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31. We thank the U.S. Office of Naval Research for their long-term support of this work. In addition this work was supported by the Air Force Office of Scientific Research, the Gatsby Foundation, the Medical Research Council, the National Institute of Mental Health, the National Science Foundation, the European Community, the Human Frontiers Science Program, the Wellcome Trust, and the Royal Society. We thank J. Anderson for reconstructions of neurons in cat striate cortex and G. Holt for help with the graphics.

16 February 1995; accepted 5 June 1995

Object-Centered Direction Selectivity in the Macaque Supplementary Eye Field

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Object-centered spatial awareness—awareness of the location, relative to an object, of its parts—plays an important role in many aspects of perception, imagination, and action. One possible basis for this capability is the existence in the brain of neurons with sensory receptive fields or motor action fields that are defined relative to an object-centered frame. In experiments described here, neuronal activity was monitored in the supplementary eye field of macaque monkeys making eye movements to the right or left end of a horizontal bar. Neurons were found to fire differentially as a function of the end of the bar to which an eye movement was made. This is direct evidence for the existence of neurons sensitive to the object-centered direction of movements.

Many behaviors and mental processes require the use of spatial information defined in an object-centered reference frame. Visual object recognition, for example, is generally thought to require explicit encoding of the locations of parts relative to the object (*1*). Visually guided motor behavior also depends on object-centered information. The hand, in reaching around an object, must move along a trajectory defined relative to the object. Likewise, the eyes, during scanning, may be directed to a featureless point defined solely by its relation to visible details elsewhere in the scene. Evidence that localized groups of neurons represent specific parts of object-centered space has been provided by studies of visual neglect in humans. In many cases of hemifield neglect, patients overlook features on the contralesional side of a visible object even when the neglected side of the object has been viewed through the good hemifield (*2*). Object-centered neglect must arise from the loss of neurons that mediated awareness of one half of the current reference object rather than one half of visual space or the retina. Such neurons could be expected to have sensory receptive fields or motor action fields defined with respect to the current reference object. Previous single-unit studies have produced only limited evidence for the existence of neurons with these properties (*3*). In this report, we demonstrate that neurons in the supplementary eye field (SEF) of the macaque monkey encode eye-movement direction with respect to an object-centered reference frame.

The SEF is an oculomotor area on the dorsomedial surface of the frontal lobe. Electrical stimulation of the macaque SEF elicits eye movements with complex properties, including dependence on initial orbital position (*4*). Neurons in the SEF discharge preferentially before and during saccades in a restricted range of directions (*5*). Some SEF neurons are selectively active during the learning of associations between visual-pattern cues and eye-movement directions (*6*). These observations suggest that the SEF mediates processes of comparatively high order that are related to oculomotor control.

We prepared two male macaque monkeys for single-unit recording by standard methods (*7*). We mapped out the SEF in both hemispheres of one monkey and in the right hemisphere of the second monkey (*8*). To assess object-centered direction selectivity, we trained the monkeys to perform an oculomotor task in which the object-centered direction of eye movements (to the left or right end of a horizontal target bar) could be dissociated from their orbit-centered direction (leftward or rightward in the orbit). The sequence of events during a representative trial is shown in Fig. 1A. A cue presented early in each trial (a spot superimposed on one end of a sample bar) instructed the monkey to look to the left or right end of the target bar. The target bar subsequently appeared at one of three locations (Fig. 1B). Across eight possible conditions (Fig. 1C), eye-centered direction (leftward or rightward in the orbit) was fully counterbalanced against object-centered direction (to the left or right end of the bar) (*9*).

