Dissociation of visual, motor and predictive signals in parietal cortex during visual guidance

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The role of the posterior parietal cortex (PPC) in the visual guidance of movements was studied in monkeys trained to use a joystick to guide a spot to a target. Visual and motor influences were dissociated by transiently occluding the spot and by varying the relationship between the direction of joystick and spot movements. We found a strong segregation of function in PPC during visual guidance. Neurons in area MST were selectively modulated by the direction of visible moving stimuli, whereas neurons in area MIP were selectively modulated by the direction of hand movement. In contrast, the selectivity of cells in the lateral intraparietal area (LIP) did not directly depend on either visual input or motor output, but rather seemed to encode a predictive representation of stimulus movement. These predictive signals may be an important link in visuomotor transformations.

The ease with which an animal captures its prey, or an athlete catches a ball, belies the complexity of the underlying visuomotor transformation in the brain. The brain integrates visual information, makes inferences about the future positions of targets, transforms visual coordinates into motor coordinates and issues motor commands. There is considerable evidence that the posterior parietal cortex (PPC) is important in this transformation[1,2]—although there is much debate as to whether its role is better characterized as 'sensory' or 'motor'. The fundamental problem is that it is difficult to dissociate these two influences in natural guidance tasks, such as eye movements and reaching, in which the visual stimulus of the target or moving limb is confounded with the act of moving itself. We studied the role of PPC in the visual guidance of movements in fixating monkeys trained to use a joystick to guide a spot to a target. To dissociate sensory and motor components, two experiments were done conjointly. In one experiment, the moving spot was transiently hidden from view. Our prediction was that PPC cells that were primarily driven by the visual stimulus should become inactive, whereas cells that were driven by nonvisual 'extraretinal' sources, such as the hand movement, should remain active and directional. Extraretinal activity of this sort has typically been attributed to the planning or execution of movements[3]. We have previously reported that some cells in PPC remain active during the transient absence of a moving visual stimulus while the animals withheld movements, but it is possible that the animals had still planned to move[4]. In the other experiment, the mapping between the direction of the hand movement and stimulus movement was varied. Our prediction was that visual cells would be unaffected by the direction of the hand movement, whereas motor-related cells would reflect the direction of the hand movement. We tested both predictions to determine the extent to which visual input and/or motor output could account for the activity of different PPC areas during visual guidance.

Results

Behavioral task

Extracellular recordings were made from the medial superior temporal area (MST), the lateral intraparietal area (LIP) and the medial intraparietal area (MIP) in two rhesus monkeys. The animals were trained to use a joystick to guide a spot of light to a circular target 17° away while fixating (**Fig. 1a**). Animals were rewarded if they completed the movement within a time limit and followed a fairly straight trajectory. Different directions were tested by rotating the spot/target axis (**Fig. 1b**). For MST neurons, the spot/target pairs were centered in or about the receptive field, which had been mapped previously while the animal passively fixated. For LIP neurons, the spot/target pairs were centered about the saccade-response field, mapped previously using a memory-saccade task. This was done to minimize differences in neuronal activity that might occur if the animals planned to saccade to the targets in the joystick task. For MIP neurons, the spot/target pairs were always centered 14° from the fovea, on the horizontal meridian contralateral to the recording chamber.

Once the spot/target pairs had been placed, twelve different directions, evenly spaced at 30° intervals, were tested by rotating the spot/target axis about its midpoint (**Fig. 1b**). Each direction was repeated two to four times, and the responses were averaged from stimulus onset until the end of movement. In all three PPC areas, the majority of cells were selective for the direction of movement. The direction that elicited the largest response (preferred) and its opposite (null) were determined on-line and selected for further analysis.

