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Spatial Updating in Area LIP Is Independent of Saccade Direction

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Heiser, Laura M. and Carol L. Colby. Spatial updating in area LIP is independent of saccade direction. *J Neurophysiol* 95: 2751–2767, 2006. First published November 16, 2005; doi:10.1152/jn.00054.2005. We explore the world around us by making rapid eye movements to objects of interest. Remarkably, these eye movements go unnoticed, and we perceive the world as stable. Spatial updating is one of the neural mechanisms that contributes to this perception of spatial constancy. Previous studies in macaque lateral intraparietal cortex (area LIP) have shown that individual neurons update, or “remap,” the locations of salient visual stimuli at the time of an eye movement. The existence of remapping implies that neurons have access to visual information from regions far beyond the classically defined receptive field. We hypothesized that neurons have access to information located anywhere in the visual field. We tested this by recording the activity of LIP neurons while systematically varying the direction in which a stimulus location must be updated. Our primary finding is that individual neurons remap stimulus traces in multiple directions, indicating that LIP neurons have access to information throughout the visual field. At the population level, stimulus traces are updated in conjunction with all saccade directions, even when we consider direction as a function of receptive field location. These results show that spatial updating in LIP is effectively independent of saccade direction. Our findings support the hypothesis that the activity of LIP neurons contributes to the maintenance of spatial constancy throughout the visual field.

INTRODUCTION

The relationship between perception and action is usually considered a forward process in which sensory information influences the generation of movement. Often overlooked, but also important, is the reverse process in which action influences perception. One striking example of the importance of this reverse process comes from our sense of vision. With each eye movement, a new image falls on the retina. As a result, a given location in the world corresponds to a new region of the retina. If visual perception were based solely on the forward processing of sensory information, our experience would be unintelligible: objects in the world would appear to shift with each eye movement, and it would be impossible to distinguish the movement of an external object from our own internally generated eye movements. In reality, our eye movements go unnoticed and our perception is that objects in the world remain stationary. This perceptual stability reflects the fact that what we see is not a direct impression of the external world, but an internal representation of it that is actively constructed. This internal representation must be updated to account for our eye movements (Goldberg et al. 1990; Ross et al. 2001). Evidence of such updating has emerged in recent years. Single-unit recording studies indicate that neurons in the lateral intraparietal cortex (area LIP) update, or “remap,” the locations

of salient stimuli when the eyes move (Duhamel et al. 1992a; Goldberg et al. 1990; Gottlieb et al. 1998; Kusunoki et al. 2000). These investigators found that neurons in area LIP became active when an eye movement shifted the receptive field (RF) onto a previously stimulated location. The neurons responded as if anticipating what the world would look like after the eye movement. Remapping has been observed in several other cortical and subcortical areas (Goldberg and Bruce 1990; Mays and Sparks 1980; Nakamura and Colby 2002; Umeno and Goldberg 1997, 2001; Walker et al. 1995). In addition to remapping, LIP neurons are modulated by many high level cognitive functions, including attention, decision-making, and behavioral relevance (Andersen et al. 1997; Bisley and Goldberg 2003; Leon and Shadlen 2003; Platt and Glimcher 1999; Shadlen and Newsome 2001; Toth and Assad 2002). These findings highlight the importance of area LIP in the creation of sophisticated representations that link incoming sensory information to motor output.

One intriguing implication of remapping is that, at the time of the eye movement, neurons are responsive to locations outside of their classical RFs. This suggests that neurons have access to information from throughout the visual field. In theory, it should be possible to observe evidence of a remapped stimulus trace every time the RF of an LIP neuron lands on a previously stimulated and attended location, regardless of the initial retinal location of the stimulus, or the direction of the saccade. Previous studies have shown that this access to visual information even extends to the opposite visual hemifield. In the original demonstration of remapping in area LIP, the stimulus was updated from one visual hemifield to the other (Duhamel et al. 1992a). Specifically, the stimulus was placed in the opposite hemifield and the saccade was directed ipsiversively.

Remapping has been tested primarily with the across-hemifield configuration described above. We hypothesized that individual LIP neurons can remap for any saccade direction. We tested this hypothesis by recording the updating activity of individual neurons in conjunction with saccades in four directions. We predicted that remapping would be equally robust regardless of saccade direction. This prediction is based on three previous findings. First, physiological studies have shown that the RFs of LIP neurons tile the entire visual field, indicating that it encodes visual stimuli located throughout the visual field (Ben Hamed et al. 2001). This is important because it is thought that remapping requires a transfer of visual information between LIP neurons that encode the location of the stimulus before and after the saccade. Second, previous studies have shown that neurons in both the frontal eye field (FEF) and

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superior colliculus represent all directions and sizes of saccades (Bruce and Goldberg 1985; Schiller and Stryker 1972; Sparks et al. 1976; Wurtz and Goldberg 1971). These are the two regions most likely to be involved in generating and supplying a copy of the eye movement command, or corollary discharge signal, to LIP. Recently it has been shown that corollary discharge signals are relayed from the superior colliculus to the FEF through the mediodorsal thalamus (Sommer and Wurtz 2002); the FEF may in turn supply this information to area LIP (Ferraina et al. 2002). The corollary discharge signal is critical for initiating the transfer of visual information (Colby 1998; Quiaia et al. 1998). If remapping is indeed independent of saccade direction, LIP must receive corollary discharge information about all directions of saccades. The third finding is related to the anatomical connections between LIP and FEF. The projections from FEF to LIP are not strictly topographic (Schall et al. 1995; Stanton et al. 1995). This finding implies that neurons representing stimuli in all portions of the visual field have access to information about all sizes and directions of saccades. Altogether, these observations support the hypothesis that updating will be robust regardless of saccade parameters.

The goal of this experiment was to investigate the degree to which individual neurons have access to information from different portions of the visual field. We hypothesized that individual LIP neurons would remap regardless of the direction in which the stimulus trace had to be updated. We addressed three experimental questions. First, we asked whether stimulus traces are remapped equally robustly in four saccade directions. Second, we asked whether the strength of remapping was affected by the direction of the saccade relative to the location of the RF. Third, we asked whether stimulus traces are updated equivalently within a hemifield as compared with across hemifields. Our prediction was that remapping would be immune to these changes. We found that the majority of LIP neurons update stimulus traces in multiple directions. In individual neurons, we typically found differences in the strength of remapping for each saccade direction. At the population level, however, remapping was equally robust for all saccade directions. Additionally, we found that the strength of remapping was largely independent of saccade direction relative to the RF location. Finally, there were no differences between within- and across-hemifield remapping.

METHODS

Animals

Two adult male rhesus macaques (8.1–9.5 kg) were used in this study. Experimental protocols were approved by the University of Pittsburgh Institutional Animal Care and Use Committee and were certified to be in compliance with the guidelines in the Public Health Service Guide for the Care of Laboratory Animals.

At the outset of the experiment, both monkeys underwent sterile surgery under general anesthesia induced with ketamine and maintained with isoflurane. The top of the skull was exposed, bone screws were inserted around the perimeter of the exposed area, and an acrylic cap was used to cover the skull and embed the bone screws. A head-restraint bar was embedded in the cap, and scleral search coils were implanted around the eyes for the purpose of monitoring eye position (Judge et al. 1980). After initial training, a recording chamber (1.8 cm diam) was installed over area LIP. The placement of the recording chamber was determined using 1) the standard stereotaxic

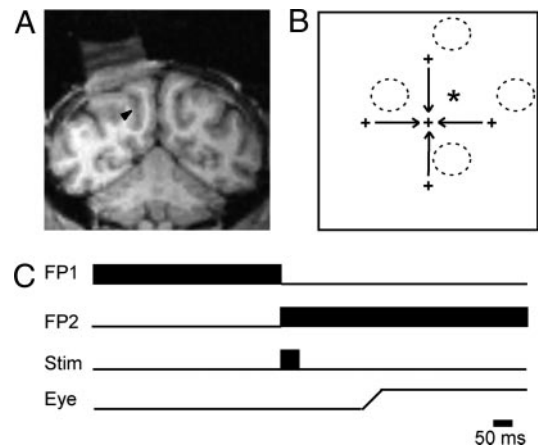


FIG. 1. Recording locations and behavioral paradigm. *A*: coronal MRI that shows recording chamber location (monkey FF). Neurons were recorded in lateral intraparietal cortex (area LIP), located on the lateral bank of the intraparietal sulcus (arrowhead). *B*: spatial configurations. Monkey begins each trial at 1 of 4 peripheral fixation points located 20° from the center of the screen. Each dashed circle represents location of receptive field (RF) when the monkey is fixating one of the peripheral fixation points. In this example, the RF is up and to the right. Arrows represent saccades to FP2. The saccade moves the RF onto the location of flashed stimulus (star). The stimulus is in the same screen location for all conditions. *C*: timing of single step task. The monkey holds its gaze on the fixation point FP1 for 300–500 ms. Three events then occur simultaneously. FP1 disappears, a new fixation point appears (FP2), and a stimulus (Stim) is flashed for 50 ms. The monkey makes a visually guided saccade to FP2, located at the center of the screen. The monkey maintains its gaze on FP2 for 500–700 ms.

location for area LIP (5 mm posterior and 12 mm lateral in Horsley Clarke coordinates) and 2) anatomical information from structural MRIs (see Fig. 1A).

Physiological methods

During recording sessions, the monkey sat in a darkened room with its head fixed in a primate chair, facing a tangent screen 25 cm away. The screen subtended 100° horizontally and 75° vertically. Visual stimuli were back-projected on the tangent screen using a LCD projector. Stimulus presentation was under the control of two computers running a C-based program, CORTEX, made available by Dr. Robert Desimone at the National Institutes of Mental Health.

We measured the phosphopersistence of the stimulus and determined the psychophysical threshold for each monkey to ensure that the stimulus was perceptible only when the eyes were at the initial fixation location. This is important because we wanted to be certain that the presence of the stimulus per se could not contribute to the response in the remapping task. The stimulus did not vanish instantaneously when it was turned off, but instead decayed over time. We used the memory-guided saccade task to determine the monkey's perceptual threshold for the stimulus. Specifically, we asked how dim the flashed stimulus could be for it to be detectable, as measured by the monkey's ability to direct a saccade to the remembered stimulus location. We used a staircase design, in which the luminance of the stimulus was gradually decreased after correct saccades to the remembered location and increased after incorrect saccades. With this standard procedure, we identified the lowest luminance at which the monkey could still perceive the stimulus, and found the time at which the stimulus decayed below this level. We determined that the stimulus used in the remapping tasks was below perceptual threshold within 40 ms of its offset for both monkeys. The monkeys' average saccade latency was 183 ± 12 (SD) ms. These observations indicate that the extinguished stimulus could not affect our measures of spatial updating.

