Prefrontal Cortex Neurons Reflecting Reports of a Visual Illusion

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Lebedev, Mikhail A., Diana K. Douglass, Sohie Lee Moody, and Steven P. Wise. Prefrontal cortex neurons reflecting reports of a visual illusion. J Neurophysiol 85: 1395–1411, 2001. When a small, focally attended visual stimulus and a larger background frame shift location at the same time, the frame’s new location can affect spatial perception. For horizontal displacements on the order of 1–2°, when the frame moves more than the attended stimulus, human subjects may perceive that the attended stimulus has shifted to the right or left when it has not done so. However, that misapprehension does not disable accurate eye movements to the same stimulus. We trained a rhesus monkey to report the direction that an attended stimulus had shifted by making an eye movement to one of the two report targets. Then, using conditions that induce displacement illusions in human subjects, we tested the hypothesis that neuronal activity in the prefrontal cortex (PF) would reflect the displacement directions reported by the monkey, even when they conflicted with the actual displacement, if any, of the attended stimulus. We also predicted that these cells would have directional selectivity for movements used to make those reports, but not for similar eye movements made to fixate the attended stimulus. A population of PF neurons showed the predicted properties, which could not be accounted for on the basis of either eye-movement or frame-shift parameters. This activity, termed report-related, began approximately 150 ms before the onset of the reporting saccade. Another population of PF neurons showed greater directional selectivity for saccadic eye movements made to fixate the attended stimulus than for similar saccades made to report its displacement. In view of the evidence that PF functions to integrate inputs and actions occurring at different times and places, the present findings support the idea that such integration involves movements to acquire response targets, directly, as well as actions guided by less direct response rules, such as perceptual reports.

INTRODUCTION

The distinction between the perception of a visual stimulus and use of the same stimulus as a target of movement has received increasing attention in recent years (Boussaoud et al. 1996; Goodale and Haffenden 1998; Goodale et al. 1991, 1994). For example, for disks of slightly different sizes, subjects may perceive that they are of the same size if the larger one is surrounded by large disks and the smaller one by small disks. However, prehension movements to the edges of those disks reflect their actual size, at least to an extent (Aglioni et al. 1995). Although the generality of this finding has been questioned (Brenner and Smeets 1996; Ellis et al. 1999; Pavani et al. 1999; van Donkelaar 1999), similar phenomena have been observed for both reaching (Bridgeman 1992; Bridgeman et al. 1981) and eye movements (Wong and Mack 1981). The present experiment was based on a report by Wong and Mack (1981), who asked subjects to focus attention on a light spot embedded in a relatively large background frame. The spot and frame briefly disappeared from the visual display and were presented again, usually at slightly displaced locations. Under these conditions, the subjects perceived that the light spot, alone, had been displaced. Moreover, the direction of this perceived motion was strongly affected by frame displacements. For example, if the light spot was displaced 1° to the left of its original location, but the frame was displaced 2° to the left, subjects reported incorrectly that the spot had moved right. According to Wong and Mack, this illusion was induced by the relative location of the spot within the frame. If the spot was first presented centered in the frame, for example, but during the second presentation appeared in the right half of the frame, subjects would report that the spot had moved to the right. Despite this faulty report, the subjects could make an accurate, leftward saccade to fixate the spot.

Activity of prefrontal cortex (PF) neurons has been suggested to reflect perceptions and their transformation into actions according to behavioral context and learned response rules (reviewed in Passingham 1993, Wise et al. 1996; Fuster 1997a,b). Taken together with the well-known spatial and directional preferences of PF neurons (Boch and Goldberg 1989; Funahashi et al. 1991), the experimental design of Wong and Mack enabled us to test a particular prediction stemming from these ideas. We hypothesized that some PF activity would reflect the reported direction of spot displacement, regardless of whether those reports accorded with its actual displacement direction or, due to visual illusions, conflicted with that direction. We also hypothesized, on the basis of the finding that accurate saccades could be made to inaccurately reported targets (Wong and Mack 1981), that some cells in PF would show different activity for saccades made to report about an attended stimulus than for saccades made to fixate it.

MATERIALS AND METHODS

Subject

A male rhesus monkey (Macaca mulatta, ~9 kg) was used. All procedures conformed to the Guide for the Care and Use of Laboratory Animals (rev. 1996, ISBN 0–309-05377–3) and an institutionally

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approved animal study proposal. The monkey sat, head fixed, in a primate chair equipped with a “bar,” i.e., a switch that the monkey could close by hand. Visual stimuli appeared on a video screen 57 cm directly in front of the monkey. A high-density neutral filter eliminated background phosphorescence of the video screen. Thus the monkey performed in total darkness without any visual frame of reference other than that provided by stimuli presented on the monitor. Horizontal gaze angle was recorded with an infrared oculometer (Bouis Instruments, Karlsruhe, Germany), sampled at 250 Hz. Vertical gaze was monitored on-line, but not recorded.

**Behavioral tasks**

**OVERVIEW.** The monkey performed three tasks, termed the Report, Track, and Track-8 tasks, conducted in blocks of ~50–100 trials. In each task, a visual stimulus appeared on the screen. As shown in Fig. 1A1, this stimulus consisted of a light spot, termed the tracking spot, embedded in a frame, which consisted of an array of similar spots. The monkey fixated the tracking spot for 1–2 s, and the screen went blank for 0.8–1.6 s (Fig. 1A2). Then, the tracking spot and the frame were presented again, usually slightly displaced relative to their previous locations (usually by different amounts). Following the second presentation of the stimulus, the monkey generated an oculomotor response. In the Report task, this response served to report whether the tracking spot had shifted to the left or to the right of its initial location. The reporting saccades were made to visible targets at the edges of the frame, one designated for “left reports”, the other for “right reports” (Fig. 1A1). The Track task required the monkey to fixate the tracking spot with a saccadic eye movement. The Track-8 task also required fixation of the tracking spot, but with displacements in eight different directions rather than the two used for the Track task.

**STIMULI.** The tracking spot was 0.13° in diameter. The surrounding frame itself consisted of light spots. In the Track and Track-8 tasks, the frame was 2° by 10° and consisted of six spots arranged in two horizontally aligned rows (Fig. 1C2). These spots were identical to the tracking spot in size and brightness. We did not measure their luminance, but they appeared dim to fully dark-adapted human observers. In the Report task, the frame contained, in addition, two 0.19° spots of the same brightness, 1° to the right and 1° to the left of the edges of the frame (Fig. 1C1). These spots served as the targets for reporting saccades and are thus termed report spots. The relative arrangement of the frame elements remained fixed for each task; that is, all of its elements were displaced by equal amounts in the same direction. In the Report task, the report spots were displayed during both the first and the second presentation of the frame (e.g., Fig. 1B1). The tracking spot was centered on the frame in the vertical, but generally not in horizontal, dimension.