The task in Fig. 1c was used to determine the source of the selectivity. While the animal fixated, two spots within two circular targets appeared, oriented along the preferred/null axis of the cell. The monkey used the joystick to move one of the spots toward the opposite target. The two directions of movement were

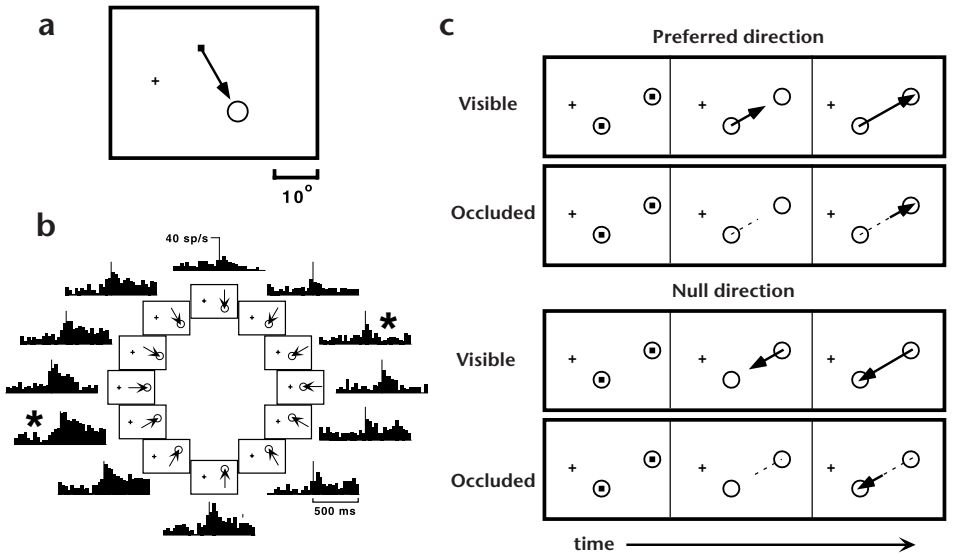

Fig. 1. Visual stimuli and behavioral tasks. **(a)** Task used to determine preferred direction. The animal fixated a small point (+) and used a joystick to guide a spot to a circular target. **(b)** Responses from a neuron in the IPS to the twelve directions of movement in the same task. Histograms were aligned to the start of joystick movement (vertical lines). The cell was direction selective, and its preferred/null axis was 30° from horizontal (asterisks). **(c)** Main task. Only preferred and null directions were tested. Arrows indicate that moving spot is visible; dashed lines indicate that moving spot is not visible.

tested in separate but interleaved blocks of trials, so that the animal knew the direction on a given trial. Two kinds of trials were randomly interleaved. On 'visible' trials, the moving spot remained visible throughout its trajectory, and the opposite spot disappeared at the start of movement. On 'occluded' trials, both spots disappeared without moving as soon as the animal moved the joystick, and the spot being guided then reappeared near the target, as if it had been moving smoothly behind an occluder. On occluded trials, the visual stimulus was identical for both directions until the reappearance of the spot. Thus up to the time that the spot reappeared, any differences in neuronal activity between the two directions could not have been due to differences in visual stimulation, and therefore must have been due to an extraretinal source, such as the hand movement.

To determine further the source of the selectivity, the animals were also trained to use two different mappings between the direction of the stimulus movement and the direction of the hand movement. In 'forward' mapping, the direction of stimulus movement corresponded to the direction of hand movement, whereas in 'reverse' mapping, the direction of stimulus movement was opposite that of the hand. In this manner, both directions of stimulus movement (with randomly interleaved visible and occluded trials) were tested with both directions of hand movement. Forward and reverse trials were presented in separate but interleaved blocks of trials, so that the animal knew the mapping on a given trial.

The animal first did a block of trials in one stimulus direction, with forward mapping in one half-block and reverse mapping in the other half-block. Four visible and four occluded trials were pseudorandomly interleaved in each half-block. The direction was then changed and the sequence repeated. The direction was alternated 2–4 times, for a total of 8–16 repetitions of each trial type.