Neural activity was recorded using tungsten microelectrodes (Fredrick Haer, Bowdoinham, ME) introduced into the cortex through stainless steel guide tubes placed flush with the dura. The guide tubes were stabilized by a nylon grid (Crist Instruments) held rigidly in the recording chamber. The grid system permitted parallel penetrations along the bank of the intraparietal sulcus (IPS) with a resolution of 1 mm. Action potentials were amplified and filtered with a band-pass of 500 Hz to 5 kHz, and digitally sampled using template matching at 20 kHz. Individual neurons were isolated by means of an on-line spike-sorting system using a template-matching algorithm (Signal Processing Systems, Prospect, Australia).

Eye position was sampled at 250 Hz. Saccades were identified on the basis of velocity criteria: saccade onset was defined as the time when velocity exceeded 50°/s; saccade offset was defined as the time when velocity fell below 20°/s. Additional spatial and temporal criteria were used to ensure that each saccade was identified correctly. The accuracy of saccade identification was verified by the experimenter. Saccade latency was defined as the difference between the onset of the saccade and the time when the initial fixation point was extinguished. Trials in which the saccade latency was <70 ms were considered anticipatory and were excluded from analysis.

IDENTIFICATION OF AREA LIP. We used the following procedure to identify recording sites within the lateral bank of the intraparietal sulcus. In initial recording sessions, we mapped the location of the intraparietal sulcus within the chamber. We systematically recorded from the anterior-most to the posterior-most part of the chamber and assessed whether neurons responded to visual or somatosensory stimuli. We localized the sulcus as the transition from somatosensory responses on the medial bank to visual responses on the lateral bank. We assessed somatosensory responses by lightly touching the monkeys' hands, feet, or face while they performed a fixation task. We assessed visual responses with the memory-guided saccade task.

Within the lateral bank, the response properties of neighboring areas 7a and VIP provided additional landmarks for the identification of area LIP. Area 7a is located superficially, and neurons there exhibit broad visual responsiveness and postsaccadic firing (Barash et al. 1991a,b). Area VIP is located in the fundus of the sulcus, and neurons here exhibit striking selectivity for direction of motion (Colby et al. 1993). Area LIP is located between these two functionally distinctive areas. We identified LIP neurons according to the conjunction of two criteria. First, the depth of the recorded neuron had to be ≥ 2 mm below the cortical surface. Second, the neuron had to respond to visual stimuli. Using these procedures, even after many months, we found neurons with similar response properties at the same grid location. Recording sites extended from 2 to 10 mm deep [average depth, 5.4 ± 1.60 (SD) mm]. Most neurons (94%) were >3 mm below the surface of the cortex.

Behavioral paradigms

MEMORY-GUIDED SACCADE TASK. We used the memory guided saccade task to search for neurons and assess their visual, memory, and saccade-related response properties (Hikosaka and Wurtz 1983). In this task, the monkey initially maintained fixation on a central fixation point. After a random delay of 300–500 ms, a stimulus flashed in the RF for 50 ms. After a second delay of 400–800 ms, the fixation point was extinguished, which cued the monkey to make a saccade to the location of the flashed stimulus. After the saccade, the stimulus reappeared, and the monkey maintained fixation for 300–500 ms. We defined RF locations using standard procedures that have been used in numerous studies of area LIP (e.g., Barash et al. 1991b; Colby et al. 1996; Eskandar and Assad 2002; Williams et al. 2003; Zhang and Barash 2000). Rather than quantify the extent of the RF, our mapping procedure focused on locating the “hot spot” in the RF. To do this, we placed stimuli at one of eight locations around the fovea; these were spaced 45° apart. We adjusted the amplitude (i.e., distance

from the fovea) as needed to identify the location with the best response. We confirmed that the location did indeed elicit a robust visual response by applying standard statistical measures (*t*-test, $P < 0.05$) to assess whether the visual activity was significantly elevated as compared to baseline.

SINGLE STEP TASK. The single step task was used to assess spatial updating (Fig. 1C). The monkey maintained fixation on an initial fixation point (FP1) for 300–500 ms. Three events then occurred simultaneously: a stimulus appeared outside of the neuron's RF for 50 ms; FP1 was extinguished; and a new fixation point (FP2) was illuminated. The offset of FP1 was the monkey's cue to make a visually guided saccade to FP2. The location of the stimulus was chosen such that the saccade moved the RF onto the location of the now extinguished stimulus. The monkey maintained its gaze on FP2 for an additional 500–700 ms. Both monkeys performed this task very well; average performance was 91% correct.

SACCADE CONTROL TASK. This task was used to measure activity related to the generation of the saccade by itself. The timing of the task is identical to the single step task, except that no peripheral stimulus was presented. The monkey maintained fixation of FP1 for 300–500 ms, after which FP1 was extinguished and FP2 was illuminated. After making a saccade to FP2, the monkey was required to maintain fixation on FP2 for 500–700 ms. The monkeys' behavior in this task was nearly identical to that in the single step task, with correct performance on 93% of trials.

STIMULUS CONTROL TASK. The stimulus control task was used to test whether the initial stimulus location used in the single step task was actually outside of the RF. In this task, the monkey maintained fixation for 300–500 ms. The stimulus was flashed for 50 ms, and the monkey was required to maintain fixation for an additional 1,200–1,500 ms. Average performance on this task was 90% correct.

Experimental design

REMAPPING IN DIFFERENT SACCADE DIRECTIONS. We used the single step task to assess remapping across changes in saccade direction. Each neuron was tested in four conditions. The saccade directions were along the horizontal and vertical meridians (right, left, up, and down). Saccade amplitude (20°), screen location of the stimulus, and final eye position were identical for all conditions (Fig. 1B). We were principally interested in neural activity generated around the time of the saccade. We avoided potential confounds with orbital position modulation by using the same final eye position for all conditions.

For each condition of the single step task, we recorded neural activity during matching control tasks. The complete data set for each neuron in this experiment is 3 tasks \times 4 conditions (directions), for a total of 12 trial types. We collected 12–20 trials for each trial type. The different tasks were run in separate blocks of trials, and always in the same order: stimulus control, saccade control, and single step. We collected data in this order because previous experiments have shown that long-term intertrial memory responses can persist after experience with the single step task (Umeno and Goldberg 2001). Within each block of trials, the different directions were always randomly interleaved.

WITHIN- AND ACROSS-HEMIFIELD REMAPPING. We were interested in knowing if remapping varies as a function of whether the stimulus must be updated within a single hemifield or from one hemifield to the other. We addressed this by analyzing two saccade directions for each neuron: one for within-hemifield and one for across-hemifield remapping. For across-hemifield remapping, we always used the ipsiversive condition: a horizontal saccade moved the representation of the stimulus from one hemifield to the other. For within-hemifield remapping, we used one of the vertical saccade conditions. With a vertical saccade, the representation of the stimulus always remains in the same

hemifield. The particular directions used were determined by the location of the RF. When the RF was located in the upper visual field, we used the downward saccade as the representative within-hemifield condition. We used the upward saccade when the RF was located in the lower visual field.

Finally, for this analysis, we selected only those neurons for which we were certain that the across-hemifield condition required an inter-hemispheric transfer of visual information. LIP has RFs that can extend $\sim 5^\circ$ into the ipsilateral visual field (Ben Hamed et al. 2001), so it was necessary that the saccade at least move the visual stimulus 5° into the opposite visual field. We always used a 20° saccade, which led to the requirement that the RF be within 15° of the fovea. From our data set, 159/281 neurons met this criterion and were included in this analysis.

Data analysis

ASSESSMENT OF REMAPPING ACTIVITY. Remapping activity in the single step task represents a response to a stimulus trace that has been updated in conjunction with the saccade. We measured activity in the single step task relative to each event of interest: the stimulus and the saccade. We used standard analysis epochs in order to have the most unbiased measure of remapping to compare across the four test directions. We assessed remapping by comparing activity in the single step task to activity generated in the stimulus and saccade control tasks. We chose the following epochs to capture the response to the remapped stimulus trace. For the comparison of the single step and saccade control tasks, the epoch was 0–300 ms relative to saccade onset. For the comparison of single step and stimulus control tasks, the epoch was 200–500 ms relative to stimulus onset. These epochs are similar to those used in previous remapping studies (Kusunoki and Goldberg 2003).

Our objective in investigating activity in area LIP was to be as inclusive as possible when selecting neurons. In the RESULTS, we describe a three-stage analysis that assesses the strength and selectivity of remapping. We used this method to assess the remapping in the entire population of neurons we recorded. We also conducted this three-stage analysis in a smaller subset of neurons that exhibited statistically significant remapping (activity in the single step significantly greater than activity in both control tasks, $n = 156$). With this more conservative approach, the findings were comparable with those obtained with the more inclusive population. Specifically, we found that in this smaller subset, as well as in the entire population, remapping is equally robust for all four saccade directions. Accordingly, we report data from the entire population, asking how updating signals are represented in area LIP as a whole.

ASSESSMENT OF VISUAL AND SACCADE-RELATED ACTIVITY IN CONTROL TASKS. We used the following method to determine if the stimulus or saccade alone elicited a significant response. We used a t -test ($P < 0.05$) to look for increases over baseline activity in stimulus or saccade-related activity during the control tasks (baseline defined as 150–350 ms after fixation attainment). We used the following epochs to capture visual or saccade-related responses. For the stimulus control task, the response epoch was 100–200 ms after the onset of the stimulus. For the saccade control task, the response epoch was -100 to $+100$ ms relative to the onset of the saccade.

CALCULATION OF REMAPPING LATENCY. Activity in the single step task can potentially reflect three factors: the stimulus, the saccade, and the remapped stimulus trace. In our analysis of latency, we excluded samples where either the stimulus or the saccade produced a significant response in the control task. This ensured that all activity in the single step task was attributable to updating. From this subset, we constructed population histograms of the single step and saccade control activity aligned on the onset of the saccade. The saccade control task served as the baseline response. We determined the onset

of the remapped response by computing the time at which activity in the single step task first became significantly greater than that in the saccade control task. To determine this time-point, we measured the response during successive 10-ms response windows beginning 100 ms before the start of the saccade. We used a t -test ($P < 0.05$) to determine if activity in the single step task was significantly greater than activity in the saccade control task. If there was no significant difference, the response window was shifted forward by 10 ms, and the procedure was repeated until a significant difference was obtained. The onset of the response was defined as the midpoint of the first of two consecutively significant bins. The appeal of this approach is that it is quite conservative. It ensures that the increase in activity in the single step task reflects spatial updating and not the generation of the saccade.

We also conducted an alternative analysis that did not rely on multiple t -tests. In this analysis, we computed the average difference in activity during the baseline epoch (-200 to -100 ms relative to saccade onset). We took the onset of the remapped response to be the time when the difference between the conditions exceeded the difference during the baseline epoch $+3$ SD. This approach yielded similar results.

ANALYSIS OF STANDARD NEURONAL RESPONSE PROPERTIES. The response in the memory-guided saccade task was analyzed to determine the visual and saccade-related responses of individual neurons. The visual epoch was the 100-ms epoch beginning at the onset of the visual response. The saccade epoch was -100 to $+100$ ms relative to the onset of the saccade. For both epochs, activity was compared with baseline with a t -test ($P < 0.05$).

