Combination of Neuronal Signals Representing Object-Centered Location and Saccade Direction in Macaque Supplementary Eye Field

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Submitted 17 January 2007; accepted in final form 23 February 2007

Moorman DE, Olson CR. Combination of neuronal signals representing object-centered location and saccade direction in macaque supplementary eye field. J Neurophysiol 97: 3554–3566, 2007. First published February 28, 2007; doi:10.1152/jn.00061.2007. Neurons in the macaque supplementary eye field (SEF) fire at different rates in conjunction with planning saccades in different directions. They also exhibit object-centered spatial selectivity, firing at different rates when the target of the saccade is at the left or right end of a horizontal bar. To compare the rate of incidence of the two kinds of signal, and to determine how they combine, we recorded from SEF neurons while monkeys performed a task in which the target (a dot or the left or right end of a horizontal bar) could appear in any visual field quadrant. During the period when the target was visible on the screen and the monkey was preparing to make a saccade, many neurons exhibited selectivity for saccade direction, firing at a rate determined by the direction of the impending saccade irrespective of whether the target was a dot or the end of a bar. On bar trials, many of the same neurons exhibited object-centered selectivity, firing more strongly when the target was at the preferred end of the bar regardless of saccade direction. The rate of incidence of object-centered selectivity (33%) was lower overall than that of saccade-direction selectivity (56%). Signals related to saccade direction and the object-centered location of the target tended to combine additively. The results suggest that the SEF is at a transitional stage between representing the object-centered command and specifying the parameters of the saccade.

INTRODUCTION

The macaque supplementary eye field (SEF), an area on the dorsomedial shoulder of the frontal lobe, is involved in the generation of saccadic eye movements. This is indicated by the fact that intracortical microstimulation at moderate levels of current (40–50 μA) elicits eye movements (Fujii et al. 1995; Lee and Tehovnik 1995; Mann et al. 1988; Martinez-Trujillo et al. 2003a; Martinez-Trujillo et al. 2004; Martinez-Trujillo et al. 2003b; Missal and Heinen 2001, 2004; Mitz and Godschalk 1989; Russo and Bruce 1996, 2000; Schall 1991a,b; Schlag and Schlag-Rey 1985, 1987b; Schlag et al. 1992; Schlag-Rey et al. 1997; Tremblay et al. 2002). It has long been thought that the SEF serves motor functions and that SEF neurons represent saccade direction with respect to a motorically relevant egocentric reference frame, either retina-centered or head-centered. Electrical stimulation at some sites elicits saccades of fixed direction regardless of initial gaze angle, a result suggestive of retina-centered coding (Martinez-Trujillo et al. 2003a, 2004; Russo and Bruce 1993; Schlag and Schlag-Rey 1987a,b). Electrical stimulation at other sites elicits saccades to a fixed endpoint, as expected from head-centered coding (Bon and Lucchetti 1992; Lee and Tehovnik 1995; Mann et al. 1988; Mitz and Godschalk 1989; Schall 1991a; Schlag and Schlag-Rey 1985, 1987a,b; Tehovnik and Lee 1993; Tehovnik and Slocum 2000; Tehovnik and Sommer 1996, 1997; Tehovnik et al. 1994, 1998, 1999). Likewise, some neurons are selective for saccades in a fixed direction regardless of starting point, as expected from retina-centered coding (Russo and Bruce 1996), whereas others are selective for saccades that bring the gaze to a given angle, as expected from head-centered coding (Mann et al. 1988). Recent studies, including studies of head-unrestrained animals, showed that the nature of the egocentric reference frame may vary regionally within the SEF (Martinez-Trujillo et al. 2004; Park et al. 2006).

Recent studies also provide evidence that the SEF serves cognitive as distinct from motor functions. In particular, they show that SEF neurons are sensitive to the location of a saccade target as determined relative to an external (object-centered) reference frame. Around half of SEF neurons exhibit object-centered spatial selectivity. These neurons fire differentially before saccades to the right or left end of a horizontal bar even with the physical direction of the saccade held constant (Moorman and Olson 2007; Olson and Gettner 1995, 1999; Olson and Tremblay 2000; Tremblay et al. 2002). Initial reports describing this phenomenon received support from recent reports by several groups (Breznen et al. 2004; Horwitz et al. 2004).

Is it possible that the SEF contains two populations of neurons, one specifying target location with respect to object-centered space and the other specifying saccade direction with respect to retina-centered or head-centered space? Previous studies revealed a few neurons sensitive to both the object-centered location of the saccade target and the direction of the
saccade (Moorman and Olson 2007; Olson and Gettner 1995, 1999; Olson and Tremblay 2000; Tremblay et al. 2002). However, what is not clear is whether the general trend is for object-centered and saccade-direction signals to combine or to remain segregated. Nor is it clear, in cases where they do combine, how they combine, for example, whether they do so by an additive or a multiplicative rule. These issues could not be addressed in previous studies because they used only the ends of bars as targets and because the bars were presented only in a restricted sector of the upper visual field. To resolve them, we have now monitored neuronal activity in the SEF while monkeys plan saccades in directions distributed around the clock to targets including both dots and the right and left ends of horizontal bars.

METHODS

Subjects

Two adult male rhesus monkeys were used (Macaca mulatta; laboratory designations Bi and Ro hereafter referred to as M1 and M2). Experimental procedures were approved by the Carnegie Mellon University Animal Care and Use Committee and were in compliance with the guidelines set forth in the United States Public Health Service Guide for the Care and Use of Laboratory Animals.

Preparatory surgery

At the outset of the training period, each monkey underwent sterile surgery under general anesthesia maintained with isoflurane inhalation. The top of the skull was exposed, bone screws were inserted around the perimeter of the exposed area, a continuous cap of rapidly hardening acrylic was laid down so as to cover the skull and embed the heads of the screws, a head-restraint bar was embedded in the cap, and scleral search coils were implanted on the eyes, with the leads directed subcutaneously to plugs on the acrylic cap (Robinson 1963). After initial training, a 2-cm-diameter disk of acrylic and skull, centered on the midline of the brain roughly at anterior 21 mm (Horsley–Clarke coordinates), was removed and a cylindrical recording chamber was cemented into the hole with its base just above the exposed dural membrane.

