Shape selectivity and remapping in dorsal stream visual area LIP

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Subramanian J, Colby CL. Shape selectivity and remapping in dorsal stream visual area LIP. J Neurophysiol. 2014;111:613–627. First published November 13, 2013; doi:10.1152/jn.00841.2011.—We explore the visual world by making rapid eye movements (saccades) to focus on objects and locations of interest. Despite abrupt retinal image shifts, we see the world as stable. Remapping contributes to visual stability by updating the internal image with every saccade. Neurons in macaque lateral intraparietal cortex (LIP) and other brain areas update information about salient locations around the time of a saccade. The depth of information transfer remains to be thoroughly investigated. Area LIP, as part of the dorsal visual stream, is regarded as a spatially selective area, yet there is evidence that LIP neurons also encode object features. We sought to determine whether LIP remaps shape information. This knowledge is important for understanding how it is used. In its simplest form, the remapped signal determines what information is retained from each glance. We identified 82 remapping neurons. First, we presented shapes within the receptive field and tested for shape selectivity in a fixation task. Among the remapping neurons, 28 neurons (34%) were selective for shape. Second, we presented the same shapes in the future location of the receptive field around the time of the saccade and tested for shape selectivity during remapping. Thirty-one (38%) neurons were selective for shape. Of 11 neurons that were shape selective in both tasks, 5 showed significant correlation between shape selectivity in the two tasks. Across the population, there was a weak but significant correlation between responses to shape in the two tasks. Our results provide neurophysiological evidence that remapped responses in area LIP can encode shape information as well as spatial information.

Although remapping is thought to contribute to visual stability, the exact content of the remapped signal is unknown. Understanding the content of the remapped signal is crucial for determining what information is retained from each glance and how it is used. In its simplest form, the remapped signal indicates the location of a previously stimulated region. However, LIP responses are far more sophisticated than merely indicating the occurrence of visual events. Several studies have shown that LIP activity may reflect reward value, uncertainty, attentional priority, or the behavioral relevance of the stimulus (Andersen et al. 1997; Bisley and Goldberg 2003, 2010; Leon and Shadlen 2003; Platt and Glimcher 1999; Toth and Assad 2002). This complexity in LIP activity is also reflected in remapping (Gottlieb et al. 1998; Mirpour and Bisley 2012). Although remapping is triggered automatically whenever a saccade is internally generated, the remapped response is affected by the attentional value of the stimulus. Just as visual responses can be enhanced, remapped responses can also be enhanced. Larger remapped responses are evoked by the sudden appearance of an object, or by a potential saccade target, than by a stable, irrelevant object.

The richness of visual activity in LIP is not limited to attentional factors. A landmark study revealed that LIP encodes shape information (Sereno and Maunsell 1998). This was a remarkable finding because until then it was assumed that LIP, as a dorsal stream area, did not process shape. Object recognition was believed to be mediated solely by the ventral stream. It continues to be unclear whether LIP neurons merely

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update locations so that they can be appropriately attended or if object information is remapped as well (Cavanagh et al. 2010; Melcher and Colby 2008; Prime et al. 2006, 2007; Wurtz et al. 2011). Is it possible that shape information is also reflected in the remapped signal?

It is already known that remapping is a mechanism by which the brain could maintain a map of important spatial locations. That map is incomplete because information about the identity of objects that occupy those locations is missing. Remapping of object information would enable the brain to maintain a map of features that were present at those locations (Melcher and Colby 2008).

There is considerable psychophysical evidence showing that visual information is maintained across saccades (Deubel et al. 2002; McConkie and Currie 1996). We retain information about important locations as well as the objects occupying those locations (Gordon and Irwin 1996). Sensory adaptations are maintained in a location-dependent manner across saccades (Melcher 2007). Feature information from presaccadic presentations may also be used in a behaviorally relevant manner (Melcher et al. 2004; Melcher and Morrone 2003; Pollatsek et al. 1984). The neural structures involved in the maintenance of feature information are just beginning to be identified. Recent studies indicate that the parietal cortex may be involved in transsaccadic memory of features (Prime et al. 2008).

In this study, we found that individual LIP neurons automatically encode and update shape information. The prevalence of shape-selective remapped responses in our data shows that the remapped information is far more detailed than previously appreciated.

METHODS

Animals

Two adult female rhesus macaques (5–8 kg) were used in this study. Monkeys were trained on no other task other than those described in this study. The 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 beginning of this study, both monkeys underwent sterile surgery under general anesthesia induced with ketamine and maintained with isoflurane. A portion 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 for monitoring eye position (Judge et al. 1980). After initial training, a recording chamber (1.8-cm diameter) was installed over area LIP. The placement of the recording chamber was determined using 1) the standard stereotaxic location for area LIP (5 mm posterior and 12 mm lateral in Horsley Clarke coordinates) and 2) anatomic information from structural MRIs.

Selection of Shape Stimuli and Stimulus Presentation

We closely followed the procedure of Sereno and Maunsell (1998) in designing a set of eight shapes (Fig. 1E). Each of the shapes extended the entire width of a 2.2° × 2.2° square. Each shape had 180 white pixels and 220 black pixels. The shapes had equal brightness and overall size. They differed only in the relative configuration of the white pixels. The luminance of the stimuli was ~63.15 cd/m², and the background was nearly completely dark, below the threshold of our photometer (sensitive to <0.01 cd/m²). Stimuli were presented on a computer-controlled 19-in. ViewSonic color cathode ray tube (CRT) monitor using an 8-bit digital-to-analog converter with an ATI Radeon X600 SE graphics card.

Phosphor Persistence

We were careful to ensure that responses in the single-step task were not visual responses to stimulus artifacts. The CRT monitors used in this study have P22 phosphors, which decay to 10% of maximum luminance between 1 and 6 ms (Elze 2010a, 2010b; Wittenberg et al. 2008). To confirm that this rapid decay occurs in our experiments, we separately measured the average response of a photodiode on 20 trials. Stimulus presentations were sampled at a rate of 1,000 Hz and low-pass Butterworth filtered at 85 Hz. Responses were measured at the center of the monitor with a refresh rate of 85 Hz. Bright white stimuli were presented for four frames (~11.76-ms duration per frame) at maximal phosphor excitation (each 8-bit gun set to maximum value, 63.15 cd/m²). Baseline background response when no stimulus was presented was <0.01 cd/m². After a stimulus was presented, phosphor excitation decayed rapidly and differed from background by <0.01 cd/m² at about 100 ms after stimulus offset.

