Representation of the Ipsilateral Visual Field by Neurons in the Macaque Lateral Intraparietal Cortex Depends on the Forebrain Commissures

Catherine A. Dunn¹, Carol L. Colby¹

¹Department of Neuroscience and Center for the Neural Basis of Cognition, University of Pittsburgh, Pittsburgh PA 15213

Running head: Receptive fields of LIP Neurons in split-brain monkeys

Address for correspondence: C.L. Colby, 115 Mellon Institute, 4400 5th Ave, Pittsburgh PA 15213 (E-mail: colby@cnbc.cmu.edu)
ABSTRACT

Our eyes are constantly moving, allowing us to attend to different visual objects in our environment. With each eye movement, a given object activates an entirely new set of visual neuron, yet we perceive a stable scene. One potential neural mechanism for stable perception is the phenomenon of remapping. Neurons in lateral intraparietal cortex (area LIP), frontal eye fields (FEF), extrastriate cortex, and the superior colliculus (SC) respond to visual stimuli outside their receptive field if a impending eye movement will bring the stimulus location into their receptive field. Remapping depends on neurons receiving visual information from outside their classic receptive field, even when the initially salient location is in the opposite visual field. If the forebrain commissures are transected, behavior dependent on accurate spatial updating is impaired but recovers over time. Additionally, neurons in LIP continue to remap information across hemifields even in the absence of the forebrain commissures. One possible explanation for the across hemifield remapping in split-brain animals is that neurons in a single hemisphere could represent visual information from both visual fields. We measured receptive fields of LIP neurons in split-brain monkeys and compared them to receptive fields in intact monkeys. We found a small number of neurons with bilateral receptive fields in the intact monkey. In comparison, we found no such neurons in the split-brain animals. We conclude that bilateral representations in area LIP following forebrain commissures transection cannot account for remapping across hemifields.
INTRODUCTION

Vision is an active process in which we move our eyes to explore the world. Eye movements introduce a complex problem for perception: they occur about three times per second, and with each eye movement a new image impinges on the retina. Even so, we perceive a stable visual world, enabling us to act. Neurons in lateral intraparietal cortex (LIP), frontal eye fields (FEF), extrastriate cortex, and the superior colliculus (SC) update spatial representations at the time of an eye movement (Duhamel et al. 1992; Goldberg and Bruce 1990; Nakamura and Colby 2002; Umeno and Goldberg 1997; Walker et al. 1995). It is thought that these areas transfer visual activity from neurons representing the salient location before the eye movement to neurons representing the salient location after the eye movement. It is hypothesized that updating contributes to the formation of a stable perception (Berman and Colby 2009).

Accurate spatial updating depends on a population of neurons that receive visual information from the entire visual scene, even when the initial and final salient locations are in opposite visual fields. For example, a visual stimulus flashed 6° up and to the right of an initial fixation point is presumably represented by neurons in the left hemisphere. If an eye movement is made 12° to the right, the location of the flashed stimulus will now be 6° up and to the left of fixation, represented by neurons in the right hemisphere. Neurons that remap in the right LIP must receive information about the visual stimulus that was original encoded by the left hemisphere. There is evidence that this is the case in the original LIP remapping study (Duhamel et al. 1992). In this study, the task was configured so that a stimulus was flashed in the hemifield opposite the one represented by the neuron being recorded. Visual information was updated from one visual hemifield to the other.
One potential route for the transfer of visual information across hemispheres is through the forebrain commissures, the fiber pathways that connect the cortical hemispheres. Berman and colleagues test this possibility by transecting the forebrain commissures (Berman et al. 2005). They found that behavior dependent on accurate spatial updating is impaired. Surprisingly, this impairment was not permanent and behavior recovered over time. Additionally, neurons in area LIP continue to remap information across hemifields even in the absence of the forebrain commissures (Heiser et al. 2005). These studies indicate that the forebrain commissures are the primary pathway for the transfer of visual information between hemispheres but they are not the only possible pathway.

The finding that LIP neurons remap visual information from the opposite visual field even in the absence of the forebrain commissures implies that the opposite cortical hemisphere is not the only direct source of information (Heiser et al. 2005). One possibility is that information from both the ipsilateral and contralateral visual fields is represented in a single hemisphere. In other words, LIP neurons could have bilateral receptive fields.