Task

Each trial of the bar-dot task proceeded through the following stages: attainment of central fixation (Fig. 1B1); presentation of a foveal cue instructing the monkey whether the saccade target would be the left or right end of a bar or a dot (Fig. 1B2); a pre-target-onset delay period (Fig. 1B3); onset of a target display, either a bar or a dot, which remained visible during a post-target-onset delay period (Fig. 1B4); offset of the central fixation spot (Fig. 1B5); and execution of a saccade (Fig. 1B6) followed at a random interval in the range 0–300 ms by disappearance of the display and juice delivery. The central and peripheral fixation windows were 5 × 5°. The size of the window was selected to ensure that if the monkey’s gaze landed anywhere on the right half of the bar the response would be classified as bar-right and if it landed anywhere on the left half the response would be classified as bar-left. This degree of tolerance was not strictly necessary. Under each trial condition, in each monkey, across all data collection sessions, the SD of the displacement of the saccade’s endpoint from the target averaged <1° with respect to the horizontal axis and likewise with respect to the vertical axis. The 24 conditions (eight dot, eight bar-left, and eight bar-right; Fig. 1A) were interleaved randomly, subject to the constraint that one trial conforming to each condition had to be completed successfully before the beginning of the next block of 24 trials. Data collection continued until 16 trials had been completed under each condition unless the neuron was lost. In the event of the neuron’s being lost, the data were retained and included in the database for subsequent analysis if at least eight trials had been completed successfully under each condition.

Stimuli

GEOMETRY. The displays were identical for the two monkeys but the distance from the eyes to the monitor was less for M2 by a factor of 0.96. In analyzing saccade trajectories, we scaled-up data from M2 by a factor of 1.04 to achieve register with data from M1. The values given here are for M1. The fixation spot was a 0.43 × 0.43° white square presented at the center of the screen. The foveal color cue was a 1.7 × 1.7° gray, green, or red square. The bar display consisted of two 1.3 × 1.3° gray squares centered on the ends of a horizontal gray bar 5.7° long and 0.28° thick. The bar display was centered at one of eight locations 11.4° above or below the 0° horizontal meridian and 8.5 or 14.2° to the right or left of the zero degree vertical meridian. The dot display consisted of a single 1.3 × 1.3° gray square placed at a location 16.1° eccentric along one of eight rays emanating from the fixation point at 45° intervals. In consequence of the preceding constraints, there were four points, located at 16.1° eccentricity along 45° oblique rays emanating from the fixation point, at which could appear a solitary dot target, a dot forming the left end of a bar, or a dot forming the right end of a bar (Fig. 1A). This design feature was critical because it allowed analysis of neuronal activity accompanying

FIG. 1. Bar-dot task. A: there were 8 conditions in which the target was at the left end of a bar, 8 in which the target was a dot, and 8 in which the target was at the right end of a bar. Data analysis focused on 12 conditions (shown in black) in which the saccade was directed along one of the 45° obliques to a location that could be occupied by a target of any of the 3 types. B: sequence of events during the trial: 1) a white fixation spot appeared at the center of the screen and monkey achieved foveal fixation; 2) after 200 ms, the fixation spot was replaced by a cue the color of which instructed the monkey whether to prepare a saccade to the left end of a bar, a dot, or the right end of a bar; 3) a delay ensued; 4) the target display (in this example, a bar in the upper right quadrant) appeared and remained on during an ensuing delay period; 5) offset of the fixation spot served as an imperative cue; 6) the monkey was required to make a saccade directly to the target. C: a green, red, or gray foveal cue instructed the monkey to prepare a saccade to the left end of a bar, a dot, or the right end of a bar.
a saccade to the same dot as a function of whether the dot was solitary or at the left or right end of a bar.

LUMINANCE AND HUE. The fixation point had a luminance of 83 cd/m² and CIE x and y chromaticity coefficients of 0.28 and 0.32. The red cue and target had a luminance of 33 cd/m² and CIE x and y chromaticity coefficients of 0.33 and 0.17. The green cue and target had a luminance of 67 cd/m² and CIE x and y chromaticity coefficients of 0.25 and 0.66. The gray bar and targets had a luminance of 57 cd/m² and CIE x and y chromaticity coefficients of 0.27 and 0.31.

**Single-neuron recording**

At the beginning of each day’s session, a varnish-coated tungsten microelectrode with an initial impedance of several megohms at 1 kHz (FHC, Bowdoinham, ME) was advanced vertically through the dura into the immediately underlying cortex using a hydraulic microdrive (Narashige, Tokyo, Japan). The electrode could be placed reproducibly at points forming a square grid with 1-mm spacing (Crist et al. 1988). Single neurons were isolated using both on-line and off-line template-matching and principal components analysis sorting (Plexon, Dallas, TX).

**Behavioral control and data collection**

All aspects of behavioral procedure, including presentation of stimuli, monitoring of eye movements, and delivery of reward, were under the control of a Pentium-based computer running Cortex software (http://www.cortex.salk.edu). Eye position was monitored by means of a scleral search coil system (Riverbend Instruments, Birmingham, AL). The X and Y coordinates of eye position were stored at 10-ms intervals. Stimuli generated by an active matrix LCD projector were rear-projected onto a frontoparallel screen 25.4 cm (M1) and 24.5 (M2) cm from the monkey’s eyes. Reward in the form of a scleral search coil system (Riverbend Instruments, Bir-

**Analysis of behavioral performance**

Behavioral data, including percent-correct score and reaction time, as well as saccade velocity, amplitude, and landing points, were calculated for each trial in both tasks. These data were compared across tasks to determine the behavioral effect of changes in task requirements. In all cases, significant differences in behavioral data were assessed using t-test or Kolmogorov–Smirnov (KS) tests as appropriate (P < 0.05).

**Analysis of saccade metrics**

The aim of this step was to characterize the properties of the saccade executed on each trial. First, the direction of gaze was determined for each 10-ms bin during a 500-ms epoch beginning with offset of the fixation spot. Then the instant of maximal velocity was identified by finding the pair of adjacent 10-ms bins (B_m and B_m+1) for which the displacement of the eye in degrees of visual angle (ΔE_v) was maximal. The maximal velocity, in degrees of visual angle per second, was given by 100 × ΔE_v. The start of the saccade was identified by moving backward in time until encountering a pair of bins, B_s and B_s+1, for which ΔE_v < ΔE_v/4. Saccadic reaction time was taken as the interval between offset of the fixation spot and the beginning of bin B_s+1. The finish of the saccade was identified by moving forward in time until encountering a pair of bins, B_f and B_f+1, for which ΔE_v < ΔE_v/4. Saccade amplitude was taken as the distance in degrees of visual angle between eye positions recorded at B_s and B_f+1. The final position of the eye was estimated on the basis of B_t+1 so as to allow time for asymptotic deceleration without exceeding the minimal reaction time for any corrective saccade.