**EVENTS COMMON TO ALL TASKS.** The intertrial interval lasted 1 s, after which a 1° red “X” appeared on the screen, signaling the monkey to press the bar with its hand (Fig. 1A2). In addition, the position of the X on the screen corresponded to the place where the tracking spot would later appear on that trial. The monkey typically fixated the X in anticipation of the tracking spot appearance. Each of the three tasks (Report, Track, and Track-8) required fixation of the tracking spot during its first presentation andfixating an appropriate spot after the second presentation of the stimulus. The spot deemed appropriate differed by task, as will be elaborated below. If the animal failed to fixate the tracking spot on the first presentation of the stimulus or failed to fixate the appropriate spot on the second presentation, the trial was terminated and a timeout period of 2–5 s ensued.

**REPORT TASK.** The monkey was operantly conditioned to make a saccade to the left report spot for a leftward tracking-spot shift and to make a saccade to the right report spot for a rightward shift. Note that the displacements of the stimuli on the screen were discrete, with a blank period between their presentations. There were no smooth movements of stimuli on the screen. The tracking spot appeared initially at 0, 1, 2, or 3° to the left or right of screen center, and the center of the frame was initially located at 0, 2, or 3° to the left or right of screen center. As illustrated in Fig. 1A2, the first presentation of the stimulus lasted 1.0, 1.5, or 2.0 s (psuedorandomly selected), and the screen went blank for 0.8, 1.2, or 1.6 s (also pseudorandomly select-ed). The displacements of the tracking spot relative to its initial location could differ in degree from those of the frame, and the displacements relative to the frame were typically 0, 2, 4, 6, or 8°, which could differ by condition, as described below. Following the second presentation of the tracking spot and the frame, the monkey was required to make a saccadic eye movement to one of the two report spots, left or right, and to maintain fixation there until that spot dimmed. The dimming occurred 1.0, 1.5, or 2.0 s after fixation, and the monkey had to release the bar within 0.8 s to receive a liquid reward and terminate the trial. This latter requirement was especially useful during training. It not only ensured that the monkey maintained fixation of the chosen report spot for more than a second, but also precluded any attempt by the monkey to examine the alternative report spot to see if it also dimmed (which it did in certain conditions, as described below).

Using different displacements of the tracking spot and the frame, four conditions were created, veridical, illusion, coherent, and saccade-opposite, selected pseudorandomly on each trial in the Report task, although not in equal proportions. The veridical condition (Fig. 1B1) was always the most common (>50%). In that condition, the frame either did not shift relative to the screen, shifted in the direction opposite to the direction of the tracking spot shift, or shifted in the same direction as the tracking spot, but to a lesser extent. In all of these three cases, the direction of the tracking-spot shift relative to the screen coincided with the direction of its shift relative to the frame. According to the results of Wong and Mack (1981), this condition should result in a report that the tracking spot had moved in the direction it had actually been displaced on the screen, thus the term veridical. During the lengthy training period (>1 yr) and the initial recording sessions, all trials were veridical. During the recording sessions, only, three additional conditions were gradually introduced, the illusion, coherent, and saccade-opposite conditions. An important feature of these conditions was that the monkey received reinforcement for either report choice. After the monkey fixated one of the report spots, both report spots dimmed, but because the dimming was very slight, the monkey could only detect dimming of the chosen report spot. Thus from the perspective of the monkey, these trials were similar to the veridical trials in that the monkey made a saccade to one of the report spots, and that spot later dimmed.

In the illusion condition, the displacement of the tracking spot relative to the frame conflicted with its displacement relative to the screen (Fig. 1B2). By analogy to the human psychophysical results of Wong and Mack (1981), this condition was expected to induce faulty perception of the tracking-spot shift. Tracking-spot shifts were either 0 or 2° (left or right) and the frame shifts were 2 to 4° (left or right), and the displacement of the tracking spot relative to the frame was 2° in the majority of the trials. Illusion trials, therefore, came in one of two varieties: 1) only the frame had shifted 2° while the stimulus reappeared on the screen; and 2) the tracking spot and the frame both had shifted in the same direction, but the frame had shifted 2° more. Illusion trials occurred relatively rarely (~12% of trials).

In the coherent condition (Fig. 1B3), the tracking spot and the frame were displaced by equal amounts (1 or 2°) in the same direction. Thus the tracking spot did not move relative to the frame. The coherent condition served as a control for neural activity correlated with the frame shift, per se, and also as a probe for the monkey’s response strategy. If, as in human psychophysical experiment of Wong and Mack (1981), the monkey’s perception was captured by the frame, then coherent displacements of the spot and the frame should lead to reports divided roughly evenly between left and right.

Trials of the saccade-opposite condition controlled for saccade
This condition was formally similar to one type of the illusion condition in that the frame shifted further than, but in the same direction as, the tracking spot. However, in the saccade-opposite condition the frame movement was so large (a 9° frame shift versus a 1° tracking-spot displacement) that the original fixation point ended up outside the frame. Therefore a response to the right report spot required a leftward saccade, as illustrated in Fig. 1B4, and vice versa (not illustrated).

Additional features of the report task precluded use of frame-shift direction, per se, as the basis for choosing the response. As a general
rule, it could have been the case that rightward frame shifts would be more commonly associated with left reports and vice versa. However, throughout all training and recording sessions, trials were equally divided between leftward and rightward frame shifts. Thus the direction of frame shift could not be used to guide the report. Leftward and rightward tracking-spot displacements were also balanced. In addition, the locations of fixation origins, endpoints, saccade amplitudes, frame shifts, and saccade directions were balanced to the extent possible, although limitations of the screen size required that saccades in the saccade-opposite condition were smaller in amplitude (in the 3 versus 4–8° range) and usually terminated nearer the center of the screen than in the other conditions.

**TRACK TASK.** In separate blocks of trials, for selected neurons, a task was employed in which the monkey merely fixated the tracking spot through changes in gaze angle. Note that because the monkey’s head was fixed, gaze angle depended only on eye position. The sequence of stimuli presentations and the stimuli were similar to those used in the Report task (Fig. 1C1), with the only difference being that the report spots were absent in the Track task (Fig. 1C2). The monkey was required to fixate the new location of the tracking spot after the second stimulus presentation. The initial locations of the tracking spot and the frame matched those in the Report task, as did the displacement directions and amplitudes of both the tracking spot and the frame. The timing of events was also matched. When the tracking spot dimmed, the monkey was required to release the bar within 0.8 s to receive a reward, as in the Report task.

