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

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Submitted 15 August 2009; accepted in final form 18 July 2010

Dunn CA, Colby CL. Representation of the ipsilateral visual field by neurons in the macaque lateral intraparietal cortex depends on the forebrain commissures. J Neurophysiol 104: 2624–2633, 2010. First published August 18, 2010; doi:10.1152/jn.00752.2009. Our eyes are constantly moving, allowing us to attend to different visual objects in the environment. With each eye movement, a given object activates an entirely new set of visual neurons, yet we perceive a stable scene. One neural mechanism that may contribute to visual stability is remapping. Neurons in several brain regions respond to visual stimuli presented outside the receptive field when an eye movement brings the stimulated location into the receptive field. The stored representation of a visual stimulus is remapped, or updated, in conjunction with the saccade. Remapping depends on neurons being able to receive visual information from outside the classic receptive field. In previous studies, we asked whether remapping across hemifields depends on the forebrain commissures. We found that, when the forebrain commissures are transected, behavior dependent on accurate spatial updating is initially impaired but recovers over time. Moreover, neurons in lateral intraparietal cortex (LIP) continue to remap information across hemifields in the absence of the forebrain commissures. One possible explanation for the preserved across-hemifield remapping in split-brain animals is that neurons in a single hemisphere could represent visual information from both visual fields. In the present study, we measured receptive fields of LIP neurons in split-brain monkeys and compared them with receptive fields in intact monkeys. We found a small number of neurons with bilateral receptive fields in the intact monkeys. In contrast, 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/s and with each eye movement a new image impinges on the retina. Even so, we perceive a stable visual world. Remapping of visual information is one neural mechanism that may contribute to visual stability (for review, see Berman and Colby 2009). 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). In each area, visual information is transferred from neurons representing the salient location before the eye movement to neurons representing the salient location after the eye movement.

Accurate spatial updating depends on the existence of neurons that can receive visual information from the entire visual scene. When the initial and final salient locations are in opposite visual fields, information is presumably transferred from one hemisphere to the other. For example, a visual stimulus flashed 6° to the right of an initial fixation point should be 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° to the left of fixation and will be represented by neurons in the right hemisphere. Neurons that remap in the right LIP must receive information about the visual stimulus that was originally encoded by the left hemisphere. In the initial LIP remapping study, the task was configured so that a stimulus was flashed in the hemifield opposite the one represented by the neuron being recorded (Duhamel et al. 1992). Visual information was updated from one visual hemifield to the other.

The main 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 (2005) tested whether remapping depends on this pathway by transecting the forebrain commissures. 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, but not the only, pathway for the transfer of remapped visual information across hemispheres.

The finding that LIP neurons in the split-brain monkey can still remap visual information from the opposite visual field indicates that the opposite cortical hemisphere is not the only source of remapped 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 (RFs). Early studies showed that the majority of parietal cortex neurons have large bilateral RFs (Motter and Mountcastle 1981; Motter et al. 1987; Steinmetz et al. 1987). In later studies, researchers identified separate areas within parietal cortex, including area LIP and area 7a (Andersen et al. 1990; Blatt et al. 1990). The proportion of cells with bilateral RFs differs between these areas. In area 7a, the majority of cells have bilateral fields, whereas only a small number of LIP neurons have bilateral RFs (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, most neurons have contralateral RFs. The ipsilateral representation
Previous studies in visual cortex show that bilateral RFs depend on the integrity of the forebrain commissures. In inferior temporal cortex (area IT), neurons have large RFs, typically ranging from $10 \times 10$ to $30 \times 30^\circ$ and they almost always include the fovea (Gross et al. 1969, 1972). Many of these cells have bilateral RFs, extending $\geq 3^\circ$ into both visual fields. Approximately one third of IT RFs extend out even further, out to $7^\circ$ in both hemifields. The ipsilateral extent of the RF 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).

The aim of the present study was to determine whether there is any ipsilateral representation in LIP in the absence of the forebrain commissures. If there were, it is possible that this ipsilateral representation could provide the basis for across-hemifield remapping. We addressed this question by recording single LIP neurons in both split-brain and intact monkeys while they performed an RF mapping task. This task allowed us to measure the extent of the ipsilateral and contralateral representation for each neuron. Consistent with previous studies, we found a small number of neurons with bilateral RFs in intact monkeys. In contrast, we found no such neurons in the split-brain animals. As in area IT, LIP neurons no longer represent the ipsilateral visual field after the hemispheres have been disconnected. Representation within a single cortical hemisphere of both the ipsilateral and contralateral visual fields is therefore not the explanation for the preserved remapping across hemifields observed in split-brain monkeys.

