Distinct Nature of Directional Signals Among Parietal Cortical Areas During Visual Guidance

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Eskandar, Emad N. and John A. Assad. Distinct nature of directional signals among parietal cortical areas during visual guidance. J Neurophysiol 88: 1777–1790, 2002; 10.1152/jn.00095.2002. We examined neuronal signals in the monkey medial superior temporal area (MST), the medial intraparietal area (MIP), and the lateral intraparietal area (LIP) during visually guided hand movements. Two animals were trained to use a joystick to guide a spot to a target. Many neurons responded in a direction-selective manner in this guidance task. We tested whether the direction selectivity depended on the direction of the stimulus spot or the direction of the hand movement. First, in some trials, the moving spot disappeared transiently. Second, the mapping between the hand direction and the spot direction was reversed on alternate blocks of trials. Third, we recorded the spot’s movement while the animals moved the joystick and then played back that movement while the animals fixated without moving the joystick. Neurons in the three parietal areas conveyed distinct directional information. MST neurons were active and directional only on visible trials in both joystick-movement mode and playback mode and were not affected by the direction of hand movement. MIP neurons were mainly directional with respect to the hand movement, although some MIP neurons were also selective for stimulus direction. MIP neurons were much less active in playback mode. LIP neurons were active and directional in both joystick-movement mode and playback mode. Directional signals in LIP were unrelated to planning saccades. The selectivity of LIP neurons also became evident hundreds of milliseconds before the start of movement. Since the direction of movement was consistent throughout a block of trials, these signals could provide a prediction of the upcoming direction of motion. We tested this by alternating blocks of trials in which the direction was consistent or randomized. The direction selectivity developed earlier on trials in which the upcoming direction could be predicted. These results suggest that LIP neurons combine “bottom-up” visual motion signals with extraretinal, predictive signals about stimulus motion.

INTRODUCTION

There is considerable evidence that the primate parietal cortex integrates visual signals to guide movement (Andersen 1995; Critchley 1953; Mountcastle et al. 1975). Determining whether neuronal activity in parietal cortex is more “sensory” or “motor” can be difficult, however, since the act of moving can itself produce visual stimulation. This can be clarified by having an animal acquire the same visual target with different types of movement (Bushnell et al. 1981; Snyder et al. 1997), or by transiently turning off the visual target (Colby et al. 1996; Gnadt and Andersen 1988; MacKay 1992; Newsome et al. 1988). Neuronal activity that is specific for particular movements or that occurs in the absence of visual stimulation might be reasonably assumed to be related to movement per se. We used a similar approach in a previous study to examine visual-guidance related signals in three parietal areas, medial superior temporal area (MST), the medial intraparietal area (MIP), and the lateral intraparietal area (LIP) (Eskandar and Assad 1999).

In that study we trained monkeys to use a joystick to guide a spot of light to a target while fixating. In all three areas, many neurons were selective for the direction of movement. Moreover, neurons in LIP and MST, but not MIP, continued to fire in a direction-selective manner if the spot disappeared over part of its trajectory. We showed that the directionality of the extraretinal signals in MIP was mainly due to the direction of the hand movement, while the directionality of the extraretinal signals in LIP was mainly due to the expected direction of the invisible moving spot. We therefore proposed that the three parietal areas convey different directional information during visual guidance.

This proposal raises several issues that are examined further here. First, if the direction selectivity of MIP neurons depends on the direction of the hand movement, then it is likely that MIP neurons would require a hand movement to respond, whereas LIP and MST neurons would not require a hand movement. To examine this, we recorded the visual traces generated when the animal was actively moving the spot with the joystick and then played back those movement traces while the animal passively fixated without moving the joystick. Second, in our previous study, we only quantitatively analyzed neuronal signals on trials in which the moving spot disappeared. Comparing responses on trials in which the spot is visible might reveal further distinctions in the origin of direction selectivity among parietal areas. For example, if the direction selectivity of a neuron depends solely on the direction of the hand movement then the neuron should respond similarly whether or not the moving spot is visible. Third, if the extraretinal signals in LIP neurons provide a predictive representation of the motion of the stimulus spot, then LIP neurons should respond differently if the animal could not predict the upcoming direction of motion. We tested this by presenting alternate blocks of trials in which the direction of motion was
either consistent or randomized from trial-to-trial. Extraretinal signals are often attributed to the planning or execution of movements. Our goal was to examine whether any extraretinal activity might also provide a more abstract, predictive representation of motion.