RESULTS

We recorded from 290 LIP neurons in two hemispheres of two monkeys (Fig. 1A). Of these, 281 (140 from monkey O; 141 from monkey F) were visually responsive in the memory-guided saccade task and were included for further analysis. Throughout the analyses described below, we used two populations of neurons: all neurons (281) and neurons with remapping in at least one condition (241/281).

Individual LIP neurons remap stimulus traces in multiple directions

Our primary finding is that individual neurons remap stimulus traces in multiple directions (Fig. 2). The neuron shown exhibits robust activity in the single step task in conjunction with each saccade direction (*top row*). The control tasks, however, indicate that some of this activity can be attributed to the presence of the stimulus (*middle row*) or the generation of the saccade (*bottom row*). In the ipsiversive condition, this neuron had minimal activity in the two control tasks. In this condition, the saccade is directed away from the RF, and the stimulus is located in the opposite visual hemifield. When neither the stimulus nor the saccade alone drive the neuron, all activity in the single step task can be attributed to a remapping of the stimulus trace. The ipsiversive condition has been the standard configuration with which to test for remapping because the control conditions are unlikely to activate the neuron. Our goal in this experiment was to determine whether neurons could remap stimulus traces in all directions, including those for which the control conditions generate responses.

How do we assess remapping activity given the presence of activity generated by the stimulus or saccade alone? We devised an analytical method to determine which single step

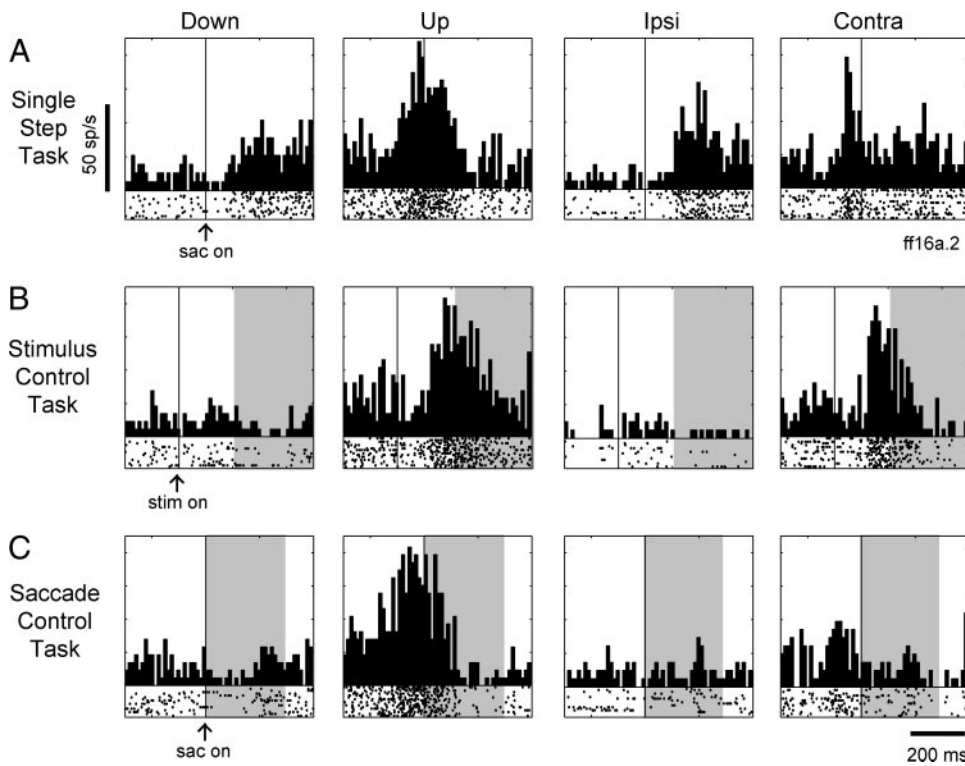


FIG. 2. LIP neuron that remaps stimulus traces in multiple directions. Each column represents data from one saccade direction (downward, upward, ipsiversive, or contraversive). *A*: single step task. Data are aligned on onset of the saccade. *Bottom* of each panel shows rasters: each row represents a single trial; each dot represents the time of an action potential. Histograms above show average activity of the neuron in 10-ms bins. There is robust activity during the single step task for all four directions. *B*: stimulus control task. Data are aligned on onset of the stimulus. The stimulus alone generates variable amounts of activity for each condition. *C*: saccade control task. Data are aligned on onset of the saccade. The saccade alone also generates variable amounts of activity. Gray shaded regions represent analysis epoch used to compare activity in control and single step tasks. This neuron remapped stimulus traces for downward, ipsiversive, and contraversive saccades.

conditions showed remapping. To be certain that we were comparing only updating activity across the four directions, it was critical that our analyses account for activity generated in the control conditions. We defined remapping as activity that cannot be accounted for by either the stimulus or the saccade alone. We use the data from the neuron in Fig. 2 to illustrate our three-step procedure.

First, we compared the activity generated in each direction of the single step task to activity generated in each of the two corresponding control conditions. We computed two indices, a stimulus index and a saccade index: $\text{Index} = (A - B)/(A + B)$, where A is the mean firing rate in the single step task and B is the mean firing rate in either the stimulus control task or the saccade control task. Index values scale from -1 to $+1$. Positive values indicate that single step activity is greater than control activity, and negative values indicate that control task activity is greater.

Second, we used the stimulus and saccade indices to assess the strength of remapping in each direction. For each saccade direction, we plot the two indices against one another (Fig. 3A). A neuron is considered to remap for a particular direction if both indices are positive, i.e., if activity in the single step task is greater than that observed in each of the control tasks. These samples fall into the top right shaded quadrant. Samples where either the stimulus or the saccade index is negative fall into one of the other three quadrants; these samples are considered nonremapping samples. We found that this particular neuron remaps for three of the four test directions.

Third, we assessed the magnitude of remapping by computing a remap index (RI) for each saccade direction. This is computed by calculating the distance of a given sample from the origin. For nonremapping samples (those that do not fall into the shaded quadrant), the RI is set to 0. The RI ranges from 0 to 1.4, where 0 indicates no detectable remapping and 1.4

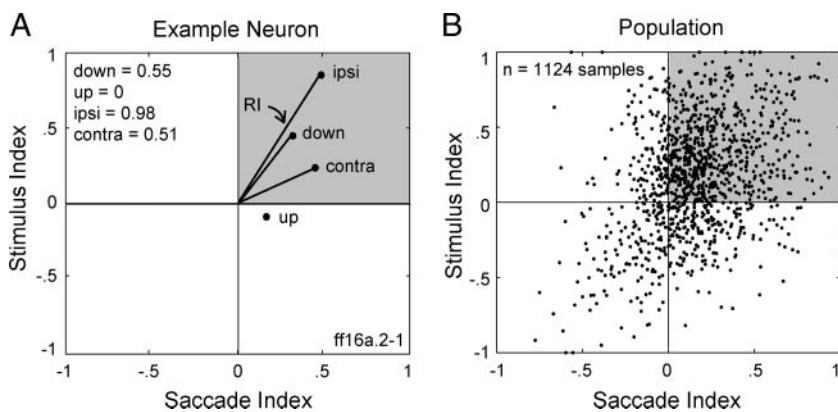


FIG. 3. Method used to calculate the remap index (RI), a measure of the strength of remapping. *A*: data from the example neuron in Fig. 2. Each dot represents data from a single condition. If single step activity is greater than that observed in each control condition, the stimulus and saccade indices are both positive. These samples fall into the top right (shaded) quadrant and are considered to show remapping. RI for these conditions is computed by calculating distance of the point from the origin. Conditions that fall into one of the other three quadrants have no detectable remapping; their RI is set to 0. For this neuron, remapping was detectable for three of the four test conditions. The most robust remapping was for ipsiversive saccades. The neuron showed no detectable remapping for upward saccades. *B*: population data. Each dot represents data from a single neuron during remapping in one direction. Each neuron was tested in 4 directions and therefore contributes 4 data points. Remapping was detectable for 57% of samples.

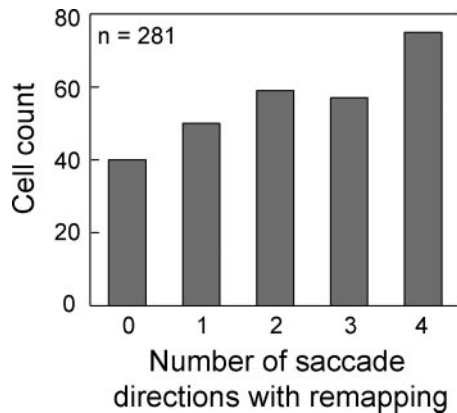


FIG. 4. Most neurons remap stimulus traces in multiple directions. Bars represent the number of neurons with remapping for 0, 1, 2, 3, or 4 saccade directions.

indicates strong remapping. A neuron with a high RI for a particular saccade direction robustly updates spatial representations in that direction. For the neuron shown in Fig. 2, the most robust remapping was for ipsiversive saccades (RI = 0.98); contraversive and downward saccades show nearly equal remapping (contra = 0.55; down = 0.51). There is no detectable remapping for upward saccades (RI = 0). The benefit of this analysis is that it provides a method to compare the strength of remapping in different directions while simultaneously accounting for activity generated in both of the control conditions.

We used the RI to assess the strength of remapping for the entire population of samples (281 neurons \times 4 test directions = 1,124 samples). If the points were equally distributed on the plot, we would expect only 25% of the samples to fall into the upper right "remapping" quadrant (Fig. 3B). Instead, we observed that 57% of the samples are in the remapping quadrant. This proportion was statistically significant (χ^2 test,

$P < 0.01$) and indicates that remapping is detectable in most samples.

We used this analysis to address the principle question of whether individual neurons can remap in multiple directions. First, we found that most LIP neurons show remapping for at least one saccade direction (Fig. 4; 86%, 241/281). Second, most of these remapping neurons (79%, 191/241) can remap stimulus traces in multiple directions. For neurons with statistically significant remapping (see METHODS), the results were similar: most (56%) remapped stimulus traces in multiple directions. These findings indicate that most LIP neurons have access to visual information from multiple regions beyond the classically defined RF.