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Fig. 1. Task design. A: fixation task. After fixation is attained, 1–4 nonrepeating shapes were presented sequentially in the receptive field (RF). Shapes were presented for 50 ms with an interstimulus interval of 350 ms. B: single-step task. The monkey maintains fixation for 300–500 ms. The fixation point (FP) is then extinguished and a new fixation point appears (FP2). Simultaneously, a stimulus is briefly flashed in the future field (FF) for 50 ms. FF is the screen location that will occupy the neuron’s RF once the saccade is completed. Offset of the initial FP cues the monkey to make a saccade to FP2. The monkey maintains gaze at FP2 for an additional 500–700 ms. C: stimulus control task. During fixation, a spot is briefly flashed (50 ms) at the FF location. The monkey continues to maintain fixation for an additional 1,200–1,500 ms. D: saccade control task. The trial begins when the monkey attains central fixation. After 300–500 ms, FP is extinguished and a new fixation point (FP2) appears. The monkey makes a saccade to FP2 and maintains fixation for 300–500 ms. No stimulus appears during the trial. E: a set of 8 stimuli were used to test for shape selectivity in fixation and single-step tasks. Each shape fit into a 2.2° square. Each shape had 180 white pixels and 220 black pixels (contrast inverted in image).
Physiological Methods

Recording sessions were conducted in a darkened room with minimal background illumination. The monkey sat with its head fixed in a primate chair, facing a CRT monitor on which stimuli were presented. Stimulus presentation was under the control of two computers running a C-based program (CORTEX). Eye position was monitored using scleral search coils (Judge et al. 1980), with a sampling rate of 250 Hz.

Neural activity was recorded using tungsten microelectrodes (FHC, Bowdoinham, ME) inserted into cortex through stainless steel guide tubes that were stabilized in a nylon grid system (Crist Instrument, Hagerstown, MD). The neural signal was amplified and filtered with a bandpass of 500 Hz to 5 kHz. Individual neurons were isolated with an on-line spike-sorting system using both on-line and off-line template matching and principal component analysis sorting (Plexon, Dallas, TX).

Identification of Saccades

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 latency was defined as the difference between the time when the initial fixation point was extinguished and the onset of the saccade. 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 area LIP. In initial recording sessions, we systematically recorded from the anterior-most to the posterior-most part of the chamber. 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 with a Q-tip 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 postaccaodic firing (Barash et al. 1991a, 1991b). Area VIP is located in the fundus of the sulcus, and neurons 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. Recording sites extended from 2 to 6 mm deep.

Behavioral Paradigms

Neural activity was recorded while the monkey performed five tasks run in separate blocks.

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 (FP). After a random delay of 300–500 ms, a spot flashed in the RF for 50 ms. After a second delay of 400–800 ms, the FP was extinguished, which cued the monkey to make a saccade to the remembered 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 (Barash et al. 1991b; Colby et al. 1996; Zhang and Barash 2000). To do this, we placed stimuli at one of 24 locations arranged in three concentric rings. We identified the peak of the RF as the location that elicited the maximum visual response. We confirmed that the location elicited a robust visual response by applying standard statistical measures (t-test, P < 0.05) to assess whether visual activity was significantly elevated compared with baseline.

Fixation task. The fixation task was used to assess whether neurons were selective for shape when the monkeys were simply fixing (Fig. 1A). The task was designed so that stimulus shape was not relevant for accurate behavior. The monkey’s only task was to maintain fixation at a central point outside the RF. We used a task design adapted from Dunn and Colby (2010). In each trial, one to four nonrepeating stimulus shapes were presented sequentially in the RF. This design enabled us to collect more trials per shape than if only a single stimulus was presented on each trial. Each stimulus was presented for 50 ms, followed by an interstimulus interval of 350 ms to allow activity to return to baseline. The trial ended with extinction of the FP. The monkey was rewarded for successfully maintaining fixation throughout the trial. The monkey performed this task until each shape had been presented at least 12 times.

Single-step task. The single-step task was used to assess remapping and shape selectivity during remapping (Fig. 1B). The trial began when the monkey attained fixation. The monkey maintained fixation on the initial FP for 300–500 ms. Three events then occurred simultaneously: a stimulus appeared outside the neuron’s RF for 50 ms, the initial FP was extinguished, and a new fixation point (FP2) was illuminated. Offset of the initial FP was the monkey’s cue to make a visually guided saccade to the FP2. The stimulus was flashed at the location that would become the peak of the neuron’s RF after the saccade. We refer to this location as the future field (FF). The monkey maintained its gaze on FP2 for an additional 500–700 ms. In each trial, one of eight stimulus shapes was randomly chosen and presented in the FF. The monkey performed the single-step task until 12 trials had been correctly performed for each of the 8 shapes. As in the fixation task, the monkey was not required to pay attention to the stimulus to perform the task.

Stimulus control task. The stimulus control task was used to ensure that the location of the flashed stimulus lay outside the initial RF (Fig. 1C). In this task, the monkey maintained fixation for 300–500 ms. A spot was flashed for 50 ms at the same location to be used in the single-step task. The monkey was required to maintain fixation for an additional 1,200–1,500 ms. The task was run until 12 correct trials had been performed for each shape stimulus.

Saccade control task. This task was used to measure activity related to the generation of the saccade itself (Fig. 1D). The design of the task was the same as for the single-step task, except that no peripheral stimulus was presented. The monkey maintained fixation for 300–500 ms when the initial FP was extinguished, and the onset of the saccade. Trials in which the saccade latency was <100 ms and the remapping latency was >150 ms. In this study, average saccade latency was 194 ms and average remapping latency was 104 ms. We conclude that neural activity in the single-step task is a genuine remapped response and not a response to phosphor persistence.

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ms, after which the initial FP was extinguished and a new fixation point (FP2) was illuminated. After making a saccade, the monkey was required to maintain fixation for 500–700 ms. The task was run until 12 correct trials had been performed.

Data Analysis

Identification of remapping LIP neurons. For a neuron to be considered as remapping, three conditions have to be satisfied: 1) activity must not be a visual response to the stimulus alone, 2) activity must not be due to the saccade itself, and 3) activity must be elicited by the conjunction of the stimulus in the FF and the saccade. We describe below the procedure used to identify neurons that satisfied each of the above three conditions.

ACTIVITY DUE TO THE STIMULUS ALONE. We used the stimulus control task to determine whether a neuron was visually responsive to the stimulus in the FF location. We calculated baseline activity in a 200-ms epoch from 150 to 350 ms after fixation attainment. We assessed whether activity in the visual epoch (50–200 ms after onset of stimulus) was greater than the baseline epoch (t-test, P < 0.05).

