OBJECT SELECTIVITY IN DORSAL VISUAL STREAM

by

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We scan the visual world by making rapid eye movements (saccades) and serially focusing on objects 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 objects around the time of a saccade. Information about salient objects is transferred from neurons that currently encode their screen locations to other neurons that will encode their locations after the 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 has been increasing evidence that LIP neurons also encode object features.

We sought to determine whether LIP remaps shape information. Such insight is required for understanding what information is retained from each glance and how the visual percept is built (transsaccadic perception). First, we presented shapes in the future location of the receptive field around the time of the saccade and tested for shape selectivity during remapping. Second, we presented the same shapes within the receptive field and tested for shape selectivity in the fixation task. Finally, we compared selectivity in the two tasks. We found that LIP neurons automatically encode and remap shape information. Selectivity in the two tasks was comparable. Our results provide critical evidence for the idea that remapping may be a mechanism for transsaccadic perception of features.

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PREFACE

Acknowledgments

As I reflect on my journey in completing this project, I cannot help but feel extremely fortunate for the kind of support I have had.

I wish to thank my advisor Carol Colby. I joined the lab as a shy girl with little experience. She has been instrumental in teaching me how to approach science and has been immensely patient as I fumbled, learned, and at last, started producing results. Under her guidance I have learnt how to articulate and communicate my thoughts clearly. Carol has been such an extraordinarily compassionate and generous mentor. Without her encouragement, I would have never had the will to make some courageous decisions. I have come to truly enjoy my weekly meetings with her. Her cheerful greeting has the ability to instantly vaporize some of the most stubborn doubts and uncertainties. I always come away feeling surer, braver and a whole lot lighter. I am yet to meet someone with a larger heart.

I would like to thank past and present members of Carol's lab. Nathan Hall taught me the art of performing experiments. From recording to MATLAB coding to maintaining monkeys, he managed to single handedly teach me. I do not think I can ever repay him for his time. I thank Jared Clemens, with whom I performed the early part of these experiments and who was always fun to have around.

1.0   INTRODUCTION

Vision is the chief sense we use to comprehend the world. It has long been recognized that we regard the scene in front of us by making a series of rapid eye movements (saccades) (Yarbus 1967). This enables us to sample critical regions of space at the fovea, where vision is sharpest. These eye movements disrupt and shift the retinal image. Artificially moving the eye produces a noticeable abrupt shift in the visual image. Yet we are oblivious to the shifts caused by internally generated saccades. How we compensate for image disruptions while extracting and retaining visual information across each saccade has been the subject of much investigation.

Early theories suggested that the "effort of will" required to make a saccade activates mechanisms to stabilize the visual image (Helmholtz 1962). Signals that carry information about the intent to make eye movements were considered critical for visual stability. Among these signals are copies of the eye movement commands, referred to as a "corollary discharge" (Sperry 1950) or as an "efference copy" (von Holst and Mittelstaedt 1950). These signals could be used to compensate or update internal representations in conjunction with the actual saccade.

Neurons that participate in spatial updating were first identified in the macaque lateral intraparietal area (LIP) (Duhamel et al. 1992). Neurons in LIP have retinally defined receptive fields (RF). Because the retina moves during a saccade, an LIP neuron will encode a new screen location at the end of the saccade. This new screen location is referred to as the future field (FF) to denote the future location of the receptive field. Duhamel and colleagues briefly flashed a

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stimulus in the future field just prior to the saccade. Many LIP neurons responded robustly, even though the stimulus was outside the actual RF. LIP neurons received information about a previous visual event and updated or remapped the memory trace of that event. In short, during remapping, neurons that encode a salient location transfer information to other neurons that will encode that same location after the saccade (Goldberg and Bruce 1990; Gottlieb et al. 1998; Kusunoki et al. 2000). Remapping may be a general property of visual processing and neurons that remap have also been found in several cortical and subcortical areas (Goldberg and Bruce 1990; Mays and Sparks 1980; Nakamura and Colby 2002; Umeno and Goldberg 1997; Walker et al. 1995).

While remapping is thought to contribute to visual stability, the exact content of the remapped signal is still a mystery. Understanding the content of the remapped signal is crucial to determine 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. But LIP responses are far more detailed than merely indicating occurrence of visual events. Several studies have shown that LIP activity may reflect reward value, uncertainty, attentional priority or behavioral relevance of the stimulus (Andersen et al. 1997; Bisley and Goldberg 2010; 2003; Leon and Shadlen 2003; Platt and Glimcher 1999; Shadlen and Newsome 2001; Toth and Assad 2002). This complexity in LIP activity is also reflected in remapping (Gottlieb et al. 1998). 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 ground-breaking study revealed that LIP encodes feature 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 encode shape information. Object recognition was believed to be mediated solely by the ventral stream. It continues to be unclear whether LIP neurons merely 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; Wurtz et al. 2011). Is it possible that feature 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 2008). Comparison of presaccadic and postsaccadic information would be possible. In effect, a usable visual percept could be built with information obtained from a series of saccades.

There is considerable psychophysical evidence showing that visual information is maintained across saccades (Deubel et al. 2002; McConkie and Currie 1996). We retain information both about important locations as well as the objects occupying those locations (Gordon and Irwin 1996). For instance, subjects show increased speed in identifying an object after a saccade if a similar object had been present before the saccade (Pollatsek et al. 1984). Likewise, decisions about motion direction are not interrupted by saccades as long as stimuli occupy the same screen locations (Melcher et al. 2004; Melcher and Morrone 2003). Another study found that sensory adaptations to tilt stimuli persist across saccades (Melcher 2007). In a

manner strikingly similar to remapping, adaptation effects were found at a peripheral location that would occupy the same retinal position as the adaptor when the saccade was completed.

Although there is psychophysical evidence for feature information being remapped, the neural structures are only just beginning to be identified. Studies indicate that parietal cortex may be involved in transsaccadic memory of features (Prime et al. 2008). When transcranial magnetic stimulation (TMS) is applied to the parietal cortex around the time of a saccade, subjects' ability to remember the features of multiple objects is disrupted

In this study, we hypothesized that remapped responses are related to the shape of the object being remapped. We show that individual neurons automatically encode and update shape information. Our results indicate that the remapped information is far more detailed than previously appreciated. These findings open up the possibility that remapping is a unified mechanism for both spatial and feature updating.

2.0   METHODS

2.1   ANIMALS

Two adult female rhesus macaques (5 – 8 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 beginning of this study, both monkeys underwent sterile surgery under general anesthesia induced with ketamine and maintained with isofluorane. 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 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) anatomical information from structural MRIs

2.2   PHYSIOLOGICAL METHODS

During recording sessions, the monkey sat in a dark room 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), made available by Dr. Robert Desimone. Eye position was monitored using scleral search coils (Judge et al. 1980).

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 band-pass 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).

2.2.1   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.

2.2.2 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 postsaccadic firing (Barash et al. 1991a; b). 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.

2.3   BEHAVIORAL PARADIGMS

Neural activity was recorded while the monkey performed 5 tasks run in separate blocks.