**Analysis of neuronal activity**

To characterize the dependency of neuronal activity on the direction of the saccade and the object-centered location of the target, we carried out ANOVAs on data from the post-target-onset epoch (target onset + 100 ms to fixation point offset + 100 ms). This epoch was chosen for analysis because during it the monkey had information about both saccade direction and object-centered location. The offset of 100 ms from key events was included to take into account the approximate latency with which visual events affect firing in the SEF. In the case of bar trials, there were two factors: saccade direction and the object-centered location of the target. In the case of dot trials, there was one factor: saccade direction. The criterion for significance was taken as P < 0.05 unless otherwise stated. In comparing counts of neurons exhibiting significant effects, we used a χ² test. In all such cases, if there was only one degree of freedom, we incorporated a Yates correction.

**Multiple regression analysis**

To determine whether firing rate was correlated with object-centered location independently of any effect arising from subtle variations in saccades between bar-left and bar-right trials, we performed a multivariate regression analysis, fitting three models to data collected from each neuron during trials in which the target (the right or left end of a bar) appeared at a given screen location

\[ Y = \beta_0 + \beta_1 \text{Obj} + \beta_2 \text{Vel} + \beta_3 \text{Amp} + \beta_4 \text{Xpos} + \beta_5 \text{Ypos} \]

where \( Y \) represents the firing rate measured during the post-target-onset period (target onset + 100 ms to saccade initiation + 100 ms); \( \text{Obj} \) is the object-centered location (0 or 1 for bar-left or bar-right); \( \text{Lat} \) is latency (from fixation spot offset); \( \text{Vel} \) is peak velocity; \( \text{Amp} \) is amplitude; and \( \text{Xpos} \) and \( \text{Ypos} \) represent the final x and y landing positions, respectively. Having fitted the parameters of each model to a neuron’s data, we determined, using an F-test, whether the full model (model 1), when compared with each of the reduced models (models 2 and 3) accounted for significantly more of the variance in the data than could be explained by its larger number of degrees of freedom. If model 1 provided a significant improvement over model 2, we concluded that neuronal activity depended significantly on object-centered location independently of any tendency for saccade variations in the saccade. We computed F as

\[
F = \frac{(SS_{reduced} - SS_{full})}{DF_{reduced} - DF_{full}} \times \frac{DF_{full}}{SS_{full}}
\]

where, for both the full and the reduced models, SS is the residual sum of squares obtained on fitting the model to the data and DF is the number of degrees of freedom on which SS is based (n − p − 1, where n is the number of trials and p is the number of free parameters in the model).

**Characterization of recording sites**

The location of the recording sites relative to gross morphological landmarks was assessed by analysis of structural MR images. Scanning was carried out in a Bruker 4.7-T magnet in which the anesthetized monkey was supported by an MR-compatible stereotaxic device. Fiducial marks made visible by means of a contrast agent included the centers of the ear bars and selected locations inside the
recording chamber. Frontoparallel and parasagittal slices (thickness 2 mm) were collected over the entire extent of the cerebral hemisphere. To determine the location of recording sites relative to functional divisions of cortex, we mapped out regions under each chamber from which oculomotor responses could be elicited at low threshold (≤50 μA) by electrical microstimulation (1.65-ms biphasic pulses delivered through the recording microelectrode at a frequency of 300 Hz in 200-ms-long trains).

RESULTS

The bar-dot task

Data were collected in the context of a single task in which, on interleaved trials, the target could be either a dot, as in standard oculomotor tests, or the right or left end of a horizontal bar, as in previous studies demonstrating object-centered spatial selectivity (Fig. 1). A foveal cue presented early in each trial (Fig. 1B, panel 2) instructed the monkey (by its color) concerning the nature of the response required at the end of the trial, either a saccade to a dot (gray cue) or a saccade to the left or right end of a bar (green or red cue, respectively). After a delay of 400–600 ms (Fig. 1B, panel 3), the target appeared—either a dot at one of eight possible locations (if the cue had been gray) or a bar at one of eight possible locations (if the cue had been green or red) (Fig. 1A). After a further delay of 600–800 ms (Fig. 1B, panel 4), offset of the foveal fixation spot signaled the monkey to execute a saccade to the instructed location (Fig. 1B, panel 5).

The essential aim of using this task was to allow analysis of how neuronal activity depended on the combination of two independent factors: saccade direction and the object-centered location of the target. To permit characterizing neuronal selectivity for saccade direction, the location of the target on the screen was allowed to vary around the clock—a feature unique to this study compared with previous studies characterizing object-centered spatial selectivity in the SEF (Moorman and Olson 2007; Olson and Gettner 1995, 1999; Olson and Tremblay 2000; Tremblay et al. 2002). Within the full set of 24 trial conditions, there was a subset of 12 conditions (targets and saccade vectors indicated by dark shading in Fig. 1A) that represented the full crossing of four saccade directions (the four 45° obliques) with three target types (dot, bar-left, and bar-right). Data analysis focused on this subset of conditions because, within it, saccade direction and the nature of the target were fully counterbalanced.

Behavior

PERCENT-CORRECT SCORE. The score for each type of target (dot, bar-left, or bar-right) during each session was taken as the number of trials on which the monkey made a saccade to the correct target expressed as a percentage of all trials on which he made any saccade in response to fixation spot offset). The monkeys performed somewhat better under dot than under bar conditions. M1 and M2 scored 99 and 98%, respectively, under dot conditions, whereas under bar-left conditions the scores were 96 and 89% and under bar-right conditions they were 94 and 86%. In both monkeys, the tendency for the percent-correct score to vary across target types was significant (Kruskal–Wallis, P < 0.01) and the significance was revealed by post hoc tests to depend on the comparison between dot and bar conditions (KS, P < 0.01) rather than on the comparison between bar-right and bar-left conditions (KS, P > 0.05). It is not surprising that performance was better overall on dot than on bar trials because the monkey could simply make a saccade to the single visible target on a dot trial whereas, on bar trials, he had to select one end of the bar on the basis of a rule conveyed by a cue presented early in the trial and held in working memory over the course of the delay.