ACTIVITY DUE TO THE SACCADE ALONE. We used the saccade control task to determine whether the saccade itself caused activity. We calculated baseline activity in a 200-ms epoch from 150 to 350 ms after fixation attainment. We compared activity in an epoch from −100 to +100 ms relative to the onset of the saccade to baseline activity (t-test, P < 0.05). Neurons that had significant activity in the saccade control task were excluded from further analysis.

ACTIVITY IN THE SINGLE-STEP TASK. For neurons that did not respond in either control task, we asked whether there was significant activity in the single-step task. Remapping occurs at a variety of times relative to the saccade (Duhamel et al. 1992; Kusunoki and Goldberg 2003). For each neuron, we had to choose an appropriate window for measuring remapping activity. For this, we used a two-stage Poisson detection method (Bisley et al. 2004; Maunsell and Gibson 1992).

In the first stage, we calculated a baseline measure from the saccade control task. We created peristimulus time histograms (10-ms bins) of activity from 100 ms before saccade onset to 500 ms after saccade onset. We found a Poisson distribution that best fit the baseline data. We used the resulting Poisson distribution to determine a threshold. We defined threshold as the level below which spike counts could be expected to lie 99% of the time.

In the second stage, we asked when activity in the single-step task exceeded threshold activity in the saccade control task. For this, we measured activity in the single-step task collapsed across all 8 shapes in an epoch from 100 ms before saccade onset until 500 ms after saccade onset. We calculated firing rate in 10-ms bins shifted every 5 ms. For each bin, we determined whether activity was greater than threshold. We defined remapping latency as the start of the first five consecutive bins that contained firing rates above threshold. The window for measuring remapping activity was a 200-ms epoch aligned on the remapping latency for each neuron.

Once we had selected an appropriate window, we were able to test whether activity in the remapping window was greater than that during the saccade control condition. We measured activity in the remapping window for each of the eight shapes. We compared this activity to that in a 200-ms window aligned at the same time in the saccade control task. We used an ANOVA with Bonferroni correction for multiple comparisons (P < 0.05) to test for significant differences between the remapping epoch and the saccade control epoch. We classified the neuron as remapping if the response in the single-step task was significantly different from saccade control for at least one stimulus shape.

Identification of neurons selective for shape during remapping. For neurons that remapped, we computed responses to each of the 8 shapes during a 200-ms window aligned on the remapping latency of that neuron. We performed a one-way ANOVA (P < 0.05) to determine whether there were significant differences between responses to the eight shapes.

Measurement of visual activity in the fixation task. In the design of the fixation task, one to four stimuli could be presented in a single trial. Instead of measuring baseline activity once at the beginning of the trial, we used a procedure adapted from Dunn and Colby (2010) to avoid a potential confound. This confound would occur if a stimulus evoked a burst of activity that gradually declined but did not reach the original single baseline before the next stimulus was flashed. In this case, the difference from prestimulus baseline would be significant. However, the activity would be due to the lingering response to the previous stimulus and not necessarily due to the current stimulus.

To avoid this confound, we used a three-stage procedure to determine visual activity. In the first stage, we chose as baseline epoch a 100-ms window beginning 50 ms before each stimulus appeared. Because one to four stimuli could be presented in a single trial, each trial could have up to four baseline epochs. We calculated baseline as the average activity across these baseline epochs in all trials. In doing so, we eliminated the possibility of a spurious result due to a sustained response.

In the second stage, we determined visual latency for each neuron using the same Poisson detection procedure described previously. Briefly, we quantified threshold activity using baseline activity. We measured responses collapsed across all 8 shapes from 0 to 400 ms after stimulus presentation. We calculated firing rate in 10-ms bins shifted every 5 ms. We defined visual latency as the start of the first five consecutive bins that contained firing rates above threshold.

In the third and final stage, we determined whether there was a significant visual response. We compared responses to each of the 8 shapes in the 200 ms window aligned on the neuron’s visual latency to activity obtained in the baseline epoch. We used an ANOVA with Bonferroni correction (P < 0.05) to test for significant differences between the visual epoch and the baseline epoch.

Identification of neurons selective for shape during fixation. To determine whether a neuron showed shape selectivity during fixation, we performed a two-way ANOVA on the responses for the 8 shapes calculated in the 200 ms window aligned on the visual latency. We used shape (8 levels) and order within trial (4 levels) as factors. We included order within trial as one of the factors to avoid a spurious suggestion of shape selectivity due to repetition suppression or enhancement.

Characterizing selectivity profile of a neuron. For each neuron, we characterized shape selectivity in the fixation and single-step tasks using two indexes: selectivity index (SI) and depth of selectivity (DOS). The first measure is indicative of the difference in responses to the most preferred and least preferred shape and has been widely used in the literature, including previous LIP studies on shape selectivity (Sereno and Amador 2006; Sereno and Maunsell 1998). The second measure is a more fine-grained measure and is indicative of the depth of tuning to the eight shapes within the stimulus set.

SELECTIVITY INDEX. We defined the SI as 

\[
SI = \frac{R_{\text{most}} - R_{\text{least}}}{R_{\text{most}} + R_{\text{least}}},
\]

where \( R_{\text{most}} \) is the response to the most preferred shape and \( R_{\text{least}} \) is the response to the least preferred shape. The SI ranges from 0 to 1 with values closer to 0 indicating no selectivity and values closer to 1 indicating strong selectivity. When the entire data set is used to select most preferred and least preferred shape and the same data set is used to calculate SI, the procedure will necessarily result in a value greater than 0. This could erroneously indicate strong selectivity. To avoid this circularity, we estimated the selectivity index using the split-half method. We used responses in one half of the trials to assign the shapes to which the neuron showed highest and lowest activity. We used responses in the other half of the trials to measure activity to the assigned shapes and calculate the selectivity index. This grouping method also ensured that the data used to select most preferred and least preferred and the data used to calculate SI had equal statistical power. For a genuinely selective neuron, most and
least preferred shapes will be consistent across trials. Resulting index values will be largely resistant to the group being used for most preferred/least preferred assignment. In contrast, for nonselective neurons, the most preferred shape will be different in each trial solely due to random variations. Occasionally, when assignment of most preferred and least preferred is made using one half and SI is calculated using responses to those assigned shapes in the second half, a negative value can be obtained. Because a different shape is randomly preferred in each trial, the most preferred and least preferred shapes may be different in each of the data halves and could sometimes reverse.