2.3.1   Memory guided saccade task
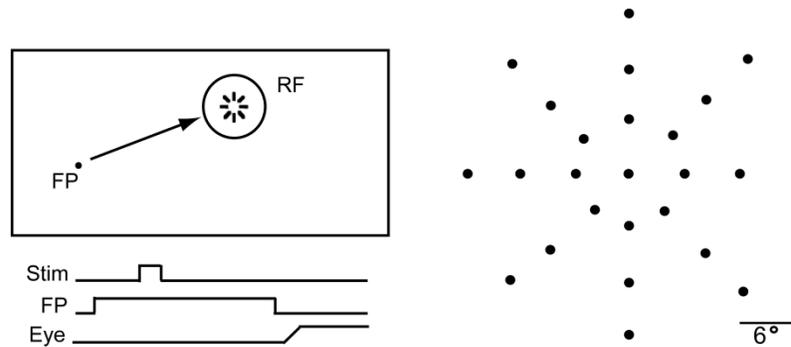
Figure 1. Memory guided saccade. Left Panel : The monkey maintains fixation at FP for 300 – 500 ms. Stimulus is briefly flashed in the receptive field (RF) for 50 ms. After a delay period (400 – 800 ms), FP is extinguished. The monkey makes a saccade into RF and maintains fixation for 300 – 500 ms. Time lines below show the sequenc of events. Right Panel: Stimuli were flashed at any one of 24 locations arranged in 3 concentric circles 6 degrees apart. RF was defined as the location that elicited the maximum visual response.

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) (Fig 1A, left panel). 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 receptive field (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 (Barash et al. 1991b; Colby et al. 1996; Zhang and Barash 2000). In each trial, we placed stimuli at one of 24 locations arranged in three concentric rings (Fig. 1B, right panel). We defined the RF as the location that elicited the

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maximum visual response during online inspection. 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 as compared to baseline.
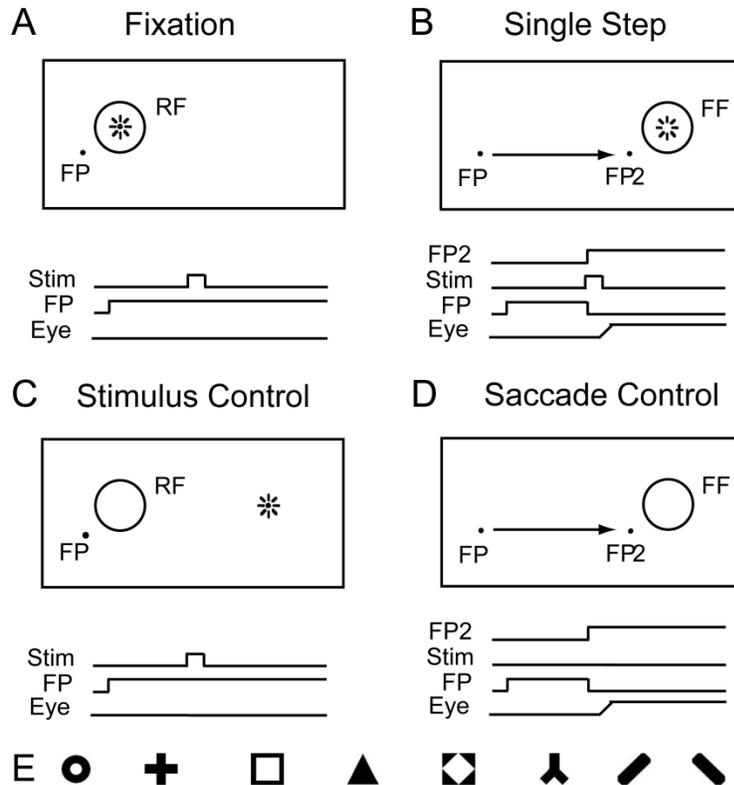
Figure 2. Task Design A: Fixation Task – Once fixation is attained, 1 – 4 non repeating shapes were presented consecutively in the receptive field. Shapes were presented for 50 ms with an interstimulus duration of 350 ms. B: Single Step Task – The monkey maintains fixation for 300 – 500 ms. Upon extinction of the initial fixation point, a new fixation point appears (FP2). Simultaneously, a shape is briefly flashed in the future field (FF) for 50 ms. FF is the screen location that will become the neuron's receptive field once saccade is completed. Offset of fixation point 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 - Following attainment of fixation (300 – 500 ms) , a spot is briefly flashed (50 ms) at the FF location to be used in the single step task. Monkey continues to maintain fixation for an additional 1200-1500 ms. D: Saccade Control Task - Trial begins when the monkey attains central fixation. After 300-500 ms, FP is extinguished and a new fixation point (FP2) appears. Location of FP2 is the same location as used in the single step task for that neuron. The monkey makes a saccade to FP2 and maintains fixation for 300-500 ms. E: A set of 8 shapes were used to test for shape selectivity in fixation and single step tasks. Each shape fit into a 2.2 degree square. Each shape had 180 white pixels and 220 black pixels (contrast inversed in image). Stimulus set was adapted from (Sereno and Maunsell, 1998)

2.3.2   Fixation Task

The fixation task was used to assess whether neurons were selective for shape when the monkeys were simply fixating (Fig 2A). We used a task design adapted from Dunn and Colby (2010). In each trial, 1-4 non-repeating stimulus shapes were presented consecutively in the receptive field. 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 inter-stimulus interval of 350 ms to allow the activity to return to baseline. The trial ended with extinction of fixation point. The monkey was rewarded for successfully maintaining fixation throughout the trial. The monkey performed this task until each of shapes had been presented at least 12 times.

2.3.3   Single Step Task

 The single step task was used to assess remapping and shape selectivity during remapping (Fig. 2B). The trial began when the monkey attained fixation. The monkey maintained fixation on the initial fixation point (FP) for $300 - 500$ ms. Three events then occurred simultaneously: a stimulus appeared outside of the neuron's RF for 50 ms; the initial FP was extinguished; and a new fixation point (FP2) was illuminated.   Offset of initial fixation point was the monkey's cue to make a visually guided saccade to FP2. The stimulus was flashed at the location that would become the receptive field of the neuron once the saccade is completed. 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 8 stimulus shapes was randomly chosen and presented in the future field. The monkey performed the single step task until 12 trials had been correctly performed for each of the 8 shapes.

2.3.4 Stimulus Control Task

The stimulus control task was used to ensure that the location of the flashed stimulus lay outside the receptive field (Fig. 2C). 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 block was run until 12 correct trials had been performed.

2.3.5 Saccade Control Task

This task was used to measure activity related to the generation of the saccade itself (Fig. 2D). The design of the task was identical to the single step task, except that no peripheral stimulus was presented. The monkey maintained fixation for $300 - 500$ ms, after which the initial fixation point 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 block was run until 12 correct trials had been performed.

2.3.6 Selection of Shape Stimuli

We closely followed the procedure of Sereno and colleagues in designing the shapes for testing for shape selectivity (Sereno and Maunsell 1998). We used a set of 8 shapes (Fig. 2E). Each of the shapes extended the entire width of a 2.2° by 2.2° square. Each shape had 180 white pixels and 220 black pixels. In this way the shapes had equal sizes and brightness and differed only in the relative configuration of the white pixels.

2.4   DATA ANALYSIS

2.4.1   Identification of remapping LIP neurons

For a neuron to be considered as remapping, three conditions must be satisfied: a) activity must not be solely a visual response to the stimulus alone; b) activity must not be solely motor activity due to the saccade and c) activity must be elicited by the conjunction of the stimulus in the future field and the saccade. We describe below the procedure used to identify neurons that satisfied each of the above three conditions.

a)   Activity due to the stimulus alone: We used the stimulus control task to determine whether a neuron was visually response to the stimulus in the future field location (FF). We calculated baseline activity in a 200 ms epoch from 150-350 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, $p<0.05$).

b)   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 150-350 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, $p <0.05$).

c)   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 chose a 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 beginning 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 our threshold measure. We defined the remapping latency of each neuron as the start of the first 5 consecutive bins that contained firing rates above threshold. Our window for measuring 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 obtained during the saccade control condition. We measured activity in the remapping window for each of the 8 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 multicomparison correction ($P < 0.05$) to test for significant differences between activity in the single step task and saccade control task. If the response in the single step task for at least one stimulus was significantly different from saccade control, we considered the neuron as remapping.