**TRACK-8 TASK.** For some neurons, tuning curves during occulomotor tracking were measured using the Track-8 task. The stimuli were like those in the Track task (Fig. 1C3), but the tracking spot always began a trial in the center of both the frame and the screen. After a period of 1.0, 1.5, or 2.0 s, the screen went blank for 0.2, 0.3, or 0.4 s. Then, the tracking spot and the frame reappeared in one of eight possible displaced locations or reappeared at their original location in the center. The eight off-center locations were equally spaced on a 2°-radius circle (arrows in Fig. 1C3). The monkey had to fixate the new position of the tracking spot and release the bar within 0.8 s of its dimming to receive a reward, as in the other two tasks.

**Surgical and recording procedures**

An initial surgery was performed to implant a head-restraint device. Later, a stainless steel recording chamber (27 by 27 mm) was implanted over the right frontal cortex. Tungsten microelectrodes (Haer Instruments, Brunswick, ME; 1–3 MΩ measured at 1 kHz) were used to record neuronal activity. Single-unit potentials were filtered with a band-pass of 600 Hz to 6 KHz, amplified and discriminated using the Multispike Detector (Alpha-Omega Engineering, Nazareth, Israel) or a time-amplitude waveform discriminator (BAK Electronics, Rockville, MD).

Most neurons were isolated as the monkey performed the Report task. Neuronal responses were also recorded during the Track and Track-8 tasks for selected cells. To confirm the cell’s properties, we tried to return to the first task studied for a given neuron after the other tasks had been studied. This goal was accomplished for 44% of the present neuronal sample.

**Data analysis**

Neuronal activity was analyzed for several task periods, each of which was selected a priori, without consideration of the activity of an individual neuron. These task periods were as follows: 1) the poststimulus interval (80–200 ms after the second presentation of the stimulus), 2) the presaccadic interval (0–100 ms before saccade onset), 3) the postsaccadic interval (0–200 ms after saccade onset), 4) the predelay interval (0–300 ms before target dimming), and 5) the prebar-release interval (0–300 ms before bar release). In addition to these preset task periods, we searched systematically for an epoch that would better represent the activity of an individual neuron. The duration of this epoch was set at 300 ms because that was the typical duration of the task-related firing-rate modulations, as judged by visual inspection of the records. A floating-window technique was implemented: A reference firing rate (the across-trial mean during the 500-ms preceding stimulus reappearance) was subtracted from each single-trial peri-event histogram. Then a 300-ms floating window was slid along the histograms in 20-ms steps within a time range of interest. For poststimulus activity, windows were tested from 20 to 1000 ms after stimulus reappearance. For peri-saccadic activity, a comparable test window was used based on the average reaction time (~320 ms). It was set from 300 ms before the mean saccade onset to 680 ms afterward. Next, single-trial activity means in this window were squared and averaged across trials to yield a measure of rate modulation irrespective of sign (excitation or inhibition). Using all trials, the window position with the highest modulation was designated as the maximum modulation window. The position of the window was then fixed and applied to the various tasks and conditions for statistical analysis. The results of this algorithm were inspected visually and were found to be in good correspondence with subjective judgment. Note that this analysis was used to identify the 300-ms epoch in which the cell, on average, was most modulated in its activity relative to a reference epoch and did not bias the comparisons between directions, tasks, or conditions.

For the Report task, directional selectivity was assessed with two separate two-factor analyses of variance (ANOVA; α = 0.05). Data were analyzed both for the epoch selected using the floating window method (Table 1) and for the fixed task periods (Table 2). The dependent variable was the trial-by-trial mean firing rate during the analysis time window. In the first ANOVA, the factors were condition (veridical, illusion, or saccade-opposite) and report (a saccade to the

### Table 1. Neuronal classification in the Report task, numbers of neurons in each class

<table>
<thead>
<tr>
<th></th>
<th>Report-Related</th>
<th>Gaze-Related</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Left</td>
<td>Right</td>
</tr>
<tr>
<td>By ANOVA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>By Wilcoxon rank-order test</td>
<td></td>
<td></td>
</tr>
<tr>
<td>veridical</td>
<td>14</td>
<td>9</td>
</tr>
<tr>
<td>illusion</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>saccade-opposite</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>MaxD in veridical vs. illusion (same/opposite)</td>
<td>7/0</td>
<td>3/0</td>
</tr>
<tr>
<td>MaxD in illusion vs. saccade-opposite (same/opposite)</td>
<td>4/0</td>
<td>2/0</td>
</tr>
<tr>
<td>MaxD in veridical vs. saccade-opposite (same/opposite)</td>
<td>3/0</td>
<td>3/0</td>
</tr>
</tbody>
</table>

Maximal-discharge direction (MaxD) is based on the report (left reports or right reports). Accordingly, gaze-related neurons that have maximal discharge for left reports in veridical and illusion trials, have maximal discharge for the “opposite” direction in saccade-opposite trials (i.e., for right reports, because they are made with left saccades).
left report spot or to the right report spot). Report should not be confused with the direction of the saccade used to make the report, which differed from the report in saccade-opposite trials. In the second ANOVA, the factors were condition and saccade direction. These analyses permitted classification of most significantly task-related neurons as either report-related or gaze-related. By the term gaze-related, we include both the saccade to and fixation of the report target. For report-related neurons, report was statistically significant, whereas for gaze-related neurons, saccade direction was significant. The terms report-related and gaze-related were chosen because they have no causal implications. Indeed, as elaborated in the DISCUSSION, the results show that activity of either type could occur substantially after the eye movement that comprised the report and thus could not participate in the generation of the oculomotor response. About 70% of task-related neurons could be classified unambiguously with this method as either report-related or gaze-related. For ~30% of task-related neurons (24 cells in the poststimulus period, for example), the effects of both saccade direction and report were significant. Typically, such cells exhibited lower directional modulations in the saccade-opposite trials than in the veridical and illusion trials, which hindered dissociation between the relationship to saccade direction or report. These cells were classified on the basis of activity in saccade-opposite trials for the purposes of population analysis. If the directional preference corresponded to the report, as observed in the veridical and illusion trials (n = 14), the cell was grouped with the report-related cells; if it corresponded to the saccade direction, the cell was classified as gaze-related (n = 10). Data from these cells are marked with open circles in Figs. 5 and 6.

Tracking-spot and frame shifts that would be expected to produce illusions in the Report task were also presented in the Track task. For the Track task, neurons were classified as described above, using a two-factor ANOVA with the saccade direction and the “predicted report direction,” as the factors. We put the phrase predicted report direction in quotes because the monkey did not make a report in the Track task, although the target-spot and frame displacement matched those that would lead to certain reports in the Report task. Finally, to compare neuronal activity in the Report and Track tasks, a two-factor ANOVA (task and saccade direction) was performed. Only trials with veridical stimuli were used in this analysis.

For the Track-8 task, preferred direction (PD) was calculated using a circular mean weighted vector-average, derived from mean firing rates with reference firing rate subtracted.