REACTION TIME. We computed the mean, for each type of target in each session, of the interval between when the fixation spot was extinguished and the saccade began. The monkeys were free to respond as soon as the fixation spot vanished. We had introduced temporal jitter (in the range 400–600 ms) into the delay period between onset of the target and offset of the fixation spot to discourage anticipatory saccades. Nevertheless, it is clear from the short durations of the reaction times that the monkeys were engaging in anticipatory behavior. In M1, the mean reaction time on dot, bar-left, and bar-right trials was 118, 101, and 106 ms, respectively. In M2, the corresponding values were 139, 105, and 80 ms. In each monkey, all pairwise differences between conditions achieved significance (Kruskal–Wallis with post hoc KS, P < 0.01).

SACCADIC LANDING POSITION. To assess whether there was a consistent discrepancy between the landing point of the saccade and the location of the target, we computed the mean location of the landing point under each condition during each electrophysiological data collection session and then computed the means across sessions. We found, as expected, that saccades to a target at a given location terminated in close proximity to the target regardless of its nature. However, on bar trials, the landing point varied slightly as a function of whether the target was the left or right end of a bar. In particular, the eyes deviated slightly from the end of the bar toward its center, with the result that they landed farther to the right on bar-left trials and farther to the left on bar-right trials. The mean horizontal difference in landing position on bar-left and bar-right trials was 1.3° in M1 and 1.8° in M2. This effect was previously reported (Moorman and Olson 2007; Olson and Tremblay 2000).

Single-neuron recording

We recorded bilaterally from a total of 233 neurons in the SEF of two monkeys (129 and 104 neurons in M1 and M2, respectively). All recording sites (as shown in Fig. 2) were within a region, straddling the interhemispheric midline 4–8 mm rostral to the genu of the arcuate sulcus, from which eye movements could be elicited by microstimulation at low levels of current (≤50 μA). They thus met criteria for assignment to the SEF as established in classic studies (Russo and Bruce 1993, 2000; Schlag and Schlag-Rey 1985, 1987a,b).

Selectivity for the object-centered location of the target

Some SEF neurons exhibited robust selectivity for the object-centered location of the target. The neuron of Fig. 3A is an example. It fired much more strongly on trials in which the monkey had been instructed to select the right end of the bar as a target than on trials in which the instruction had been to select

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the bar’s left end. It did so both before onset of the bar, when the monkey knew the object-centered location of the target but could not yet know the direction of the saccade (Fig. 1B, panel 3), and after onset of the bar, when both the target’s object-centered location and the direction of the saccade were known (Fig. 1B, panel 4). It is on activity during the post-target-onset epoch that the bulk of the subsequent data analysis will focus. Inasmuch as both the direction of the saccade and the target’s object-centered location were known during this epoch, we are in a position to ask whether the two kinds of information simultaneously affected neuronal activity and, if so, how the two influences interacted.

To assess the dependency of firing rate on the object-centered location of the target, we carried out an ANOVA on data collected from each neuron during trials in which the target was the left or right end of a bar. The analysis was confined to the post-target-onset epoch, when both the saccade direction and the object-centered location of the target were known. It was confined to conditions in which the targeted end of the bar, whether left or right, was at one of the four standard locations (black arrows in Fig. 1A). Across these conditions, the object-centered location was fully counterbalanced against the saccade direction. Results are presented in Table 1. The key finding is that firing was significantly dependent on object-centered location in 76/233 (33%) of neurons.

Could SEF neurons have exhibited object-centered selectivity simply because they were sensitive to subtle differences between saccades to the left and right ends of bars? This was ruled out in a previous study (Tremblay et al. 2002), although the range of target locations in that study was more restricted than that in the present case. To resolve this issue, we carried out a multivariate regression analysis, factoring out the impact of object-centered location from the impact of several saccadic attributes including latency, velocity, amplitude, and the horizontal and vertical landing positions. The analysis focused on 76 neurons exhibiting a significant main effect of object-centered location during the post-target-onset epoch. Each neuron contributed one set of data for each quadrant; thus the analysis concerned 304 cases. This analysis lacked the statistical power of the ANOVA on the basis of which the neurons had originally been classified in consequence of the data’s having been divided into quadrant-specific subsets. Nevertheless, the general trend was clear. The neuronal firing rate was much more frequently dependent on object-centered location than on the parameters of the saccade. There was a significant dependency on object-centered location with saccade metrics factored out in 86 cases. The converse was true in only 20 cases. In only seven of the latter cases did firing depend solely on saccade parameters.

We conclude that the firing of SEF neurons was genuinely dependent on the object-centered location of the target even under the unique conditions of the present experiment, notably the requirement that monkeys make saccades to bar targets in all four visual-field quadrants.

**Selectivity for the direction of the impending saccade**

Some SEF neurons were robustly selective for the direction of the impending saccade. The neuron of Fig. 3A is an example. After onset of the target, which determined the direction of the impending saccade, this neuron fired strongly in the event that the planned saccade was up and to the right but not otherwise. It did so irrespective of whether the saccade was to be directed to a dot or to the right or left end of a bar.

To assess the dependency of firing rate on saccade direction, we carried out ANOVAs on data collected from each neuron during dot and bar trials. Both analyses were confined to data collected in the epoch that the bulk of the subsequent data analysis will focus. Inasmuch as both the direction of the saccade and the target’s object-centered location were known during this epoch, we are in a position to ask whether the two kinds of information simultaneously affected neuronal activity and, if so, how the two influences interacted.

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collected during trials requiring saccades in the four 45° oblique directions (black arrows in Fig. 1A) because those were the directions in which the monkeys executed saccades to both dot and bar targets. Selectivity for saccade direction turned out to be common under both dot and bar conditions (Tables 1 and 2). When a dot was the target, 105/233 (45%) of neurons exhibited significant selectivity for the direction of the impending saccade during the post-target-onset epoch. The corresponding rate of incidence on bar trials was 131/233 (56%). The tendency for saccade-direction selectivity to occur more

![Bar Left](Fig_3_A.png)

![Dot](Fig_3_B.png)

![Bar Right](Fig_3_C.png)

**FIG. 3.** Firing rate as a function of time during the trial under 12 critical conditions for 3 representative neurons. A: a neuron sensitive primarily to the object-centered location of the target, firing most strongly on bar-right and least strongly on bar-left trials. B: a neuron sensitive primarily to the direction of the impending saccade, firing most strongly before saccades up and to the right regardless of whether they are directed to the left end of a bar, a dot, or the right end of a bar. C: a neuron considerably sensitive to both the object-centered location of the target and the direction of the impending saccade, firing most strongly when the target is the left end of a bar if the saccade is in a leftward direction. For each neuron, the 3 tetrads of panels represent data collected when the target was at the left end of a bar (left), was a dot (middle), or was at the right end of a bar (right). In each tetrad of panels, the location of each component panel corresponds to the direction of the required saccade, so that the panel up and to the right represents data collected under a condition requiring a saccade up and to the right and so on. In each panel, rasters from successive trials are shown at the top and spike density functions at the bottom. Both are aligned on the time of onset of the target display (either bar or dot). Times of cue onset and saccade initiation varied within the ranges indicated by the correspondingly labeled gray bars.