Early studies showed that majority of parietal neurons have large bilateral receptive fields (Motter and Mountcastle 1981; Motter et al. 1987; Steinmetz et al. 1987). In later studies, researchers separated parietal cortex in to smaller sub-regions, including area LIP and area 7a (Andersen et al. 1990; Blatt et al. 1990). Between these two sub-regions, the proportion of cells with bilateral receptive fields is different. In area 7a, the majority of cells have bilateral fields, while only a small number of LIP neurons have bilateral receptive fields (Andersen et al. 1990; Barash et al. 1991; Ben Hamed et al. 2001; Blatt et al. 1990; Platt and Glimcher 1998; Quraishi et al. 2007). In area LIP, ipsilateral representation is predominately within 5° of the vertical meridian.
Since even in the intact monkey the ipsilateral representation is restricted to areas close to the vertical meridian, it seems unlikely that connections within one hemisphere are sufficient for across hemifield remapping. Additionally, prior to the current study, we examined the role of the forebrain commissures in updating representations across hemifields in these split brain monkeys (Berman et al. 2005). We had the monkeys perform a task that depends on accurate updating, the double-step task. In the double-step task, the monkey must make two sequential saccades. The target of the second saccade is turned off before the first eye movement is made. This creates a mismatch between the retinal representation of the second target, and the saccade vector required to reach the second target. The representation of the second target must be updated to take the first saccade into account. During the initial split-brain study, the monkeys performance was measured on three separate across-hemifield double-step configurations. The target for the second saccade was placed either 6 degrees from the midline, 3 degrees from the midline, or on the midline. We found a deficit in performance for both the 6 and 3 degree configurations. Therefore, even in the zone that contains ipsilateral representation in the intact animal, the split-brain monkey is unable to perform the task. While this behavioral task is not a direct measurement of remapping, we have demonstrated that remapping activity is related to double-step performance (Berman et al. 2007). These results suggest that the across hemifield remapping, even within the region of normal ipsi representation, is reduced in the split-brain animal. However, the possibility remains that some ipsilateral representations remain in the split-brain monkey. The aim of the present study was to determine whether there is any ipsilateral representation in LIP in the absence of the forebrain commissures.

While it is unknown what role the forebrain commissures play in the construction of bilateral receptive fields in area LIP, it has been examined in inferotemporal cortex (IT). In area
IT, neurons have large receptive fields, typically ranging from 10° by 10° to 30° by 30°, and they almost always include the fovea (Andersen et al. 1990; Gross et al. 1969; Gross et al. 1972). Many of these cells have bilateral receptive fields, extending at least 3° degrees into both visual fields. Approximately one-third of IT receptive fields extend out even further, out to 7° in both hemifields. The ipsilateral extent of the receptive field is dependent on interhemispheric connections. Ipsilateral representations are eliminated when the forebrain commissures are transected or when the contralateral striate cortex is removed (Gross et al. 1977; Rocha-Miranda et al. 1975). This means that the information about the ipsilateral visual field is coming from the contralateral visual cortex.

The goal of the current study was to determine whether neurons in area LIP retain bilateral representation in the absence of the forebrain commissures. We addressed this question by recording single LIP neurons in both split-brain and intact monkeys while they performed a receptive field mapping task. This task allowed us to measure the extent of the ipsilateral and contralateral representation of each neuron. Consistent with previous studies, we found a small number of neurons with bilateral receptive fields in the intact monkey. In contrast, we found no such neurons in the split-brain animals. Similar to area IT, LIP neurons no longer represent the ipsilateral visual field. Representation in a single cortical hemisphere of both the ipsilateral and contralateral visual fields is not the explanation for the preserved remapping across hemifields following the transaction of the forebrain commissures. We conclude that a subcortical structure must be the source of the across hemifield remapping.
METHODS

General Procedures

Four rhesus macaques (*Macca Mulatta*, 5-9 kg) were used in this study. The forebrain commissures of monkey EM and CH were surgically transected at the beginning of a set of previous experiments (Berman et al. 2007; Berman et al. 2005; Heiser et al. 2005). In the control animals FF and OP, the forebrain commissures remained intact. Animals were cared for and handled in accordance with NIH guidelines and all experimental protocols were approved by the University of Pittsburgh Institutional Animal Care Use and Committee.