Responses Of PPC neurons

We recorded from cells in areas MST, MIP and LIP (**Fig. 2**). A typical MST cell was selective for the direction of stimulus movement only when the stimulus was visible and not when the stimulus was occluded, irrespective of the hand movement (**Fig. 2a**). In contrast, cells in MIP and LIP were frequently active and direction selective during occluded trials. In MIP, this extraretinal direction selectivity was largely related to the direction of hand movement. A typical MIP cell was active on occluded trials when the hand was moving in one direction and not when the hand was moving in the other direction, irrespective of the direction of stimulus movement (**Fig. 2b**). LIP cells were also active and direction selective on occluded trials, but the selectivity did not depend on either differences in visual stimulation or the direction of hand movement. A typical LIP cell was direction selective on occluded trials, but its selectivity matched that of visible trials, regardless of the direction of hand movement (**Fig. 2c**). Because the visual stimulus on occluded trials was identical between directions until the reappearance of the spot, we will refer to this as selectivity for the 'inferred' stimulus direction. Further analyses focused on the selectivity observed while the moving spot was not visible during occluded trials. In MIP and LIP, direction-selective responses were evident before and after the start of movement. Because the directionality was generally similar during both time periods, further analyses focused on the activity after the start of movement.

Transmitted information was calculated to assess the degree to which the direction-selective extraretinal signals depended on hand direction or inferred stimulus direction[5,6]. The input code was the two directions, and the output code was the spike counts from the start of joystick movement until the reappearance of the moving spot. Information is a useful measure because it captures the reliability of the directional modulation. A neuron that gives a reliably different response for the two directions would transmit a maximum of one bit of information. A neuron that gives the same response for the two directions, or responds unreliably, will transmit low amounts of information. For example, the cell in Fig. 2b conveyed 0.640 bits of information about hand direction and 0.066 bits about inferred stimulus direction, whereas the cell in Fig. 2c conveyed 0 and 0.897 bits, respectively.

Anatomical segregation of function in PPC

Transmitted information about hand direction and inferred stimulus direction was calculated for the occluded-trial responses of each cell (**Fig. 3a**). Neurons predominantly conveyed information about either hand direction or inferred stimulus direction, but not both. Furthermore, there was a clear anatomical segregation. MST cells conveyed little extraretinal information about

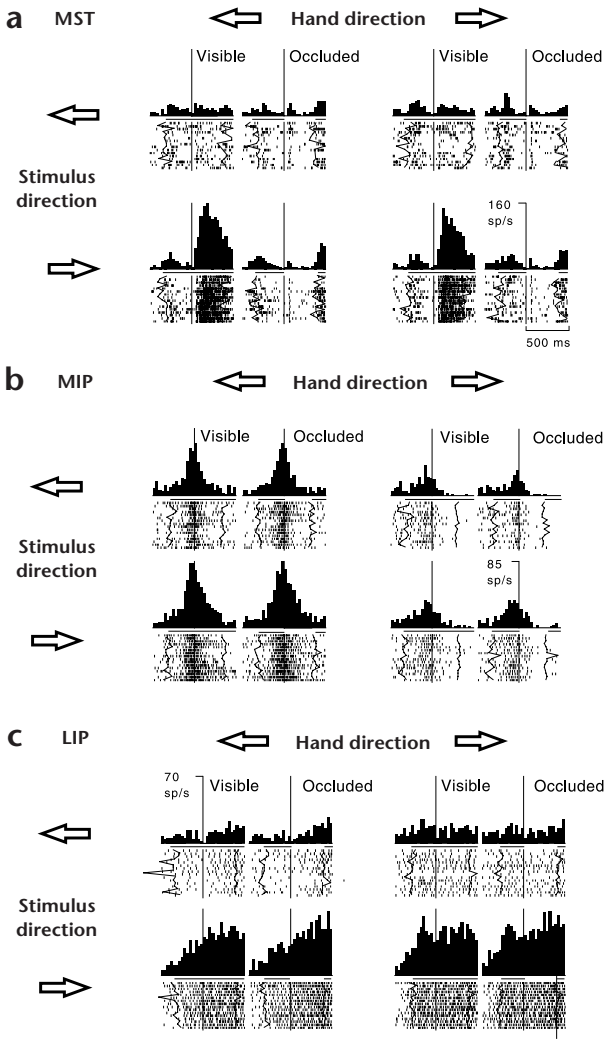

Fig. 2. Responses of single neurons in MST, MIP and LIP. Each combination of hand direction and stimulus direction (indicated by arrows) was tested, for both visible and occluded trials. The two directions are shown as right and left, although the actual preferred direction varied among cells. The rasters and histograms are synchronized at the start of joystick movement, which was when the spots disappeared on the occluded trials (long vertical line). The thick black line beneath the histograms indicates the time during which the spot was visible, averaged across trials; the gap in the thick black line beneath the occluded histograms indicates the time during which the moving spot was not visible, averaged across trials. The jagged lines in the rasters indicate spot/target onset and spot reappearance on individual trials.