<table>
<thead>
<tr>
<th>Saccade</th>
<th>Object</th>
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<tbody>
<tr>
<td>C &gt; I</td>
<td>1 &gt; C</td>
</tr>
<tr>
<td>M1 (n = 129)</td>
<td>45 (35%)</td>
</tr>
<tr>
<td>M2 (n = 104)</td>
<td>32 (31%)</td>
</tr>
<tr>
<td>Total (n = 233)</td>
<td>77 (33%)</td>
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Results of an ANOVA carried out on data from all 233 neurons with firing rate as the dependent variable and with the saccade direction (upper left, upper right, lower left, or lower right) and the object-centered location of the target (bar-left or bar-right) as two factors. The analysis was based on data from the post-target-onset epoch (target onset + 100 ms to fixation point offset + 100 ms). “Saccade”: main effect of saccade direction. “Object”: main effect of object-centered location. “Int”: interaction between saccade direction and object-centered location. C > I: stronger firing when the target was in the visual field contralateral to the recording hemisphere (in the case of saccade direction selectivity) or at the end of the bar contralateral to the recording hemisphere (in the case of object-centered selectivity). I > C: the opposite pattern. Neurons preferring ipsilateral and contralateral directions are distinguished in this and subsequent tables as a general point of information. The distinction is not relevant to the main line of argument in the paper. The criterion for significance was $P < 0.05$. 

J Neurophysiol • VOL 97 • MAY 2007 • www.jn.org
TABLE 2. Counts of neurons exhibiting selectivity for the direction of the impending saccade (dot trials, post-target-onset epoch)

<table>
<thead>
<tr>
<th></th>
<th>C &gt; I</th>
<th>I &gt; C</th>
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</thead>
<tbody>
<tr>
<td>M1</td>
<td>39 (30%)</td>
<td>24 (19%)</td>
</tr>
<tr>
<td>M2</td>
<td>27 (26%)</td>
<td>15 (14%)</td>
</tr>
<tr>
<td>Total</td>
<td>66 (28%)</td>
<td>39 (17%)</td>
</tr>
</tbody>
</table>

Results of an ANOVA carried out on data from all 233 neurons with firing rate as the dependent variable and with saccade direction (upper left, upper right, lower left, or lower right) as a single factor. The analysis was based on data from the post-target-onset epoch (target onset + 100 ms to fixation point offset + 100 ms). C > I (or I > C): main effect of saccade direction, with stronger firing overall when the target was in the visual field contralateral (or ipsilateral) to the recording hemisphere. The criterion for significance was $P < 0.05$.

Commonly, the strongest firing overall when the target was in the visual field contralateral (or ipsilateral) to the recording hemisphere. The criterion for significance was $P < 0.05$.

To determine whether the neurons exhibiting selectivity for saccade direction on bar trials did so on dot trials as well, we compared the outcomes of the ANOVAs. We found that there was a very strong tendency for a neuron exhibiting a main effect of saccade direction under one condition to do so under the other condition (Fig. 4A). The concordance was highly significant ($\chi^2$ test, $P \ll 0.0001$).

To assess whether saccade-direction selectivity was concordant between bar and dot trials, we generated for each neuron a vector representing its saccade-direction selectivity. This was obtained by $I$ multiplying unit vectors pointing toward the four target locations by the associated firing rates and 2) summing the resulting vectors. There was a highly significant ($r = 0.88, P \ll 0.0001$) correlation between the magnitudes of the vectors on bar and dot trials (Fig. 4B). Furthermore, the directions matched closely. The median angular difference was only 29° across all neurons and 17° among neurons with significant saccade-direction selectivity (Fig. 4C). Thus the strength of the signal and the preferred direction were conserved across bar and dot trials.

The fact that we collected data during trials requiring saccades to dot targets at eight evenly spaced locations allowed us to resolve an important tangential issue. It has been common to characterize selectivity for saccade direction in the SEF by measuring neuronal activity during saccades to four targets spaced around the clock at 90° intervals (Chen and Wise 1995a,b, 1996, 1997; Olson and Gettner 2002; Olson et al. 2000). To evaluate the dependability of this approach, we compared results obtained with four targets at 90° intervals (as described earlier) to those obtained with eight targets at 45° intervals. The magnitude of the directional vector was positively and highly significantly correlated across the four- and eight-direction analyses ($r = 0.97, P \ll 0.0001$). There was no systematic trend for the estimate of magnitude to be greater or less when based on eight instead of four target locations. The estimates of preferred direction also matched closely: for neurons with a significant main effect of saccade direction, the median difference was 7.4°. Sampling direction with 90° resolution therefore appeared to be an adequate means for characterizing saccadic directional tuning.

Thus many SEF neurons exhibited selectivity for the direction of the planned saccade. Moreover, the magnitude of the signal and the preferred direction were nearly identical across bar and dot conditions.

**Co-occurrence of signals reflecting object-centered location and saccade direction**

The results described up to this point establish that the SEF contained neurons sensitive to both the object-centered location of the target and the direction of the impending saccade. However, they do not address the issue of whether the same neurons carried both kinds of signal. There were in fact cases in which the signals were clearly commingled. For example, the neuron of Fig. 3C was sensitive to both the object-centered location of the target (favoring the bar’s left end) and the direction of the planned saccade (favoring saccades into the left visual field).