**METHODS**

**General procedures**

Four rhesus macaques (*Macaca mulatta*, 5–9 kg) were used in this study. In monkeys EM and CH, the entire corpus callosum and the anterior commissure (AC) were surgically transected (Berman et al. 2005). In the control animals FF and OP, the forebrain commissures remained intact. Animals were cared for and handled in accordance with National Institutes of Health 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 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 capillary that was stabilized in a nylon grid system (Crist Instrument, 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 a template-matching algorithm (Signal Processing Systems, Prospect, Australia) or with both on-line and off-line template matching and principal component analysis sorting (Plexon, Dallas, TX).

**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 onto a tangent screen using a liquid crystal display 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 (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 a template-matching algorithm (Signal Processing Systems, Prospect, Australia) or with both on-line and off-line template matching and principal 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 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 MR 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.

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 a central point (FP) for 300 to 500 ms. 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 stimulus. 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 50 ms, with an interstimulus interval of 200 ms. 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 a 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 ≥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 in area LIP are enhanced when the monkey is attending to a stimulus (Bushnell et al. 1981; Colby et al. 1996). Neurons fire more when a stimulus is behaviorally relevant compared with the firing rate when the monkey can simply maintain fixation 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 RF.

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 100 ms window starting 50 ms 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 prestimulus 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 measuring the baseline immediately before the presentation of each stimulus we eliminated the possibility of a spurious result due to a sustained response. The stimulus was presented ≥12 times at each of the 24 locations. The baseline measure for a given neuron was the average activity over ≥288 epochs.

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 (PSTHs) with a 10 ms bin width. 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 \( P < 0.01 \) 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 through individual 10 ms bins from 50 to 200 ms after stimulus onset. The latency was defined as the beginning of the first of three consecutive bins that contained firing rates above the threshold.

The third step was to determine whether there was a significant visual response at a given stimulus location by comparing activity in the visual epoch to baseline. The visual epoch was 100 ms starting at the neural latency. We used an ANOVA with Bonferroni multicomparison correction \( (P < 0.05) \) to test for significant differences between the visual epoch and the baseline epoch.

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

![Figure 3](http://jn.physiology.org/)

**FIG. 3.** Responses from a single left-hemisphere neuron in an intact monkey. Conventions as like those in Fig. 2. This neuron had a receptive that was down and to the left (ipsilateral visual field).
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 created a new epoch that was not tied to the neural response latency. Instead, we used a standard epoch from 70 to 200 ms after stimulus onset for each stimulus location that yielded a measurable response. For locations that did not yield a visual response, we interpolated the data. 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. These values were 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 only. The interpolation procedure created a linear grid of responses based on data from a polar grid, which produces a difference in the spatial resolution across the plot. To avoid inaccuracy due to the limitations of the interpolation, further analysis is based only on the collected data points.

RESULTS

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

LIP neurons represent only 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 appeared in the lower visual field, either on the midline or in the contralateral field. The peak location for this cell was on the vertical meridian and 7° down. To visualize the RF, we created a contour plot for each neuron (Fig. 2B; see METHODS). An asterisk appears at each location in the contour plot where the visual response exceeded 75% of peak activity. Although this neuron responded strongly to visual stimuli at contralateral and midline positions, it did not respond to ipsilateral stimuli.

In the intact monkey, most LIP neurons also have contralateral RFs. In addition, we found a small number of cells with bilateral or even predominantly ipsilateral RFs. An example of a strongly ipsilateral cell is shown in Fig. 3. This

FIG. 4. Number of lateral intraparietal cortex (LIP) neurons with responses to stimuli in ipsilateral, contralateral, or both hemifields. A: in the split-brain monkey, no neurons respond to stimuli in the ipsilateral field. B: in the intact monkey, a small number of neurons have bilateral RFs, and even fewer are ipsilateral only.

FIG. 5. Location of peak response for LIP neurons in split-brain and intact monkeys. Positive values on the x-axis represent contralateral space; negative values represent ipsilateral space. A: in split-brain monkeys, the location of peak response varies from 0 to 20°. B: in intact monkeys, the location of peak firing varies from 16° in the ipsilateral field to 20° in the contralateral field.
atypical neuron responded strongly to stimuli at ipsilateral and midline positions and weakly to contralateral stimuli. The strongest response was to stimuli presented 10° to the left and 10° down (peak location).