**Histology**

Electrolytic lesions (15 μA for 10 s, anodal current) were made at two depths along five tracks. Ten days later, the monkey was deeply anesthetized with barbiturates, then perfused with buffered formaldehyde (3% by wt). Steel pins were inserted at known electrode-penetration coordinates. The brain was removed, photographed, and sectioned on a freezing microtome at 40-μm thickness. The sections were later mounted on glass slides and stained for Nissl substance with thionin. We did not attempt a cytoarchitectonic analysis or an estimate of recording depths.

### Table 2. Temporal distribution of report-related and gaze-related activity during each trial, classed according to ANOVA using main effects

<table>
<thead>
<tr>
<th>Task Period</th>
<th>Report-Related</th>
<th>Gaze-Related</th>
</tr>
</thead>
<tbody>
<tr>
<td>Post-stimulus</td>
<td>16</td>
<td>19</td>
</tr>
<tr>
<td>Pre-saccadic</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>Post-saccadic</td>
<td>40</td>
<td>46</td>
</tr>
<tr>
<td>Pre-saccadic delay</td>
<td>35</td>
<td>9</td>
</tr>
<tr>
<td>Post-bar release</td>
<td>36</td>
<td>13</td>
</tr>
</tbody>
</table>

Values are number of neurons of each class in each task period.

As shown in Fig. 2B, the monkey’s performance in the task matched that of human subjects under similar experimental conditions (Wong and Mack 1981). Although either report was rewarded in the illusion condition, the monkeys usually chose the response that human subjects experiencing an illusion would have chosen. Note that for the purpose of Fig. 2B, the “correct” response in the illusion condition was defined as that reporting the predicted illusion and was correct only in that sense. Indeed, it was incorrect in the sense that the tracking spot had actually moved in the direction opposite to that reported by the monkey or had not moved at all. Overall, the course of recording neural activity, the predicted illusion was reported 1,508 times for left reports and 1,592 times for right reports, whereas the alternate report was observed 208 and 323 times, respectively. This difference is highly statistically significant (χ² = 1.823; df = 1; P < 0.001).

In the coherent condition, i.e., the condition in which the tracking spot position relative to the frame was unchanged, the monkey’s performance was also consistent with human psychophysical results. For this condition, the correct response was defined, for heuristic purposes only, as the direction in which the tracking spot (and the frame) was displaced on the monitor screen. Although both responses were rewarded, the monkey’s reports were not predominantly correct in that sense. If, as predicted based on the human psychophysical results, the monkey’s perception was captured by the frame, then coherent displacements of frame and tracking spot should lead to reports divided roughly evenly between left and right, regardless of the direction that the array had shifted. This was, approximately, the case (Fig. 2B), although there was a slight bias toward correct responses when the space and the frame shifted to the left.

The prediction that the tracking spot displacement relative to the frame would be the most significant factor determining the monkey’s reports was confirmed, in addition, by the following analysis. Veridical trials were subdivided into three groups that corresponded to the amplitudes of relative displacement of 2, 4, and >4”, respectively. For these groups of trials, the percentage of correctly performed trials increased with the increase in the relative displacement amplitude [80.3 ± 0.9 (SE)% correct, 93.7 ± 1.0% correct, and 96.2 ± 1.5% correct, respectively).

In addition, we ruled out the possibility that the monkey chose the response based on the final position of the tracking spot relative to the frame (closer to the left or right report spot), rather than based on the displacement information. In the cases of the more distant report target being the correct one, the percent correct was high: 84 and 88% for left and right reports, respectively. In the cases of the closer report target being correct, the corresponding values were also high: 93 and 82% for left and right reports, respectively.

In the Track task, performance was nearly perfect. Errors were sufficiently rare that it was difficult to characterize any common feature among them.

The monkey’s oculomotor behavior generally accorded with the original experimental design. However, there were two features that merit comment. First, the monkey maintained gaze at the location of the tracking spot, even when it disappeared during the blank period prior to stimulus reappearance.
Although never explicitly required, this behavior was maintained throughout recording. Second, on approximately half of the trials in the Report task, the monkey responded to stimulus reappearance with two saccades in quick succession: the first to the tracking spot and the second to the report spot. We allowed this behavior to persist because we thought that it might prove useful to compare activity during these two kinds of response (as shown in Fig. 11B versus 11C).

Saccadic reaction times are shown in Fig. 2A. For the veridical condition, the mean saccadic reaction time, combining correct left and correct right reports, was 321 ± 92 ms (SD). Note that reaction times were relatively short for the saccade-opposite condition. This effect probably reflects ease of recognition and choice of response in that condition. Longer reaction times were observed in the illusion and coherent conditions, probably reflecting more the difficult response choice in those conditions. Saccadic reaction times in the Track task were comparable to those in the veridical and saccade-opposite conditions of the Report task. Bar-release reaction times, averaged over all report and track trials, were 480 ± 50 ms (SD), which did not differ materially by task, condition, report, or saccade direction.

Report task: cell-by-cell analysis

A substantial number of PF cells, classified as report-related, reflected the report and not the direction of eye movement (Table 1). Figure 3 illustrates a neuron that had a vigorous modulation in activity for left-report trials (Fig. 3A, left column) and showed much less modulation for right reports (Fig. 3A, right column). In illusion trials, activity was comparable to or greater than that in the veridical condition (Fig. 3A, middle row versus top row), but only for left reports. The data from saccade-opposite trials show that the cell’s activity reflects left reports even when the monkey makes those reports with rightward saccades (Fig. 3A, bottom row). The cell illustrated in Fig. 3 had a relatively long response latency, but for the population of response-related neurons as a whole, activity modulation followed stimulus reappearance by a mean of 156 ± 48 ms (SD) in the veridical condition and became directionally selective (i.e., activity levels distinguished between “maximal” and “minimal” directions) at a mean of 173 ± 35 ms. Similar values were obtained for the other conditions. Given a grand mean saccadic reaction time of 321 ms in veridical trials, the directional signal preceded the onset of saccade by a mean of 148 ms. Population histograms presented below show similar timing.

Other neurons reflected the eye movements and/or gaze angle and were collectively classified as gaze-related (Table 1). In the illustrated case, the activity was postsaccadic, but examples of pre-, peri-, and postsaccadic gaze-related activity were also observed (Table 2).

When the cells were classed as report- or gaze-related by ANOVA, these two classes were represented in approximately equal numbers in the 1-s period immediately following stimulus presentation 2 (Table 1). However, relative propor-
tion of neurons in the two classes changed as the trial progressed. Table 2 shows that report-related neurons became significantly more prevalent later in the trial ($\chi^2 = 20.2; df = 4; P < 0.001$).