To assess how frequently selectivity for saccade direction and the object-centered location of the target coexisted, we carried out an analysis on data from the post-target-onset epoch on bar trials. On counting cases in which a significant (S) or nonsignificant (NS) object-centered effect was combined with

**Fig. 4.** Across all 233 neurons, there was a strong tendency for measures of selectivity for saccade direction obtained with bar targets to match measures obtained with dot targets. A: during the post-target-onset epoch, neurons exhibiting significant saccade-direction selectivity (S) or not exhibiting it (NS) under bar conditions tended to do the same under dot conditions, as indicated by the fact that counts on the match diagonal exceed the number expected on the basis of the null hypothesis that the 2 traits were distributed independently at a highly significant level ($\chi^2$ test, $P \ll 0.0001$). B: estimates of the magnitude of the saccade-direction signal based on trials with bars and dots as targets were correlated at a highly significant level ($P \ll 0.0001$). C: estimates of preferred saccade direction based on firing rates from bar and dot trials were closely similar, as indicated by the fact that the distribution of angular differences was distributed in a small range around zero. This was especially true for neurons selected according to the criterion that they exhibited significant saccade-direction selectivity on dot trials (gray bars).
a significant (S) or nonsignificant (NS) saccade-direction effect (Fig. 5A), we found that matches (S + S and NS + NS) were much more frequent than expected by chance ($\chi^2$ test, $P \ll 0.0001$). This trend, although highly significant, was comparatively weak. Accordingly, we considered the possibility that it might have arisen from either of two causes: 1) the two traits might have been distributed independently across neurons with task-related activity but were correlated as a result of their common confinement to task-related neurons or 2) the two traits might have tended to occur together even within the population of neurons with task-related activity. To decide between these interpretations, we repeated the analysis on a subset of neurons classified by an independent measure as having task-related activity. The criterion for selection was that there should be a highly significant difference in firing rate between the post-target-onset epoch and a baseline epoch preceding onset of the foveal cue ($t$-test, $P < 0.001$). We found that the tendency for neurons exhibiting object-centered selectivity also to exhibit saccade-direction selectivity remained significant even when attention was confined to this population. We conclude that the positive correlation between the two traits was not simply a secondary consequence of their both occurring in neurons with task-related activity.

To assess whether there was a match in amplitude between object-centered and saccade-direction signals, we plotted an index of the magnitude of object-centered selectivity against an index of the magnitude of saccade-direction selectivity across all neurons (Fig. 5B). In a majority of neurons, the saccade-direction signal was stronger. There was a positive and highly significant correlation between the strengths of the two signals ($r = 0.41$, $P \ll 0.0001$).

To determine whether there was a consistent relation between the preferred object-centered location (the right or left end of the bar) and the preferred horizontal direction of the planned saccade (rightward or leftward), we carried out an analysis on data from the post-target-onset epoch on bar trials for all 233 recorded neurons. We computed an index of object-centered selectivity: $(R - L)/(R + L)$, where $R$ and $L$ represent the firing rates on trials when the target was on the bar’s right and left end, respectively. We also computed an index of saccade-direction selectivity: $(R - L)/(R + L)$, where $R$ and $L$ represent the firing rates on trials requiring rightward and leftward saccades, respectively. We then plotted the index of object-centered selectivity against the index of saccade-direction selectivity (Fig. 5C). Correlation analysis revealed a weak ($r = -0.13$) but significant ($P = 0.04$) negative correlation. With consideration restricted to 60 neurons with significant selectivity for both the object-centered location of the target and the direction of the saccade, the effect became extremely weak ($r = -0.02$) and insignificant ($P = 0.9$).

We conclude that signals reflecting the object-centered location of the target and the direction of the impending saccade coexisted in the same population of neurons, varying together in strength but showing no tendency to match with respect to preferred direction.

**Interaction of signals reflecting object-centered location and saccade direction**

The strength of the object-centered signal varied to some degree across saccade direction. An example in support of this point is afforded by Fig. 3C. This neuron fired more strongly on bar-left than on bar-right trials regardless of which quadrant the target was in, although the strength of the signal (the excess of spikes fired on bar-left compared with bar-right trials) was much greater with the target in the left visual field than when it was in the right visual field.

To systematically assess the degree to which the strength of the object-centered signal varied across quadrants, we carried out the following analysis. In each of 76 neurons exhibiting a significant main effect of object-centered location, we ranked the quadrants according to the magnitude of the object-centered signal: $\text{Abs}(R - L)/(R + L)$, where $R$ and $L$ represent the mean firing rates on bar-right and bar-left trials, respectively. Then we normalized the signal in each quadrant to the signal in the best quadrant, retaining the sign, so that a positive normal-

![Fig. 5](https://www.jn.org/content/jn/97/5/3561/F5.large.jpg)

**Fig. 5.** Measures of object-centered selectivity, obtained on bar trials, were correlated with measures of saccade-direction selectivity obtained on the same trials. **A:** during the post-target-onset epoch, neurons exhibiting (S) or not exhibiting (NS) significant dependency on the object-centered location of the target tended to do the same with respect to saccade direction, as indicated by the fact that counts along the match diagonal significantly exceed the number expected on the basis of the null hypothesis that the 2 traits were distributed independently ($\chi^2$ test, $P \ll 0.0001$). **B:** magnitude of the object-centered signal is plotted against the magnitude of the saccade-direction signal for all 233 neurons. SAC Magnitude Index = Abs($B$ - $O$)/(B + O), where B is the firing rate for best saccade direction and O is the firing rate for opposite saccade direction as averaged across bar-left and bar-right conditions. OBJ Magnitude Index = Abs($R$ - $L$)/(R + L), where R is the firing rate on bar-left trials and L is the firing rate on bar-right trials averaged across all 4 saccade directions. C: object-centered directional signal is plotted against the saccade-direction signal for all 233 neurons. SAC Direction Index = $(R - L)/(R + L)$, where R is the average firing rate for saccades into the right visual field and L is the firing rate for saccades into the left visual field as averaged across bar-left and bar-right conditions. OBJ Direction Index = $(R - L)/(R + L)$, where R is the firing rate on bar-right trials and L is the firing rate on bar-left trials as averaged across all 4 saccade directions.
ized value indicated a preference for the same object-centered direction as in the best quadrant. Distributions of values across the ranked quadrants are shown in Fig. 6A. That the median of the distribution moves steadily to the left with progress from the best to the worst quadrant is a direct consequence of the fact that the quadrants were sorted on the basis of the strength of the object-centered signal. Other aspects of the display are not, however, predictable from the sorting procedure and are therefore informative. We note, in particular, that, in every test quadrant, the median of the distribution is displaced significantly away from zero in a positive direction (signed-rank test, \( P < 0.05 \)). This indicates a tendency for the preferred object-centered direction in the test quadrant to match that in the best quadrant. Moreover, for the second- and third-best quadrants, the effect is very nearly total (75/76 and 70/76 neurons). Finally, we constructed a pair of curves representing mean population firing rate as a function of time during the trial under conditions in which the target was at the preferred or the nonpreferred end of the bar (Fig. 6B). Thus neurons tend to exhibit consistent object-centered selectivity regardless of the quadrant into which the saccade is directed but the strength of the signal varies across quadrants.