**METHODS**

Single-unit recordings were made from MIP, LIP, and MST of two male rhesus monkeys. The animals were trained to use a joystick to guide a spot of light to a target on a monitor. The vertically mounted joystick allowed full two-dimensional control of the displacement of the spot and was hidden from the animal’s view by the neck plate of the primate chair. Before each trial, the animals had to return the spring-loaded joystick to the center position, so the hand movements were always made relative to the starting center position. During training, both animals developed an exclusive hand preference that was maintained throughout the experiments. Once the animals mastered the task, an aseptic surgery was performed, following National Institutes of Health and Harvard Medical School guidelines, to implant a titanium head-post, celux recording chamber (Crist Instruments), and scleral search coil (Judge et al. 1980). The recording chamber was dorsally positioned at stereotactic coordinates P3,L10 in the hemisphere contralateral to the hand used to move the joystick.

**Behavioral paradigm**

Once a single unit was isolated, we first mapped its receptive/response field and then examined the cell’s direction selectivity online using a simple version of the joystick task. Most cells in MIP, LIP, and MST were at least qualitatively direction selective. Only the preferred and null directions were tested in the main task (Fig. 1). The animals began a trial by fixating a small spot to within 0.5°. Fixation had to be maintained throughout each trial, or the trial would abort without reward. After a delay of 500 ms, two pairs of stimulus spots (0.3° diam) and round targets (2.5° diam) were displayed, separated by 16°. The two pairs were centered about the midpoint of the receptive field (if the receptive field could be determined) and oriented parallel to the preferred/null axis of the cell. Throughout a given block of trials, the monkey used the joystick to guide one of the spots toward

![Diagram of the behavioral paradigm](image-url)
the opposite target. The direction of movement was thus dictated by the position of that spot relative to the target. The animals received a juice reward if they completed the movement within 2000 ms, did not deviate from the straight trajectory by more than $5^\circ$ (visual angle), and held the spot within the target for 300 ms.

Both spot-target pairs were shown at the start of each trial so that the initial visual stimulus was the same regardless of the upcoming direction of movement. However, since there was no visual cue to indicate which direction to move, the animal had to remember the appropriate direction to move on each trial within a block of trials. Once a block of trials in one direction was complete, the direction was switched (Fig. 1). In this way, preferred and null directions were tested in alternating blocks of trials. Changes in direction were indicated by two “training” trials in which only a single spot and opposing target were shown. Both spot/target pairs were presented on subsequent trials in the block, and the training trials were not included in the main analysis.

Within a block of trials in a particular direction (24 correct trials/block) there were three different experimental modes presented in sequential, smaller blocks of eight correct trials so that the animal knew the mode on a given trial (Fig. 1). In forward mode, the direction of the joystick movement was the same as the direction of the stimulus movement. For example, a rightward joystick movement moved the stimulus spot to the right. In reverse mode, the mapping between the joystick and the stimulus movement was reversed. For example, a rightward joystick movement moved the stimulus spot to the left. In playback mode, the movements of the stimulus spot recorded in the previous trials were played back to the animal while it passively fixated. On playback trials, the visual stimulus was identical to what the animal had just observed while moving the joystick; however, the animal was not permitted to move the joystick else the trial would abort. Typically, the animals released the joystick throughout the playback trials and kept their hands in their laps. Within each of these modes, two kinds of trials, visible and occluded, were interleaved pseudorandomly (Fig. 1). On visible trials, when the animal began moving the joystick, the appropriate spot began moving while the opposite spot disappeared. The moving spot remained visible throughout its trajectory. Occluded trials began identically to visible trials, but when the animal started moving the joystick, both spots disappeared. The disappearance was not a gradual occlusion: both spots disappeared within one video frame without either one moving. The animal still controlled the displacement of the invisible spot. When the spot was within $3.5^\circ$ of its target, it became visible again for the final approach to the target. The reappearance was presented as if the spot was reappearing from behind an occluder. On occluded trials, the visual stimulation was exactly the same for both directions of movement until the moving spot reappeared. Thus on occluded trials, until the reappearance of the moving spot, any differences in neuronal activity between the two directions could not be due to differences in the visual stimulation. While the perception of motion on occluded trials would have been enhanced if the stimulus spot had moved a short distance before becoming occluded, it would be impossible to guarantee equivalent visual stimulation under those conditions.