DEPTCH OF SELECTIVITY INDEX. The DOS describes the overall tuning to all eight shapes (Rainer et al. 1998; Rainer and Miller 2000). We defined DOS as \[
\frac{n}{H(1 - R_{\text{most}})} = \left(\frac{\sum R_i}{n} - \frac{1}{n}\right) \left(\frac{R_i}{R_{\text{most}}} - 1\right)
\] where \(n\) is the number of shapes (8 in this study), \(R_i\) is the response to each shape, and \(R_{\text{most}}\) is the response to the most preferred shape. DOS ranges from 0 to 1 with values closer to 0 indicating broad tuning and values closer to 1 indicating sharp tuning. To estimate the reliability of our procedures we used a split-half method. We computed DOS indexes separately for the odd- and even-numbered trials. We then correlated the DOS across neurons. We corrected for the correlation measure obtained by computing the Spearman-Brown split-half coefficient (Lord and Novick 1968). The coefficient is obtained by calculating 
\[r_{sb} = \frac{1}{2} \left(\frac{\text{Spearman-Brown coefficient}}{\text{Spearman-Brown coefficient}}\right)
\] where \(r_{sb}\) is the corrected split-half reliability coefficient and \(r_{xy}\) is the correlation between DOS indexes for the odd and even repetitions.

RESULTS
The goal of these experiments was to determine whether LIP neurons encode and remap information about stimulus shape. We recorded from 117 neurons that had visual activity in a memory-guided saccade task (\(t\)-test, \(P < 0.05\)). Of these, 82 neurons had significant remapping activity in the single-step task (ANOVA, \(P < 0.05\) compared with saccade control task). We performed all our analyses on the 82 remapping neurons.

Response in Fixation Task

**Individual LIP neurons are selective for shape during fixation.** We first asked whether LIP neurons are selective for shape. In the fixation task, between one and four different shapes per trial were presented sequentially in the RF while the monkey maintained fixation (Fig. 1A). The response of many neurons depended on the shape of the stimulus (ANOVA, \(P < 0.05\), 28 of 82, 34%).

Visual activity of two LIP neurons is shown in Fig. 2. Visual responses to each of the eight shapes in the fixation task are plotted as rasters and histograms aligned on stimulus onset. Activity was measured during a 200-ms epoch aligned on the beginning of the visual response. The neuron in Fig. 2A responds most strongly to the square and least strongly to the inverted Y. The neuron in Fig. 2B responds most strongly to the left oblique bar and least strongly to the right oblique bar. To determine whether these neurons were truly shape selective, we submitted their responses to a two-way ANOVA. Because more than one shape could appear within a single trial, we included both shape and order within trial as factors. In this way, we were able to determine whether differences in activity...
arose from stimulus shape or from repetition suppression or enhancement. The neuron in Fig. 2A had a main effect of shape (ANOVA, $P = 1.51e^{-10}$) but no main effect of or interaction with order within trial. Similarly, the neuron in Fig. 2B has a main effect of shape (ANOVA, $P = 0.0002$) but no main effect of or interaction with order within trial. We categorized such neurons as shape selective. In most of the recording sessions for the second monkey, only one stimulus was presented in a given trial. There was no difference between the proportions of shape-selective neurons in the second monkey compared with the first ($P = 0.0699$, $\chi^2$ test).

LIP neurons showed impressive shape-selective responses even though we used a limited and arbitrary stimulus set. The proportion of shape selectivity is greater than that expected by chance ($\chi^2$ test at 10% chance, $P < 0.0001$).

Strength of shape-selective responses during fixation. Twenty-eight of 82 neurons (34%) were classified as significantly shape selective using ANOVA. For each neuron ($n = 82$), we also computed two measures of shape selectivity. The first measure is the SI, a normalized score indicative of the difference in response to the most preferred and least preferred shapes. Scores closer to 1 indicate preference for a single shape, and scores closer to 0 indicate no preference for shape. We used a split-half method to measure SI (see Methods). Briefly, one half of the data from a neuron were used to select the most preferred and least preferred stimulus. Responses to the selected shapes were then measured using the remaining half of the data, and SI was calculated. The SI of the neuron in Fig. 2A was 0.47. The SI of the neuron in Fig. 2B was 0.25.

SI of all selective neurons is plotted in Fig. 3A. Despite being significantly selective according to ANOVA, a few cells have a low SI value. This may be due to the stimulus set being nonoptimal for that particular cell’s selectivity profile. As control, we also calculated and plotted SI of all nonselective neurons. If a neuron is not truly selective, it may respond slightly more to a different shape on each trial due to trial-to-trial variability. Therefore, the split-half procedure may occasionally yield a negative SI (see Methods). As can be seen in Fig. 3A, many neurons that were nonselective according to the ANOVA have a negative value. Plotting SI values of selective as well as nonselective cells reveals a prominent rightward shift in the distribution of selective neurons (median SI = 0.22) compared with that of nonselective neurons (median SI = 0.04) ($P < 7.33e^{-5}$, Wilcoxon rank sum test). This shift also assured us of the validity of our classification procedures.

We used a second measure to quantify shape selectivity in more detail. DOS is a more sensitive measure of shape selectivity because it takes into account the responses to all eight shapes. It is indicative of the depth of tuning within the stimulus set. Values closer to 0 denote neurons that respond to all shapes equally, whereas values closer to 1 denote neurons that respond to only one shape. The DOS of the neuron in Fig. 2A was 0.55. The DOS of the neuron in Fig. 2B was 0.38. Distribution of DOS values of all neurons is plotted in Fig. 3B. The Spearman-Brown split-half reliability coefficient was 0.77 and assured us of the consistency of our calculations. A similar rightward shift in the distribution of selective neurons (median DOS = 0.30) compared with that of nonselective neurons (median DOS = 0.18) was observed ($P < 0.00023$, Wilcoxon rank sum test).

The difference between responses of selective and nonselective neurons is illustrated in Fig. 3C. For each neuron, we used the data set for calculating DOS to obtain order of shape preference. One half of the data were used to calculate shape preference from most preferred (rank 1) to least preferred (rank 8). We used the other half of the data to measure responses to each of those shapes. In Fig. 3C, averaged, ranked, normalized responses for neurons categorized as selective according to ANOVA ($n = 28$) are plotted separately from average ranked responses of neurons categorized as nonselective according to ANOVA ($n = 54$). As can be expected, for selective neurons, the heights of the bars fall sharply from rank 1 to rank 8 (Fig. 3C, black bars). This observation also confirms that the order of preference in one half of the trials is consistent with the order of preference in the other half of the trials, thereby reflecting genuine selectivity. In contrast, for nonselective neurons, the heights of the bars are flatter across rank, indicating lack of selectivity (Fig. 3C, gray bars). The exact distance between each of the shapes in feature space is not known. Consequently, we did not attempt to fit curves to response profiles.