2.4.2   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 1 way ANOVA (p <0.05) to determine whether there was a significant difference between responses to the 8 shapes.

2.4.3   Measurement of visual activity in the fixation task

In the design of the fixation task, 1-4 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 (Dunn and Colby 2010) in order 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. The activity would be due to the lingering activity of the previous stimulus and not necessarily due to the current stimulus.

In order 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 1 – 4 stimuli could be presented in a single trial, each trial could have upto 4 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 - 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 5 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 multicomparison correction ($P < 0.05$) to test for significant differences between the visual epoch and the baseline epoch.

2.4.4   Identification of neurons selective for shape during fixation

To determine whether a neuron showed shape selectivity during fixation, we performed a 2-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 in order to avoid a spurious suggestion of shape selectivity due to repetition suppression or enhancement.

2.4.5   Characterizing selectivity profile of a neuron

For each neuron, we characterized shape selectivity in the single step and fixation tasks using two indices: selectivity index and depth of selectivity. The first measure is indicative of the difference in responses to the most preferred and least preferred shape. The second measure is indicative of the overall depth of tuning to all 8 shapes.

2.4.5.1 Selectivity Index

We defined the selectivity index as $(R_{most} - R_{least})/(R_{most} + R_{least})$, where R_{most} is response to most preferred shape and R_{least} is response to least preferred shape. The selectivity index ranges from 0 to 1 with indices closer to 0 indicating no selectivity and indices closer to 1 indicating strong selectivity.

We estimated the selectivity index using the split-half method. We used responses in one half of the trials to pick the shapes to which the neuron showed highest and lowest activity. We used responses in the other half of the trials to calculate the selectivity index.

2.4.5.2 Depth of Selectivity Index

The depth of selectivity index describes the overall tuning to all 8 shapes (Rainer et al. 1998; Rainer and Miller 2000). We defined depth of selectivity as $[n - \sum R_i/R_{most}]/(n\text{-}1)$, where n is the number of shapes (8 in this study), R_i is the response to each shape, R_{most} is the response to the most preferred shape. DOS ranges from 0 to 1 with indices closer to 0 indicating broad tuning and indices closer to 1 indicating sharp tuning.

To estimate the reliability of our procedures we used a split half method. We computed DOS indices separately for the odd numbered and even numbered trials. We then correlated the DOS across neurons. We then corrected for the correlation measure obtained by computing the Spearman-Brown split-half coefficient (Lord and Novick 1968). The coefficient is obtained by calculating $r_{sb} = 2\ r_{xy}/(1 + r_{xy})$, where r_{sb} = corrected split-half reliability coefficient and r_{xy} = correlation between DOS indices for the odd and even repetitions.

3.0   RESULTS

The goal of these experiments was to determine whether LIP neurons are capable of encoding shape information about a remapped stimulus. We recorded from 117 LIP neurons that had visual activity in a memory guided saccade task. Of these, 82 neurons also had significant remapping activity.

3.1   ARE INDIVIDUAL LIP NEURONS SELECTIVE FOR SHAPE?

3.1.1   Individual LIP neurons show shape selectivity during remapping

Our primary finding is that individual neurons are shape selective during remapping. In the single step task, a stimulus is briefly flashed outside the RF of a neuron (Fig. 2B). At the same time, a new fixation point appears (FP2). When the monkey make a saccade to the new fixation point, the receptive field moves onto the screen location where the stimulus had previous appeared (future field, FF). A typical remapping neuron is shown in Fig. 3. Responses to each of the 8 shapes in the single step task are plotted as rasters and histograms aligned on saccade onset (Fig. 3A). 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. 3B).

Likewise, the neuron did not respond when a saccade was made but no stimulus appeared in the future field (Fig. 3C). The combination of a stimulus in the future field and an eye movement is required for the neuron to remap (Fig. 3A).
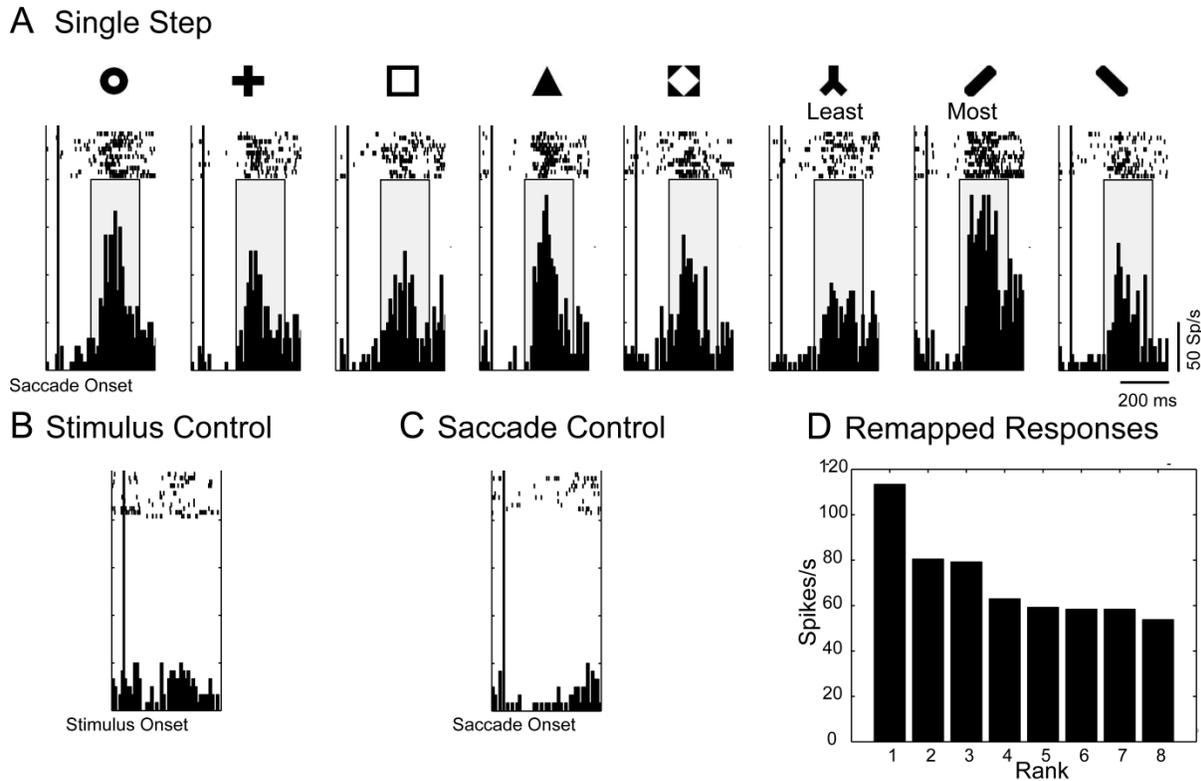
Figure 3. Response of a shape selective neuron in the Single Step Task. A-D: Histograms are plotted in 10 ms bins and are aligned on saccade onset (A, C, vertical black line) or stimulus onset (B, vertical blue line). Each row in the raster plots indicates the time of individual spikes for each trial. A: Responses to each of the 8 shapes in single step task. A 200 ms epoch aligned on beginning of visual response (box) was used to measure average firing rate ; *Most* - The shape for which the neuron had the strongest response; *Least* – Shape to which neuron had the weakest response. B: Response of neuron in the stimulus control task when stimulus was presented in the future field but no saccade was made. 3C: Response of neuron 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).