hand direction or inferred stimulus direction (0.045 ± 0.014 and 0.069 ± 0.018 bits, respectively; mean ± standard error). MIP cells conveyed significantly more information about hand direction than about inferred stimulus direction (0.187 ± 0.022 versus 0.071 ± 0.010 bits; Mann-Whitney test, $p < 0.001$), whereas LIP cells conveyed significantly more information about inferred stimulus direction than about hand direction (0.167 ± 0.021 versus 0.059 ± 0.010 bits; Mann-Whitney test, $p < 0.0005$). Cells were assigned to MST, MIP or LIP based on pre-experimental magnetic resonance imaging (MRI; **Fig. 3b**) and depth measurements (see Methods). Twenty-three cells were recorded from MST, 102 cells from MIP and 96 cells from LIP. To confirm our distinction between LIP and MIP cells, 115 cells were tested with the memory-saccade task using at least six directions. Spatially selective delay-period activity in this task is commonly found in LIP, but not in MIP[7]. In general, cells assigned to LIP were activated on stimulus onset, and that activity persisted throughout the delay period, whereas MIP cells were less responsive throughout (**Fig. 4**). Twenty-nine of 44 LIP cells (66%) were significantly modulated with respect to saccade direction during the delay period, whereas only 12 of 71 MIP cells (17%) were significantly modulated (ANOVA, $p < 0.05$).

Controls for block effects and planned eye movements

Because occluded trials were interleaved with visible trials of the same direction over a block of trials, it is possible that the selectivity was a nonspecific consequence of the block organization. To control for this possibility, 10 LIP cells were also recorded while the monkey performed trials with the two directions randomized. The direction on a given trial was indicated by presenting only one spot and one target. Average information about inferred stimulus direction was not different between blocked and randomized tasks, indicating that the selectivity did not result from nonspecific block effects (Mann-Whitney test; $p > 0.25$).

For LIP cells, it was important to determine whether the selectivity was due to the animals' intention to saccade to, or otherwise attend, the different target locations for the two directions of movement, even though the animals maintained fixation throughout the trials. Early in training, the animals had a tendency to break fixation and saccade to the target of the movement. This behavior was virtually eliminated with further training, and we did not notice systematic patterns of eye movements once the fixation spot was turned off at the end of trials. However, we cannot exclude that the animals still planned to look at the target during the trial, but suppressed the movement. Although we tried to place the two targets symmetrically about the center of the saccadic response field, it is possible that one target was placed in a less responsive part of the field than the other target; when the animals shifted their attention to the target locations, the LIP cell would have been differentially activated in a manner that mimicked direction selectivity. If this scenario were true, then the cells should be at least as selective if the animals were required to saccade to the targets. We tested this directly. For 60 LIP cells, the animals also did blocks of 'saccade' trials, without moving the joystick, interleaved with the blocks of joystick trials. During saccade trials, the spot/target pairs appeared at the same locations as in the previous joystick block, and then disappeared. After a variable delay, one spot reappeared at the location of one of the targets, to which the animal was required to make a saccade. Only one target was tested throughout the block of saccade trials so the animal could plan which direction to saccade; the other target was tested following the next block of joystick trials. Twenty-nine of 60 LIP cells were selective on occluded trials of the joystick task (**Fig. 5a**; two-way ANOVA for effect of inferred stimulus direction and hand direction; $p < 0.05$), and the same 29 cells were tested on the saccade task (**Fig. 5b**). The population histograms diverged for the two directions in the joystick task, but nearly overlapped in the saccade task. Among all 60 cells, responses were more selective during the occluded trials of the joystick task than for saccades made to the targets of the two directions of movement (0.140 ± 0.022 versus 0.057 ± 0.009 bits; Mann-Whitney test, $p < 0.005$; spike counts determined during delay periods). These data argue that the intention to saccade to