Twenty-nine neurons in one monkey were studied while the monkey performed this task. The neuron shown in Fig. 2 fired more strongly when the eye movement was to the left end of the target bar (left column) than when it was to the right end (right column). This was true regardless of the orbital direction of the movement (rightward in the first and third rows; leftward in the second and fourth rows). Firing was stronger in bar-left trials, not only during the period between the cue and the

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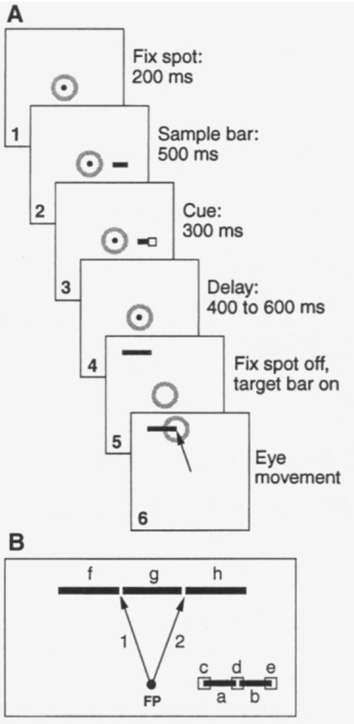
target, when the monkey was remembering an abstract instruction, but also around the time of the response, when the monkey was preparing and executing an eye movement to the target. In each of the 29 neurons, an analysis of variance (ANOVA) was carried out to assess the dependence of neuronal firing rate on the direction of the eye movement as defined with respect to the target (right or left end of bar) and with respect to the orbit (rightward or leftward). Separate analyses were carrried out on activity occurring during (i) a "delay" epoch 500 ms long, terminating with onset of the target; (ii) a "preparation" epoch extending from onset of the target to initiation of the eye movement; and (iii) a "response" epoch extending from initiation of the eye movement to a point in time 100 ms after its termination (*10*). The rate of firing showed significant ($P < 0.05$) dependence on bar-centered direction, or a significant interaction of bar-centered and orbit-centered direction, during at least one of the epochs, in 23 out of 29 neurons. Additional statistical information is given in Table 1 and in (*11*). These results indicate that the activity of SEF neurons is influenced to a major degree by the direction of an impending eye movement as defined with respect to the target, regardless of orbital direction (*12*, *13*).

It is striking that bar-centered direction selectivity was present not only during the delay epoch, when only bar-centered information was available, but also during the preparation and response epochs, when the target had appeared and the orbital direction of the impending eye movement was known. However, because the preparation and response periods were comparatively brief in the task described above, bar-centered activity during these periods might be a carry-over of delay-period firing. To ad-



Condition	1	2	3	4	5	6	7	8
Sample bar	b	a	b	a	a	b	a	b
Cue	d	d	d	d	c	e	c	e
Target bar	h	g	g	f	h	g	g	f
Eye movement	2	2	1	1	2	2	1	1
Direction with respect to bar	L	R	L	R	L	R	L	R

Fig. 1. Neurons were tested for object-centered direction selectivity by monitoring of their activity while the monkey performed the task summarized in this figure. (**A**) Panels 1 to 6 represent the screen in front of the monkey during successive epochs of a single trial. The center of the hatched circle indicates the monkey's direction of gaze. All other items are patterns visible to the monkey. Panel 1: A white fixation spot (0.8° by 0.8°) appears at the center of the screen; when the monkey has achieved foveal fixation of this spot, data collection begins. Panel 2: A horizontal red sample bar (4° by 0.2°) appears in the visual field lateral to the fixation spot. Panel 3: A white cue (1.6° by 1.6°) appears superimposed on one end of the sample bar. Panel 4: During an ensuing delay period of variable length, the monkey must remember whether the right or left end of the sample bar was marked by the cue. Panel 5: The fixation spot is extinguished and a horizontal red target bar (8° by 0.4°) simultaneously appears in the upper visual field at one of three possible locations. Panel 6: The monkey must respond by making an eye movement to the end of the target bar corresponding to the cued end of the sample bar. A reward is delivered only if the first eye movement is to the correct end of the target bar and if fixation at this point is maintained until the display is extinguished, 300 to 450 ms later. (**B**) Eight experimental conditions are differentiated by the following features: The sample bar is centered either 8° (a) or 12° (b) to the right of fixation. The cue is centered 6° (c) or 10° (d) or 14° (e) to the right of fixation. The target bar, always at a height of 12°, is centered 8° to the left of fixation (f) or directly above fixation (g) or 8° to the right of fixation (h). The required eye movement is made either 12° up and 4° to the left (1) or 12° up and 4° to the right (2). The fixation spot (FP) is presented at the center of the screen in all conditions. (**C**) For each of the eight conditions, the location of the cue, the location of the target bar, and the direction of the required response are given. Note that the orbit-centered direction of the eye movement (1 versus 2) and its object-centered direction (L versus R) vary orthogonally across conditions.