In individual neurons, strength of remapping varies with saccade direction

How does the magnitude of remapping compare across the four directions? We addressed this question by computing a selectivity index for each neuron (modified from Cook and Maunsell 2002). The first step in computing this index is to construct, for each neuron, a polar plot that compares the strength of remapping in the four directions (Fig. 5A). The RIs for each test direction are plotted along the cardinal axes. Some neurons remap equally robustly for all saccade directions (*left*). Other neurons are highly selective (*right*) and effectively remap for only a single direction. We calculate the selectivity index by first normalizing the RI for each direction by the sum of the RIs for all directions. Next, we sum the normalized RIs as vectors, where each vector points in the direction of the saccade. This results in a single vector. The length of this vector is a measure of the neuron's selectivity and is referred to as the selectivity index. If a neuron remaps equally robustly for all directions, then the selectivity index is 0. Conversely, if a neuron remaps stimulus traces for only a single direction, then the selectivity index is 1. The direction of the vector

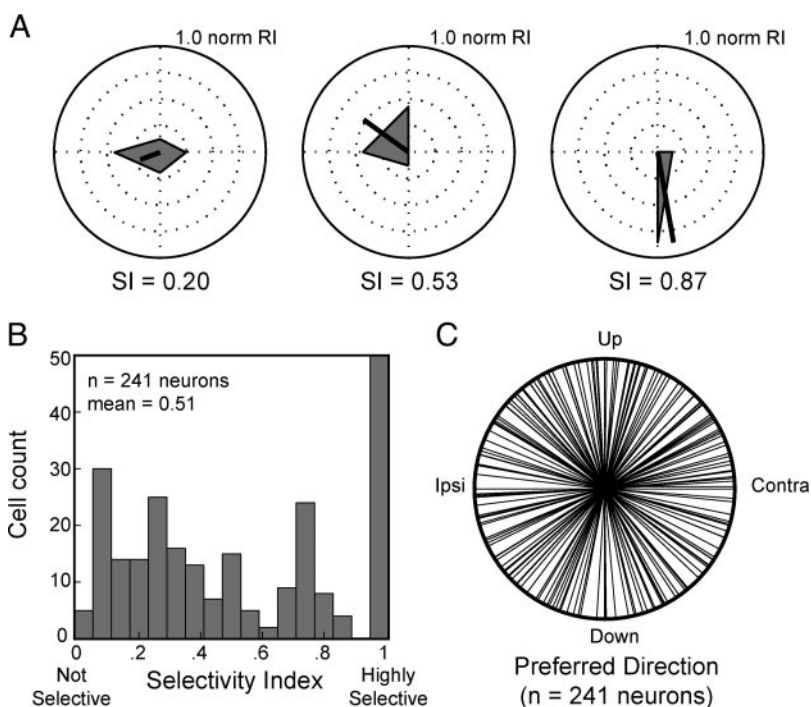


FIG. 5. In individual neurons, the strength of remapping is variable. *A*: each polar plot represents data from a single neuron. Some neurons remapped stimulus traces nearly equally in all 4 saccade directions (*left*), whereas others were more selective (*right*). Normalized RIs for the 4 test directions are plotted along cardinal axes. Thick black line represents selectivity index (SI), a measure of the strength of remapping across the 4 test directions. SI values near 0 indicate that the neuron remapped stimulus traces equally robustly for all directions tested, whereas values near 1 indicate that the neuron remapped stimulus traces for only 1 saccade direction. *B*: distribution of SIs for neurons with detectable remapping in at least 1 condition. Population of neurons showed a broad range of selectivities. *C*: distribution of preferred remapping directions. Across the population, preferred directions are distributed equally throughout the visual field.

indicates the saccade direction with the most robust remapping for the neuron and is referred to as the preferred remapping direction.

We found a broad distribution of selectivities for the population (Fig. 5B). The large bar at 1 represents neurons that remap for only a single direction ($n = 50/241$). Overall, the distribution of selectivity indices is quite broad, indicating that neurons show a variable range of tuning (mean $SD = 0.51 \pm 0.33$; median = 0.42). This result indicates that remapping is effectively universal for many neurons in LIP, whereas for others, remapping is restricted to a single saccade direction.

The preferred remapping direction calculated from the polar plots can be used to make inferences about all saccade directions. We found that preferred directions are represented throughout the entire visual field (Fig. 5C). In this analysis, we included all neurons with detectable remapping in at least one direction ($n = 241/281$). Statistically, the distribution of preferred directions is uniform (Rayleigh's test, $P > 0.05$). These observations indicate that stimulus traces are remapped in conjunction with saccades of all directions. Furthermore, across the population, there is no bias toward a preference to remap stimulus traces in any particular direction. These results support the hypothesis that remapping is independent of saccade direction.

Strength and selectivity of remapping are related

We were intrigued by the finding that a relatively large subset of the population (50/241, 21%) remapped stimulus traces for only a single saccade direction and considered the possibility that these neurons are highly specialized. Perhaps they have spatially restricted but exceptionally robust access to information from outside their classically defined RFs. We compared the RIs for the unidirectional neurons to the indices observed for the multidirectional neurons (Fig. 6). Unidirectional neurons have positive RIs for only a single direction ($n = 50$), whereas multidirectional neurons have positive RIs for more than one direction ($n = 191$). For each neuron, we used the maximum RI (of the 4 directions) to represent its ability to update stimulus traces. On average, multidirectional

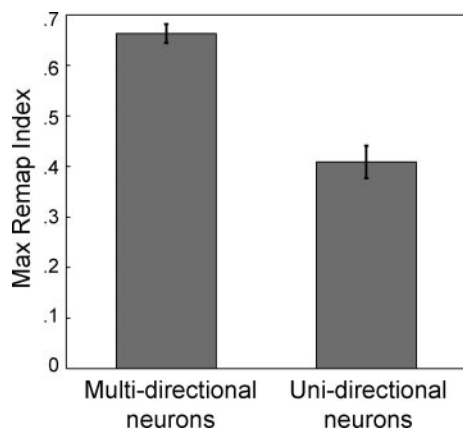


FIG. 6. Comparison of remapping strength and selectivity. Bars represent the average maximum RI for neurons that remapped stimulus traces in multiple directions (left bar, $n = 191$) and for neurons that remapped stimulus traces in only 1 direction (right bar, $n = 50$). Error bars represent SE. Neurons that remapped in multiple directions carried significantly stronger signals associated with spatial updating than those that remapped in only a single direction.

neurons carried a more robust remapping signal than did the unidirectional neurons (Wilcoxon rank sum, $P < 0.01$). This indicates that neurons that remap in multiple directions tend to remap more robustly than neurons that remap in only a single direction.

Population remaps stimulus traces for all saccade directions

The analyses above show that individual neurons can remap stimulus traces in all saccade directions. We next extended our analyses to consider the signals present in the entire population of LIP neurons. Of particular interest is whether, at the population level, stimulus traces are updated in conjunction with all saccade directions. The analyses described here parallel those used for single neurons. We compared activity in the single step task to that in each of the corresponding control tasks. Here, however, we treat each direction tested in each neuron as a separate sample. With this analysis we can assess whether the population of neurons shows universal remapping as opposed to whether individual neurons do so. If activity in the single step task is significantly greater than that generated in each of the control conditions (t -test, $P < 0.025$, Bonferroni correction), we conclude that the population remaps stimulus traces for that particular direction. In Fig. 7, we plot activity in the single step task against that generated in the matching control conditions for each sample. For all four directions, average firing rate in the single step task is significantly greater than that generated by either the stimulus or saccade alone (t -test, all comparisons, $P < 0.0001$). These data indicate that at the population level, stimulus traces are remapped in conjunction with all tested saccade directions.

We next used the RIs to determine whether there are differences in the strength of remapping when activity in the two control conditions is accounted for simultaneously. We compared three features of remapping: 1) the frequency of remapping; 2) the average remapping signal carried in each direction; and 3) the magnitude of the remapping signal carried by remapping neurons.

The first issue was whether remapping occurs with equal frequency for all directions. To address this, we analyzed the frequency of positive RIs observed for each direction. We found that remapping occurs in nearly equal frequency for the four test directions (down = 53%, up = 57%, ipsi = 62%, contra = 62%). Furthermore, for each direction, the proportion of remap samples is greater than that expected by chance (χ^2 test, $P < 0.05$, all directions). We used a χ^2 test to compare these frequencies statistically and found no significant differences in the proportions of neurons that remapped for each of the test conditions (χ^2 test, $P > 0.05$). We conclude that remapping occurs with equal frequency for the four directions.

To address the second issue, we analyzed the entire population of LIP neurons (Fig. 8), including samples with and without detectable remapping. This approach yields 281 samples per direction. This tells us whether, across the entire population, there are any differences in the average remapping signal carried in each direction. In each panel, the thick arrow indicates the average RI of the entire population (means: down = 0.26, up = 0.27, ipsi = 0.32, contra = 0.30). We compared the four distributions with a Kruskal-Wallis repeated-measure ANOVA, with direction as the factor of interest. There was no effect of direction ($df = 3$, $\chi^2 = 4.84$, $P >$

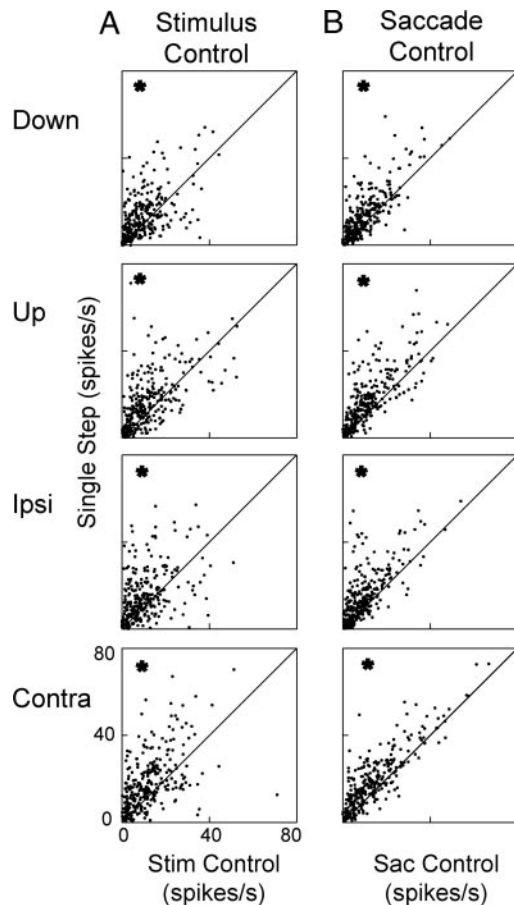


FIG. 7. At the population level, stimulus traces are remapped in conjunction with all saccade directions. Each row of panels represents data from one saccade direction. Four samples from each neuron are included ($n = 281$ neurons). *A*: comparison of single step activity and stimulus control activity. Each dot represents activity of a single neuron in the single step task plotted against its activity in the stimulus control task. Asterisks indicate that activity in the single step task is significantly greater than that observed in the stimulus control task (t -test, $P < 0.025$). For all 4 directions, single step activity is greater than stimulus control activity. *B*: comparison of single step and saccade control activity. For all directions, single step activity is significantly greater than saccade control activity. Conventions as in *A*. If single step activity is greater than activity in both control tasks, the population is considered to remap stimulus traces for that direction. This criterion is met for all 4 directions. Axes are identical on all plots (0–80 spikes/s).

0.18), indicating that the population remaps equally robustly for all directions.