In the population of LIP neurons, there was no consistent preference for any one shape over another (Kruskal-Wallis test, $P > 0.05$). We verified and confirmed results of previous

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Fig. 3. Population measures of strength of selectivity in fixation task. In A–C, gray bars represent values and responses of nonselective cells, and black bars represent values and responses of selective cells. A: selectivity index (SI) values. B: depth of selectivity (DOS) index values. Gray arrowheads indicate median index of nonselective neurons; black arrowheads indicate median index of selective neurons. C: for each neuron, responses to each shape from each task were divided by the response to the most preferred shape in that task. Normalized responses are plotted as a function of rank.
studies that demonstrated shape selectivity in LIP (Sereno and Maunsell 1998). We conclude that shape information is automatically encoded in LIP. We extended these results and showed that shape selectivity is an inherent property of LIP neurons by using monkeys with no previous task experience with stimulus shape.

Response in Single-Step Task

Many LIP neurons had remapping activity that significantly depended on stimulus shape (ANOVA, $P < 0.05$, 31 of 82, 38% of all remapping neurons). As in the fixation task, many neurons were shape selective in the single-step task even though we used a limited and arbitrary stimulus set. There was no difference between the proportions of shape selective neurons in the second monkey compared with the first ($P = 0.0762$, 2 test). The proportion of shape selectivity is greater than that expected by chance ($2$ test at 10% chance, $P < 0.0001$). Some neurons were shape selective in both the fixation and single-step tasks. A summary of these neuron classes is presented in Table 1. Below, we present detailed analysis of shape selectivity in the remapping condition.

Individual LIP neurons show shape selectivity during remapping. For each of the 82 neurons, we asked whether it was capable of remapping information about shape. In the single-step task, a stimulus is briefly flashed outside the RF of the neuron (Fig. 1B). At the same time, a new fixation point appears (FP2). When the monkey saccades to the new fixation point, the RF moves onto the screen location where the stimulus had previously appeared (FF). A typical remapping neuron is shown in Fig. 4. Responses to each of the eight shapes in the single-step task are plotted in rasters and histograms aligned on saccade onset (Fig. 4A). The stimulus was turned off $\sim 194$ ms (SD 47 ms) before the saccade began. Although the stimulus was extinguished long before the saccade, this neuron had a strong response that lasted several hundred milliseconds around the time of the saccade. This response was absent in the two control conditions. The neuron did not respond when a stimulus was presented but no saccade was made (Fig. 4B). Likewise, the neuron did not respond when a saccade was made but no stimulus appeared in the FF (Fig. 4C). The combination of a stimulus in the FF and a specific eye movement is required for the neuron to remap (Fig. 4A).

Our main question was whether the strength of remapping is related to stimulus shape. We approached this question by manipulating the shape of the flashed stimulus from trial to trial. Remapping activity was measured in a 200-ms epoch

<table>
<thead>
<tr>
<th>Task</th>
<th>Selective</th>
<th>Nonselective</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single step</td>
<td>11</td>
<td>20</td>
</tr>
<tr>
<td>Nonselective</td>
<td>17</td>
<td>34</td>
</tr>
</tbody>
</table>

Table 1. Number of neurons selective for shape in each task

Fig. 4. Response of a shape-selective neuron in the single-step task. Histograms are plotted in 10-ms bins and are aligned on saccade onset (A and C) or stimulus onset (B). A: responses to each of the 8 shapes in the single-step task. A 200-ms epoch aligned on the beginning of remapped response (outlined box) was used to measure average firing rate. For the neuron shown, stimulus was turned off $\sim 194$ ms (SD 47 ms) before saccade onset. B: response in the stimulus control task when the stimulus was presented in the future field but no saccade was made. C: response in the saccade control task when no stimulus was presented in the future field. D: tuning of shape selectivity during remapping. Responses are ranked from most preferred (rank 1) to least preferred (rank 8).
aligned on the beginning of the remapped response. The response of the LIP neuron in Fig. 4A was significantly modulated by stimulus shape (ANOVA, $P = 0.0006$). The neuron fired most strongly to the right oblique bar (113 spikes/s). In contrast, the neuron fired only half as much to the inverted Y (54 spikes/s). This shape selective activity was present even for the brief stimulus duration of 50 ms. Remapped responses to shapes were ranked from highest to lowest, in order of preference (Fig. 4D). The decline in the height of the bars further illustrates that this neuron had a remapped response that depended on the shape of the stimulus. The response of a second shape-selective remapping neuron is plotted in Fig. 5 (ANOVA, $P = 0.00003$). The remapped response of this neuron was strongest for the triangle and weakest for the square. As can be seen in Fig. 5D, the response of the neuron is far lower for nonpreferred shapes than preferred shapes.

Strength of shape-selective remapped responses. We used the same procedures to analyze selectivity in the single-step task as we used in the fixation task. Neurons were first classified as selective or nonselective using ANOVA. For each neuron, we then computed two measures of shape selectivity, the SI and DOS. The SI of the neuron in Fig. 4 was 0.32. The SI of the neuron in Fig. 5 was 0.57. DOS values of all remapping neurons were calculated using the split-half procedure (Fig. 6A). The prominent rightward shift in the distribution of selective neurons (median SI = 0.24) compared with that of nonselective neurons (median SI = 0.03) assured us of

**Single Step Task**

![Graphs showing single step task](image)

Fig. 6. Population measures of strength of selectivity in single-step task. Conventions are the same as in Fig. 3.

![Graphs showing remapped responses](image)

Fig. 5. Response of a shape-selective neuron in the single-step task. Conventions are the same as in Fig. 4. For the neuron shown, stimulus was turned off $\sim 262$ ms (SD 47 ms) before saccade onset.
the validity of our classification procedures \( (P < 6.43 \times 10^{-7}) \), Wilcoxon rank sum test).

For each neuron, we also calculated its DOS, which takes into account responses to all eight shapes. The DOS of the neuron in Fig. 4 was 0.43. The DOS of the neuron in Fig. 5 was 0.55. The distribution of DOS values of all remapping neurons is plotted in Fig. 6B. The Spearman-Brown split-half reliability coefficient was 0.80. A similar rightward shift in the distribution of selective neurons (median DOS = 0.32) compared with that of nonselective neurons (median DOS = 0.17) was observed \( (P < 4.65 \times 10^{-7}) \), Wilcoxon rank sum test.

The difference in responses of selective neurons compared with nonselective neurons is illustrated in Fig. 6C. For selective neurons, bar height falls sharply from the most preferred shape (rank 1) to least preferred shape (rank 8; Fig. 6C, black bars). The height of the bars remains flat for ranked responses of nonselective neurons (Fig. 6C, gray bars).