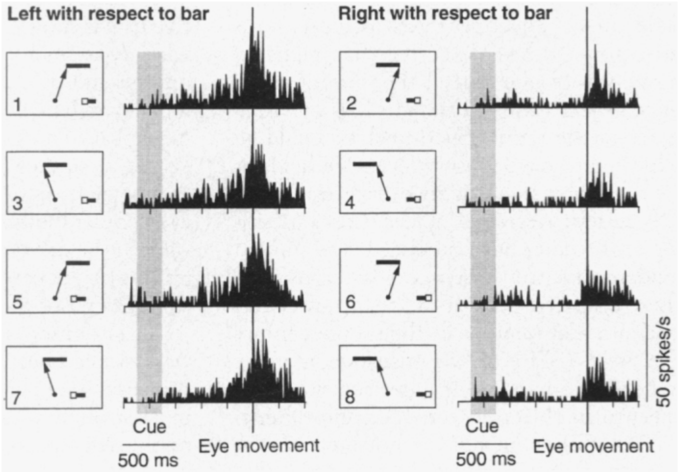


Fig. 2. Data collected from a neuron during the test for object-centered direction selectivity. Each panel represents the location of sample bar, location of cue, location of target bar, and direction of the eye movement for one condition. Panels are numbered according to the conditions listed in Fig. 1C. Each histogram represents neuronal firing rate as a function of time during successfully completed trials for the condition indicated to its left. Data from successive trials are aligned on the time of onset of the eye movement (vertical line). The time of onset of the cue (vertical shaded bar) varied across trials because of randomization of the interval between cue onset and target onset. Firing depended primarily on the direction of the eye movement relative to the bar (leftward in the left column; rightward in the right column) and not on its direction relative to the orbit (rightward in rows 1 and 3; leftward in rows 2 and 4). Note that conditions 1 and 2 are matched for both the retinal location of the cue and the orbital direction of the eye movement, as are conditions 3 and 4.

Table 1. Fraction of neurons in which firing rate showed a significant ($P < 0.05$) main effect for eye-movement direction as defined with respect to the target bar (row 1) or the orbit (row 2) or a significant ($P < 0.05$) interaction between these two factors (row 3). A separate two-factor ANOVA was carried out for each of three trial epochs defined in the text. Twenty-three out of 29 neurons exhibited a significant effect of bar-centered direction (see text). Out of these 23 neurons, 15 showed only a main effect, 1 showed only an interaction effect, and 7 showed both types of effect; 5 showed a main or interaction effect in all three periods, 12 showed an effect in two periods, and 6 showed an effect in only one period. A neuron exhibiting more than one type of effect or exhibiting effects in more than one period contributed to multiple entries in this table. Orbit-centered effects during the delay period (left column, second and third rows) must have been false positives because orbital direction was unknown to the monkey until the appearance of the target bar at the end of the delay period. The number of positive observations (two) does not deviate significantly from the number of false positives expected on the basis of the significance level used and the number of neurons tested.