Finally, for the population of neurons that remap for each direction, does the magnitude of the signal vary with changes in direction? To answer this question, we compared only the positive RIs for each direction. In each panel of Fig. 8, the thin arrow indicates the mean RI of the population of positive samples (down = 0.52, up = 0.49, ipsi = 0.53, contra = 0.49). We used a one-way ANOVA with direction as the factor of interest to compare the distributions of positive RIs. We found no significant differences between any of the directions when the data were analyzed this way ($df = 3$, $\chi^2 = 1.44$, $P > 0.70$). We observed similar results when we conducted these analyses on the subset of neurons with statistically significant remapping (see METHODS): the frequency and magnitude of remapping does not vary with changes in saccade direction. Altogether, the results of our analyses of the RI reveal that, at the popu-

lation level, both the frequency and strength of remapping are independent of saccade direction.

Remapping latency does not vary across saccade directions

When do neurons in LIP first respond to the updated stimulus trace? If activity in area LIP is related to the perception of spatial constancy, the timing of updating responses should be comparable, regardless of saccade direction. We compared the latency and time-course of remapping by constructing population histograms using only those samples for which neither the stimulus nor the saccade generated a response (see METHODS). We found that the latency of remapping did not change with direction (Fig. 9). This figure shows three main points. First, for all directions, activity in the single step task (solid lines) is greater than activity in the saccade control task (dotted lines). Second, activity in the single step task begins to exceed saccade control activity before the beginning of the saccade and remains elevated until well after the saccade is completed. Third, the latency of remapping does not vary with direction. We quantified the onset of remapping by calculating the time at which activity in the single step task first exceeded that in the saccade control task (down = -15.5 ms, up = -5.5 ms, ipsi = -15.5 ms, contra = $+4.5$ ms). In an alternative analysis (see METHODS), we achieved similar results: the latency of remapping is effectively the same for the four test directions. We conclude that across the four test directions, there is little variability in the time at which signals associated with spatial updating first become available.

Remapping is independent of RF location

We were interested in whether the selectivity (selectivity index) or magnitude (RI) of remapping varies as a function of the distance of the RF from the fovea. For instance, do neurons with more central RFs have greater access to remapped stim-

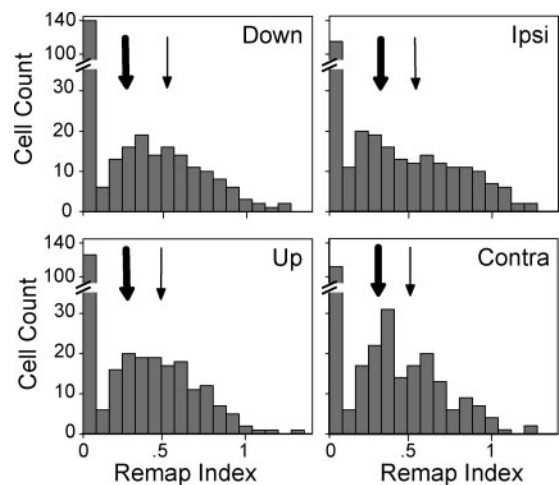


FIG. 8. Comparison of the distribution of RIs for the 4 test directions. RI is a measure of how robustly a neuron remaps stimulus traces for saccades of a particular direction. Positive values indicate that remapping was detectable; values of 0 indicate that remapping was not detectable. Thick arrows indicate the mean of all samples; thin arrows indicate the mean of positive samples only. For each direction, the distribution of indices is broad. Bar at 0 represents neurons with no detectable remapping. There were no differences between any distributions. This was true both for comparisons of the entire population and for comparisons of just those neurons with detectable remapping.

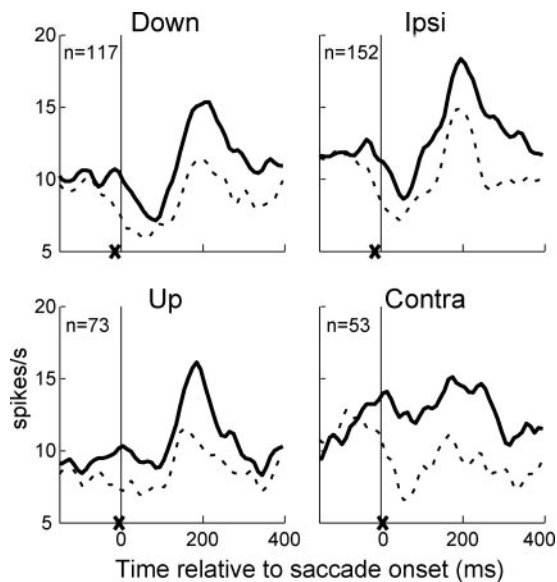


FIG. 9. Time-course of remapping. Data from single step (solid lines) and saccade control (dotted lines) tasks are shown aligned on onset of eye movement. Only samples with no significant response in the visual or saccade epoch of the control tasks are included. For all directions, activity in the single step task first begins to rise above saccade control activity before start of eye movement. Marker along x -axis indicates the time at which activity in the single step task is first significantly greater than saccade control activity. In all 4 directions, remapping begins before the saccade and persists until after it is completed.

ulus traces? To address this issue, we focused on the population of neurons with detectable remapping in at least one condition ($n = 241$). We divided these neurons into three groups. Neurons with RFs located within 10° of the fovea were categorized as central. Those with RFs $>20^\circ$ from the fovea were categorized as peripheral. Neurons with RFs between these were considered intermediate. With these categories, we had a reasonable population of neurons in each group (central = 84, intermediate = 110, peripheral = 47). There were no differences in the distributions of selectivity indices across the groups of neurons (Fig. 10A; Wilcoxon rank sum, all comparisons $P > 0.5$). This indicates that, regardless of eccentricity, neurons show equally selective remapping responses. We also compared the strength of remapping for these groups of neurons (Fig. 10B). We found that the strength of remapping does not vary with changes in RF eccentricity (Wilcoxon rank sum, all comparisons $P > 0.5$). Finally, we compared neurons with RFs in the upper and lower visual fields. We found no differences in the selectivity or magnitude of remapping between these two groups of neurons (Wilcoxon rank sum, both comparisons $P > 0.05$). Taken together, these results indicate that neurons with RFs located throughout the visual field carry equally selective and robust spatial updating signals.

Remapping is independent of response properties

Neurons in LIP exhibit a range of responses in the memory-guided saccade task. While most neurons carry visual signals, many also fire in conjunction with the saccade (Barash et al. 1991b; Colby et al. 1996). All neurons included in our analysis had significant visual responses: 32% had only visual responses and 68% had visuomovement responses. We were interested in whether the response properties of these neurons

would provide insight into their remapping properties. We therefore asked whether the strength or selectivity of remapping varies between visual and visuomovement neurons. We found no differences in either feature of remapping (Wilcoxon rank sum, both comparisons $P > 0.05$). This provides further evidence that remapping is ubiquitous in area LIP.

LIP remaps for most saccade directions relative to the RF location

In the original remapping paradigm, the stimulus was always placed in the hemifield opposite from the RF and the saccade was always directed away from the RF (Duhamel et al. 1992a). The rationale behind this approach was that neither the stimulus nor the saccade alone would drive the neuron. In this experiment, we tested the same four saccade directions, regardless of the location of the RF. As a result, for any given neuron, some saccades are directed toward the RF, whereas others are directed away from it. We anticipated that there might be systematic differences in responses according to whether the saccade was directed toward or away from the RF. For example, if the saccade is directed toward the RF, it usually will drive the neuron. Likewise, because the outer edge of the RF is often unbounded (Ben Hamed et al. 2001), the stimulus alone frequently drives the neuron in configurations where the saccade is directed toward the RF. On the other hand, if the saccade is directed away from the RF, it is unlikely that there will be activity present in either control task. As discussed in previous sections, the presence of activity in the control tasks influences the detectability of remapping. This raised the pos-

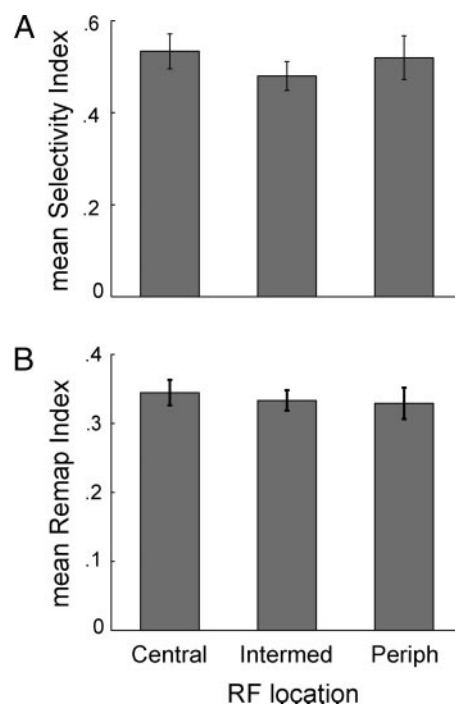


FIG. 10. Comparison of remapping properties for neurons with RFs in central, intermediate, and peripheral visual fields. A: comparison of selectivity indices. There was no difference in selectivity of remapping for neurons with RFs in different regions of the visual field. B: comparison of strength of remapping. Bars represent the average RI for each group of neurons; error bars represent SE. There were no differences in strength of remapping for any groups.

sibility that we might see differences in remapping if we accounted for the relationship between saccade direction and RF location. We normalized saccade direction relative to the RF location to determine whether there was any systematic relationship between remapping and the direction of the saccade relative to the RF.

During data collection, we mapped the RF to one of eight cardinal locations around the fovea. This produced two classes of neurons: those with RFs on one of the cardinal axes (cardinal neurons, $n = 96$), and those with RFs along one of the oblique axes (oblique neurons, $n = 185$). We computed the angular offset between the saccade direction and the angle of the RF. This angular offset is the normalized saccade direction and represents the direction of the saccade relative to the RF location. After normalization, the saccade directions for cardinal neurons become 0, 90, 180, and 270. The saccade directions for oblique neurons become 45, 135, 225, and 315. We refer to the normalized saccade directions as "saccade categories."

The first question we asked was whether the population remaps stimulus traces for all saccade categories. We addressed this by comparing activity in the single step task to that in each of the corresponding control tasks (t -test, $P < 0.025$, Bonferroni correction). Remapping is considered significant only if both comparisons are found to be significant. We separately compared the saccade categories from each class of cells. For all eight saccade categories, activity in the single step task is significantly greater than activity in the stimulus control task (Fig. 11, *A* and *C*). Activity in the single step task was significantly greater than saccade control activity for all categories except the 180° category (Fig. 11, *B* and *D*). We conclude that, at the population level, there is significant remapping for most saccade directions relative to the RF.

Remapping is less detectable when the saccade is directly opposite the RF.