The commissurotomy is described in detail elsewhere (Berman et al. 2005; Vogels et al. 1994). Briefly, the monkeys were prepared for this surgery with dexamethasone, and anesthesia was induced with ketamine and maintained with isoflurane. Mannitol was administered throughout the surgery to minimize tissue swelling. The corpus callosum was transected along its full length using a small glass pipette with suction; the anterior commissure was fully transected. In the two weeks following the surgery, analgesics and antibiotics were administered daily.

All four monkeys underwent sterile surgery to implant an acrylic cap with an embedded head restraint bar, scleral search coils and a recording chamber. General anesthesia was induced with ketamine and was maintained with isoflurane. The recording chamber was placed over the lateral bank of the intraparietal sulcus (area LIP, 5mm posterior and 12mm lateral in Horsley Clarke coordinates). We used MRI to guide and verify correct placement of the chambers.
Physiological Methods

During recording sessions, the monkey sat in a darkened room with its head fixed in a primate chair, facing a tangent screen. Visual stimuli were back-projected on a tangent screen using a LCD projector. Stimulus presentation was under the control of two computers running a C-based program, CORTEX, made available by Dr. Robert Desimone. 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 (Frederick Haer, Bowdoinham, ME) inserted into cortex through stainless steel guide tubes that were stabilized in a nylon grid system (Crist Instruments). 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 a template-matching algorithm (Signal Processing Systems, Prospect, Australia) or with both on-line and off-line template matching and principle component analysis sorting (Plexon, Dallas, Tx).

Reconstruction of Recording Locations

We reconstructed recording locations within the lateral bank of the intraparietal sulcus with structural MRI images. For three out of the four monkeys, prior to the MRI scan, the nylon grid system used for neural recording was placed within the recording chamber. Two to four metal wires were inserted into the cortex through grid holes spaced throughout the chamber. The wires and the outline of the recording chamber were clearly visible in coronal magnetic resonance images. We used the wires and the outline of the chamber to determine the center of the LIP recording chamber. We used the center as a reference point to determine the recording locations. In the fourth monkey, the recording chamber was removed before the MRI scan. A
depression left by the absence of the chamber was clearly visible on MRI scans. This depression was used to approximate the chamber location. The MRI scans were coronal sections 2mm thick.

Behavioral Paradigm

Single unit activity in LIP was recorded while the monkey performed a task designed to map the visual RF of the neuron rapidly. The trial began when the monkey fixated on a central point (FP) for 300 to 500ms. While the monkey fixated, stimuli were presented sequentially at 1 to 9 locations (Fig. 1A). When the fixation point was extinguished, the monkey had to make a saccade to the location of the most recently presented stimuli. Because the number of stimuli presented was unpredictable, the monkey was forced to attend to the location of each stimulus. Each stimulus was presented for 50ms, with an interstimulus interval of 200ms. The stimuli were presented at 24 possible locations (Fig. 1B). A given location was not repeated within a trial. If the monkey landed within ±2.5° of the target location he received a liquid reward.

The advantage of this RF mapping task was that multiple displays of visual stimuli in each trial yielded a large number of target locations and large number of trials for each location without the requirement of holding a single neuron for a long period of time. Data collection for a single neuron was complete when the stimulus was presented at least 12 times at each of the locations. In addition to decreasing the time for each session, the unpredictability of when the final target would appear in each trial forced the monkey to attend to each stimulus presentation, which is important for LIP. Neural responses are enhanced in area LIP when the monkey is attending to a stimulus (Bushnell et al. 1981; Colby et al. 1996; Mountcastle et al. 1981). A neuron fires more when a peripheral stimulus is relevant compared to when the monkey can
passively fixate centrally and ignore the stimulus. By requiring the monkey to attend to each stimulus we ensured that we were not underestimating the extent of the visual receptive field.

Data Analysis

Determining Significant Locations. We used a three step process to determine whether a neuron had a significant visual response to stimuli presented at a particular location. First, we determined the baseline activity of the cell. The baseline activity was defined as the average activity in a 100ms window starting 50ms before each stimulus appeared. This means that the number of baseline epochs in a single trial varied depending on the number of stimuli presented. We used this method instead of a baseline measured only once at the beginning of the trial 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. If we were comparing visual activity only to the first pre-stimulus baseline, then the response to the second stimulus presented might appear to be significant, when in fact it is a lingering elevated response to the first stimulus. By using an epoch that occurred before the presentation of each stimulus we eliminated the possibility of a spurious result due to a sustained response. The stimulus was presented at least 12 times at each of the 24 locations. Each presentation had a baseline measurement. Therefore, the baseline measure contained at least 288 measurements.