Our main question was whether the strength of remapping was 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 aligned on the beginning of the remapped response. The response of the LIP neuron in Fig. 3A was significantly modulated by stimulus

shape (ANOVA, p <0.05). The neuron fired most strongly to the 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. 3D). The exact distance between each of these shapes in feature space is not known. Consequently, we did not attempt to fit curves to response profiles. Ranked response plots used in Fig. 3D and in subsequent figures provide useful visual illustrations for our results.

Many LIP neurons in this study had remapping activity that significantly depended on stimulus shape (ANOVA, p< 0.05; 31 of 82, 38 % of all remapping neurons). This was true even though we used a limited and arbitrary stimulus set. The proportion of shape selectivity is greater than that expected by chance (chi-squared test, p <0.05).

3.1.2 Strength of shape selective remapped responses

Neurons were first classified as selective or non-selective using ANOVA. For each neuron, we also computed two different measures of shape selectivity. The first measure is the Selectivity Index (SI). SI is a normalized score indicative of the difference in response to the most preferred and least preferred shapes. Scores closer to 1 indicate preference for only 1 shape and scores closer to 0 indicate no preference for shape. We used a split-half method to measure SI (see METHODS). For noisy responses, the most preferred and least preferred shapes obtained using one half of the trials may not be consistent with that obtained from the other half of the trials. In those cases, the index can have a negative value. The SI of the neuron in Fig. 3 was 0.32. Distribution of selectivity indices of all remapping neurons is plotted in (Fig. 4D). The prominent rightward shift in the distribution of selective neurons (Black bars, median SI = 0.24) compared

to that of non-selective neurons (Gray bars, median SI = 0.03) assured us of the validity of our classification procedures.
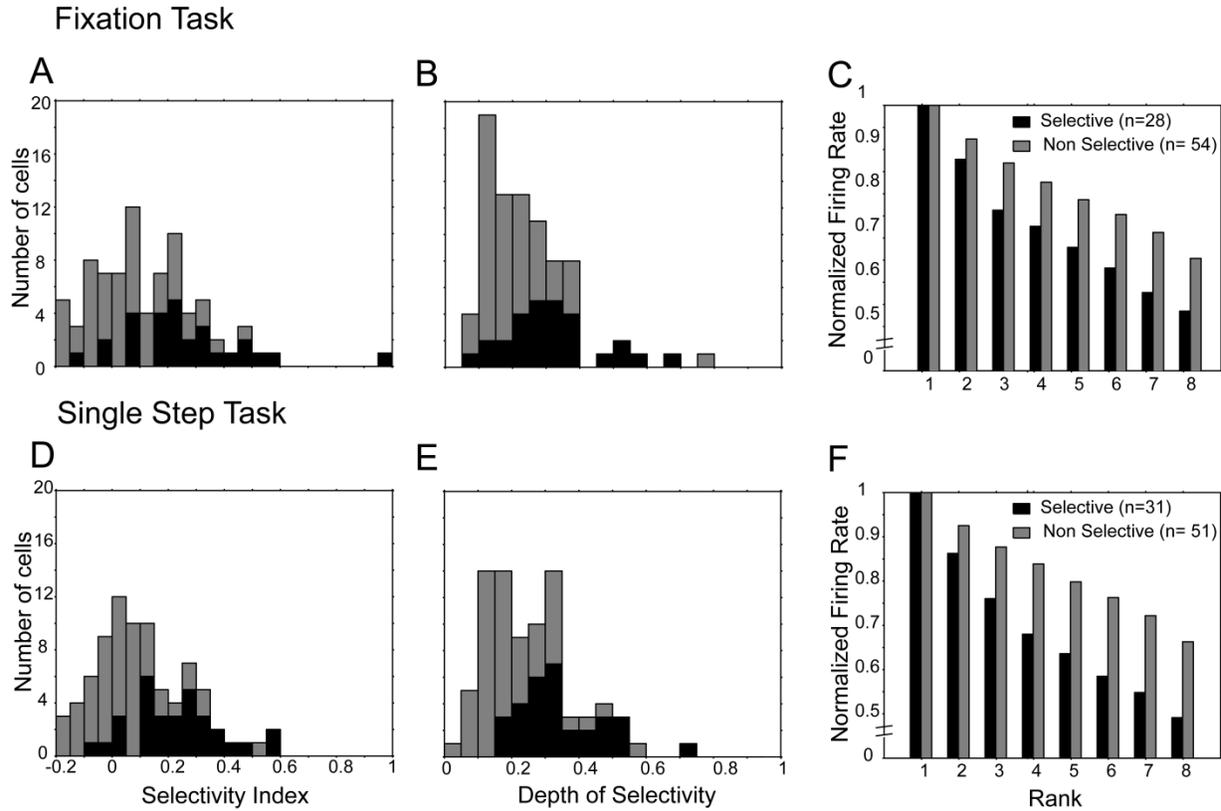
Figure 4. Population measures of strength of selectivity. *Top Row* A – C: Fixation Task. *Bottom Row* D- F: Single step Task. Distribution of Selectivity Index values in the fixation task are plotted in A and in single step task are plotted in D. Distribution of Depth of Selectivity Index values in fixation task are plotted in B and in single step task are plotted in E. For each neuron, responses to shape from each task were divided by the response to the most preferred shape in that task. Normalized responses plotted as a function of rank are shown in C (fixation task) and F (remapping task). In all panels, gray bars represent values and responses of non-selective cells. Black bars represent values and responses of selective cells.

We also used a second measure, Depth of Selectivity (DOS), to characterize shape selectivity. DOS is a more sensitive measure of shape selectivity as it takes into account response to all 8 shapes. Values closer to 0 denote neurons that respond to all shapes equally while values closer to 1 denote neurons that respond to only one shape. The DOS of the neuron in Fig. 3 was 0.43. Distribution of DOS values of all remapping neurons is plotted in Fig. 4E. The Spearman-

Brown split-half reliability coefficient was 0.80. A similar rightward shift in the distribution of selective neurons (Black bars, median DOS = 0.32) compared to that of non-selective neurons (Gray bars, median DOS = 0.17) was observed.

The average response of selective neurons is distinct from population averaged responses of non selective neurons. For each neuron, responses were ranked from highest to lowest. Ranked responses were averaged separately for selective and non selective populations (Fig. 4F). Bar height decreases from most preferred (Rank 1) to least preferred (Rank 8) shape (Fig. 4F, Black bars). Because ranking necessarily orders responses from high to low, we can expect the procedure to produce a declining trend even for non selective cells. The decrease in height, however, is not as pronounced as that of selective neurons.

Many neurons exhibited impressive shape selective responses. Because representation in LIP is viewed as a priority map of salient locations, we wondered if the shape selective responses reflected behavioral significance of the stimulus rather than feature information. We designed the tasks so that stimulus shape was not relevant for accurate behavior. The stimulus in the future field was never a target for the saccade. The monkey's only task was to make a saccade from an initial fixation point to a new fixation point. In addition, we performed the saccade control task to ensure that the new fixation point was not in the receptive field of the neuron. The sudden appearance of the stimuli made each of them equally salient. It is unlikely that task design encouraged the monkey to pay more attention to some shapes than others. Further, the monkeys in this study had never been trained on any other task other than those described in this study. In particular, they had never been trained to pay attention to stimulus shape. We conclude that training history could not have contributed to shape selectivity. We had also designed the shapes so that they were equal in all other aspects other than their relative configuration. The only

feature differentiating the stimuli was their shape. In the population of remapping neurons, there was no consistent preference for any one shape over the other (Kruskal-Wallis test, p >0.05). We conclude that selective responses reflect genuine shape selectivity during remapping.