	Delay period	Preparation period	Response period
Bar-centered	18/29	9/29	16/29
Orbit-centered	1/29	6/29	3/29
Interaction	1/29	2/29	6/29

dress this issue, we recorded from 73 neurons in two monkeys performing a version of the bar task with a second delay period. This version of the task was identical to the one described above except that the fixation spot remained on for more than half a second after onset of the target bar. We found that significant ($P < 0.05$) dependence on bar-centered direction, or a significant interaction of bar-centered and orbit-centered direction, was at least as frequent (38 out of 73 neurons) during the second delay period, following onset of the target bar, as during the first delay period, before its appearance (25 out of 73 neurons). Additional statistical information is given in Table 2 and in (*14*). The finding that SEF neurons carry bar-centered signals even when the orbital direction of the impending eye movement is known establishes that they are fundamentally different from classic oculomotor neurons (*15*).

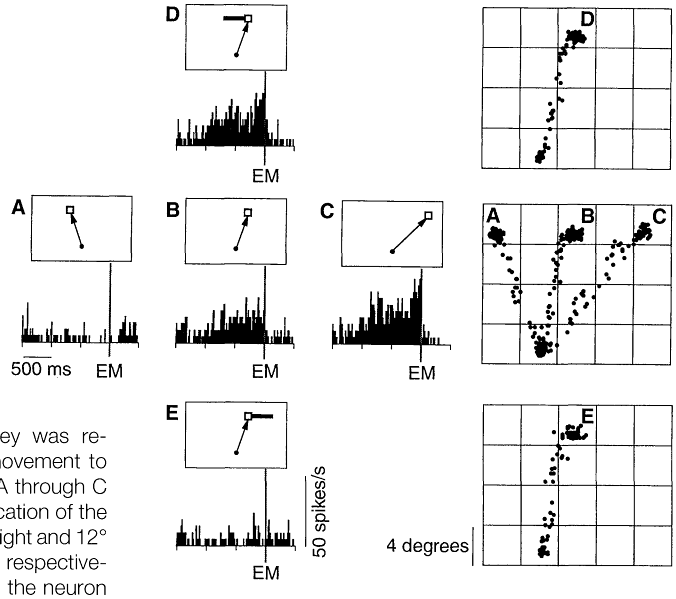


Fig. 3. Data from a neuron exhibiting selectivity for both orbit-centered and object-centered direction in a task not requiring a decision based on object-centered information. In every trial, while the monkey fixated a white central spot, a white target spot came on. The target spot remained on for the duration of the trial. The fixation spot was extinguished after a variable interval (1300 to 1700 ms), whereupon the monkey was required to execute an eye movement to the target spot. Conditions A through C varied with respect to the location of the target (4° left and 12° up, 4° right and 12° up, and 12° right and 12° up, respectively). Across these conditions, the neuron exhibited clear selectivity for orbit-centered direction, firing more strongly before rightward than before leftward eye movements. In conditions D and E, the location of the target was 4° right and 12° up. In these conditions, a bar appeared on the screen 500 ms before the onset of the target and remained on for the duration of the trial. In condition D, the bar was positioned so that the target was superimposed on its right end. In condition E, the bar was positioned so that the target was superimposed on its left end. Although the bar did not serve as a cue or target, its presence markedly affected the activity of the cell. Firing during the delay period was much stronger when the target was on the bar's right end than when it was on the bar's left end. Each histogram represents the average firing rate as a function of time during 16 successfully completed trials for a given condition. Data from successive trials are aligned on the time of eye movement onset (EM, vertical line). The eye movements to each target were highly stereotyped regardless of the presence of the bar. In the panels at the right, the groups of dots labeled A through E represent eye positions sampled at 10-ms intervals during 16 eye movements performed under conditions A through E. Eye movements B, D, and E were nearly identical. Thus, differential activity across conditions B, D, and E cannot be accounted for in terms of differences among the eye movements.