On average, saccades began between 150 and 270 ms after the stimulus had been extinguished. For all 82 neurons, the stimulus was extinguished well before the saccade brought the new location into the RF. In addition, the monkeys were not required to pay attention to the stimulus, or more specifically, to its shape. Over 37% of neurons (31 of 82) showed selectivity for shape. To our knowledge, these are the first single-unit studies to show selectivity for shape during the remapping task.

Relation Between Shape Selectivity in Visual and Remapped Responses

We asked whether shape selectivity was comparable in the two tasks. Similar proportions of neurons were selective for shape in the fixation and single step tasks (Table 1). Selectivity in the population is illustrated in Fig. 7. Neuronal responses to the most preferred shape in each task were binned in 10-ms intervals. Peak firing rate was identified as the 10-ms bin that contained the highest firing rate. Binned responses were normalized by dividing by peak firing rate. A grand average of all neurons’ normalized responses was obtained and plotted with a smoothing filter. This procedure was repeated for the least preferred shape for each neuron, and binned responses were divided by peak firing rate to the most preferred shape. Population responses to most preferred and least preferred shapes are plotted in Fig. 7.

For shape-selective neurons, averaged responses differ for most preferred and least preferred shapes (Fig. 7A, fixation; Fig. 7B, single step). When responses from all neurons are averaged, this difference is reduced (Fig. 7C, fixation; Fig. 7D, single step). These data indicate that shape information is likely encoded by a subset of LIP neurons.

How do shape selectivity in the visual and remapped responses of single neurons compare? Some neurons were selective in both tasks (11 of 82, 13%). Visual activity in the fixation task and remapping activity in the single-step task for one sample neuron are shown in Fig. 8. The neuron was selective for shape in both the fixation (Fig. 8, top; 2-way ANOVA, main effect of shape, \( P = 3.56 \times 10^{-3} \)) and the single-step tasks (Fig. 8, bottom; ANOVA, \( P = 1.8 \times 10^{-8} \)). In the fixation task, this neuron had an SI of 0.21 and a DOS of 0.30. In the single-step task, the neuron had an SI of 0.29 and a DOS of 0.33. In both tasks, the neuron preferred the same shape, the circle. Although the least preferred shapes are different in the two tasks, the responses are so diminished as to be statistically indistinguishable. When responses to all eight shapes are compared across both tasks for this neuron, a strong and significant correlation is revealed (Pearson’s \( r = 0.82, P = 0.01 \)).

Single-neuron-level relation between shape selectivity in visual and remapped responses. At the single-neuron level, we first focused our analysis on neurons that were shape selective in both tasks (\( n = 11 \)). We used a procedure similar to that described by Peng et al. (2008) to determine whether individual neurons were selective for the same shapes in each task. For each neuron, we selected the two most preferred shapes and one least preferred shape in the single step. Only one least preferred shape was chosen since signal strength for nonpreferred shapes are expected to be statistically indistinguishable. We then compared the responses to those same shapes in the fixation task. The question is whether, for these three shapes, shape preference was conserved across tasks. For 7 of the 11 dual-selective neurons, the two shapes that were more preferred in the single-step task compared with the third shape were also more preferred in the fixation task. These results suggested that there is at least some correspondence in shape preference between tasks.
Next, we compared shape preference across all eight shapes. This time, we included data from all 82 remapping neurons regardless of shape selectivity. For each neuron, we performed a correlation analysis to compare shape selectivity in the two tasks. For 52 of the 82 neurons, there was a positive correlation. The correlation was significant in 10 of those neurons (Pearson’s $r$, $P < 0.05$). No neuron in the population had a statistically significant negative correlation. The summary of the various neuron classes to which these 10 neurons belong is shown in Table 2 along with the range of correlation values.

Five neurons belong to the neuron classes that were selective in both conditions. Three neurons, including the neuron in Fig. 8, also had the same most preferred shape in both tasks. We used a standard but limited stimulus set that may have been nonoptimal for most neurons. Therefore, we extended our analysis to the population because of the increased statistical power available.

**Population-level comparison of shape preference.** We first focused our analysis on the subset of neurons that were selective in both tasks (11 of 82, 13%). For each neuron, we first computed the mean firing rate across all eight shapes in a particular task (fixation or single step). Responses were normalized by dividing the firing rate by the response to the most preferred shape in that task. We followed this procedure for both tasks. For each neuron, we calculated a pair of normalized responses to each shape in the two tasks. By this method, each neuron yields eight pairs of responses corresponding to the eight shapes. We plotted these pairs of responses for all the neurons that were selective in both tasks and computed correlation values. We found a significant positive correlation (Fig. 9A, $n = 11$, Pearson’s $r = 0.57$, $P = 7.72e^{-9}$). We repeated this analysis on the entire remapping population regardless of selectivity. We found a weaker but significant correlation (Fig. 9B, $n = 82$, Pearson’s $r = 0.26$, $P = 9.27e^{-12}$).

We followed this analysis with a robust regression that used iteratively reweighted least squares. This method is sensitive to outliers and yielded similar results. A significant positive correlation was found when we compared the cells selective in both tasks ($n = 11$, correlation estimate = 0.65, $P = 5.22e^{-9}$). When we performed the analysis on normalized responses for all the cells ($n = 82$), we obtained a correlation estimate of 0.28 ($P = 7.1e^{-15}$).

**Table 2. Neurons with significant correlation in responses between tasks**

<table>
<thead>
<tr>
<th>Cell Class</th>
<th>Selective</th>
<th>Nonselective</th>
</tr>
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<tbody>
<tr>
<td>Single step</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Selective</td>
<td>5 [0.71–0.85]</td>
<td>1 [0.82]</td>
</tr>
<tr>
<td>Nonselective</td>
<td>2 [0.80–0.82]</td>
<td>2 [0.69–0.96]</td>
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Data show the subset of cells in each cell class (see Table 1) that also had significant correlation in responses to shape between the two tasks. Values in parentheses indicate the range of correlation values (Pearson’s $r$).
As an additional measure, we performed a bootstrap analysis by resampling the normalized responses of neurons 1,000 times and computing correlation values. We calculated a confidence interval for the resulting distribution of correlation values. For the subset of neurons that were selective in both tasks (n = 11), a confidence interval of 0.37–0.71 was obtained. The confidence interval for distribution of correlation values of all neurons (n = 82) regardless of selectivity was 0.17–0.35. The results of the bootstrap analysis agreed with the results illustrated in Fig. 9. We found significant correlation between preferences for shape in the two tasks irrespective of methodology. For the limited stimulus set used in this study, we conclude that shape preferences in the two tasks are comparable at the population level.