Second, we determined the onset of neural activity (neural latency) for each stimulus using a Poisson detection method (Bisley et al. 2004; Maunsell and Gibson 1992). The first step was to compile the neural responses at each stimulus location into peristimulus time histograms (PSTH) with a 10ms binwidth. The next step was to find a Poisson distribution that best fit the
baseline data. From the Poisson distribution a threshold was determined. The threshold was the level at which the spike count would be expected to lie 99% of the time. Therefore if a firing rate was greater than the threshold it had a probability of p<.01 that it was different from the fitted Poisson distribution of the baseline activity. Once the threshold was determined we went back to the raw PSTH and searched in individual 10ms bins from 50ms to 200ms after stimulus onset. The latency was defined as the beginning of the first of 3 consecutive bins that contained firing rates above the threshold.

The third step was to determine if there was a significant visual response at a given stimulus location by comparing the visual epoch to the baseline population. The visual epoch was defined as the activity in 100ms starting at the neural latency. We tested for significant difference between the visual epoch and the baseline epoch using an ANOVA test with Bonferroni multicomparison correction (p<.05).

CREATING CONTOUR PLOTS. For each cell, a contour plot of actual data points and interpolated data points was constructed. To construct the contour plots, we need a firing rate for each location. In the previous analysis we used a visual epoch that started at the neural latency. However, not every location yields a visual response and so not every location has a latency measurement. To construct the contour plots, we chose a new epoch. For each actual data point, the firing rate was equal to the mean firing rate across all trials in an epoch from 70 to 200ms after stimulus onset.

The interpolated data points are a weighted average of the four closest measured data points. The mean firing rate at the actual points was multiplied by the inverse of the distance to the interpolated point. This value was then summed and divided by the sum of the inverse of the
distance to give a weighted average. The mean baseline firing rate was subtracted from both the
known and interpolated points for the final plot.

The contour plots were used for visualization purposes. The interpolation procedure
created a linear grid of responses based on data from a polar grid. This creates a difference in the
spatial resolution across the plot. In order to avoid inaccuracy due to the limitation of the
interpolation, further analysis is based only on the collected data points.
RESULTS

The goal of these experiments was to determine if LIP neurons in split-brain monkeys have bilateral visual representations. We recorded from 268 visually responsive LIP neurons in four monkeys while they performed a receptive field mapping task. For the two split-brain animals, we recorded 52 neurons from monkey EM and 70 in monkey CH. For the intact animals, we recorded 25 neurons in monkey FF, and 121 in monkey OP.

LIP neurons only represent the contralateral visual field in split-brain monkeys.

Our primary finding is that in the split-brain monkey LIP neurons represent only the contralateral visual field. We measured the response of LIP neurons to a visual stimulus that was presented at 24 locations. A typical cell from the left-hemisphere of a split-brain monkey is shown in Fig. 2A. Each histogram represents the response of the neuron to a stimulus presented at that spatial location. This neuron fired when a stimulus was present in the lower visual field, either on the midline, or in the contralateral field. To quantify the RF, we calculated the RF’s width, peak and center of mass based on the contour plots of each neuron (Fig. 2B, see methods). For this example cell, the width of the RF was 9.27°. The peak activity was located at 1° to the right and 1° down. The center of mass of the RF was located at 3° to the right and 8° down.

An example cell from the left hemisphere of an intact monkey is shown in Fig. 3. Similar to the split-brain example cell, this neuron fired when the stimulus was presented in the lower visual field. This neuron was also active when the stimulus was presented in right visual field (the contralateral field). Its strongest activity was for stimuli presented in the left visual field (the ipsilateral field). The width of the RF was 15°, slightly larger than a typical cell. The peak
activity was located 11° to the left and 16° down. The center of mass was located 9° to the left
and 16° down.