Table 2. Fraction of neurons in which firing rate showed a significant ($P < 0.05$) main effect for eye movement direction as defined with respect to the target bar (row 1) or the orbit (row 2) or a significant ($P < 0.05$) interaction between these two factors (row 3). A separate two-factor ANOVA was carried out for each of three trial epochs. Fifty-six out of 73 neurons exhibited a significant effect of bar-centered direction during at least one trial epoch. Out of these 56 neurons, 30 showed only a main effect, 10 showed only an interaction effect, and 16 showed both types of effect; 13 showed a main or interaction effect in all three periods, 16 showed an effect in two periods, and 27 showed an effect in only one period. A neuron exhibiting more than one type of effect or exhibiting effects in more than one period contributed to multiple entries in this table. Orbit-centered effects during the delay period 1 (left column, second and third rows) must be false positives because orbital direction was unknown to the monkey until the appearance of the target bar at the beginning of delay period 2. The number of observations (three) does not deviate significantly from the number of false positives expected on the basis of the significance level used and the number of neurons tested.

	Delay period 1		Delay period 2		Response period	
	Monkey 1	Monkey 2	Monkey 1	Monkey 2	Monkey 1	Monkey 2
Bar-centered	17/49	6/24	18/49	10/24	23/49	5/24
Orbit-centered	1/49	0/24	13/49	5/24	11/49	4/24
Interaction	0/49	2/24	12/49	3/24	11/49	3/24

In the tasks described so far, monkeys were required to remember an instruction formulated in bar-centered terms. Thus, the bar-centered direction selectivity of SEF neurons might be specific to situations involving active memory of a bar-centered instruction. To assess this possibility, we used a task in which the monkey made a visually guided eye movement to a spot that appeared in isolation in some trials and was superimposed on the end of a bar in others. In each "bar" trial, a bar appeared in isolation for 500 ms; a target spot was then presented on one end of it. During the remainder of the trial, both the bar and the spot remained on. The monkey was required to maintain central fixation until the fixation light was turned off and then to make an eye movement to the target spot. "Spot" trials were identical in all respects except that a bar never appeared. Spot trials were included to permit characterization of orbital direction selectivity under standard conditions and to provide a baseline against which to assess the effects of the bars. Data from a neuron studied while the monkey performed this task are shown in Fig. 3. This neuron displayed direction-selective preparatory activity during the period of more than 1 s between the appearance of the target spot and initiation of the eye movement. In trials when no bar was present, the neuron fired most strongly before rightward eye movements (Fig. 3, conditions A through C). In trials in which the target was a spot superimposed on a bar, the firing rate was enhanced if the bar was positioned so that the spot appeared on its right end (Fig. 3, condition D) and was reduced if the bar was positioned so that the same spot appeared on its left end (Fig. 3, condition E). Statistically significant dependence on bar-centered direction ($P < 0.05$) was present in 24 out of 45 neurons tested by this procedure. We conclude that SEF neurons manifest bar-centered direction selectivity even when the monkey is performing a task that is not dependent on the use of bar-centered information (*16*).

In all of the tasks described above, each eye movement was preceded by the appearance of a spot superimposed on one end of a bar. The configuration of this stimulus (spot on left or right end of a bar) and the bar-centered direction of the impending eye movement (to the left or right end of a bar) were completely correlated across trials. Consequently, neuronal activity varying with bar-centered direction might conceivably represent a pattern-selective visual response or a visual memory signal. To assess this possibility, we trained one monkey to perform a version of the task using colored squares as cues (blue instructing a bar-left response and yellow instructing a bar-right response). In all other respects, this task was identical to the version of the bar task with two delay periods (see above). Electrical activity was monitored in each of 21 neurons during performance of both tasks. Eleven of these neurons exhibited statistically significant dependence on bar-centered direction during the same trial-epoch in both tasks. In all 11 neurons, the preferred bar-centered direction was identical in both tasks (6 neurons favored bar-right and 5 favored bar-left). Thus, neuronal activity was related to the bar-centered direction of the impending eye movement rather than to the physical attributes of the cues.