The animal first performed a block of trials in one stimulus direction, with forward mode followed by reverse mode, followed by playback mode. Four visible and four occluded trials were pseudorandomly interleaved in each mode. Once a block was completed, the direction was reversed and the entire sequence repeated. Changes in mode and direction were signaled by a full-field flash of the stimulus monitor. The direction was usually alternated 4 times, for a total of 16 repetitions of each unique trial type. (There were $2 \times 2 \times 3 = 12$ unique trial types—every combination of preferred/null direction, visible/occluded, and forward/reverse/playback). Once trained, the animals learned to switch readily between modes and directions and performed all aspects of the task extremely well. For both animals, there were no systematic differences in movement latency or peak movement velocity among the various trial types [analysis of variance (ANOVA); $P > 0.05$].

Data analysis

For quantitative analyses, average spike rates were computed from the start of movement until the spot was $3.5^\circ$ away from the target, the point at which the spot reappeared on occluded trials. This ensured that on occluded trials, the visual stimulation was identical between the two directions over the period of analysis. On playback trials, the spike rate was measured over the same epochs as in the joystick task. The direction selectivity of individual neurons was measured by calculating transmitted information about direction using the spike rates from single trials. Transmitted information expresses the reduction in uncertainty about the stimulus (direction) with a given response (spike rate) (Abramson 1963; Optican and Richmond 1987). Because transmitted information is based on the reliability of differences between two sets of spike rates rather than the mean spike rates, it is closely related to the statistical significance of the differences. The maximum amount of transmitted information for two directions is $\log_2(2) = 1$ bit.

It is possible that the distributions of spike rates between the two directions differed by chance alone, causing the absolute information to be overestimated. To compensate, information expected from chance was estimated using a bootstrap technique. For each calculation, spike rates from trials in the two directions were randomly re-shuffled into two sets, and information calculated exactly as above. The average value of 1,000 shuffles was taken as an estimate of the information expected from chance and was subtracted from the measured information. For each data set, the average information expected from chance was around 0.1 bits.

For each unit, we calculated six transmitted information values about direction. For playback trials we calculated transmitted information for stimulus direction separately for visible and occluded trials. (For occluded trials “stimulus direction” could only be inferred by the animal, since the actual moving stimulus spot was not visible over the period of analysis.) For trials in which the animal moved the joystick (i.e., nonplayback trials), we calculated transmitted information independently for the direction of stimulus-spot movement and the direction of hand movement. As for playback trials, this was also done separately for visible and occluded trials. To calculate transmitted information about stimulus direction when the animal moved the joystick, we needed to ensure that the hand movement was the same and the only difference was the stimulus direction. Therefore we compared forward trials in one stimulus direction with reverse trials in the other stimulus direction. To calculate transmitted information about hand direction, we needed to ensure that the stimulus direction was the same and the only difference was the direction of the hand. Therefore we compared forward and reverse trials in the same stimulus direction. For both of these comparisons there were therefore two possible forward/reverse pairings. Transmitted information for the two pairings was generally similar, so we averaged the two values. In addition to calculating transmitted information, we also used two-way ANOVA to independently assess the effects of the stimulus direction and the hand direction. Visible and occluded trials were analyzed separately.

Mapping of receptive fields/response fields and direction selectivity

Before running the main task, we first attempted to map the receptive field using manually controlled moving spots or bars while the animal passively fixated. This was generally effective for mapping receptive field boundaries and assessing preferred direction in MST. LIP neurons generally had weaker responses to passive stimulation. To better define the response fields of LIP neurons we used a memory delayed-saccade task (Barash et al. 1991). In this task, the animal made a saccade after 500 ms to the remembered location of a target that had been flashed for 200 ms. Six to eight directions were tested with targets placed at $6^\circ$, $12^\circ$, or $18^\circ$ from the fovea. Most LIP neurons were strongly modulated by this task and were broadly spatially selective for the contralateral visual field. Once the receptive/
response field was determined on-line from the neuronal responses, we determined the direction preference of the neuron in the joystick task by testing 12 directions of joystick movement evenly distributed at 30° intervals. Only one spot and its opposing target were presented on each trial to indicate the direction unambiguously. For each direction, the stimulus and target were placed so that a perfectly straight trajectory would cross through the center of the receptive/response field. Most MIP cells were unresponsive during either manual mapping or the saccade task. However, MIP neurons were active and direction selective during the 12-direction joystick-mapping task. Therefore for all MIP cells, the stimulus/target array was centered 14° from the fixation point within the contralateral hemisphere.