Visual activity was completely absent for the ipsilateral hemifield in the split-brain
monkeys (Fig. 4A). In the intact monkeys, we found 25 (17%) neurons with bilateral receptive
fields and 5 (3%) neurons with ipsilateral receptive fields. The bar graphs in Fig. 4 shows the
number of neurons that have significant visual activity for locations separated into three
categories: ipsilateral, contralateral and both hemifields. If an individual neuron had a
significant response for a stimulus at least one location in the ipsilateral side of space, it was
included in the ipsilateral group. If the neuron had at least one significant response for a
stimulus at a location in the contralateral side of space it was included in the contralateral group.
If there was a significant response to both the ipsilateral and contralateral side of space it was
included in the both group. A neuron that only responded when the stimulus was presented at a
midline location was not classified as either ipsilateral or contralateral; therefore, those cells
were not included in the bar plot (midline cells: Intact, 4%, split-brain, 10%).

The spatial distribution of the LIP receptive fields are different for intact and split-brain
monkeys.

We calculated the spatial distribution of the RFs in two ways. First, we determined the
location that had the peak firing rate. Second, we determined the distance from the vertical
meridian. The main focus of this study was to examine ipsilateral and contralateral
representation; therefore, we focused on the horizontal coordinates of both measurements. The
distribution of the horizontal coordinates of the peak firing rate for split-brain and intact animals
is show in Fig. 5. When we compared the distribution of the split-brain monkeys to that of the
intact monkeys we found that the two populations were significantly different (p=0.02, Wilcoxon rank-sum test). This difference was due to the small number of neurons in the intact animals that had a peak in the ipsilateral field. If those neurons were removed from the intact population, then there was no significant difference between split-brain and intact animals (p=.81, Wilcoxon rank-sum test).

We next compared the distributions for the horizontal distance from the vertical meridian (Fig. 6). If the cell had a response in the ipsilateral field, the distance from the vertical meridian is the location in the ipsilateral field that had a significant response that is closest to the vertical meridian. If the cell had no response in the ipsilateral field, then distance from the vertical meridian is the first location in the contralateral field that had a significant response. When we compared the distribution from the split-brain monkeys to that of the intact monkey we found a significant difference between the two populations (p<.001, Wilcoxon rank-sum test). In the intact monkey, there majority of cells had activity close to the vertical meridian. A few cells had a distance beyond 4 degrees into the ipsilateral field. These few cells, when examined more closely, appear to have RF that are at the edge of the measured area. It is possible that the cell responses to a location closer to the vertical meridian that was not measured. It we only analyze the cells with RFs that have distinct boundaries; we find no distances beyond 4 degrees into the ipsilateral field of the intact monkey. This suggest that in the intact animal, the ipsilateral representations are close to the vertical meridian.

In sum, the horizontal spatial distributions of LIP receptive fields, as measured by peak activity, are significantly different for intact and split-brain animals. This difference was due to neurons with ipsilateral representations. This further suggests that ipsilateral representations in LIP depend on the forebrain commissures.
The widths of LIP receptive fields were not different for intact and split-brain monkeys.

We measured the RF width of each neuron. The width was defined as the horizontal distance between the two locations that are furthest apart from each other. Since we only displayed visual stimuli in a portion of the visual field it is possible that we did not capture the full extent of the RF. When the RF is only partially measured it is impossible to determine an accurate measure of RF width. Therefore, we only included cells where a clear boundary of the RF could be determined. We compared the distribution of RF widths from the split-brain monkey (n=20) to that of the intact monkey (n=45) (Fig. 7). We found no significant difference between the two populations (p= .63, Wilcoxon rank-sum test). Even though neurons in the split-brain animal lose their ipsilateral representation, the overall sizes of the RFs are comparable between the split-brain and intact monkeys.

The recording locations in LIP in the split-brain monkeys overlap with the recording locations in the intact monkeys.

As discussed above, we found a small number of LIP neurons with ipsilateral RFs in the intact monkeys, but none in the split-brain monkeys. Before we attribute the loss of ipsilateral representation to the absence of the forebrain commissures we first must address another potential explanation. It is possible that we recorded from different portions of the parietal cortex. If ipsilateral representations are restricted to a localized portion of LIP, and we missed this spot when recording from the split-brain monkeys, it would appear that the LIP neurons in the split-brain monkey had no ipsilateral representations when in fact they do. The most
complete mapping study of area LIP indicates no segregation of ipsilateral representations (Ben Hamed et al. 2001). We wanted to verify that our results matched this previous finding.