The finding that neurons of the macaque supplementary eye field exhibit bar-centered direction selectivity in tasks requiring the monkey to look to the right or left end of a horizontal bar provides by far the most robust and direct evidence to date for the existence of cortical neurons that carry object-centered signals.

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3. A few intriguing but ambiguous findings bearing on this issue have been reported. Niki, recording from prefrontal neurons in monkeys trained to reach in alternation for left and right targets, noted that intertrial activity reflected the location relative to the other target, and not just relative to the visual field, of the target chosen during the preceding trial [H. Niki, *Brain Res.* **68**, 197 (1974)]. The activity of these neurons might be construed as encoding the object-centered direction of the previous response if the two targets are thought of as the right and left components of a single object. Connor *et al.* recorded from neurons in area V4 of monkeys performing a spatial attention task [C. E. Connor *et al.*, *Soc. Neurosci. Abstr.* **20**, 1054 (1994)]. They noted that the strength of the response to an optimal stimulus varied as attention was focused to one side or another of the receptive field. They interpret this result as indicating that neurons of V4 are selective for the location of the stimulus with respect to the current focus of attention.
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7. Each monkey was prepared for chronic single-unit recording by standard methods, including surgical implantation of a head-holding device, a recording chamber overlying the SEF, and ocular search coils [R. S. Remmel, *IEEE Trans. Biomed. Eng.* **31**, 388 (1984); D. A. Robinson, *ibid.* **10**, 137 (1963)]. Recordings were made with varnish-coated tungsten electrodes introduced into the cortex through the dura. Penetrations were placed in a square array at 1-mm intervals under guidance of a nylon grid held rigidly in the recording cylinder [C. F. Crist *et al.*, *J. Neurosci. Methods* **26**, 117 (1988)].
8. During each daily session, an electrode was lowered into the SEF. The electrical signal was processed by a template-matching action-potential discriminator, from which pulses were led to the data-collection computer. Before testing for bar-centered direction selectivity, we characterized each neuron in the context of the following standard oculomotor task. Each trial began when the monkey fixated a central spot. Shortly after attainment of fixation, a cue was flashed briefly at one of four peripheral locations (20° right or up or left or down). The monkey was required to wait for approximately 500 ms, until extinction of the fixation spot, to make an eye movement to the cued location. Vigorous, directionally selective task-related activity was taken as evidence that the neuron was in the SEF. We mapped out a zone several millimeters in extent, close to the sagittal midline and approximately 28 mm anterior to the Horsley-Clarke interaural plane, in which neuronal activity conformed to this pattern. This zone was bounded posteriorly and medially by sites at which neurons fired primarily during movements of the face and arm. It was bounded anteriorly and laterally by sites at which little or no neural activity accompanied the monkey's observable movements.
9. The eight conditions were imposed in pseudorandomly interleaved sequence. Data collection commonly continued until 32 trials had been completed successfully for each condition. Analysis was carried out only on data collected during successfully completed trials. During sessions in which neuronal data were collected, the monkey made correct choices on 95% of trials in which a response occurred.
10. These epochs were chosen to allow separate analysis of neuronal activity during periods when the orbital direction of the impending eye movement was not known (delay), could at the earliest have been known (preparation), and was definitely known (response). They do not necessarily coincide with discrete stages of neural processing or behavior.
11. We used two measures to characterize the strength of the bar-centered signal in neurons exhibiting a significant effect of bar direction: (i) The absolute value of the difference $R - L$, between the firing rate during bar-right conditions (R) and the firing rate during bar-left conditions (L). During delay, preparation, and response epochs, respectively, the mean values were: 5.5 ($SD = 4.3$), 10.5 ($SD = 7.6$), and 4.7 ($SD = 3.5$) spikes per second. (ii) The absolute value of $(R - L)/(R + L)$, a measure normalized to the neuron's average firing rate. During delay, preparation, and response epochs, respectively, the mean values were: 0.25 ($SD = 0.16$), 0.37 ($SD = 0.16$), and 0.15 ($SD = 0.10$).