3.1.3 LIP neurons are also shape selective during fixation

We asked whether our population of remapping neurons were also selective for shape when tested in the fixation task. In each fixation trial, between 1 and 4 different shapes were consecutively presented in the receptive field while the monkey maintained fixation on a central spot. To determine whether a neuron was shape selective in the fixation task, responses were submitted to a 2-way ANOVA. We included shape and order-within-trial as factors to rule out spurious shape selective effects from repetition suppression or enhancement.

Many remapping neurons were also shape selective in the fixation task. Neurons could have combinations of selectivity in the fixation and single step tasks (Table 1). We describe three of the four possibilities below.

Fixation / Single Step	Selective	Non Selective
Selective	11	20
Non Selective	18	34

Table 1. Number of neurons selective in each task

First, we found that neurons could be selective in both tasks (11 of 82, 13 %). Visual activity in the fixation task and remapping activity in the single step task of one example neuron is plotted in Fig. 5.
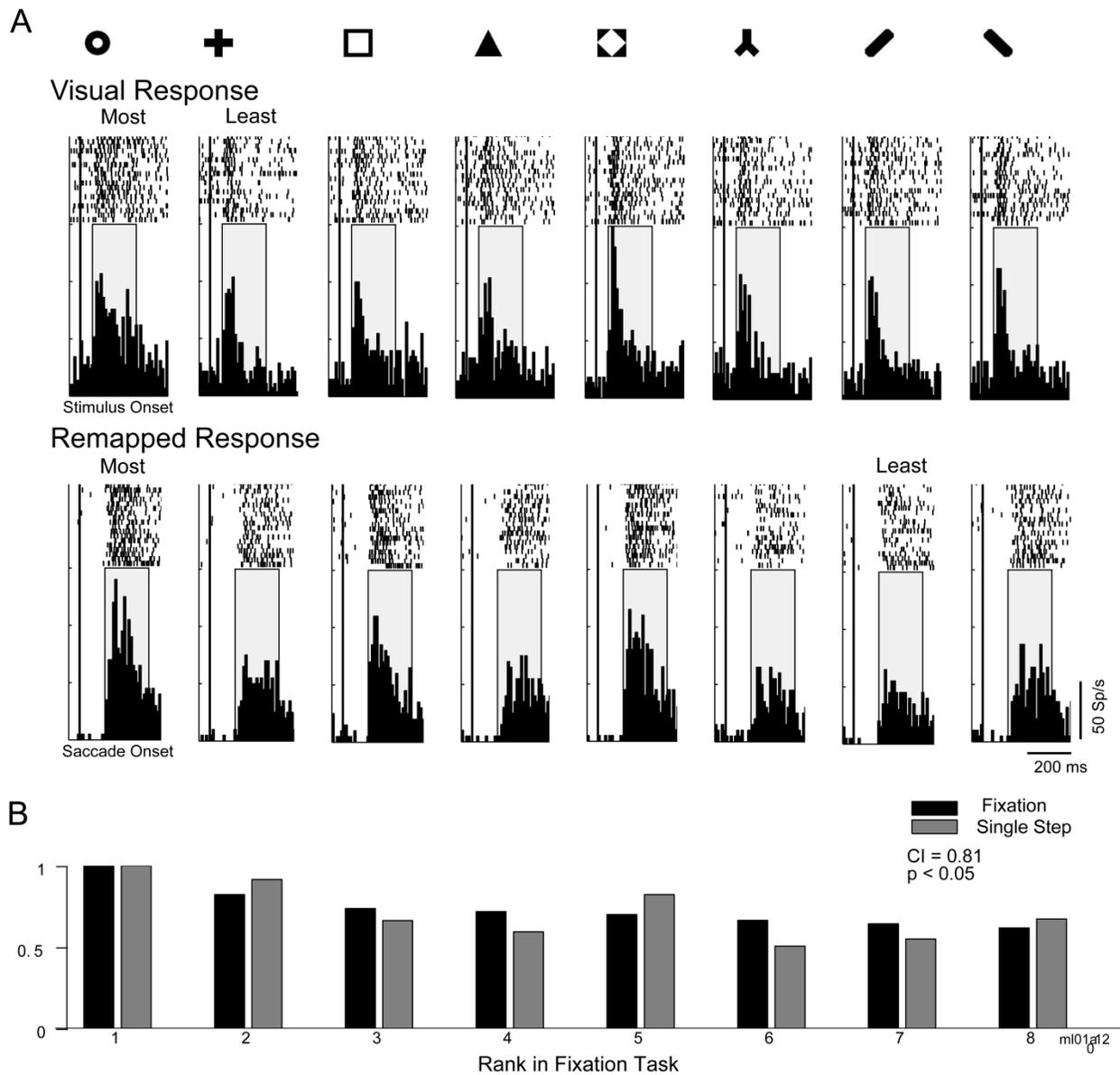
Figure 5 Response of a neuron selective in both fixation and single step tasks. Visual responses in the fixation task are shown in A, *Top Row*. Remapped responses in single step task are shown in B, *Bottom Row*. Histograms are plotted in 10 ms bins and are aligned on stimulus onset (top row) and saccade onset (bottom row). Boxes indicate the 200 ms epoch during which average firing rates were measured. *Most* and *Least* refer to the shape to which the neuron fired most strongly and least strongly in each task. B: Responses to shapes in each task were divided by response to most preferred shape in that task. Normalized responses in the fixation task were ranked from highest to lowest and are plotted as a function of rank (Black bars). Normalized responses to the corresponding shapes in the single step task are also plotted (Gray bars).

The neuron was selective for shape in both fixation (top row, 2 way ANOVA, main effect of shape, $p<0.05$) and single step tasks (bottom row, ANOVA, $p<0.05$). In both tasks, the neuron

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preferred the same shape, the annulus. The neuron's least preferred shape differed in the two tasks. In the fixation task, the least preferred shape was the cross. In the single step task, the least preferred shape was the right oblique bar.

When responses to only the most preferred and least preferred shapes are compared, there appears to be no relation between preferences in the two tasks. When responses to all 8 shapes are compared across both tasks, however, a strong and significant correlation is revealed (Pearson's r = 0.82, p <0.05). To illustrate this result, visual activity in the fixation task was ranked from highest to lowest (Fig. 5B, Black bars). As can be expected from the ranking procedure, normalized response in fixation task decreases from Rank 1 to Rank 8. Rank order in the fixation task was imposed on remapped responses in the single step task (Fig. 5B, Gray bars). Overall, as the preference for a shape in the fixation task decreases, preference for that shape in the single step task also decreases. With decreasing preference (higher rank), height of the gray bars also tend to get shorter. This negative trend is present even though the ordering is based on preference in the fixation task. Further analysis of the relation between preferences is presented in the next section.

We characterized strength of shape selectivity in the fixation task using the same two measures used in the single step task. This neuron had an SI of 0.21 and a DOS of 0.30 in the fixation task. It had an SI of 0.29 and a DOS of 0.33 in the single step task.