Identification of parietal areas

We obtained a T1-weighted coronal MRI scan (1-mm sections) with mineral-oil filled capillary tubes placed at specific locations within the recording grid to reconstruct the electrode penetrations. Recordings were made from the posterior intraparietal sulcus (IPS) and the posterior superior temporal sulcus (STS). While we were searching for units, the animals continually ran the 12-direction joystick direction-tuning task. Once we isolated a unit, we tried to map its receptive field and then ran the memory delayed-saccade task. Cells were then assigned to LIP, MIP, and MST based on their location within the IPS or STS and their physiological responses. MST neurons were identified based on their location in the anterior bank of the STS, their strong, direction-selective responses during passive receptive field mapping, and their large receptive fields that often included the fovea. With our dorsal approach to the IPS, we would typically first encounter gray matter of the medial bank of the IPS, then a brief quiet stretch consistent with the sulcus itself, then gray matter of the lateral bank of the IPS. Subjectively, the responses of the neurons between the two banks of the IPS were strikingly different. Neurons in the medial bank were generally unresponsive to either passive visual stimulation or the delayed memory-saccade task. Neurons in the lateral bank were more active during passive mapping and responded strongly during the delayed memory-saccade task. Seventy-one percent of neurons from the lateral bank were selective for the spatial location of the saccade target during the delay period (ANOVA; P < 0.05), whereas only 18% of neurons from the medial bank were spatially selective. Thus based on anatomic criteria plus the strong, spatially selective activity during the delayed memory-saccade task (Barash et al. 1991), the lateral bank neurons were assigned to LIP. The medial bank neurons were assigned to MIP based on their location compared with the anatomic description of Colby et al. (1988). A few neurons were also recorded from the fundus of the IPS, probably from the ventral intraparietal area (VIP) (Colby et al. 1993; Cook and Maunsell 2002). These neurons were distinct in that they had strong, direction-selective responses during receptive field mapping with a manually controlled bar-stimulus, but only responded transiently to stimulus onset and offset during the memory delayed-saccade task. VIP responses are not examined further in this report.

RESULTS

A total of 123 cells were recorded from MIP and 119 cells from LIP. For comparison, a smaller sample of 23 cells was recorded from MST. The response properties of neurons from the joystick-movement trials and playback trials differed in a consistent way among the three areas.

MST

Figure 2 shows responses to all experimental conditions for a single MST neuron. Average population responses for all 23

FIG. 2. Response of a single medial superior temporal area (MST) neuron. Responses are aligned on the start of movement, indicated by the vertical lines. The open arrows indicate the direction of movement of the hand or stimulus spot. In the raster displays, the lines to the left of the vertical line indicate the onset of the spots and targets and the lines to the right of the vertical line indicate the time at which the spot moved to within 3.5° of the target.
MST units were also compiled after sorting by the preferred direction determined during the direction-tuning task (Fig. 3A). MST neurons were most active and direction selective when the moving stimulus was visible, whether on joystick-movement trials or playback trials, but were not selective for the direction of hand movements. For each unit, we measured transmitted information about direction for the six experimental conditions. The distributions of these information values are displayed in three pair-wise comparisons in Fig. 3B. MST neurons generally conveyed information about direction whenever the stimulus was visible, including playback trials (Fig. 3B). MST neurons conveyed much less information about hand direction or occluded stimulus direction. (On occluded trials “stimulus direction” could only be inferred by the animal, since the actual moving stimulus spot was not visible over the period of analysis.)

MIP

Responses of a single MIP cell are shown in Fig. 4. Average population responses for all 123 MIP neurons are shown in Fig. 5A. In general, MIP neurons were direction selective for both visible and occluded trials, but the direction selectivity depended more on the direction of the hand movement than on the direction of the stimulus movement. MIP neurons were much less active and selective on playback trials, when there was no hand movement, consistent with the direction selectivity being dependent on the direction of the hand movement. While MIP neurons mainly conveyed information about the direction of the hand movement many MIP neurons were also informative about the direction of the stimulus movement (Fig. 5B). This raises the possibility that distinct sets of MIP neurons could encode hand direction or stimulus direction. Of the MIP neurons that were significantly modulated by the direction of the stimulus spot during joystick-movement trials (visible trials, 50/123; occluded trials, 42/123; ANOVA; \( P < 0.05 \)), most of those cells also had significant hand-movement modulation (visible trials, 33/50; occluded trials, 27/42). Moreover, across the population, the preferred stimulus direction was not different from the preferred hand direction (sign test, \( P > 0.4 \)). Thus if the stimulus motion was in the preferred direction, the responses tended to be larger by the same amount regardless of the direction of the hand movement, as expected for a main (i.e., additive) effect of both hand direction and stimulus direction. This is evident in the population histograms for the subset of 50 MIP neurons that were selective for the direction of the stimulus spot during visible trials (Fig. 6A). These data suggest that hand direction and stimulus direction have independent effects on the MIP neurons. Consistent with this, while the average responses on playback trials for those 50 units were
much smaller than responses on joystick-movement trials, the playback responses were nonetheless selective for the direction of stimulus motion (Fig. 6A). For visible trials, the average difference in firing between preferred and null directions was quantitatively similar for playback trials and joystick-movement trials (Fig. 6C), and individual MIP cells tended to be selective for stimulus direction on both playback trials and joystick-movement trials (Fig. 6D). For occluded trials, the average difference in firing between preferred and null directions was smaller for playback trials (Fig. 6B and C), but individual MIP cells could still be quite selective for stimulus direction on playback trials (Fig. 6D).