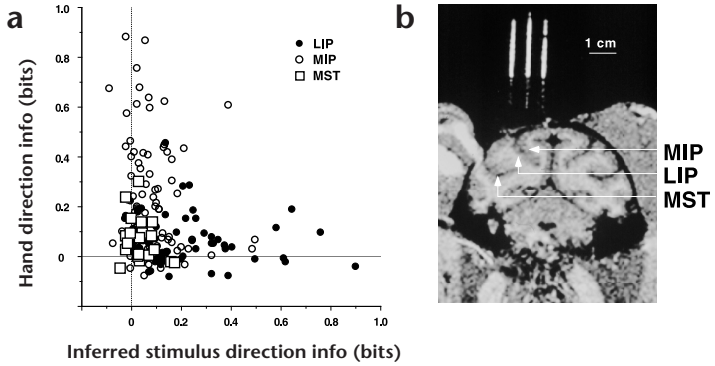

Fig. 3. Quantitative comparison of parietal areas. **(a)** Information for hand direction versus inferred stimulus direction for all 221 cells in MST, LIP and MIP. All data are from occluded trials. For MST, 0/23 cells were significantly modulated by hand direction, and 6/23 cells were significantly modulated by inferred stimulus direction. For MIP, 59/102 cells were significantly modulated by hand direction and 39/102 by inferred stimulus direction, whereas for LIP, 20/96 and 50/96 were modulated, respectively (two-way ANOVA; $p < 0.05$). **(b)** Coronal T-1-weighted, 1-mm MRI section through parietal cortex. The three bright parallel lines above the cortex were capillary tubes filled with mineral oil that served as fiducial marks.

the targets does not explain the selectivity during the joystick task. It is possible that the animals planned to saccade to an intermediate point along the trajectories, for example the midpoint. However, because the trajectories in the two directions overlapped, that should not have produced a difference in activity. More generally, we would expect only smaller differences for saccades planned to intermediate locations, as the targets were the most extreme points along the trajectories. These data do not mean that the LIP neurons were not selective for saccade direction; the cells were generally selective when tested over a broader range of saccade directions (**Fig. 4**).

Discussion

Our results reveal a striking segregation of function in PPC during visual guidance. Cells in MST were primarily modulated by the direction of visible moving stimuli and did not show extraretinal activity. Cells in dorsal MST (MSTd) convey extraretinal signals during smooth pursuit eye movements[8]; it is possible that we did not record from MSTd among our 23 MST neurons, or that extraretinal signals in MST are related exclusively to eye movements. Cells in MIP had direction-selective extraretinal activity that was modulated primarily by hand direction, similar to the directional responses in MIP and superficial area 5 during reaching[9,10]. In contrast, LIP cells were modulated by stimulus direction, both visible and inferred. This differs from previous views concerning LIP neurons, that they encode attention to particular locations[11,12] or the specific intention to saccade to those locations[3]. Although we have referred to the LIP signals as 'direction selective', we should emphasize that the direction selectivity differs from that of other visual areas, such as MT or MST. First, LIP cells were not direction selective while the animals passively fixated but were direction selective when the animals had to attend to the trajectories during the joystick task. Second, the direction selectivity on occluded trials was distinct from either visual or motor sources, because the visual stimulus was identical between directions and the responses were largely independent of hand movement. The selectivity was also unrelated to saccade planning or attention to one or the other target, although the same population of cells was selective for saccade direction when examined over the full 360° range of directions.

Although planning to saccade to the targets could not explain the selectivity we observed in LIP neurons, there may still be some relationship between the direction selectivity and the saccadic response field. We did not find evidence for separate populations of LIP cells selective for either joystick or saccade tasks, because there was no correlation between the degree of selectivity in the joystick task and either the multi-direction memory-saccade task or the saccade control experiment (data not shown). However, because we consistently centered the spot/target pairs on the saccade response field, we cannot address the detailed spatial relationship between the direction selectivity and the saccadic response field. More experiments will be needed to examine whether the preferred direction is uniform, or whether directional responses can be elicited over the entire saccadic response field.