Detectability of remapping is affected for saccades opposite the RF

The finding that remapping is less robust when the saccade is directly opposite the RF prompted us to explore the 180° category further. The neuron in Fig. 12 shows why it is often difficult to detect remapping for the 180° saccade category: the saccade alone generates a robust response during our analysis epoch (0–300 ms relative to saccade onset; Fig. 12*C*). This response occurs at nearly the same latency as the response in the single step task. This activity cannot be considered pure motor activity because the eye movement is not in the direction of the response field. The response instead is attributable to remapping the representation of the first fixation point. As schematized in the *left panels*, if the saccade is directly opposite the RF, it will move the RF onto the location of the initial fixation point, as well as the stimulus location. The fixation point itself is a salient visual stimulus and therefore is remapped. The analysis of remapping as a function of normalized saccade direction reveals a pattern in the data that was previously unrecognized. Furthermore, it provides insight into why remapping of the stimulus trace is sometimes not detectable, namely that this signal can be obscured by activity related to updating the fixation point.

Strength of remapping is similar across saccade categories

We were next interested in directly comparing the strength of the remapping signal associated with each saccade category. The central issue is to assess whether the strength of remapping varies with changes in saccade direction relative to RF loca-

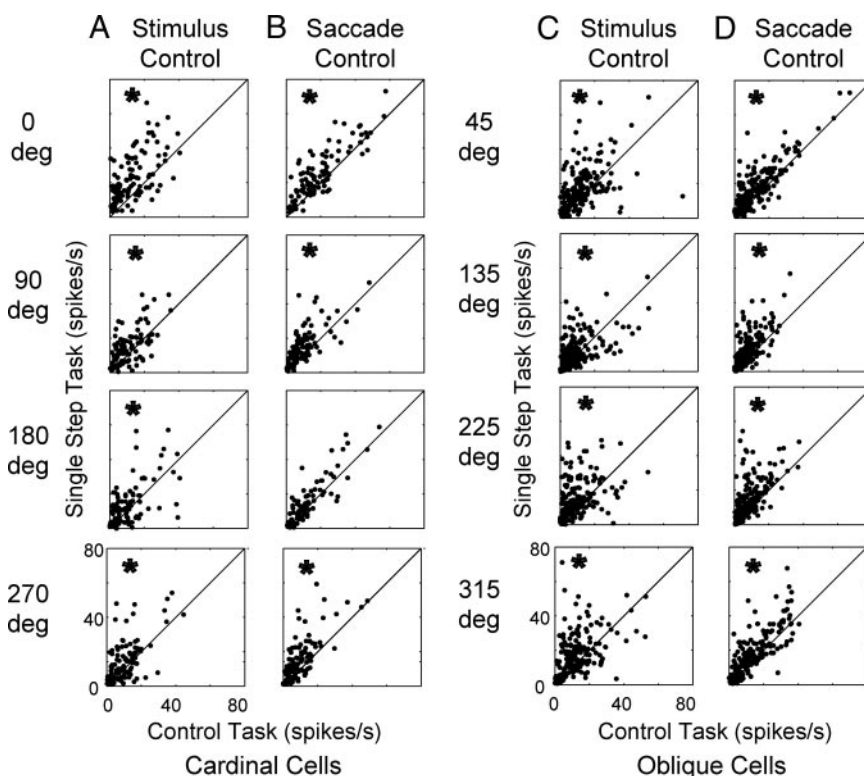


FIG. 11. Population level assessment of remapping for the 8 saccade categories. All 4 samples from all neurons are included in order to assess how the entire population of neurons responds in different conditions. *A* and *B*: cardinal cells ($n = 96$). *C* and *D*: oblique cells ($n = 185$). *A* and *C*: single step and stimulus control tasks. Each dot represents activity of a single neuron. Conventions as in Fig. 7. Activity in the single step task is significantly greater than that observed in the stimulus control task. This is true for all saccade categories from both classes of cells. *B* and *D*: activity in the single step task compared with activity in the saccade control task. Conventions as in *A* and *C*. For all saccade categories except the 180° category, activity in the single step task is significantly greater than activity in the saccade control task. Stimulus traces are remapped for all saccade directions relative to the RF location, except when saccade is directly opposite the RF. Axes are identical on all plots (0–80 spikes/s).

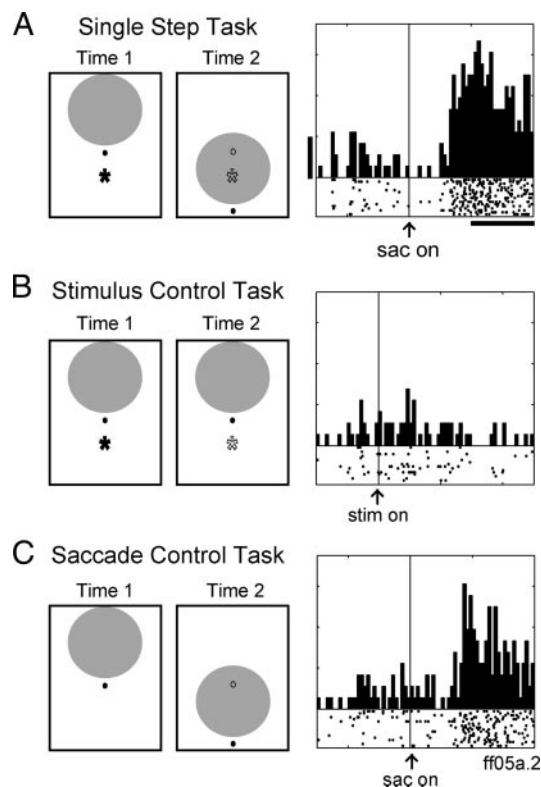


FIG. 12. Remapping the location of the initial fixation point obscures remapping of stimulus trace. This occurs often for the 180° saccade category, in which saccade is directly opposite the location of RF. In each row of panels, cartoons represent spatial configuration of the task. Two time-points are shown: before and after the stimulus is flashed. For the single step and saccade control tasks, these times correspond to the monkey fixating at FP1 (time 1) or FP2 (time 2). Gray circle represents RF. Dots represent FP1 (top) and FP2 (bottom). Star represents the stimulus that will be updated. *A*: single step task. Data are aligned on onset of saccade. Neuron exhibits a robust response after eye movement. *B*: stimulus control task. Stimulus is outside of the classically defined RF; it does not drive the neuron. *C*: saccade control task. Saccade moves RF onto location where FP1 had been. The neuron responds in conjunction with the execution of the saccade, even though the stimulus is not presented. This response is attributed to remapping the location of the initial fixation point. Vertical scale bar, 20 spikes/s; horizontal scale bar, 200 ms. Conventions for histograms as in Fig. 2.

tion. Here, we focus on separate analyses of the two classes of neurons. We can exploit the fact that each neuron is tested in four of the saccade categories and, when appropriate, use repeated measures statistics to determine whether there are any differences between the categories. We analyzed the RIs from each saccade category to compare three features of remapping: 1) the frequency of remapping; 2) the average remapping signal; and 3) the magnitude of the signal carried by neurons with detectable remapping.

First, does remapping occur with equal frequency for the four different saccade categories? We addressed this question by comparing the percentages of neurons with positive RIs (Fig. 13, *A* and *B*). For all saccade categories, the proportion of remapping samples is greater than that expected by chance (χ^2 test, $P < 0.05$, all categories). Additionally, there were no differences in the frequency of remapping according to category (χ^2 test, $P > 0.05$ for both cardinal and oblique cells). These data show that remapping is equally likely to occur for all saccade directions relative to the location of the RF.

The second issue is whether the strength of remapping varies as a function of saccade category. We used a Kruskal-Wallis repeated-measure ANOVA to compare the mean RI for each saccade category for the two classes of neurons (Fig. 13, *C* and *D*). We found a main effect of saccade direction for each class ($P < 0.05$, both classes). For the cardinal cells, we found that the strength of remapping for the 180° category is significantly diminished compared with the other saccade categories ($P < 0.05$, Tukey's HSD). For the oblique cells, we found that the RI for the 225° saccade category was significantly greater than for the other three categories ($P < 0.05$, Tukey's HSD). There were no differences between any of the other saccade categories. Together, these results indicate that if the saccade is directed toward the RF, or is only partially offset from it, the magnitude of the remapping signal carried by the population is largely invariant. If the saccade is made directly away from the RF, as it is in the 180° category, the detectability of remapping is diminished. This finding parallels the observations reported in earlier sections: remapping is reduced when the saccade is directly opposite the RF because this signal is obscured by remapping the fixation point.

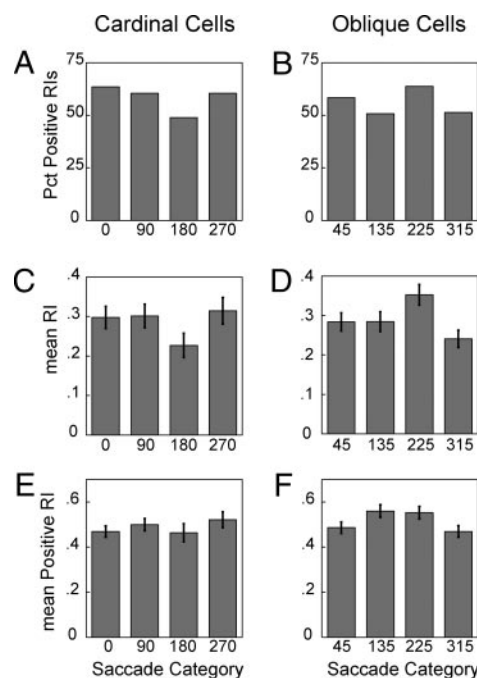


FIG. 13. Comparison of RI, a measure of strength of remapping, across all 8 saccade categories. All 4 samples from all neurons are included to assess the response of the entire population of LIP neurons. Data from cardinal cells are plotted on the left ($n = 96$); oblique cells are plotted on the right ($n = 185$). *A* and *B*: comparison of the number of neurons with positive RIs, the neurons with detectable remapping. There are no significant differences in frequency of remapping for either population of neurons. *C* and *D*: comparison of average population RI for each category. This is the updating signal carried by the entire population of LIP neurons; it includes neurons with and without remapping. Error bars represent SE. For cardinal cells, the 180° RI is significantly smaller than the other 3 categories. For oblique cells, updating for the 225° saccade category is significantly greater than for the other 3 categories. There are no differences between any other categories for either group of neurons. *E* and *F*: comparison of average positive RI for each saccade category. This is the signal carried by the population of remapping neurons. There are no significant differences between any saccade categories. Error bars represent SE. Overall, direction of saccade relative to location of RF has little bearing on the strength of remapping.

Finally, for those neurons that remap stimulus traces for each saccade category, does the strength of the remapping signal vary? We compared only the positive RIs for each saccade category to address this question (Fig. 13, *E* and *F*). There were no significant differences between the saccade categories of either class of neurons ($P > 0.05$, 1-way ANOVA). This shows that, for neurons for which remapping is detectable, the strength of this signal does not vary as a function of saccade category.