**LIP**

Responses of a single LIP neuron are shown in Fig. 7, and average population responses are shown in Fig. 8A. LIP neurons were generally active and direction selective during both visible and occluded trials. In contrast to MIP neurons, however, the direction selectivity LIP neurons did not depend on the direction of the hand movement, and the cells were still active and directional on playback trials, when there was no hand movement at all. On occluded trials, therefore, the direction selectivity of the LIP neurons was not related to either the hand movement or differences in the visual stimulation, since the visual stimulus was identical between both directions of movement until the moving spot reappeared. In addition, LIP neurons were already selective for the direction of the upcoming stimulus direction hundreds of milliseconds before the movement actually began (Fig. 8A). This premovement activity was related to the upcoming hand movement since it could be used to “predict” the upcoming direction of the stimulus spot.

Individual LIP neurons generally conveyed more information about stimulus direction than hand direction (Fig. 8B). Most LIP neurons were also more directional for visible trials than occluded trials, but many LIP neurons were strongly selective for stimulus direction on occluded trials. The pattern of direction selectivity in the main task is summarized for the three parietal areas in Fig. 9. Average transmitted information is shown for each condition, along with the percentage of units showing significant modulation for direction, as assessed using ANOVA.

**Controls for potential alternate explanations for direction selectivity in LIP**

The responses of the LIP neurons seemed to encode the direction of the stimulus spot, independent of the hand movement. However, there are several alternative explanations that must be considered. First, LIP neurons are also selective for the direction of saccadic eye movements (Andersen 1995) and/or attention to particular locations (Colby et al. 1996). Although the animals maintained fixation throughout the trials, it was important to ensure that the apparent direction selectivity was not an artifact of the animal planning to saccade to one of the two target locations. For example, if one of the targets was inadvertently positioned in a stronger part of the response field than the other target, then a systematic plan by the animal to saccade to the target of the movement could be misinterpreted as direction selectivity. For 83 LIP neurons, we directly controlled for this possibility by requiring the animal to actually make saccades to each of the targets (Fig. 10A).
block of joystick-movement and playback trials in a particular direction, the target of that movement served as the saccade target for an additional block of trials. If the apparent direction selectivity observed during the joystick and playback trials was due to a covert plan to saccade to the targets, then the same selectivity should also be present when the animals actually made saccades to the targets. Individual saccade-control trials began exactly like occluded trials: both spots/target pairs appeared and then both spots disappeared, leaving only the targets. After a delay (chosen from the distribution of spot-reappearance times on occluded trials), the fixation point disappeared, signaling the animal to make a saccade to the remembered target location for that particular block of trials. The same saccade target was tested throughout a block of trials so that the animals could plan the upcoming saccade on each trial. Most LIP neurons responded briskly to the onset of the spot/targets and during the delay period but were not very selective between the two targets (Fig. 10B). Across the population, LIP neurons were significantly more selective for stimulus direction on joystick-movement trials (visible trials, 0.27 ± 0.020 bits; occluded trials, 0.19 ± 0.017 bits) or playback trials (visible trials, 0.22 ± 0.018 bits; occluded trials, 0.15 ± 0.015 bits) than for saccades made to the targets of the two directions of movement (0.12 ± 0.009 bits; pairwise Wilcoxon signed-rank tests; P < 0.05; Fig. 10C). More importantly, while the four directional information values were mutually correlated across the population of LIP cells (pairwise correlations, P < 0.05), there was no correlation between any of the four directional information values and the information on saccade-control trials (P > 0.2). There was also no systematic preference for the target of the preferred or null direction movement to elicit the larger response during saccade-control trials (Wilcoxon signed-rank test, P > 0.8). These results argue that the intention to saccade to the targets does not explain the selectivity observed during joystick-movement trials. This does not mean that LIP neurons were not selective for saccade direction: most LIP neurons were indeed selective for saccade direction when tested with a broader range of saccade directions (see METHODS).