One interpretation of the LIP responses is that the directionality of LIP neurons provides a predictive signal about the direction of moving objects, which is not directly driven by sensory input or motor output. This predictive signal may be a correlate of the animal's expectation that an object is moving, or will move, even if the movement is not overt. This view is supported by the observation that the directionality was already evident several hundred milliseconds before the start of movement in the joystick task (**Figs 2c** and **5a**)—presumably because the animals

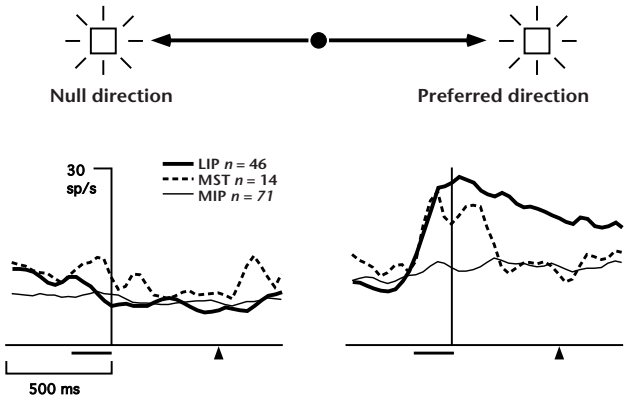

Fig. 4. Responses to the multidirection memory-saccade task. Population histograms are shown for LIP (thick line), MIP (thin line) and MST cells (dashed line). Only two directions are shown, the preferred direction (which gave the largest response) and the opposite direction. Histograms were aligned to the offset of the target spot before averaging (vertical lines). Thick lines beneath the histograms indicate the time that the target spot was on, vertical lines indicate the offset of the target spot, and triangles indicate the offset of the fixation spot. MST cells had a transient response on stimulus onset/offset when the stimulus fell within their receptive fields, and then were silent during the delay. LIP cells were activated on stimulus onset, and that activity persisted throughout the delay period. MIP cells were much less responsive throughout.

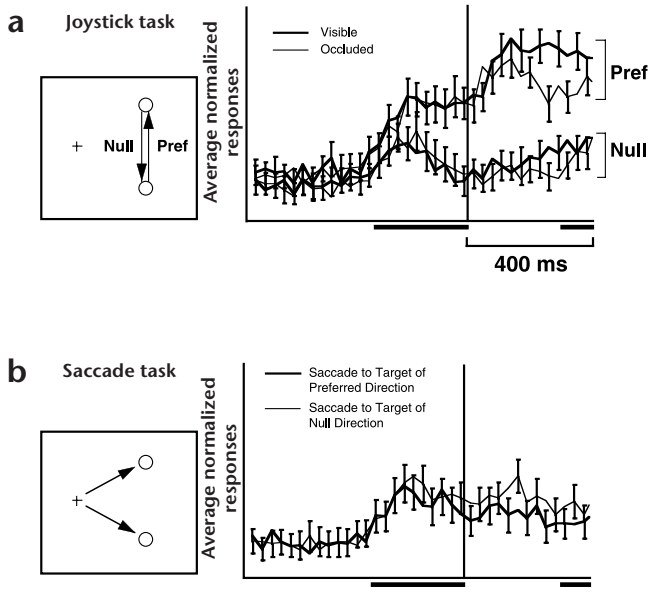

Fig. 5. Comparison of responses to the joystick and saccade-control tasks. **(a)** Population histograms of 29 LIP cells in the joystick task. Before averaging, the histograms were sorted by the preferred direction determined from visible trials, normalized to peak response on visible trials, and synchronized to the start of joystick movement (vertical line). Preferred and null directions are indicated by brackets. Thick and thin lines indicate visible and occluded trials, respectively. Error bars indicate standard error. The gap in the thick black line beneath the histograms indicates the average time during which the moving spot was not visible on occluded trials. **(b)** Population histograms of the same 29 cells in the saccade task, sorted and normalized as in (a)**.** Histograms were synchronized to the disappearance of the two spots, which was the start of the delay period (vertical line). The gap in the thick black line beneath the histograms indicates the average delay before the signal to saccade.

could anticipate the impending direction because of the direction-blocked organization. Consistent with this interpretation, for the ten cells in which the direction was varied unpredictably from trial to trial, the difference between preferred and null directions developed ~175 ms later than when the two directions were presented in separate blocks of trials (data not shown). This delay presumably occurs because, in the randomized trials, the animal could not anticipate the direction of movement but rather had to inspect the orientation of the spot/target array to determine the appropriate direction of movement.