**Population-level comparison of strength of selectivity.** In the final set of analyses, we asked whether the strength of selectivity as measured by the SI and DOS were comparable between the two tasks. We plotted the index in the single-step task as a function of the corresponding index in the fixation task. We found a strong correlation between SI when we compared neurons selective in both tasks (Fig. 10A; Pearson’s r = 0.70, P < 0.05). This result indicates that the strength of selectivity in the two tasks is related. This was true when we compared DOS indexes, as well (Fig. 10C; Pearson’s r = 0.81, P < 0.01). When we compared indexes of all neurons regardless of selectivity, a significant but weaker correlation was found (Fig. 10, B and D; Pearson’s r for SI = 0.24, P < 0.05; Pearson’s r for DOS = 0.40, P < 0.01). Correlation between strength of selectivity in the two tasks was found irrespective of index used. We conclude that at the level of the population, both preferences for shape as well as strength of selectivity are related in the two tasks.

**DISCUSSION**

Our primary question was whether remapping is sensitive to stimulus shape. Psychophysical evidence has suggested that it may be (Prime et al. 2006, 2007). There have been no previous single-unit studies on this topic. Our main finding is that shape sensitivity does exist for a subpopulation of LIP neurons that remap (31 of 82, 37% of remapping neurons). We were inspired in this set of experiments by the original observations of Sereno and Maunsell (1998), who found that 57% of LIP neurons were shape selective during a fixation task. Using the same stimuli that they used, we tested whether LIP encodes and remaps shape information. Two experimentally naïve monkeys were trained to perform fixation and single-step tasks in which stimulus shape was irrelevant for behavior. LIP neurons were recorded while the monkeys performed these tasks. We showed that shape selectivity is automatic in LIP, in the sense that the animals had never been trained to use shape information. In addition to encoding shape information in the fixation task (28 of 82 neurons, 34%), we also showed that remapped responses contain shape information (31 of 82 neurons, 37%).

Remapping is one of the mechanisms that contributes to visual stability (Berman and Colby 2009; Sommer and Wurtz 2002, 2008). Considerable progress has been made in identifying the underlying structures and mechanisms that produce remapping (Hall and Colby 2011). As yet, the actual content of the remapped signal remains to be thoroughly determined.
In this study, we showed that remapping neurons are selective for shape. The functional significance of these observations requires further study. Parietal cortex has primarily spatial and attentional functions. It remains an open question how shape information might contribute to these functions.

When we compared selectivity between the two tasks, they did not necessarily match at the single-cell level. This is not the first observation of noncorrespondence in shape selectivity. In a frontal eye field study where cells were tested for object selectivity in a fixation task and a delay match to sample task (DMTS), only 5 of 65 neurons had selectivity in both tasks (Peng et al. 2008). When only most and least preferred shapes in the two tasks were compared, selectivity seemed largely consistent, but when the order of preference across the range of shapes was compared, the correspondence was far less consistent. In the present study, 7 of 11 cells were comparable in their most and least preferred shapes between tasks. Five of those neurons were significantly correlated between tasks in their order of preference. Finally, three of those five had the same most preferred shape in both tasks. There are at least three possible reasons for this apparently weak correspondence.

One reason could be the limited stimulus set. We used the same eight stimuli previously used to test LIP for shape selectivity. Any limited stimulus set may be nonoptimal for most neurons. We cannot know the actual percentage of LIP neurons that are shape selective. While there is a prevalence of shape selective neurons in the fixation task and the single step task, it may be premature to impute any functional meaning to the presence or absence of comparable selectivity across different tasks.

A second reason could be the mechanism of remapping. The essential mechanism of how stimulus information is maintained between cell populations remains to be investigated. One view, the shifting receptive field view, postulates that the neuron changes its RF through some type of dynamic gating mechanism. If this were true, then it could be expected that the neuron maintains its selectivity profile across a saccade. However, a mechanism for how a neuron can dynamically change its RF remains to be elucidated. An alternate view is that information is transferred from one population of neurons to another. If this were the case, then activity recorded from a neuron in the remapping task is the “reflection” of activity in a different population of neurons (which may have different shape selectivity). This leads to a deeper question of whether neurons of similar selectivity are connected. Both views would produce the same “remapping burst of activity” but have very different implications for what shape selectivity corresponds to. Conclusive evidence for either or a combination of the two remapping mechanisms is still to be found. The evidence is likely important in understanding the functional significance of shape-selective remapped responses.

A third, related reason for noncorrespondence at the single-neuron level could be the mechanism of shape information encoding. It is not clear whether shape information is encoded locally in LIP or whether it arises from other brain areas and is transmitted to LIP.

We set out to determine whether remapping is sensitive to stimulus shape and found that it is in more than one-third of LIP neurons. Further studies are needed to test whether shape selectivity exists in other parts of the dorsal visual stream. Our results indicate that LIP responses contain information about both stimulus location and shape, thereby revealing the sophisticated nature of remapping.

**Representation of Space in LIP**

Visual information is processed by two independent pathways (Ungerleider and Mishkin 1982). The ventral visual pathway mediates object recognition. The dorsal visual pathway, to which LIP belongs, processes information about space and action (Goodale et al. 1991). Information about salient locations is thought to be encoded in a priority map in LIP (Bisley and Goldberg 2010; Kusunoki et al. 2000). In this priority map, neurons that represent relevant locations fire more than other neurons that represent irrelevant locations. The retinal positions of these locations change with every eye movement. Remapping enables the locations of relevant locations to be continuously updated. Remapping has been studied most extensively in LIP. Consistent with the framework of the priority map, remapping signals in LIP are affected by both top-down and bottom-up attention (Gottlieb et al. 1998; Mirpour and Bisley 2012). For instance, when stimuli suddenly appear (bottom-up attention) or if they are relevant for behavior (top-down attention), the amplitude of the remapped response is larger than the response to an irrelevant stimulus. Remapping allows information about salient locations to be maintained across saccades.

**Representation of Features in LIP**

A ground-breaking study by Sereno and Maunsell (1998) showed that LIP neurons also represent feature information. In the simplest of circumstances, when shapes merely appear in the RF, many neurons were found to exhibit shape selectivity. These findings challenged the notion that LIP solely encodes information about which location is salient. If LIP represents information about salient locations as well as objects in those locations, is all this information remapped during saccades?

In this study, we determined that many LIP neurons (37%) show selectivity for shape during remapping. Shape information is automatically present in the remapped responses, even when it is irrelevant for the task. In our study, the stimuli were made salient by their sudden appearance. In addition, the stimuli were carefully controlled for size, area, and brightness. The stimuli were presented equally often and were always irrelevant for task performance. We conclude that remapped responses are shape selective.