Another potential explanation for the apparent direction selectivity in LIP is that it could be due to nonspecific changes in the animals’ vigilance or arousal. For example, the animals may have had difficulty making movements in particular directions, which could have produced more firing in LIP neurons for those directions. However, the average performance of both animals was good across all directions of movement (≥80% correct), and the performance was closely matched between any pair of opposing directions (≤7% differences in correct trials). More importantly, for both animals we found LIP units with preferred directions in any of the 12 possible directions. Most LIP neurons (64%) that were significantly direction selective for joystick-movement trials were also significantly direction selective for playback trials, for which the animal had only to fixate. Thus it is unlikely that the direction selectivity in LIP was an artifact of nonspecific changes in the animal’s state.
Predictive activity in LIP

In Fig. 7, LIP responses were already direction selective even before the spot began to move. The premovement selectivity did not seem to depend on the direction of the hand movement and was present on playback trials. This is revealed in more detail by subtracting the population-response histograms for the null direction from the population-response histograms for the preferred direction (Fig. 11A) to yield difference histograms (Fig. 11B). Starting approximately 600 ms before the start of movement, the average response was larger when the upcoming movement was in the preferred direction than in the null direction, for both joystick-movement trials and playback trials. The difference developed even before the onset of the spots/targets and rapidly increased following the onset of the spots/targets (Fig. 11C). After the movement began, the difference increased further for visible trials and decreased to zero as the spot slowed and reached the target (Fig. 11B). (The transient difference is further evidence that the selectivity is for direction of motion and not for attention to the two different static target locations. If the selectivity were due to attention to the two different target locations, then the difference obtained for the 2 hand directions were averaged. Difference histograms were smoothed by convolving with a Gaussian function with an SD of 30 ms. D: stimulus-direction information for joystick-movement trials vs. playback trials for the same 50 MIP cells. Diagonal lines indicate unity slope.)
**FIG. 7.** Response of a single lateral intraparietal area (LIP) neuron. Same conventions as in Fig. 2.

**FIG. 8.** Population responses in LIP.

**A:** population histograms calculated by averaging responses among all 119 LIP neurons. Same conventions as in Fig. 3A.

**B:** transmitted information for direction. Same conventions as in Fig. 3B.
tion, which the animal could predict. Before the ANOVA calculations, we pooled visible and occluded trials for the same direction of movement, since these trials were indistinguishable until the start of movement. For the 300-ms period from the start of fixation until the onset of the spots and targets, 21/119 LIP neurons (18%) were significantly selective for the upcoming stimulus direction on joystick-movement trials and 16/119 (13%) were significantly selective on playback trials. For the period from the onset of the spots/targets until the start of movement (approximately 300 ms), 51/119 (43%) were significantly selective on joystick-movement trials and 36/119 (30%) were significantly modulated on playback trials. For comparison, no more than 2/23 (9%) MST neurons or 30/123 (25%) MIP neurons were significantly selective for the upcoming stimulus direction during either premovement period for joystick-movement trials or playback trials. Since the visual stimulus was always the same regardless of the upcoming direction of movement, the premovement selectivity in LIP could not be due to differences in the visual stimulus.

The fact that LIP neurons were selective before the start of movement suggests that LIP could provide a predictive representation of the upcoming direction of stimulus motion. If so, the LIP neurons should respond differently if the animals could not predict the upcoming direction of motion before a trial. To examine this, 11 LIP units from one monkey were tested with trials in which the direction of motion was randomized from trial-to-trial between preferred and null directions. The direction on each trial was indicated to the animal by presenting only one spot and its opposite target. For each unit we first had the monkey complete the standard task with blocked directions (Fig. 12A), and then switched to the trials with randomized directions (Fig. 12B). To avoid confusing the monkey, we had him make movements only in forward mode during the randomized trials. As before, for blocked directions (i.e., predictable) the population neuronal activity for preferred and null directions diverged slightly from the beginning of the trial, then diverged more rapidly following the onset of the spots/targets. When the direction was randomized, the difference between preferred and null directions did not emerge until after the spot/target appearance, and then was delayed approximately 100 ms compared with the blocked-direction population response (Fig. 12C). Later in the trials, as movement began, the

FIG. 9. Summary of responses in the main task. Left column: mean transmitted information for direction for the 6 experimental conditions, averaged among all neurons in MST, MIP, or LIP. Error bars are ±1 SE. Right column: percentage of cells from the 3 areas that showed significant direction selectivity in the 6 experimental conditions [analysis of variance (ANOVA); P < 0.05].
response amplitudes and directionality were similar between blocked and randomized directions. Thus the early selectivity in LIP neurons depended on whether the upcoming direction could be anticipated.