We estimated the approximate recording location using MRI images and compared across monkeys. In Fig. 8, we matched the MRI images from split-brain monkey EM to images from intact monkey OP. We recorded from the left hemisphere in both animals. We aligned the images based on anatomical landmarks. The recording sites from these two animals aligned (red arrows). We found neurons with ipsilateral representation at all the recording locations in the intact monkey OP. This suggests that ipsilateral representations are not restricted to a localized location in LIP, but instead are scattered throughout. Fig. 9 shows the MRI images for split-brain monkey CH and intact monkey FF. We recorded from the right hemisphere in these two monkeys. We recorded from more posterior locations in split-brain monkey CH compared to the other three monkeys. Between the two split-brain monkeys, we covered a large posterior-to-anterior extent of LIP. Additionally, the recording sites in the split-brain monkeys overlapped with the recording sites in the intact monkeys. These two pieces of evidence make it unlikely that LIP in split-brain monkeys have ipsilateral representations that we missed during this experiment.

The neural latencies are different between the split-brain and intact monkeys

We compared the distributions of the neural latencies for the split-brain and intact monkeys. For each cell we determined the neural latencies at every stimulus location. For this analysis we only used the latencies for the location with the greatest response. We found that the latencies for the split-brain animals were significantly longer than the latencies for the intact animals (Fig. 10: 106 ms vs 86 ms, p < .001, Wilcoxon rank-sum test). This suggests that neural properties, even within one hemisphere, is modified in the absence of the forebrain commissures.
Our aim was to determine if connections within a single cortical hemisphere in the split-brain monkeys account for the persevered across hemifield remapping. We asked, do LIP neurons retain bilateral receptive fields after the forebrain commissures have been transected? We addressed this question by having both split-brain and intact monkeys perform a receptive field mapping task while we recorded from LIP neurons. We found that a small minority of LIP neurons in the intact animals encoded both the ipsilateral and contralateral visual fields. In contrast, LIP neurons in the split-brain animals only encoded the contralateral visual field. These results are significant because they eliminate the possibility that connections within one hemisphere can explain the intact across hemifield remapping in the split-brain monkeys.

LIP neurons represent the contralateral visual field in intact monkeys

We found that even in the intact monkeys the majority of the neurons fire only for visual stimuli in the contralateral visual field. This is consistent with previous studies. In one of the original papers that characterized the properties of cells in LIP, the lack of large bilateral receptive fields was used to distinguish LIP from a neighboring region, area 7a (Blatt et al. 1990). The first rigorous, quantitative analysis of LIP receptive fields was conducted by Ben Hamed and colleagues (2001). They found that the representation of LIP neurons extend to about 5° into the ipsilateral visual field (2001). Our results are consistent with the finding of Ben Hamed et al. Even in intact animals, it seems unlikely that connections within a single hemisphere contribute to across hemifield remapping. Only a minority of cells have bilateral receptive fields, but the majority of cells are capable of remapping.
LIP neurons represent only the contralateral visual field in split-brain monkeys

Our results indicate that the forebrain commissures are necessary for ipsilateral representation in LIP. These results are consistent with anatomical studies that show that ipsilateral projecting ganglion cells contribute to only a 1-degree strip around the vertical meridian (Stone et al. 1973). Our results are also consistent with two other split-brain studies in monkeys. First, as we described in the introduction, ipsilateral representations by neurons in the inferotemporal cortex depend on the forebrain commissures (Rocha-Miranda et al. 1975). The forebrain commissures also play a role in RF construction in area V4 (Desimone et al. 1993). V4 neurons in an intact animal typically do not represent the ipsilateral visual field. However, the classically defined RFs are often surrounded by a large suppressive surround. This surround can extend beyond the vertical meridian into the ipsilateral field. When Desimone et al. transected the corpus callosum, the suppressive surround was greatly reduced.

Ipsilateral representation and remapping

We found that in the split-brain monkeys there is no representation of the ipsilateral visual field in area LIP, and that there is only a limited about in the intact animal. These results have stronger implications for the circuitry of remapping. Visual activity in one hemisphere is not sufficient for across hemifield remapping. In the intact animal, activity could be transferred using the forebrain commissures. This is not the case for the split-brain monkeys. Therefore, the source for the across-hemifield remapping in the split brain monkeys must be subcortical.