In the same neurons, we also evaluated the extent of shape selectivity when the stimuli were presented within the RF (fixation task). Since the initial study by Sereno and Maunsell (1998) that revealed shape selectivity, several studies have replicated and reaffirmed those findings (Janssen et al. 2008; Lehky and Sereno 2007). The monkeys in all these previous studies had also been trained in other tasks in which stimulus shape was relevant. There is evidence, at least in the case of color, that neurons can develop sensitivity as a result of training with tasks in which color is relevant (Toth and Assad 2002). It is interesting to ask whether shape selectivity is present in the absence of task experience with shape. We were able to eliminate training history as contributing to shape selectivity, because we used monkeys that had not been previously trained on any other task. We conclude that shape...
selectivity is inherent in area LIP and that shape information is automatically updated during remapping.

Significance of Shape Representation in LIP

In view of these findings, it is important to address the functional significance of feature selectivity in the dorsal visual stream. Visual and remapped responses of LIP neurons can be enhanced by a variety of task relevant features (Gottlieb et al. 1998, 2009). Neurons are selective for shape when the monkey is performing a match to sample task based on shape (Sereno and Amador 2006). When the match is to be made based on location, shape selectivity is attenuated. LIP neurons are also sensitive to relative arrangements of objects when monkeys are to identify arrangements of a particular orientation (Yokoi and Komatsu 2009). In another instance, monkeys were trained to report the direction of a moving stimulus as belonging to one or two categories along an arbitrary boundary (Freeman and Assad 2006, 2009). Many LIP neurons were found to be selective for directions of one category and not the other.

Previous results indicate that shape selectivity is not only task dependant but also dependant on the timing within a trial. Sensitivity to features changes as the trial progresses. In the delayed match to sample task, a population of LIP neurons showed different degrees of selectivity during different epochs within the task. (Sereno and Amador 2006). The authors suggest that the finding was related to the specific computation needed at that stage of the trial (e.g., memory of sample stimulus, comparison to test stimulus, preparation to make a saccade). In a recent study, monkeys were required to decide the direction of a stimulus and indicate their decision by an eye movement (Bennur and Gold 2011). In the beginning of the trial, during the perception phase, LIP neurons were selective for motion direction. Toward the end of the trial, when monkeys were planning an eye movement, direction selectivity decreased and spatial selectivity emerged. It is evident that neurons have access to feature information and use it in a behaviorally relevant manner.

As we have shown in this study, shape selectivity can be found in the absence of task demands. The same is also true of selectivity for direction of motion (Fanini and Assad 2009). LIP receives inputs from multiple visual regions including ventral visual areas and directionally selective neurons in MT (Blatt et al. 1990; Lewis and Van Essen 2000; Ungerleider and Desimone 1986). It has been suggested that feature selectivity in the absence of task demands may represent inputs from other visual areas (Ferrera and Grinband 2006). These inputs may be dynamically modulated according to the needs of the task.

Transsaccadic Memory for Shapes and Locations

Given that the information encoded in LIP is so elaborate, what happens to it when the eye moves? Ever since the realization that we make multiple eye movements per second, psychophysicists have asked what information is retained from each saccade. Early results suggested that the world is perceived afresh after every saccade (Bridgeman et al. 1975; Irwin et al. 1983). Later studies clarified these findings and indicated that we retain information about salient locations while remaining oblivious to most of the visual scene (Henderson 1994; Irwin 1991; Pollatsek et al. 1984; Rayner 2009). For instance, human subjects show increased speed in identifying an object if the same object had been present before the saccade (Germes et al. 2002; Henderson and Siefert 2001). This speed improvement is greatest when the object continues to occupy the same screen location through the saccade, even when it is the object feature that is to be discriminated. It was apparent that there is some relation between transsaccadic memory of object location and that of object feature.

The link between object location and features in transsaccadic memory has begun to receive more attention (Melcher et al. 2004; Melcher and Morrone 2003). For instance, the time to decide the direction of a moving stimulus is not affected by an intervening eye movement as long as the stimulus occupies the same retinal location or the same screen location. This effect was also found for sensory information that did not involve higher order computations (Melcher 2007, 2008, 2009). Sensory adaptation to tilt stimuli was found to persist across saccades. After the saccade, the adaptation was found both at the original screen location of the adaptor and the screen location corresponding to the retinal location of the adaptor. Moreover, adaptation at this new screen location was found even before the saccade had been completed. These studies suggest that feature information is retinotopically organized and remapped during saccades.

Evidence implicating specific brain regions in transsaccadic memory has come from transcranial magnetic stimulation (TMS) studies (Prime et al. 2007, 2008, 2009). When TMS was applied to human parietal and frontal eye fields around the time of the eye movement, the ability to remember orientations of objects was affected. Monkey analogs of both these regions have a large proportion of remapping neurons.

How might remapping be involved in transsaccadic memory? One view is that a map of attentionally significant locations is updated during each saccade. Once a saccade is completed, feature information can be selectively extracted from these locations (Cavanagh et al. 2010). A map of attentionally significant locations does seem to be remapped during saccades (Rolfs et al. 2011). These authors adapted the classic Posner task in which faster reaction times and improved accuracy for discrimination were found at previously cued locations (Posner 1980). The authors were interested in determining where attentional benefits would be found if a saccade intervened between the cue and probe presentation. They probed screen locations that corresponded to retinal RFs of neurons that would eventually encode the cue location after the saccade. In those locations, compared with equally eccentric but unrelated control locations, attentional benefits were observed. These results provide evidence that a remapped store of attentionally significant locations is used in a behaviorally relevant manner. Recent physiological data provide evidence for the same conclusion (Mirpour and Bisley 2012).

An alternate view is that shape information along with spatial information is remapped during a saccade (Mayo and Sommer 2010; Melcher and Colby 2008). This idea requires evidence that there is remapping of shape information. In this study we show that shape information is remapped in LIP. Our findings indicate that LIP keeps track of both locations and features of salient objects. Memory for object features may be distributed within the LIP population and other brain areas rather than encoded by single neurons.

A growing body of literature suggests that dorsal stream areas have access to shape information and use it according to...
the task at hand. We extend these findings by showing that shape information is also updated during the saccade. Furthermore, shape selectivity itself is an inherent property of LIP neurons and requires no previous training. In light of recent physiological and psychophysical findings, the prevalence of shape-selective remapped responses is striking. Our results provide critical neurophysiological evidence that LIP remaps both spatial and shape information.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.S. and C.L.C. conception and design of research; J.S. performed experiments; J.S. analyzed data; J.S. and C.L.C. interpreted results of experiments; J.S. prepared figures; J.S. drafted manuscript; J.S. and C.L.C. edited and revised manuscript; J.S. and C.L.C. approved final version of manuscript.

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