Second, many neurons were selective in only one of the tasks (38 of 82, 46 %). Responses of an example neuron are plotted in Fig. 6. This neuron was selective for shape in the fixation task (2 way ANOVA, main effect of shape p < 0.05) but not selective in the single step task (1 way ANOVA, p <0.05). In the fixation task, the neuron was most responsive to the square and the least responsive to the inverted Y (Fig. 6A, top row). It had an SI of 0.47 and a

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DOS of 0.55. The neuron was not selective in the single step task (Fig. 6A, bottom row). SI was 0.08 and DOS was 0.16. As expected, no significant correlation was seen between the responses to shapes in the two tasks. Ranked responses in the fixation task are plotted in Fig. 6B (Black bars). When responses of the corresponding shapes in the single step task are plotted, no decreasing trend is observed, illustrating lack of selectivity (Fig. 6B, Gray bars)
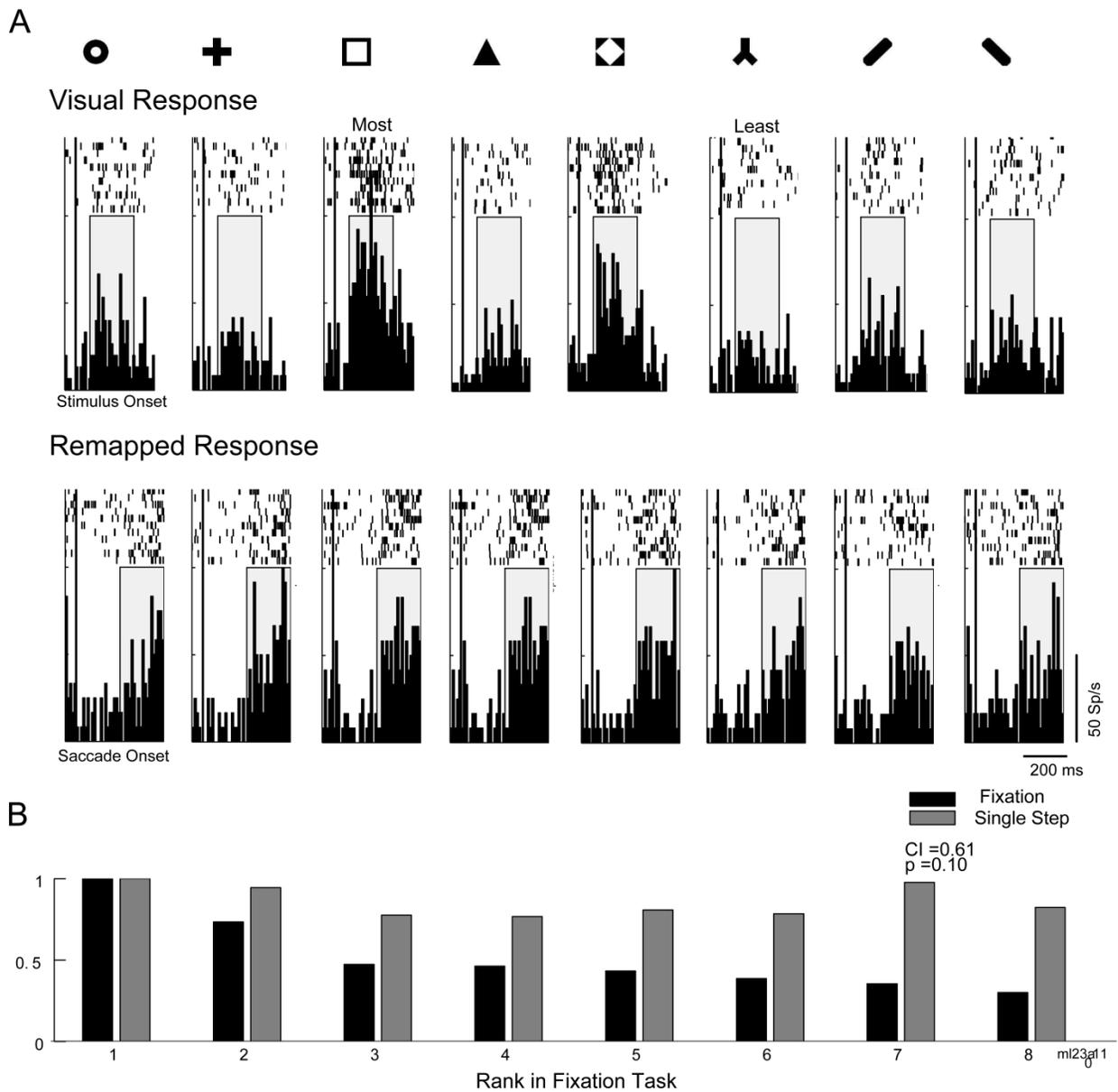
Figure 6. Response of a neuron selective in fixation task but not single step task. Conventions as in Fig. 5.

Third, we found examples of neurons that were selective in the single step task but not in the fixation task. The neuron in Fig. 7 was selective for shape in the single step task (1 way ANOVA, p <0.05) but not shape selective in the fixation task (2 way ANOVA, main effect of order-within-trial, p<0.05).
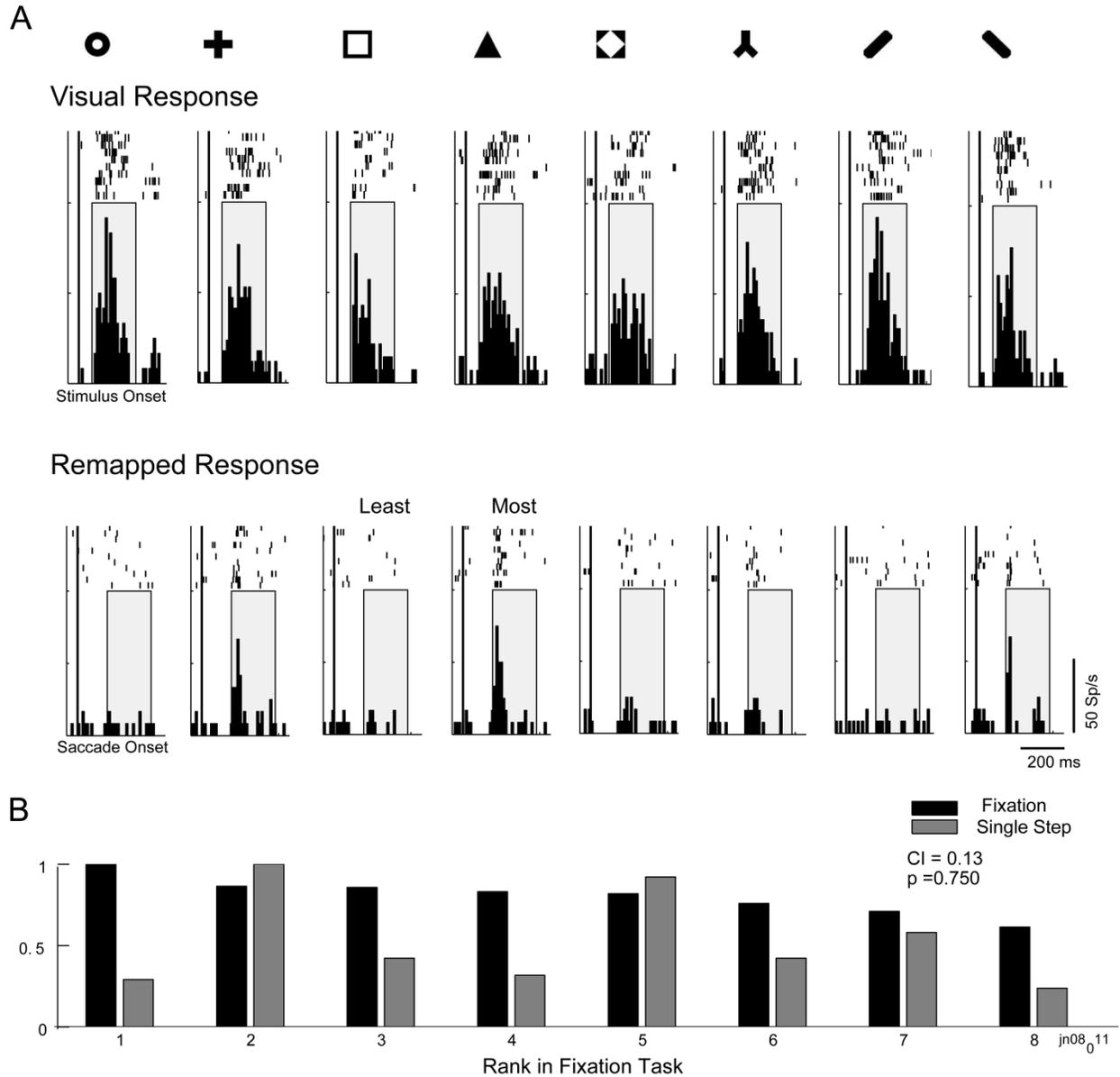
Figure 7. Response of a neuron selective in single step task but not in fixation task. Conventions same as Fig. 5