12. Chen and Wise (*6*) recently demonstrated that some SEF neurons preferentially active during eye movements in a certain direction fire especially strongly during a period when the monkey is learning to produce those eye movements in response to a novel visual stimulus, whereas others begin firing only after the association has become established. In light of this finding, it might be argued that SEF neurons showing modulation of activity during performance of our task are mediating arbitrary learned associations between visual stimuli and eye movements. However, our task can be construed as one in which visual stimuli are associated arbitrarily with eye movements only if the cue and the target bar together are considered as a single stimulus. In this view, four combinations of cue and target would be associated with eye movements up and to the left (conditions 1, 3, 5, and 7) whereas four would be associated with eye movements up and to the right (conditions 2, 4, 6, and 8). There are strong arguments against this interpretation. First, bar-selective activity begins before onset of the target. Second, each neuron prefers a set of conditions in which the eye movement is to the same end of the bar but varies in direction as defined with respect to the orbit. Finally, the neuronal pattern of bar-centered direction selectivity is unaffected by manipulations of the testing situation that alter the range of the eye movements produced by the monkey, for instance, incorporation of conditions in which eye movements are directed to the outer ends of target bars f and h (Fig. 1B).
13. Because all eye movements in our task contain an upward component, the question arises whether bar-centered signals represent modulation of activity associated with upward eye movements. This does not appear to be the case. We have observed cases in which a neuron did not fire at all during upward eye movements to a spot target and yet fired vigorously during upward eye movements to the preferred end of a horizontal bar. Moreover, across the entire population of neurons studied, there was no tendency for bar-centered direction selectivity to occur predominantly among neurons that fired preferentially during upward eye movements.
14. Among the 73 neurons studied during performance of this version of the bar task, 26 were in the left hemisphere and 47 were in the right hemisphere. There was a marked preponderance of neurons that fired preferentially in conjunction with eye movements to the end of the bar opposite the recording hemisphere (chi square test; $P < 0.01$). Similarly, in the standard oculomotor test (*8*), there was a marked preponderance of neurons that fired preferentially during eye movements in a contralateral orbital direction (chi square test; $P < 0.01$).
15. Neurons carrying signals related only to saccade amplitude and direction might appear to carry bar-centered signals if a monkey performing the bar task employed a mnemonic strategy based on picturing eye movements. Following a bar-left instruction, for example, the monkey might imagine an eye movement directed to the left in the orbit, with concomitant elevation of activity in cortical oculomotor neurons having leftward preferred directions. However, following onset of the target, the activity of neurons carrying simple oculomotor signals would be reset to reflect the orbital direction of the impending eye movement.
16. Because the monkey was highly trained on other tasks requiring the use of bar-centered information, it is possible that in this task he actively attended to the bar-relative location of the spot despite its irrelevance. This issue could be resolved only by recording from SEF neurons in a monkey performing this task without previous training in tasks requiring the active use of bar-centered information.

17. Supported by grants to C.R.O. from NSF (IBN 9312763) and NIH (RO1 NS27287). S.N.G. was supported by a National Research Service Award postdoctoral fellowship (1 F32 NS09452). We thank F. Castro, C. Cordes, and G. Haynes for technical help; R. Desimone and E. Miller for providing Cortex software and aiding us in its use; C. Colby for comments on the manuscript; and members of the Laboratory of Sensorimotor Research, NIH, and Laboratory of Neuropsychology, NIMH, for their insightful comments on our results. A protocol covering these studies was approved by the Institutional Animal Care and Use Committee of the College of Dental Surgery, University of Maryland at Baltimore, as being in accord with Public Health Service guidelines for the care and use of laboratory animals.

27 March 1995; accepted 12 June 1995