For all cells tested, visual activity was completely absent for the ipsilateral hemifield in the split-brain monkeys. This finding contrasts with our results in the intact monkeys, where we found 25 (17%) neurons with bilateral RFs and 5 (3%) neurons with ipsilateral RFs. The bar graphs in Fig. 4 show the number of neurons that have significant visual activity, separated into three mutually exclusive categories: ipsilateral hemifield locations only, contralateral hemifield only, and both. Neurons were included in the ipsilateral group if they had a significant response to a stimulus presented at any ipsilateral location. Neurons were categorized as contralateral if they had a significant response to a stimulus at any contralateral location. Neurons were categorized as “both” if there was a significant response to locations on both the ipsilateral and contralateral sides of space. Neurons that responded only to midline stimulus locations are not included in the bar graphs (midline cells: intact, 4%; split-brain, 10%).

Spatial distribution of LIP receptive fields differs for intact and split-brain monkeys

We calculated the spatial distribution of the RFs in two ways. First, we determined the stimulus location that yielded the peak response. The main focus of this study was to examine ipsilateral and contralateral representation and thus we focused on the horizontal coordinates of both measurements. The distribution of the horizontal coordinates of the peak location for split-brain and intact animals is shown in Fig. 5. When we compared the distributions of the peak locations for split-brain and intact monkeys, we found that the two populations were significantly different ($P = 0.02$, Wilcoxon rank-sum test). This difference was attributed to the small number of neurons in the intact animals that had a peak location in the ipsilateral field. When those neurons are removed from the intact population, there is no significant difference between the populations ($P = 0.81$, Wilcoxon rank-sum test). In sum, the horizontal spatial distributions of LIP RFs, as measured by peak activity, are significantly different for intact and split-brain animals. This difference was due to neurons with ipsilateral RFs. This result suggests that ipsilateral representations in LIP depend on the forebrain commissures.

In the second analysis, we determined the distance from the vertical meridian to the nearest stimulus location that yielded a response (Fig. 6). This measure was intended to capture the distance of the “inner edge” of the RF from the vertical meridian. If a neuron had any significant response in the ipsilateral field, we used the distance from that location to the vertical meridian. If a neuron had no response in the ipsilateral field, then we measured the distance from the vertical meridian to the nearest location in the contralateral field that had a significant response. This analysis produced three main results. First, we found a significant difference between the two pop-
ulations when we compared the distribution from the split-brain monkeys with that of the intact monkeys ($P < 0.001$, Wilcoxon rank-sum test). Once again, the intact animals have RFs that extend into the ipsilateral field, whereas the split-brain animals do not. Second, for the majority of neurons in both the intact and split-brain monkeys, even when the peak location is in the periphery, the inner edge is close to the midline. The distributions for the distance from vertical meridian are skewed toward the midline compared with the distributions for peak locations (Fig. 6 compared with Fig. 5). For both the intact and split-brain animals, the majority of cells had activity close to the vertical meridian. Third, in the intact monkeys, a few cells had an RF inner edge beyond 4° into the ipsilateral field. These few cells, when examined more closely, appear to have RFs that are at the edge of the measured area. It is possible that these cells would have responded to a stimulus location closer to the vertical meridian that was not measured. If we analyze only the cells with RFs that have distinct boundaries, we find no neurons with an inner boundary beyond 4° into the ipsilateral field. This indicates that in the intact animal, the ipsilateral RFs are close to the vertical meridian.

**Widths of LIP receptive fields are not different for intact and split-brain monkeys**

We measured the RF width for each neuron. The width was defined as the horizontal distance between the two responsive locations furthest apart from each other. Because visual stimuli were presented in only a portion of the visual field, it is possible that we did not capture the full extent of the RF. Therefore we included in the analysis only cells for which clear RF boundaries could be determined. We compared the distribution of RF widths from the split-brain monkeys ($n = 20$) with that of the intact monkeys ($n = 45$) (Fig. 7). We found no significant difference between the two populations ($P = 0.63$, Wilcoxon rank-sum test). Even though neurons in the split-brain animals lose their ipsilateral representation, the overall sizes of the RFs are comparable between the split-brain and intact monkeys.