Alternative source for across hemifield remapping

One possible source of across hemifield remapping activity in LIP of the split-brain monkeys is the superior colliculus (SC). It has been demonstrated that the SC is important for
visual representation in at least one cortical area, the superior temporal polysensory area (STP) (Bruce et al. 1981). In the intact monkey, STP neurons have large bilateral receptive fields. Even when striate cortex is removed unilaterally, these neurons retain their representation of the contralateral space. It is only when the superior colliculus was also removed that activity in these neurons was abolished. The SC can provide visual information to cortical areas independent of the geniculostriate system.

In addition to providing visual information, it is also possible that the SC provides a remapping signal to cortex. SC neurons are capable of remapping and the SC has projections to LIP through thalamic structures (Clower et al. 2001; Walker et al. 1995). In the absence of the forebrain commissures, neurons in the superficial and intermediate layers of the SC are capable of remapping across hemifields (Dunn et al. 2009). In the current study, we have ruled out the possibility that connections within a single cortical hemisphere can account for across hemifield remapping in the split brain monkey. Neurons in the superior colliculus are the likely source of the preserved remapping.

Although SC seems like the most likely subcortical structure to contribute to remapping, other subcortical regions may be involved. The intertectal commissure contains fibers that connect other subcortical structures, such as the substantia nigra par reticulate (SNr) (Antonetty and Webster 1975; Edwards 1975; 1977; Glickstein et al. 1980; Jayaraman et al. 1977; Mower et al. 1980; Wallace et al. 1990; 1989). It is also possible that the cerebellum provides a pathway for remapping. Both the cerebellum and the SNr have connections to the cortical areas and play a role in visual orienting and saccadic eye movements (Basso and Liu 2007; Basso et al. 2005; Hikosaka and Wurtz 1983a; b; Liu and Basso 2008; Wallace et al. 1990; 1989). Remapping
activity in these pathways has yet to be explored. It is possible that one of these areas is the source of across hemfield remapping in the split brain animals.
Acknowledgments

We thank N. Hall, K. McCracken and Dr. Kevin Hitchens for technical assistance, and J. Patrick Mayo and other colleagues at the Center for the Neural Basis of Cognition for constructive comments.

Grants

This work was supported by National Institutes of Health Grants EY-12032 and MH-45156, technical support was provided by core grant EY-08908, and collection of MR images was supported by P41RR-03631. Support was also provided by National Aeronautics and Space Administration Fellowships to C.A. Dunn.
Figure 1. Receptive field mapping task. A. Monkey begins each trial fixating a central location (black circle). While the monkey fixates, a random number (1-9) of visual stimuli (red circle) are presented for 50ms with a 200ms interstimulus interval. Once the fixation point is turned off the monkey is free to make an eye movement (arrow) to the last stimulus presented. B. The stimulus was placed at one of eight locations in three rings with amplitudes of 7°, 14° or 21°, for a total of 24 locations. Each red dot represents a possible target location.

Figure 2. Cell from split brain monkey. A. Each histogram and rasterplot represents the activity of the same LIP neuron for one particular stimulus location. This cell was recorded from the left hemisphere. Histograms are red when the activity during the visual epoch is significantly greater than the baseline epoch (see methods). The data are aligned on stimulus onset. The vertical line represents the neural latency for that location. If a neural latency could not be determined, then no line is present. B. Contour plot of the same neuron as in A. The x-axis represents the horizontal location in real degrees. The y-axis represents the vertical location. The color represents the firing rate of the neuron. The black asterisks indicates that the firing rate at the location was at least 75% of the peak firing rate. This neuron had a receptive that was down and slightly to the right (contralateral visual field).

Figure 3. Cell from an intact monkey. A. The activity of an LIP neuron recorded from left hemisphere of an intact monkey. The conventions are the same as Fig. 2. B. Contour plot of the same neuron as in A. This neuron had a receptive that was down and to the left (ipsilateral visual field).
Figure 4. The number of neurons with ipsilateral, contralateral, or both representations. The bars represent the number of neurons with ipsilateral, contralateral, or both representations. If the neuron fires in response to a stimulus presented at least one location in the ipsilateral field, it is in the ipsilateral group. If the neuron fires in response to a stimulus presented at least one location in the contralateral field, it is in the contralateral group. If the neuron fires response to a stimulus when it is present in the ipsi- and contra-lateral field, it is in the both group. If the neuron only responds to cell on the midline it is not included. Each group is mutually exclusive.