Attentional factors in remapping

Attention plays a critical role in updating. As shown by Gottlieb et al. (1998), stimulus traces are remapped only if they attract attention. This can be the result of the intrinsic salience of the stimulus. In the single step task, for example, the stimulus to-be-updated attracts attention because it is briefly flashed on an otherwise uniform background. A stimulus can also attract attention if it is the target for an upcoming eye movement. In either case, LIP neurons can exhibit remapping. In contrast, LIP neurons do not remap a stable, nontarget stimulus that is embedded in an array of other stimuli. These findings attest to a close link between spatial updating and attentional processes. It is important to note, however, that the influence of attention is spatially specific. Neurons do not remap in the single step task if the stimulus is flashed at a location that will not be encompassed by the RF after the saccade to the new fixation point (Kusunoki and Goldberg 2003). Therefore, while attention is a critical factor in remapping, its effects are only observed when the neuron's RF is brought onto the previously stimulated location, eliciting a response to the updated trace of the salient stimulus.

Attention is one of several higher-order processes attributed to area LIP. Activity in LIP may also reflect other factors related to the monkey's behavioral state, such as task demands or expected reward (Colby et al. 1996; Gottlieb and Goldberg 1999; Platt and Glimcher 1999; Sugrue et al. 2004; Toth and Assad 2002; Zhang and Barash 2000). Therefore it was important to determine whether activity in the single step task compared with the saccade control task is specific to updating or to generalized changes in behavioral state. In both tasks, the monkey is required to make a single visually guided saccade from the first fixation point to the second. The only difference between the two tasks is that, in the single step task, a stimulus appears briefly. This stimulus, while salient, is not a target for the monkey's subsequent behavior and does not alter the monkey's performance of the visually guided saccade. In keeping with these comparable task demands, the monkeys had excellent performance on both the saccade control and single step tasks (93% and 91% correct, respectively). These findings indicate that task difficulty, and thus expected reward, were equivalent for the two tasks. We explored this issue further by asking whether there was any correlation, on a session-by-session basis, between the monkeys' behavior (percent correct score in the single step task) and the strength of remapping (RI). We found that behavior was a poor predictor of the strength of remapping ($R^2 = 0.035$, $P < 0.05$).

Furthermore, we did not observe any shift in baseline activity between the saccade control and single step tasks, as would be expected if there were a generalized change in task difficulty, reward expectation, or arousal. We assessed this by

comparing, across the population, baseline activity in the single step and saccade control tasks (t -test, $P > 0.05$, all 4 directions). Additionally, baseline firing rate was only weakly correlated with the strength of remapping ($R^2 = 0.032$, $P < 0.05$). Taken together, these observations reinforce the conclusion that increased activity in the single step task is specific to the remapping of a salient stimulus trace.

LIP updates both within and across hemifields

In the previous sections, we established that stimulus traces can be updated in conjunction with saccades of all directions. Our paradigm also allowed us to determine the influence of another important variable: whether the stimulus was updated within a single hemifield or across hemifields. In within-hemifield updating, the representation of the stimulus remains within the same hemifield both before and after the saccade (Fig. 14A). In contrast, for across-hemifield updating, the representation of the stimulus is moved from one hemifield to the other (Fig. 14B). We reasoned that these two conditions must require different circuitry. Specifically, across-hemifield remapping must involve a transfer of information from one hemisphere to the other. When the stimulus remains in the same hemifield, however, the information transfer can occur between neurons in a single hemisphere. Does this mode of transfer affect remapping signals? We addressed this question by directly comparing within- and across-hemifield conditions. For this analysis, we used a subset of neurons (159/281) and compared just two of the four test conditions: one for across and one for within. Additionally, we used the canonical saccade directions, and not the normalized saccade directions for this analysis.

The first question we asked was whether LIP at the population level shows significant remapping for both within and

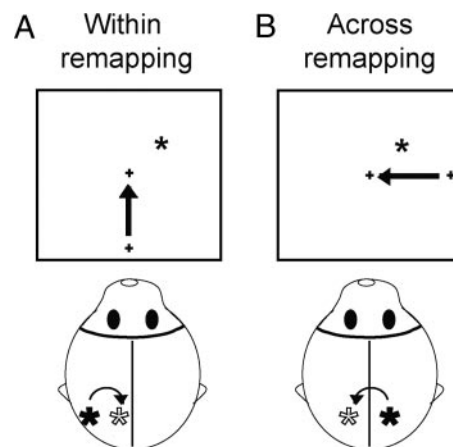


FIG. 14. Schematic representation of within and across hemifield updating. *A*: within-hemifield updating. The stimulus is located in the right visual field when the eyes are at FP1. It is represented by neurons in the left hemisphere (black star). When the eyes reach FP2, the location where stimulus appeared is still in the right visual field and continues to be represented by neurons within the left hemisphere (white star). Updating in this condition involves a transfer of visual signals between neurons located within the same cortical hemisphere. *B*: across-hemifield updating. Stimulus is located in the left visual field when the eyes are at FP1; it is represented by neurons in the right hemisphere (black star). When the eyes reach FP2, the screen location where the stimulus appeared is now in the right visual field. This location is represented by neurons in the left hemisphere (white star). Here, updating involves a transfer of visual information across hemispheres.

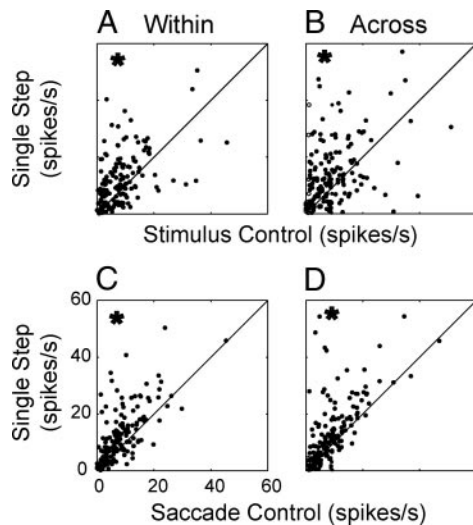


FIG. 15. The population remaps stimulus traces both within and across hemifields. *A* and *B*: comparison of activity in single step and stimulus control tasks. Each dot represents data from a single neuron. *Activity in the single step task is significantly greater than activity in the stimulus control task. *C* and *D*: comparison of activity in saccade control and single step tasks. Single step activity is greater than saccade control activity for both conditions. LIP shows significant remapping both within and across hemifields ($n = 159$ neurons in each panel).

across conditions. We addressed this question by comparing, for each condition, single step activity to that of the corresponding controls. For both within- and across-hemifield updating, we found significant remapping at the population level (Fig. 15). Single step activity is significantly greater than activity in either control task (t -test, $P < 0.001$, all comparisons). These data show that, at the population level, stimulus traces are robustly updated both within and across hemifields.

INDIVIDUAL NEURONS CAN UPDATE BOTH WITHIN AND ACROSS HEMIFIELDS. The second question we asked was whether individual neurons can remap stimulus traces both within and across hemifields. We compared the frequency of neurons that showed remapping for within-hemifield only, for across-hemifield only, and for both types of remapping (Fig. 16*A*). Most neurons with updating activity remapped stimulus traces in both the within- and across-hemifield conditions (67/120, 56%). This shows that, although the circuitry underlying these two conditions must differ, neurons are capable of updating stimuli both within and across hemifields. Similar proportions showed remapping for within only and for across only [within = 18% (22/120), across = 26% (31/120)], supporting the idea that there is no cost associated with updating from one hemifield to the other.

MAGNITUDE OF REMAPPING IS SIMILAR FOR WITHIN AND ACROSS UPDATING. The third question we asked was whether the magnitude of remapping differs for the within- and across-hemifield conditions. Our analysis of the RI for these two conditions revealed that they are essentially the same (Fig. 16, *B* and *C*). We found that a significant number of neurons remap for both conditions (χ^2 test, $P < 0.05$, both conditions). There is no significant difference in the frequency with which neurons remap within- and across-hemifields (within = 56%, across = 62%, χ^2 , $P > 0.05$). Moreover, there is no difference in the magnitude of remapping for these two conditions. We found no

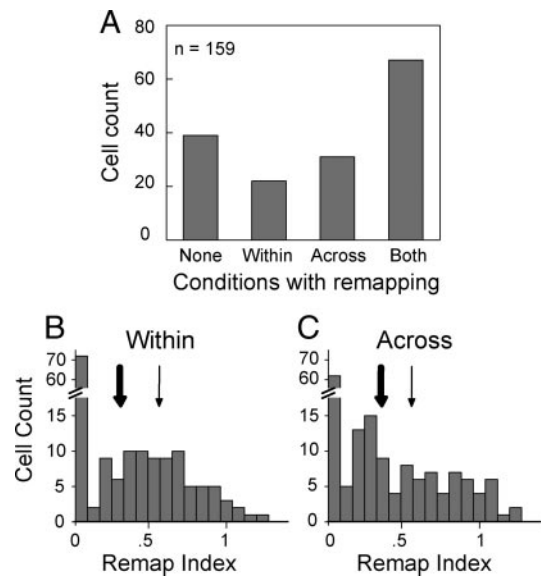


FIG. 16. Comparison of the frequency and magnitude of within- and across-hemifield remapping. *A*: individual neurons can remap stimulus traces both within and across hemifields. Bars represent the number of neurons with no remapping, only within, only across, or both within and across. Groups are mutually exclusive; each neuron is represented only once. Most neurons update stimuli both within and across hemifields. *B* and *C*: distribution of RIs. Thick arrow indicates mean RI of all samples; thin arrow indicates mean RI of samples with remapping (positive samples). There are no differences in the strength of remapping, both when the entire population is considered and when just those neurons with detectable remapping are compared.

difference in the average RI when we compared the entire population [within = 0.31 ± 0.027 (SE); across = 0.34 ± 0.029 ; Wilcoxon matched test, $P > 0.80$]. We also found no difference in the strength of remapping even when we analyzed just those neurons with detectable remapping (within = 0.55 ± 0.029 (SE); across = 0.55 ± 0.032 ; Wilcoxon rank sum, $P > 0.70$). Taken altogether, these results show that neurons in LIP remap stimulus traces within and across hemifields with equal frequency and strength.