Report task: population analysis

To compare activity profiles of report- and gaze-related neurons across different conditions of the Report task, we computed population histograms. In this computation, histograms for individual neurons were first calculated and the population average was then derived by summing them and dividing them by the number of neurons. In the analysis shown in Figs. 5 and 6, only trials deemed correct in the sense used for Fig. 2 are included. Figure 5 shows activity for the populations of report-related neurons during three of the conditions in the Report task: the veridical condition in which reports matched the actual displacements on the screen (Fig. 5A1), the illusion condition in which reports differed from the actual event (Fig. 5A2), and the saccade-opposite condition in which the report was dissociated from the direction of the saccade used to make...
that report (Fig. 5A3). As a population, report-related neurons retained their directional preference for the report (e.g., a report that the tracking spot had moved left), even when that report conflicted with the actual displacements of the tracking spot (as they did in the illusion condition, Fig. 5A2) and when the saccade directions and reports conflicted (as they did in the saccade-opposite condition, Fig. 5A3). Figure 5A1 also shows that for the population average the response latency to stimulus reappearance was 120 ms for the veridical condition, with the directional difference emerging after 160 ms (161 ms prior to the mean saccade onset). These population-level onset times reflect contributions from the earliest modulations within the population and therefore are somewhat different from the cell-by-cell averages presented above.

Contributions from individual cells comprising the population averages of Fig. 5A are depicted by the scatterplots of Fig.

FIG. 5. Report-related neurons: population analysis. A: population directionality for neurons classified as report-related. Each cell’s maximal direction is determined by the report associated with the largest modulation in activity; its minimal direction is for the opposite report. The degree and time course for the development of this directionality can be appreciated by the difference between the unfilled population histograms (population average for the maximal direction) and shaded population histograms (average for minimal direction). Computations are bin-by-bin means over the population with no normalization. Bin width, 40 ms. Arrows mark the mean onset of the monkey’s response (black, for the maximal direction, emphasized by the dotted vertical line; shaded, for the minimal direction). A1: veridical condition; A2: illusion condition; A3: saccade-opposite condition. See Fig. 7 for data from the coherent condition. B: correspondence between maximal directions in the veridical, illusion, and saccade-opposite conditions, confirmed by correlational statistics for the individual neurons. Delta firing rate: difference in mean firing rate between the right and left reports for the maximum modulation window (see METHODS). Positive values correspond to a preference for right reports, and negative values correspond to left reports. Unfilled circles are for cells that had significant main effects, by analysis of variance (ANOVA), for both gaze and report.

FIG. 6. Gaze-related neurons: population analysis. A: in format of Fig. 5, but for cells classified as gaze-related. The maximal direction by saccade is the saccade direction associated with the largest modulation in activity; minimal direction is for saccades in the opposite saccade direction. Unlike the report-related population (Fig. 5), which maintains its directional signal according to the direction of the report, gaze-related activity maintains directionality according to the direction of the saccade. B: correlational analysis in format of Fig. 5B. Unfilled circles are for cells that had significant main effects, by ANOVA, for both gaze and report.
The strength of the directional signal was quantified for the individual neurons by an index termed *delta firing rate* \( \Delta r \), the firing rate within the maximum-modulation window (see Methods) for right reports minus left reports. For report-related neurons, taken cell-by-cell, \( \Delta r \) was positively correlated for the veridical and illusion conditions, as well as for the veridical and saccade-opposite conditions. This correlation shows that cells with maximal activity for left reports in the veridical condition (negative values) typically maintained that preference in the illusion condition.

Figure 6 shows population averages and \( \Delta r \), values for the cells classified as gaze related. That population maintains its directional preferences when the data are sorted according to the saccade direction associated with the cell’s maximal activity (termed “maximal direction by saccade” in Fig. 6). A directional signal is not observed when the data are sorted according to the report (not illustrated). For gaze-related neurons, \( \Delta r \) was positively correlated between the veridical and illusion conditions, but was negatively correlated between the veridical and saccade-opposite conditions (Fig. 6B). The negative correlation reflects the fact that, for gaze-related neurons, left reports were made with rightward eye movements and vice versa.

As shown above (Fig. 2B), left and right reports occurred with approximately equal probabilities in the coherent condition, regardless of the direction that the array of tracking spot and frame shifted (by equal amounts). This indicates that the monkey did not base the response choice on the frame displacement, per se. Nevertheless, frame displacement might have been reflected in neuronal activity and could, theoretically, account for the results presented above. To test this possibility, population histograms were calculated for the coherent condition (Fig. 7). These average histograms for report-related neurons showed that the direction of the coherent displacement of the tracking spot and the frame was not a significant factor, whereas the generated report was. As shown in Fig. 7C, the report-related population did not show an average directional signal when the frame and tracking spot shifted in each cell’s maximal versus minimal direction, but the monkey made both left and right reports. In contrast, as shown in Fig. 7B, the directional signal was evident when reports were made that corresponded to each cell’s maximal versus minimal direction, even though the tracking spot and the frame shifted to the left in some trials and to the right in others.

Figure 7D summarizes the results obtained for the Report task. The curves in that figure show the difference between population activity in the maximal and minimal directions as a function of time, relative to the second stimulus presentation. For all four conditions, the directional signal appears substantially before the eye movement made to make the report (downward pointing arrows indicate movement onsets for each condition). Note that the directional signal observed in the illusion condition, when the tracking spot moved differently than the monkey had reported, developed with a similar time course and eventually became larger than that observed in the veridical condition.

We also examined whether eye movement parameters, specifically saccade amplitude, starting and ending position, determined directionality. That analysis was focused mainly on veridical trials because they provided the widest range of saccade parameters, and data were analyzed separately for report- and gaze-related neurons, as classed by ANOVA. For a given saccade direction, Pearson correlation coefficients were computed that related an eye-movement parameter (amplitude,
origin, or endpoint) with the corresponding firing rate on a trial-by-trial basis for the maximum modulation window. For report-related neurons, only 3/35 cells exhibited a statistically significant correlation for amplitude, 5/35 for starting position and 4/35 for ending position (7/35 for at least one parameter). Analysis of the population activity confirms these conclusions. As a population, the report-related activity could be attributed to neither the direction (Fig. 5A3), amplitude (Fig. 8A), origin (Fig. 8B), or endpoint (Fig. 8B) of the saccadic eye movement used to make the report. By contrast, gaze-related neurons did depend on eye movement and position parameters (not illustrated). Further, the relative displacement of the frame and tracking spot was the most important factor in generating the directional signal observed in the population of report-related neurons (Fig. 8, C and D) and relative displacement was reflected in the monkey’s behavior as well (Fig. 8E). Performance on illusion trials with 2° relative displacement of tracking spot and frame was comparable to that on veridical trials with 2° relative displacement (Fig. 8E). Variation in that relative displacement accounts for most of the variability seen in the veridical condition. Interestingly, 2° relative shifts in frame and tracking spot induced only a weak directional signal in the veridical condition, on the order of 10%, but induced a much larger signal in the illusion condition, on the order of 30%. This difference corresponds to the larger directional signal observed for the illusion condition in Fig. 7D.

