at the same time) be directed (as an effect)? For this to make sense, another process must be invoked that moves attention that causes effects. This confusion hinders progress.

It seems sensible to assert that attention must refer to the manifestation of a particular process or state of the brain during a behavior in the context of alternative stimuli. This interpretation seems necessary for the word to have meaningful reference at the behavioral or phenomenal level. Accordingly, the allocation of attention across the image need be no more or less than the selective differential activation of neurons in the appropriate network that includes FEF. In other words, attention can be said to be allocated when certain neurons enter a certain state. Hence, when particular FEF neurons (as well as neurons in other parts of the network) signal the location of the stimulus of interest or the endpoint of an upcoming gaze shift, it can be said that attention was allocated. Thus, attention is allocated when and to the extent that the activity of particular neurons represent one as opposed to another location. This can be tested more directly by using a secondary response to probe stimuli at the location of different elements of an array (e.g., Bichot, Cave, & Pashler, 1999; Bisley & Goldberg, 2003). This measure of the allocation of attention can be distinguished in time and neural process from when, whether and where gaze shifts.

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