**DISCUSSION**

We examined the nature of neuronal direction selectivity during visually guided arm movements in parietal cortex. We determined the extent to which the selectivity was related to the movement of the arm or the movement of the spot being guided through the receptive field. We found consistent differences in MST, MIP, and LIP that suggest that the three areas play distinct roles in visual guidance.

The direction selectivity of MST neurons was dominated by the direction of visual motion. MST neurons were direction selective on visible trials, but not occluded trials, regardless of whether the animals made a hand movement. Many previous studies have shown that MST neurons are sensitive to visual motion (reviewed in Albright 1993; Andersen 1997; Maunsell and Newsome 1987). MST neurons are also affected by non-visual influences that may reflect inputs from occulomotor (Bradley et al. 1996; Bremmer et al. 1997; Newsome et al. 1988) or vestibular sources (Duffy 1998; Thier and Erikson 1992). We did not see extraretinal modulation of MST responses in our experiment: MST neurons were not modulated by the direction of hand movement and did not respond after the stimulus spot disappeared on occluded trials, save for a small off-transient that was similar across all conditions (Fig. 3A). However, in our experiment the animals fixated throughout the trials. Extraretinal signals in MST may thus be specific for eye movements such as smooth pursuit (Newsome et al. 1988). It is also possible that our sampling of MST neurons...
was too limited to have included units with extraretinal activity. For example, Newsome et al. (1988) reported neurons that continued to fire during smooth pursuit eye movements if the pursuit target was turned off or stabilized on the retina. These neurons, which were preferentially located in dorsal MST, were also selective for the motion of a single spot rather than wide-field motion (Komatsu and Wurtz 1988). Most of the MST neurons in our sample were strongly activated by the motion of a single spot, suggesting that at least some of them were from dorsal MST.

The direction selectivity of MIP neurons was mainly related to the direction of hand movement. MIP is part of the superior parietal lobule, which contains many neurons that are activated during arm movements (Kalaska et al. 1990; Snyder et al. 2000). Strictly speaking, we could not distinguish whether the selectivity for hand direction was related to the movement per se or to sensory feedback from the arm. After our study, we recorded EMG activity from one of the animals during a similar joystick-movement task and found that arm-muscle activation leads the joystick movement by no more than 150 ms (I. H. Lee and J. A. Assad, unpublished observations). On average, MIP neurons began to activate approximately 250 ms before the first detectable joystick movement (Fig. 5A), which suggests that the MIP activity was not solely due to sensory feedback from the moving arm.

The responses of many MIP neurons were also modulated by the stimulus-spot direction. MIP receives input from the parietal occipital area and VIP (Colby and Duhamel 1991; Colby et al. 1988), both of which contain visually responsive neurons. While we only found weak responses from most MIP neurons on playback trials, many of those responses were still direction selective. Moreover, the small modulation on playback trials could account reasonably well for the effect of stimulus-spot direction on joystick-movement trials, providing further evi-
because many cells were directional on occluded trials or were the direction of the visual stimulus or the direction of the hand movement, and that direction selectivity did not depend on either hand-related directional influences in MIP. However, the modulation by the stimulus-spot direction was not a purely visual effect since modulation by the inferred stimulus direction was also present on occluded trials. The stimulus-direction modulation might represent the “goal” of the movement, as previously suggested for neurons in motor cortex or striatum (Alexander and Crutcher 1990). By integrating hand-related directional information with stimulus- or goal-related information, MIP could contribute to controlling ongoing movements.