Report versus track tasks

Both the Report and Track tasks required saccadic eye movements of comparable parameters. However, according to the design of the experiments, in the Report task the monkey generated those saccades to the report spots based on its judgment about the displacement of the attended (tracking) spot, whereas in the Track task the monkey merely followed that spot with shifts in gaze angle. The fact that the stimuli presented in the Report and Track tasks were matched, except for the absence of report spots in the latter, allowed us to compare activity patterns across tasks for trials matched for stimulus locations and displacements (input matching) as well as saccade direction (output matching). Figure 9 shows activity contrasts for the Report and Track tasks in four PF neurons. Histograms and rasters presented in Fig. 9 are matched for both input and output because they display only the trials matching the veridical condition. Note that both directional (Fig. 9, A, B, and D) and nondirectional neurons (Fig. 9B) showed differences between the two tasks and that preferences were observed for both the Report task (Fig. 9, A and B) and the Track task (Fig. 9, C and D). Preferences for both tasks were observed in comparable numbers (Table 3).

Report- and gaze-related neurons both showed preferences for either the Report or the Track task, but differed in the way their activity patterns changed from task to task. Figure 10 shows the population averages for report-related (Fig. 10A) and gaze-related (Fig. 10B) neurons. The directional signal, as observed for the report-related population in the Report task (Fig. 10A1), was not observed when the same neuronal population was studied in the Track task. This was the case when the averages were matched for outputs, i.e., saccade direction (Fig. 10A2), or for inputs, i.e., the pattern of tracking-spot and frame displacements (Fig. 10A3). By contrast, activity patterns of gaze-related neurons in the Report task were directional when matched by saccade direction in the Track task (Fig. 10B2, although not when matched for the pattern of tracking-spot and frame displacements, Fig. 10B3).

In the analyses described above, neurons were classified as report- or gaze-related according to their activity patterns in the Report task. A similar classification could be made in the Track task. Of course, the monkey was not making a report about tracking-spot displacement in the track task, but merely making a saccade to fixate it. The gaze-related neuronal population, selected on the basis of directional selectivity during the track task, was tested against data obtained during the Report task for the 34 cells recorded in both tasks. In this analysis we took advantage of a peculiarity in the monkey’s behavior described above. In the Report task, the monkey performed the task in two ways. In the first, as intended by the task design, the
monkey made a single saccade to one of the two report targets, left or right. We term these “report-only” trials in Fig. 11. In the second, which occurred about half the time, the monkey first made a saccade to fixate the tracking-spot, then made a second saccade to a report target. We call these “track, then report” trials. The population of gaze-related neurons that showed a presaccadic directional signal in the track task (Fig. 3A) lost part of its directionality in the Report task (Fig. 11, B and C). Specifically, we measured the directional signal on veridical trials for the 200-ms preceding saccade onset. These neurons exhibited directional signals of 6.4 ± 1.4 spikes/s (mean ± SE) in the track trials, but only 3.1 ± 1.5 spikes/s in the report-only trials of the Report task and 4.7 ± 2.2 spikes/s in the track-then-report trials of the Report task (Fig. 11D). The difference between these values was statistically significant ($\chi^2 = 9.5$, df = 2, $P < 0.01$; Friedman repeated measures ANOVA) with the track trials being statistically different from the report-only trials of the Report task (Dunn’s post hoc comparison). Further, the two kinds of trials in the Report task were not statistically different from each other.

Note that, as a population, directional selectivity was dimin-

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**TABLE 3. Report vs. Track task activity**

<table>
<thead>
<tr>
<th>Directional in:</th>
<th>Report &gt; Track</th>
<th>Track &gt; Report</th>
</tr>
</thead>
<tbody>
<tr>
<td>Report task</td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td>Track task</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>Either task</td>
<td>18</td>
<td>12</td>
</tr>
</tbody>
</table>

Values are number of neurons with significant differences depending on task.
ished in the Report task mainly because the differences between directions observed in the Track task decreased, not because the cells lost their task-related modulation. Figure 11, A and B, also shows that this decrease in directional selectivity was maintained when amplitude of saccades was matched for the two tasks (±5.5°, on average).

Track-8 task

The majority of cells recorded in the Report task had leftward maximum directions (Table 1). This bias was contralateral to the recording site and was especially strong for gaze-related neurons. Using more detailed information about directional tuning available from the Track-8 data, we computed PD for all cells studied in the Track-8 task (n = 23, not illustrated). This sample also showed a strong bias toward the left (with a vector mean of 0.46 at 140°, where 0° is to the right).

Histological analysis

We plotted the surface projections of the recording sites and the estimated track of each penetration by reference to the recovered electrolytic lesions and the pin holes (Fig. 12). Three of the five electrolytically marked tracks were identified in the histological material, with good agreement between the marking pins, electrolytic lesions, and sulcal landmarks. Nearly the entire population of task-related neurons was recorded in the ventral prefrontal cortex, designated PFv, with none in the banks of the principal sulcus. Figure 12C shows the locations of the cells with report-related and gaze-related activity in the Report task. In the area with report- and gaze-related neurons, report-related cells appeared slightly more commonly in its rostromedial parts. However, overlap was extensive, and there were many penetrations having both report-related and gaze-related neurons. There was not any clearly biased distribution of cells with preferential activity in the Report versus Track task (Fig. 12D).

DISCUSSION

Using experimental conditions that evoke visual illusions in human subjects (Wong and Mack 1981), we tested the hypothesis that the activity of at least some PF neurons should reflect reported perceptions, even when they conflict with veridical events. Testing the hypothesis involved a comparison among conditions in the Report task, in which the monkey reported its perception, as operationally defined here, about whether a tracking spot had been displaced to the left or to the right. In the majority of trials (the veridical condition), there was no conflict between the actual and the perceived direction of tracking-spot shift. In a minority of trials (the illusion condition), the psychophysical results of Wong and Mack (1981) predicted such conflicts. The experiment was thus based on two fundamental assumptions: first, that the conditions inducing displacement illusions in human subjects also did so in our monkey; and, second, that the monkey, which had been trained to report the direction of tracking-spot displacement during extensive training in the veridical condition, continued to do so in the illusion condition.

As summarized in Table 1, a substantial percentage of the directional cells in PF showed activity that reflected the re-
ported rather than the actual direction of tracking-spot displacement (Fig. 5A2). Activity in the saccade-opposite condition showed that this directional preference did not merely represent the direction of eye movement used to make the report (Fig. 5A3). The finding of this report-related activity, therefore, confirmed the hypothesis. Other PF cells, however, reflected the metrics of the eye movement used to make the report. The finding of such gaze-related activity in PF confirms several previous reports (e.g., Asaad et al. 2000; Funahashi et al. 1991) and will not be discussed in detail, except to note that although these cells were well represented, they were by no means dominant in the parts of PF explored.