TIME-COURSES FOR WITHIN AND ACROSS UPDATING ARE SIMILAR. Finally, we asked whether the latency of remapping affected by whether the stimulus must be updated within or across hemifields. We considered, for example, that across-

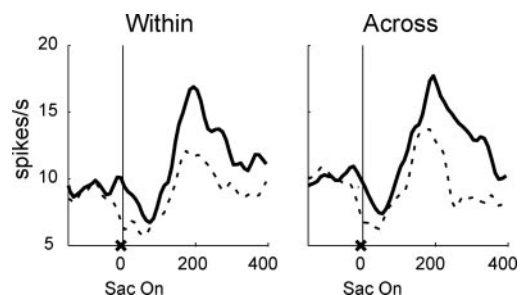


FIG. 17. Comparison of the time-course of within- and across-hemifield remapping. Data from single step (solid lines) and saccade control tasks (dotted lines) are aligned on onset of the saccade. Marker along x -axis indicates the time at which activity in the single step task is first significantly greater than activity in the saccade control task. This time-point is the same for the 2 conditions (-5 ms). For both within and across conditions, activity in the single step task begins to rise above saccade control activity before onset of the saccade. This activity persists until well after the saccade has been completed ($n = 60$ neurons in each panel).

hemifield remapping may require longer transmission times and thus may be delayed relative to within-hemifield remapping (Poffenberger 1912; Zaidel 2003); but see also (Braun et al. 2003). We addressed this possibility by constructing smoothed population histograms (spike density functions) using only those neurons with no significant activity in any control task. In other words, if a neuron was included in this analysis, it contributes to both the within- and across-population histograms (Fig. 17). For both within and across updating, activity in the single step task (solid line) begins to rise above activity in the saccade control task (dotted line) even before the onset of the saccade. Updating activity persists for many hundreds of milliseconds after the completion of the saccade. We calculated the latency of remapping by determining the time at which activity in the single step task is first significantly greater than that of the saccade control task. This time-point was the same for the two conditions (-5 ms relative to the beginning of the saccade).

The population histograms can be used to summarize the observations described above: first, neurons in LIP carry robust signals related to updating stimulus traces both within and across hemifields; second, remapping activity begins before the onset of the saccade for both conditions; third, updating signals persist until well after the saccade is completed. Based on the findings described here, we conclude that there is no difference in the magnitude or latency of within- and across-hemifield updating.

DISCUSSION

Our aim was to determine whether neurons in the lateral intraparietal cortex can access information from throughout the visual field. We addressed this aim by asking whether remapping is independent of the direction over which a stimulus trace must be updated. We found that individual neurons can update spatial locations in conjunction with saccades of multiple directions. In individual neurons, the strength of this signal often varied with saccade direction. At the population level, remapping was equally robust for all saccade directions. Furthermore, the strength of remapping was largely independent of two other factors: the direction of the saccade relative to the RF location and the mode of transfer required—within or across hemispheres.

LIP neurons can access information from throughout the visual field

We found that, at the population level, stimulus traces can be updated in conjunction with saccades of all directions. The classically defined RFs in LIP are restricted in extent and are primarily confined to the contralateral hemifield (Barash et al. 1991b; Ben Hamed et al. 2001). When an eye movement is executed, these neurons must receive information that allows them to respond to visual stimuli presented virtually anywhere in the visual field. We found that the visual responsiveness of the neuron can be shifted in any direction relative to the RF location. This implies that any given LIP neuron must be interconnected with other neurons with RFs distributed throughout the visual field. Furthermore, this finding supports the hypothesis that the activity of LIP neurons can contribute to the maintenance of spatial constancy throughout the visual field.

Our expectation was that remapping would be equally robust for all saccade directions in all neurons. Instead, we found that, in individual neurons, the strength of remapping often varied with changes in saccade direction. In particular, we found that many neurons showed significant remapping for only a subset of the test directions. One major source of variability is related to detectability. In our paradigm, the amount of activity generated in the control conditions varied considerably. For some saccade directions, remapping was difficult to detect because this signal co-occurred with robust stimulus or saccade-related activity.

The analysis of normalized saccade direction provided some insight into why the activity in the saccade controls sometimes varied by condition. Specifically, it was often difficult to detect remapping in conjunction with a saccade directly opposite the RF (the 180° category). In this configuration, the saccade moved the RF onto the location of the initial fixation point (FP1), a salient visual stimulus that had been extinguished just before the saccade. During the saccade alone task, many neurons remapped the location of the fixation point and consequently exhibited a robust response. For this configuration, therefore we often could not detect a single step response that was significantly greater than the saccade alone task. Early experiments on spatial updating shed light on this observation.

One of the first remapping studies used spatial configurations similar to our 180° category (Goldberg and Bruce 1990). In this study, experimenters measured updating activity under different conditions. Of particular interest is the “back-and-forth” condition of the updating task (the double step task). In this condition, the location of the new fixation point was chosen so that the saccade would move the RF onto the location of FP1. The new fixation point was directly opposite the RF, as it is in our 180° configuration. Neurons in FEF responded robustly just after the onset of the first eye movement that moves the RF onto the location of the previously extinguished FP1. In other words, neurons updated the location of FP1 in conjunction with the first saccade. These observations are in agreement with our conclusion that neural activity in the saccade alone task for the 180° condition is attributable to remapping the representation of the central fixation point.

LIP subserves spatially accurate behavior for all saccade directions

Our experience of spatial constancy suggests that there are no perceptual differences associated with making eye movements toward objects located in different regions of the visual field. Our finding that stimulus traces are robustly updated with all saccade directions indicates that the population activity of LIP could guide spatially accurate behavior in conjunction with all saccade directions. Behavioral experiments indicate that this is indeed the case: spatial locations are updated in conjunction with all saccade directions (Baizer and Bender 1989; Baker et al. 2003; Hallett and Lightstone 1976). This ability is measured behaviorally with the double step task. In this task, two sequentially flashed targets must be acquired by two consecutive saccades. The critical factor in this task is that the targets are presented so briefly that they are extinguished before the eye movements begin. The first saccade can be easily attained using retinal coordinates. The second saccade, however, can only be attained correctly if the first saccade is

taken into account. Experiments in both monkeys and humans indicate that the double step task is accurately performed for saccades of varying directions, including horizontal, vertical, and oblique.

What are the neural underpinnings of this ability? Remapping the stimulus trace of the second target accomplishes the required transformation: the stimulus trace can be shifted from the coordinates of the initial eye position to the coordinates of the new eye position. If remapping subserves spatially accurate behavior, lesions in areas responsible for generating this signal should impair the ability to perform the double step task. This prediction was verified in studies of patients with unilateral parietal lobe lesions (Duhamel et al. 1992b; Heide et al. 1995). These patients performed both saccades accurately when the first saccade was directed into the spared (ipsilesional) hemifield. The second saccade was inaccurate only when the first was directed into the contralesional hemifield. They failed on the double step task because they could not update the location of the second target. Similar observations have been made in monkeys: performance of the double step task is impaired after temporary lesions to LIP (Li and Andersen 2001). These findings support the hypothesis that parietal cortex is necessary for spatial updating.

Anatomical findings lend further credence to the idea that the remapped representation generated in LIP could be used to guide accurate eye movements. LIP is strongly interconnected with both the superior colliculus (Clower et al. 2001; Lynch et al. 1985) and FEFs (Cavada and Goldman-Rakic 1989; Schall et al. 1995; Stanton et al. 1995), areas that are intimately involved in saccade generation (Schall 1997; Wurtz and Albano 1980). Through these connections, updating activity in LIP could be used to generate accurate eye movements toward targets of interest. Recent experiments have begun to shed light on the nature of the signals transferred between these areas (Pare and Wurtz 2001; Sommer and Wurtz 2002; Wurtz et al. 2001). Our finding that remapping in LIP is effectively independent of saccade direction supports the hypothesis that this activity is important for spatially accurate behavior.

Implications for a remapping model

A mechanism for remapping in LIP has been proposed by Goldberg and colleagues (Quaia et al. 1998). The logic behind the model is simple. During the single step task, the to-be-updated stimulus activates a set of neurons that encode its location when the monkey's eyes are at the initial fixation point. At the time of the eye movement, this activity is shifted from the first group of neurons to a new set of neurons whose RFs will encompass the stimulated location once the eyes are at the new fixation point. The basic claim of the model is that neurons should remap every time a saccade moves the RF onto a previously stimulated location in the visual field. The critical feature of the model is that it works as a coincidence detector: remapping happens if and only if a neuron receives both a visual signal and a corollary discharge signal—a copy of the eye movement command. Remapping results in a transfer of visual information between neurons in LIP.

Our data speak to two predictions of the model. The first prediction is that individual neurons in LIP should remap stimulus traces regardless of saccade direction. Consistent with this prediction, we observed that individual neurons can remap

stimulus traces in conjunction with saccades of multiple directions. We also found, however, that many neurons showed remapping for only a subset of the test directions. Based on this observation, we conclude that there must be additional factors, not accounted for by the model, that contribute to remapping. It is possible, for example, that individual cells in area LIP do not receive corollary discharge signals regarding all saccade directions. Likewise, single neurons may not be linked to neurons representing all other regions of the visual field. These possibilities indicate that the perception of spatial constancy must not rely on signals from selected individual neurons but must be based on information present in the population as a whole.

The second prediction of the model is that remapping should occur for stimuli located anywhere in the visual field. In the single step task, the location of the stimulus is determined by the location of the RF. Consequently, our analysis of neurons with RFs at different eccentricities can speak to the issue of stimulus location. We found that neurons at all eccentricities show robust remapping. This indicates that there is no bias for neurons at a particular location in the visual field to prefer to remap in conjunction with a 20° saccade. Instead, neurons with RFs located throughout the visual field have equal access to information brought into the RF with a 20° eye movement.

Some of our observations were not consistent with the model. In particular, we observed that the detectability of remapping is influenced by the presence of other neural signals, including those related to the stimulus alone, saccade alone, and remapping of other stimuli. One of the more unexpected findings in this study is that neurons sometimes remap not only the flashed stimulus but also the central fixation point. This remapping occurs when a saccade brings the neuron's RF onto the location where the original fixation point had been, and therefore elicits a response in the saccade control task as well as the single step task. This finding, while perplexing at first, speaks to the limited spatial resolution of individual neurons in area LIP. Given that RFs can be relatively large (Barash et al. 1991b; Ben Hamed et al. 2001), a single LIP neuron can respond to stimuli at multiple locations within the visual field. Likewise, a single neuron can exhibit a remapped response to multiple stimulus locations brought into the RF by an eye movement. How these signals are resolved at the level of the population, and read out by downstream structures, is a compelling issue that deserves consideration in future studies. Modeling these many signals may provide a greater understanding of how they influence one another.

Final conclusions

The goal of this experiment was to determine whether neurons in LIP have access to visual information throughout the visual field. We addressed this by asking whether neurons in LIP update stimulus traces equally robustly in conjunction with saccades of different directions. We can draw four main conclusions. First, individual neurons have access to visual information from multiple regions beyond their classically defined RFs. This conclusion is supported by our observation that single cells in LIP can remap stimulus traces in multiple directions. A second, parallel conclusion is that spatial updating in LIP is effectively independent of saccade direction: at the population level, stimulus traces are updated in conjunction

with all saccade directions, even when we consider direction as a function of RF location. Third, despite these findings that remapping is virtually universal, we obtained evidence that the detectability of updating signals can vary. We observed this variability both at the level of single neurons and in the population, and found that it was attributable to the strength of activity in the stimulus and saccade control tasks. Our fourth conclusion is that neurons in LIP have equal access to visual information, whether it originates in the same or opposite hemifield. Specifically, we compared the updating of stimulus traces within- and across-hemifields. We found no differences in the magnitude or timing of remapping in these two conditions. Taken together, our findings support the hypothesis that the activity of LIP neurons can contribute to the maintenance of spatial constancy throughout the visual field.

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