Are object-centered signals simply added to saccade-direction signals or do they interact with saccade-direction signals in a multiplicative fashion? The idea that the signals combine multiplicatively was advanced in a model of the SEF developed by Deneve and Pouget (2003). Multiplicative models predict that the strength of the object-centered signal will vary across quadrants in a specific way. When the monkey is planning a saccade in the neuron’s most-preferred direction, the object-centered signal will be strongest; when the monkey is planning a saccade in the neuron’s least-preferred direction, the object-centered signal will be weakest. This pattern did indeed appear to be present in some individual neurons including the one shown in Fig. 3C. This neuron’s object-centered signal (the difference in firing rate between bar-left and bar-right trials) was strongest when the bar was in one of the two quadrants (upper left and lower left) eliciting strong firing on dot trials. In general, the results for individual neurons were not as clear as in this exceptional case. Moreover, when we attempted to fit the data from an individual neuron with an additive or multiplicative model, the difference between the fits commonly did not attain significance because of a lack of statistical power. Thus there is a limit to the conclusions we can draw about individual neurons. To circumvent this problem, we adopted a population-based approach.

To determine whether there was a trend across the neuronal population for interactions to be multiplicative, we considered data from all 76 neurons exhibiting a significant main effect of object-centered location during the post-target-onset epoch (Table 1). On the basis of firing on dot trials, we first ranked the quadrants for each neuron from “best” (planning a saccade to a dot in this quadrant was associated with the highest firing rate) to “worst” (planning a saccade to a dot in this quadrant was associated with the lowest firing rate). Then we computed indices of object-centered selectivity (Fig. 7A) and constructed a population histogram (Fig. 7B) for bar trials requiring a saccade into the best, second-best, second-worst, and worst quadrants. Note that in Fig. 7 quadrants are ranked according to how strongly the neuron fired when a saccade was directed into the quadrant, whereas in Fig. 6 they are ranked according to how strong the object-centered signal was when the bar was located in the quadrant. Contrary to the prediction of the multiplicative model, the median of the object-centered indices was actually lower when the target was in the preferred saccadic direction than when it was in the other directions. On fitting a line to object-centered indices plotted as a function of...
quadrant rank, we found that the slope was positive (indicating a trend for the object-centered index to increase as the quadrant rank became worse), although its difference from zero did not approach significance ($P = 0.28$). These results are incompatible with the idea that object-centered signals and saccade-direction signals combine multiplicatively and suggest, rather, that the signals combine in an additive fashion.

It might have been the case that multiplicative interactions were confined to a subset of neurons in which object-centered signals and saccade-direction signals combined nonlinearly. These would have been tagged in the ANOVA by exhibiting a significant interaction between the effects of object-centered location and saccade direction. Interaction effects were present in 58 neurons (Table 1), including 26 that did not exhibit a significant main effect of object-centered location and so were not included in the previous analysis. On analyzing data from these 58 neurons (Fig. 8), we obtained results essentially identical to those obtained in the previous analysis (Fig. 7). In particular, when the indices of object-centered selectivity were plotted as a function of rank, a line fitted to them had a slightly positive slope (indicating a trend for the object-centered index to increase as the quadrant rank became worse), although the effect did not approach significance ($P = 0.79$). Thus even among neurons selected by a criterion that should have been sensitive to multiplicative interactions, there was no multiplicative effect at the population level.

A final piece of evidence favoring an additive over a multiplicative model is the observation that neurons exhibited object-centered spatial selectivity before onset of the bar, when the direction of the impending saccade was not yet known and when, in consequence, no saccade-direction signal was present.

**FIG. 7.** There was no tendency, among 76 neurons exhibiting a significant main effect of object-centered location, for the object-centered signal to be stronger when saccade was in the preferred direction (best quadrant). Quadrants are ranked by the strength of firing on trials when the monkey was planning a saccade to a dot target located in the quadrant. Red curve superimposed on each population histogram in $B$ represents firing on dot trials. All other conventions as in Fig. 6.

**FIG. 8.** Even among 58 neurons exhibiting a significant interaction between the object-centered location of the target and saccade direction, there was no tendency for the object-centered signal to be stronger when the saccade was in the preferred direction (best quadrant). Quadrants are ranked by the strength of firing on trials when the monkey was planning a saccade to a dot target located in the quadrant. All other conventions as in Fig. 7.
If the interaction between object-centered and saccade-direction signals had been multiplicative, then, in the absence of a saccade-direction signal, there should have been no object-centered signal. Contrary to this prediction, 36% of recorded neurons exhibited significant object-centered selectivity during the pre-target-onset epoch (Table 3). These were, for the most part, the same neurons that exhibited object-centered selectivity during the post-target-onset epoch: the occurrence of significant object-centered selectivity during the pre-target-onset epoch was strongly predictive of its occurrence during the post-target-onset epoch ($\chi^2$ test, $P < 0.0001$). Furthermore, the preferred object-centered direction during the pre-target-onset epoch was strongly predictive of the preferred object-centered direction during the post-target-onset epoch ($\chi^2$ test, $P < 0.0001$). All of the preceding observations led us to reject the idea that object-centered selectivity is expressed through multiplicative modulation of saccade-direction signals, leading us instead to the conclusion that, with the exception of some unsystematic nonlinearities, object-centered signals are simply added to saccade-direction signals.

**DISCUSSION**

**Overview**

Previous studies of object-centered spatial selectivity in the SEF were carried out in monkeys making saccades to the ends of horizontal bars at a restricted range of locations in the upper visual field (Moorman and Olson 2007; Olson 2003; Olson and Gettner 1995, 1999; Olson and Tremblay 2000; Tremblay et al. 2002). Because these studies did not place targets at a broad range of screen locations or use dots as well as bars as targets, they did not allow direct comparison of object-centered selectivity and selectivity for saccade direction. By circumventing these limitations, the present study allowed us to directly compare the two forms of selectivity. The results indicate that object-centered and saccade-direction signals are carried by a largely overlapping population of SEF neurons and that the two signals combine, on average, by simple summation.