Many LIP neurons were also selective for the direction of movement, and that direction selectivity did not depend on either the direction of the visual stimulus or the direction of the hand. The direction selectivity did not require a moving visual stimulus, because many cells were directional on occluded trials or were selective for the upcoming direction of motion even before the movement began. On every occluded trial both stimulus spots were visible at the start of the trial, and both spots disappeared simultaneously. Thus the direction selectivity after the disappearance of the spots could not have been due to the previous visual stimulation, such as a response transient following the offset of the stimulus spots. The direction selectivity in LIP likewise did not depend on the direction of hand movement, because on joystick-movement trials the responses of most cells were unaffected by the hand direction, and many cells were directional on playback trials. What then is the nature of the direction selectivity in LIP? Because the same direction of motion was presented repeatedly within a block of trials, the animals could predict the direction on a given trial. Thus the directional signals in LIP may in part reflect the animal’s expectation or working memory that the stimulus is moving, or will move, in a particular direction. This interpretation was supported by the observation that the direction selectivity was present even before the start of movement when the animal could predict the upcoming direction of motion, but was reduced when the animal could not predict the upcoming direction of motion. A predictive representation of this sort may play an important role in visual perception and visual guidance. More generally, these results suggest that extraretinal signals should not be automatically ascribed to motor and/or nonvisual sensory sources. They may instead relate to the animal’s internal state, similar to the effects of attention on neuronal responses (Moran and Desimone 1985; Treue and Maunsell 1996).

Direction selectivity is not a property commonly attributed to LIP. Rather, there is considerable evidence that LIP neurons encode eye movements or attention to specific locations in the visual field (Gottlieb et al. 1998; Kusunoki et al. 2000; Snyder et al. 2000). It is thus important to consider whether spatial selectivity could account for the apparent direction selectivity we have observed in LIP. In our experiment, the trajectories of the preferred and null directions of motion were spatially overlapping. However, the animals almost certainly attended to different locations on the screen for the two directions of motion. For example, before the animals were trained to hold gaze on the fixation spot, they would invariably fixate the target of the movement. Even when trained, animals would occasionally break fixation and make a saccade to the target of the movement, especially near the end of the trajectory as the spot approached the target. Planned saccades and/or attention to the two targets could have produced different activity for the two directions of motion. However, this scenario was unlikely for several reasons. First, we tried to place the two targets symmetrically about the strongest part of the response field so that any activity related to planning eye movements/attention to the two targets would be balanced. Second, we showed that memory-delayed saccades to the two target locations could not account for the selectivity observed during the joystick-movement and playback trials. Third, the difference in firing rate between the preferred and null directions declined to zero as the spot’s movement slowed near the end of the trajectory, despite the fact that the animals must have closely attended the target location for the final precise approach of the spot to the target. Fourth, the directionality was generally stronger on visible than occluded trials, even though attention was presumably directed to the target of the movement in either case. Thus the simplest explanation is that the selectivity we observed in LIP was for the direction of motion rather than for a static spatial location.

We should emphasize that direction selectivity and spatial
selectivity are not mutually exclusive attributes. Most of the direction-selective LIP neurons in our study were also selective for spatial location when tested with a memory delayed saccade task over the full 360° range of saccade directions. In the main experiment, we deliberately placed the two targets symmetrically about the center of the response field so as to minimize the effect of spatial selectivity, so we could only test movements spanning the center of the response field. Thus we cannot yet address the detailed spatial relationship between the saccade-response field and the direction selectivity. For example, it will also be interesting to examine whether LIP neurons are direction selective throughout their response fields, and if so, whether the direction selectivity is spatially uniform or varies in some way. On the other hand, we did not notice any obvious relationship between the preferred direction of LIP neurons and the location of the center of the saccade response field, which suggests that the directional signals may be independent of the spatial specificity of LIP neurons. In fact, a closer look at the averaged LIP responses suggests that the directional signals might be superimposed or combined with spatial signals (Fig. 11). For all conditions, including saccade-control trials, there was an increase in activity at the onset of the stimulus/target pairs that was maintained throughout the trial. This may be due to the presence of a visual stimulus in the response field of the neurons and/or attention directed toward the response field. On top of that pedestal of activity there were further variations in activity which depended on the presence and direction of movement. For example, in all conditions in which the monkeys could expect the spot to move in the preferred direction of the neurons, there was an increase in activity very early in the trial that continued through the start of movement. If the stimulus spot was visible and moved in the preferred direction, there was an abrupt further increase in activity at the start of movement. This view is interesting that the extraretinal, predictive directional signals were comparable in strength to the “additional” signal evoked by the visible moving spot (Fig. 11B). Thus a reasonable description of the LIP activity is that it reflected a confluence of visual motion signals and “top-down” signals related to predicting or inferring stimulus movement. These results add to an increasing body of work suggesting that extraretinal signals may be at least as important as visual signals in revealing functional distinctions among cortical areas in later stages of visual processing.

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