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In the single step task, the neuron preferred the triangle the most and the square the least. It had an SI of 0.57 and DOS of 0.55. The neuron showed no significant selectivity in the fixation task. When the rank ordered responses in the fixation task are plotted, a very shallow decreasing trend is observed (Fig. 7B, Black bars). When remapped responses for the corresponding shapes are plotted, the heights of the bars vary widely, demonstrating shape selectivity in the single step task.

In our population of remapping neurons, 28 of 82 (34 %) neurons were shape selective in the fixation task. There was either a main effect of shape or a main effect of order-within-trial. None of our neurons showed any interaction between shape and order within trial. The distribution of selectivity indices in the fixation task are plotted in Fig. 4. Neurons that were significantly shape selective in the fixation task are denoted by the black bars (Fig. 4A, median SI of selective neurons = 0.22). Histograms of DOS values are plotted in a similar manner in Fig. 4B (median DOS of selective neurons = 0.30). Our results confirm previous observations (Sereno and Maunsell 1998) that LIP neurons are selective for shape during fixation. When we ranked responses of selective neurons, we found a steep decline in responses as preference for shape decreased (Fig. 4C, Black bars). The decline in the response of non selective responses is not so pronounced (Fig. 4C, Gray bars). The lack of a completely flat response for non selective neurons in either task may also indicate a continuum of shape selectivity within the population.

3.2 IS THERE A RELATION BETWEEN RESPONSES IN FIXATION AND SINGLE STEP TASKS?

We compared selectivity in fixation and single step tasks in two ways. First, we compared strength of selectivity in the two tasks. Second, we compared preference for shape in the two tasks.

3.2.1 Comparison of strength of selectivity
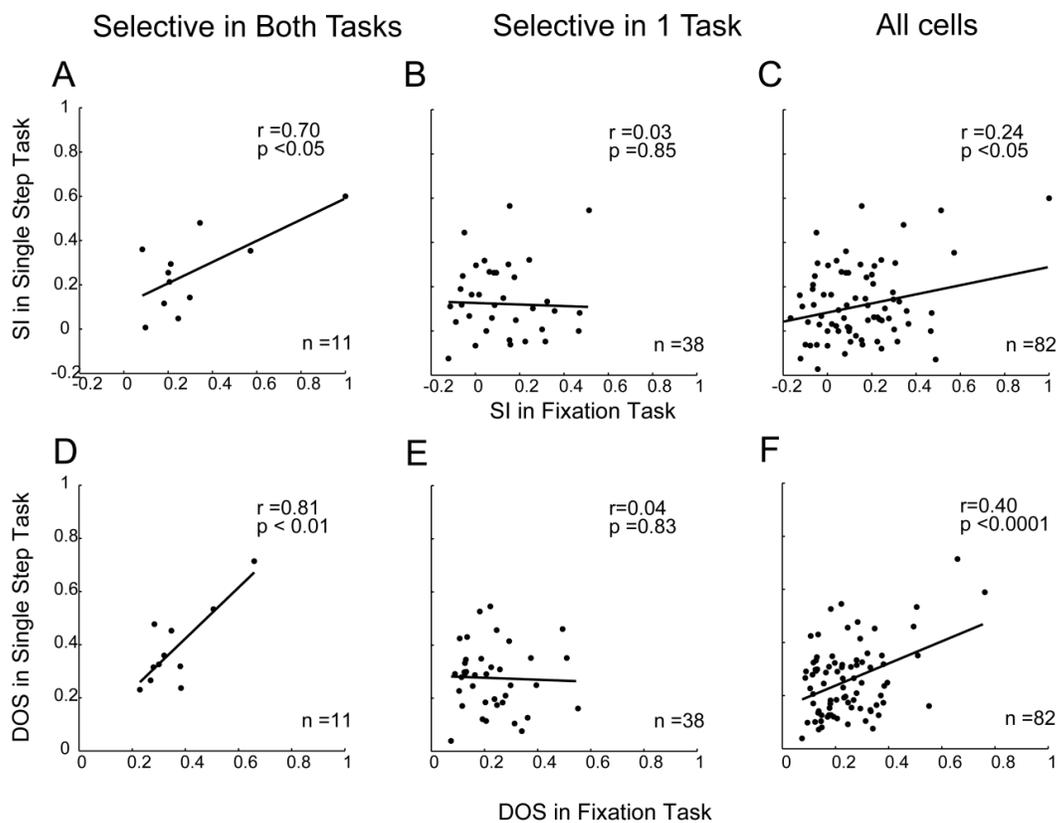
Figure 8. Population level comparison of strength of selectivity between fixation and single step task. Two measures were computed. A- C show comparison of Selectivity Index. E – F shows comparison of Depth of Selectivity. Value of index of neurons in the single step task is plotted as a function of value of index in the fixation task. In A, D, Selectivity Index and Depth of Selectivity of neurons selective in both tasks are compared. In B, E, Strength of selectivity of neurons selective in only 1 task are compared. In C, F Strength of Selectivity of all neurons are compared.

We asked whether the strength of selectivity as measured by 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. For neurons selective in both tasks, we found a strong correlation between SI (Fig. 8A; Pearson's r = 0.70, p<0.05). This result suggests that the updating mechanism does not dampen the extent of shape selectivity. This was true when we compared DOS indices as well (Fig. 8D; Pearson's r = 0.81, p<0.01). We found no correlation when we compared neurons that were selective in only one task and not the other (Fig. 8 B, E; Pearson's r = .03, p >0.05). When we compared indices of all neurons regardless of selectivity, we found a weak but significant correlation (Fig. 8C, F; Pearson's r for SI = 0.24 p<0.05, Pearson's r for DOS = .4031, p <0.01). We found a stronger and more significant correlation when we compared DOS values owing to the more sensitive nature of the index. Even though only a small percentage of neurons were selective in both tasks, a correlation was still observable at the level of the entire population. We conclude that the extent of feature information encoded in the two tasks are related.

3.2.2 Comparison of shape preference in individual neurons

We asked whether neurons tended to prefer the same shapes in the two tasks. We calculated a correspondence index (CI) for each neuron. Each neuron's CI is the Pearson's correlation co-efficient between responses to the same shapes in the two tasks. CI ranges from − 1 to 1. Many of our neurons (52 of 82, 63%) showed a trend towards positive correlation. In 10 of 82 neurons the CI was statistically significant (Pearson's r, p <0.05). No neuron in the population had a statistically significant negative CI.