**Recording locations in LIP in the split-brain monkeys overlap with the recording locations in the intact monkeys**

As discussed earlier, 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 sub-regions of LIP in different animals. If ipsilateral RFs are restricted to a subregion of LIP, and we missed this spot when recording from the split-brain monkeys, then it would appear that the LIP neurons in the split-brain monkey had no ipsilateral representations, when in fact they do. The most

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**FIG. 8.** Coronal magnetic resonance images of monkeys EM and OP. Gray arrows indicate recording locations. A: images from split-brain monkey EM. The chamber was removed before the magnetic resonance imaging (MRI) scan. The location of the chamber was estimated based on the depression that remained after the chamber was removed. B: images from intact monkey OP. Recording locations in the split-brain monkey were aligned with recordings in the intact monkey.
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 from each monkey. 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 were well matched (gray arrows). We found neurons with ipsilateral RFs at all recording locations in the intact monkey OP. This suggests that ipsilateral RFs are not restricted to a subregion in LIP but instead are scattered throughout.

Figure 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 monkey CH compared with the other three monkeys. Between the two split-brain monkeys, we covered the entire posterior-to-anterior extent of LIP. Additionally, recording sites in the split-brain monkeys generally overlapped with those in the intact monkeys. These two pieces of evidence make it unlikely that LIP in split-brain monkeys has an ipsilateral representation that was missed.

Neural latencies are different between the split-brain and intact monkeys

We compared the distributions of neural latencies for split-brain and intact monkeys. For each cell we determined response latency at every stimulus location. For this analysis we used only the latency for the location with the greatest response. We found that latencies for the split-brain animals were significantly longer than latencies for the intact animals (Fig. 10; 106 vs. 86 ms, \( P < 0.001 \), Wilcoxon rank-sum test). This indicates that response properties, even within a hemisphere, are modified in the absence of the forebrain commissures.

DISCUSSION

Our aim was to determine whether there is any ipsilateral representation in area LIP in the absence of the forebrain commissures. We asked whether LIP neurons retain bilateral RFs after the corpus callosum and AC were transected. We addressed this question by doing an RF mapping task in both split-brain and intact monkeys. In accord with previous results, we found that a small number of LIP neurons in the intact animals have RFs that extend into the ipsilateral hemifield. In contrast, in the split-brain animals, RFs were limited to the contralateral visual field. These results are significant because...
also consistent with two other split-brain studies in monkeys. Around the vertical meridian (Stone et al. 1973). Our results are consistent with anatomical studies that show that ipsilateral projecting ganglion cells contribute to only a 1° strip of the ipsilateral visual field. When the corpus callosum is transected, the suppressive surround is greatly reduced.

**Ipsilateral representation and remapping**

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

**Alternative source for across-hemifield remapping**

One possible source of across-hemifield remapping activity in LIP of split-brain monkeys is the superior colliculus (SC). The SC is important for visual activity 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 RFs. When striate cortex was removed unilaterally, these neurons retained visual responsiveness. Visual activity in these neurons was abolished only when the SC was also removed. The SC can thus 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. 2010). 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 a likely source of the preserved remapping.

Although SC is 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 pars reticulata (SNr) (Antonetto and Webster 1975; Edwards 1975, 1977; Glickstein et al. 1980; Jayaraman et al. 1977; Mower et al. 1980; Wallace et al. 1981). In the intact monkey, STP neurons have large bilateral RFs. When striate cortex was removed unilaterally, these neurons retained visual responsiveness. Visual activity in these neurons was abolished only when the SC was also removed. The SC can thus provide visual information to cortical areas independent of the geniculostriate system.

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**LIP neurons primarily represent the contralateral visual field in intact monkeys**

In intact monkeys, most LIP neurons respond to visual stimuli only in the contralateral visual field. This is consistent with previous studies. In one of the original studies that characterized the properties of LIP neurons, the presence of large bilateral RFs was used to distinguish area 7a from LIP (Blatt et al. 1990). A quantitative analysis of LIP RFs showed that the representation in area LIP extends only about 5° into the ipsilateral visual field (Ben Hamed et al. 2001).

**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. We found no LIP neurons with RFs that crossed the vertical meridian. These results are consistent with anatomical studies that show that ipsilateral projecting ganglion cells contribute to only a 1° strip around the vertical meridian (Stone et al. 1973). Our results are also consistent with two other split-brain studies in monkeys.
ACKNOWLEDGMENTS

We thank N. Hall, K. McCracken, and Dr. Kevin Hitchens for technical assistance and J. P. 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 National Eye Institute Core Grant EY-08908; provision of the collection of magnetic resonance images was supported by Division of Research Resources Grant P41-RR-03631; and National Aeronautics and Space Administration Fellowships to C. A. Dunn.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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