A predictive representation would be invaluable for guiding movements of the eyes or hands toward visual targets, particularly if those targets are themselves moving or are temporarily occluded from view[13,14]. In acquiring a moving target, relying on instantaneous visual information alone could cause errors due to reaction-time delays; predicting the trajectory of the target allows more accurate guidance. Neurons in area LIP may provide such a predictive representation. Moreover, prediction may be important in visual perception, supporting constancy of object representation when visual information is incomplete.

Methods

ELECTROPHYSIOLOGY. Two adult male rhesus monkeys weighing 9 and 13 kg were used for these experiments. Before training and recording, a plastic recording chamber, titanium headpost and scleral search coil[15] were surgically implanted, following Harvard Medical School and NIH guidelines. The recording chambers were centered at stereotactic coordinates P3, L10 and allowed a dorsal approach to parietal cortex. Before recording, a T-1-weighted, thin-slice MRI scan (1 mm sections) was obtained. Capillary tubes filled with mineral oil were placed in the same grid used later for physiological recording, to serve as fiducial marks to guide electrode penetrations. Single-unit recordings were made with tungsten microelectrodes using a guide-tube and grid system[16]. The grid was placed within the chamber in the same orientation as the pre-experimental MRI. The coronal section in Fig. 3b was in the center of the chamber along the anterior-posterior axis. Penetrations were made at this location and at locations 3–4 mm anterior and posterior to this slice. A total of 221 cells were recorded from MST, LIP and MIP (137 from the first animal and 84 from the second animal).

RECEPTIVE FIELD AND SACCADIC RESPONSE-FIELD MAPPING. Once a unit was isolated, we attempted to map its receptive field using flashed and moving spots or bars, under the experimenter's control, while the animal passively fixated. In MST, this was effective for mapping receptive field boundaries and assessing preferred direction. In LIP, only weak visual responses were evoked, which were not appreciably direction selective. Therefore, most cells were also tested with a memory-saccade task[7], with 6–8 directions, evenly spaced about the full 360°, and 1–3 eccentricities (6, 12 and 18°) to map the saccadic response field. The animal first fixated a point at the center of the screen. After a 500-ms delay, a spot was flashed for 200 ms at one location, randomly interleaved from trial to trial. After another 500-ms delay, the fixation spot was extinguished, and the animal made a saccade in the dark to the remembered location of the target. Spikes were counted during the delay period from the offset of the flashed target to the offset of the fixation spot. Responses to different saccade targets were analyzed by ANOVA. Most LIP cells gave strong, selective responses in the saccade task, both to stimulus onset and during the delay period while the animal had to remember the target location, whereas cells in MST were activated only transiently by stimulus onset or offset. MIP cells were generally unresponsive to either passive mapping or memory saccades, although their preferred direction was readily assessed with a 12-direction joystick task.

BEHAVIORAL TASK. In both the twelve-direction joystick mapping task and the main task, the animals moved a spot of light to a circular target, 17° away from the starting location of the spot. The direction of movement was indicated by the orientation of the spot/target axis. All stimuli were presented on a computer monitor placed 57 cm from the animal. The animal had full two-dimensional control of the displacement of the joystick, and neither the joystick nor the animal's hand were visible to the animal. The animals did not track the movement, but rather actively moved the spot to the target. All trials began with the onset of a small fixation point. The animal fixated the point within 0.5° and maintained fixation throughout every trial until the fixation point was turned off. After a 500-ms delay, the spot/target pair(s) appeared, and the animal could begin moving the joystick. The minimum latency to move was set to 200 ms to discourage anticipatory movements. After the start of movement, the animals were required to keep the spot within an invisible narrow corridor (± 5°) centered on the spot/target axis, and to reach the target within 2000 ms, although they usually completed the movement in less than 500–600 ms. On occluded trials, the moving spot reappeared 3.5° from the target, which occurred ~300–450 ms after the start of movement, depending on how quickly the animal moved the joystick. Once

the spot reached the target, the animal was required to hold the spot within the target for 300 ms, at which time the juice reward was delivered, and the spot, target(s) and fixation point were turned off. Trials were aborted without reward if the animals broke fixation, moved the joystick prematurely, failed to hold the spot in the target during the final 300-ms hold period or, most commonly, strayed from the corridor boundaries. The same constraints were enforced regardless of whether a trial was visible or occluded or whether the mapping was forward or reverse. Overall, the animals did the task correctly on 75–85% of trials. Performance was slightly better on visible trials than on occluded trials. Only correct trials were considered in the analysis.