There have been several previous reports that interpret single-neuron activity in PF in terms of sensory perception, recently (e.g., Hasegawa et al. 1998; Hoshi et al. 1998; Kim and Shadlen 1999; Quintana and Fuster 1999; Rainer et al. 1999) and in the more distant past, as summarized in several reviews (Fuster 1997a,b; Miller 2000; Wise et al. 1996). However, the present study is the first to report that cells in PF have activity corresponding to a monkey’s perceptions during induced illusions, as well as the first to contrast activity for perceptual reports about stimuli with that for similar movements made to acquire the same stimuli. These findings support the view that PF functions to integrate inputs and actions across time and space (Fuster 1997a), possibly including information from all types of memory (Gaffan 1994). On the basis of the present data, we conclude that PF neurons process information relevant to responses based on perceptions about stimuli as well as responses made directly to those stimuli. We further conclude that PF cells tend to be specialized for one of those two functions, although this distinction is by no means absolute.

It is also noteworthy that the report-related activity we observed in PF neurons persisted longer during the trial than did the gaze-related activity. Toward the end of each trial, the report choice had already been made and the reporting movement (the saccade) executed. During this late stage of the trial, the report-related activity predominated over gaze-related activity (Table 2). Obviously, activity during this period could not have played any role in the decision or in generating the report. We speculate that report-related activity during this period of the trial reflects a monitoring function involved in response learning (Owen et al. 1998; Passingham 1993).

We emphasize that the directional effects seen in the activity of individual report- and gaze-related neurons and their corresponding populations were quantitative ones and do not represent an all-or-none distinction between these cell classes. For some cells in the Report task, it was difficult to classify them as either report-related or gaze-related. In those cases, the greatest directional tuning occurred in veridical and illusion trials, and directional tuning in saccade-opposite trials was less pronounced. For example, there might have been significantly more activity for left reports than for right reports, but little directionality in the saccade-opposite condition. This impression was confirmed by testing the significance of directional activity.
incorporates both the perceptual and the executive aspects of behavior.

**Alternative accounts of report-related activity**

Additional factors that need to be considered in interpreting report-related activity include possible accounts in terms of eye-movement parameters, receptive fields, responses to the frame shift, or responses to the relative motion of tracking spot and frame. As argued below, all of these possibilities can be excluded. Further, several issues concerning the animal’s behavior need to be addressed, including the question of whether an illusion was induced, whether the monkey adopted strategies involving responses in the direction opposite to that of the frame shift, or strategies involving responses to the nearest report target. An additional issue involves the possibility that the monkey was operantly conditioned to report the illusion.

To address the issue of spatial or directional tuning in the sense implied by the concept of receptive, spatial, or movement fields, the locations of stimuli on the screen were manipulated to rule out, to the extent possible, the interpretation that a response-related cell’s activity or that the population as a whole reflected the amplitude, origin, or endpoint of the reporting saccade (Fig. 8). Cell-by-cell analysis ruled this out for individual report-related neurons, as well for the population. By contrast, the activity patterns of gaze-related units did depend on saccade parameters and/or gaze (not illustrated).

As for frame shifts, data from the coherent condition, in which the frame and tracking spot moved equally, ruled out an account of report-related activity simply in terms of frame displacement. As shown in Fig. 7C, no directional signal was observed when the stimuli were matched for the direction of frame shift. A separate problem concerns the behavioral response to the direction of frame shifts, which was also addressed by the coherent condition as well as by specific features of the experimental design. If displacements of the frame were completely randomized, there would be a tendency for rightward frame shifts to be associated with left reports and vice versa. Accordingly, we balanced the trials throughout training and recording so that each direction of frame shift was associated with left and right reports in equal proportions. The monkey’s relatively balanced choice of responses in the coherent condition (Fig. 2B) validated the assumption that report decision was not strongly influenced by the direction of frame shift. Had the monkey responded in the direction of frame shift or the opposite, there would have been significantly more consistency in its response to the coherent tracking spot and frame shifts. Further, had the directional signal at the time of the report simply reflected the relative motion of tracking spot and frame, the directional activity seen in Fig. 7B (in the coherent condition) would have been lacking. The monkey’s behavior in the coherent condition also rules out the possibility that the monkey reported the direction of tracking spot or frame shift in retinocentric coordinates or in allocentric (screen-centered) coordinates. This finding probably results from the small amplitude of the shifts and the lack of any reference other than that provided by the frame. As intended by the experimental design, then, the relative displacement of the tracking spot and frame led to the report and perception was captured by the frame.

We studied neuronal activity in operantly conditioned mon-
keys. Accordingly, we cannot take for granted that a report reflects anything beyond a conditioned response. Our experimental design was drawn from the human psychophysical studies of Wong and Mack (1981). However, from a strict behaviorist perspective, any response could be based on the reinforcement history concerning stimuli and responses. Accordingly, we incorporated into the design of our experiment elements that make an interpretation in terms of instrumentally conditioned stimulus-response associations unlikely. In the majority of report trials and throughout the monkey’s training, there was never a conflict between the veridical displacement of the tracking spot and the reported one. Once the frame-shift induced illusions were instituted, either report (left or right) was accepted and reinforced. The monkey could not detect this contingency, because the requirement to foveate one report spot precluded detection of the subtle dimming of the other report spot. This was tested during the training sessions by showing that the monkey never responded (with bar release) to the dimming of the nonfoveated report spot when it alone dimmed. Furthermore, had the monkeys responded by arbitrary association, reports in the illusion trials would not have followed the pattern predicted by Wong and Mack’s psychophysical data from human subjects. As noted in the results, the correspondence of the monkey’s behavior to that predicted was highly significant in the illusion condition and was comparable to that observed for similar magnitudes of relative tracking spot and frame shifts in the veridical condition. Accordingly, we can exclude the possibility that the monkey had simply been trained or conditioned to report the illusory displacements of the tracking spot under a given set of stimulus-response contingencies. In further support of the view that humans and monkeys experience these general phenomena similarly, Zivotofsky et al. (1998) have demonstrated in monkeys that moving visual backgrounds affect saccades made to remembered targets as if the monkeys perceive Duncker’s illusion, which is related to the displacement illusion studied here.

Alternative strategies, such as responding to the report target nearest the final position of the tracking spot, were also ruled out.

Limitations of the Report-task design

We restricted our Report task to shifts along the horizontal axis. In part we did this to match the psychophysical study of Wong and Mack and, in part, to simplify the experimental design. This limited the proportion of cells in which we could detect directional effects.

The saccade-opposite condition was designed to control for the direction of reporting saccade. However, the relative ease and speed with which the monkey recognized this condition and chose its response (Fig. 2) suggests that the monkey may have treated that condition as a separate task, which limits its value as a control.