3.2.3 Population level comparison of shape preference
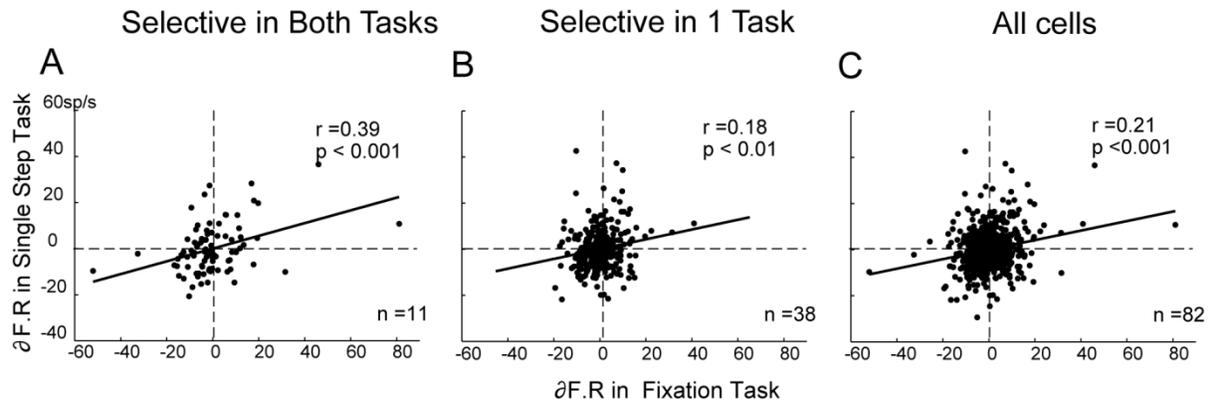
Figure 9. Population level comparison of preference for shape. For each neuron, average firing rate across all 8 shapes was computed for each task. For each task, average firing rate in that task was subtracted from response to each individual shape. For each neuron, difference in firing rate (δ F. R) for each shape in single step task was plotted as a function of δ F.R for each shape in fixation task. A : Comparison of preference for neurons selective in both tasks. B: Comparison of preference for neurons selective in only 1 task. C: Comparison of preference for neurons selective in both tasks.

We next asked if the trend towards matching order of shape preference was present at the level of the population. For each neuron, we centered the response in a particular task by subtracting the mean firing rate across all 8 shapes from the response to each shape. As a result, the corrected average response of each neuron in our population was 0 spikes/s. This correction prevented neuron to neuron differences in overall firing rate from contributing to the correlation calculation. We calculated the population correlation by correlating all the neurons' corrected responses to the 8 individual shapes in the fixation and single step tasks. For each neuron and each shape, we plotted the centered firing rate in the single step task as a function of the centered firing rate in the fixation task (Fig. 9)

We compared preferences of neurons that were shape selective in both tasks. A significant positive correlation is seen (Fig. 9A; Pearson's r = 0.39, p <0.05). The level of correlation decreased when we compared neurons that were shape selective in only one of the

two tasks (Fig 9B; Pearson's r = 0.17, p <0.05). A significant positive correlation was apparent when we compared all neurons in our population. Despite including neurons that were not selective for shape in either task, we still observed a significant correlation (Fig. 9C; Pearson's r = .21, p<0.05). Similar results were obtained when we used normalized responses. We conclude that both strength as well as preference is maintained in the two tasks. Our results suggest that when neurons are selective for shape in both tasks, they have similar strengths of selectivity. Moreover, their order of preference is maintained in both tasks. Although only a small proportion of neurons are selective in both tasks, significant correlation in selectivity is still observable at the level of the population.

We were interested in determining whether feature information is remapped. LIP neurons were tested under conditions of fixation and remapping. We show that shape selectivity is automatic in LIP. Further, shape information is remapped. Comparison of selectivity between the two tasks indicates that shape information may be maintained during remapping. These results reveal the sophisticated nature of remapping. Our results suggest that LIP may contribute to the transsaccadic perception of features.

4.0   DISCUSSION

Remapping is one of the mechanisms that may contribute to visual stability (Sommer and Wurtz 2002; Wurtz 2008). Much 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 examined.

4.1   REPRESENTATION OF SPACE IN LIP

It has been traditionally held that vision 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. 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. Because the retinal positions of these locations change with every eye movement, remapping enables the map to be 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). 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 if the stimulus is irrelevant. In this way, remapping allows information about salient locations to be maintained across saccades.

4.2 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 receptive field, many neurons were found to exhibit shape selectivity. These findings challenged the notion that LIP solely encoded information about which location was 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 do show selectivity for shape during remapping. Shape information is automatically remapped, even when it is irrelevant for the task. All our shapes were equally salient due to their sudden appearance. In addition, the stimuli were carefully controlled for size, area and brightness. We ruled out attentional difference between stimuli as a factor that contributes to shape selectivity. Our results demonstrate that remapped responses are not modulated by attentional considerations alone.

In the same neurons, we also evaluated the extent of shape selectivity when the stimuli were presented within the receptive field (fixation task). Since the landmark study by Sereno and Maunsell (1998) that revealed feature selectivity in the absence of task demands, many studies have replicated and reaffirmed those findings (Janssen et al. 2008; Lehky and Sereno 2007). The monkeys in those studies had also been trained in other tasks in which shapes were 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 task whether shape selectivity is present in the absence of training history. Because we used monkeys that had not been previously trained on any other task, we were able to eliminate training history as contributing to shape selectivity. We conclude that shape selectivity is innate to area LIP and that shape information is automatically updated during remapping.

4.3 SIGNIFICANCE OF FEATURE 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 have been found to be enhanced by a variety of task relevant features (Gottlieb et al. 2009; Gottlieb et al. 1998). 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. Neurons are 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 (Freedman and Assad 2009; 2006). Many LIP neurons were found to be selective for directions of one category and not the other.

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, the LIP population showed different degrees of selectivity in different epochs within the task. (Sereno and Amador 2006). The authors suggested 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 more 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. Towards 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 pathway and directionally selective neurons in MT (Blatt et al. 1990; Lewis and Van Essen 2000; Ungerleider and Desimone 1986). It has been suggested that 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.

4.4   TRANSSACCADIC PERCEPTION

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 a 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 (Germeys 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 was some relation between transsaccadic memory of object location and that of object feature.

The link between object location and feature 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 2008; 2007; 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.

4.5   ROLE OF LIP IN TRANSSACCADIC PERCEPTION

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

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How might remapping be involved in transsaccadic perception? One idea 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 second idea is that feature information along with spatial information is remapped during a saccade (Mayo and Sommer 2010; Melcher and Colby 2008). There is evidence supporting both ideas.

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 receptive fields of neurons that would eventually encode the cue location after the saccade. In those locations, compared to equally eccentric but unrelated control locations, attentional benefits were observed. These results provide evidence that a remapped store of attentionally significant is used in a behaviorally relevant manner.

The second idea requires evidence that there is remapping of feature information. In this study we show that shape information is remapped in LIP. Further, we were able to compare selectivity in the fixation and remapping tasks within the same neuron. Not all neurons were selective in both tasks. Neurons selective in both tasks, tended to maintain preference. When we compared selectivity within the population we found a significant correlation between preferences in the two tasks. Memory for object features may be distributed within the LIP population rather than completely encoded within a single neuron.

Our findings indicate that LIP keeps track of both locations and features of salient objects. A parsimonious explanation is that remapping is simply a transfer of encoded information between populations of neurons. Consequently, remapping of different aspects of an object (shape, direction, salience) is unlikely to employ separate updating mechanisms.

A growing body of literature suggests that dorsal stream areas have access to feature 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. Further, shape selectivity itself is an innate property of LIP requiring no previous training. Our results are significant because they provide critical neurophysiological evidence for the possibility that remapping mechanisms in LIP are involved in transsaccadic memory and perception.

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