A. In the split brain monkey, there are no neurons that fire when the stimulus is in the ipsilateral field. B. In the intact monkey, a small number of cells are bilateral, and even fewer are ipsilateral only.

Figure 5. Distributions of the location of peak firing of LIP receptive fields in split brain and intact monkeys. On the x-axis, the horizontal coordinates of spatial location of peak firing rate. Positive values represent contralateral space, negative values represent ipsilateral space. A. In the split brain monkey the location of peak firing varies from 0 to 20 degrees. B. In the intact monkey the location of peak firing varies from 12 degrees in the ipsilateral field to 20 degrees in the contralateral field. There is a significant difference between the split brain and intact populations.

Figure 6. Distributions of the distance from the vertical meridian of LIP receptive fields in split brain and intact monkeys. On the x-axis, the horizontal coordinates of spatial location of the center of mass. Positive values represent contralateral space, negative values represent ipsilateral space. A. In the split brain monkey the center of mass varies from 0 to 20 degrees. B. In the
intact monkey the location of peak firing varies from 12 degrees in the ipsilateral field to 20
degrees in the contralateral field. There is a significant difference between the split brain and
intact populations.

Figure 7. Distributions of LIP receptive field widths in split brain and intact monkeys. A. In split
brain monkeys and B. Intact monkeys receptive field widths vary from a few degrees to as much
as twenty degrees. There is no significant difference between the two populations. Even in the
absence of ipsilateral representations, split brain and intact monkeys have comparable RF sizes.

Figure 8. Coronal magnetic resonance images of monkeys EM and OP. The images are in order
from top to bottom, from posterior to anterior. A. The images from split brain monkey EM. The
recording chamber was over left parietal cortex. The chamber was removed before the MRI
scan. The location of the chamber was estimated based on the depression the remained after the
chamber was removed. B. The images from intact monkey OP. The recording chamber was
over left parietal cortex. The red arrows indicate the estimated recording locations. Recordings
in the split brain monkey were aligned with the recordings in the intact monkey.

Figure 9. Coronal magnetic resonance images of monkeys CH and FF. The conventions are the
same as Fig. 8 A. The images from split brain monkey CH. The recording chamber was over
right parietal cortex. B. The images from intact monkey FF. The recording chamber was over
right parietal cortex. The red arrows indicate the estimated recording locations. Recording in
the split brain monkey were more posterior, while the recordings in the intact animal was more
anterior.
Figure 10. Distributions of the neural latency in split brain and intact monkeys. On the x-axis, the latency of neural response. Positive values represent contralateral space, negative values represent ipsilateral space. A. In the split brain monkey mean latency is 106ms. B. In the intact monkey the mean latency is 86ms. There is a significant difference between the split brain and intact populations.
REFERENCES


Fig. 4

Split Brain

Intact

<table>
<thead>
<tr>
<th></th>
<th>Ipsilateral</th>
<th>Both</th>
<th>Contralateral</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>109</td>
<td>20</td>
<td>140</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Ipsilateral</th>
<th>Both</th>
<th>Contralateral</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>140</td>
<td>20</td>
<td>140</td>
</tr>
</tbody>
</table>
Fig. 5

A

Split Brain

# of neurons

-20 -16 -12 -8 -4 0 4 8 12 16 20

B

Intact

# of neurons

-20 -16 -12 -8 -4 0 4 8 12 16 20

Horizontal Peak (deg)
A

Split Brain

# of neurons

0 10 20 30 40 50 60

-20 -16 -12 -8 -4 0 4 8 12 16 20

B

Intact

# of neurons

0 20 40 60 80

-20 -16 -12 -8 -4 0 4 8 12 16 20

Distance from Vertical Meridian (deg)
A. Split Brain

B. Intact

Receptive Field Width (deg)

# of neurons

# of neurons

Fig. 7
Fig. 8

A  Split Brain Monkey EM
    Posterior

B  Intact Monkey OP
    Anterior
Fig. 10

A

Split Brain

Latency of Neural Response (ms)

# of neurons

0 5 10 15 20 25 30 35

60 70 80 90 100 110 120 130 140 150 160

B

Intact

Latency of Neural Response (ms)

# of neurons

0 10 20 30 40 50

60 70 80 90 100 110 120 130 140 150 160