On saccade-control trials, the visual stimulus and time epochs were identical to the main joystick task until the disappearance of the spot/target pairs. After a variable delay, the fixation spot disappeared and one spot simultaneously reappeared at the location of one of the targets. The animal had to saccade directly to the location of the spot within 500 ms, and then hold its gaze on the stimulus for 300 ms before reward. The same saccade target was presented throughout a block of saccade trials so that the animals could know which target to expect. The delay time before the reappearance of the spot was chosen from the set of times during which the moving spot was not visible from the occluded trials of the preceding joystick block. Trials were aborted without reward if the animals broke fixation before the fixation spot was turned off, moved the joystick, failed to complete the saccade within the allotted time or looked away prematurely from the saccade target.

Changing between the two directions or between forward and reverse mapping was signaled by two initial practice trials at the start of the block in which only one spot and one target appeared. The start of saccade-control blocks were signaled by practice trials in which one spot appeared without any targets. Practice trials were not analyzed further.

IDENTIFICATION OF PPC AREAS. The animals used in this study are still alive, so recording sites have not yet been confirmed histologically. However, parietal areas were readily distinguished based on the following criteria. The pre-experimental MRI allowed an absolute distinction between the intraparietal sulcus (IPS) and the superior temporal sulcus, which contains MST. Within the IPS, we used a dorsal approach, which passed through both medial and lateral banks of the sulcus. With the exception of four units, which were excluded from the study, we were readily able to discern medial and lateral banks of the IPS based on the presence of a quiet intervening sulcus. This allowed us to distinguish MIP from LIP. In addition, delay activity in the memory-saccade task is diagnostic of LIP[3,7] (compared with 7A and the medial bank of the IPS, for example). We found delay activity in the memory-saccade task primarily in cells that had been independently assigned to LIP based on their location relative to the IPS, and to a much lesser extent in areas MIP and MST (**Fig. 4**). Finally, although we could use the MRI to locate the fundus of the IPS, we could not radiographically distinguish the border between LIP and the ventral intraparietal area (VIP). However, a few cells were recorded near the fundus of the IPS that were clearly distinct from responses more laterally. These cells had strong, direction-selective responses during passive mapping, suggesting that they were in VIP[17]. In the main task, their responses were very similar to those of MST neurons; the cells were strongly direction selective during visible trials, but were largely unresponsive during occluded trials, irrespective of hand direction.

DATA ANALYSIS. In the main joystick task, spikes were counted on occluded trials from the start of movement—which was when the two spots disappeared—until the reappearance of the moving spot. On saccade-control trials, spikes were counted during the identical period, from the disappearance of the two spots until the appearance of the one spot that served as the saccade target. Transmitted information about direction was calculated from the spike counts[5]. Transmitted information is less prone to noise than traditional modulation indices, in that it is based upon the reliability of response differences. For example, the values of transmitted information for inferred stimulus direction and hand direction were highly correlated with the *F*-scores from the two-way ANOVA (data not shown). Transmitted information was calculated after binning the spike counts into ten-bin histograms; above ten bins the amount of transmitted information is relatively insensitive to the number of bins[6]. However, because only 8–16 repetitions were gathered for each condition, it is likely that the distributions of spike counts between the two directions would differ by chance alone, causing the absolute information to be overestimated. To compensate, information expected from chance was estimated using a bootstrap technique: Spike counts from trials in the two directions were randomly reshuffled into two sets, and information calculated exactly as above. The average value of 1000 such resamplings was taken as an estimate of information expected from chance, which was subtracted from the measured information. This correction accounts for the occasional negative information values in Fig. 3. However, we should emphasize that for a given cell the absolute information values are not important; rather, the relative information about hand direction versus stimulus direction is relevant.

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