**Relative incidence of signals reflecting object-centered location and saccade direction**

In previous studies of neuronal activity during performance of a task in which 1) only the ends of bars were targets and 2) the bars were presented only in the upper visual field, fewer SEF neurons were found to be sensitive to saccade direction than to the object-centered location of the target (Moorman and Olson 2007; Olson and Gettner 1995). This result might have arisen from any of several causes, including 1) a genuine preponderance of neurons sensitive to object-centered location, 2) a damping of saccade-direction selectivity when the target was one end of a bar, or 3) the use of a limited range of saccade directions. In light of the current results, the last explanation seems closest to the truth. When saccade direction was allowed to vary around the clock, neurons exhibiting saccade-direction selectivity considerably outnumbered those exhibiting object-centered selectivity and the saccade-direction signals were somewhat more robust. Furthermore, requiring the monkey to make a saccade to the end of a bar rather than to a dot did not in the least reduce saccade-direction selectivity. Instances of significant selectivity were actually more numerous on bar than on dot trials. We conclude that saccade-direction signals are, overall, slightly more robust than object-centered signals even when monkeys are selecting targets by an object-centered rule.

**Gain fields, basis sets, and explicit representations**

Deneve and Pouget (2003) described a simulated neural network, consisting of several layers of units, that is able to perform the object-centered task. Critical to the operation of this network is a hidden layer in which each unit represents a particular combination of object-centered location and saccade direction. Mechanistically, these units operate by a gain-field or multiplicative mechanism, becoming active only if two conditions are met simultaneously: 1) one active input line signals that the neuron’s preferred end of the bar is in the response field and 2) another active input line signals that the instruction on this trial is to move to the preferred end. Computationally, the population of units as a whole can be thought of as forming a basis set representing all possible combinations of object-centered location and saccade direction. Deneve and Pouget suggest that the hidden layer in their network corresponds to the SEF. They argue that if this is so then the representation of object-centered space in the SEF is not explicit, which is to say, not pure. How well does their argument bear up in light of results from the present study?

**Gain fields.** Do SEF neurons have object-centered gain fields? In answering this question, it is helpful to begin by considering the classic case from which the idea of gain fields arose: modulation of visual responses by angle-of-gaze signals in parietal cortex. In parietal areas 7a and LIP, neurons respond to visual stimuli within fixed retina-centered receptive fields and also exhibit changes in firing rate in conjunction with changes in the direction of gaze (Andersen and Mountcastle 1983; Andersen et al. 1985, 1990; Brodtie et al. 1995; Sakata et al. 1980). The function relating firing rate to gaze angle (typically a monotonic function peaking as the gaze achieves maximal eccentricity in some direction) was previously described as a “gain field.” This might be taken as implying that gaze-angle and visual inputs act asymmetrically, with the gaze-angle input modulating the response to visual input. However, there are neural net models that instantiate gain modulation without any functional asymmetry between the two signals (Andersen and Zipser 1988; Zipser and Andersen 1988). In these models, visual and gaze signals sum at the input stage to the hidden unit. Superadditive effects arise when the

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**Table 3. Counts of neurons exhibiting object-centered selectivity (bar trials, pre-target-onset epoch)**

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<tr>
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<th>C &gt; I</th>
<th>I &gt; C</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1 ($n = 129$)</td>
<td>27 (21%)</td>
<td>28 (22%)</td>
</tr>
<tr>
<td>M2 ($n = 104$)</td>
<td>22 (21%)</td>
<td>6 (6%)</td>
</tr>
<tr>
<td>Total ($n = 233$)</td>
<td>49 (21%)</td>
<td>34 (15%)</td>
</tr>
</tbody>
</table>

Results of an ANOVA carried out on data from all 233 neurons with firing rate as the dependent variable and with the object-centered location of the target (bar-left or bar-right) as the factor. The analysis was based on data from the pre-target-onset epoch (cue onset + 100 ms to target onset + 100 ms). C > E: stronger firing when the instruction was to select as target the end of the bar contralateral to the recording hemisphere. I > C: the opposite pattern. The criterion for significance was $P < 0.05$. 

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**Note:** The content provided is a transcription of the text from the image, ensuring that the layout and formatting are preserved as accurately as possible. This approach allows for a natural reading experience, suitable for further analysis or citation.
summed input is converted to an output under conditions in which the strength of the summed input is below the level at which the logistic activation function becomes quasi-linear. If, against this backdrop, we now ask whether SEF neurons have object-centered gain fields, the essential answer is that they do not. On average, across the neuronal population, signals reflecting the object-centered location of the target and the direction of the impending saccade combine additively. In terms of the neural net model described earlier, it is as if 1) the two signals sum linearly at the input stage to the neuron and 2) the values assumed by the summed input remain, across trial conditions, within the range in which the neuron’s activation function is quasi-linear.

**BASIS SETS.** Do SEF neurons form a basis set embodying all possible combinations of object-centered location and saccade direction? Strictly speaking, the answer to this question is “no.” The properties of SEF neurons deviate in at least two ways from the properties of units in the hidden layer of Deneve and Pouget’s model. 1) SEF neurons are not sharply selective for particular conjunctions of object-centered location and saccade direction, often exhibiting object-centered selectivity over several visual-field quadrants. 2) The interaction of object-centered and saccade-direction signals, considered on average across the neuronal population, is additive rather than multiplicative. However, the mere fact that the two kinds of signals are combined in the SEF—even if the pattern of combination deviates from the predictions of the basis set model—does argue, in the general spirit of Deneve and Pouget’s proposal, that the area is at a transitional functional stage between the object-centered command and specification of the direction of the required saccade.

**EXPlicit REPRESENTATION.** Most SEF neurons carry a combination of signals reflecting object-centered location and saccade direction. From the fact that the signals are commingled, it follows that the representation of object-centered space in the SEF is not pure or, to use Deneve and Pouget’s term, not “explicit.” We would note only that few if any representations in the brain are explicit in this stringent sense. The representation of edge orientation in primary visual cortex, for example, which the logistic activation function becomes quasi-linear. If, against this backdrop, we now ask whether SEF neurons have object-centered gain fields, the essential answer is that they do not. On average, across the neuronal population, signals reflecting the object-centered location of the target and the direction of the impending saccade combine additively. In terms of the neural net model described earlier, it is as if 1) the two signals sum linearly at the input stage to the neuron and 2) the values assumed by the summed input remain, across trial conditions, within the range in which the neuron’s activation function is quasi-linear.

**ACKNOWLEDGMENTS**

We thank K. McCracken for excellent technical assistance.

**GRANTS**

This work was support by National Eye Institute (NEI) Grant ROI EY-11831. D. Moorman received stipendary support from National Institute of Mental Health Grant F31 MH-65052. Technical support was provided by an NEI Core Grant EY-08098. Collection of MR images was supported by a Division of Research Resources Grant P41 RR-03631.

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