The present results come from a single subject, which remains a controversial practice. In the present study, we tested a hypothesis predicting that we would observe certain signals in PF. Having observed the predicted signals in the first subject, we decided not to confirm the observation in a second subject. Nevertheless, the fact that the result was not replicated needs to be acknowledged.

Neuronal sampling was confined to PF. Accordingly, we make no claim that report-related activity is confined to PF. Indeed, related phenomena have been reported in parietal cortex (Powell et al. 1998). Notwithstanding the suggestion that PFv plays a role in exclusively nonspatial visual information processing (O Scalaidhe et al. 1997, 1999; Wilson et al. 1993), the present results accord with the idea that spatial and nonspatial signals are strongly intermixed in the monkey’s PF (Rainer et al. 1998; Rao et al. 1997; White and Wise 1999), as they are in human subjects (Rushworth and Owen 1998) and elsewhere in the neocortex.

Report versus Track tasks

As a subsidiary experiment, we also tested the prediction that some PF neurons would be preferentially active when the monkey made reports about visuospatial stimuli, compared with when the monkey made visually guided movements to the same stimuli. This test involved a comparison of activity during the Report and Track task. The Track task involved fixating the tracking spot, which was contained within a frame similar to that used in the report task. Shifts of the frame and tracking spot were matched in the two tasks.

Some PF neurons showed a preference for the Report task, others for the Track task. Cells preferring the Report task were found in approximately equal numbers and in roughly the same locations as neurons preferring the Track task (Fig. 12D). In a population analysis, we matched the Track- and Report-task data for either the saccade direction or the stimuli presented (combinations of both shifts and locations of the tracking spot and frame). The presaccadic directional signal observed for report-related neurons in the Report task (Fig. 10A1) could not be observed in the same neuronal population as the monkey performed the track task. This directional signal was lost when the trials were matched for either saccade direction (Fig. 10A2) or for the stimuli presented (Fig. 10A3). Along the same lines, neurons classified as gaze-related in the Track task (Fig. 11A) were significantly less directional, at least for the presaccadic period, in the Report task (Fig. 11B).

The comparison of activity during the Report and Track task raises a number of interpretational issues that differ in some ways from those raised by comparison among the Report-task conditions. The design of the Report task depends on the coherent motion of the elements comprising the frame. In this sense, the frame and the tracking spot both act like objects. For example, the monkey could perform the Report task by reporting changes in the spatial relationship between these two objects. In addition, the response can be construed as being directed to a part of one of those objects in the Report task (the report spots), but to a different object in the Track task. In view of object-oriented spatial information processing in cortical neurons (Olson and Gettner 1995), it is possible that this factor contributed to preferences for the Report task. Additionally, report spots were present in the Report task, but not in the Track task, and to this extent the stimuli were not identical in the two tasks. Spatial attention might also differ, three spots being behaviorally relevant in the Report task as opposed to one in the Track task. The difference between track and report could also be interpreted as a rule or context effect, which has been documented for PF (Asaad et al. 2000; Boussaoud and Wise 1993; Hoshi et al. 1998; White and Wise 1999). Under this interpretation, the activity differences among tasks could...
reflect the different response rules for a given set of inputs. In addition, it is possible that the monkey attempted to perform the Report task with a strategy that involved memorizing the configuration of the tracking spot relative to the frame (for comparison with its configuration at the time of reappearance) or one that involved computation of an egocentric coordinate frame. If so, then these processes would be neither required nor expected in the Track task.

Relation to previous reports

A large number of previous neurophysiological studies have recorded the activity of PF neurons during tasks involving sensory perception (e.g., Niki 1974, as reviewed by Fuster 1997a and Miller 2000). The directional signal observed (Fig. 7D) may reflect a neuronal correlate of the perceptual decision, in accord with previous reports on frontal cortex activity during response-selection tasks, including PF, frontal eye fields (FEF), and primary motor cortex (Bichot and Schall 1999; Bichot et al. 1996; Gold and Shadlen 2000; Kim and Shadlen 1999; Romo et al. 1999; Salinas and Romo 1998). A particularly pertinent study has been published recently by Thompson and Schall (1999, 2000). Using a backward-masking paradigm, they found cells in the FEF that responded to a target stimulus presented briefly prior to mask. However, these responses were ~20% higher on trials during which the monkey presumably perceived the stimulus (as demonstrated by a correct report of the target’s presence). Although this finding, taken alone, could be ascribed to visually guided movements rather than perception, additional properties of FEF cells indicate that these cells play a role in sensory information processing rather than in response selection or execution (Bichot and Schall 1999; Bichot et al. 1996; Thompson et al. 1996, 1997).

A preliminary report on parietal cortex neurons (Sakai et al. 1978) described activity similar to the report-related cells observed here. Unlike the present study, which employed discrete displacements, that study used smoothly moving focal stimuli and background frames. While intriguing, the activity of only one cell is illustrated and there is no indication of the cell-to-cell variability in the reported effect, no description or illustration of trial-to-trial variability for any neuron, and no statistical test of the significance of the reported phenomenon. Goldberg and his colleagues have recently reported a similar phenomenon in the lateral intraparietal area (Powell et al. 1998).

Several previous neurophysiological studies have probed the neuronal correlates of perception in areas outside the frontal lobe. Logothetis and his colleagues (Logothetis 1998; Logothetis et al. 1996; Sheinberg and Logothetis 1997) have reported cell activity in inferior temporal cortex that corresponds to a monkey’s report during binocular rivalry. In the spatial domain, Bradley et al. (1998) found neurons in the middle temporal area (MT) that reflected the reported direction of surface motion, for ambiguously rotating transparent cylinders, even though the visual input remained identical. Previous work in visual areas also shows, in accord with the present study, that visual background information can be important to neuronal activity and its correlation with behavior. Born et al. (1999) have reported cells in MT that respond mainly to movements of either focal objects or larger backgrounds. Their findings suggest that the background shifts contributed to perception opposite to background movement.

Conclusion

Although some neuroimaging research have suggested that visual areas alone are sufficient to subserv visual perception (Tong et al. 1998; Zeki and Bartels 1998), other evidence supports the idea, derived from a wide variety of neurophysiological and other studies, that PF also plays a central role in visual perception of stimuli (Crick and Koch 1995, 1998; Elliott et al. 1999; Fuster 1997a and et al. 2001). The observation that report-related neurons, as a population, lost their directional signal when the subject used the tracking stimulus as the target of movement (Fig. 10A) suggests that these PF neurons function relatively specifically in the generation and monitoring of perceptual reports. Report-related cells were, nevertheless, thoroughly intermixed with another population of PF neurons, one that seemed relatively selective for the use of visual inputs as the target of movement (Fig. 11). Our findings thus support the hypothesis that PF plays a role in both perceptual reports about visual inputs, as exemplified by report-related neurons, and in actions directly guided to visual stimuli, as exemplified by gaze-related neurons (Boussaoud et al. 1996; Milner and Goodale 1996).

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